Florencia Montagnini

RESEARCH ARTICLES

(August 1997)

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1- Published refereed articles

Montagnini, F. and Mendelsohn, R. 1997. Managing forest fallows: improving the economics of swidden agriculture. *Ambio* **26(2): 118-123.**

Montagnini, F., Eibl, B., Woodward, C., Szczipanski, L. and Ríos, R. 1997. Tree regeneration and species diversity following conventional and uniform spacing methods of selective cutting in a subtropical humid forest reserve. *Biotropica.* **In Press.**

Montagnini, F., Eibl, B., Grance, L., Maiocco, D. and Nozzi, D. 1997. Enrichment planting in degraded forests of the Paranaense region of Misiones, Argentina. *Forest Ecology and Management.* **In Press.**

+ Montagnini, F., and Porras, C. 1997. Evaluating the role of plantations as carbon sinks: an example of an integrative approach from the humid tropics. *Environmental Management.* **In Press.**

Montagnini, F. and Muñiz-Miret, N. 1997. Vegetation and soils of tidal floodplains of the Amazon estuary: a comparison of *varzea* and *terra firme* forests in Pará, Brazil. *Journal of Tropical Forest Science.* **In Press.**

Fernández, R., Montagnini, F., and Hamilton, H. 1997. The influence of native tree species on soil chemistry in a subtropical humid forest region of Argentina. *Journal of Tropical Forest Science.* **In Press.**

Kershnar, R. and Montagnini, F. 1997. Leaf litter decomposition, litterfall and effects of leaf mulches from in mixed and monospecific plantations in Costa Rica. *Journal of Sustainable Forestry.* **In Press.**

Montagnini, F., Eibl, B., Grance, L, Maiocco, D, and Nozzi, D. 1997. Técnicas de enriquecimiento de bosques degradados en la selva subtropical Paranaense de Misiones, Argentina. *Yvyraretá* (Argentina) 8. **In press.**

Muñiz-Miret, N., Vamos, R., Hiraoka, M., Montagnini, F., and Mendelsohn, R. 1996. The economic value of managing Acai (*Euterpe oleracea* Mart.) in floodplain lands of the Amazon estuary, Pará, Brazil. *Forest Ecology and Management* **87: 163-173.**

Byard, R., Lewis, L. C., and Montagnini, F. 1996. Leaf litter decomposition and mulch performance from mixed and monospecific plantations of native tree species in Costa Rica. *Agriculture, Ecosystems and Environment* **58: 145-155.**

Eibl, B. Montagnini, F., Woodward, C., Szczipanski, L. and Ríos, R. 1996. Evolución de la regeneración natural en dos sistemas de aprovechamiento y bosque nativo no perturbado en la Provincia de Misiones - República Argentina. *Yvyraretá* (Argentina) **7(7): 63-78.**

Montagnini, F., González, E. and Sancho, F. 1996. Relación entre área basal arbórea y propiedades químicas del suelo en un bosque tropical secundario de 10 años de edad. *Yvyraretá* (Argentina) **7(7): 47-56.**

Montagnini, F., González, E., Rheingans, R. and Porras, C. 1995. Mixed and pure forest plantations in the humid neotropics: a comparison of early growth, pest damage and establishment costs. *Commonwealth Forestry Review* **74(4): 306-314.**

Montagnini, F., Fanzeres, A. and da Vinha, S. G. 1995. The potential of twenty indigenous tree species for reforestation and soil restoration in the Atlantic Forest region of Bahia. *Journal of Applied Ecology* **32: 841-856.**

Guariguata, M. R., Rheingans, R., and Montagnini, F. 1995. Early woody invasion under tree plantations in Costa Rica: implications for forest restoration. *Restoration Ecology* **3(4): 252-260.**

Montagnini, F., Fernández, R. and Hamilton, H. 1995. Relaciones entre especies nativas y la fertilidad de los suelos. Parte 1: Contenido de elementos en la biomasa. *Yvyraretá* (Argentina) **6 (6): 5-12.**

Baker, D. and Montagnini, F. 1995. Estimación de la fijación de nitrógeno por el árbol tropical Stryphnodendron microstachyum Poepp. Et Endl. *Yvyraretá* (Argentina) **6 (6): 93-96.**

Montagnini, F. and Sancho, F. 1994. Above-ground biomass and nutrients in young plantations of four indigenous tree species: implications for site nutrient conservation. *Journal of Sustainable Forestry* **1 (4): 115-139.**

Montagnini, F., Fanzeres, A. and da Vinha, S. G.. 1994. Studies on Restoration Ecology in the Atlantic Forest region of Bahia, Brazil. *Interciencia* **19(6): 323-330.**

Asbjornsen, H. and Montagnini, F. 1994. Vesicular-arbuscular mycorrhizal inoculum potential affects the growth of Stryphnodendron microstachyum seedlings in a Costa Rican humid tropical lowland. *Mycorrhyza* **5: 45-51.**

Baker, D. and Montagnini, F. 1994. Estimation of nitrogen fixation by the tropical legume tree *Stryphnodendron microstachyum* Poepp. et Endl. *Nitrogen Fixing Tree Research Reports* **12: 139-141.**

Montagnini, F. and Sancho, F. 1994. Net nitrogen mineralization in soils under six indigenous tree species, an abandoned pasture and a secondary forest in the Atlantic lowlands of Costa Rica. *Plant and Soil* **162: 117-124.**

Montagnini, F., Fanzeres, A. and da Vinha, S. G. 1994. Estudios de restauración ecológica en la región del bosque Atlántico de Bahía, Brasil. *Yvyraretá* (Argentina) **5(5): 9-23.**

Montagnini, F., Ramstad, K. and Sancho, F. 1993. Litterfall, litter decomposition and the use of mulch of four indigenous tree species in the Atlantic lowlands of Costa Rica. *Agroforestry Systems* **23: 39-61.**

Montagnini, F. and Sancho, F. 1993. Reciclaje de nutrientes en plantaciones jóvenes con árboles nativos: estrategias para un manejo sustentable. *Yvyraretá* (Argentina) **4(4): 9-23.**

Montagnini, F., Haines, B., and Swank, W. T. 1991. Soil solution chemistry in black locust, pine-hardwoods and oak-hickory forest stands in the southern Appalachians. *Forest Ecology and Management* **40: 199-208.**

Montagnini, F., and Sancho, F. 1990. Impacts of native trees on tropical soils: a study in the Atlantic lowlands of Costa Rica. *Ambio* **19(8): 386-390.**

Montagnini, F., and Sancho, F. 1990. Influencia de seis especies de árboles nativos sobre la fertilidad del suelo en una plantación experimental en la llanura del Atlántico en Costa Rica. *Yvyraretá* (Argentina) **1(1): 29-49.**

Montagnini, F., Haines, B., Swank, W., and Waide, J. 1989. Nitrification rates in undisturbed mixed hardwoods and manipulated forests in the southern Appalachian Mountains of North Carolina, USA. *Canadian Journal of Forest Research* **19: 1226-1234.**

Montagnini, F., Haines, B., and Swank, W.T. 1989. Factors controlling nitrification in soils of early successional and oak/hickory forests in the southern Appalachians. *Forest Ecology and Management* **26: 77-94.**

Montagnini, F. and Buschbacher, R. 1989. Nitrification rates in two undisturbed tropical rain forests and three slash and burn sites of the Venezuelan Amazon. *Biotropica* **21(1): 9-14.**

Montagnini, F., Haines, B. L., Boring, L. R., and Swank, W. T. 1986. Nitrification potentials in successional black locust and mixed hardwood forest stands in the southern Appalachians, U. S. A. *Biogeochemistry* **2: 197-210.**

Montagnini, F., Neufeld, H., and Uhl, C. 1984. Heavy metal concentrations in some non-vascular plants in an Amazonian rain forest. *Water, Air and Soil Pollution* **21: 317-321.**

Montagnini, F. and Jordan, C. 1983. The role of insects in productivity decline of cassava (*Manihot esculenta* Crantz) on a slash and burn site in the Amazon Territory of Venezuela. *Agriculture, Ecosystems and Environment* **9: 293-301.**

Jordan, C., Caskey, W., Escalante, G., Herrera, R., Montagnini, F., Todd, R. and Uhl, C. 1983. Nitrogen dynamics during conversion of primary Amazon rain forest to slash and burn agriculture. *Oikos* **40: 131-139.**

Jordan, C., Caskey, W., Escalante, G., Herrera, R., Montagnini, F., Todd, R. and Uhl, C. 1982. The nitrogen cycle in a "tierra firme" rain forest on oxisol in the Amazon Territory of Venezuela. *Plant and Soil* **67: 325-332.**

2- Articles in circulation

Montagnini, F. and Muñiz-Miret, N. Vegetación y suelos de las planicies inundables del estuario amazónico: una comparación de bosques de várzea y terra firme en Pará, Brasil. *Agrotrópica.* **Submitted**, July 1996.

Montagnini, F., Sancho, F., González, E., Porras, C., Moulaert, A. and del Mónaco, A. Plantaciones forestales puras y mixtas con especies nativas para la reforestación de terrenos degradados en Costa Rica: estudio comparativo del crecimiento, daños por plagas, regeneración natural y costos de establecimiento. *Biocenosis* (Costa Rica). **Submitted,** Oct. 1996.

Horn, N. and Montagnini, F. 1997. Litterfall, litter decomposition and maize bioassay of mulches from four indigenous Costa Rican tree species in mixed and monospecific plantations. *Journal of Applied Ecology.* **Submitted, June 1997.**

Eibl, B., Fernández, R., Kozarik, J. C., Lupi, A., Montagnini, F. and Nozzi, D. Agroforestry systems with *Ilex paraguariensis* (American Holly or Yerba Mate) and native trees in small farms in Misiones, Argentina. *Agroforestry Systems.* **In Preparation.**

3- Review articles/book chapters

Montagnini, F., Jordan, C.F. and Matta Machado, R. 1997. Nutrient cycling and nutrient-use efficiency in agroforestry systems. In: Ashton, M. and Montagnini, F. (Eds.). *The Silvicultural Basis for Agroforestry Systems.* Winrock/Oxford & IBH Series in Agroforestry. **In Press.**

Montagnini, F. 1997. Silvicultural plantations. In: McClain, M. E., Martinelli, L. A. and Richey, J. E (Eds.). *The Biogeochemistry of the Amazon Basin and its Role in a Changing World.* Oxford University Press. **In Press.**

Vogt, K., Asbjornsen, H., Ercelawn, A., Montagnini, F., and Valdes, M. 1997. Roots and mycorrhizas in plantation ecosystems. In: Nambiar, E. K. S. and Brown, A. G. (eds.) *Better Management of Soil, Water and Nutrients in Tropical Plantation Forests.* **In press.**

Montagnini, F. 1994. Agricultural systems in the La Selva Region. **pp. 307-316** In McDade, L. A., Bawa, K., Hespenheide, H. A., and Hartshorn, G. S. (eds.). *La Selvà: Ecology and Natural History of a Neotropical Rainforest.* University of Chicago Press.

Montagnini, F. and Sancho, F. 1994. Nutrient budgets of young plantations with native trees: strategies for sustained management. **pp. 213-233** In Bentley, W. & Gowen, M. (eds.). *Forest Resources and Wood-Based Biomass Energy as Rural Development Assets.* Winrock International and Oxford & IBH Publishing Co. New Delhi. 347 pp.

Montagnini, F., Sancho, F., Ramstad, K. and Stijfhoorn, E. 1991. Multipurpose trees for soil restoration in the humid lowlands of Costa Rica. **pp. 41-58** In Taylor, D. A. & Mc Dicken, K. G. (eds.). *Research on Multipurpose Trees in Asia.* Winrock International Institute for Agricultural Development. Bangkok. 259 pp.

Montagnini, F. 1990. Ecology applied to agroforestry in the humid tropics. **pp. 49-58** In Goodland, R. A. (ed). *Race to Save the Tropics. Ecology and Economics for a Sustainable Future.* Island Press. Washington, D.C.

Uhl, C., Jordan, C. F. and Montagnini, F. 1983. Traditional and innovative approaches to agriculture in the Amazon Basin. **pp. 73-95** In Lowrance, R. Todd, R. Asmussen, L. and Leonard, R. (eds.). *Nutrient Cycling in Agricultural Ecosystems.* University of Georgia, College of Agric. Exp. Stations, Spec. Pub. 23.

4- Published non-refereed publications

Montagnini, F., Eibl, B., Fernández, R., Kozarik, J. C., Lupi, A., and Nozzi, D. Agroforestry systems with *Ilex paraguariensis* (.Aamerican holly or yerba mate) and native timber trees in small farms in Misiones, Argentina. **pp. 67-72** In: *Proceedings of the International workshop: Agroforestry for Sustainable Land-use.* CIRAD/INRA, Agropolis International, Montpellier (France), 23-29 June 1997.

Montagnini, F. 1996. Recuperación de áreas degradadas con la utilización de árboles nativos: experiencias en tres regiones de Latinoamérica. In *Proceedings of III Congreso Latinoamericano de Ecología.* Mérida, Venezuela. October 19-21, 1995. **In press.**

Eibl, B. Montagnini, F., Woodward, C., Szczipanski, L. and Ríos, R. 1996. Evolución de la regeneración natural en dos sistemas de aprovechamiento y bosque nativo no perturbado en la Provincia de Misiones - República Argentina. In *Proceedings of III Congreso Latinoamericano de Ecología*. Mérida, Venezuela. October 19-21, 1995. **In press.**

Muñiz-Miret, N, Vamos, R., Hiraoka, M. and Montagnini, F. 1996. Las várzeas del estuario amazónico: extracción y cultivo de la palma de assaí (*Euterpe oleracea* Mart.) y su factibilidad financiera. In *Proceedings of III Congreso Latinoamericano de Ecología*. Mérida, Venezuela. October 19-21, 1995. **In press.**

Soto, G., Alvarado, A. y Montagnini, F. 1996. Encalado de especies forestales nativas. **p. 144** En: Bertsch, F., Badilla, W. y Bornemisza, E. (Eds.). Suelos: ¿Puede la Agricultura Sostenible ser Competitiva?. Memorias, X Congreso Nacional Agronómico y de Recursos Naturales/II Congreso de Suelos. Volumen III. Ed. Universidad Estatal a Distancia/Ed. de la Universidad Nacional. San José, Costa Rica.

Delgado, G., Soto, G. y Montagnini, F. 1996. Impacto de plantaciones forestales de especies nativas en monocultivo y en forma mixta sobre las poblaciones de microartrópodos del mantillo. **p. 96** En: Bertsch, F., Badilla, W. y Bornemisza, E. (Eds.). Suelos: ¿Puede la Agricultura Sostenible ser Competitiva?. Memorias, X Congreso Nacional Agronómico y de Recursos Naturales/II Congreso de Suelos. Volumen III. Ed. Universidad Estatal a Distancia/Ed. de la Universidad Nacional. San José, Costa Rica.

Montagnini, F. 1995. Initiatives in ecosystem rehabilitation and forest management in Tropical America. Tropical Resources Institute, Yale University School of Forestry and Environmental Studies. Internal Document. **15 pp.**

Montagnini, F., Eibl, B., Woodward, C., Szczipanski, L. and Ríos, R. 1995. Natural regeneration under two systems of selective cutting and undisturbed forest in Misiones, Argentina. *IUFRO XX World Congress. Tampere, Finland.* August 6-12, 1995. Available from the Internet: http//iufro.boku.ac.at/procee/s107/s10700.htm.

Montagnini, F. 1994. Rehabilitating forest ecosystems in the humid tropics: Recent experiences from Latin America. **Pp. 224-234** In *Proceedings from IUFRO International Symposium on Growth and Yield of Tropical Forests*. Sept. 26-Oct. 1, 1994. Tokyo University of Agriculture and Technology. Fuchu, Tokyo, Japan.

Montagnini, F., González, E., Porras, C., Rheingans, R. and Sancho, F. 1994. Mixed-tree plantations in the humid tropics: Growth, litterfall and economics of experimental systems in Latin America. **Pp. 125-135** In *Proceedings from IUFRO International Symposium on Growth and Yield of Tropical Forests*. Sept. 26-Oct. 1, 1994. Tokyo University of Agriculture and Technology. Fuchu, Tokyo, Japan.

Montagnini, F. and Sancho, F. 1995. Nutrientes en plantaciones jóvenes con árboles nativos. *Vetas* (Argentina) **155: 54-58**.

Fernández, R., Eibl, B., Montagnini, F., O'Lery, H. and Friedl, R. 1994. Native species planted in degraded areas in the province of Misiones, Argentina. **Pp. 633** In Balensiefer, M., de Araujo, A. J., and Rosot, N. C. (eds.). *Recuperacao de areas degradadas.* I Simposio Sul Americano e II Simposio Nacional. Foz do Iguacu. FUPEF. Curitiba, Brazil.

Montagnini, F. 1994. Tropical forests and climate. Book review. *Forest Ecology and Management* **65: 293-299**.

Montagnini, F. 1994. La salud humana y la utilización efectiva de los bosques tropicales. *Desarrollo Forestal y Comunidad Campesina* **3(10): 6-7**.

Montagnini, F. 1993. Shifting agriculture and sustainable development: an interdisciplinary approach from northeastern India. Book review. *Environmental Conservation* **20(1): 93-94**.

Montagnini, F., Singer, B., Auer, B., and Muñiz-Miret, N. 1993. A Tropical Resources Institute Initiative. Human health and effective utilization of tropical forests. *TRI News* **12(1): 1-2**.

Montagnini, F., Sancho, F., González, E., and Moulaert, A. 1993. El uso de especies maderables nativas en plantaciones mixtas para la reforestación de terrenos degradados: resultados preliminares de experiencias en la llanura del Atlántico de Costa Rica. **Pp. 190-210** In *VII Jornadas Técnicas: Ecosistemas Forestales Nativos: Uso, Manejo y Conservación.* 10-12 Noviembre, 1993. Universidad Nacional de Misiones, Facultad de Ciencias Forestales. Eldorado, Misiones, Argentina.

Montagnini, F., Sancho, F., González, E., and Moulaert, A. 1993. Mixed-tree plantations with indigenous trees in the Atlantic lowlands of Costa Rica. **Pp. 161-169** In Parrotta, J. A. and Kanashiro, M. (eds.). *Management and rehabilitation of degraded lands and secondary forests in Amazonia.* Proceedings of an International Symposium. Santarem, Pará, Brazil. 18-22 April, 1993. IITF. USDA - Forest Service. Puerto Rico.

Montagnini, F., Eibl, B., Friedl, A., Fernández, R, O'Lery, H. and Parussini, M. 1993. Ciclaje de nutrientes en plantaciones puras y mixtas con especies nativas. *Vetas* (Argentina) **134: 39-41**.

Montagnini, F., Fernández, R., O'Lery, H., Maiocco, D., Eibl, B. and Grance, L. 1993. Sistemas agrosilviculturales con especies nativas: yerba, timbó y guatambú. *Vetas* (Argentina) **135: 50-53**.

Montagnini, F. 1992. Mixed-tree plantations with native trees: land-use systems for economic returns and soil restoration. Experiments in Costa Rica and Argentina. *Agroforestry Today* **4(3): 4-6**.

Montagnini, F. 1992. Restauración de los bosques y los suelos con especies nativas- experimentos en Costa Rica y Argentina. *El Ecologista* (Costa Rica), dic/ene-1991/92, **pp. 3-5**.

Montagnini, F. 1991. Ecological restoration of degraded tropical pastures: experiences with native trees in the humid lowlands of Costa Rica. *Research and Exploration* (National Geographic Society), Summer **1991: 367-368**.

Montagnini, F. 1991. Collaboration in Costa Rica and Argentina: Forest and soil restoration experiments. *TRI News*, Fall **1991: 2-4**.

Montagnini F., Fanzeres, A., Beardsley, D., and da Vinha, S.G. 1991. Reforestation and soil restoration in the Atlantic Region of Bahia, Brazil. *Belowground Ecology Bulletin* **2(1): 15-17**.

Montagnini, F. and Sancho, F. 1990. Ensayos forestales con especies nativas: impacto sobre la fertilidad del suelo en la llanura del Atlántico de Costa Rica. *Biocenosis* (Costa Rica) **7(1): 11-16**.

Montagnini, F. 1989. Sistemas agroforestales: prioridades actuales de la investigación. Actas, Tomo 2. *V. Jornadas Técnicas: Uso Múltiple del Bosque y Sistemas Agroforestales*. Instituto Subtropical de Investigaciones Forestales (ISIF), Facultad de Ciencias Forestales, Universidad Nacional de Misiones, Eldorado, Misiones, Argentina. 4-7 Octubre, 1989.

Montagnini, F., Stijfhoorn, E., and Sancho, F. 1989. Soil chemical properties and root biomass under plantations of native tree species, grass cover and secondary forest vegetation in the Atlantic lowlands of Costa Rica. *Belowground Ecology Bulletin* **1(1): 6-8**.

Montagnini, F. 1985. Nitrogen turnover and leaching from successional and mature ecosystems in the southern Appalachians. *Ph.D. Dissertation*. University of Georgia, Athens, Georgia, U.S.A. **251 pp**.

Montagnini, F. 1980. Influencia de los insectos sobre el ciclo de nutrientes y productividad primaria en los ecosistemas de conucos de San Carlos de Río Negro, Territorio Federal Amazonas. *Trabajo de Grado para Magister Scientiarum en Biología, Mención Ecología*, Instituto Venezolano de Investigaciones Científicas (IVIC), Caracas, Venezuela. **238 pp**.

Montagnini, F. 1974. Insectos que afectan al cultivo de la soja en la zona de Pergamino. *Trabajo de Grado de Ingeniero Agrónomo*. Universidad Nacional de Rosario, Argentina. **37 pp**.

Article

Florencia Montagnini and Robert O. Mendelsohn

Managing Forest Fallows: Improving the Economics of Swidden Agriculture

The use of improved fallows has been proposed as a management alternative to shifting cultivation in the tropics. Managed fallows are quite widespread in the Americas, producing biological and economic benefits, however, cases in which both advantages are realized are scarce. In this article we evaluate the economic viability of forest fallows managed with planted timber tree species to replenish soils and provide economically valuable timber. At a 5% real interest rate, the enriched fallow-subsistence agriculture system yields land values from USD 5000–12 000 ha^{-1}. The results suggest that managing forest fallows in this manner can make shifting agriculture sustainable and economically competitive. Although the experiences are site-specific, the species used have broad distribution in Latin America and we expect that the systems could be transferred to other areas with similar ecological and socioeconomic conditions.

INTRODUCTION

Anthropologists have evidence that shifting agriculture has been practiced in the tropics for many centuries. Today, shifting (also called "swidden", "slash-and-burn") agriculture is the dominant land-use practice on about 30% of the arable soils of the world and provides sustenance for an estimated 300 million of the world's poorest people (1). Traditional shifting agriculture uses long forest fallows between short periods of farming. The long fallows make the traditional technique sustainable, but it also requires extensive amounts of land. When land is scarce, tropical farmers shorten the forest fallows and lengthen the agricultural periods. The modified approach yields higher immediate economic returns, but because it depletes the soil, it is nonsustainable with low long-run economic returns (2). Alternative farming techniques geared to sustaining agricultural productivity have been developed for several humid tropical regions, but frequently these are not attainable by rural farmers with limited resources, and often they are discontinued after the initial help or subsidies are terminated (2). The model presented in this article uses indigenous resources to produce short- and long-term returns in a land-use system accessible to small farmers in a rural region of Central America, in a pattern that could be applicable in other tropical humid regions with similar ecological and socioeconomic conditions.

Improved fallows have been proposed as a management alternative to shifting cultivation in the tropics (3, 4). Traditionally, shifting cultivators have encouraged the presence of certain tree or herb species in fallows to restore site fertility, suppress weeds and increase economic yields. Several types of traditional "enriched" fallows have been described, including those techniques involving planting or tending selective species for fruit, fuelwood or timber in fallow fields or secondary forests which are maintained by local populations over long periods of time, for local consumption, for markets or both (4–11). Some of these systems produce crops for local consumption and for a

The use of managed fallows based on a single species is quite widespread in the Americas, occurring from subtropical areas of Brazil to highland regions of Central America (4, 11). These systems include both biologically and economically enriched fallows. Some of the economically enriched fallows of the Amazon require more intensive management by which certain trees are protected during clearing or planted during the cropping period and maintained during the fallow (7). In the planted fallows, one or more species with biological or economic value are introduced to shorten the fallow regeneration period or increase its economic value (12, 13).

In this article we evaluate a system in which forest fallows are managed for timber and soil regeneration. A general economic model is developed in the next section which captures the sequential nature of agriculture and forestry in shifting agriculture. We utilize the economic model to evaluate the viability of managing the forest fallow for timber and soil fertility. We examine specific indigenous trees for the fallows, which both replenish the soil and provide high economic returns. Using results from experiments in the Atlantic lowlands of Costa Rica, we demonstrate that enriched fallows can return soil to agricultural productivity and make shifting agriculture economically competitive. Although we test only a single site, the timber species used here have broad geographical distribution throughout tropical America and we believe the technique can be used in other regions with comparable socioeconomic and ecological situations. Finally, it is important to recognize that shifting agriculture with managed fallows is particularly well suited for assisting the rural poor. The method requires some initial capital, but it can sustain income, works well in conjunction with subsistence farming, and provides income safely by relying on a portfolio of outputs.

ECONOMIC MODEL OF SHIFTING AGRICULTURE

Although the practice of using periods of fallow to replenish soils is used in agriculture throughout the world, shifting agriculture is unique in using a secondary forest during the fallow period. Starting with a forested hectare, an initial expenditure, CA, is made to clear and burn the forest. This is then followed by an intense agricultural period of a few years. In general, the most valuable and nutrient-demanding crops, e.g., rice, maize, are grown in the first 1–2 years during which the productivity of the soils gradually declines. This is then followed by a more resilient, less demanding crop (e.g., cassava) which can survive in the deteriorating soil for another 1–2 years. The net annual returns from agriculture we denote as RA_t. The land is then abandoned and the natural forest gradually reclaims the plot. After a period of 5–15 years of fallow, the farmer may return to harvest something from the secondary forest, R_F, such as timber or medicinal plants. The process of clearing and planting is then repeated.

Because this process takes a long time, in order to make it comparable with other land uses with different timing, we disthen can compare their present values. The present value, V_S, of shifting agriculture is:

$$V_S = \frac{-CA + \int_0^{t_1} RA_t\, e^{-rt}\, dt + \int_{t_1}^{t_2} (RF_t - CF_t)\, e^{-rt}\, dt}{[1 - e^{-rt_2}]} \qquad \text{Eq. 1}$$

where t_1 is the period in which agriculture is grown and t_2–t_1 is the period in which the forest grows. There are two explicit types of costs in the model, an initial clearing cost, CA, and a forest fallows management cost, CF_t. If the fallows are not managed, this forest fallow cost is zero. There are two types of net revenue. During the period of agriculture, the farmer collects annual net revenue from crops. The value of this net revenue generally falls with time, ending usually in the third year. There is also revenue from the forest, especially if it is managed. If the forest is being managed for nontimber forest products, this revenue can persist over a few years near the end of the rotation. If the forest is being managed for timber, the revenue comes in the last year of the rotation as the forest is harvested. The expression in the numerator is the present value of a single cycle. Dividing this by the denominator gives the present value of all future cycles.

Shifting agriculture, because it sequences a period of agriculture and forestry is a general model of which agriculture and forestry are special cases. When there is no forest fallow, chemical fertilizers and weed control replace the period of fallow. If there is no agricultural production, the model turns into the traditional Faustmann model of even-aged forestry. The model weighs initial planting costs against a large future timber harvest. Pure agricultural land use is characterized as a constant flow of net revenue per year, pure forestry as large intermittent incomes, and the managed swidden system as periods of annual flow followed by a long period of waiting and a large timber harvest. The present value calculation adjusts for the timing of costs and revenues to make the values of each of the land uses comparable. The calculation depends upon the interest rate (assumed to have a real value of 5% in this paper). Higher (lower) interest rates imply society places a relatively lower (higher) value on future income. Given a specific interest rate, the land use with the highest present value is the most valuable.

In addition to the market costs listed above, it is possible that there would be additional environmental impacts from shifting agricultural activities. Harvesting the forest is likely to affect local wildlife. For example, species which depend on an undisturbed tropical forest are likely to be harmed by a shifting system. Effects on wildlife, however, need not be all negative as some forest animals may benefit from the relatively young stands associated with a shifting system. Depending on local conditions, it is also possible that a shifting system would increase soil erosion while the ground is cleared. In contrast, the shifting system is less likely to cause water contamination problems than continuous agriculture because of the long period in forest and because it uses little fertilizer or pesticides. Although these additional factors should be quantified and included in the analysis, there is almost no information about the magnitude or value of these impacts. We have consequently omitted them from the analysis.

SOIL IMPACTS OF MANAGED FOREST FALLOWS

When a secondary forest replaces an abandoned crop or pasture, the production of biomass by the vegetation and the cooler soil temperature under the forest canopy act favorably on both the needed for the restoration of the soil organic matter after abandonment from agriculture or pasture depends on the rate at which the secondary forest fallow establishes itself. This rate in turn depends on rainfall, soil physical and chemical conditions, topography and erosion: typically, fallow periods of 5 to 15 years are required in most tropical humid areas for soils to recover organic matter to levels similar to those of the original rain forest (11, 14, 15).

Successional processes can be manipulated to achieve sustainable forest productivity, a prime goal in ecosystem rehabilitation projects (16). The length of the fallow period can be decreased, the rate of soil recovery can be enhanced, and the economic return from the forest can be improved through judicious forest management (11). For example, in an experimental fallow system in the Peruvian Amazon, selected soil-improving tree species were planted in abandoned shifting agriculture fields (12). The species planted were acid-tolerant woody legumes, *Cajanus cajan* and *Inga edulis*. Two years after planting, the total ecosystem levels of Mg and Ca declined, while total N and K increased, and the levels of P increased after 4.5 years. In these experiences, weed control was achieved more rapidly with herbaceous species (*Pueraria phaseoloides, Desmodium ovalifolium*), however good suppression of weeds was also eventually obtained by the woody legumes. Experiences such as those described by Szott et al. (12) are especially relevant in Central America and other regions where land becomes scarce and the fallows are not long enough to restore soils to their productive capacity (11, 15).

A key to the success of these systems is the choice of fast-growing trees with good economic potential and positive impacts on soil properties (17, 18). In the present article we have used results from experimental fallow systems at La Selva Biological Station in the Atlantic humid lowlands of Costa Rica. The soils are Inceptisols, great group Fluventic Dystropepts (US Soil Taxonomy) derived from volcanic alluvium; they are deep, well-drained, stone-free, acid (pH in water < 5.0), with low or medium organic matter (2.5–4.5%), cation exchange capacity 10–14 cmols kg^{-1}, 10–15% base saturation, and moderately heavy texture (50–60% sand, 5–15% silt and 25–45% clay) (19, 20). The area was cleared in the mid-1950s and grazed until 1981, a land-use pattern common in the region. At the time of abandonment, soil fertility levels of the site were too low to allow for conventional agriculture (21).

The tree species planted in the abandoned pasture fields included leguminous, nitrogen fixing trees as well as species of other families: *Stryphnodendron microstachyum* Poepp. et Endl. (sinon: *excelsum*), *Vochysia ferruginea* Mart., *Vochysia guatemalensis* Donn. Sm. (sinon: *hondurensis*) and *Hyeronima alchorneoides* (O). Soils were sampled just after the trees had closed canopies (1.5–2 years after planting), and annually thereafter for 5 more years. Composite samples were taken in each of five replicate plots per treatment, at 0–15, 15–30 and 30–60 cm depth. Soil fertility was examined using standard procedures for acid tropical soils (21). The pH was measured in a 1:2.5 mixture of soil:deionized water. The exchangeable Ca and Mg were extracted with a 1 N KCl solution, while the exchangeable P and K were extracted with a modified Olsen solution (19–21). Organic matter was measured with the Walkley-Black technique, and total N was measured using a semi-Micro-Kjeldahl technique (21). Analysis of variance and LSD tests were run to compare the means for each variable and soil depth ($n = 5$, $P < 0.05$) among sites.

The results showed that in just 2.5 years, soil conditions improved in the tree plots compared to abandoned pasture. In the top 15 cm, soil nitrogen and organic matter were higher under the trees than in nearby pasture, with values close to those found in adjacent 20-year-old forests (Table 1). The highest values for

***Hyeronima alchorneoides* in a farmer's land, 2-year-old stands (notice cassava interplanted among the *Hyeronima*). Photo: F. Montagnini.**

A 2-year-old stand of *Vochysia ferruginea*. Notice the dark understory and lack of weeds. Photo: F. Montagnini.

ferruginea, a species of the Vochysiaceae family, common in mature and secondary forests in the region (19, 20). Subsequent measurements revealed similar trends in the soil parameters in the three following years.

Based on the standards determined by the Ministry of Agriculture of Costa Rica for soil fertility assessments (21), the cation levels (Ca, Mg and K) under most of the tree species were at or above the critical values for agriculture. In contrast, the cation levels in the adjacent abandoned pasture soils were too low for the subsistence crops preferred in the region, i.e. rice and beans (22, 23). The standards set by the Ministry of Agriculture do not include N or organic matter. However, an indication of the importance of the improvement of the soil organic matter levels is given by the close relation found between organic matter content and the sum of bases (Ca+Mg+K), showing that the organic matter was responsible for much of the cation retention capacity (19). For example, based on this relationship, a 1–2% increase in soil organic matter (in the 4–6% range) would more than double the base content, reaching values in the range recommended for agriculture (21). The higher soil organic matter under the trees can contribute to better retention of cations recycled from tree leaf litter and roots, as described below.

Low crop yields in the humid tropics are often a result, in part, of unfavorable physical properties such as soil compaction (24). In our site at La Selva, soil organic matter also had positive influences on soil physical properties: the soil bulk density was lower, i.e. lower compaction, while soil moisture was higher under the trees than in abandoned pasture (Table 1). This may appear to be irrelevant in a humid region with an average annual rainfall of 4000 mm yr^{-1}. However, even in rainy climates, occasional dry spells may affect the growth of young tree seedlings or interplanted crops, therefore, better water retention becomes an advantage, especially in the early stages of system establishment.

Nitrogen fertilizers are heavily used in the La Selva region, especially for the most demanding commercial crops such as bananas, in which case capital is available for fertilizer in a more extensive land-use system (22, 23). From the results shown in Table 1, *S. microstachyum*, a N-fixing tree, did not have an important effect on total N, but its litter decomposes faster than the other species, resulting in increased soil mineral nitrogen under its canopy (25). Evaluating the effects of trees on soil P availability is even more difficult, although experiments with test crops can determine soil impacts. For example, in other experimental research, maize seedlings, grown in plots mulched with *S. microstachyum* and *H. alchorneoides* versus the litter of other species, showed the greatest initial growth and the highest N and P plant uptake (26). In these and in other related research at La Selva, the maize seedlings grown without mulch or fertilizer on soils from abandoned shifting agriculture fields grew very poorly, reaffirming the need for soil improvement techniques for growing conventional crops in the impoverished abandoned lands.

Table 1. Top-soil (0–15 cm) characteristics in 2.5 year-old tree stands of indigenous species, grass and adjacent 20-year-old secondary forest at La Selva, Costa Rica (19, 20).

Species/Site	Organic matter (%)	Total N (%)	P ($mg\ kg^{-1}$)	Ca ($cmol\ kg^{-1}$)	Mg	K	pH	Bulk density ($g\ cm^{-3}$)	H_2O (%)
Stryphnodendron microstachyum	6.0ab	0.29b	5.6a	0.45a	0.63ab	0.27a	5.4ab	0.80a	42.9bc
Vochysia ferruginea	6.6a	0.32a	7.1a	0.73a	0.61ab	0.22a	5.4ab	0.75b	45.2a
Vochysia guatemalensis	5.5ab	0.29b	5.2a	0.25a	0.37ab	0.11a	5.3ab	0.75b	45.3a
Hyeronima alchorneoides	5.2c	0.23b	1.5b	0.31b	0.21b	0.09a	5.1b	0.78ab	41.9c
Pasture	4.8c	0.22b	4.9a	0.32b	0.27b	0.19a	5.3ab	0.81a	41.1c
Forest	7.6a	0.33a	3.6b	0.68a	0.55ab	0.17a	5.3ab	0.70c	44.6ab

Note: For each variable, differences between sites are statistically significant as determined with analysis of variance, when means are followed by different letters ($n = 5$, $P < 0.05$).

Stryphnodendron microstachyum, 3-year-old stand in an abandoned pasture field. Photo: F. Montagnini.

An aerial view of the region showing fields abandoned from conventional shifting agriculture. Photo: F. Montagnini.

The impacts of trees on soil fertility depend on their nutrient recycling characteristics such as litter chemistry and decomposition. Tree litter can act as mulch with differing objectives: a fast mulch decomposition rate may accelerate the growth of associated crops on poor soils, while in other cases a more persistent litter may be desired. For example, high rates of litterfall and slower decomposition result in high litter accumulation and high soil organic matter under *V. ferruginea*, making this species well suited for protecting soils against erosion. In contrast, *H. alchornoides* litter, although less abundant than the other three species, with its relatively faster decomposition and high nutrient content, promotes fast nutrient recycling, especially of N, Ca, Mg, K and P, while *V. guatemalensis* litter may be especially important for Ca and Mg recycling (26).

Apart from their beneficial effects on soils, the tree species with their rapid canopy closure decreased the growth of weeds after 2–3 years, however with differences among species: the growth of understory vegetation was less in *V. ferruginea* and *V. guatemalensis* than in *H. alchorneoides* or *S. microstachyum* plots (27, 28). The canopy characteristics of the tree species will affect their suitability for interplanting with annual crops and the management required when used in agroforestry systems.

ECONOMIC ANALYSIS

Using the economic model described above, we calculate the present value of a forest fallow for two of the species explored in Costa Rica, *V. ferruginea* (*V.f.*) and *H. alchorneoides* (*H.a.*). In this analysis, we convert prices in colones to USD using an official exchange rate of 152 colones per dollar. The stumpage price, the amount paid to farmers for the right to cut mature trees, is USD 44 per m^3 for *V.f.* and USD 43 per m^3 for *H.a.* (29). The cost of establishing and maintaining plantations of these species was estimated from field observations by Rheingans (March-October 1994) (30). The bulk of these costs are needed to establish the trees in the first year (Table 2). The remaining costs entail weeding and pruning which occur in the first, second, third, and fifth years. The forest begins to close after this period suppressing the growth of weeds so that no further costs for weeding are incurred.

Precise yield functions for these two species are not available. The trees in the experimental plots are still too young to determine their long-term growth rate. However, based on growth and volume data for these species from the same experiment as well as from other plantations on similar soils and with the same spacing (32–34), we estimate that *V.f.* would mature to an optimal yield of 260–300 m^3 ha^{-1} in approximately 10–12 years and *H.a.* would mature to 260–300 m^3 ha^{-1} in 15–20 years. These growth rates are within ranges found for other native species in the region and throughout Costa Rica (35). Taking the mid-point of these ranges, this implies an average growth rate of 25 m^3 ha^{-1} yr^{-1} for *V.f.* and 16 m^3 ha^{-1} yr^{-1} for *H.a.*

Whether farming is profitable in this region is not clear. Given regional prices paid to farmers, productivity, and wages, if farmers hire local help to do their farming, the farms would lose money (Table 3). That is, at competitive wage rates, farming re-

Table 2. The economics of managing forest fallows.

Forest fallow costs[a] (per ha)

	Year 1		Year 2		Year 3		Year 5	
Task	Days	Cost	Days	Cost	Days	Cost	Days	Cost
Clearing	52.4	581						
Planting/ Digging	20.8	231						
Replanting	3.6	40						
Weeding/ Pruning[b]	29.3	325	14.6	162	8.8	97	8.8	97
Seedlings/ Transport		150						
Sub-total	106.1	1328	14.6	162	8.8	97	8.8	97

Timber revenue (per hectare)

Species	Year	Yield	Price	Revenue
V. ferrug.	11	280 m^3	44 USD m^{-3}	USD 12 320
H. alchor.	17	280 m^3	43 USD m^{-3}	USD 12 040

[a] Source: (30)

[b] Source: (31)

quires so much labor, that the farms are not viable. This is consistent with observed behavior as most cash crop farmers are moving out of agriculture. The majority of agricultural activity remaining in the region is subsistence farming, people growing food for their own consumption (36). Subsistence agriculture is economically viable because of lower labor costs and higher prices. Subsistence farmers rely on the labor of spouses and children whose wage (next best employment opportunity) is lower than men's (hired help) (36). Meanwhile, the value of the produced food is higher than for cash farmers because there are no transport and middlemen costs. The farmer is the consumer. If the farmer is paid the retail value of his crops, the activity becomes profitable. Assuming that subsistence wages are one third of market wages and that retail prices are twice what farmers are paid on the farm, subsistence rice and bean farming generate positive annual returns of USD 496 and USD 174, respectively (Table 3). As women and children demand higher wages or as subsistence farmers try to sell a fraction of their crops for cash, one moves from subsistence farming towards modern farming, lowering net values.

Because each land use provides income in different time periods, it is necessary to compare the present value of the stream of income from each land use in order to determine their relative economic value. We assume a real interest rate (the interest after inflation is removed) of 5%. Using Equation 1 and estimating the present value of shifting agriculture with subsistence farming and enriched fallows yields the estimates shown in Table 4.

The value of traditional swidden fallows, where the forest is not managed, is presented in the first column of Table 4. The farmer saves all the costs of preparing the forest for the fallow period, but in turn collects no revenue when it is time to clear the forest again. This was attractive when labor was scarce and land was plentiful. The present value of this practice yields values of USD 0.5–USD 1.7 thousand per ha when combined with crops and a negative value when combined with cattle. Columns 2 and 3 of Table 4 provide estimates of the value of managed fallow-subsistence agriculture. When the forests are managed, present values rise to USD 5–12 000 depending upon the agriculture and tree species adopted.

Given current market conditions, managing *V.f.* is more profitable than *H.a.* However, *H.a.* is currently plentiful in natural forests. As *H.a.* gets harvested out of existing natural forests, its price will gradually rise making it more competitive in the future. An additional aspect influencing the choice of species for the fallow is the length of their growth period. In our example, *V.f.* takes 6 less years to reach harvestable size than *H.a.*, which is a distinct economic advantage. In the agricultural part of the cycle, growing rice is more profitable than beans, which in turn, is more profitable than cattle. This too can change as economic conditions fluctuate in the region and the world. Compared to the returns from other land-use activities, shifting agriculture with enriched fallows is a competitive land use.

Table 3. Annual net farm income (USD ha^{-1} yr^{-1}).

	Modern farm[a] (hired labor)			Subsistence (family labor)		
	Rice	Beans	Cattle	Rice	Beans	Cattle
Inputs	33	26	73	33	26	73
Labor costs	536	268	78	177	88	26
Revenue	353	144	46	706	288	92
Net revenue	–215	–150	–105	496	174	–7

[a] Source: (36)
Subsistence calculation assumes labor costs are one-third of modern farm costs because they rely on women and children rather than hired help and that revenue is twice modern farm revenue because output is consumed by the farmer at retail value.

Table 4. Net present value of shifting agriculture (USD ha^{-1})[a].

Farm output	Traditional	Managed tree species	
		V.f.	*H.a.*
Rice	696	12 413	6778
Beans	447	11 162	5805
Cattle	–256	10 459	5257

[a] Estimates developed from Tables 2 and 3, using Equation 1 and assuming repeated cycles of two years of subsistence agriculture followed by 12, 11, and 17 years, respectively, for traditional, *V.f.*, and *H.a.* management.

DISCUSSION

Traditional shifting agriculture may be sustainable but its land-intensive nature makes it unprofitable when there is a scarcity of land. By enriching forest fallows with timber species of economic value and positive impacts on soils, the economics of shifting agriculture can be substantially improved. After cutting and extracting timber from the tree plantation, leaving slash on the ground to protect soils, farmers can plant subsistence crops on the improved soils. By growing trees on one portion of the farm while growing crops on others, the farmer can maintain a consistent flow of food while following the rotational scheme being recommended in this article. Further, by carefully select-

be preserved ensuring the sustainability of the entire process. Even with careful management, and depending on the nutrient-supplying capacity of the soils, the application of low levels of lime or fertilizers may be needed to restore nutrients extracted at harvest in the long run. However, the surplus generated from the timber sales is expected to allow farmers to purchase fertilizers to accommodate these needs.

Other advantages of tree planting are likely to favor the adoption of the present system. Apart from being a source of cash, trees also serve as savings and insurance for individual farmers living in these regions (37). Fuelwood from thinning and pruning would be an additional source of farm income. In fact, the species involved in the experiment currently account for the majority of small-farm reforestation in the region.

This article has presented evidence that shifting agriculture with planted fallows can be an economically viable and sustainable activity in a Costa Rican forest region. By managing the forest fallows, farmers can increase the present value of swidden agriculture from the traditional levels of USD 0.5–1.7 to USD 5000–12 000 thousand per ha. Further, by relying on multiple outputs, shifting agriculture gives portfolio protection against price swings in any one product. Finally, by including subsistence agriculture as part of its land use, the technique is accessible even to relatively poor farmers who must rely on some cash to fulfill household needs.

Many existing managed fallow systems are quite site-specific and have limited distribution, while others occur over large geographical areas and could be adapted to other regions (4, 6, 11). Our model applies to the particular experimental site in Costa Rica, and we expect the conditions will vary according to economic access and ecological characteristics. However the species used here have broad natural ranges throughout tropical America (32, 38) and thus we expect that this system could be applied in other regions with comparable ecological and sociosities, indicating their volcanic origin, while in other parts of Latin America different soils occur (Ultisols and Oxisols) which have different constraints. The particular characteristics of the site will dictate what species, rotation length and management strategies are adequate. For example, experiments are now underway in Misiones, NE Argentina and Bahia, Brazil (39, 40) to explore whether this system can be adapted to other humid tropical and subtropical forest regions. Initial feedback on soil recovery rates suggest that managed forest fallows will generally be sustainable (40, 41). Economic analyses of these sites will test whether enriched fallows-shifting agriculture will be broadly competitive.

Because the system proposed here involves the plantation of selected trees in the fallows, initially some capital will be needed to cover 2–3 years of establishment costs. This requirement can be a problem if farmers have no access to capital. As a mechanism to help the poorest segment of rural populations, some assistance may be required to help farmers make the up-front expenditures required to plant the trees. Small subsistence farmers often have no access to loans and so cannot afford to make even profitable investments. In Costa Rica, programs such as the Fondo de Desarrollo Forestal (FDF), Forestry Development Fund provides loans for planting trees to small farmers (31, 42). The farmers repay the loan by giving 30% of the income from harvesting the trees at maturity. Such programs could make sustainable development a reality by allowing small farmers to make good long-term investments in their land.

References and Notes

1. Andriesse, J.P. and Schelhaas, R.M. 1987. A monitoring study of nutrient cycles in soils used for shifting cultivation under various climatic conditions in tropical Asia. III. The effects of land clearing through burning on the fertility level. *Agric. Ecosyst. Environ. 19*, 311–332.
2. Bandy, D.E., Garrity, D.P. and Sanchez, P.A. 1993. The worldwide problem of slash and burn agriculture. *Agrofor. Today 5*, 2–9.
3. Nair, P.K.R. 1990. *The Prospects and Promise of Agroforestry in the Tropics, a Review of Technical and Socioeconomic Information with Special Emphasis to Africa.* Report to the World Bank, Washington, DC.
4. Kass, D.C.L., Foletti, C., Szott, L.T., Landaverde, R. and Nolasco, R. 1993. Traditional fallow systems of the Americas. *Agrofor. Syst. 23*, 207–218.
5. Denevan, W.D, Treacy, J.M., Alcorn, J.B., Padoch, C., Denslow, J. and Paitan, S.F. 1984. Indigenous forestry in the Peruvian Amazon: Bora Indian management of forest fallows. *Interciencia 9*, 346–357.
6. Padoch, C., Chota Inuma, J., De Jong, W. and Unruh, J. 1985. Amazonian agroforestry: a market-oriented system in Peru. *Agrofor. Syst. 3*, 47–58.
7. Padoch, C. and De Jong, W. 1987. Traditional agroforestry practices of native and ribereno farmers in the lowland Peruvian Amazon. In: *Agroforestry, Realities, Possibilities and Potentials*. Gholz, H. (ed.). Martinus Nijhoff, Dordrecht, The Netherlands, pp.179–194.
8. Raintree, J.B. and Warner, K. 1986. Agroforestry pathways for intensification of shifting agriculture. *Agrofor. Syst. 4*, 39–54.
9. Unruh, J.D. 1990. Iterative increases of economic tree species in managed swidden-fallows of the Amazon. *Agrofor. Syst. 11*, 175–197.
10. Del Amo, R.S. and Ramos, P.J. 1993. Use and management of secondary vegetation in a humid-tropical area. *Agrofor. Syst. 21*, 27–42.
11. Sips, P.A. 1993. *Management of Tropical Secondary Rain Forests in Latin America. Today's Challenge, Tomorrow's Accomplished Fact!?* Werkdocument IKC-NBLF Nr.27. Stitching BOS, Wageningen, The Netherlands, pp.16–55.
12. Szott, L.T., Palm, C.A. and Sanchez, P.A. 1991. Agroforestry in acid soils of the humid tropics. *Advanc. Agron. 45*, 275–300
13. Vergara, N.T. 1987. Agroforestry: a suitable land use for fragile ecosystems in the humid tropics. In: *Agroforestry, Realities, Possibilities and Potentials*. Gholz, H. (ed.). Martinus Nijhoff, Dordrecht, The Netherlands, pp. 7–20.
14. Van Wambeke, A. 1992. *Soils of the Tropics. Properties and Appraisal*. McGraw-Hill, New York, pp. 69–95
15. Watters, R.F. 1971. *Shifting Cultivation in Latin America*. FAO Forestry Development Paper No. 17. Food and Agriculture Organization of the United Nations, Rome.
16. Lugo, A.E. 1988. The future of the forest. Ecosystem rehabilitation in the tropics. *Environ. 30*, 17–20 and 41–45.
17. Sanchez, P.A., Palm, C.A., Davey, C.B., Szott, T.C. and Russell, C. 1985. Tree crops as soil improvers in the humid tropics? In *Attributes of Trees as Crop Plants*. Cannell, M.G.R. and Jackson, J.E. (eds). Institute of Terrestrial Ecology, Natural Environmental Research Council, Abbots Ripton, Huntingdon, England, pp. 327–350
18. Young, A. 1989. *Agroforestry for Soil Conservation*. C.A.B. International and International Council for Research in Agroforestry, Wallingford, UK.
19. Montagnini, F. and Sancho, F. 1990. Impacts of native trees on tropical soils: a study in the Atlantic lowlands of Costa Rica. *Ambio 19*, 386–390.
20. Montagnini, F. and Sancho, F. 1990. Influencia de seis especies de árboles nativos sobre la fertilidad del suelo en una plantación experimental en la llanura del Atlántico en Costa Rica. *Yvyraretá (Argentina)1*, 29–49. (In Spanish).
21. Bertsch, F.H. 1986. *Manual para Interpretar la Fertilidad de los Suelos en Costa Rica.* Universidad de Costa Rica, Escuela de Fitotecnia, San José, Costa Rica. (In Spanish).
22. Universidad de Costa Rica. 1984. *Caracterización Ambiental y de los Sistemas de Cultivo en Fincas de la Región de Río Frío, Horquetas, Sarapiquí, Heredia, Costa Rica.* Facultad de Agronomía, UCR, San José, Costa Rica. (In Spanish).
23. Van Sluÿs, F.R., Waaijenberg, H., Wielemaker, W.G. and Wienk, J.F. 1989. *Agricultura en la Zona Atlántica de Costa Rica*. Serie técnica, Informe técnico No. 21, Programme paper No. 4. CATIE, Turrialba, Costa Rica and Wageningen Agricultural University. (In Spanish).
24. Cassel, D.K. and Lal, R. 1992. Soil physical properties of the tropics: Common beliefs and management restraints. In: *Myths and Science of Soils of the Tropics*. Lal, R. and Sanchez, P.A. (eds). Soil Science Society of America Special Publication Number 29, SSSA and American Society of Agronomy, Madison, Wisconsin, pp. 61–90.
25. Montagnini, F. and Sancho, F. 1994. Net nitrogen mineralization in soils under six indigenous tree species, an abandoned pasture and a secondary forest in the Atlantic lowlands of Costa Rica. *Plant Soil 162*, 117–124.
26. Montagnini, F., Ramstad, K. and Sancho, F. 1993. Litterfall, litter decomposition and the use of mulch of four indigenous tree species in the Atlantic lowlands of Costa Rica. *Agrofor. Syst. 23*, 39–61.
27. Montagnini, F. and Sancho, F. 1994. Above-ground biomass and nutrients in young plantations of four indigenous tree species: implications for site nutrient conservation. *J. Sustain. For. 1*, 115–139.
28. Montagnini, F. and Sancho, F. 1994. Nutrient budgets of young plantations with native trees: strategies for sustained management. In: *Forest Resources and Wood-based Biomass Energy as Rural Development Assets*. Bentley, W. and Gowen, M. (eds).
29. Dirección General Forestal. 1994. *Lista de Precio en Pie, en Patio de Industria y Aserrada de las Especies que Comunmente se Industrializaron en Costa Rica en 1993.* Min. de Recursos Nat., Energía y Minas, DGF, Dept. de Ind. For, San José, Costa Rica. (In Spanish).
30. Rheingans, R. 1994. *Analysis of Establishment and Maintenance Costs in an Experimental Setting*. Project Progress Report, March 15, 1994.
31. Morales Soto, O. 1992. *Análisis de Costos e Incentivos CAF-FDF*. Ministerio de Recursos Naturales, Energía y Minas, Dirección General Forestal, San José, Costa Rica. (In Spanish).
32. González, E., Butterfield, R., Segleau, J. and Espinoza, M. (eds). 1990. *Primer Encuentro Regional sobre Especies Forestales Nativas de la Zona Norte y Atlántica.* Memoria, 28–29 Julio 1990, Chilamate, Costa Rica. Inst. Tecnol. Costa Rica, Cartago, Costa Rica. (In Spanish).
33. González, E. and Fisher, R. 1994. Growth of native species planted on abandoned pasture land in Costa Rica. *For. Ecol. Mgmt 70*, 159–167.
34. Butterfield, R.P. and Espinoza C.M. 1995. Screening trial of 14 tropical hardwoods with an emphasis on species native to Costa Rica: fourth year results. *New For. 9*, 135–145.
35. Alfaro, M. 1991. Evaluación financiera de la inversión en plantaciones forestales. *Silvoenergía 48 (CATIE, Turrialba, Costa Rica)*, 1–4. (In Spanish).
36. Schelhas, Jr. J.W. 1991. *Socio-economic and Biological Aspects of Land Use Adjacent to Braulio Carrillo National Park, Costa Rica*. PhD Dissertation, University of Arizona.
37. Chambers, R. and Leach, M. 1990. Trees as savings and security for the rural poor. *Unasylva 41*, 39–52.
38. Chudnoff, M. 1984. *Tropical Timbers of the World*. USDA Forest Service, Agricultural Handbook 605, Washington, DC.
39. Montagnini, F. 1992. Mixed-tree plantations with native trees: land-use systems for economic returns and soil restoration. Experiments in Costa Rica and Argentina. *Agrofor. Today 4*, 4–6.
40. Montagnini, F., Fanzeres, A. and da Vinha, S.G. 1994. Studies on restoration ecology in the Atlantic Forest region of Bahia, Brazil. *Interciencia 19*, 323–330.
41. Montagnini, F., Fernández, R. and Hamilton, H. 1995. Relaciones entre especies nativas y la fertilidad de los suelos. Parte 1: contenido de elementos en la biomasa. *Yvyraretá (Argentina) 6*, 5–12. (In Spanish).
42. Segleau, J. and Gómez, A. 1990. Incentivos fiscales para la reforestación. In: *Primer Encuentro Regional sobre Especies Forestales Nativas de la Zona Norte y Atlántica.* González, E., Butterfield, R., Segleau, J. and Espinoza, M. (eds). Memoria, 28–29 Julio 1990, Chilamate, Costa Rica. Inst. Tecnol. Costa Rica, Cartago, Costa Rica, pp. 40–43. (In Spanish).

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Mixed and pure forest plantations in the humid neotropics: a comparison of early growth, pest damage and establishment costs

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SUMMARY

Three plantations, each with four indigenous tree species, were established in the humid lowlands of Costa Rica to compare growth, pest damage and economics in pure and mixed stands, with the objective of developing suitable plantation models for small farms. In measurements taken at 2-4 years of age, DBH was larger in mixed than in pure plots of the fastest growing species of each combination. Pest damage was less severe in mixed than in pure stands for three of the twelve species tested, and there was no damage or no difference between pure and mixed conditions for the other species. Establishment costs were lower for the slower growing species in mixture than alone. In comparison with pure stands of the fastest growing species, mixtures had relatively high yields, with the additional advantage of including other species of high economic value.

Keywords: establishment costs, mixed plantations, native trees, pest damage, tree growth.

INTRODUCTION

Mixed plantations yield more diverse forest products than monospecific stands, helping to diminish farmers' risks in unstable markets. Species diversification in plantations also may be desirable because of uncertainties about species performance, scarcity of seedlings, or potential pest damage. Species diversification can be achieved by planting species mixtures or planting sets of monospecific plots. If planned with consideration for each species' response to mixed conditions, mixed designs can be more productive than monospecific systems (Smith 1986, Burkhart and Tham 1992, Wormald 1992). Stratified mixtures that combine rapidly growing overstorey species with slow-starting but higher producing species are likely to exhibit greater total productivity than pure stands of shade-intolerant species (Smith 1986). When mixtures combine tree species that differ in growth requirements and production, they can reduce inter-specific competition and can outyield monospecific stands (Kelty 1992). Mixed stands can improve the survival and growth of a species in nutrient poor soils when combined with a suitable accompanying species (Matthews 1989, Binkley *et al.* 1992). Mixed stands may also contribute to higher landscape diversity.

Severity of pest damage is expected to be lower in mixed than in pure plantations because monospecific stands favour the spread and build up of populations of individual pests. Nevertheless, there are many instances in which pure stands are more resistant to certain pests than stands of the same species mixed with other, more susceptible ones (Smith 1986, Perry and Maghembe 1989, Watt 1992). Experiences comparing monospecific and mixed species plantations are still few, and their advantages and disadvantages appear to be site specific (Wormald 1992). Yields of mixed and pure designs should therefore be evaluated in the context of other potential advantages or disadvantages attained by each system.

In this paper we report results from three experimental plantations with native trees in mixed and pure stands in the Atlantic humid lowlands of Costa Rica. Research at this site also involves studies of nutrient cycling and effects on soil chemical and physical properties (Montagnini *et al.* 1994). Here we examine the growth, production, pest damage and economics of twelve indigenous species in pure and mixed conditions. Although the plantations were young (2-4 years old), for fast growing species in humid tropical sites this age range often represents about 20% of a rotation length. Establishment is also one of the most critical phases in the life of a plantation because it includes relatively high costs with no immediate returns. The results offer suggestions for design and management which can be useful for the success of these systems.

STUDY SITE

Experiments were established on abandoned pasture at La Selva Biological Station, Costa Rica (10°26'N, 86°59'W, 50 metres mean altitude, 24°C mean annual temperature, 4000 mm mean annual rainfall). Soils are Fluventic Dystropepts derived from volcanic alluvium; they are deep, well drained, stone-free, acid (pH in water <5.0), with low or medium organic matter (2.5-4.5%), cation exchange capacity 10-14 cmols kg^{-1}, 10-15% base saturation, and moderately heavy texture (50-60% sand, 5-15% silt and 25-45% clay) (Sancho and Mata 1987). The area was cleared in the mid-1950s and grazed until 1981, a land use pattern common in the region. The area is on flat, uniform terrain (<1 m average difference between lowest and highest points). At the time of clearing for plantations, the area was covered with shrubs and early successional trees interspersed with patches of grass and ferns. In comparisons of soil chemical characteristics before planting, results showed that there were no significant differences among blocks within each plantation (Montagnini *et al.* 1993). According to standards set by the Costa Rican Ministry of Agriculture, fertility levels of the site were too low for conventional agriculture.

METHODS

Plantation establishment and management

In each mixture of four tree species there was at least one nitrogen-fixing tree, a relatively fast growing species and a slower growing species (Table 1). Additionally, species were combined so as to have trees of different branching pattern and crown shape and size in each mixture. The criteria for species selection were: growth rate, economic value and preference by farmers (Chudnoff 1984, González *et al.* 1990); presence of root nodules in the leguminous species; potential impacts on soils and nutrient cycling (Montagnini and Sancho 1990, 1994a, 1994b); and seedling availability. Other characteristics of the twelve species of this research can be found in Montagnini *et al.* (1993).

Plantations were set in randomized blocks, with four replicates and six treatments: four pure plantation plots of each species, a mixed-species plot (with the four species), and a fallow (natural forest regrowth) plot. Each plot was 32 m x 32 m. Initial planting distance was 2 m x 2 m to speed canopy closure and obtain early impacts on soils, with 50% thinning planned after canopy closure.

TABLE 1. *Characteristics of tree species grown in mixed and pure plantations at La Selva Biological Station.*

Scientific name	Common name	Family	Native range	Growth, habitat
Plantation 1				
Stryphnodendron microstachyum Poepp. et Endl.	vainillo	Leguminosae (Mimosoid)	Costa Rica, Nicaragua, Panama	Upper canopy of mature forest. Also on secondary forest. Fast growth.
Vochysia guatemalensis Donn.Sm.	mayo, chancho	Vochysiaceae	Mexico to Panama	Upper canopy, early-mid successional. Fast growth.
Jacaranda copaia (Aubl.)D.Don.	jacaranda	Bignoniaceae	Guatemala to Brazil	Pioneer, early successional. Secondary forest. Very fast growth.
Callophylum brasiliense Cambess.	cedro Maria	Guttiferae (Clusiaceae)	Mexico to N. South America	Mature forest. Slower growth.
Plantation 2				
Albizia guachapele (H.B.K.)Little	cenizaro, guayaquil	Leguminosae (Mimosoid)	Guatemala to Ecuador	Pioneer. Common in low secondary forest. Fast growth.
Terminalia amazonia (J.F.Gmel.)Exell.	roble coral	Combretaceae	S. Mexico to N.South America	Upper canopy, mid-successional. Relatively fast growth.
Virola koschnyi Warb	fruta dorada	Myristicaceae	Central America	Upper canopy, mid-successional. Slower growth.
Dipteryx panamensis (Pittier)Record & Mell	almendro	Leguminosae (Papilionoid)	Nicaragua to Colombia	Upper canopy, mid- to late successional. Slower growth.
Plantation 3				
Pithecellobium elegans D.C.Benth	ajillo, guaitil	Leguminosae (Mimosoid)	Tropical America	Mid- to late successional. Slower growth.
Genipa americana L.	genipa	Rubiaceae	Tropical America	Late successional. Slower growth.
Vochysia ferruginea Mart.	botarrama	Vochysiaceae	Nicaragua to Brazil	Early to mid-successional. Fast growth.
Hyeronima alchorneoides Fr. Allemao	pilon	Euphorbiaceae	S. Mexico to S. Brazil	Early to mid-successional. Fast growth.

Sources: González *et al.* 1990, Holdridge and Poveda 1975.

Within each mixed-tree plot, trees of the four species were planted alternating two species per row. The sequential order of the species within rows was systematically reversed every other row. In that manner, each column contained the four species of the mixture in a sequence:

1 3 2 4
2 4 1 3
1 3 2 4
2 4 1 3

The site was cleared manually with no burning. Slash was left on the ground to protect against soil erosion and to delay the growth of weeds. Seeds were collected from trees at La Selva forest or from other areas in the region, and seedlings were grown at La Selva nursery. Plantations were weeded manually as needed (including the natural regrowth plots for consistency) with no herbicides.

Since no border effects were expected initially, all 256 trees of each plot were measured for total height and diameter at breast height (DBH) every six months for the first two years. Thereafter, subplots containing at least 40 trees were established for measurements to avoid border rows. Analysis of variance and tests for means (LSD, $P<0.05$) were run using the means of each variable from each of the four replicate plots. Total height, DBH and survival were compared among the four species of each plantation and also between pure and mixed-species plots of each species. Additionally, basal area and volume estimates per hectare were compared between the four pure-species plots and the mixed-species plots. Since form factors were not known for these species, a volume index was calculated following Newbould (1967): Volume index=basal area x height x 0.5.

Pest damage

Pest damage was evaluated in plantations up to two years of age. Each plantation was examined at least twice, at two different times of the year. Damage was visually examined in all plots of each plantation. Arthropods associated with damage were taken to the laboratory for identification. Two damage indices were calculated for each pest: damage frequency and damage severity (Moulaert and Arguedas 1993). Damage frequency was calculated as the number of affected individuals divided by the total number of individuals in each plot. For each affected individual, damage severity was calculated as the percentage of the total number of leaves or branches that manifested a particular type of damage. Individual estimates were averaged for each species. Analysis of variance and tests for means (LSD, $P<0.05$) were run for comparisons of damage frequency and severity among species in pure and mixed plots. For brevity, only results of the second evaluations performed on the three plantations in 1993 are presented here.

Costs

Establishment and maintenance cost estimates (work-days/ha and US dollars/ha), calculated from field observations of activities carried out by workers, have been published in Montagnini *et al.* (1994). In the present paper we show a comparison of establishment costs between pure and mixed conditions for Plantation 1. The costs of exclusively research oriented tasks were subtracted from the final calculations. Labour costs were calculated using rates commonly paid for similar tasks in the country, instead of the relatively higher wages paid to project employees. Clearing and site preparation costs vary according to the original condition of the site (old pasture or young secondary forest); values used here correspond to a clearing of a 10 year-old secondary forest. Pruning costs were added in years 3 and 5 from estimates taken from Morales Soto (1992).

RESULTS

Tree growth

Forty-eight months after planting in Plantation 1, trees of *Jacaranda copaia* (Aubl.)D.Don. were the tallest, followed by *Vochysia guatemalensis* D.Sm. and *Callophylum brasiliense* Cambess, with no significant differences between pure and mixed conditions for any species (Table 2). *Stryphnodendron microstachyum* Poepp. et Endl. showed the lowest survival (calculated after seedling replacements), in part related to deer browsing before a fence was built for protection. A fungal disease resulted in substantial mortality of *S. microstachyum* after 2 years (see pest damage, below), and at 4 years trees of this species had survived only in the mixed plots (Table 2). Trees of *J. copaia* and *V. guatemalensis* had greater DBH in mixed than in pure plots, a difference that became evident after canopy closure. In contrast, *C. brasiliense* was suppressed by the overstory species in the mixture and had greater DBH in pure than in mixed plots.

Thirty-nine months after planting in Plantation 2, the tallest trees were those of *Terminalia amazonia* (Gmell.)Exell., followed by *Dipteryx panamensis* (Pittier) Record&Mell and *Virola koschnyi* Warb. Trees of *Albizia guachapele* (H.B.K.) Little were taller in mixed than in pure stands, a trend detected just after canopy closure. There were no statistically significant differences in height between pure and mixed plots of the other three species at any age (Figure 1). *T. amazonia* showed the lowest survival because of attacks by leaf-cutting ants, with no differences between pure and mixed plots. At 39 months the largest DBH was found in *T. amazonia* mixed plots; this was significantly higher than in pure plots (Table 2). The DBH of *A. guachapele* was also greater in mixed than in pure plots, a trend that was apparent at 21 months (Figure 2).

At 24 months of age, the trees with greater height and diameter in Plantation 3 were *Hyeronima alchorneoides* Fr. Allemao, followed by *Pithecellobium elegans* D.C.Benth., *Genipa americana* L. and *Vochysia ferruginea* Mart. (Table 2). *G. americana* had the lowest survival, mostly attributed to slow initial growth just after planting, which made it susceptible to unfavourable (hot and dry) weather conditions. Its survival was higher in mixed than in pure plots.

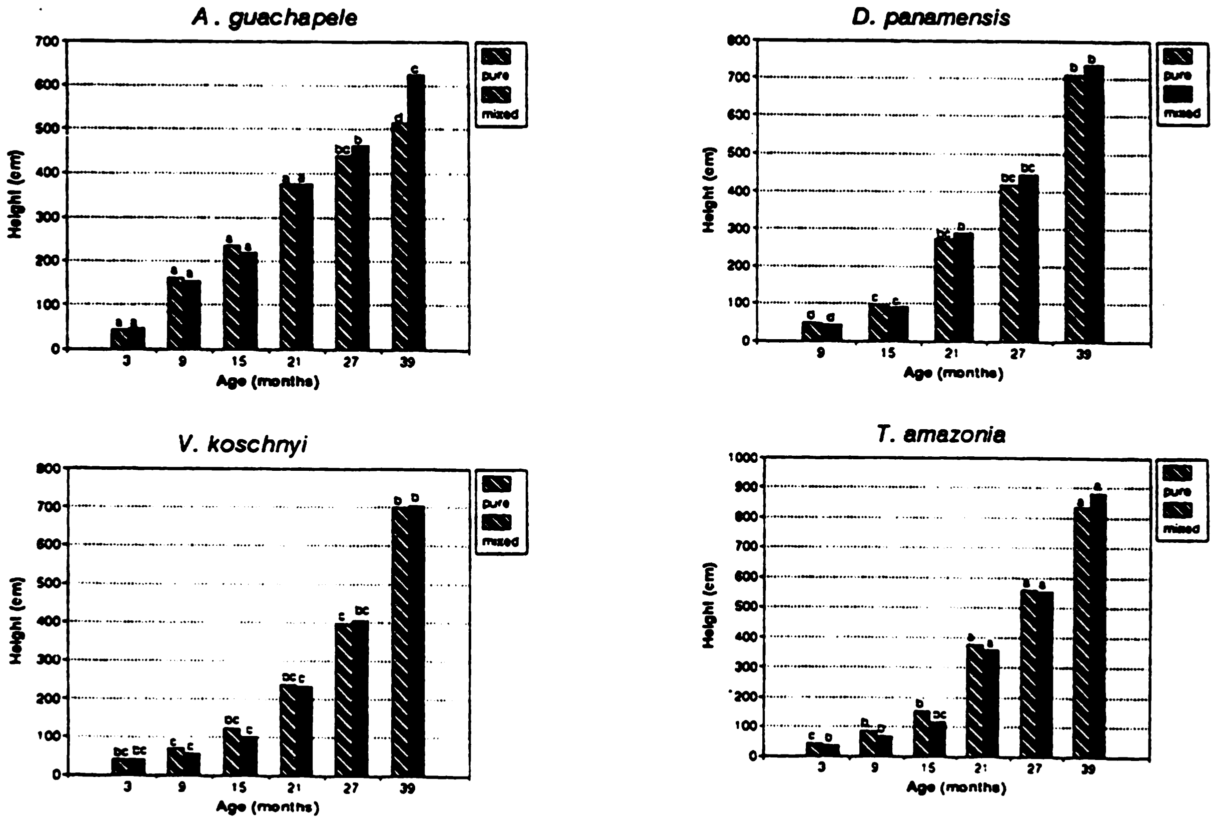

FIGURE 1. *Total height of the four species of Plantation 2 in pure and mixed plots. For each date, differences in total height among species and between pure and mixed plots are statistically significant when the bars are marked with different letters. (Notice that the scales in the vertical axes differ among the species).*

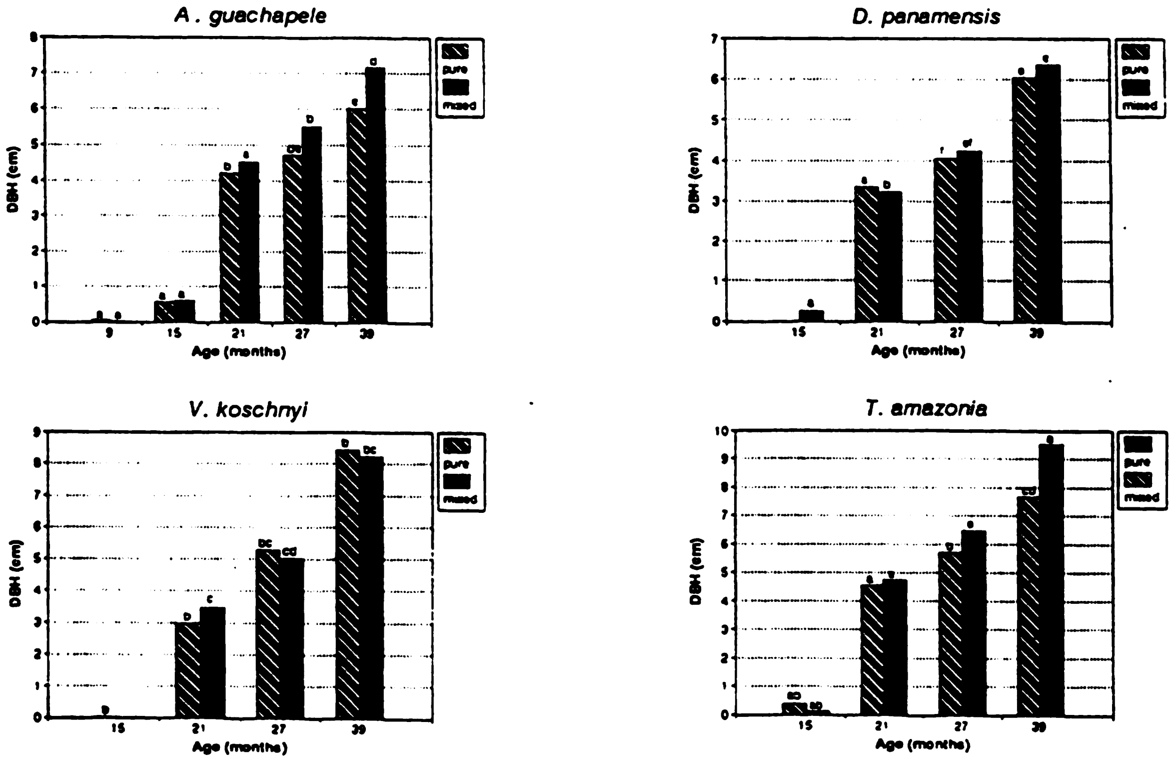

FIGURE 2. *DBH of the four species of Plantation 2 in pure and mixed plots. For each date, differences in DBH among species and between pure and mixed plots are statistically significant when the bars are marked with different letters. (Notice that the scales in the vertical axes differ among the species).*

The DBH of *H. alchorneoides* was greater in mixed than in pure conditions. There were no statistically significant differences in height between pure and mixed plots for any species.

TABLE 2. *Growth and survival.*

Species/Plots	Total height (m)	DBH (cm)	Survival (%)
Plantation 1: 48 months			
S. microstachyum			
pure	0	0	0
mixed	5.73(0.35)c	6.38(0.82)c	42.2(7.49)c
V. guatemalensis			
pure	11.6(0.52)b	11.8(0.30)b	97.6(0.97)a
mixed	11.4(0.22)b	18.0(0.24)a	97.7(1.50)a
J. copaia			
pure	14.4(0.19)a	12.7(0.19)b	97.0(1.50)a
mixed	15.4(0.58)a	18.8(0.76)a	97.7(1.50)a
C. brasiliense			
pure	5.38(0.13)cd	6.09(0.11)c	74.4(4.99)b
mixed	4.58(0.14)c	3.80(0.18)d	77.3(5.00)b
Plantation 2: 39 months			
A. guachapele			
pure	5.15(0.08)d	6.02(0.14)c	83.8(4.24)b
mixed	6.25(0.12)c	7.15(0.31)d	90.2(2.58)a
D. panamensis			
pure	7.10(0.29)b	6.04(0.13)e	75.5(2.54)bc
mixed	7.36(0.20)b	6.35(0.24)e	72.7(3.38)b
V. koschnyi			
pure	7.01(0.35)b	8.44(0.41)b	87.9(3.17)a
mixed	7.06(0.09)b	8.24(0.23)bc	76.6(2.50)bc
T. amazonia			
pure	8.35(0.33)a	7.64(0.06)cd	66.3(6.71)cd
mixed	8.82(0.18)a	9.51(0.23)a	58.9(3.02)d
Plantation 3: 24 months			
G. americana			
pure	3.36(0.36)cd	4.51(0.19)de	64.2(10.0)d
mixed	3.77(0.27)c	4.79(0.27)d	79.3(3.02)c
H. alchorneoides			
pure	5.96(0.17)a	6.96(0.13)b	97.3(1.33)a
mixed	5.47(0.20)ab	7.76(0.34)a	99.2(0.45)a
V. ferruginea			
pure	2.59(0.09)e	4.05(0.10)ef	88.2(3.36)b
mixed	2.99(0.09)de	3.78(0.12)f	91.4(2.67)ab
P. elegans			
pure	4.98(0.49)b	6.58(0.26)bc	95.7(0.55)ab
mixed	5.14(0.28)b	6.33(0.40)c	97.7(1.01)a

Note: For each plantation variables are compared among 4 species and between pure and mixed plots. Means are significantly different when standard errors are followed by different letters (n=4. $P < 0.05$)

In Plantation 1, tree basal area was larger in *J. copaia* pure plots and in the mixture of four species. Volume index was larger in *J. copaia*, and the mixture ranked second (Table 3). In Plantation 2, although *T. amazonia* ranked first in height and DBH, *V. koschnyi* pure plots had the largest basal area because of greater survival. *T. amazonia* pure plots and the mixture followed, with no statistically significant differences in basal area between them (Table 3). Volume indices were larger in *V. koschnyi*, *T. amazonia* and the mixture (Table 3). In Plantation 3, basal area was larger in *H. alchorneoides* and *P. elegans* pure plots, followed by the mixture. Volume index was larger in *H. alchorneoides* pure plots, followed by *P. elegans* and the mixture (Table 3).

TABLE 3. *Basal area and volume estimates for pure plots and mixtures for Plantations 1, 2 and 3.*

Species/ Plots	Basal area (m^2/ha)	Volume index (m^3/ha)
Plantation 1: 48 months		
S. microstachyum	0	0
V. guatemalensis	28.4(1.20)b	172(15.2)c
J. copaia	34.1(0.32)a	272(6.77)a
C. brasiliense	5.53(0.46)c	16.1(1.71)d
Mix of 4 spp.	34.8(1.64)a	232(12.9)b
Plantation 2: 39 months		
A. guachapele	6.12(0.45)cd	17.7(1.40)b
D. panamensis	5.38(0.41)d	21.1(2.36)b
V. koschnyi	12.0(1.07)a	45.1(6.61)a
T. amazonia	8.08(0.85)bc	37.2(4.96)a
Mix of 4 spp.	9.24(0.47)b	36.5(5.88)a
Plantation 3: 24 months		
G. americana	2.66(0.56)c	4.78(1.33)c
H. alchorneoides	9.26(0.37)a	27.7(1.86)a
V. ferruginea	2.84(0.20)c	3.70(0.37)c
P. elegans	8.18(0.68)a	20.9(4.05)b
Mix of 4 spp.	6.43(0.36)b	15.9(1.50)b

Note: Means are significantly different when standard errors are followed by different letters (n=4, $P<0.05$).

Pest damage

In Plantation 1, *V. guatemalensis* and *C. brasiliense* had higher damage frequency by leaf chewing insects in mixed than in pure plots (Table 4); however, the overall frequency was relatively low and did not seem to reduce growth or survival (Table 2). In contrast, damage severity was lower in mixed than in pure plots of *S. microstachyum*. The anthracnosis that affected *S. microstachyum*, caused by the fungus *Glomerella* spp. (M. Arguedas, pers.comm.), resulted in complete mortality in pure plots, while 42.2% of the trees survived in mixed plots at 4 years. Damage severity was relatively low (<20%) in *V. guatemalensis* and *C. brasiliense*, with no significant differences between pure and mixed plots. No damage was recorded on *J. copaia* trees.

In Plantation 2, damage frequency was higher in mixed than in pure plots of *V. koschnyi* and *A. guachapele* (Table 4). Severity of damage by leaf chewing insects was almost twice as high in pure than in mixed plots of *V. koschnyi*, and there were no differences between pure and mixed plots of *A. guachapele*. Although frequency and severity of root damage by gophers (*Orthogeomys* spp.) on *A. guachapele* were high, the attacked trees apparently recovered, showing good growth in height and DBH (Table 2). There were no differences in frequency or severity between pure and mixed plots for *D. panamensis*, but both frequency and severity were lower than for the other species.

In Plantation 3 there was a higher frequency and lower severity of pest damage in the mixed than in the pure plots of *G. americana*; there were no differences between pure and mixed plots of *V. ferruginea*, and neither *H. alchorneoides* nor *P. elegans* showed signs of pest damage (Table 4). *H. alchorneoides* and *V. ferruginea* seedlings had been affected by leaf cutting ants, but the seedlings had recovered by the time these measurements were taken. In all cases, pest damage frequency and severity in Plantation 3 were less than 10%.

Costs

The adjusted costs estimated for the mixture and three of the single species treatments of Plantation 1 are shown in Table 5. The only difference was the cost of weeding during years 2 and 3. The amount of labour required for the establishment of pure plots of *C. brasiliense*, which began to close canopy after 3 years, was 40% greater than that of pure plots of *J. copaia*, which closed canopy after the first year. The costs for *V. guatemalensis* and the mixture were intermediate between the two.

TABLE 4. *Damage incidence and severity for twelve species at establishment time. Within each plantation, both variables are compared among 4 species and also among pure and mixed conditions.*

Species/Plots	Incidence %	Severity %	Type of damage
Plantation 1			
S. microstachyum			
pure	11.6 (4.43)b	86.7(4.50)a	Anthracnosis
mixed	8.56(1.00)bc	41.2(2.39)b	
V. guatemalensis			
pure	5.0(1.11)c	9.48(1.15)d	Leaf damage, mostly circular holes
mixed	18.9(3.03)a	12.3(1.80)cd	
J. copaia			
pure	0.0	0.0	No visible signs
mixed	0.0	0.0	
C. brasiliense			
pure	8.94(0.9)bc	14.1(1.07)cd	Leaf damage, yellowing of tips
mixed	17.1(1.72)c	15.3(1.72)c	
Plantation 2			
A. guachapele			
pure	25.4(0.79)b	70.0(2.04)a	Chlorosis, associated with root damage by gophers
mixed	31.2(3.14)a	70.6(1.88)a	
D. panamensis			
pure	20.3(1.87)cd	11.7(0.68)c	Leaf damage, mostly circular holes
mixed	21.9(1.52)bc	10.4(1.25)c	
V. koschnyi			
pure	13.2(1.26)e	24.7(4.74)b	Same as above
mixed	17.3(1.28)d	13.7(1.05)c	
T. amazonia			
pure	0.0	0.0	No visible signs
mixed	0.0	0.0	
Plantation 3			
G. americana			
pure	3.32(0.62)b	8.83(0.40)a	Burnt tips, folded leaves. Damage on leaf veins
mixed	5.08(0.86)a	6.67(1.20)b	
H. alchorneoides			
pure	0.0	0.0	No visible signs
mixed	0.0	0.0	
V. ferruginea			
pure	2.54(0.52)b	6.25(0.80)b	Leaf damage from cutting ants
mixed	3.13(0.64)b	5.50(0.50)b	
P. elegans			
pure	0.0	0.0	No visible signs
mixed	0.0	0.0	

Note: Means are significantly different when standard errors are followed by different letters (n=4, P<0.05).

TABLE 5. *Comparison of establishment and maintenance costs per hectare by species in mixed and pure treatments for Plantation 1.*

Year	Species/treatment							
	V. guatemalensis		*J. copaia*		*C. brasiliense*		Mixture	
	Work-days	US$	Work-days	US$	Work-days	US$	Work-days	US$
1	108.7	1329.2	108.7	1329.2	108.7	1329.2	108.7	1329.2
2	14.6	162.1	0	0	29.3	325.2	14.6	162.1
3	0	0	0	0	14.6	162.1	7.3	81.0
TOTALS	123.3	1491.3	108.7	1329.2	152.6	1816.5	130.6	1572.3

DISCUSSION

Tree growth and yield in pure and mixed stands

The growth rates shown here agree with those reported earlier for these species in pure plantations at La Selva and elsewhere in Costa Rica (González *et al.* 1990, González and Fisher 1994, Butterfield and Espinoza 1995). The highest values of basal area and volume were in the pure plots of the fastest growing, shade-intolerant species of each of the three plantations (*J. copaia, V. koschnyi, T. amazonia* and *H. alchorneoides*). Mixtures ranked second, or in the case of Plantation 2, volume of the mixture was not statistically different from the pure plots of the two leading species (*V. koschnyi* and *T. amazonia*).

The larger DBH of faster growing species in mixed than in pure plots (Table 2) probably resulted from less intra-specific competition and from higher spatial variation of light micro habitats in mixed plots, associated with crown structure and vertical foliage distribution (Guariguata *et al* 1995). The crowns of *J. copaia* trees are shallow and their small leaflets are widely spaced in a horizontal plane, while the crowns of *V. guatemalensis* are deep, with densely-packed simple leaves; *S. microstachyum* is open-crowned, and *C. brasiliense* is deep-crowned. In the mixed plots, differences in crown structure among species appeared responsible for creating intermediate illumination conditions (Guariguata *et al.* 1995). Since tree height is mainly influenced by site, it was not expected to vary between mixed and pure conditions; this was the case for all species except for *A. guachapele.* This species tended to branch out in the pure plots while it had better form (straighter and taller stems) in mixed conditions due to interspecific competition.

The relatively slower growing species of each plantation were probably subject to competition by the faster growing species in the mixtures. This was particularly the case of *C. brasiliense*, the only species with significantly lower DBH in mixed than in pure plots. This relatively slower growing species was apparently suppressed by the other overstorey species in the mixture. The most successful mixed plantings are stratified mixtures composed of faster-growing, shade-intolerant species above slower-starting tolerants (Smith 1986). If the trees in the upper canopy are not too dense, they grow more rapidly in diameter than if crowded into the single canopy of a pure plantation; lower-stratum species can influence stem form and self pruning of upper-stratum species similar to that of a pure stand (Burkart and Tham 1992).

Management operations such as thinning and pruning can also favor the growth of suppressed species. Preliminary results showed that 18 months after thinning, the DBH and height of *C. brasiliense* were significantly higher in thinned than in non-thinned subplots, with more marked effects in mixed than in pure plots, indicating the importance of inter-specific competition. *J. copaia* and *V. guatemalensis* had higher DBH but no increases in height as a response to thinning, with greater effects on DBH in pure than in mixed plots, presumably as a result of higher intra-specific competition in the pure plots.

Competition for resources below ground may also influence the relative success of each species; therefore, the species' root architecture and density and water and mineral needs also should be considered in the design of tree mixtures. Tree mixtures can be more productive than pure plantations if the species are combined to complement soil mineral demands and effects on nutrient cycling. The N-fixing species of this research (*S. microstachyum, A. guachapele* and *P. elegans*) were found to nodulate in the field; *D. panamensis*, a leguminous (Papilionoid) species, has not been reported to nodulate (Allen and Allen 1981). The N-fixing ability of *S. microstachyum* was measured in a separate field experiment (Baker and Montagnini 1994), and the positive impacts of this species on soil N availability and nutrient cycling in pure stands have already been documented (Montagnini and Sancho 1994a, 1994b). Due to its high mortality (Table 2), the influence of *S. microstachyum* on nutrient cycling was probably limited to the first two years in the present experiment. However, the remaining species might have benefitted from its early presence, and results from current nutrient use efficiency studies may clarify this point. In general, results of investigations on litter fall, litter decomposition, whole-tree biomass and soil chemistry will help elucidate the advantages and disadvantages of mixed and pure plantations with regard to nutrient resource use.

As seen here, growth responses may vary according to species and site conditions. The outcome may depend on whether soil factors or light are most limiting for a particular species, or whether production is measured in terms of weight or volume of wood (Smith 1986). In some cases, tree species may not differ enough to reduce competition significantly, or important interactions may occur but may not be of enough magnitude to cause mixtures to outyield a pure plantation of a highly productive species (Kelty 1992). The results presented here reflect responses at an early stage. Long-term measurements are expected to show other effects, making the interactions among species more evident. Other results of studies comparing thinned and non-thinned subplots may also help to elucidate the relative influence of spacing and intra- and inter-specific competition on tree growth.

Pest damage incidence and severity in pure and mixed plots

Except for early damage by leaf cutting ants, results shown in Table 4 were similar to those of previous measurements for the three plantations (data not shown). Leaf-cutting ants, *Atta cephalotes*, initially affected 7 out of the 12 species examined, with a frequency of 7-20% and a severity of 10-65%. This coincides with earlier findings by Moulaert and Arguedas (1993), where leaf cutting by *A. cephalotes* was the most important damage agent on young tree plantations at La Selva. No pest control measures were taken, but the infestations ceased after about three months, generally with the onset of heavy rains.

The expected pattern of lower severity of pest and disease damage in mixed than in pure plots was found for three species: *S. microstachyum*, *V. koschnyi* and *G. americana*. Four species did not show visible signs of damage in either pure or mixed conditions (*J. copaia*, *T. amazonia*, *H. alchorneoides* and *P. elegans*), and in the other five species, differences between pure and mixed plots were not statistically significant. Growing conditions (mixed or pure stands) may have different effects on pest infestations depending on the causal agent: the fungal disease spread faster in pure stands, while the chewing insects present in the plantations probably fed on a variety of trees and weeds and did not reach outbreak levels in either pure or mixed conditions.

Economic advantages and disadvantages of pure and mixed plantation designs

While establishment costs differed mainly in weeding requirements between pure and mixed designs in Plantation 1, the costs associated with other silvicultural activities will probably vary by species. The present discussion is limited to information from one plantation. However, the results suggest that the use of mixed designs could help reduce establishment costs for slower growing species, which take longer to close canopies, resulting in higher weeding costs in pure than in mixed conditions. This benefit should be weighed against the potential decrease in growth rate of the slower growing (and potentially more valuable) species when associated with shade-intolerant, more aggressive species.

The majority (68%) of establishment costs for both pure and mixed plots occurred in year 1, due to the initial dominance of aggressive grasses and the relatively long growing season (Montagnini *et al.* 1994). These initial costs were relatively high (US$1329 per ha, corresponding to 108.7 work-days per ha), but they were similar to other estimates for the region, and they fell within the range that the Costa Rican Forest Service fixes for reforestation projects. Costs declined in the second year to US$162 per ha (14.6 work-days), and in the third year there were no costs for the maintenance of pure plots of the fast-growing species (Table 5). This decrease was mostly a result of reduced weed growth caused by rapid canopy closure. It is worth noting that these costs include social benefits as stipulated by law (35-40% of gross salaries). As a result, costs to small farmers who rely on family labour are considerably less.

Although little price differentiation currently exists among the twelve species, prices are expected to rise as timber availability from natural forests decreases. At present, local markets generally accept logs with a minimum small end diameter of 40 cm; however, logs of as little as 15 cm are also purchased, though at one-third the price. With estimated rotation times of 15-25 years and expected volumes at harvest of 250-300 m^3 ha^{-1}, planting of these species is attractive for small farmers in the region. Fuelwood from thinning and pruning would be an additional source of farm income. In fact, the species involved in the experiment currently account for the majority of small farm reforestation in the region, and interest has recently developed for mixed designs that include some of the fastest growing trees with good timber value (*T. amazonia*, *V. guatemalensis* and *H. alchorneoides*).

CONCLUSIONS

Although it is still early to assess the performance of some of the slower growing species of these experiments, some of the advantages and disadvantages of mixed-species systems were evident. The mixed designs apparently favoured growth in diameter of the fastest growing species, starting just after canopy closure. In comparison with pure species plots of the fastest growing species, the mixtures had relatively high yields, with the additional advantage of including other species of higher economic value. Management practices, such as thinning and pruning, could favour the future growth of the most suppressed species. While patterns of pest damage depend on both the plant and pest species, mixed species designs may be advantageous in reducing risks of pest or disease damage, as was the case with anthracnosis and leaf cutting ants.

Despite relatively high establishment costs, the estimated rotation times and timber prices suggest that these systems are financially attractive to farmers. Savings in establishment costs could be gained when slower-growing species are part of the mixed design. Mixed-species systems could also provide more flexibility by offering a variety of products in an uncertain market.

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REFERENCES

ALLEN, O.N. and ALLEN, E.K. 1981 *The Leguminosae: a source book of characteristics, uses, and nodulation.* University of Wisconsin Press, Madison, Wisconsin. 812 pp.

BAKER, D. and MONTAGNINI, F. 1994 Estimation of nitrogen fixation by the tropical legume tree *Stryphnodendron microstachyum* Poepp. et Endl. *Nitrogen Fixing Tree Research Reports* 12: 139-141.

BINKLEY, D., DUNKIN, K.A, DEBELL, D. and RYAN, M.G. 1992 Production and nutrient cycling in mixed plantations of *Eucalyptus* and *Albizia* in Hawaii. *Forest Science* 38: 393-408.

BURKHART, H.E. and THAM, Å. 1992 Predictions from growth and yield models of the performance of mixed-species stands. *In:* Cannell, M.G.R., Malcolm, D.C. and Robertson, P.A. (eds.). *The ecology of mixed-species stands of trees.* Blackwell Scientific, Boston. pp.21-34.

BUTTERFIELD, R. P., and ESPINOZA, M. 1995 Screening trial of 14 tropical hardwoods with an emphasis on species native to Costa Rica: fourth year results. *New Forests* 9: 135-145.

CHUDNOFF, M. 1984 *Tropical timbers of the world.* USDA Forest Service, Agricultural Handbook 605, Washington, DC.

GONZÁLEZ, E., BUTTERFIELD, R., SEGLEAU, J. and ESPINOZA, M. 1990 *Primer encuentro regional sobre especies forestales nativas de la zona Norte y Atlántica.* Memoria, 28-29 Julio 1990, Chilamate, Costa Rica. I.T.C.R., Cartago, Costa Rica, 46pp.

GONZÁLEZ, E. and FISHER, R. 1994 Growth of native species planted on abandoned pasture land in Costa Rica. *Forest Ecology and Management* 70: 159-167.

GUARIGUATA, M. R., RHEINGANS, R. and MONTAGNINI, F., 1995. Patterns of understorey woody invasion in plantations of native tree species in lowland Costa Rica: implications for restoration. *Restoration Ecology*, in press.

HOLDRIDGE, L.R. and POVEDA, L.J. 1975 *Arboles de Costa Rica.* Centro Científico Tropical, San José, Costa Rica.

KELTY, M. J. 1992 Comparative productivity of monocultures and mixed-species stands. *In:* Kelty, M.J., Larson, B.C., and Oliver, C.D. (eds) *The ecology and silviculture of mixed-species forests.* Kluwer Academic Publishers, Dordrecht, pp. 125-141.

MATTHEWS, J. D. 1989 *Silvicultural systems.* Clarendon Press, Oxford.

MONTAGNINI, F. and SANCHO, F. 1990 Impacts of native trees on tropical soils: a study in the Atlantic lowlands of Costa Rica. *Ambio* 19: 386-390.

MONTAGNINI, F., SANCHO, F., GONZÁLEZ, E. and MOULAERT, A. 1993 Mixed-tree plantations with indigenous trees in the Atlantic lowlands of Costa Rica. *In:* Parrotta, J.A. and Kanashiro, M. (eds.) *Management and rehabilitation of degraded lands and secondary forests in Amazonia.* USDA Forest Service. Puerto Rico. pp. 161-169.

MONTAGNINI, F. and SANCHO, F. 1994a Above-ground biomass and nutrients in young plantations of four indigenous tree species: implications for site nutrient conservation. *Journal of Sustainable Forestry* 1: 115-139.

MONTAGNINI, F. and SANCHO, F. 1994b Net nitrogen mineralization in soils under six indigenous tree species, an abandoned pasture and a secondary forest in the Atlantic lowlands of Costa Rica. *Plant and Soil* 162: 117-124.

MONTAGNINI, F., GONZÁLEZ, E. PORRAS, C., RHEINGANS, R. and SANCHO, F. 1994 Mixed-tree plantations in the humid tropics: growth, litterfall and economics of experimental systems in Latin America. *IUFRO International Symposium on growth and yield of tropical forests.* Sept. 26-Oct. 1, 1994. Tokyo University of Agriculture and Technology. Tokyo, Japan. pp.125-135.

MORALES SOTO, O. 1992 *Análisis de costos e incentivos CAF-FDF, San José, Costa Rica.* Dirección General Forestal, San José, Costa Rica.

MOULAERT, A. and ARGUEDAS, M. 1993 Insectos herbívoros asociados con diez especies forestales en la Región Norte de Costa Rica. *Revista Forestal Centroamericana* 2: 24-26.

NEWBOULD, P.J. 1967 *Methods for estimating the primary production of forests.* IBP Handbook 2. Blackwell Scientific, Oxford, UK.

PERRY, D. A. and MAGHEMBE, J. 1989 Ecosystem concepts and current trends in forest management: time for reappraisal. *Forest Ecology and Management* 26 123-140.

SANCHO, F. and MATA, R. 1987 *Estudio detallado de suelos. Estación Biológica La Selva.* Organización para Estudios Tropicales, San José, Costa Rica, 162 pp.

SMITH, D.M. 1986 *The practice of silviculture.* John Wiley and Sons, New York.

WATT, A.D. 1992 Insect pest population dynamics: effects of tree species diversity. *In* Cannell, M.G.R., Malcolm, D.C. and Robertson, P.A.(eds.) *The ecology of mixed-species stands of trees.* Blackwell Scientific, Boston. pp. 267-275.

WORMALD, T. J. 1992 *Mixed and pure forest plantations in the tropics and subtropics.* FAO Forestry Paper 103. FAO Technical Papers. Food and Agriculture Organization of the United Nations, Rome, 152 pp.

Early Woody Invasion Under Tree Plantations in Costa Rica: Implications for Forest Restoration

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Abstract

The role of tree plantations as facilitators of tropical forest restoration in degraded lands has been explored recently, but there are few data on the effect of different tree species on invasion of the plant understory. We evaluated early patterns of understory composition in three-year-old native tree plantations in lowland Costa Rica using two pure-species treatment (*Jacaranda copaia* and *Vochysia guatemalensis*) and one mixed-species treatment (*J. copaia, V. guatemalensis, Stryphnodendron microstachyum,* and *Calophyllum brasiliense*). We also monitored woody invasion in unplanted control areas dominated by grasses. The understory of the different plantation treatments differed in light environment, woody-plant growth and recruitment, and quantity and quality of woody regeneration. Forest tree invasion appeared to be enhanced under *Vochysia,* while shrubs were more abundant under the *Jacaranda* and mixed-species treatments. Woody plant growth, herbaceous cover, and understory light availability were highest under *Jacaranda,* intermediate under mixed species, and lowest under *Vochysia.* Soil-stored seeds seemed an important source for woody plant recruitment in *Jacaranda* and mixed species and of minimal importance under *Vochysia,* probably due to light suppression. It appears that competition from grasses is a major factor influencing early woody invasion in our study area. We found no woody recruitment after one year in the unplanted controls. We suggest that to promote the use of plantations as tools of forest restoration, there is a need to gather basic ecological information on how different tree species may influence patterns of plant understory colonization.

Introduction

Research on tropical forest restoration has focused, to date, on evaluating biological barriers to natural forest regeneration in degraded pastures (Nepstad et al. 1990; Aide and Cavelier 1994) and on investigating the role of tree plantations in expediting plant succession in biologically impoverished lands (Lugo 1992*a*; Parrota 1992). In particular, tree plantations have been recognized for their ability to restore soil fertility and ameliorate microclimatic conditions, and their potential for directly facilitating forest regeneration also appears promising. In one of the few published experiments designed to examine this potential directly, Parrota (1992) found significantly higher seedling densities and species richness under plantations of the exotic legume tree *Albizzia lebbek* than in nonforested controls in lowland Puerto Rico. There are, however, few experimental or observational data on the effect of different planted tree species on plant understory composition in tropical tree plantations.

Establishment of plant colonists under tree plantations depends on the combination of on-site mechanisms (germination from the seed bank, resprouts) and off-site propagule dispersal. The relative contribution of these two processes may influence the quantity and quality of understory regeneration. Therefore, to promote the use of tree plantations as tools of tropical forest restoration, there is a need to obtain basic ecological information on how different tree species may influence the establishment and growth of other plant invaders, as a first step in delineating restoration guidelines in degraded, terrestrial tropical ecosystems.

We document early patterns of woody plant invasion, life-form composition, and dynamics of the herb layer in the understory of native tree plantations – three years of age at the start of this study – in wet Costa Rica. We also document both the possible role of the seed bank and the early effects of thinning on understory plant dynamics. Because research on the silviculture of many native trees for commercial reforestation is currently increasing in Costa Rica (Butterfield & Fisher 1994), the information presented in this study can be useful at both the local and regional levels when there is need to restore plant diversity by using tree plantations as potential successional catalysts.

Study Site and Methods

This study is part of an ongoing project on the use of mixed and pure native tree plantations for timber production and

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il rehabilitation (Montagnini & Sancho 1990; Montag- i 1992). Seedlings of four tree species – *Calophyllum* *asiliense* (Guttiferae), *Jacaranda copaia* (Bignoniaceae), *yphnodendron microstachyum* (Mimosoideae), and *chysia guatemalensis* (Vochysiaceae) – were planted dur- g June 1991 in an abandoned pasture at La Selva Biologi- l Station (10° 26'N, 84° 00'W), operated by the Organi- tion for Tropical Studies (OTS), Heredia Province, Costa ca. Annual rainfall and temperature average 4000 mm d 26°C, respectively (Sanford et al. 1994).

The study site was logged in the early 1950s and subse- ently cleared for rice cultivation for three years. The rice lds were burned lightly and seeded to pasture for beef d dairy cattle with the grasses *Cynodon nlemfuensis*, *Pen- setum maximum*, *P. purpureum*, *Brachiaria* spp., and *elinis minutiflora*. Cattle raising lasted for about 20 years til the property was sold to OTS in 1981 with no further man intervention (Pierce 1992). Ten years before planta- n establishment, secondary vegetation was dominated shrubs and ferns, and tree regeneration was patchy. The rain is flat, and soils are derived from volcanic alluvium; ey are well drained, acidic (pH < 5.0), and infertile (San- o & Mata 1987). Currently, the forested surroundings are minated by secondary vegetation (10–15 meters tall) in rly and mid-successional stage, and by pasture with scat- ed remnant trees.

Prior to tree planting, all existing vegetation was cleared anually, and the debris was left in place; the site was not rned. The plantations were set in randomized blocks, th four replicates and six treatments: four pure-species ots of each species, a mixed-species plot (with the four ecies), and a control plot (natural regrowth). Inter-tree stance was 2 meters by 2 meters to speed up canopy clo- re. Within each block, plot size was 32 meters by 32 meters 56 trees total). In the mixed-species plot, trees of the four ecies were planted, alternating two species per row, and e sequential order of the species was systematically versed every other row.

The pure-species treatments of *Calophyllum* and *Stryph- dendron* were not used in this study. *Calophyllum* trees re planted six months later than the other treatments, t they have grown very slowly: on average, plants had ly grown to 3 meters in average height after two years comparison, *Jacaranda* and *Vochysia* had averaged 12 eters and 10 meters in height, respectively). The pure- ecies treatment of *Stryphnodendron* suffered severe fun- l infection, and most trees had died after two years (the ngal spread occurred at a much lower frequency in the ixed-species treatment). The results presented here will limited to four treatments: two pure-species (*Jacaranda* d *Vochysia*), one mixed-species, and the unplanted control.

Twenty-six months after the plantations were established, hinning operation was performed in the study treatments. each 32-meter-by-32-meter plot across all blocks, every her row of trees was removed in only half of the plot's area. This allowed us to examine the early effects of thinning on canopy structure and understory plant dynamics compared to adjacent, unmanipulated sections.

Understory Light Environment. We predicted that species-specific effects in crown structure of the planted tree species would influence density, establishment, and growth of woody invaders due to differences in the amount of incident light reaching the plantation understory. We characterized light levels 1 meter above ground at eight random points in each treatment replicate (only in the unthinned sections), except in the control (since there was little or no vegetation above 1 meter), by means of black and white (ASA 400) hemispherical photography using a Nikkor 8-mm fish-eye lens. The photographic negatives were analyzed with the CANOPY software (Rich 1990). This program calculates both direct (the proportion of direct light potentially reaching a point relative to the open) and indirect site factors (the proportion of diffuse light potentially reaching a point relative to the open).

In addition, we described the canopy structure – the vertical distribution of foliage – of each plantation treatment. Foliage profiles were created by recording the presence or absence of vegetation layers intercepting a 15-meter-tall telescopic tube at 2-meter height intervals from the ground to the canopy in eight random points that were systematically distributed in thinned (four points) and unthinned (four points) area, 10 months after thinning (data from all treatment replicates were pooled).

Understory Regeneration. In August 1993, prior to thinning, we quantified and marked all woody plants (individual $\geq$ 0.2 m tall) in each treatment replicate in four permanent quadrats (1 m by 2 m; $n = 16$ quadrats total per treatment). Two of these four plots were laid out in rows that would be thinned two months later. We distinguished resprouted stems from "true" recruits by visual inspection of discontinuities of the stem diameter at the root collar and above; we included in our analyses only those individuals that showed no obvious evidence of past damage. Therefore, we reduced the chance of including woody stems that were present before plantation establishment (about 5% of all sampled woody individuals were resprouts). To characterize the herbaceous vegetation, we subsampled each 1-meter-by-2-meter quadrat with a 1-meter-by-1-meter frame subdivided into 25 points and measured height of the vegetation (the distance to the highest leaf intercepting five randomly chosen points) and percentage cover by life form by visual interception of all 25 points. The categories were grass (sedges included), vine, fern, herb, and woody. Woody plant recruitment, growth, and changes in herb cover were assessed one year later.

Preliminary observations in the three plantation treatments suggested that, in contrast to shrubs, seedlings of most canopy tree species had a patchy distribution in the understory, making our initial sampling effort (four 1-meter-by-2-meter permanent plots per treatment replicate) inadequate to fully characterize their abundance and richness. In August 1994, we surveyed all tree seedlings (individuals $\geqslant 0.2$ but $\leqslant 1$ m tall) present in 25% of the total area of each treatment replicate (four 2-meter-by-32-meter plots) only in the thinned sections. We also included shrub species for comparison.

To assess the potential contribution of buried seeds to woody regeneration, we documented species abundance and composition of the germinable seed bank present in the top 10 cm of soil in all four treatments. Four randomly located cores were taken with a soil bulk density sampler in each replicate ($n = 16$ cores total per treatment). Soil cores were thinly spread in plastic trays over a 2-cm-deep layer of heat-sterilized sand, and they were watered daily in order to monitor seedling emergence in a shadehouse at La Selva Biological Station (about 20% of full sunlight). Two control trays with sterilized soil were used to check for airborne seed contamination. Seedling emergence was followed for 12 weeks. Species identification was carried out by seedling reference collections and with the aid of local naturalists. Nomenclature follows that of Wilbur (1994).

Results

Understory Light Environment. Light environments at 1 meter aboveground were very different among the three plantation treatments. Both direct and indirect site factors differed statistically, being highest in *Jacaranda*, intermediate in the mixed-species plantation, and lowest in *Vochysia* (Table 1; Tukey, $p < 0.01$ in all comparisons). In addition, we found a higher spatial heterogeneity of light microhabitats (a larger coefficient of variation) in the mixed-species plantation than in the other two treatments. These findings appear to be related to structure of the tree crown and distribution of the foliage vertical. At our given planting density, the crowns of *Jacaranda* trees are open, and their small leaflets are widely spaced in a horizontal plane. In contrast, the crowns of *Vochysia* trees are deep, with densely-packed simple leaves. In the mixed-species plantation, crown structure (*Vochysia*, deep-crowned; *Jacaranda*, *Stryphnodendron*, open-crowned) appeared responsible for creating intermediate illumination conditions. Ten months after the thinning operation, only the *Vochysia* treatment showed a statistically significant response to changes in the vertical distribution of foliage (Fig. 1; Komolgorov-Smirnov, $p < 0.05$).

Table 1. Understory light environments expressed as mean values ($n = 32$ in each treatment) of indirect site factors (ISF) and direct site factors (DSF). For both variables, all treatments differ statistically at $p < 0.01$ (Tukey's test).

Treatment	*ISF*	*Range*	*CV (%)*	*DSF*	*Range*	*CV (%)*
Jacaranda	0.17	0.12–0.22	16.0	0.15	0.11–0.20	15.5
Mixed	0.09	0.05–0.17	32.9	0.12	0.04–0.27	38.7
Vochysia	0.04	0.03–0.06	18.5	0.05	0.03–0.07	21.3

Understory Regeneration. At the first sampling date (prethinning; August 1993), the density of understory woody seedlings recorded in the permanent quadrats differed among the three plantation treatments (Table 2). No woody seedlings were recorded under *Vochysia*. In contrast, many

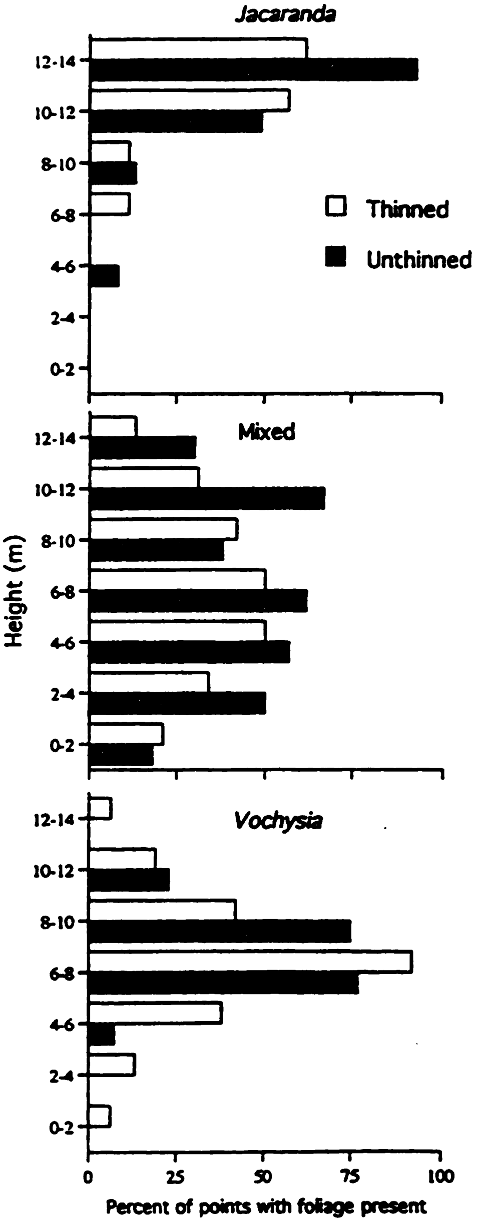


Figure 1. Vertical profiles of foliage in the three plantation treatments taken simultaneously from the unthinned sections (solid bars) and thinned sections (open bars), 10 months after thinning.

Table 2. Changes in woody seedling density (individuals ≥ 0.2 m but ≤ 1 m tall) and absolute height growth of vegetation present in 1993 (first census) in unthinned and thinned sections of the three plantation treatments. Paired comparisons within treatments were performed with a Wilcoxon test (two-sided p values). Values are means and ranges (in parentheses).

	Individuals/m²						*1-Year Height Growth (m)*		
	Unthined Section			*Thinned Section*					
Treatment	*1993*	*1994*	p	*Pre-thinning*	*Post-thinning*	p	*Unthinned*	*Thinned*	p
Jacaranda	2.4 (0.0–6.5)	2.6 (0.0–7.0)	0.34	0.8 (0.0–3.0)	1.5 (0.5–2.5)	0.04	1.2 (0.4–2.2)	1.1 (0.3–1.2)	0.92
Mixed	0.9 (0.0–4.5)	1.4 (0.0–6.5)	0.11	0.6 (0.0–1.5)	2.3 (1.0–6.0)	0.01	0.8 (0.3–1.8)	0.98 (0.5–1.6)	0.09
Vochysia	0.0 (0.0–0.0)	0.1 (0.0–0.5)	0.31	0.0 (0.0–0.0	0.9 (0.0–3.0)	0.05	—	0.5 (0.2–1.8)	—

ly species were present in the understory of the *Jaca-* a and mixed-species treatments. One year later, this rn was still consistent across treatments. Thinning ioted woody plant invasion in all three plantation treat- s (Table 2). No woody seedlings were recorded in the ·ol treatment, which was dominated by dense, grassy ls of *Penisetum* spp. and *Melinis minutiflora*.

:ere were differences in the number of one-year recruits ıg plantation treatments ($\chi^2 = 14.5$, 2 d.f., $p < 0.001$). : recruits were recorded in the mixed-species planta- (39), than in *Jacaranda* (17), and *Vochysia* (15) treat- s. Overall, woody vegetation was taller in *Jacaranda* :y, $p < 0.01$; mean height: 1.1 m; range: 0.4–1.2) than ixed species (mean height: 0.8 m; range: 0.5–1.5) and *ysia* (which did not differ from each other; Tukey, p = mean height: 0.5 m; range: 0.2–1.8). There were no ;tical differences in absolute height growth in thinned ıs unthinned sections of established woody vegetation ıth *Jacaranda* and mixed-species treatments (Table 2). e was no block effect in the height of woody vegeta- for the plantation treatments (ANOVA, $p > 0.2$ in all ;).

both *Jacaranda* and mixed-species treatments, shrubs *:ostegia, Leandra*: Melastomataceae; *Piper*, Piperaceae; *hotria*, Rubiaceae) comprised more than 75% of all s recorded either during the initial vegetation sampling recruits one year later (Fig. 2). Shrub species also domi- l the seed bank (Table 3); for example, seeds of *Conoste- ıbcrustulata* accounted for 40% of all seedlings emerged seed bank samples taken from all four treatments. This b species is abundant in active and abandoned pastures ss the area, and it is likely that a constant propagule t into the soil since pasture creation may have kept soil numbers of this species at high levels. It is interesting ɔte that the grasses that dominate the unplanted con- treatment appear to inhibit buried seed germination use we found comparable densities and species com- tion of the germinable seed bank in the control and the tations (Table 3). Although we did not measure the light oenvironment in the control, low light levels at the soil

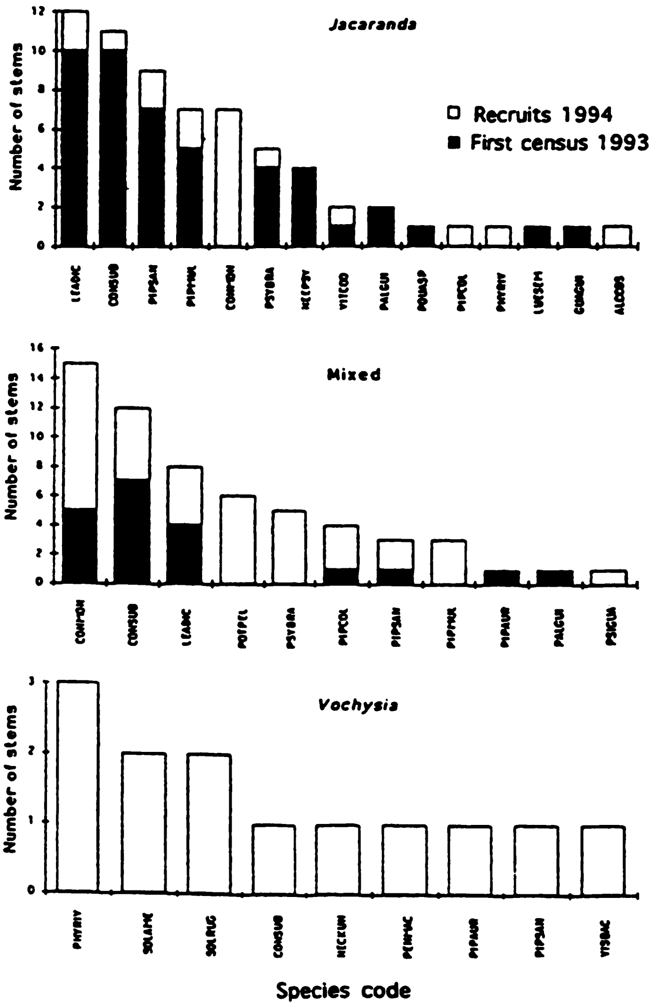


Figure 2. Total number of woody stems (except *Phytolacca rivinoides* and *Potomorphe peltata*, which are giant herbs; ≥ 1 m tall as adults) recorded initially in 1-meter-by-2 meter regeneration plots in 1993 (solid bars). The open bars are the 1994 recruits (individuals ≥ 0.2 m tall) that were distributed within treatments as follows: *Jacaranda*, 60% in thinned sections; mixed species, 79% in thinned sections; *Vochysia*, 93% in thinned sections. Note that the y axis is on different scales. Species codes are given in Appendix 1.

Table 3. The absolute number of seedlings that emerged in sixteen 0.0026-m^2 samples per treatment taken from the upper 10 cm of soil in August 1993.

		Number of Emerged Seedlings			
	Life Form	Jacaranda	Mixed	Vochysia	Control
Clibadium sp (Compsitae)	Shrub	4	3	4	4
Conostegia subcrustulata (Melastomataceae)	Shrub	163	164	165	172
Diodia sp. (Rubiaceae)	Herb	3	6	15	6
Hyptis sp. (Labiatae)	Herb	9	3	2	11
Lindernia sp. (Scrophulariaceae)	Herb	14	7	9	24
Scleria sp. (Cyperaceae)	Grass	53	86	91	72
Leandra dichotoma (Melastomataceae)	Shrub	76	96	65	74
Paspalum sp. (Gramineae)	Grass	5	6	5	3
Phytolacca rivinoides (Phytolaccaceae)	Herb	4	7	6	2
Piper auritum (Piperaceae)	Shrub	7	12	6	6
Palicourea guianensis (Rubiaceae)	Shrub	33	21	28	17
Rubiaceae sp. 1	Shrub	13	16	16	2
Unidentified (nonwoody)		20	22	6	40
Total		404	449	418	443
Mean number/m^2		14,595	16,221	14,668	15,607
Range		7,080–16,470	8,800–19,480	5,340–17,300	5,635–20,830

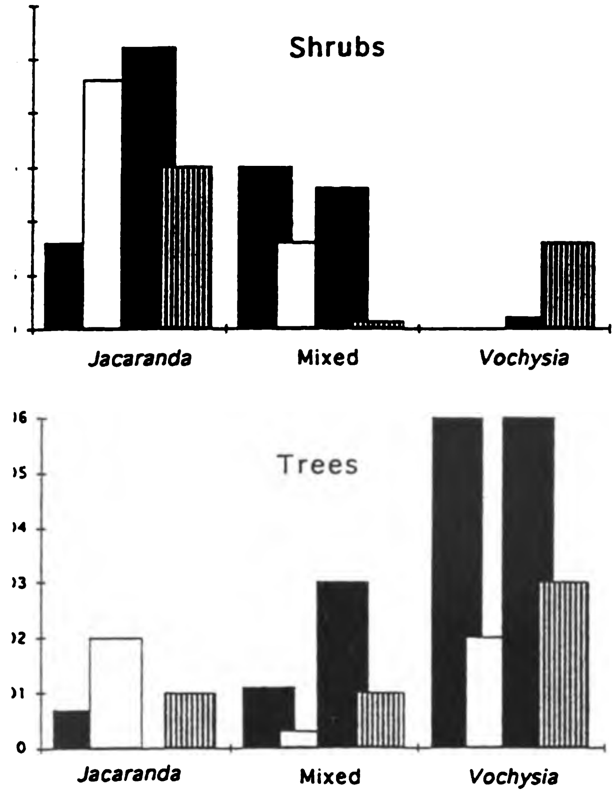
surface due to the dense grass canopy may play a role in inhibiting germination from the seed bank. Similarly, the presence of high soil seed densities in the *Vochysia* treatment, along with the paucity of shrubs in its understory, also suggest that light may be a limiting factor for shrub and herb regeneration from buried seeds.

Results from the more extensive seedling sampling (four 2-meter-by-32-meter plots per treatment replicate) revealed that, although we found differences in the absolute numbers of woody seedlings across all four treatments ($\chi^2 = 58.6$, 3 d.f., $p < 0.001$), the understory of *Vochysia* showed—in contrast to the shrub life form—the highest tree seedling density (Tuley, $p < 0.05$; Fig. 3). This could imply that the quantity and quality of woody regeneration may be influenced by the kind of plantation itself. For example, tree species that are dispersed by bats appear overrepresented under *Vochysia* (Table 4). The presence of clumped seedlings, indicative of bat feeding behavior, was especially noticeable in the large, seeded tree species *Dipteryx panamensis* (Papilionoideae) and *Nectandra kunthiana* (Lauraceae). The preponderance of bat-dispersed species under *Vochysia* suggests that its crown architecture may provide more opportunities for feeding roosts than do the other two plantation treatments.

In short, it appears that shrub species are more likely to recruit from the seed bank, while most tree species are being dispersed, particularly under *Vochysia*. None of the tree seedlings surveyed across all treatments were observed to germinate from the soil samples, suggesting that off-site seed dispersal may account for their presence as understory invaders.

Herbaceous Component. At the start of the study, percentage cover of the herbaceous layer was highest in the control treatment (mean = 93%), intermediate in *Jacaranda* and mixed species (which did not differ from each other; Tukey, $p = 0.6$; mean = 61% and 59%, respectively), and lowest in *Vochysia* (mean = 9%; Tukey, $p < 0.01$). Block effects on percentage herbaceous cover were detected only in the *Jacaranda* treatment (ANOVA, $p = 0.02$) but were not significant in the other treatments (ANOVA, $p > 0.1$ in all cases).

Height of the herbaceous vegetation was highest in the control (mean = 1.20 m), intermediate (but statistically different) in *Jacaranda* and mixed species (mean = 0.53 m and 0.42 m, respectively) and lowest in *Vochysia* (mean = 0.2 m; Tukey, $p < 0.01$ in all cases). There was no block effect in height of herbaceous vegetation in the *Jacaranda*, *Vochysia*, and control treatments (ANOVA, $p > 0.1$ in all



·e 3.. Density of shrub and tree seedlings (individuals ≥ n but ≤ 1 m tall) in the three plantation treatments. .in treatments, different bars represent density estimates ach block. Shrub and tree density was statistically differ- ıcross treatments (ANOVA, $p < 0.03$ in both cases). Note the y axis is on different scales.

;), but it was detected in the mixed-species treatment ƆVA, $p = 0.04$). Finally, Figure 4 shows that thinning ficantly increased herb cover (Wilcoxon, $p < 0.01$ in ses), although *Vochysia* still maintained the lowest herb ꞉ of all treatments.

ussion

ound contrasting patterns in the quantity and quality ırly woody regeneration in the understory of three rent plantation treatments. The understory of *Vochysia* tations had a higher density of tree seedlings than both *·anda* and mixed-species treatments. In contrast, shrub ies were dominant under *Jacaranda* and mixed-species ments. It is interesting to note that seedlings of *Cecro- ›btusifolia*, a small-seeded (< 0.1 g), light-demanding eer tree, appeared more abundant under *Vochysia* than ꞉r *Jacaranda* and mixed species, even though *Vochysia* ved the darkest understory of all plantations. Although annot separate the combined effects of differential seed ›sition of *Cecropia* under *Vochysia* from understory effects (low herb cover may facilitate seedling establishment), our results suggest that small-seeded pioneers like *Cecropia* could encounter more-suitable sites for early establishment under *Vochysia* than in the other two plantation treatments. Once weeds have been suppressed, a careful opening of the canopy in *Vochysia* could release *Cecropia* seedlings that may serve as additional attracting points to vertebrate frugivores later in time. *Cecropia* trees are visited by a wide variety of birds and bats; they grow rapidly in height and reproduce precociously (Estrada et al. 1984; Alvarez-Buylla & Martinez-Ramos 1992).

From our results it appears that competition from herbaceous vegetation is a major factor influencing early woody invasion (either from the seed bank or from seed rain) in abandoned pastures, and that a species' capacity for rapid canopy closure stands out as an important attribute for restoration purposes in our study area. We found no woody recruitment over one year in the nonplanted control treatment, which was dominated by grasses. Our results contrast with those of Aide and Cavelier (1994), who reported that germination and early establishment of woody seedlings were not inhibited but rather facilitated by grasses in highly degraded areas in the Sierra Nevada de Santa Marta, Colombia. Extreme soil impoverishment on that site appears linked to severe loss of the upper soil horizons due to deforestation and repeated fire. There, grasses may act as poor competitors to woody plant invasion and possibly as nurse sites for seedling establishment. In our case, extreme soil degradation did not occur before plantation establishment, which may explain the extensive cover and thickness of the grass canopy.

Other authors have suggested the use of fast-growing, fleshy-fruited trees as habitat-forming islands where tree seed deposition by visiting frugivores could accelerate successional processes in abandoned pastures (Nepstad et al. 1991). Although *Vochysia guatemalensis* trees may not fruit early, this species looks promising as an effective forest restoration tool in the study area because it appears to provide perching and roosting sites for frugivore birds and bats while rapidly suppressing grass cover. Furthermore, thinning modifies *Vochysia* crown structure but does not seem to stimulate immediate lateral crown expansion, therefore maintaining adequate understory light levels for plant growth. Our observations in other *Vochysia* plantations at La Selva (seven years old at the time of the study) suggest that inter-crown spacing after thinning is kept for a few years.

Compared to *Vochysia*, we found much higher herbaceous cover under the *Jacaranda* and mixed-species plantations, and a higher density of shrub species. Shrub dominance in these two treatments is probably due to their high light-regeneration requirements and presence in the seed bank. At La Selva, shrubs in secondary-growth areas provide an adequate food supply to frugivore birds when food becomes scarce in mature forest (Levey 1988). Although this

Table 4. Total number of tree seedlings (individuals ≥ 0.2 m but ≤ 1 m tall) sampled in four 2-meter-by-32-meter plots in each treatment replicate (32 m × 32 m total area per replicate) in the thinned sections of the three plantation treatments in 1994.

Species	*Dispersal Mode**	Treatment: Vochysia	*Treatment*: Jacaranda	*Treatment*: *Mixed*	*Treatment*: *Control*
Alchornea costaricensis (Euphorbiaceae)	F	6	6	2	0
Casearia arborea (Flacourtiaceae)	F	3	1	0	0
Cecropia obtusifolia (Moraceae)	B, F	12	2	6	1
Cordia bicolor (Boraginaceae)	F	0	1	0	0
Dipteryx panamensis (Papilionoideae)	B, R	5	0	0	0
Luehea seemannii (Tiliaceae)	W	3	1	1	0
Nectandra kunthiana (Lauraceae)	F, B	8	1	2	0
Ochroma pyramidale (Bombacaceae)	W	0	0	1	0
Pentaclethra macroloba (Mimosoideae)	G	1	4	0	0
Pourouma aspera (Moraceae)	F	1	0	0	0
Psidium guajava (Myrtaceae)	F	1	0	0	0
Soroceae pubivena (Moraceae)	F	0	1	0	0
Vismia panamensis (Guttiferae)	B,F	10	3	2	0
Unknown		0	0	1	0
Total		50	21	15	1

*B = bats; F = frugivore birds; R = rodents; W = wind; G = gravity.
Sources: Croat 1978; Janzen 1983; Snow 1981; O. Vargas, personal communication.

suggests that these two plantation treatments can be important in terms of diversifying the shrub layer and as a frugivore food source, they do not seem to enhance the tree component as much as under *Vochysia*. In fact, shrubs may strongly compete with trees for belowground resources (Putz & Canham, 1992), potentially inhibiting tree invasion in the long term. Canopy opening in *Vochysia* stands could subsequently trigger the germination of dormant shrub seeds, and we expect shrub recruitment to increase in our *Vochysia* plantations over time. Therefore, we speculate that, with respect to life-form diversity, a more structurally complex plant community is likely to develop under *Vochysia* than under the other two plantation treatments at our study site.

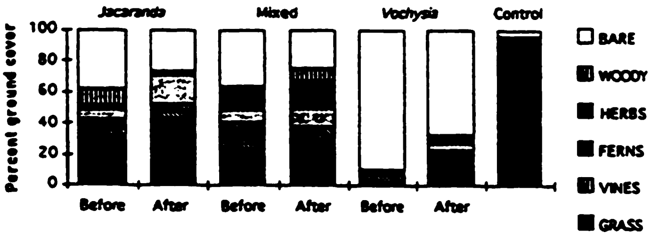


Figure 4. Changes in percentage ground cover by life form before and 10 months after thinning in the plantation treatments. The control treatment is included as a comparison.

The mixed-species treatment showed the highest spatial variation in the amount of incident light in the understory, and a more vertically complex foliage stratification. Even though spatial heterogeneity in the light resource is thought to promote plant species diversity in tropical wet forests (Denslow 1987), and structural complexity of the vegetation could be associated with high rates of seed deposition by vertebrate frugivores (McDonnell & Stiles 1983), we found no evidence of increased plant diversity in terms of species or life forms in the mixed-species treatment. Again, it appears that herbaceous cover—which was about three times higher in the mixed-species than in the *Vochysia* treatment—is playing a more important role than structural or light heterogeneity in controlling early woody invasion in our study location.

The use of tree plantations in ecosystem restoration is receiving increased attention as a biological tool in tropical degraded areas because they may accelerate natural plant succession (Lugo 1992*b*). But there is little ecological information about different plantation scenarios under which the re-creation of diverse forest ecosystems may occur. Although we have shown some evidence of species-specific effects of tree plantations on plant understory invasion in this study, it should be noted that these patterns may vary—for example, with degree of isolation from forested areas, species richness and abundance of soil-stored seeds, and land-use history. Our study site is not likely to be limited by off-site plant propagules due to its proximity to protected secondary and mature forest (at La Selva Biological Station), and there is additional regeneration potential from the seed bank. We hope, however, that our preliminary results stimulate further research about how to couple tree species attributes, and silvicultural practices to the recovery of biological integrity on degraded sites in the wet tropics.

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LITERATURE CITED

Aide, T. M., and J. Cavelier. 1994. Barriers to lowland tropical forest restoration in the Sierra Nevada de Santa Marta, Colombia. Restoration Ecology 2:219-229.

Alvarez-Buylla, E. R., and M. Martínez-Ramos. 1992. Demography and allometry of *Cecropia obtusifolia*, a neotropical pioneer tree: an evaluation of the climax-pioneer paradigm for tropical rain forests. Journal of Ecology 80:275-290.

Butterfield, R. P., and R. F. Fisher. 1994. Untapped potential: native species for reforestation. Journal of Forestry 92:37-40.

Croat, T. B. 1978. Flora of Barro Colorado Island. Stanford University Press, Stanford, California.

Denslow, J. S. 1987. Tropical rainforest gaps and tree species diversity. Annual Review of Ecology and Systematics 18:421-451.

Estrada, A., R. Coates-Estrada, and C. Vazquez-Yanes. 1984. Observations on fruiting and dispersers of *Cecropia obstusifolia* at Los Tuxtlas, Mexico. Biotropica 16:315-318.

Janzen, D. H., editor. 1983. Costa Rican natural history. University of Chicago Press, Chicago, Illinois.

Levey, D. J. 1988. Spatial and temporal variation in Costa Rican fruit and fruit-eating bird abundance. Ecological Monographs 58: 251-269.

Lugo, A. E. 1992*a*. Comparison of tropical tree plantations with secondary forests of similar age. Ecological Monographs 62:1-41.

Lugo, A. E. 1992*b*. Tree plantations for rehabilitating damaged forest lands in the tropics. Pages 247-255 in M. K. Wali, editor. Ecosystem rehabilitation, vol. 2: Ecosystem analysis and synthesis. SPB Academic Publishing, The Hague, The Netherlands.

McDonnell, M. J., and E. W. Stiles. 1983. The structural complexity of old-field vegetation and the recruitment of bird-dispersed plant species. Oecologia 56:109-116.

Montagnini, F. 1992. Mixed-tree plantations: experiments with native trees in Costa Rica and Argentina. Agroforestry Today 4(3):4-6.

Montagnini, F., and F. Sancho. 1990. Impacts of native trees on tropical soils: a study in the Atlantic lowlands of Costa Rica. Ambio 19:386-390.

Nepstad, D., C. Uhl, and E. A. Serrao. 1990. Surmounting barriers to forest regeneration in abandoned, highly degraded pastures: a case study from Paragominas, Pará, Brazil. Pages 215-229 in A. B. Anderson, editor. Alternatives to deforestation: steps toward sustainable use of the Amazon rain forest. Columbia University Press, New York.

Nepstad, D. C., C. Uhl, and E. A. S. Serrao. 1991. Recuperation of a degraded Amazonian landscape: forest recovery and agricultural restoration. Ambio 20:248-255.

Parrota, J. A. 1992. The role of plantation forests in rehabilitating degraded tropical ecosystems. Agriculture, Ecosystems and Environment 41:115-133.

Pierce, S. M. 1992. La Selva Biological Station history: colonization/land use/deforestation of Sarapiquí, Costa Rica. Thesis, Colorado State University, Fort Collins, Colorado.

Putz, F. E., and C. D. Canham. 1992. Mechanisms of arrested succession in shrublands: root and shoot competition between shrubs and tree seedlings. Forest Ecology and Management 49:267-275.

Rich, P. M. 1990. Characterizing plant canopies with hemispherical photographs. Remote Sensing Reviews 5:13-29.

Sancho, F., and R. Mata. 1987. Estudio detallado de suelos. Estación Biológical La Selva. Organización de Estudios Tropicales, San José, Costa Rica.

Sanford, R. L., Jr., P. Paaby, J. C. Luvall, and E. Phillips. 1994. Climate, geomorphology, and aquatic systems. Pages 19-33 in L. A. McDade, K. S. Bawa, H. A. Hespenheide, and G. S. Hartshorn, editors. La Selva: ecology and natural history of a neotropical rainforest. University of Chicago Press, Chicago, Illinois.

Snow, D. W. 1981. Tropical frugivorous birds and their food plants: a world survey. Biotropica 13:1-14.

Wilbur, R. L. 1994. Plants: an interim checklist. Pages 350-378 in L. A. McDade, K. S. Bawa, H. A. Hespenheide, and G. S. Hartshorn, editors. La Selva: ecology and natural history of a neotropical rainforest. University of Chicago Press, Chicago, Illinois.

Appendix. Plant species codes.

Life Form	*Code*	*Species Name*	*Family*
Giant Herbs	POTPEL	*Potomorphe peltata*	Poperaceae
	PHYRIV	*Phytolacca rivinoides*	Phytolaccaceae
Shrubs	CONMON	*Conostegia montana*	Melastomataceae
	CONSUB	*Conostegia subcrustulata*	Melastomataceae
	LEADIC	*Leandra dichotoma*	Melastomataceae
	NEEPSY	*Neea psychotrioides*	Nyctaginaceae
	PALGUI	*Palicourea guianensis*	Rubiaceae
	PIPAUR	*Piper auritum*	Piperaceae
	PIPCOL	*Piper colonense*	Piperaceae
	PIPMUL	*Piper multiplinervium*	Piperaceae
	PIPSAN	*Piper sancti-felicis*	Piperaceae
	PSYBRA	*Psychotria brachiata*	Rubiaceae
	SOLAME	*Solanum americanum*	Solanaceae
	SOLRUG	*Solanum rugosum*	Solanaceae
Trees	ALCCOS	*Alchornea costaricensis*	Euphorbiaceae
	GUAGUI	*Guarea guidonia*	Meliaceae
	LUESEM	*Luehea seemannii*	Tiliaceae
	NECKUN	*Nectandra kunthiana*	Lauraceae
	PENMAC	*Pentaclethra macroloba*	Mimosoideae
	PSIGUA	*Psidium guajava*	Myrtaceae
	POUASP	*Pourouma aspera*	Cecropiaceae
	VISBAC	*Vismia panamensis*	Guttiferae
	VITCOO	*Vitex cooperi*	Verbenaceae

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Leaf litter decomposition and mulch performance from mixed and monospecific plantations of native tree species in Costa Rica

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Abstract

An experiment with native trees was established in 1991 on degraded pasture in the Atlantic lowlands of Costa Rica to examine the influence of mixed and monospecific plantation designs on tree growth and nutrient cycling. As part of this study, leaf litter decomposition rates and mulch performance were compared among four native tree species, *Callophylum brasiliense* Cambess, *Jacaranda copaia* (Aubl.) D. Don, *Vochysia guatemalensis* J.D. Smith, and *Strypnodendron microstachyum* Poepp. et Endl. Leaf litter of *V. guatemalensis*, *J. copaia* and the mixed plantation decomposed the fastest, with less than 16% of the initial weight remaining at 12 months. *C. brasiliense* had the slowest decomposition rate with 23% of the leaf litter remaining at 12 months. *V. guatemalensis* had the greatest amount of annual leaf litter fall and accumulation. *J. copaia* showed high levels of annual litter fall but fluctuating forest-floor litter accumulation, and the mixture showed intermediate patterns of annual leaf litter fall and accumulation. All mulch treatments improved maize seedling performance in comparison with unmulched controls. *S. microstachyum* mulch was found to have the most beneficial effect on initial maize seedling height growth and N uptake. Recommendations are drawn from the results to suggest potential uses of these species in forestry and agroforestry systems.

Keywords: Litter decomposition; Mulch; Mixed plantation; Native trees; Costa Rica

1. Introduction

The main source of nutrient transfer from trees to soils is through the decomposition of leaf litter and roots (Ewel, 1976; Montagnini, 1990). The performance and potential role of individual tree species on nutrient cycling affects the suitability of each species for soil rehabilitation and for its combination with agricultural crops. Knowledge of each species potential, then, is important in influencing tree species choice. Experiments with alley cropping systems have shown positive effects on crop yield when leguminous tree leaves were used as 'green manure' or mulch. Mulches can protect soils against erosion, decrease weed growth, release nutrients to the soil via decomposition, and moderate soil moisture loss and temperature fluctuations (Budelman, 1988; Budelman, 1989; Montagnini et al., 1993). Farmers frequently use leaf litter as mulch when inorganic fertilizers are too expensive and livestock manure is not available.

Mulch and leaf litter decomposition studies have not traditionally compared mixtures with monospecific systems. Montagnini et al. (1993) found a trend

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that a mixture of two species decomposed faster than either species alone. In addition, mulches of a mixture of species can provide more diverse benefits to crop growth and soil protection than mulches of a single species. For example, the mulch of a rapidly decomposing N-fixing species may provide higher N availability, and the mulches of other species may release other nutrients important to plant nutrition such as P or K, or may decompose more slowly and contribute better protection against soil erosion.

In the present article, decomposition rates and mulch experiments focused on four native tree species growing in an experimental plantation on abandoned pasture soils: Cedro Maria (*Callophylum brasiliense* Cambess.), Mayo or Chancho (*Vochysia guatemalensis* J. D. Smith), Vainillo (*Strypnodendron microstachyum* Poepp. et Endl), and Jacaranda (*Jacaranda copaia* (Aubl.)D.Don). The plantation was part of a larger project to compare growth, nutrient cycling, effects on soil chemical and physical properties, pest damage, and economics in pure and mixed stands, with the objective of developing suitable plantation models for small farms (Montagnini et al., 1994; Montagnini et al., 1995). In the region of study, farmers grow trees in a portion of their land for tree products and also as an investment (Rheingans, 1996). Farmers generally grow crops between the lines of trees if tree spacing and canopy and nutrient cycling characteristics favor intercropping, or they plant crops in the area previously covered by trees in a rotational scheme (Montagnini and Mendelsohn, 1996). In the present research, decomposition rates were compared among species in pure plots and in mixture (a combination of all four species). Additionally, a mulch experiment was used as a bioassay to measure the effects of nutrient release from decomposing leaf litter on initial growth of maize seedlings. The results are discussed in context with growth rates of the tree species, and suggestions are offered on land use options including these species.

2. Study site

The plantation used in this study was established in June 1991 on a cattle pasture which had been abandoned in 1981. The site is located at La Selva Biological Station in the Atlantic Lowlands of Costa Rica (10°26′N, 86°59′W; 50 m altitude, 24°C mean annual temperature, 4000 mm mean annual rainfall). Soils are Fluventic Dystropepts derived from volcanic alluvium. They are deep, well-drained, stone-free, with low or medium soil organic matter, moderately heavy texture, and are generally acidic and infertile (Sancho and Mata, 1987). The plantation plots were set in randomized blocks, with four replicates and six treatments: four pure plantation plots of each species, a mixed-species plot (with the four species), and a fallow (natural forest regeneration) plot which was used as a control treatment. Each plot was 32 m × 32 m. Initial planting distance was 2 m × 2 m to speed canopy closure and obtain early impacts on soils, with 50% thinning planned after canopy closure.

3. Tree species

The criteria for species selection were growth rate, economic value and preference by farmers;

Table 1
Characteristics of tree species grown in mixed and pure plantation at La Selva Biological Station

Scientific name	Common name	Family	Uses/economic value	Growth, habitat
Stryphnodendron microstachyum Poepp. et Endl.	Vainillo	Leguminosae (Mimosoid)	General construction, medium value	Upper canopy of mature forest. Abundant modulation, N-fixer. Also in secondary forest. Fast growth
Vochysia guatemalensis Donn.Sm.	Mayo, chancho	Vochysiaceae	Plywood, high value	Upper canopy, early–mid successional. Fast growth
Jacaranda copaia (Aubl.)D.Don.	Jacaranda	Bignoniaceae	Boxes, fuelwood, low value	Pioneer, early successional. Secondary forest. Very fast growth
Callophylum brasiliense Cambess.	Cedro Maria	Guttiferae	Furniture, very high value	Mature forest. Slower growth

presence of root nodules in the leguminous species; potential impacts on soils and nutrient cycling; and seedling availability (Montagnini et al., 1995). The four native species (*C. brasiliense*, *V. guatemalensis*, *S. microstachyum*, and *J. copaia*) fulfill different ecological and economic criteria (Table 1). In plots of *V. guatemalensis*, canopy closure occurs quickly because of its deeply crowned canopy architecture and its large, densely packed leaves. In the monospecific treatment, this closed canopy allows limited light penetration so that little is able to grow on the thick litter layer beneath it. In contrast, *J. copaia* has a tall, relatively open canopy from its smaller, widely spaced compound leaves and lack of branching, allowing thick herbaceous growth in the ground storey. Similar observations in this plantation were described and quantified by Guariguata et al. (1995), who found the highest values for understorey light environment under *J. copaia*, an intermediate light environment in the mixtures, and the lowest light levels under *V. guatemalensis*. *C. brasiliense*, a slower growing tree with medium-sized leaves, had not yet achieved canopy closure by the time of this experiment, allowing for a grassy ground storey. Almost all *S. microstachyum* trees planted in monospecific plots died in early 1994 from anthracnosis (a fungal disease) but many individuals survived in the mixed plots. Therefore decomposition of *S. microstachyum* leaves was only studied in the mixed plots, and decomposition data from an earlier study was used for comparison (Montagnini et al., 1993).

4. Methods and materials

4.1. Litter decomposition: litter bag experiment

Litter bags measuring 20 cm × 20 cm were made from 1 mm fiberglass mesh (window screen) and sewn with nylon thread. Fresh leaves were collected from several perimeter trees of each species in each of the four replicate blocks. Before placement in bags, litter was oven-dried to constant weight at 70°C. In previous research, leaves were air-dried and air/oven-dried weight ratios were used to correct the leaf weights, but this procedure introduced high variability among leaf samples (Ruvinsky, 1995); therefore oven-drying was preferred in the present study. Eight grams of dry litter of each species (except *S. microstachyum*) were placed in litter bags. For the mixed litter treatments, 2 g of each species (including *S. microstachyum*) were mixed and placed in litter bags. In each monospecific plot of *V. guatemalensis*, *C. brasiliense*, and *J. copaia*, 15 bags of that species' litter were placed in two randomly selected subplots; the four plots of dead *S. microstachyum* were not used. The top litter layer was moved aside before laying the bags down and the removed litter was then set on top of the litter bags. Three subplots were used in each of the four replicate mixed plots. These sites were chosen randomly from the inner portion of each replicate plot, leaving at least three rows of trees on each side as buffer rows. A total of 540 bags were used (15 bags × 2 subplots × 3 pure species × 4 replicate blocks + 15 bags × 3 subplots × 4 replicates of the mixtures). One bag was collected from each site every 2 weeks for the first 2 months, and once a month for a further 11 months.

After each collection, litter bags were taken to the laboratory, dried to constant weight at 70°C, and weighed. The percentage of the original weight remaining at each collection time was then calculated. Values for each subplot were averaged to give one value per plot for each monospecific and mixed plot. To compare weight loss of the mixed and monospecific treatments *t*-tests and ANOVAs were used ($n = 4$, $P < 0.05$) for each collection date.

4.2. Soil and air temperature

Between 11:00 and 13:00 h (the time of maximum temperatures) during July and August 1994, air temperature at ground level was measured with ambient thermometers, and soil temperature was measured with Wexler™ soil thermometers at 5 cm depth, for a total of 20 soil and 20 air temperature measurements for each plot. In addition, soil moisture was measured gravimetrically by taking samples at 0–5 cm depth with a 2.5-cm-diameter soil corer at each site; soil samples were then oven-dried at 105°C in the laboratory. ANOVAs and *t*-tests were used to examine differences in soil and air temperature among treatments.

4.3. Mulch experiment

To prepare for maize planting, about 300 g of soil were placed in each of 60 pots (11.5 cm top diameter, 6 cm bottom diameter, 12.5 cm high). For the experiment, soil was taken from the border of the plantations at depths between 10 and 30 cm because it was expected that a more distinct response to the addition of mulch would be detected with soil from this depth than if the more nutrient-rich topsoil was used. Soils were homogenized with a trowel and a sifter. Ten replicates were used for each mulch treatment. The treatments were: mulch from each of the four species, a mixture of the four species, and a control without mulch. Leaves were collected from at least four different trees from each plot in the plantation. Leaves were oven-dried at 70°C and ground in a mill with a 1 mm sieve. Two grams of mulch were added 1 week before planting maize and mixed into the top half of the soil in the pots. This addition corresponds to 8000 kg ha^{-1}, an amount similar to the quantity of litter fall which might be collected under tree plots of similar age and spacing (Montagnini et al., 1993). For mixed species mulches, half a gram of mulch from each species was mixed together and then mixed into the soil. The control soil was stirred in the same way without adding mulch. The soil was watered daily, and at the end of the week another 2 g of mulch per pot were added to the top of the soil without mixing it. This second application was expected to prolong the effects of mulching and obtain a longer term nutrient release.

A local cultivar of maize was used, for which the germination rate was approximately 95%. The day before the second mulch treatment, maize kernels were left to soak in water overnight. Immediately

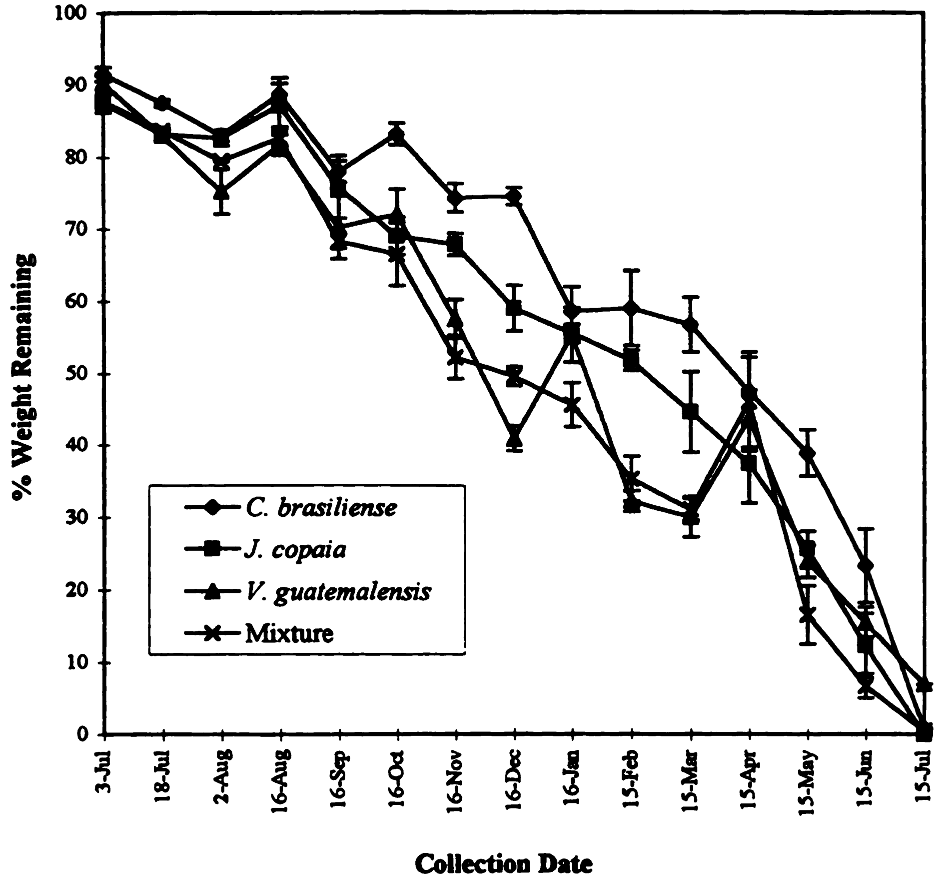

Fig. 1. Leaf litter decomposition from July 1993 to July 1994: percent weight remaining at each collection (means and standard error bars).

after the second mulch treatment, two seeds per pot were planted at 1–2 cm depth. Seedling height was measured from the base of each plant to the tip of the longest leaf when fully extended. In the first week following seed planting, seedling height was measured daily, and heights were measured every 3 days for 2 more weeks because initial differences in responses of maize seedlings to mulch application were expected to be evident early in the experiment (Montagnini et al., 1993). Thereafter, seedlings were measured every week. The height of the two seedlings in each pot was averaged for every date and the data were analyzed using a one-way ANOVA. At the end of the experiment, each plant was harvested and rinsed, oven dried at 100°C, and weighed. The N and P content of the maize shoots were analyzed using Kjeldahl digestion and an autoanalyzer, and the data were compared using one-way ANOVA.

5. Results

5.1. Litter decomposition

C. brasiliense showed slower initial weight loss than the other species and the mixture for the first 6 months of the experiment. This difference became significant in the fourth month (October) of collection (Fig. 1). Statistically significant differences in weight loss between *J. copaia* and *V. guatemalensis* were found after 5 months. At the seventh month all single species showed similar percentages of weight loss with 55–58% of the initial weight remaining. Thereafter, weight loss among species again diverged. *C. brasiliense* continued to show the slowest weight loss; *J. copaia* showed intermediate weight loss; and *V.guatemalensis* and the mixture had the most rapid weight loss. From month 10 to 13, leaf litter of *V. guatemalensis* and *J. copaia* had similar rates of weight loss, with less than 16% of the initial weight remaining at 12 months. *C. brasiliense* had the slowest decomposition rate with 23% of the leaf litter remaining at 12 months.

The weight loss of the mixture was similar to that of the other species in the first 2 months. Thereafter, the mixture began to show the greatest weight loss in comparison with the single species. By month 5, the mixture had significantly greater weight loss than *J. copaia*, and in month 7 the mixture was significantly less than all the others: 45.5% of its initial weight remained (Fig. 1). From month 11 to 13, the mixture decomposed the fastest with only 6.7% of its weight remaining at 12 months.

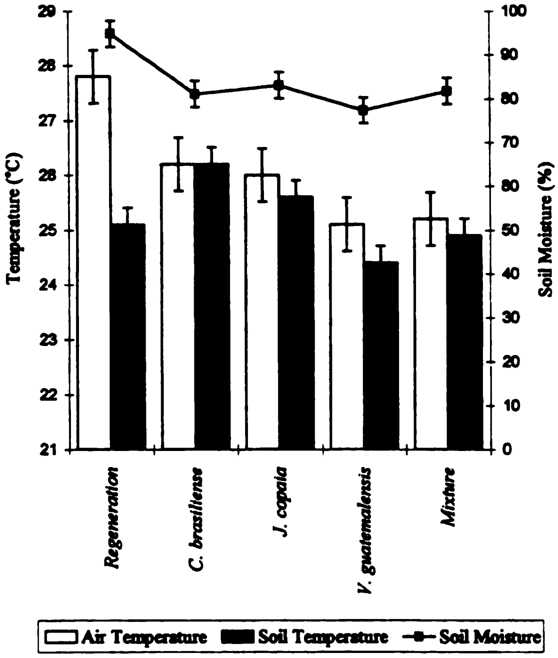

Fig. 2. Air temperature, soil temperature, and soil moisture in pure and mixed tree stands, and regeneration control (means and standard error bars).

Increases in weight loss followed by a decrease in the next collection were found throughout the experiment (Fig. 1). These most likely reflect inaccuracies in recording the remaining leaf weights at times of the year when small particles of mud would adhere to the bags because of high rainfall. A higher number of replicates could serve to decrease the influence of such weighing errors.

Air temperature and soil moisture did not vary significantly among species or the mixture (Fig. 2), but the regeneration (control) plots had significantly higher air temperatures (27.8°C) and soil moisture (94.8%) than the tree plots. The highest average soil temperature (26.2°C) was found in *C. brasiliense*, and the lowest in *V. guatemalensis* (24.4°C) (Fig. 2).

5.2. Maize seedling growth under mulch treatments

Seedlings grown in the *S. microstachyum* mulch treatment grew fastest initially, as shown by the

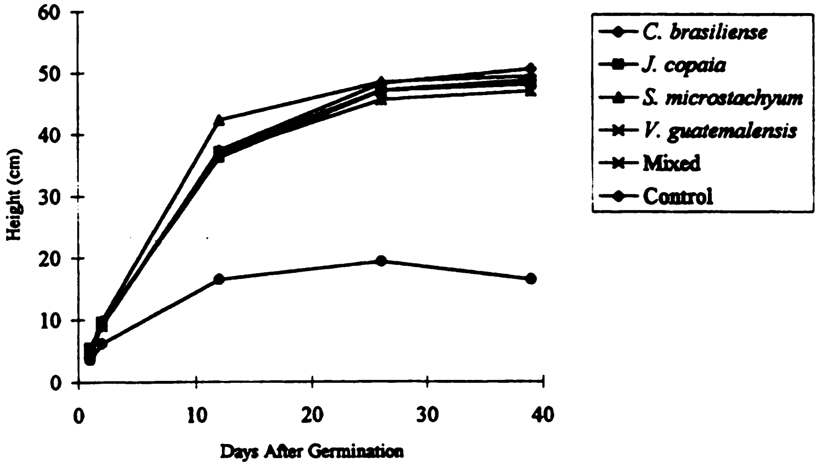

Fig. 3. Height of maize seedlings in soils mulched with leaves from a single tree species, a mixture and an untreated (no mulch) control.

steeper slope of their growth curve (Fig. 3). These seedlings were the tallest from days 2–16. After this point, all the treated seedlings except the mixture attained similar heights. Throughout the experiment, the control seedlings were significantly shorter than the treated seedlings. The greatest difference among treatments was found 12 days after germination when *S. microstachyum*-treated seedlings were significantly taller than all other treatments. *J. copaia*-and *V. guatemalensis*-treated seedlings showed intermediate growth and were not statistically different from each other at any point during the experiment. At the last measurement (day 39), seedlings treated with *C. brasiliense* mulch were the tallest and significantly surpassed seedlings treated with the mixture. By this time there was a large gap in height between the control and the treated seedlings. The control seedlings incurred a much higher mortality rate (46.7%) compared with *J. copaia* and *S. microstachyum* (a maximum of 3.3% mortality).

Mulch treated seedlings had higher above-ground seedling biomass (g per seedling) than unmulched seedlings, with the highest values in *C. brasiliense*, followed by *V. guatemalensis*, the mixture, *S. microstachyum* and *J. copaia*, in that order (Table 2). Control seedlings had approximately 1.5% higher N concentrations than any of the mulch-treated seedlings (Table 2). The next highest N concentration was found in *S. microstachyum*-treated seedlings, followed by the *J. copaia*-treated seedlings. When total N uptake per seedling was calculated by multiplying percent N by dry seedling

Table 2
Above ground biomass, nitrogen concentration, total N uptake, phosphorus concentration and total P uptake of maize seedlings in different mulch treatments

Treatment	Aboveground biomass (g per seedling)	N (%)	Total N uptake (mg)	P (%)	Total P uptake (mg)
C. brasiliense	0.25a	1.05d	2.66b	0.076bc	0.19a
J. copaia	0.21c	1.16c	2.40b	0.092b	0.19a
S. microstachyum	0.22bc	1.53b	3.41a	0.086bc	0.19a
V guatemalensis	0.24ab	1.02d	2.50b	0.072c	0.17a
Mixture	0.24ab	1.06d	2.55b	0.058d	0.14b
Control	0.05d	3.04a	1.62c	0.26a	0.14b

For each variable, means are significantly different between treatments when followed by different letters ($P < 0.05$).

Table 3
Mass fraction (%) of nutrients in leaves of the four species studied

Species	N	P	Ca	Mg	K
S. microstachyum	1.94(0.07)a	0.21(0.01)a	0.44(0.05)bc	0.21(0.01)c	0.90(0.08)a
C. brasiliense	1.09(0.03)d	0.09(0.01)c	0.63(0.09)b	0.15(0.01)d	0.74(0.06)a
J copaia	1.70(0.20)b	0.18(0.02)ab	0.35(0.03)c	0.32(0.02)b	0.72(0.08)a
V. guatemalensis	1.43(0.09)c	0.14(0.01)bc	1.39(0.14)a	0.47(0.05)a	0.43(0.11)b

For each variable, means are significantly different between treatments when followed by different letters ($P < 0.05$).

weight, *S. microstachyum*-treated seedlings had the highest total N uptake, and the control had the lowest value (less than 50% of the total N uptake by *S. microstachyum*- treated seedlings) (Table 2). This difference was statistically significant. Therefore, although N concentration was high in the control seedlings, they did not grow as much and the total N taken up by each plant was lower than any of the other treated seedlings. The other mulch treatments showed an intermediate performance in N uptake, with no statistically significant differences among them.

The control seedlings had the highest P concentration by weight, followed by *J. copaia* treatments, and *S. microstachyum* (Table 2). When total P uptake was calculated, the control and the seedlings treated with mixed mulch had the lowest P uptake (Table 2). There were no statistically significant differences in P uptake among the four single species mulch treatments ($P < 0.05$).

6. Discussion

6.1. Leaf litter decomposition

In the present study, the mixture and *V. guatemalensis* had the fastest rates of decomposition, a finding consistent with results from an earlier study including these species (Ruvinsky, 1995). *J. copaia* ranked third over the first 9 months, but thereafter its decomposition rate was similar to that of *V. guatemalensis*. *J. copaia* was expected to decompose relatively quickly because of its pioneer status, its high leaf N and P concentrations (Table 3) and its small, tender leaflets. In a separate study, the leaf rachis of *J. copaia* decomposed slower than the leaflets, but when averaged over a 4 month period their rates of weight loss were similar (Ruvinsky, 1995).

The slowest decomposition rates, found in *C. brasiliense*, could be the result of an unfavorable microclimate resulting from the lack of canopy closure (Ewel, 1976; Anderson et al., 1983). However, air temperatures in the *C. brasiliense* plots were similar to those in the *J. copaia* plots. Although soil temperature in the *C. brasiliense* plots was significantly higher than in the other treatments, soil temperature differences were slight (1°C); therefore this factor was not likely to affect litter decomposition. Alternatively, *C. brasiliense* leaf characteristics may retard decomposition. The leaves of this species are waxy and thick, and contained the lowest levels of N, P and Mg of the species of the present study (Table 3).

It was expected that decomposition rates would be faster in the mixture than in any single species because a mixture would have a better chance of satisfying the demands of decomposing organisms with its more diverse chemical and nutrient make-up. Decomposition of the mixture was intermediate throughout the collection period, and it decomposed faster than any of the single species tested between the third and fifth months, and again during the last three collection months (Fig. 1). The high N concentrations in *S. microstachyum* leaves in the mixed plots may have provided a nitrogen source favoring decomposition. However, some authors (Ewel, 1976; La Caro and Rudd, 1985) have found that species with high leaf N content do not always decompose faster than those with lower N concentration; lignin and polyphenol concentrations may be more important factors for determining decomposition rates (Singh, 1969; Palm and Sanchez, 1990; Palm and Sanchez, 1991; Constantinides and Fownes, 1994). Of the species studied, *S. microstachyum* also had

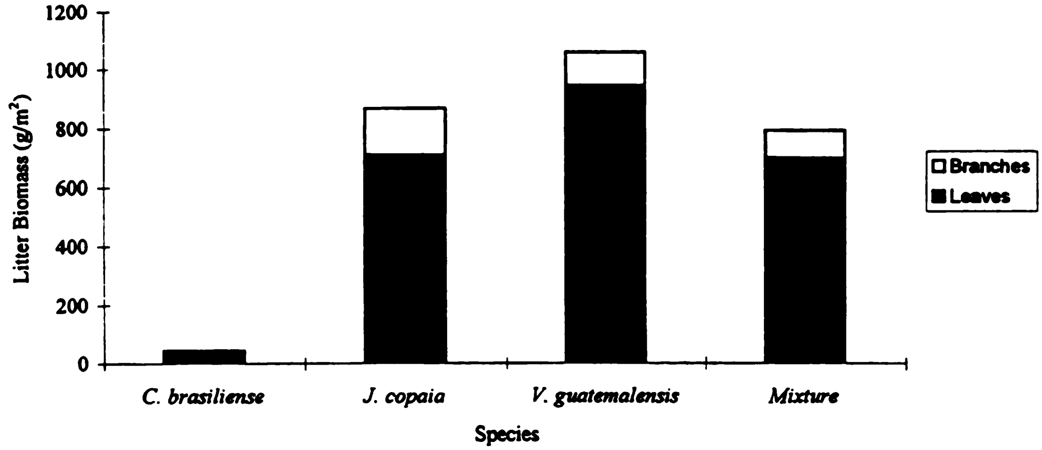

Fig. 4. Total annual litter fall from August 1993 to July 1994 (means and standard error bars). Source: Montagnini et al. (1994).

the highest levels of leaf K and P, which probably favored decomposition rates. It also has soft, small leaves. The presence of this species could have compensated for the slower decomposing *C. brasiliense* present in the mixture. In the present research, the mix could not be compared to the *S.*

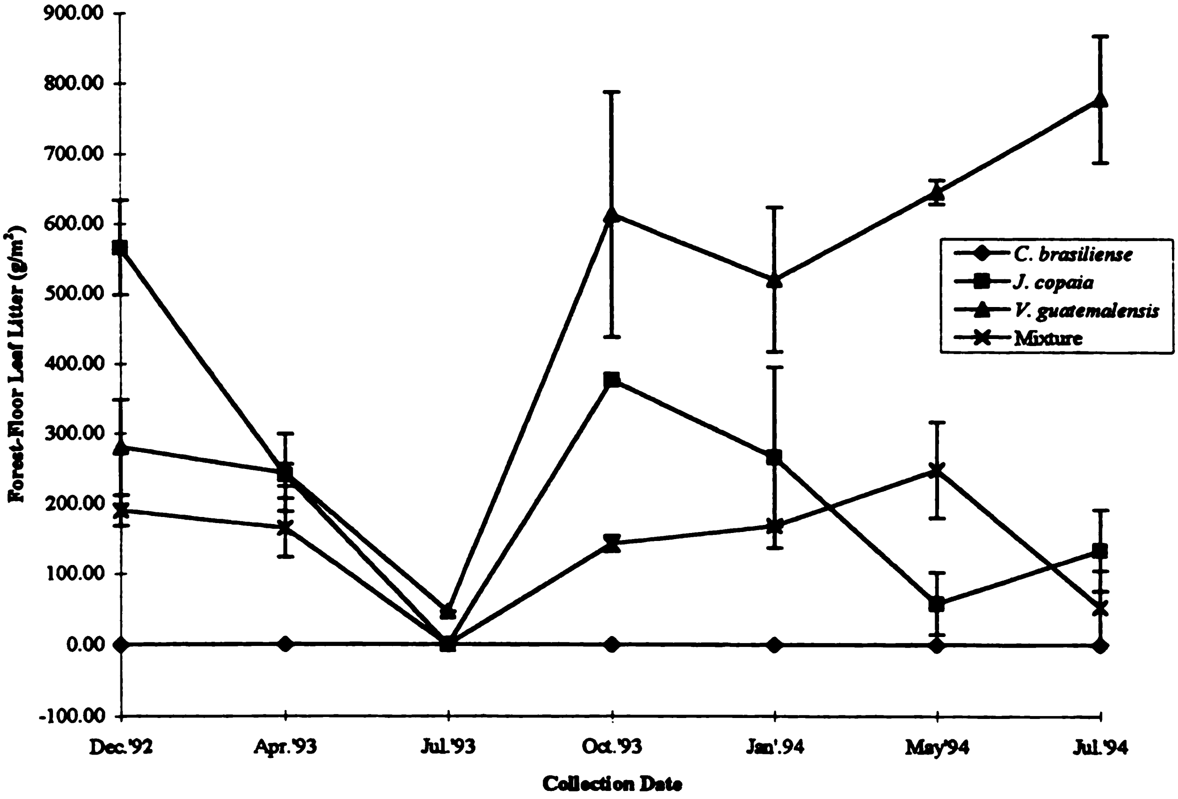

Fig. 5. Forest-floor leaf litter. Data are from collections made every 3 months from January 1992 to August 1994 (means and standard error bars). Source: F. Montagnini, unpublished data. Note: Except for a small amount under *V. guatemalensis*, there was no leaf litter on the forest floor in July 1993, possibly because of unusually high rainfall during that month.

microstachyum grown in pure plots. However, a comparison with previous research is valid: data for *V. guatemalensis* in Montagnini et al. (1993) are similar to results found in the present study. A comparison of research by Montagnini et al. (1993) on *S. microstachyum* in monospecific plots with the current study suggests that *S. microstachyum* might have been the fastest to decompose had it remained part of the present study.

6.2. Litter fall and forest-floor litter

Data from the same experimental plantation (Montagnini et al., 1994) showed that *V. guatemalensis* and *J. copaia* had the highest annual litter fall (Fig. 4). Despite similar amounts of litter fall, *J. copaia* plots had about half the total amount of litter found on the forest floor as *V. guatemalensis* plots (Fig. 5). This may imply that the overall rate of litter decomposition is faster in *J. copaia* than in *V. guatemalensis*, even though initially *V. guatemalensis* had a faster rate of weight loss than *J. copaia*. This finding suggests that even when examining species with rapid decomposition rates, at least a full year of a study is needed to corroborate initially observed trends. In the present experiment, 87–93% of litter had disappeared after 13 months, making further collections unfeasible.

The mixed plots had intermediate values and less pronounced peaks of forest-floor litter than *V. guatemalensis* and *J. copaia*, therefore contributing year-round litter coverage. However, *V. guatemalensis* and *J. copaia* plots, despite their peaks and depressions, had more litter on the ground than the mixture at every point measured; these two species can therefore also provide good soil protection. On the other hand, if faster nutrient return to the soils is desired, the mixture would be preferred because its annual litter fall was only slightly less than that of *J. copaia*, yet significantly less litter was found on the ground, suggesting that the mixed litter decomposed more quickly than *J. copaia*. The mixture probably also decomposed more quickly than *V. guatemalensis* because these plots did not accumulate as much forest floor material. *V. guatemalensis* plots accumulated about 700 g m^{-2} on the forest floor between July 1993 and July 1994; the mixture only gained 53 g m^{-2} during the same period.

6.3. Mulch experiment

Initial growth of the maize seedlings was improved by all the mulch treatments in comparison with the unmulched controls. Apparently, the application of any mulch, independent of the species used, improves nutrient availability and moisture retention, favoring initial seedling growth. Among the mulches used in the present research, during the early stage of growth of maize seedlings the most pronounced results were found with *S. microstachyum* mulches. Similar results were obtained by Montagnini et al. (1993) in a short-term field experiment comparing *S. microstachyum*, *V. guatemalensis*, *Hyeronima alchorneoides* and *V. ferruginea*, where *S. microstachyum* mulch treated seedlings showed the fastest growth in height and the largest total aerial and root biomass.

The total N uptake for the *S. microstachyum* treated seedlings was much higher than the other treatments or the controls because of the combination of faster growth rates and high levels of N in the mulch. Montagnini et al. (1993) found that seedlings mulched with *S. microstachyum* had over five times as much N uptake as control seedlings. Although differences were not as marked in the present study, it was clear that high N concentration favored the initial growth of maize.

Phosphorus uptake was also favorably influenced by mulches, with the single species mulches showing the highest P uptake in comparison with either the mixture or the unmulched controls. Although seedlings treated with the mixed mulch did not have high P uptake, their growth was significantly better than the controls, suggesting that factors other than P uptake such as improved soil moisture or higher availability of nutrients other than P were more important for seedling success.

Toward the end of the experiment, as seen in Fig. 3, the maize seedling height reached a plateau in all mulch-treated pots, possibly because of depletion of soil and mulch nutrients or the restriction of the small pot and soil volume available to root systems. The initial release of nutrients from the mulches was probably accelerated because the leaves were ground for the mulch experiment before each application. In a field situation nutrient release from mulches of whole leaves is expected to be slower and also their effects on plant growth would presumably last longer than in the present experimental conditions.

The control seedlings were never as tall as the mulched seedlings during the experiment, and mortality rates were high. The control seedlings appeared weak and progressively deteriorated. Thus, it is likely that maize could not be grown in very infertile soils without mulch or fertilizers. The experiment successfully corroborates the expectation that seedlings treated with mulches receive an early addition in nutrients that can make a difference between crop survival and failure on poor and acidic soils like those used in this experiment.

6.4. Application to species choice for site rehabilitation

The species tested in these experiments showed differences in litter decomposition, annual litter fall, forest-floor litter accumulation, and in nutrient release from mulch and nutrient uptake by maize seedlings. In context with additional information on tree growth and economic value, these differences are important in planning site restoration and agroforestry systems with these species. For example, if rapid tree growth, fast canopy closure, and deep litter cover are desired, *V. guatemalensis* appears to be the preferred species. In recent experiments testing over ten indigenous and exotic species for their suitability for reforestation in the region, *V. guatemalensis* was ranked as one of the most outstanding species in terms of growth rate, form and survival (González and Fisher, 1994; Butterfield and Espinoza, 1995). This tree was surpassed by the fast height growth of *J. copaia*, although diameters were similar (Montagnini et al., 1995). However, *J. copaia* has a much more open canopy, allowing the growth of herbaceous plants in the understorey. These conditions under *J. copaia* may be desirable for intercropping because more light is available than under *V. guatemalensis* at the same planting density. If the objective is to obtain timber with large diameters, the best growing condition may be in mixture as diameters of both species were greater in mixed plots (Montagnini et al., 1995).

S. microstachyum may also be a good choice for site restoration and agroforestry because of its quick leaf litter decomposition rate and high litter nutrient levels as shown in the mulch experiment. However, it has poor form, and, as in the present experiment, it is susceptible to pest problems. Beneficial effects may still be achieved if planted in mixture because pest problems were less severe in mixed designs than in monospecific plots (Montagnini et al., 1995). When the aim of a restoration project is to build a litter layer and canopy cover as soon as possible, *C. brasiliense* in pure plantations does not appear to be a good choice, because it had the lowest rate of litter decomposition and the smallest annual litter fall, resulting in an absence of forest-floor cover. It may be more advantageous to plant this species in a mixture rather than in monospecific stands: higher economic returns can be obtained from the relatively high timber quality of *C. brasiliense*, and other species in the combination can provide other ecological benefits from higher rates of litter fall and faster nutrient release to the soils. The mixed design provides intermediate to fast decomposition rates, releasing nutrients to the soil and allowing a litter layer to protect the soil. The leaf mixture provides a balance of nutrients for recycling.

Apart from their beneficial effects on nutrient cycling, tree species with rapid canopy closure can decrease the growth of weeds after 2–3 years, thus decreasing the cost of weeding during plantation establishment. Alternatively, annual crops can be grown between the tree lines for 2–3 years, a relatively widespread system in the region. Some of the species involved in the present experiment (*V. guatemalensis, C. brasiliense, S. microstachyum*) currently account for a great proportion of the species used in small farm reforestation in the region (Montagnini et al., 1995). Intercropping of young tree plantations apparently encourages farmers to reforest abandoned pastures (Rheingans, 1996).

The canopy characteristics of the tree species will affect their suitability for interplanting with annual crops and the management required when used in agroforestry systems. In cases where intercropping is not feasible or desired, farmers can follow a rotational scheme: after cutting and extracting timber from the tree plantation, leaving slash on the ground to protect soils, farmers can plant subsistence crops on the improved soils (Montagnini and Mendelsohn, 1996). Fuelwood from thinning and pruning would be an additional source of farm income. These alternatives allow farmers to make choices that can provide both economic and ecological benefits within future systems.

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References

Anderson, J.M., Proctor, J. and Wallack, H.W., 1983. Ecological studies in four contrasting lowland rain forests in Gunug Mulu National Park. Sarawak. J. Ecol., 71: 503–527.

Budelman, A., 1988. The decomposition of the leaf mulches of *Leucaena leucocephala*, *Gliricidia sepium*, and *Flemingia macrophylla* under humid tropical conditions. Agrofor. Syst., 7: 33–45.

Budelman, A., 1989. The performance of selected leaf mulches in temperature reduction and moisture conservation in the upper soil stratum. Agrofor. Syst., 8: 53–66.

Butterfield, R.P. and Espinoza, M., 1995. Screening trial of 14 tropical hardwoods with an emphasis on species native to Costa Rica: fourth year results. New For., 9: 135–145.

Constantinides, M. and Fownes, J.H., 1994. Nitrogen mineralization from leaves and litter of tropical plants: relationship to nitrogen, lignin and soluble polyphenol concentrations. Soil Biol. Biochem., 26: 49–55.

Ewel, J.J., 1976. Litter fall and leaf decomposition in tropical forest succession in Eastern Guatemala. J. Ecol., 64: 293–308.

González, E. and Fisher, R.F., 1994. Growth of native forest species planted on abandoned pasture land in Costa Rica. For. Ecol. Manage., 70: 159–167.

Guariguata, M.R., Rheingans, R., and Montagnini, F., 1995. Early woody invasion under tree plantations in Costa Rica: implications for forest restoration. Restor. Ecol., 3: 252–260.

La Caro, F. and Rudd, R.L., 1985. Leaf litter disappearance rates in Puerto Rican montane rain forest. Biotropica, 17: 269–276.

Montagnini, F., 1990. Ecology applied to agroforestry in the humid tropics. In: R. Goodland (Editor), Race to Save the Tropics. Ecology and Economics of a Sustainable Future. Island Press, Washington, DC, pp. 49–58.

Montagnini, F. and Mendelsohn, R., 1996. Managing forest fallows: improving the economics of swidden agriculture. Ambio, in press.

Montagnini, F., Sancho, F. and Ramstad, K., 1993. Litter fall, litter decomposition and the use of mulch of four indigenous tree species in the Atlantic lowlands of Costa Rica. Agrofor. Syst., 23: 39–61.

Montagnini, F., González, E., Porras, C., Rheingans, R. and Sancho, F., 1994. Mixed-tree plantations in the humid tropics: Growth, litter fall and economics of experimental systems in Latin America. IUFRO International Symposium on Growth and Yield of Tropical Forests, Tokyo University of Agriculture and Technology, Fuchu, Tokyo, Japan, pp. 125–135.

Montagnini, F., González, E., Rheingans, R. and Porras, C., 1995. Mixed and pure forest plantations in the humid neotropics: a comparison of early growth, pest damage and establishment costs. Common. For. Rev., 74: 306–314.

Palm, C.A. and Sanchez, P.A., 1990. Decomposition and nutrient release patterns of leaves of three tropical legumes. Biotropica, 22: 330–338.

Palm, C.A. and Sanchez, P.A., 1991. Nitrogen release from leaves of some tropical legumes as affected by their lignin and polyphenolic contents. Soil Biol. Biochem., 23: 83–88.

Rheingans, R.D., 1996. The ecological, economic and political effects of tree plantation intercropping on small farm forestry in the Atlantic lowlands of Costa Rica. Doctoral Dissertation, Yale University, School of Forestry and Environmental Studies, 187 pp.

Ruvinsky, J., 1995. Relative leaf litter decomposition of four indigenous tree species in pure and mixed plantations in the Atlantic humid lowlands of Costa Rica. Working Paper No. 82, Tropical Resources Institute, Yale School of Forestry and Environmental Studies, New Haven, CT, 14 pp.

Sancho, F. and Mata, R., 1987. Estudio detallado de suelos. Estación Biológica La Selva. Organización para Estudios Tropicales, San José, Costa Rica, 162 pp.

Singh, K.P., 1969. Studies in decomposition of leaf litter of important trees of tropical deciduous forests at Varanasi. Trop. Ecol., 10: 292–311.

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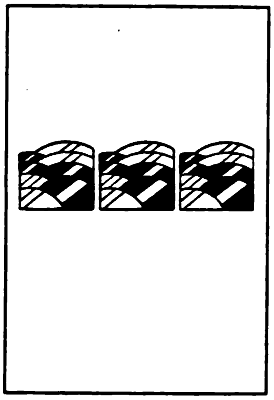

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Estimation of nitrogen fixation by the tropical legume tree *Stryphnodendron microstachyum*

Introduction

Stryphnodendron microstachyum Poepp. et Endl. (ex *S. excelsum* Harms) is a native leguminous tree of the humid tropics of Costa Rica. This species is currently under trial for its use in forestry as well as in agroforestry combinations in the Atlantic humid lowlands region (Gonzalez et al. 1990, Montagnini 1992). Like many other leguminous trees it obtains nitrogen through a root-nodule symbiosis with the azotrophic bacteria of the Rhizobiaceae. The magnitude of N input via symbiotic fixation is not well documented under field conditions. We undertook a modest field study to estimate the magnitude of nitrogen fixation by stryphnodendron using an isotope dilution methodology.

Materials and methods

Estimation of nitrogen fixation was undertaken under field conditions using a ^{15}N-dilution methodology as described by Parrotta et al. (1994). Seeds of *Stryphnodendron microstachyum* (the N^2-fixing species) and *Vochysia guatemalensis* Donn. Sm. (ex *V. hondurensis* Sprague; the non-fixing reference species) were planted in polyethylene bags. *V. guatemalensis* seedlings were seven months old and *S. microstachyum* seedlings were three months old at the time of planting.

Plantation establishment. In July 1991, the two tree species were transplanted into 6 m x 6 m plots in a mixed plantation installed on abandoned pastures at La Selva Biological Station of the Organization of Tropical Studies, Costa Rica. The site is located at 10°26'N, 86°59'W, at 50 m mean elevation, and is characterized by a mean annual temperature of 24°C and a mean annual rainfall of 4000 mm, with the maximum in July and the minimum in March. Soils are Fluventic Dystropepts derived from alluvially deposited volcanic materials; they are deep, well drained, stone-free, of low or medium organic matter content, of moderately heavy texture, and generally acidic and infertile (Sancho and Mata 1987). The area had been cleared in the mid-1950s and grazed until 1981. The two tree species were alternated in each row on a 1 m x 1 m spacing. Four replicate plots were established originally, but because of seedling mortality due to deer browsing in two of the four plots, only two replicates were followed.

Within each 6 m x 6 m plot, one 2 m x 2 m subplot had been created which was isolated to a depth of 60 cm in the soil by multiple layers of plastic construction sheeting. This subplot became the ^{15}N-enriched fertilizer application area for purposes of isotope dilution estimation. Beginning in August 1992 and continuing every six months thereafter, applications of ^{15}N-enriched fertilizer were made at the rate of 0.092 g/m^2 in a total N application of 1 g/m^2.

Sampling. Sampling of leaf tissues was undertaken just prior to each enriched fertilizer application. Random leaf samples (Parrotta et al. 1994) were taken from each of the four trees within the subplots and pooled by species. The leaves were dried at

70°C to constant weight and ground in a Tecator food mill to fine powder. Analyses for N and ^{15}N were made at the University of Saskatchewan Soil Analysis Laboratory using an ANCA-MS.

Estimation of nitrogen fixation. The proportion of nitrogen derived from atmosphere (pNdfa) was estimated using the formula of Fried and Middelboe (1977).

Results

In May 1993, at the time of the final harvest, *S. microstachyum* trees ranged in size from 2 to 7 cm diameter at breast height (dbh) and 1 to 5.4 m in height; and *V. guatemalensis* ranged in size from 4.3 to 6.6 cm dbh and 4.4 to 5.6 m in height. Stryphnodendron growth was more variable than that of vochysia, a pattern similar to that found in a nearby experimental plantation on the same soils.

pNdfa values for stryphnodendron after 6 and 12 months growth in this Costa Rican plantation are shown in Table 1. Differences in pNdfa were observed between trees of the two plots which were followed, suggesting differences in available nitrogen in the soils of the two plots. Plot 1 consistently had higher values of pNdfa than plot 2. This would indicate that plot 2 had a larger pool of available N than did plot 1. The values obtained for pNdfa in this study are similar in magnitude to those reported by Parrotta et al. (1994) for leucaena and casuarina, by Sanginga et al. (1989) for leucaena, or by Baker et al. (1992) for paraserianthes, leucaena, and enterolobium. Because stryphnodendron is a rapidly growing tree species, the contribution of litter or fine root turnover to the N economy of environments where it grows can be considerable.

Results of other studies conducted in four-year-old, mono-specific plantation stands on abandoned pastures at La Selva showed that *S. microstachyum* had fast growth (over 3.0 cm dbh per year), high N concentration in leaf (2.25%) and branch (0.93%) tissue, high rates of litter fall, and relatively fast leaf litter decomposition rates (Montagnini et al. 1993). In other research on the same experimental plantation, soils under *S. microstachyum* had higher net nitrification potential rates (1.1-1.9 mg/kg/day) than those under non-N fixing species in the same experiment (Montagnini and Sancho 1994a). Additionally, total above-ground biomass N accumulation by *S. microstachyum* was 176 kg/ha larger than *V. guatemalensis* growing in the same plantation (Montagnini and Sancho 1994b, 1994c). Furthermore, maize seedlings grown in soils mulched with *S.*

Table 1. The proportion of nitrogen derived from the atmosphere (pNdfa) by *Stryphnodendron microstachyum* at two times from planting in Costa Rica.

Age	Plot No.	pNdfa	Mean
18 months	1	69.2	61.2
	2	54.1	
22 months	1	76.7	51.9
	2	32.5	

microstachyum leaves showed better growth and extracted more N from the soil than those mulched with non-N-fixing tree species, or than the unmulched controls (Montagnini et al. 1991, 1993). We have demonstrated that the majority of this N is provided by symbiotic nitrogen fixation and a lesser amount from N uptake from the soil available-N pool.

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References

Baker, D. D., R. A. Wheeler, and M. Fried. 1992. Estimation of biological nitrogen fixation by three legume tree species, using the ^{15}N dilution method. In: K. Mulongoy, M. Gueye, and D. S. C. Spencer (eds), Biological nitrogen fixation and sustainability of tropical agriculture. John Wiley and Sons, London. p. 259–264.

Fried, M., and V. Middelboe. 1977. Measurement of amount of nitrogen fixed by a legume crop. Plant and Soil 47:713–715.

Gonzalez E., R. Butterfield, J. Segleau, and M. Espinoza. 1990. Primer Encuentro Regional sobre Especies Forestales Nativas de la Zona Norte y Atlantica. Memoria. Julio 1989. Chilamate, Costa Rica. Instituto Tecnologico de Costa Rica. Cartago, Costa Rica. 76 p.

Montagnini, F. 1992. Mixed-tree plantations with native trees: land-use systems for economic returns and soil restoration. Experiments in Costa Rica and Argentina. Agrofor. Today. July-September, 1992, p. 4–6.

Montagnini, F., F. Sancho, K. Ramstad, and E. Stijfhoorn. 1991. Multipurpose trees for soil restoration in the humid lowlands of Costa Rica. In: D. A. Taylor and K. G. Mac Dicken (eds), Research on multipurpose trees in Asia. Winrock International Inst. for Agricultural Development. Bangkok. p. 41–58.

Montagnini, F., K. Ramstad, and F. Sancho. 1993. Litterfall, litter decomposition and the use of mulch of four indigenous tree species in the Atlantic lowlands of Costa Rica. Agrofor. Sys. 23:39–61.

Montagnini, F., and F. Sancho. 1994. Soil nitrogen mineralization under six indigenous tree species, an abandoned pasture and secondary forest in the Atlantic lowlands of Costa Rica. Plant and Soil (in review).

Montagnini, F., and F. Sancho. 1994b. Above-ground biomass and nutrients in young plantations of four indigenous tree species: implications for site nutrient conservation. J. Sustain. For. In press (v. 4:1).

Montagnini, F., and F. Sancho. 1994c. Nutrient budgets of young plantations with native trees: strategies for sustained management. In: W. Bentley and M. Gowen (eds), Forests and wood-based biomass energy as rural development assets. Winrock International Inst. for Agricultural Development. Morrilton, Arkansas, USA. In press.

Parrotta, J. A., D. D. Baker, and M. Fried. 1994. Application of ^{15}N-enrichment methodologies to estimate nitrogen fixation in *Casuarina equisetifolia*. Can. J. For. Res. 24.

Sanginga, N., K. Mulongoy, and A. Ayanaba. 1989. Nitrogen fixation of field-inoculated *Leucaena leucocephala* (Lam.) de Wit. estimated by the ^{15}N and the difference methods. Plant and Soil 117:269-274.

Mycorrhiza (1994) 5:45–51

ORIGINAL PAPER

Heidi Asbjornsen · Florencia Montagnini

Vesicular-arbuscular mycorrhizal inoculum potential affects the growth of *Stryphnodendron microstachyum* seedlings in a Costa Rican human tropical lowland

Abstract This study used a plant bioassay to investigate the vesicular-arbuscular mycorrhizal (VAM) inoculum potential of soil from three vegetation types (fern, secondary forest, and grass) in an abandoned pasture in the tropical humid lowlands at La Selva, in northeastern Costa Rica. Growth, measured as seedling height, number of leaves, and total (above- and belowground) biomass, of *Stryphnodendron microstachyum* Poepp. et Endl. (Synon. *S. excelsum* Harms) seedlings was significantly lower when grown in soil inoculum from the fern areas than in soil inoculum from the forest and grass areas. However, *S. microstachyum* seedlings grown in the fern inoculum had significantly greater VAM colonization than seedlings grown in the forest and grass inoculum. In addition, roots collected from a dominant plant species from each of the three vegetation types showed that the fern (*Nephrolepsis biserrata*) had significantly greater mycorrhizal colonization than the tree (*Pentaclethra macroloba* (Willd.) Kuntze or the grass (*Brachiaria* spp.). The results of this study suggest that differences in mycorrhizal inoculum potential among vegetation types and its effects on seedling growth may have important implications for the restoration and management of degraded lands.

Key words Inoculum potential · Ecosystem restoration · *Stryhphnodendron microstachyum* Vesicular-arbuscular mycorrhizae

Introduction

Vesicular-arbuscular (VA) mycorrhizae play an important role in nutrient cycling, in particular, by facilitating plant uptake of phosphorus (Hayman 1983; Bolan 1991). The close link between nutrient cycling and ecological succession has stimulated interest in the potential importance of VA mycorrhizae in ecosystem restoration and in efforts to influence successional pathways.

Plant species from different successional communities exhibit varying degrees of dependency on VA mycorrhizae (Gange et al. 1990) and the capacity to regulate mycorrhizal colonization of their roots (Ratnayake et al. 1978; Koide and Li 1990). Mycorrhizal species composition and abundance may also change as succession proceeds (Hayman 1983; Hayman and Tavares 1985; Högberg and Piearce 1986). Furthermore, disturbance has been shown to affect the composition and function of mycorrhizal populations in the soil environment (Moorman and Reeves 1979; Hafeel and Gunatilleke 1988; Evans and Miller 1990; Fairchild and Miller 1990; Cuenca and Lovera 1991). These observations suggest that VA mycorrhizae-plant interactions may have an important role in influencing successional processes (Janos 1980a, 1985; Allen and Allen 1988; Allen et al. 1989; Gange et al. 1990; Perry and Amaranthus 1990).

VA mycorrhizal inoculation studies have shown that early mycorrhizal colonization may provide a competitive advantage for plant establishment and growth in the field (Reeves et al. 1979; Clarke and Mosse 1981; Koske and Polson 1984; Sieverding 1989). Several workers have demonstrated positive effects of VA mycorrhizal inoculation in the restoration of degraded lands in temperate regions (Reeves et al. 1979; Koske and Polson 1984; Perry and Amaranthus 1990; Sylvia 1990). Knowledge about the role of VA mycorrhizae in influencing ecosystem response to disturbance and successional pathways can provide important information for restoring and managing tropical degraded lands.

Assessment of mycorrhizal inoculum potential, defined here as the capacity of mycorrhizal propagules in the soil to colonize plant roots, provides a means to investigate the role of mycorrhizae in ecosystem processes across different habitats or microsites. Differences in mycorrhizal inoculum potential across vegetation

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types is hypothesized to affect the establishment and growth of plants and, consequently, to have implications for the restoration and management of those areas.

A bioassay was used to investigate the mycorrhizal inoculum potential of soil (and fine roots) collected from three successional vegetation types (fern, secondary forest, and grass) and its effects on seedling growth. The experiment was conducted in a shade house under controlled conditions in order to minimize potentially confounding effects of abiotic factors. *Stryphnodendron microstachyum* Poepp. et Endl. (Synon. *S. excelsum* Harms; "vainillo"), a leguminous, nitrogen-fixing tree species native to the region and characterized as an obligate mycotroph (Janos 1980b), was used as the test plant. *S. microstachyum* has soil-ameliorating properties (Montagnini and Sancho 1990) and exhibits relatively fast growth (Espinoza and Butterfield 1989), suggesting that it is a suitable species for restoring degraded tropical areas.

Materials and methods

Site description

The study was conducted at the La Selva Biological Research Station of the Organization for Tropical Studies in northeastern Costa Rica, located at 10°26′N, 86°59′W and at 50 m mean elevation. The mean annual temperature is 24° C. Mean annual rainfall is approximately 4000 mm, with a maximum in July and a minimum in March (La Selva weather reports). The soils are derived from alluvially deposited volcanic materials (Fluventic Dystropepts), and are deep, well drained, and stone free. Soils have low to medium organic matter content, moderately heavy texture, and are generally acid and infertile (Sancho and Mata 1987).

The 10-ha study site had been converted from forest to grassland in the 1950s, and was grazed until 1980, after which it was left to regenerate naturally (Pierce 1992). Within the regeneration site, the predominant vegetation type was grass, interspersed with patches of fern and approximately 20-year-old secondary forest. The dominant species in the fern vegetation were *Hypolepsis repens* and *Nephrolepsis biserrata*, with few other plant species present. The grass vegetation comprised both native species (*Paspalum fasciculatum*, and *Cynodon*) and introduced species (*Brachiaria*, *Melinis minutiflora*, *Panicum maximum*). The dominant secondary forest species was *Pentachlethra macroloba* (Willd.) Kuntze, with some *Piper culebranum*, *Psidium guajava*, and species of the Melastomataceae family, with ferns and tree seedlings in the understory.

Soil analysis

The soils and VA mycorrhizal propagule abundance within the study site were characterized by establishing four 200- to 250-m transects. Along each transect, a sampling area representing each of the three dominant vegetation types (fern, secondary forest, and grass) was selected (4 transects × 3 vegetation types = 12 sampling areas). At each sampling area, five soil samples were collected with a trowel from the surface horizon, to an approximate depth of 15 cm in March 1991. Sampling was conducted by taking one sample from an arbitrarily chosen center point of the sampling area, and four additional samples approximately 7 m from the center in each of the cardinal directions. Soils were air dried and passed through a 2-mm sieve prior to analysis. Soils were analyzed for phosphorus on soil extracts prepared by mixing 4 g of soil with 20 ml of Mehlich's solution and analyzed on a Milton Roy Spectronic-501 spectrophotometer (Anderson and Ingram 1989). Total carbon and total nitrogen content were determined by dry combustion using a LECO CHN-600 elemental analyzer. The pH was measured on 1:2.5 mixtures of soil:deionized water with an Orion 701A digital analyzer. Exchangeable cation concentrations (Mg, Ca, K, and Al) were determined on the Mehlich extracts using a Thermo Jarrell Ash AtomScan-25 Inductively Coupled Plasma Spectrophotometer.

Mycorrhizal analysis

From each sampling area, entire root systems of five plants were excavated in March 1991 from the dominant plant species within each vegetation type: *Nephrolepsis biserrata* (fern), *Pentaclethra macroloba* (secondary forest) and *Brachiaria* spp. (grass). The roots were cleared with potassium hydroxide and hydrogen peroxide and stained with 0.05% trypan blue in lactoglycerol solution (Kormanik and McGraw 1982). Roots were analyzed for percent VA mycorrhizal colonization using the ± slide method (Giovannetti and Mosse 1980), in which 10 1-cm root segments were randomly selected from each root sample, and VA mycorrhizal colonization expressed as the percent of root segments colonized for each root sample. The average percent colonization of the five root samples from each sampling area was used for subsequent analyses.

Mycorrhizal spores in the soil were quantified using a wet-sieving technique (Gerdemann and Nicolson 1963) modified with centrifugation. Four soil samples approximately 15 cm deep were collected and pooled from each of the sampling areas along the four transects to produce four replicate 100-g (air dry weight) samples from each vegetation type. Each soil sample was agitated with a strong stream of water in a beaker, allowed to settle for 45 s, and decanted through three sieves (425 µm, 106 µm, and 45 µm). After repeating this procedure three times, the 45–106 µm and 106–425 µm fractions were combined and centrifuged with water for 3 min at 3000 rpm, followed by centrifugation with a 40% sucrose solution for 1 min at 3000 rpm. The supernatant (containing suspended spores) was poured through the 45-µm sieve and the spores washed thoroughly to remove the sucrose solution. The spores from each soil sample were placed into separate petri dishes, and the dishes coded to allow for blind scoring of the samples. The total number of VA mycorrhizal spores in each soil sample was determined under a dissecting microscope. The average number of spores of the four soil samples from each sampling area was used for subsequent analyses.

Inoculum potential

In order to assess the inoculum potential of the three dominant vegetation types and its influence on plant growth, VA mycorrhizal root colonization, seedling height and number of leaves, and biomass were compared over time for *S. microstachyum* seedlings grown in: (1) nonfumigated soil, which included fine root fragments, and (2) fumigated soil (described below), which included fine root fragments. The soil inoculum was collected to a depth of approximately 15 cm from sampling areas outside the experimental regeneration site supporting each of the three vegetation types in June 1991. The soil and fine roots were mixed thoroughly by cutting roots into small pieces and mixing by hand. Soils for the fumigated group were treated with methyl bromide gas with 2% chloropicrin at a concentration of 1 kg gas/45 l soil. Methyl bromide gas has been used effectively to eliminate viable mycorrhizal fungi (Janos 1980b). Transplanting to the nonfumigated soils occurred within 1 day after the soil and roots were collected from the field. Fumigated soils were allowed to stand at least 2 days before transplanting occurred to ensure complete volatilization of the gas.

Table 1 The vesicular-arbuscular (VA), mycorrhizal colonization (% VAM) of *Stryphnodendron microstachyum* seedlings grown in fern, forest, and grass soil inocula, the VA mycorrhizal colonization of dominant plant species collected from the fern (*N. biserrata*), forest (*P. macroloba*), and grass (*Brachiaria* spp.) vegetation, and the number of spores in soil collected from beneath these vegetation types. Standard deviation and sample size shown in parentheses. Matching lowercase letters indicate no significant difference at $P \leq 0.05$ across each row

	Fern	Forest	Grass
% VAM in soil inoculum	10.56a (11.6, 18)	0.20b (0.3, 18)	0.18b (0.5, 18)
% VAM of dominant plant species	*Nephrolepsis biserrata* 0.42 a (0.1, 4)	*Pentaclethra macroloba* 0.10b (0.1, 4)	*Brachiaria* spp. 0.05b (0.1, 4)
Spores/100 g soil	25.5a (10.0, 4)	16.25a (6.1, 4)	10.25a (10.0, 4)

S. microstachyum seedlings not colonized by VA mycorrhizae were obtained by propagating seedlings from seed in a fumigated. 50:50 sand:soil mixture in an enclosed shade house. At the age of 6 weeks, *S. microstachyum* seedlings of uniform size (approximately 7–9 cm in height, with 3–5 leaves) were transplanted to plastic cups (approximately 0.35 l) containing either nonfumigated or fumigated soil from each of the three vegetation types as described above. Each soil group contained 30 replicates. The fumigated soils received 100 ml of a microbial suspension prepared by soaking soil and roots from each vegetation type overnight in water and filtering the solution through a 45-μm sieve the following day. The filtrate served to replace soil microorganisms eliminated by fumigation (Janos 1980b).

Growth analysis

Seedling height and the number of leaves per seedling were recorded prior to each harvest. Three harvests of 10 seedlings from each soil group were conducted 49 days, 103 days, and 160 days after the transplant date. Visual observations of the roots verified that there had been no restriction of root growth. The roots were immediately cut off, rinsed with water, and preserved in individual bottles with FAA solution (90 ml 50% ethanol, 5 ml acetic acid, and 5 ml formalin). The stems and leaves were dried for 48 h at 70° C and weighed.

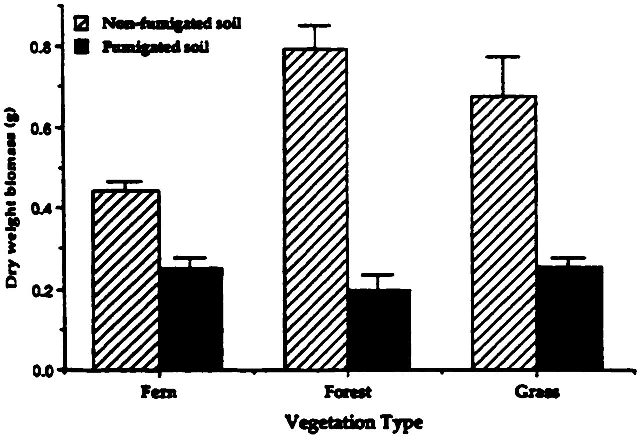


Fig. 1 Total biomass (above and below ground) of *S. microstachyum* seedlings grown in nonfumigated and fumigated soil inoculum collected from beneath fern, forest, and grass vegetation, 160 days after transplanting. The sample size for each treatment group was 6–10 seedlings. Significant differences between treatment groups are indicated by standard error bars

Root colonization

Root colonization of the entire root mass of harvested plants was assessed using the grid-line intersect technique (Giovannetti and Mosse 1980). After clearing and staining the roots as described above, the roots were cut into small pieces and spread evenly in a petri dish with a grid of 0.5-inch squares marked on the bottom. Petri dishes were coded to allow for blind scoring of the samples. The presence of a vesicle with a hyphal attachment was used as the criterion for VA mycorrhizal colonization. The percent of the total number of root-line intersections that were mycorrhizal was determined for each seedling using a MicroZoom II Microscope (Cambridge Instruments) at ×30–1000 magnification. Roots of seedlings grown in the fumigated soils were also scanned under the microscope to verify the absence of mycorrhizal colonization. Two seedlings from the fumigated soils were contaminated with mycorrhizae and were not included in the analyses. After mycorrhizal colonization was scored, the roots were rinsed with distilled water on Whatman No. 1 filter paper, dried for 4 days at 70° C, and weighed.

Statistics

One-way analysis of variance (ANOVA) was performed using SYSTAT to determine significant differences at the 95% level (SYSTAT 1989, Evanston, Ill.). Data for percent VA mycorrhizal colonization of *S. microstachyum* seedlings and of the dominant plant species collected from the field were subjected to arcsin transformations. Data on the number of spores in the soil were subjected to square-root transformations (Sokal and Rohlf 1981). Differences between treatments were confirmed using a Tukey test.

Results

S. microstachyum seedlings grown in the fern soil had significantly greater($P<0.01$) percent VA mycorrhizal colonization than seedlings grown in the forest or grass soils (Table 1). Similarly, roots collected from the dominant plant species within each vegetation type in the field indicated that fern roots supported significantly greater mycorrhizal colonization ($P<0.01$) than either the secondary forest or grass roots. In contrast, the numbers of spores present in the soils collected from beneath the fern, secondary forest, and grass vegetation were not significantly different ($P>0.05$).

The total biomass (above- and below-ground) of *S. microstachyum* seedlings grown in the nonfumigated forest and grass soils was significantly greater ($P<0.05$)

Fig. 2 Height of *S. microstachyum* seedlings grown in nonfumigated and fumigated soils collected from beneath fern, forest, and grass vegetation 49, 103, and 160 days after transplanting. The sample size for each treatment group was 6–10 seedlings. Significant differences between treatment groups are indicated by standard error bars. Fern, Forest, and Grass, indicate nonfumigated soil inocula; FFern, FForest, and FGrass, indicate fumigated soil inocula

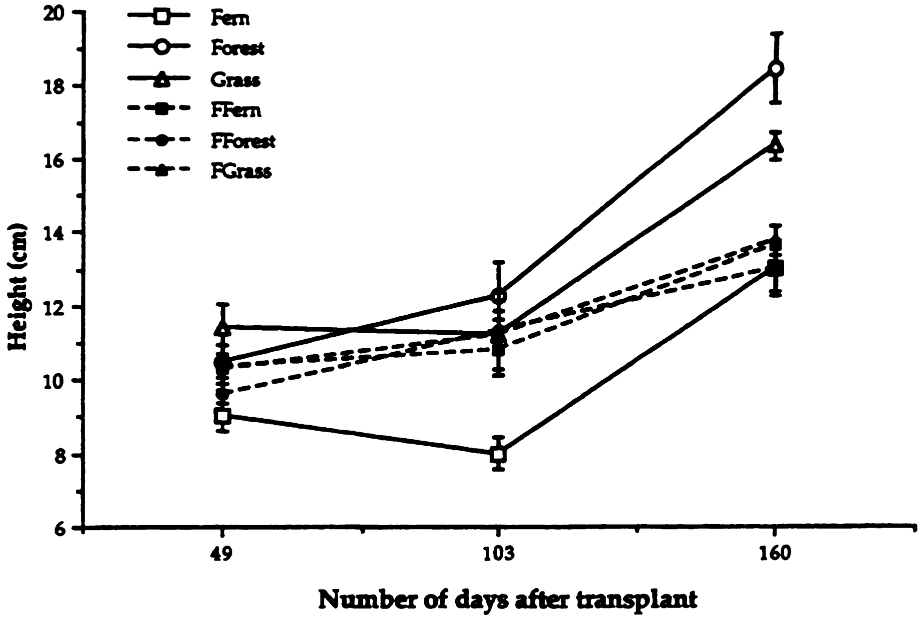
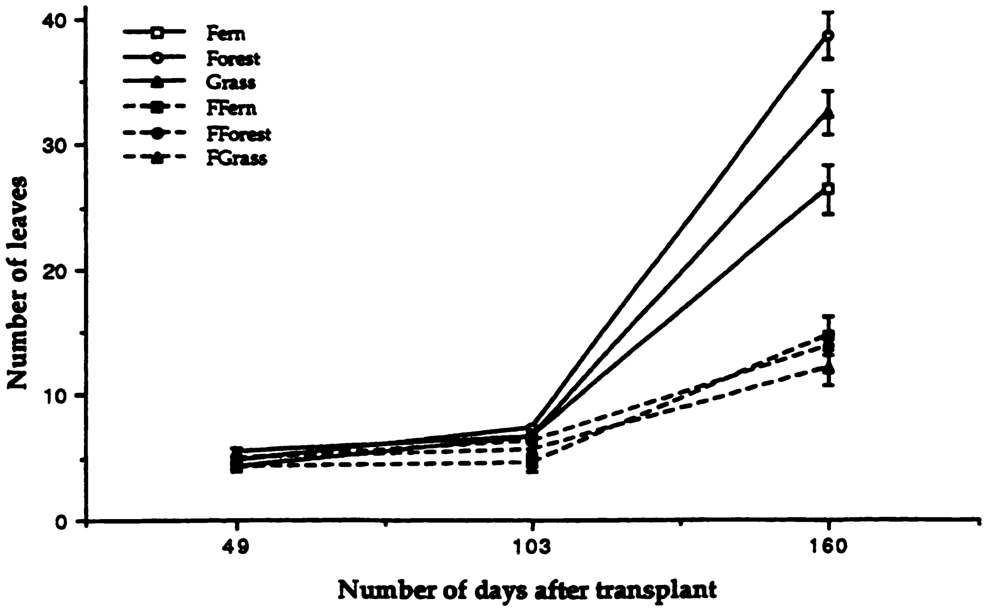


Fig. 3 Number of leaves of *S. microstachyum* seedlings grown in nonfumigated and fumigated soil inoculum collected from beneath fern, forest, and grass vegetation 49, 103, and 160 days after transplanting. The sample size for each treatment group was 6–10 seedlings. Significant differences between treatment groups are indicated by standard error bars. Fern, Forest, and Grass, indicate nonfumigated soil inocula; FFern, FForest, and FGrass, indicate fumigated soil inocula



than that of seedlings grown in the fumigated fern soil for all three harvests (Fig. 1). There was no significant difference in the biomass of seedlings grown in the nonfumigated forest and grass soils. The total biomass of *S. microstachyum* seedlings grown in the nonfumigated forest and grass soils was significantly greater ($P<0.05$) than the respective seedlings grown in the fumigated soils for all three harvests. Seedlings grown in the nonfumigated fern soil had significantly greater ($P<0.05$) biomass than seedlings grown in the fumigated fern soil in the second and third harvests. There was no significant difference in the biomass of seedlings grown in the fumigated soils among the three vegetation types. Root:shoot ratios, leaf weight ratios and root weight ratios reflected the same trends as the biomass data, and are not presented here.

The height of seedlings grown in the nonfumigated fern soil was significantly ($P<0.05$) than the height of seedlings grown in the nonfumigated forest and grass soils in the second and third harvests (Fig. 2). The height of seedlings grown in the fumigated fern soil was significantly lower than the height of seedlings grown in the nonfumigated fern soil for the second harvest, but by the third harvest there was no significant difference. Seedlings grown in the nonfumigated fern soils had significantly fewer leaves than seedlings grown in the nonfumigated forest soil (third harvest) or nonfumigated grass soil (first harvest; Fig. 3). Seedlings grown in the fumigated soils from all three vegetation types had significantly fewer leaves than seedlings grown in the nonfumigated soils by the third harvest.

Table 2 Nutrient concentrations in soils collected from beneath fern, secondary forest, and grass vegetation within the regeneration site. The sample size for all analyses was 20. Matching lower case letters indicate no significant difference at $P \leq 0.05$

	Nutrient							pH
	C (%)	N (%)	P (mg/kg)	Ca (cmol/kg)	Mg (cmol/kg)	K (cmol/kg)	Al (cmol/kg)	
Fern	4.4a	0.50a	2.5a	0.41a	0.32a	0.19a	5.8a	46b
Forest	4.4a	0.47a	1.3a	0.38a	0.42a	0.19a	5.8a	4.7ab
Grass	4.5	0.48a	1.9a	0.56a	0.66b	0.28a	5.8a	4.8a

Chemical analysis of the soil samples indicated that the concentrations of exchangeable P, Ca, and K and total N in the fern, secondary forest, and grass soils were not significantly different ($P > 0.05$). Only exchangeable Mg in the grass soils was significantly higher ($P < 0.05$) than the forest and fern soils. The pH for the fern soils was significantly lower than the grass soil ($P < 0.05$), but was not significantly different ($P > 0.05$) from the secondary forest soil (Table 2).

Discussion

Mycorrhizal propagule abundance, mycorrhizal inoculum potential, and growth of the test plant *S. microstachyum* were found to vary among soils from the three dominant vegetation types within the regeneration site. The significantly higher VA mycorrhizal root colonization of *S. microstachyum* seedlings grown in the fern soil as compared to seedlings grown in the forest and grass soils suggests that the fern soil has a greater mycorrhizal inoculum potential. The significantly lower biomass of seedlings grown in the fumigated soil as compared to the nonfumigated soils, and the lack of significant difference in seedling biomass among the three vegetation types for the fumigated soils, suggests that growth differences may be related to mycorrhizal interactions. However, the consistently poorer growth performance of seedlings grown in the fern soil as compared to seedlings grown in the grass and forest soils suggests that the mycorrhizae-plant associations formed in the fern soil may be less effective at enhancing plant growth than those which formed in the forest or grass soils.

The occurrence of VA mycorrhizae in ferns has been extensively documented (Cooper 1976; Iqbal et al. 1980; Haefeel and Guantilleke 1988; Gemma et al. 1992). The relatively high inoculum potential of fern soil may be a result of the dense rhizomatous mat typical of fern vegetation, as the greater surface area for contact between the seedling and fern roots could facilitate the transfer of VA mycorrhizal colonization. Hafeel and Gunatilleke (1988) hypothesized that the thick root mat of ferns in a *Pinus* spp. plantation in Sri Lanka increased the degree of VA mycorrhizal colonization and spore production as compared with the natural forest. The fern soil inoculum potential may be further accentuated by the greater mycorrhizal propagule abundance in the form of colonized root fragments observed in the fern soil. In addition, the slow rate of root turnover in ferns may have contributed to their high rates of mycorrhizal colonization by allowing a build up of colonization to occur (D. P. Janos, personal communication).

The relatively low inoculum potential of the grass and forest soils may be related to the mycorrhizal dependency of species within these vegetation types. Grasses are commonly facultative mycotrophs (Miller 1987), and are hypothesized to be the most independent of mycotrophic plants (Baylis 1975), and thus to tolerate low fertility in spite of low mycorrhizal colonization (Janos 1980a). Mycorrhizal dependency of obligate plant species is hypothesized to decrease after maturity (Janos 1980a), possibly accounting for the lower mycorrhizal colonization observed in the roots of the secondary forest vegetation.

The inverse relationship between inoculum potential and *S. microstachyum* seedling growth may reflect differences in the infectivity and effectivity of mycorrhizal species among the fern, forest, and grass soils. VA mycorrhizal species composition has been hypothesized to vary across habitats and microsites (Sieverding 1989; Janos 1992). Different mycorrhizal species may also vary in their capacity to colonize plant roots (infectivity) and to enhance phosphorus uptake or provide other benefits to the host plant (effectivity; Hayman 1983). Mycorrhizal species in soils supporting fern vegetation may be more effective at colonizing plant roots, while less effective at enhancing phosphorus uptake, resulting in a lower capacity of fern soil inoculum to stimulate seedling growth in the initial stages of plant development. In addition, specificity between the mycorrhizal species and *S. microstachyum* may have contributed to the differential seedling growth response if mycorrhizal species in the fern vegetation established more beneficial associations with *S. microstachyum* than mycorrhizal species in the grass and forest vegetation (Hayman 1983; Sieverding 1989).

Another possible explanation for the different growth rates of seedlings grown in the fern, forest, and grass soils is the ability of *S. microstachyum* seedlings to regulate mycorrhizal colonization of its roots. *S. excelsum* is characterized as an obligate mycotroph (Janos 1980a). Obligate mycotrophs are hypothesized to have a poor capacity to regulate mycorrhizal colonization of their roots (Janos 1985). If *S. microstachyum* is adapted to relatively low VA mycorrhizal inoculum conditions in its natural habitat, it may be less able to regulate colonization of its roots, which may allow mycorrhizal colonization to exceed optimum levels for plant growth under the conditions of high inoculum potential present in the fern soils.

A final factor which may affect seedling growth in the fern soil inoculum is allelopathic interactions, a phenomenon which has been documented for several fern species and geographic regions (Bohm and Tryon 1967; Munther and Fairbrothers 1980; Rice 1984). Phytotoxins leached from dead, standing bracken fronds and transferred by the soil medium was found to cause herb suppression (Gliessman and Muller 1972, 1978). Allelopathic chemicals have been shown to influence soil microorganisms (Rovira 1969), and both ecto- and endo-mycorrhizae appear to be sensitive to allelochemicals in litter and soil organic material (Perry and Choquette 1987). However, *Pteridium aquilinum* (bracken fern) did not affect the rate or degree of mycorrhizal colonization nor the foliar phosphorus concentration of black cherry seedlings (Horsely 1992). If phytotoxins are produced by the fern vegetation, they may influence VA mycorrhizal colonization and subsequent plant growth, possibly through effects on plant regulatory mechanisms as determined by membrane permeability and root exudation.

Although rapid VA mycorrhizal colonization of roots may be expected to provide a competitive advantage to seedlings, the degree of mycorrhizal colonization is not necessarily positively correlated with seedling growth (Hayman 1983; Saif 1987). It has been suggested that a growth depression may occur if the costs of mycorrhizal colonization to the host plant outweigh the benefits provided by the mycorrhizal symbiont (Snellgrove et al. 1982; Bethlenfalvay et al. 1983; Koide and Elliott 1989). The mycorrhizal associations of seedlings grown in the fern soils may have posed a greater photosynthetic cost to the plant as compared with the mycorrhizal associations of seedlings grown in the forest or grass soils, possibly due to the high infectivity and low effectivity of VA mycorrhizal species, the inability of *S. microstachyum* seedlings to maintain VA mycorrhizal colonization of its roots within the optimum range for plant growth, or the presence of allelopathic interactions. However, the relatively short duration of this experiment precludes determination of whether the *S. microstachyum* seedlings may eventually benefit from the symbiosis once sufficient photosynthetic capacity is established to support the higher levels of colonization.

This study suggests that it may be important to consider differences in the VA mycorrhizal inoculum potential across vegetation types, and its influence on plant establishment, growth, and competitive interactions, in designing restoration and management strategies for degraded areas. In sites where inoculum potential is low, reforestation efforts may be facilitated by inoculating seedlings with VA mycorrhizae prior to transplanting to the field. However, for certain plant species, such as *S. microstachyum*, inoculation does not appear to be necessary, and may even reduce plant growth rates during the early stages of establishment. Excessively high inoculum potential in some successional communities may require other measures to ensure successful initial establishment and growth of transplanted seedlings, particularly if the VA mycorrhizae species are relatively ineffective, if plant species transplanted to the site are adapted to conditions of low mycorrhizal inoculum potential, or if phytotoxins interfere with the establishment of plant-mycorrhizal associations.

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References

Allen BE, Allen MF (1988) Facilitation of succession by the nonmycotrophic colonizer *Salsola kali* (Chenopodiaceae) on a harsh site: effects of mycorrhizal fungi. Am J Bot 75:257–266

Allen MF, Allen EB, Friese CF (1989) Response of the non-mycotrophic plant *Salsola kali* to invasion by vesicular-arbuscular mycorrhizae fungi. New Phytol 1:45–49

Anderson JM, Ingram SI (1989) Tropical soil biology and fertility: a handbook of methods. University of Zimbabwe, Harare, Zimbabwe

Baylis GTS (1975) The magnolioid mycorrhiza and mycotrophy in root systems derived from it. In: Sanders FE, Mosse B, Tinker PB (eds) Endomycorrhizas. Academic Press, London, pp 373–389

Bethlenfalvay GJ, Bayne HG, Pacovsky RS (1983) Parasitic and mutualistic associations between a mycorrhizal fungus and soybean: the effect of phosphorus on host plant-endophyte interactions. Plant Physiol 57:543–548

Bohm BA, Tryon RM (1967) Phenolic compounds in ferns. I. A survey of some ferns for cinnamic acid and benzoic acid derivatives. Can J Bot 45:585–593

Bolan NS (1991) A critical review on the role of mycorrhizal fungi in the uptake of phosphorus by plants. Plant Soil 134:189–207

Clarke C, Mosse B (1981) Plant growth responses to vesicular-arbuscular mycorrhiza. XII. Field inoculation responses of barley at two soil P levels. New Phytol 87:695–703

Cooper KM (1976) A field survey of mycorrhizas in New Zealand ferns. N Z J Bot 14:169–81

Cuenca G, Lovera M (1991) Vesicular-arbuscular mycorrhizae in disturbed and revegetated sites from La Gran Sabana, Venezuela. Can J Bot 70:73–79

Espinoza CM, Butterfield R (1989) Adaptabilidad de 13 especies nativas maderables bajo condiciones de plantacion en las tierras bajas humedas del Atlántico, Costa Rica. In: Salazar R (ed) Manejo y aprovechamiento de plantaciones forestales con especies de uso multiple. Actas Reunion IUFRO, Guatemala, 3–7 April 1989. Catie, Turrialba, Costa Rica, pp 159–172

Evans DG, Miller MH (1990) The role of the external mycelial network in the effect of soil disturbance upon vesicular-arbuscular mycorrhizal colonization of maize. New Phytol 114:65–71

Fairchild GL, Miller MH (1990) Vesicular-arbuscular mycorrhizas and the soil-disturbance-induced reduction of nutrient absorption in maize. III. Influence of P amendments to soil. New Phytol 114:641–650

Gange AC, Brown VK, Farmer LM (1990) A test of mycorrhizal benefit in an early successional plant community. New Phytol 115:85–91

Gemma JN, Koske RE, Flynn T (1992) Mycorrhizae in Hawaiian pteridophytes: occurrence and evolutionary significance. Am J Bot 79:843–852

Gerdemann JW, Nicolson TH (1963) Spores of mycorrhizal endogone species extracted from soil by wet sieving and decanting. Trans Br Mycol Soc 46:235–244

Giovannetti M, Mosse B (1980) An evaluation of techniques for measuring vesicular-arbuscular mycorrhizal infection in roots. New Phytol 84:489–500

Gliessman SR, Muller CH (1972) The phytotoxic potential of bracken, *Pteridium aquilinum* (L.) Kuhn. Madroño 21:299–304

Gliessman SR, Muller CH (1978) The allelopathic mechanisms of dominance in bracken (*Pteridium aquilinum*) in Southern California. J Chem Ecol 4:337–362

Hafeel KM, Gunatilleke IAUN (1988) Distribution of lendomycorrhizal spores in disturbed sites of a lowland rain forest in Sri Lanka. Mycorrhizae for Green Asia. First Asian Conference on Mycorrhizae, 29–31 January, Madras, India, pp 37–45

Hayman DS (1983) The physiology of vesicular-arbuscular endomycorrhizal symbiosis. Can J Bot 61:944–963

Hayman DS, Tavares M (1985) Plant growth responses to vesicular-arbuscular mycorrhiza. XC. Influence of soil pH on the symbiotic efficiency of different endophytes. New Phytol 100:367–377

Högberg P, Piearce GD (1986) Mycorrhizas in Zambian trees in relation to host taxonomy, vegetation type and successional patterns. J Ecol 74:77–785

Horsley SB (1992) Mechanisms of interference between hayscented fern and black cherry. US Deparment of Agriculture Forestry Service, Northeast Forstry Experimental Station

Iqbal SH, Yousaf M, Younusi M (1981) A field survey of mycorrhizal associations in ferns of Pakistan. New Phytol 87:69–79

Janos DP (1980a) Mycorrhizae influence tropical succession. Biotropica 12 [Suppl]:56–64

Janos DP (1980b) Vesicular-arbuscular mycorrhizae affect lowland tropical rain forest plant growth. Ecology 61:151-162

Janos DP (1985) Mycorrhizal fungi: agents or symptoms of tropical community composition. In: Molina R (ed) Proceedings of the 6th North American Conference on Mycorrhizae. Forest Research Laboratory, Corvallis, Ore, pp 98–103

Janos DP (1992) Heterogeneity and scale in tropical vesicular-arbuscular mycorrhiza formation. In: Read DJ, Lewis DH, Fitter AH, Alexander IJ (eds) Mycorrhizas in ecosystems. CAB, Wallingford, UK

Koide R, Elliott G (1989) Cost, benefit and efficiency of the vesicular-arbuscular mycorrhizal symbiosis. Funct Ecol 3:252–255

Koide RT, Li M (1990) On host regulation of the vesicular-arbuscular mycorrhizal symbiosis. New Phytol 114:59–74

Kormanik PP, McGraw A-C (1982) Quantification of vesicular-arbuscular mycorrhizae in plant roots. In: Schenk NC (1982) Methods and principles of mycorrhizal research. American Phytopathological Society, St Paul, Minn

Koske RE, Polson WR (1984) Are V-A mycorrhizae required for sand dune stabilization? BioScience 34:420–424

Miller RM (1987) The ecology of vesicular-arbuscular mycorrhizae in grass- and shrublands. In: Safir GR (ed) Ecophysiology of VA mycorrhizal plants. CRC Press, Boca Raton, Fla, pp 136–170

Montagnini F, Sancho F (1990) Impacts of native trees on tropical soils: a study in the Atlantic lowlands of Costa Rica. Ambio 19:386–389

Moorman T, Reeves FB (1979) The role of endomycorrhizae in revegetation practices in the semi-arid west. II. A bioassay to determine the effect of land disturbance on endomycorrhizal populations. Am J Bot 66:14–18

Munther WE, Fairbrothers DE (1980) Allelopathy and autotoxicity in three Eastern North American ferns. Am Fern J 70:124–135

Perry DA, Amaranthus MP (1990) The plant-soil bootstrap: microorganisms and reclamation of degraded ecosystems. In: Berger JJ (ed) Environmental restoration. Island Press, Washington, DC, pp 94–102

Perry DA, Choquette C (1987) Allelopathic effects on mycorrhizae: influence on structure and dynamics of forest ecosystems. In: Waller GR (ed) Allelochemicals: role in agriculture and forestry. American Chemical Society, Washington, DC, pp 185–194

Pierce SM (1992) La Selva Biological Station history: colonization/land use/deforestation of Sarapiquí, Costa Rica. MSc thesis, Colorado State University, Fort Collins, Colo

Ratnayake M, Leonard RT, Menge JA (1978) Root exudation in relation to supply of phosphorus and its possible relevance to mycorrhizal formation. New Phytol 81:543–522

Reeves FB, Wagner D, Moorman T, Kiel J (1979) The role of endomycorrhizae in revegetation practices in the semi-arid west. I. A comparison of incidence of mycorrhizae in severely disturbed versus natural environments. Am J Bot 66:6–13

Rice EL (1984) Allelopathy. Academic Press, New York

Rovira AD (1969) Plant root exudates. Bot Rev 35:35–59

Saif SR (1987) Growth responses of tropical forage plant species to vesicular-arbuscular mycorrhizae. I. Growth, mineral uptake and mycorrhizal dependency. Plant Soil 97:25–35

Sancho F, Mata R (1987) Estudio detallado de suelos Estación Biológica La Selva. Organización para Estudios Tropicales, San José, Costa Rica

Sieverding (1989) Ecology of VAM fungi in tropical agrosystems. Agric Ecosyst Environ 29:369–390

Snellgrove RC, Splittstoesser WE, Stribley DP, Tinker PB (1982) The distribution of carbon and the demand of the fungal symbiont in leek plants with vesicular-arbuscular mycorrhizas. New Phytol 92:75–87

Sokal RR, Rohlf FJ (1981) Biometry. Freeman, New York

Sylvia DM (1990) Inoculation of native woody plants with vesicular-arbuscular mycorrhizal fungi for phosphate mine land reclamation. Agric Ecosysts Environ 31:253–261

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The economic value of managing the açaí palm (*Euterpe oleracea* Mart.) in the floodplains of the Amazon estuary, Pará, Brazil

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The economic value of managing the açaí palm (*Euterpe oleracea* Mart.) in the floodplains of the Amazon estuary, Pará, Brazil

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Abstract

Extraction of non-timber forest products (NTFPs) can provide important income for the inhabitants of tropical developing countries. The present research focuses on NTFP extraction in the Amazon estuary by evaluating the economics of managing açaí (*Euterpe oleracea*), a predominant palm species of the Amazon floodplains. The productivity, revenues and costs associated with traditional household management of açaí were examined in secondary forests and in homegardens. The present value of the net revenue (NPV) of lands managed for fruit and palm-heart was calculated at different distances from the central market of Belém, Pará, Brazil. Intensity of açaí management was dependent on distance from the market and household resources, ranging from simple collection in natural forest to intense cultivation. All calculations of revenues accounted for variation in prices due to seasonality of production. Açaí was found to be a highly valuable production system even at high rates of interest. At a 15% interest rate, the net present values were US$ 1337–2693 ha^{-1} in managed secondary forests and US$ 4266–6930 ha^{-1} in homegardens.

Keywords: Euterpe oleracea; Amazon; Palms; Non-timber forest products

1. Introduction

In an effort to find appropriate land use options for tropical regions, economic analyses of development alternatives have focused on tree plantations, agricultural activities and cattle ranching. More recently, researchers have also begun to examine the economics of harvesting non-timber forest products (NTFPs) such as medicinal plants, vines and fruits (Peters et al., 1989; Hecht, 1992; Balick and Mendelsohn, 1992; Grimes et al., 1994; Neil Adger et al., 1995). These studies have found that extraction of NTFPs provides substantial income to local economies and can provide incentives for the conservation of natural forests. The present research contributes to these studies by examining the economic sustainability of managing açaí (*Euterpe oleracea* Mart., Palmae), a predominant species in the palm

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forests of the Amazon estuary floodplains. Specifically, it examines the productivity, costs and revenues associated with managing açaí for fruit and palm heart in secondary forests and homegardens. In order to determine the value of these production systems and compare them with similar studies in non-flooded areas, the Net Present Value (NPV) of managing açaí was calculated at different distances from the main market in Belém, Brazil. The results of this paper provide a framework for understanding the economic and ecological dynamics of managing açaí and explain its current prevalence in the estuary.

A common misconception is that NTFP collection does not involve any manipulation of the natural forest. Yet forest management under NTFP collection ranges from minimum disturbance to enrichment planting in secondary forests. Furthermore, while some NTFP species are ecologically dependent on a diverse forest environment, others may eventually be cultivated in monospecific plantations where they are no longer considered NTFPs. For example, *Euterpe edulis*, harvested for its palm-heart, requires the shade of the forest and does not withstand intensive management (Anderson, 1988; Brucher, 1989), while *Bactris gasipaes*, which also produces quality palm-heart, is extensively grown in plantations throughout the Latin American tropics (Leon, 1987). A different case was found in the Amazon estuary, where the management of açaí for fruit and palm-heart ranges from forest collection in more remote communities to intense cultivation near the market.

In the present study, calculations of revenue from açaí accounted for seasonal production because prices fluctuate rapidly from the peak to the lowest point of harvest. Because prices are lowest at production peaks, studies which examine annual average prices and production may overestimate revenues. This potential bias is corrected by adjusting prices as a function of supply over time. The final analysis includes circumstances that may increase or decrease profitability of açaí production.

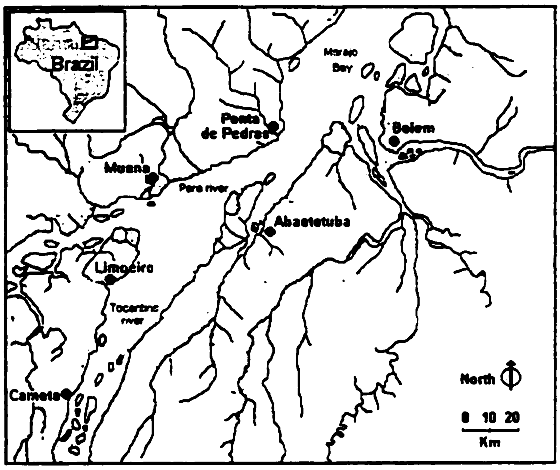

Fig. 1. Southeast portion of the Amazon estuary, Pará, Brazil.

2. Methods

2.1. Site description and management of açaí

Field work was conducted in the Amazon estuary, in the floodplain region comprised of the two margins of the Pará River and the mouth of the Tocantins River (Fig. 1). Average rainfall is approximately 2700 mm year^{-1}, with highs from January to May (more than 200 mm month^{-1}) and lows in September to November (less than 100 mm month^{-1}) (Anderson and Ioris, 1992). Because of their proximity to the Atlantic Ocean, the water masses that constitute this region are heavily tidal, and islands and lands along rivers and channels are flooded twice a day.

Daily floods in the estuary greatly restrict agricultural possibilities. The highly acidic alluvial soils (pH 4–6) common to this area have a low cation exchange capacity and are often waterlogged, creating unsuitable conditions for most conventional crops of the region, such as manioc (*Manihot esculenta* Crantz). Agricultural crops are limited to a few choices, such as rice (*Oryza* spp.) and sugarcane (*Saccharum* spp.).

Açaí is one of the most naturally abundant species in the Amazon estuary floodplains (Cavalcante, 1991; Khan and Granville, 1992), where in 1972 the coverage of açaí-dominated forests was estimated conservatively at 10 000 km^2 (Anderson, 1988). The management of açaí is evident throughout the estuary. Homes along the channels and rivers are surrounded by dense stands of açaí, called *terreiros* or homegardens. While fruit trees such as mango, lemon and cacao are interspersed, açaí dominates the homegardens. Although some açaí are planted, forest management favoring the palm is mostly responsible for the nearly monospecific stands. Beyond the homegardens, part of the secondary forest surrounding the household is also intensively managed for açaí. These managed forests, called 'matos', are larger than the homegardens but have lower açaí density. Producers may also extract açaí from lands beyond the managed forests, where the forest vegetation has not been altered to favor the palm.

The fruit of açaí is a primary staple food for the region's riverine inhabitants (Brabo, 1979; Anderson, 1988)[1]. Açaí is also the main source of palm-heart in Brazil, and its domestic and export value was estimated at US$ 300 million annually (Pollack et al., 1995). Açaí is still exploited for palm-heart in certain areas of the estuary (Anderson, 1988; Pollack et al., 1995; De Albuquerque dos Santos, 1995); however, the traditional household management examined in this article favors more sustainable fruit production, with palm-heart sold as a by-product.

2.2. Data collection and analysis

Data were collected during two periods, September–December, 1993 and August 1994–February 1995. All information was gathered through interviews and field measurements in three different communities along the estuary and in the city of Belém. Data on the prices received by producers and costs associated with producing and marketing açaí were used to calculate the net present value of hypothetical 1-ha plots, of homegardens and managed secondary forests at different distances from Belém.

The codes D1–D3 were assigned to locations that supply açaí to the market according to their distance from Belém. D1 was 0–60 km, D2 was 60–85 km, and D3 was 85–115 km from Belém (Fig. 1). The average distance from Belém was 26 km for D1, 79 km for D2, and 101 km for D3.

All prices and costs in Brazilian currency were translated into US dollars. During the study, there was a change in the Brazilian currency from Cruzeiro Real to Real on 1 July 1994. This increased the stability of the Brazilian currency and its dollar values, which averaged US$ 1.00 = Brazilian Real 0.87 between July 1994 and February 1995.

2.3. Production

Assessments of production as described by Grimes et al. (1994) were conducted in açaí stands located at three sites, each representing a different distance range: Ponta de Pedras (D1), Abaetetuba (D2), and Muaná (D3) (Fig. 1).

Four to eight representative farms were selected at each location. In each farm, one 10 m × 30 m plot was randomly selected in both the managed forest and the homegarden. Landowners were asked to estimate how many 18 kg baskets each açaí clump would produce within a plot, based on the number of racemes and immature fruits present. Most açaí producers felt comfortable with this task as they were experienced in harvesting and placing the açaí into baskets.

Estimated production from the plots was extrapolated to production per hectare per year. Test for means ($P < 0.05$) were used to compare production of managed forests between sites and production of homegardens between sites. Production of managed forests and homegardens were also compared within sites. For this last comparison, production from D2 and D3 were pooled to obtain a larger sample size.

Results of an independent 2 year survey were used to estimate the relative monthly availability of açaí (M. Hiraoka, personal communication, 1995). One limitation to this particular calculation is that the results are based on only one farm. Starting in August 1992, the survey recorded the number of baskets sold from a representative farm in the Abaetetuba area (D2). The numbers of baskets extracted from the 4.36 ha farm were recorded on a monthly basis during a 2 year period (Fig. 2). Monthly production was averaged for the two years and percentage of production was also calculated.

2.4. Cost of management and transportation

Data on costs and management activities for açaí were obtained by surveying 11 small- and medium-scale producers near the town of Abaetetuba (D2). Surveys in D2 were corroborated with informal interviews in D1, D3 and the Belém market. During these interviews, producers were asked to identify all costs incurred by the management of açaí. Accurate estimates of annual time spent in weeding and other

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[1] The juice of the açaí fruit is consumed as a cold soup with manioc flour, tapioca and fish or shrimp.

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References

Anderson, A.B., 1988. Use and management of native forests dominated by açaí palm (*Euterpe oleracea* Mart.) in the Amazon estuary. Adv. Econ. Bot., 6: 144–154.

Anderson, A.B. and Ioris, E.M., 1992. The logic of extraction: resource management and income generation by extractive producers in the Amazon. In: K. Redford and C. Padoch (Editors), Conservation of Neotropical Forests: Working from Traditional Resource Use. Columbia University Press, New York, pp. 175–199.

Balick, M. and Mendelsohn, R., 1992. The economic value of traditional medicines from tropical rain forests. Conserv. Biol., 8: 128–130.

Brabo, M.J.C., 1979. Palmiteiros de Muaná-Estrudo Sobre o Processo de Produção no Beneficiamento do Açaizeiro. Bol. Mus. Paraense Emílio Goeldi: Ser. Antropol., 73: 1–29.

Brucher, H., 1989. Useful Plants of Neotropical Origin and Their Wild Relatives. Springer, Berlin.

Cavalcante, P.B., 1991. Frutas Comestíveis da Amazônia, 5th edn. Coleão Adolpho Ducke, MCT/CNPq/Museu Paraense Emílio Goeldi, Belém, Brazil.

De Albuquerque dos Santos, A., 1995. Caxiuana: State and Local Relations in Policy Development and Implementation in the Brazilian Amazon. Ph.D. Dissertation, Yale University, New University Microfilms International, Ann Arbor, MI, 169 pp.

Foster, A., 1995. Economic reform starts to bite Brazil. Financial Times, October 11, 1995.

Grimes, A., Loomis, S., Jahnige, P., Burnham, M., Onthank, K., Alarcón, R., Palacios Cuenca, W., Cerón Martinez, C., Neill, D., Balick, M., Bennet, B. and Mendelsohn, R., 1994. Valuing the rain forest: The economic value of nontimber forest products in Ecuador. Ambio, 23: 405–410.

Hecht, S.B., 1992. Valuing land uses in Amazonia: colonist agriculture, cattle and petty extraction in comparative perspective. In: K. Redford and C. Padoch (Editors), Conservation of Neotropical Forests: Working from Traditional Resource Use. Columbia University Press, New York.

Hiraoka, M., 1995. Land use changes in the Amazon estuary. Global Environ. Change, 5 (4): 323–336.

Khan, F. and Granville, J.J., 1992. Palms in Forest Ecosystems of Amazonia. Springer, Berlin.

Leon, J., 1987. Botánica de los cultivos tropicales. Instituto Interamericano de Cooperación para la Agricultura, San José, Costa Rica.

Neil Adger, W., Brown, K., Cervigni, R. and Moran, D., 1995. Total economic value of forests in Mexico. Ambio, 24: 286–293.

Peters, C., 1992. The ecology and economics of oligarchic forests. Adv. Econ. Bot., 9: 15–22.

Peters, C., Gentry, A. and Mendelsohn, R., 1989. Valuation of an Amazonia rainforest. Nature, 339: 655–656.

Pollack, H., Mattos, M. and Uhl, C., 1995. A Profile of Palm-Heart Extraction in the Amazon Estuary. IMAZON, Belém, Brazil.

where Q is the amount of produce that reaches the market. In this case, Q was the averaged monthly yield recorded during a 2 year period (Fig. 2). P represents the price observed in the market for the second week of each month for either producers (D1) or middlemen (averaged prices for D2 and D3), and the parameters a_0 and a_1 are estimated demand function coefficients. Separate demand functions were estimated for producers who sell açaí in Belém (D1) and for producers who sell to middlemen (D2–D3 pooled). Demand functions for D2 and D3 were pooled because there was not enough variation in prices. These functions were then used to predict açaí prices in each month for D1 and D2–D3. Revenues from açaí fruit were then calculated by multiplying predicted monthly prices by the percent of production expected for each month at each site, according to the intensity of management. Annual revenues were calculated for managed forests in D1, D2, and D3 and in homegardens in D1 and D2–D3 (pooled).

2.6. *Net present value calculations*

Assuming that the producers must prepare an açaí stand from a young fallow, the formula used for calculating the net present value was

$$\mathrm{NPV} = \frac{\sum_{0}^{5} \frac{C_i}{(1+r)^t} + \sum_{5}^{15} \frac{\mathrm{NAR}}{(1+r)^t}}{1 - \frac{1}{(1+r)^{15}}}$$

where C_i is an establishment cost (for the first 5 years in secondary forest, and first 3 years in homegardens); NAR is the net annual revenue of an ongoing açaí system; r is the discount rate; and t is time.

To illustrate the economic potential of producing açaí, a hypothetical example is presented in which all productive stems are harvested for palm-heart at year 15. This is based on the assumption that old açaí stems (15 years and older) decrease in fruit production, although younger sprouts would continue to be productive. The expression in the denominator implicitly assumes that this 15 year cycle repeats itself indefinitely. Because inflation-adjusted prices were used to estimate revenues, calculations of present value used an inflation-adjusted interest rate of 5%, which has been used in other recent financial evaluations of NTFPs (Peters et al., 1989; Hecht, 1992; Balick and Mendelsohn, 1992; Grimes et al., 1994). However, in practice, small-scale farmers may not have access to capital, and so may face a much higher personal interest rate. Economic evaluations of smallholders' activities in Latin America have revealed interest rates as high as 30% (Foster, 1995). To demonstrate the impact high interest rates would have on local farmers' decisions and land values, NPVs are also calculated using 15 and 30% interest rates.

3. Results

3.1. *Production*

Rapid appraisals of production on 10 m × 30 m plots near Abaetetuba (D2) estimated a total of 511 baskets in a managed forest ha^{-1} $year^{-1}$. However, long-term studies indicate production levels are about

Table 1
Average açaí productivity in managed secondary forests, by site

Site	No. of observations	Avg. no. of baskets [a]	
		Per plot [b]	ha^{-1} $year^{-1}$
D1 (Ponta de Pedras)	4	10.84 (2.34)a	680
D2 (Abaetetuba)	8	7.67 (2.04)b	480
D3 (Muana)	4	6.58 (2.06)b	413

[a] Baskets of açaí weigh about 18 kg.

[b] Plot size 10 m × 30 m.

Numbers in parentheses are standard errors. Values followed by the same letters are not significantly different ($P < 0.05$).

ranged from US$ 11265 near Belém (D1) to US$ 5702 on lands that were 100 km away (D3). The value of homegardens cultivated for açaí ranged from US$ 24155 near Belém to US$ 14936 on lands 100 km away. However, more relevant figures to Brazil are obtained using a 30% interest rate since the new currency plan of the Brazilian government has set real interest rates above 30% a year (Foster, 1995). At a 30% interest rate, the value of a managed forest was US$ 879 near Belém and US$ 386 on lands 100 km away. At this same rate of interest the value of homegardens was US$ 2781 near Belém and US$ 1690 on lands 100 km away. NPVs for interest rates of 5, 15 and 30% are presented in Table 5.

4. Discussion

Our rapid estimate of production in D2 was compared with a previous long-term study in the same area (Hiraoka, 1995). In the long-term study, açaí yields were measured in thirteen 30 m × 30 m plots and then extrapolated to 1 ha totaling 480 baskets ha^{-1} $year^{-1}$ in managed forests. Our rapid appraisals of productivity in D2, which account for immature fruit on the tree, overestimate measured yields by only 6%. The higher production measured in D1 probably reflects higher stand density resulting from financial incentives of the proximity to Belém. The higher productivity in homegardens was associated with typical household management as well as higher density. For example, the soils were fertilized by farm animal waste and food remains. Also, viable açaí seeds were discarded near households after they were processed for consumption.

The açaí production data (Fig. 2) revealed strong seasonal patterns and when seasonal supply rises (or falls), prices fall (or rise). Because of this negative correlation, it is important to take seasonal variation into account when estimating revenue. For example, the gross annual revenue for 1 ha of managed forest in D1 is US$ 2303, if it is estimated by adjusting prices to monthly production. However, for the same system, if the average annual price is multiplied by the average annual production, total revenues are US$ 3420. The use of annual average prices and quantities in the calculation results in an overestimate of annual revenues by US$ 1117 or 50%.

When comparing the land values found in this study with other NTFP sites, floodplain lands managed for açaí were found to be more economically valuable. Grimes et al. (1994) estimated that NTFP extraction in a terra firme forest in Ecuador was worth US$ 2939 ha^{-1} $year^{-1}$. Peters et al. (1989) found that NTFPs in a secondary forest of the Peruvian Amazon were worth US$ 6330 ha^{-1} $year^{-1}$. Balick and Mendelsohn (1992) found that medicines collected from secondary forests in Belize were worth US$ 726–3325 ha^{-1} $year^{-1}$. Comparatively, at a 5% discount rate (the rate used in the above mentioned studies) the production of açaí in secondary forest ranged from US$ 5702 ha^{-1} $year^{-1}$ for sites far from Belém to US$ 11265 ha^{-1} $year^{-1}$ for sites nearest Belém.

The comparatively high values for açaí found in this study may have several explanations: First, the unique ecological conditions found in the floodplains of the Amazon estuary favor the establishment and production of açaí (Peters, 1992); the daily floods which provide soil nutrients and moisture allows for fruit production even in young fallows. Additionally, the use of organic fertilizers (a byproduct of household activities) and continuous weeding are common in homegardens leading to high production levels; and the management for açaí can be intense, as it requires the removal of other trees in order to favor the palms. Furthermore, many açaí production systems have shifted from forest extraction to intense management and cultivation, triggered by a large urban market that has developed over the last 25 years (Hiraoka, 1995). Açaí, therefore, seems to have higher economic value than other NTFPs which serve smaller rural markets.

The profitability and management intensity of açaí was clearly tied to proximity to the main market. Net present values were almost twice as high near Belém compared with 100 km away. Even in distant localities, the value of an açaí plantation appeared to be significantly higher than bare land prices in this region. Land was selling for US$ 100–400 ha^{-1} in D2. One explanation for this is that not all biotopes within floodplain lands are suited for the cultivation of açaí. While açaí is well adapted to the daily floods of the estuary, it does not grow well their own baskets. Owing to the high variability in the number of baskets used by farmers, 40 baskets ha^{-1} were assumed to be purchased, twice as many as the average estimated from our interviews. This would result in higher costs, yielding a more conservative profit estimation. The total cost of 40 collection baskets was US$ 19.20 $year^{-1}$ (Table 3).

Açaí fruit harvesting involves climbing the trunks and cutting the mature raceme. Although there are professional harvesters, in most cases the producers' children or local youths were hired for harvesting. The harvesters were paid by the number of baskets filled. In 1993 the harvesting cost was about US$ 0.18 per basket, and in 1994 it increased dramatically to US$ 1.16. The cost of harvesting the fruit at each site is included in Table 3.

Although açaí is brought to Belém from surrounding communities up to 24 h away by boat, most producers who sold their açaí directly in the Belém market came from localities within the D1 zone. Although some transported their produce in their own boats, most used one of the many private passenger–cargo boats that connect Belém with the surrounding region. Because of variation in fuel consumption and distances between different localities and the Belém market, the cost of transporting açaí in private boats varied widely. The market survey revealed that passenger–cargo boats charged very consistent fees, which, during our interview, averaged US$ 0.57 per basket throughout the D1 zone. Therefore, this figure has been adopted as the transportation cost incurred by producers from the D1 zone. Producers living beyond the D1 zone tended to sell their açaí to middlemen, who pay for the fruit as they pick up the baskets from producers' doorsteps. Therefore, producers in zones D2 and D3 did not incur direct transportation costs.

3.3. Revenues

The observed average weekly prices obtained by producers (D1) and middlemen (D2–D3) are pre-

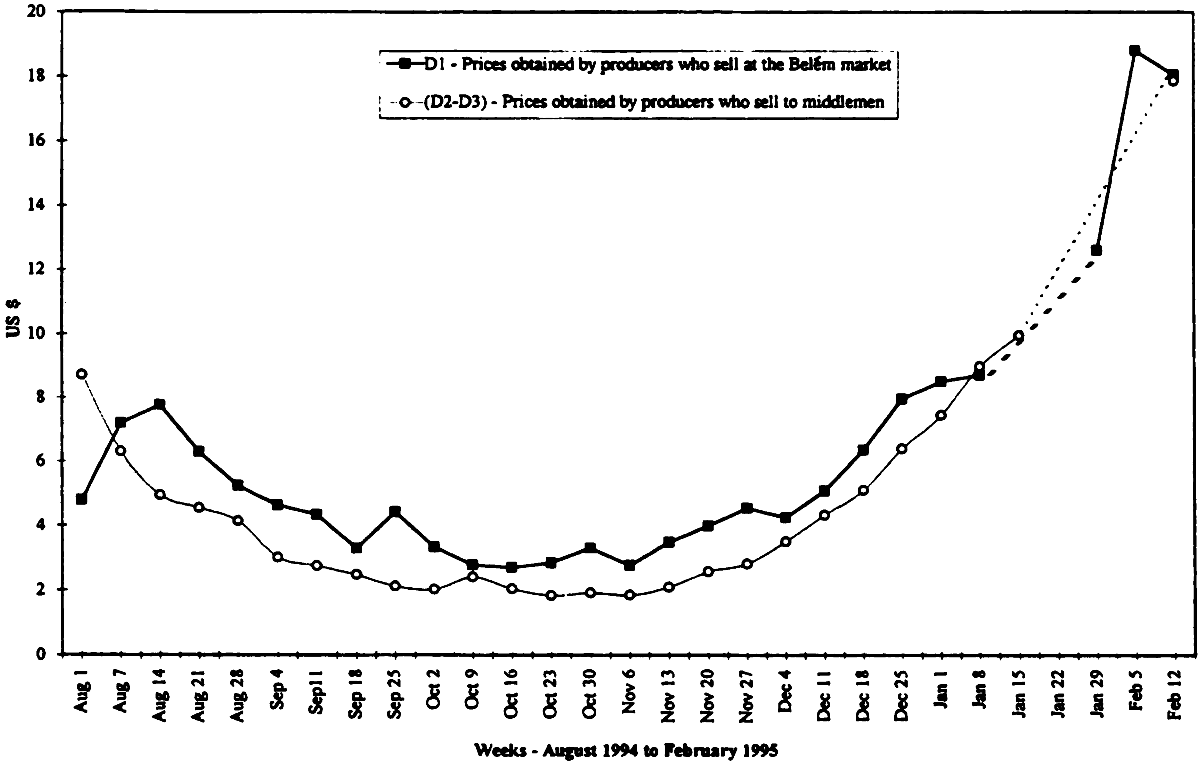

Fig. 3. Recorded average weekly prices of açaí at the Ver-o-Peso market in Belém, Pará, Brazil.

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The potentials of 20 indigenous tree species for soil rehabilitation in the Atlantic forest region of Bahia, Brazil

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Summary

1. The goal of this research was to identify indigenous tree species with a positive influence on soil fertility, in order to design mixed-tree and tree/crop systems for the Atlantic forest region of Bahia, Brazil. The study focused on 20 native tree species growing in 14–15-year-old stands in an arboretum at Pau Brasil Ecological Station. Although the small size of the areas sampled and the lack of adequate replication limits the interpretation of the results, the pure tree stands offered a unique opportunity to evaluate the nutrient cycling characteristics of several species which could be useful for their future utilization in land rehabilitation systems.

2. Soils for chemical analysis and bulk density were sampled under a 25-year-old secondary forest, a mixed-species plantation, the native forest and under the 20 species in question. Forest-floor litter and live leaf samples were analysed for N, P, K, Ca, Mg and Al.

3. Soil fertility was higher in secondary than in primary forest. The mixed plantation had similar soil pH, C, N and Mg, slightly higher P, and lower K and Ca than the primary forest. Litter accumulation on the floor was larger in secondary than in primary forest. Litter nutrients were also higher in secondary than in primary forest.

4. Positive effects on soils were noted under 15 out of the 20 species studied, among those *Inga affinis*, *Parapiptadenia pterosperma* (N-fixing species); *Arapatiella psilophylla*, *Caesalpinia echinata*, (leguminous, non-N-fixing); *Eschweilera ovata*, *Lecythis pisonis*, *Licania hypoleuca* (of other families).

5. Among the 20 species in the arboretum, the highest dry weights of forest-floor litter were found under *Arapatiella psilophylla*, *Bombax macrophyllum*, *Inga affinis*, *Licania hypoleuca* and *Pithecellobium pedicellare*; positive effects on soils were found under all these species, with *P. pedicellare* having the least influence. This suggests that forest-floor nutrients were incorporated in the soil via decomposition under these species.

6. Species that contribute to increased C and N, such as *Caesalpinia echinata*, *Inga affinis*, *Parapiptadenia pterosperma* and *Plathymenia foliolosa*, could be combined with those that increase soil pH, basic cations or both, such as *Copaifera luscens*, *Eschweilera ovata*, *Lecythis pisonis* and *Licania hypoleuca*. The inclusion of *Arapatiella psilophylla*, *Bombax macrophyllum*, *Buchenavia grandis*, *Caesalpinia echinata*, *Cassia* spp., *Hymenaea aurea* and *Inga affinis* could contribute to increased levels of extractable P in the surface soils. In addition to their potential effects on soil fertility, species choices must be guided by seed and seedling availability, as well as by farmers' preferences, local uses for the species and economic aspects (cost of establishment and market potential).

Key-words: nutrient cycling, plantations, primary rain forest, secondary forest.

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Introduction

Four-hundred years ago, the forest of the Atlantic coast of Brazil covered about 100 million ha. Today, it has been reduced to <12% of its original size (McNeely *et al.* 1990). The Atlantic rain forest is one of the world's most biologically diverse ecosystems and it is also one of the most endangered (Brooke 1993). In the south of Bahia, the site of the present study, the original extent of the forest was 140 000 ha and is today reduced by about 95%. The Atlantic coastal zone of Brazil became isolated from the Amazon basin during the Pleistocene epoch and, presently, its flora contains species common to the Amazon, as well as many endemics (Mori & Silva 1980; Jacobs 1988). In spite of current conservation and development efforts, in southern Bahia the primary forest is still cleared mainly for agriculture (Silva 1981; Quintela 1990; Brooke 1993; Montagnini, Fanzeres & da Vinha 1994); following timber extraction, the area is slashed, burned and planted with subsistence crops or grazed by cattle. Within a few years, signs of erosion, and low crop and cattle yields are apparent, leading to abandonment. To decrease pressure on the remaining natural forest it is necessary to increase the productivity of the degraded areas, thus making food, wood and fodder available to the people who are exerting pressure on the primary forest.

Tree plantations are a feasible land use option for the recovery of degraded forest regions, especially in areas with poor natural forest regeneration (Evans 1987; Gladstone & Ledig 1990; Montagnini 1990, 1992; Parrotta 1992). The presence of certain tree species in a production system can result in better soil structure and increases in soil nutrient availability (Sánchez *et al.* 1985; Nair 1989; Young 1989; Montagnini & Sancho 1990). In southern Bahia, previous research has shown the potential of certain tree species for their incorporation in productive land use systems (Silva 1983, 1988). The present study focuses on the species-site relationships of 20 native tree species growing in pure stands on the same soils at the Pau Brasil Ecological Station in Porto Seguro, Bahia (16°23′S, 39°11′W). The goal was to identify those species with a positive influence on soil fertility, that could be used in mixed-tree and agroforestry land use systems. Each soil variable was compared among the plantation species, and secondary and primary forest. Additionally, a mixed-tree plantation was evaluated to obtain a heterogeneous pattern contrasting with the pure species plots. Although the small size of the areas sampled, and the lack of adequate replication limits the interpretation and possible extrapolation of results to other sites, the pure tree stands offered a unique opportunity to evaluate nutrient cycling characteristics of several species which could be useful for their future utilization in land rehabilitation systems.

Site description

The Pau Brasil* Ecological Station, administered by CEPLAC†, extends to 1145 ha, with an arboretum including nearly 200 indigenous species, experimental plantings, and a reserve with areas in primary and secondary forest. The climate is classified as Af in the Köppen system (da Vinha & Lobão 1989). The mean annual rainfall is 1696 mm, there is no defined dry period and the daily temperature averages 23 °C (with a 30 °C maximum and a 20 °C minimum). The topography is flat and the soils are Oxisols (Haplorthox in the US Soil Taxonomy) originating from Tertiary sediments. These soils are deep (>1 m), acid (pH 4·5–5·0) and infertile, with relatively low organic matter and low base content (Cadima Zeballos, da Silva & Lobão 1982; da Vinha & Lobão 1989; Leão & Melo 1990). In the Brazilian soil classification these well drained Oxisols are called Latosols, and they are equivalent to the Ferralsols of the FAO-UNESCO soil map legends (van Wambeke 1992).

Our study focused on 20 native tree species chosen for their good growth and economic potential (da Vinha & Pereira 1983; da Vinha, de Carvalho & Silva 1985; da Vinha & Lobão 1989; Table 1). All the species could be found in the natural forest reserve of the Station. The plantation stands were part of the arboretum and were planted in 1974–75; thus, all the trees were 14–15 years old at the time this research was conducted (June 1990). The 20 species were in pure stands of 36 individuals spaced 2 × 2 m, all on the same soils. Seedlings were produced at the station's nursery from seed collected at the reserve.

There were no unplanted areas that could serve as a control; therefore, for comparison, soils were also sampled in a 25-year-old secondary forest, in a primary forest and in a mixed-species plantation, all located at the station and on the same soils. The secondary forest (about 0.5 ha) was adjacent to the arboretum. Among the most frequent species in the secondary forest were some also present in the arboretum (e.g. *Eschweilera ovata*‡, *Pithecellobium pedicellare*, *Inga affinis*); other abundant species included *Byrsomina sericea*, *Stryphnodendron pulcherrimum* and *Miconia* spp. (da Vihna & Lobão 1989). The primary forest was part of the station's forest reserve, which has been classified as evergreen tropical rain forest, similar to the Amazon forest in its structure and physionomy (Mori & Silva 1980). Some of the most frequent species in the primary forest at the station included *Hydrogaster trinerve*, *Parkia pendula*, *Cariocar edulis*, *Ocotea* spp., *Sloanea* spp.; among those also found in the arboretum stands were *Arapatiella psilophylla*, *Eschweilera ovata*, *Lycania hypoleuca* and *Pithecellobium pedicellare* (da Vinha, Ramos & Hori 1976; da Vinha & Lobão 1989). The arboretum, secondary forest and mixed plantation were located in an area of the Station where the primary forest had been cut and burned, utilized for agriculture for 3–4 years and then abandoned when the station was purchased by CEPLAC in 1969 (Cadima Zeballos *et al.* 1982; da Vihna & Lobão 1989). The mixed-species plantation was the same age, with the same initial spacing and was composed of many of the same species used in the plantation monocultures (e.g. *Parapiptadenia pterosperma*, *Platymenia foliolosa*, *Caesalpinia echinata* and *Bombax macrophyllum*, among others), plus other native species and a few exotics which were also on trial at the station, such as *Pinus caribaea* var. *hondurensis* and

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* Brazil's national tree, *Caesalpinia echinata*.

† Comissao Executiva do Plano da Lavoura Cacaueira (Centre for Cacao Promotion and Research).

‡ Authorities for the names of the 20 tree species of this study are given in Table 1.

Table 1. Species studied in monoculture stands at the arboretum in the Pau Brasil Ecological Station, Porto Seguro, Bahia (da Vinha *et al.* 1976; Mori & Silva 1980; da Vinha & Lobão 1989)

Common name	Scientific name	Family	Sub-family	Successional status
Nitrogen-fixing leguminous species				
Sucupira	*Bowdichia virgilioides* (Vog.) Yakovl.	Leguminosae	Papilionoideae	Early to late successional
Putumuju castanho	*Centrolobium minus* Presl.	Leguminosae	Papilionoideae	Mature forest
Putumuju gigante	*Centrolobium robustum* Mart.ex Benth.	Leguminosae	Papilionoideae	Mature forest
Inga cipó	*Inga affinis* DC.	Leguminosae	Mimosoideae	Pioneer
Viola	*Parapiptadenia pterosperma* (Benth.) Brenan	Leguminosae	Mimosoideae	Early-mid succesional
Juerana branca	*Pithecellobium pedicellare* (DC) Benth.	Leguminosae	Mimosoideae	Early successional/mature forest
Vinhático	*Plathymenia foliolosa* Benth.	Leguminosae	Mimosoideae	Late successional/mature forest
Non-nitrogen-fixing leguminous species				
Arapati	*Arapatiella psilophylla* (Harms) Cowan	Leguminosae	Caesalpinioideae	Mature forest
Pau brasil	*Caesalpinia echinata* Lam.	Leguminosae	Caesalpinioideae	Mature forest
Faveira	*Cassia* spp.	Leguminosae	Caesalpinioideae	Pioneer
Pau oleo	*Copaifera lucens* Dwyer	Leguminosae	Caesalpinioideae	Mature forest
Angelim	*Dimorphandra jorgei* M.F.Silva	Leguminosae	Caesalpinioideae	Early successional
Jatobá	*Hymenaea aurea* Lee et Laug.	Leguminosae	Caesalpinioideae	Early-mid successional
Oleo cumumbá	*Macrolobium latifolium* Vogel	Leguminosae	Caesalpinioideae	Early-mid successional
Species of other families				
Imbiruçu	*Bombax macrophyllum* K. Schum	Bombacaceae		Early-mid successional
Pequi doce	*Buchenavia grandis* Ducke	Combretaceae		Mid-late successional
Biriba	*Eschweilera ovata* (Cambess.) Miers	Lecythidaceae		Early to late successional
Sapucaia	*Lecythis pisonis* Cambess.	Lecythidaceae		Mature forest
Oiti	*Licania hypoleuca* Prance	Chrysobalanaceae		Mature forest
Buranhém	*Pradosia lactescens* Radkl.	Sapotaceae		Mid-late successional

Eucalyptus spp. The mixed-species plantation was established using a randomized design, with no fixed proportion of each species.

Materials and methods

NODULATION, FOREST-FLOOR LITTER, LIVE LEAVES AND TREE SIZE

Superficial roots (0–15 cm depth) of all the leguminous species in this study (Table 1) were excavated and examined for the presence of root nodules. At least five trees of each species were examined.

The forest-floor litter was collected in the area demarcated by a 16-cm-diameter plastic frame (area 201 cm^2). Two samples were taken from under the same trees chosen for soil sampling and were bulked into a single sample (402 cm^2) per tree, resulting in five samples per species. Samples from secondary forest, primary forest and the mixed-plantation were collected in the same manner, using the same five locations in each as for soil sampling. The samples were dried to constant weight at 60 °C, and were sorted into branches, whole leaves and fragments. Each fraction was weighed and subsamples were processed for chemical analysis. Nutrient concentrations were multiplied by the weight of each fraction and summed to obtain the total nutrient accumulation in the forest-floor in each site.

Leaf samples were collected from the same trees; a pole pruner was used to cut two fully-grown branches from opposite sides of the tree. Leaves from all parts of the branches were pooled into one sample per tree, five samples per species. The leaves were dried at 60 °C and stored for chemical analyses. The total height and the diameter at breast height of each sampled tree were also measured.

SOIL SAMPLING

Soils for chemical analysis and bulk density were sampled under the 20 species in the arboretum stands, and in plots located in the 25-year-old secondary forest, the primary forest and the mixed-species plantation. In each of the 20 species stands in the arboretum, soil samples were taken beneath five randomly selected trees. At the other three sites, soil samples were collected at five randomly selected points scattered throughout each site. In all 23 sites (20 species stands, secondary and primary forest, mixed plantation) two samples were taken within 1 m of a tree stem and pooled to form a single composite sample and the procedure was repeated for a total of five locations within each site. Thus, $n = 5$ for each variable measured under each species in the arboretum, as well as in the other three sites.

For soil chemistry, samples were taken with a 2·5-cm-diameter Edelman auger, at 0–5, 5–15, 15–30 and 30–60-cm depths, giving a total of 23 sites × 5 locations × 4 depths = 460 samples for chemical analyses. Soils were air-dried and passed through a 2-mm sieve.

The bulk density was measured with a 5·5-cm-diameter Soil Core Sampler (Soil Moisture Equipment, Santa Barbara, California), which allowed superficial samples to be taken at 2–6 cm soil depth. Only this superficial layer was sampled, for a total of 23 sites × 5 locations = 115 sam-ples. Although they were not from exactly the same soil depth, the bulk density values were used to calculate total nutrient stocks (kg ha^{-1}) for the 0–5-cm soil layer of each site.

CHEMICAL ANALYSES

All tissue and soil samples were transported to the US for analysis. Chemical analyses were conducted in laboratories at Yale School of Forestry and Environmental Studies, CT, USA.

Forest-floor and live leaves chemistry

All tissue material (forest-floor litter parts and live leaves) was ground (1-mm sieve) and digested in a heater block using a H_2SO_4 digestion mixture (Anderson & Ingram 1989). The Ca, Mg, K and Al in the digests were estimated using an inductively coupled atom scan spectrometer (Thermo Jarrell Ash, Franklin, Massachussetts). P was estimated colorimetrically at 880 nm wavelength after reacting with $(NH_4)_2MoO_4$ and ascorbic acid (Anderson & Ingram 1989), using a spectrophotometer (Spectronic 501, Milton Roy, Rochester, New York). Total N was estimated colorimetrically using a spectrophotometer (Anderson & Ingram 1989).

Soil chemistry

The pH was measured in a 1:2·5 mixture of soil and deionized water using a combination electrode and a digital pH meter (Accumet 915, Fisher Scientific, Pittsburgh, Pennsylvania). The extractable P, K, Ca and Mg were estimated following extraction using a 1:5 proportion of soil and Mehlich's (double-acid) solution (0·025 N H_2SO_4 and 0·05N HCl)(Santana, Periera & Morais 1977: Anonymous 1980). To ensure clear samples for the colorimetric determination of P, 0·07 g of activated charcoal was added to each 4 g of soil (Briceño & Pacheco 1984). The charcoal was leached with Mehlich solution before using to avoid P contamination; charcoal was also added to the blanks (Mehlich solution alone). The soils were shaken for an hour and then filtered. K, Ca and Mg were estimated in the extracts using similar procedures to those used for tissue digests. Total soil carbon and total nitrogen were estimated by dry combustion using a carbon hydrogen nitrogen determinator (CNH-600, Leco Corp., St. Joseph, Michigan).

STATISTICAL ANALYSES

Since in the arboretum there was only one stand per species, and just one site was available for each secondary, primary forest and mixed plantation, the five replicate samples taken within each site provided a single mean per site for each variable measured. Because of the lack of proper site replication, conventional analysis of variance was not appropriate (Hurlbert 1984). Instead, the calculated means for each variable and site were used to compare the results from the 20 species, secondary forest, primary forest and mixed plantation. The standard errors of the means are also shown in the tables. The results were grouped for the leguminous N-fixing tree species, the leguminous non-N-fixing species, species of other families and control sites (Table 1).

Results

NODULATION AND TREE SIZE

The presence of root nodules was evident in all the mimosoid and papilionoid leguminous trees; these were apparently active N-fixing nodules, as suggested by their reddish coloration in laboratory observations. No nodules were found in any of the caesalpinoid tree roots examined; these species have not been reported to nodulate (Allen & Allen 1981).

Diameters at breast height ranged from a mean of 9·3 cm in *Centrolobium robustum* to 24·1 cm in *Inga affinis* (Table 2). Mean total tree height ranged from 7·3 m to 14·2 m; the tallest trees were in the *Bombax macrophyllum*, *Cassia* spp. and *Parapiptadenia pterosperma* stands (Table 2).

FOREST-FLOOR LITTER

Total litter accumulation (whole leaves, branches and fragments) was higher under secondary than under primary forest and mixed plantation (Fig. 1). Litter accumulation was more than twice as high on the floor under *Licania hypoleuca* than under secondary forest. Forest-floor litter was also higher than in secondary forest under *Arapatiella psilophylla*, *Bombax macrophyllum*, *Hymenaea aurea*, *Inga affinis*, *Macrolobium latifolium*, *Parapiptadenia pterosperma* and *Pithecellobium pedicellare* (Fig. 1). Among these eight species, a similar proportion of the three litter fractions sampled (whole leaves, fragments and branches) was found under *Arapatiella psilophylla* and *Licania hypoleuca*. In contrast, the litter fragments weighed 3–6 times more than the whole leaves fraction under *Bombax macrophyllum*, *Hymenaea aurea*, *Inga affinis* and *Macrolobium latifolium* (Fig. 1), possibly indicating a faster litter turnover. No fragments of litter were found in *Parapiptadenia pterosperma* and *Pithecellobium pedicellare*: these mimosoid species had very small leaflets (<5 mm long) which were apparently incorporated into the soil without breaking down into sizeable fractions.

Table 2. Diameter at breast height and total height of the trees in the arboretum and in the mixed-species stand. Means and standard errors, $n = 5$

Species	Diameter at breast height (cm)	Height (m)
N-fixing leguminous species		
Bowdichia virgilioides	11·4 (2·2)	9·4 (2·0)
Centrolobium minus	14·5 (1·8)	10·3 (1·1)
C. robustum	9·3 (1·1)	7·9 (1·4)
Inga affinis	24·1 (12·6)	9·5 (1·1)
Parapiptadenia pterosperma	16·6 (5·3)	12·4 (2·4)
Pithecellobium pedicellare	10·4 (1·4)	7·7 (0·3)
Plathymenia foliolosa	15·8 (0·9)	7·3 (1·6)
Non-N-fixing leguminous species		
Arapatiela psilophylla	11·1 (0·2)	7·5 (1·3)
Caesalpinia echinata	9·7 (3·5)	8·0 (1·7)
Cassia spp.	21·4 (3·1)	13·2 (1·2)
Copaifera lucens	10·6 (1·9)	7·7 (1·4)
Dimorphandra jorgei	14·0 (2·6)	8·8 (1·6)
Hymenaea aurea	10·8 (2·3)	8·5 (2·1)
Macrolobium latifolium	14·3 (1·2)	9·7 (1·0)
Other families		
Bombax macrophyllum	22·8 (2·5)	14·2 (1·2)
Buchenavia grandis	12·3 (1·8)	8·6 (1·5)
Eschweilera ovata	11·1 (1·8)	9·4 (0·5)
Lecythis pisonis	12·9 (2·6)	7·5 (1·2)
Licania hypoleuca	9·5 (1·5)	7·9 (0·7)
Pradosia lactescens	10·9 (1·6)	8·1 (1·2)
Mixed-species plantation	11·8 (2·5)	10·9 (2·6)

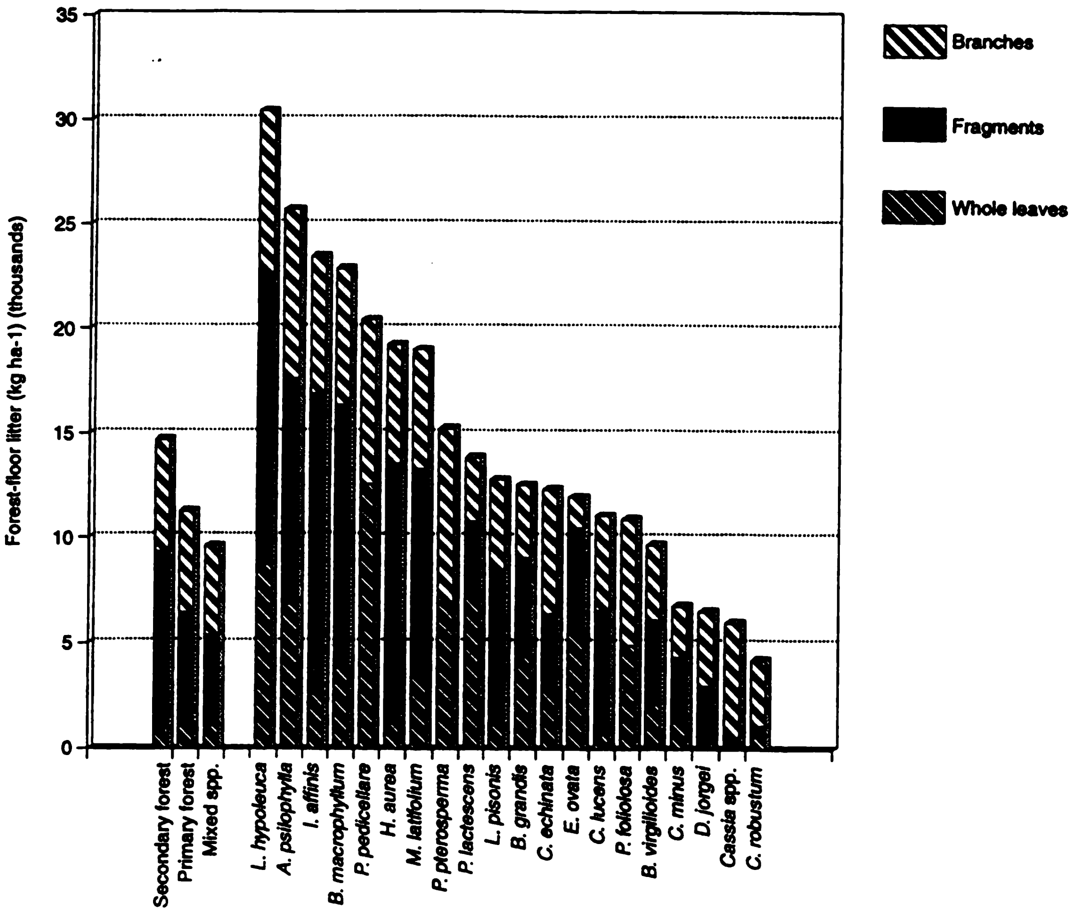

Fig. 1. Dry weight of total forest-floor litter (whole leaves, branches and fragments) under 20 tree species in the arboretum, secondary forest, primary forest and mixed-species plantation at the Pau Brasil Ecological station. See Table 1 for names of genera.

LIVE LEAVES AND FOREST-FLOOR LITTER CHEMISTRY

Live leaves

In live leaves, the highest N concentration was found in two N-fixing legumes: *Inga affinis* and *Parapiptadenia pterosperma* (Table 3). Except for *Pithecellobium pedicellare*, all N-fixing leguminous trees tended to have higher leaf N concentration than the non-N-fixing legumes or the species of other families. Among the non-N-fixing legumes, the highest leaf N concentrations were found in *Dimorphandra jorgei* and *Hymenaea aurea*. Among the other families of trees, the highest leaf N was in *Buchenavia grandis*. *Inga affinis* also had the highest leaf P concentration, along with *Centrolobium robustum*, another N-fixing legume: these species were followed by *Centrolobium minus* and *Buchenavia grandis*. *C. robustum* and *Bombax macrophyllum* showed the highest K in leaves, followed by *Arapatiella psilophylla*. The highest Ca was found in *Parapiptadenia pterosperma*, followed by *Buchenavia grandis* and *Caesalpinia echinata*. *Bombax macrophyllum* had the highest Mg, followed by *Parapiptadenia pterosperma* and *Centrolobium minus*. *Arapatiella psilophylla* showed the highest Al concentration in leaves (Table 3).

Forest-floor litter

The highest N in whole leaves from forest-floor litter was found in *Bowdichia virgilioides*, *Centrolobium minus* and *Ingá affinis* (all leguminous, N-fixing species) (Table 4). These values were slightly higher than those found under secondary and primary forests. The highest P in forest-floor litter was found under the leguminous, N-fixing species *Centrolobium minus*, *C. robustum* and *Inga affinis*. the two leguminous, non-N-fixing species *Copaifera luscens* and *Hymenaea aurea*, and two species *Buchenavia grandis* and *Lecythis pisonis* from other families. The highest K in whole leaves of forest-floor litter was found under *Centrolobium minus*, with values four times higher than those under primary forest. Ca was highest beneath *Bombax macrophyllum*, *Buchenavia grandis* and *Caesalpinia echinata*, all with values higher than those from primary and secondary forests; but *Inga affinis* showed values similar to those of the two forest sites. The values for Mg in whole leaves from forest-floor litter were higher under *Bombax macrophyllum*, *Eschweilera ovata* and *Macrolobium latifolium* than under the two forest types.

In fragments from forest-floor litter, N and Ca concentrations were slightly higher while P, K and Mg were comparable to those of entire leaves (F. Montagnini

Table 3. Nitrogen, phosphorus, potassium, calcium, magnesium and aluminium concentrations in live leaves of the 20 species from the arboretum (means and standard errors, *n* = 5)

Species	N (%)	P (%)	K (%)	Ca (%)	Mg (%)	Al (mg kg⁻¹)
Nitrogen-fixing leguminous species						
Bowdichia virgilioides	2·18 (0·05)	0·07 (0·004)	0·62 (0·09)	0·72 (0·11)	0·16 (0·02)	100 (0·0)
Centrolobium minus	2·05 (0·23)	0·10 (0·032)	0·90 (0·39)	1·08 (0·23)	0·30 (0·02)	100 (0·0)
C. robustum	2·16 (0·08)	0·14 (0·020)	1·46 (0·23)	0·50 (0·07)	0·24 (0·02)	40 (24·5)
Inga affinis	2·61 (0·08)	0·12 (0·018)	0·67 (0·13)	1·11 (0·18)	0·19 (0·02)	280 (20·0)
Parapiptadenia pterosperma	2·46 (0·11)	0·05 (0·004)	0·58 (0·05)	1·67 (0·23)	0·35 (0·07)	120 (20·0)
Pithecellobium pedicellare	1·76 (0·03)	0·05 (0·003)	0·32 (0·02)	0·48 (0·03)	0·18 (0·01)	180 (58·3)
Plathymenia foliolosa	2·17 (0·05)	0·07(0·004)	0·64 (0·04)	0·24 (0·03)	0·14 (0·01)	80 (20·0)
Non nitrogen-fixing leguminous species						
Arapatiella psilophylla	1·42 (0·03)	0·08 (0·015)	1·02 (0·18)	0·36 (0·12)	0·15 (0·03)	420 (58·3)
Caesalpinia echinata	1·88 (0·09)	0·08 (0·006)	0·67 (0·07)	1·38 (0·15)	0·16 (0·01)	260 (40·0)
Cassia spp.	1·80 (0·17)	0·07 (0·006)	0·33 (0·05)	0·90 (0·08)	0·25 (0·03)	200 (54·8)
Copaifera lucens	1·99 (0·13)	0·08 (0·005)	0·71 (0·04)	1·04 (0·14)	0·14 (0·01)	120 (20·0)
Dimorphandra jorgei	2·16 (0·18)	0·09 (0·021)	0·56 (0·13)	0·36 (0·09)	0·14 (0·03)	100 (0·0)
Hymenaea aurea	2·02 (0·07)	0·09 (0·003)	0·62 (0·02)	0·61 (0·08)	0·21 (0·01)	100 (0·0)
Macrolobium latifolium	1·50 (0·09)	0·08 (0·007)	0·52 (0·14)	0·69 (0·13)	0·31 (0·03)	80 (20·0)
Other families						
Bombax macrophyllum	1·52 (0·09)	0·06 (0·004)	1·31 (0·24)	1·02 (0·22)	0·54 (0·10)	120 (20·0)
Buchenavia grandis	2·02 (0·10)	0·09 (0·010)	0·79 (0·17)	1·56 (0·16)	0·25 (0·03)	100 (31·6)
Eschweilera ovata	1·42 (0·08)	0·06 (0·003)	0·40 (0·04)	1·01 (0·18)	0·28 (0·05)	200 (31·6)
Lecythis pisonis	1·73 (0·05)	0·08 (0·007)	0·59 (0·07)	1·03 (0·13)	0·26 (0·02)	140 (24·5)
Licania hypoleuca	1·42 (0·07)	0·06 (0·000)	0·95 (0·05)	0·98 (0·10)	0·31 (0·04)	100 (0·0)
Pradosia lactescens	1·19 (0·14)	0·08 (0·022)	0·67 (0·19)	0·66 (0·09)	0·15 (0·01)	300 (94·9)

Note: SE = 0 when there was insufficient material for chemical analysis and just one sample was processed.

Table 4. Percentages of nitrogen, phosphorus, potassium, calcium and magnesium in forest-floor litter leaves for the 20 species from the arboretum, primary and secondary forest, and mixed plantation (means and standard errors, *n* = 6)

Species/sites	N	P	K	Ca	Mg
Nitrogen-fixing leguminous species					
Bowdichia virgilioides	1·84 (0·02)	0·01 (0·0)	0·08 (0·008)	1·06 (0·03)	0·13 (0·005)
Centrolobium minus	1·89 (0·03)	0·04 (0·002)	0·41 (0·031)	1·20 (0·04)	0·21 (0·008)
C. robustum	1·51 (0·19)	0·04 (0·010)	0·08 (0·0)	1·31 (0·09)	0·19 (0·015)
Inga affinis	1·86 (0·04)	0·04 (0·003)	0·11 (0·006)	1·58 (0·04)	0·15 (0·003)
Parapiptadenia pterosperma	1·65 (0·06)	0·03 (0·002)	0·05 (0·003)	1·23 (0·08)	0·17 (0·006)
Pithecellobium pedicellare	1·54 (0·03)	0·02 (0·003)	0·04 (0·002)	0·45 (0·01)	0·10 (0·003)
Plathymenia foliolosa	1·81 (0·03)	0·03 (0·002)	0·04 (0·002)	0·41 (0·01)	0·02 (0·008)
Non nitrogen-fixing leguminous species					
Arapatiella psilophylla	1·18 (0·04)	0·02 (0·002)	0·08 (0·007)	0·85 (0·07)	0·10 (0·007)
Caesalpinia echinata	1·49 (0·02)	0·03 (0·002)	0·07 (0·003)	2·05 (0·11)	0·10 (0·003)
Cassia spp.	1·10 (0·0)	0·02 (0·0)	0·06 (0·0)	0·74 (0·0)	0·10 (0·0)
Copaifera lucens	1·37 (0·09)	0·04 (0·002)	0·20 (0·020)	1·16 (0·09)	0·17 (0·011)
Dimorphandra jorgei	1·69 (0·12)	0·01 (0·003)	0·05 (0·006)	0·68 (0·08)	0·16 (0·025)
Hymenaea aurea	1·35 (0·06)	0·04 (0·002)	0·12 (0·008)	0·87 (0·05)	0·17 (0·007)
Macrolobium latifolium	1·04 (0·03)	0·02 (0·003)	0·05 (0·005)	1·21 (0·07)	0·27 (0·011)
Other families					
Bombax macrophyllum	1·15 (0·04)	0·02 (0·004)	0·02 (0·003)	2·08 (0·03)	0·47 (0·010)
Buchenavia grandis	1·50 (0·07)	0·04 (0·003)	0·10 (0·016)	1·77 (0·04)	0·18 (0·006)
Eschweilera ovata	0·97 (0·03)	0·02 (0·002)	0·12 (0·011)	1·09 (0·09)	0·26 (0·010)
Lecythis pisonis	1·23 (0·08)	0·04 (0·003)	0·09 (0·008)	1·31 (0·08)	0·16 (0·003)
Licania hypoleuca	0·82 (0·02)	0·02 (0·003)	0·15 (0·009)	1·36 (0·04)	0·16 (0·004)
Pradosia lactescens	0·71 (0·02)	0·02 (0·0)	0·11 (0·009)	0·81 (0·02)	0·14 (0·006)
Control sites					
Primary forest	1·71 (0·11)	0·02 (0·003)	0·09 (0·006)	1·49 (0·21)	0·18 (0·011)
Secondary forest	1·78 (0·24)	0·03 (0·005)	0·13 (0·044)	1·53 (0·10)	0·23 (0·029)
Mixed-species plantation	1·15 (0·22)	0·02 (0·004)	0·06 (0·021)	0·82 (0·15)	0·17 (0·027)

Note: SE = 0 when there was insufficient material for chemical analysis and just one sample was processed.

et al. unpublished data). In branch litter, the N concentrations were generally lower than those of whole leaves, the Ca concentrations were generally higher, and the concentrations of Mg, K and P were more similar to whole leaves (F. Montagnini *et al.* unpublished data). For forest-floor litter fragments and branches, trends in differences among species were similar to those found for whole leaves.

SOIL CHEMICAL PROPERTIES

The soil pH, total C and N, and extractable Ca, Mg and P were all higher in secondary than in primary forest while the K was similar (Table 5). The mixed plantation gave lower values of soil pH, total C and cations than the primary forest, but similar total N and higher extractable P. The greatest differences among sites were found in the top 0–5 and 5–15 cm, although for some variables (e.g. Ca, Mg, the pH) the differences sometimes reached depths of 15–30 cm and even 30–45 cm depths (Table 5).

The pH in the 0–45 cm soil profile under *Caesalpinia echinata*, *Copaifera luscens*, *Eschweilera ovata*, *Lecythis pisonis* and *Licania hypoleuca* was between 5·0 and 5·3, comparable to secondary forest (Table 5). Soil total C under *Caesalpinia echinata*, *Inga affinis*, *Parapiptadenia pterosperma* and *Plathymenia foliolosa* was similar to secondary forest at all four depths sampled. Soil total C under *Bowdichia virgilioides*, *Copaifera luscens* and *Hymenaea aurea* was slightly lower than in secondary forest at 0–5 and 5–15-cm depths. Soil total N was highest under *Eschweilera ovata* at 0–5 cm depth and *Caesalpinia echinata* in the 5–45-cm layer. Soil total N was also relatively high under *Arapatiella psilophylla*, *Dimorphandra jorgei*, *Inga affinis*, *Lecythis pisonis*, *Parapiptadenia pterosperma*, *Plathymenia foliolosa* and *Pradosia lactescens*, with values ranging between 0·18 and 0·2% in the top soil (0–5 and 5–15 cm) (Table 5).

The highest soil-extractable P was found under *Inga affinis* at 0–5 and 5–15 cm, with values up to 3·6 mg kg^{-1} (Table 5). These sample values were followed by those of secondary forest, *Hymenaea aurea* and *Buchenavia grandis*, in that order. Extractable P was very low under the other species, with less than 1–2 mg kg^{-1} soil. Soil-exchangeable K was highest under *Eschweilera ovata*, *Parapiptadenia pterosperma*, primary forest, *Licania hypoleuca*, *Caesalpinia echinata*, *Inga affinis* and secondary forest (Table 5). The highest soil-exchangeable Ca was found in secondary forest, *Bowdichia virgilioides*, *Lecythis pisonis*, *Eschweilera ovata*, *Licania hypoleuca* and primary forest. The highest soil-exchangeable Mg was found under *Parapiptadenia pterosperma*, secondary forest and *Inga affinis* (Table 5).

Soil bulk density was lower under secondary than under primary forest (Table 6). Soils under *Macrolobium latifolium* had lower bulk density than under primary forest. Soil bulk density was similar to that in primary forest under *Hymenaea aurea*, another leguminous non-N-fixing species.

TOPSOIL AND FOREST FLOOR NUTRIENT STOCKS

The total N stocks (kg ha^{-1}) in the topsoil (0–5 cm depth) were higher than the total N stocks in forest-floor litter in all the tree species and forest sites (Fig. 2). The highest topsoil N stocks were in *Eschweilera ovata*, a non N-fixing species, where they were even higher than in secondary forest. Other species with high topsoil N stores were *Arapatiella psilophylla*, *Dimorphandra jorgei*, *Lecythis pisonis* and *Pradosia lactescens*, all non N-fixing species; and *Parapiptadenina pterosperma* and *Plathymenia foliolosa* among the leguminous, N-fixing trees. Several species had higher forest-floor N stocks than secondary forest: *Arapatiella psilophylla*, *Bombax macrophyllum*, *Buchenavia grandis*, *Hymenaea aurea*, *Inga affinis*, *Licania hypoleuca*, *Macrolobium latifolium* and *Pithecellobium pedicellare*.

In contrast to this, P stocks were higher in the forest-floor than in the topsoil at all sites except for *Dimorphandra jorgei*, *Cassia* spp. and *Centrolobium robustum*. In further contrast, only a few species had higher topsoil P stores than secondary forest: these were *Buchenavia grandis*, *Inga affinis* and *Hymenaea aurea* (Fig. 3). The highest forest-floor P stocks were under *Inga affinis*, a leguminous N-fixing species, however most of the species with highest forest-floor P reserves belonged to other families (Fig. 3).

Similarly, the K reserves in forest-floor litter were higher than in the topsoil under several species, with amounts higher than those in secondary forest in many instances (Table 6). In contrast to the other nutrients considered, topsoil K was higher in primary than in secondary forest. Several individual species had higher topsoil K than secondary forest, including *Cassia* spp., *Caesalpinia echinata*, *Eschweilera ovata*, *Inga affinis*, *Licania hypoleuca* and *Parapiptadenia pterosperma*, among others. As with K, the forest-floor Ca was higher than topsoil Ca for many species, most of them non-leguminous. Again, *Licania hypoleuca* showed the highest amounts with more than twice the forest-floor Ca stocks than secondary forest. Forest-floor Ca stocks were also substantial under *Arapatiella psilophylla*, *Bombax macrophyllum* and *Inga affinis*, among others (Table 6). In contrast to the other nutrients, none of the tree species of the arboretum had higher topsoil Ca stores than secondary forest. Finally, for Mg the forest-floor litter reserves were also larger than those in the topsoil under several species (Table 6). The Mg stocks in forest-floor litter were higher than in secondary forest under *Bombax macrophyllum*, *Licania hypoleuca*, *Macrolobium latifolium* and *Pradosia lactescens*. Topsoil Mg reserves were higher than in secondary forest under only two species, *Eschweilera ovata* and *Parapiptadenia pterosperma*.

Table 5. Soil chemical characteristics under the 20 monospecific stands in the arboretum, primary and secondary forest and mixed plantation (means and SEs, $n = 5$). Carbon and nitrogen concentrations are given as gravimetric fractions; data on phosphorus, potassium, calcium and magnesium as extractable fractions. SE = 0 when there was insufficient material for chemical analysis and only one sample was processed.

	Depth (cm)	pH	C (%)	N (%)	P (mg kg^{-1})	K (μmol kg^{-1})	Ca(μmol kg^{-1})	Mg (μmol kg^{-1})
N-fixing leguminous species								
Bowdichia virgilioides	0–5	5·0	1·98 (0·11)	0·16 (0·008)	1·32 (0·15)	0·06 (0·007)	1·35 (0·30)	0·39 (0·04)
	5–15	5·1	1·52 (0·05)	0·17 (0·003)	1·14 (0·15)	0·06 (0·006)	1·08 (0·25)	0·35 (0·05)
	15–30	5·0	1·14 (0·06)	0·12 (0·007)	0·43 (0·11)	0·03 (0·002)	1·04 (0·19)	0·36 (0·02)
	30–45	5·0	0·89 (0·03)	0·09 (0·008)	0·03 (0·01)	0·02 (0·003)	0·92 (0·11)	0·32 (0·02)
Centrolobium minus	0–5	4·7	1·87 (0·06)	0·16 (0·005)	1·19 (0·07)	0·05 (0·004)	0·53 (0·18)	0·21 (0·01)
	5–15	4·6	1·57 (0·08)	0·15 (0·005)	1·00 (0·07)	0·04 (0·002)	0·35 (0·04)	0·16 (0·02)
	15–30	4·5	0·94 (0·05)	0·10 (0·007)	0·07 (0·03)	0·02 (0·002)	0·32 (0·01)	0·17 (0·01)
	30–45	4·5	0·76 (0·03)	0·09 (0·007)	0·00 (0·0)	0·02 (0·003)	0·34 (0·02)	0·16 (0·01)
C. robustum	0–5	4·6	1·65 (0·06)	0·13 (0·006)	1·07 (0·15)	0·05 (0·002)	0·40 (0·04)	0·16 (0·01)
	5–15	4·5	1·39 (0·07)	0·13 (0·009)	0·92 (0·05)	0·04 (0·002)	0·31 (0·03)	0·14 (0·01)
	15–30	4·5	1·02(0·09)	0·09 (0·006)	0·35 (0·05)	0·03 (0·004)	0·22 (0·02)	0·09 (0·01)
	30–45	4·5	0·89 (0·05)	0·08 (0·004)	0·13 (0·07)	0·02 (0·0)	0·24 (0·02)	0·08 (0·01)
Inga affinis	0–5	4·9	2·10 (0·05)	0·18 (0·006)	3·64 (0·29)	0·07 (0·005)	0·76 (0·13)	0·49 (0·04)
	5–15	4·9	1·85 (0·13)	0·17 (0·012)	3·48 (0·26)	0·06 (0·004)	0·59 (0·15)	0·43 (0·05)
	15–30	4·9	1·46 (0·12)	0·14 (0·008)	1·41 (0·23)	0·05 (0·006)	0·54 (0·11)	0·33 (0·05)
	30–45	4·9	1·01 (0·07)	0·12 (0·008)	0·29 (0·02)	0·03 (0·006)	0·51 (0·09)	0·25 (0·04)
Parapiptadenia pterosperma	0–5	5·0	2·38 (0·12)	0·20 (0·016)	0·78 (0·16)	0·08 (0·016)	1·40 (0·12)	0·60 (0·03)
	5–15	4·9	1·76 (0·06)	0·18 (0·010)	0·63 (0·16)	0·06 (0·004)	1·01 (0·10)	0·49 (0·03)
	15–30	4·9	1·29 (0·09)	0·14 (0·006)	0·12 (0·07)	0·03 (0·006)	0·81 (0·11)	0·42 (0·02)
	30–45	4·9	1·09 (0·06)	0·11 (0·012)	0·00 (0·0)	0·02 (0·003)	0·79 (0·07)	0·39 (0·03)
Pithecelobium pedicellare	0–5	4·8	1·67 (0·07)	0·15 (0·005)	0·59 (0·26)	0·05 (0·005)	0·79 (0·09)	0·40 (0·03)
	5–15	4·9	1·48 (0·07)	0·13 (0·004)	1·41 (0·50)	0·04 (0·002)	0·73 (0·14)	0·28 (0·02)
	15–30	4·7	1·10 (0·06)	0·12 (0·007)	1·98 (0·23)	0·02 (0·002)	0·56 (0·13)	0·17 (0·02)
	30–45	4·7	0·79 (0·02)	0·11 (0·004)	0·93 (0·40)	0·02 (0·002)	0·44 (0·10)	0·12 (0·01)
Plathymenia foliolosa	0–5	4·7	2·08 (0·09)	0·18 (0·007)	0·13 (0·08)	0·05 (0·003)	1·05 (0·15)	0·42 (0·04)
	5–15	4·8	2·17 (0·11)	0·17 (0·007)	0·10 (0·08)	0·05 (0·004)	1·19 (0·24)	0·40 (0·04)
	15–30	4·8	1·35 (0·08)	0·12 (0·006)	0·01 (0·01)	0·03 (0·004)	0·95 (0·18)	0·32 (0·04)
	30–45	4·7	1·08 (0·14)	0·11 (0·008)	0·00 (0·0)	0·02 (0·004)	0·67 (0·11)	0·24 (0·04)

Table 5. *Continued*

	Depth (cm)	pH	C (%)	N (%)	P (mg kg^{-1})	K (µmol kg^{-1})	Ca(µmol kg^{-1})	Mg (µmol kg^{-1})
N-fixing leguminous species								
Arapatiella psilophylla	0–5	4·7	1·94 (0·12)	0·18 (0·007)	1·45 (0·11)	0·06 (0·007)	0·38 (0·11)	0·37 (0·03)
	5–15	4·7	1·76 (0·09)	0·17 (0·010)	1·31 (0·11)	0·05 (0·006)	0·35 (0·07)	0·30 (0·03)
	15–30	4·7	1·18 (0·04)	0·12 (0·007)	0·63 (0·23)	0·03 (0·002)	0·36 (0·09)	0·23 (0·03)
	30–45	4·7	1·00 (0·06)	0·11 (0·002)	0·14 (0·11)	0·02 (0·002)	0·39 (0·08)	0·16 (0·02)
Caesalpinia echinata	0–5	5·1	2·41 (0·34)	0·17 (0·024)	1·54 (0·39)	0·07 (0·014)	1·17 (0·27)	0·39 (0·06)
	5–15	5·1	1·97 (0·21)	0·18 (0·011)	2·04 (0·44)	0·07 (0·005)	0·77 (0·04)	0·43 (0·02)
	15–30	5·1	1·36 (0·16)	0·15 (0·016)	1·16 (0·20)	0·04 (0·005)	0·42 (0·06)	0·39 (0·04)
	30–45	5·2	1·89 (0·34)	0·16 (0·012)	0·56 (0·18)	0·04 (0·014)	0·56 (0·30)	0·29 (0·05)
Cassia spp.	0–5	4·7	1·94 (0·82)	0·16 (0·007)	1·40 (0·10)	0·07 (0·008)	0·56 (0·02)	0·34 (0·01)
	5–15	4·7	1·79 (0·08)	0·16 (0·007)	1·12 (0·09)	0·06 (0·005)	0·47 (0·02)	0·28 (0·02)
	15–30	4·7	1·23 (0·04)	0·13 (0·003)	0·34 (0·08)	0·03 (0·003)	0·41 (0·06)	0·20 (0·01)
	30–45	4·7	0·90 (0·04)	0·10 (0·005)	0·09 (0·09)	0·02 (0·002)	0·39 (0·07)	0·15 (0·01)
Copaifera lucens	0–5	5·0	2·02 (0·12)	0·17 (0·013)	0·63 (0·06)	0·06 (0·005)	1·15 (0·26)	0·34 (0·05)
	5–15	5·0	1·88 (0·09)	0·14 (0·009)	0·38 (0·06)	0·04 (0·002)	0·94 (0·18)	0·27 (0·02)
	15–30	5·1	0·89 (0·12)	0·06 (0·007)	0·00 (0·0)	0·02 (0·004)	1·06 (0·19)	0·26 (0·03)
	30–45	4·9	0·80 (0·10)	0·05 (0·009)	0·00 (0·0)	0·01 (0·002)	1·01 (0·19)	0·23 (0·04)
Dimorphandra jorgei	0–5	5·0	1·97 (0·10)	0·19 (0·009)	0·97 (0·10)	0·03 (0·003)	0·98 (0·07)	0·32 (0·02)
	5–15	5·0	1·74 (0·11)	0·16 (0·015)	0·74 (0·09)	0·03 (0·0)	0·92 (0·05)	0·26 (0·01)
	15–30	5·0	1·15 (0·05)	0·13 (0·006)	0·10 (0·06)	0·02 (0·0)	0·75 (0·04)	0·20 (0·01)
	30–45	4·9	0·84 (0·03)	0·11 (0·007)	0·00 (0·0)	0·01 (0·0)	0·54 (0·03)	0·15 (0·01)
Hymenaea aurea	0–5	4·4	2·00 (0·08)	0·16 (0·005)	2·03 (0·14)	0·06 (0·006)	0·26 (0·06)	0·24 (0·02)
	5–15	4·4	1·60 (0·06)	0·15 (0·004)	1·28 (0·06)	0·05 (0·002)	0·17 (0·02)	0·15 (0·01)
	15–30	4·1	1·15 (0·09)	0·12 (0·007)	0·56 (0·10)	0·04 (0·004)	0·13 (0·01)	0·12 (0·01)
	30–45	4·4	0·89 (0·05)	0·13 (0·012)	0·00 (0·0)	0·02 (0·003)	0·11 (0·01)	0·10 (0·01)
Macrolobium latifolium	0–5	4·8	1·90 (0·05)	0·16 (0·005)	0·67 (0·07)	0·04 (0·003)	0·36 (0·12)	0·25 (0·03)
	5–15	4·7	1·59 (0·10)	0·15 (0·013)	0·59 (0·08)	0·03 (0·003)	0·28 (0·12)	0·15 (0·02)
	15–30	4·7	1·34 (0·06)	0·12 (0·006)	0·23 (0·07)	0·02 (0·0)	0·30 (0·18)	0·11 (0·04)
	30–45	4·6	0·97 (0·07)	0·11 (0·006)	0·06 (0·04)	0·02 (0·002)	0·24 (0·10)	0·09 (0·03)

Table 5. *Continued*

	Depth (cm)	pH	C (%)	N (%)	P (mg kg^{-1})	K (µmol kg^{-1})	Ca(µmol kg^{-1})	Mg (µmol kg^{-1})
Other Families								
Bombax macrophyllum	0–5	4·8	1·78 (0·10)	0·13 (0·005)	1·42 (0·06)	0·06 (0·009)	0·84 (0·08)	0·33 (0·04)
	5–15	4·7	1·68 (0·14)	0·13 (0·006)	1·24 (0·08)	0·06 (0·011)	0·57 (0·06)	0·24 (0·04)
	15–30	4·6	1·41 (0·10)	0·09 (0·004)	0·59 (0·17)	0·04 (0·008)	0·34 (0·03)	0·13 (0·02)
	30–45	4·6	1·09 (0·05)	0·08 (0·009)	0·05 (0·03)	0·03 (0·003)	0·34 (0·03)	0·10 (0·01)
Buchenavia grandis	0–5	4·6	2·06 (0·13)	0·14 (0·012)	2·09 (0·12)	0·06 (0·009)	0·80 (0·19)	0·33 (0·04)
	5–15	4·5	1·90 (0·05)	0·15 (0·008)	1·89 (0·19)	0·05 (0·009)	0·42 (0·09)	0·25 (0·03)
	15–30	4·5	1·18 (0·07)	0·12 (0·012)	1·01 (0·14)	0·03 (0·006)	0·22 (0·04)	0·18 (0·01)
	30–45	4·5	0·89 (0·04)	0·09 (0·005)	0·12 (0·06)	0·02 (0·002)	0·21 (0·04)	0·16 (0·01)
Eschweilera ovata	0-5	5·3	1·82 (0·10)	0·31 (0·084)	0·58 (0·11)	0·11 (0·035)	1·38 (0·16)	0·53 (0·07)
	5–15	5·2	1·65 (0·06)	0·15 (0·002)	0·42 (0·12)	0·06 (0·014)	1·18 (0·16)	0·39 (0·05)
	15–30	5·0	1·18 (0·06)	0·09 (0·003)	0·10 (0·07)	0·04 (0·003)	0·81 (0·19)	0·22 (0·04)
	30–45	4·6	0·79 (0·06)	0·09 (0·002)	0·00 (0·0)	0·02 (0·003)	0·37 (0·11)	0·09 (0·03)
Lecythis pisonis	0–5	5·3	1·99 (0·13)	0·18 (0·007)	0·23 (0·03)	0·04 (0·004)	1·46 (0·26)	0·32 (0·02)
	5–15	5·3	1·61 (0·06)	0·17 (0·005)	0·08 (0·03)	0·03 (0·003)	1·31 (0·01)	0·29 (0·01)
	15–30	5·9	1·00 (0·10)	0·13 (0·007)	0·00 (0·0)	0·02 (0·0)	1·12 (0·09)	0·25 (0·02)
	30–45	4·9	0·84 (0·06)	0·12 (0·003)	0·00 (0·0)	0·01 (0·002)	0·79 (0·16)	0·20 (0·03)
Licania hypoleuca	0–5	5·0	1·63 (0·10)	0·14 (0·007)	1·61 (0·12)	0·07 (0·007)	1·31 (0·20)	0·35 (0·03)
	5–15	5·0	1·33 (0·07)	0·12 (0·006)	1·34 (0·06)	0·05 (0·002)	1·08 (0·16)	0·27 (0·02)
	15–30	4·9	0·93 (0·03)	0·09 (0·004)	0·32 (0·05)	0·02 (0·003)	0·78 (0·15)	0·24 (0·03)
	30–45	4·9	0·82 (0·06)	0·09 (0·003)	0·04 (0·02)	0·01 (0·003)	0·70 (0·10)	0·24 (0·03)
Pradosia lactescens	0–5	4·9	2·15 (0·08)	0·18 (0·004)	0·81 (0·11)	0·05 (0·002)	0·84 (0·18)	0·24 (0·04)
	5–15	4·8	1·76 (0·10)	0·11 (0·017)	0·51 (0·08)	0·04 (0·002)	0·60 (0·15)	0·17 (0·03)
	15–30	4·7	1·23 (0·09)	0·10 (0·008)	0·02 (0·02)	0·03 (0·004)	0·58 (0·20)	0·14 (0·05)
	30–45	4·7	0·91 (0·04)	0·10 (0·004)	0·00 (0·0)	0·01 (0·003)	0·45 (0·12)	0·12 (0·04)
Control sites								
Primary forest	0–5	4·7	1·99 (0·07)	0·15 (0·010)	0·96 (0·07)	0·08 (0·010)	1·23 (0·18)	0·36 (0·06)
	5–15	4·7	1·42 (0·07)	0·12 (0·020)	0·43 (0·07)	0·05 (0·005)	0·54 (0·09)	0·21 (0·03)
	15–30	4·7	1·02 (0·04)	0·10 (0·004)	0·06 (0·05)	0·05 (0·021)	0·34 (0·04)	0·12 (0·02)
	30–45	4·7	0·77 (0·03)	0·09 (0·008)	0·00 (0·0)	0·03 (0·008)	0·25 (0·02)	0·10 (0·02)
Secondary forest	0–5	5·2	2·25 (0·21)	0·22 (0·011)	2·46 (0·42)	0·07 (0·006)	2·20 (0·41)	0·62 (0·11)
	5–15	5·0	1·68 (0·07)	0.16(0.014)	1.71 (0.28)	0.05 (0.007)	0.93 (0.15)	0.32 (0.05)
	15–30	4.8	1.03 (0.08)	0·11 (0·008)	0·60 (0·07)	0·03 (0·006)	0·52 (0·08)	0·21 (0·04)
	30–45	4·6	0·78 (0·07)	0·11 (0·005)	0·03 (0·01)	0·02 (0·003)	0·32 (0·04)	0·20 (0·04)
Mixed-species plantation	0–5	4·7	1·74 (0·06)	0·16 (0·007)	1·97 (0·18)	0·04 (0·002)	0·59 (0·15)	0·33 (0·07)
	5–15	4·6	1·69 (0·03)	0·17 (0·004)	1·52 (0·30)	0·03 (0·002)	0·40 (0·10)	0·25 (0·04)
	15–30	4·6	0·97 (0·10)	0·13 (0·012)	0·34 (0·09)	0·02 (0·0)	0·28 (0·09)	0·15 (0·02)
	30–45	4·6	0·79 (0·03)	0·11 (0·009)	0·00 (0·0)	0·01 (0·002)	0·25 (0·08)	0·11 (0·02)

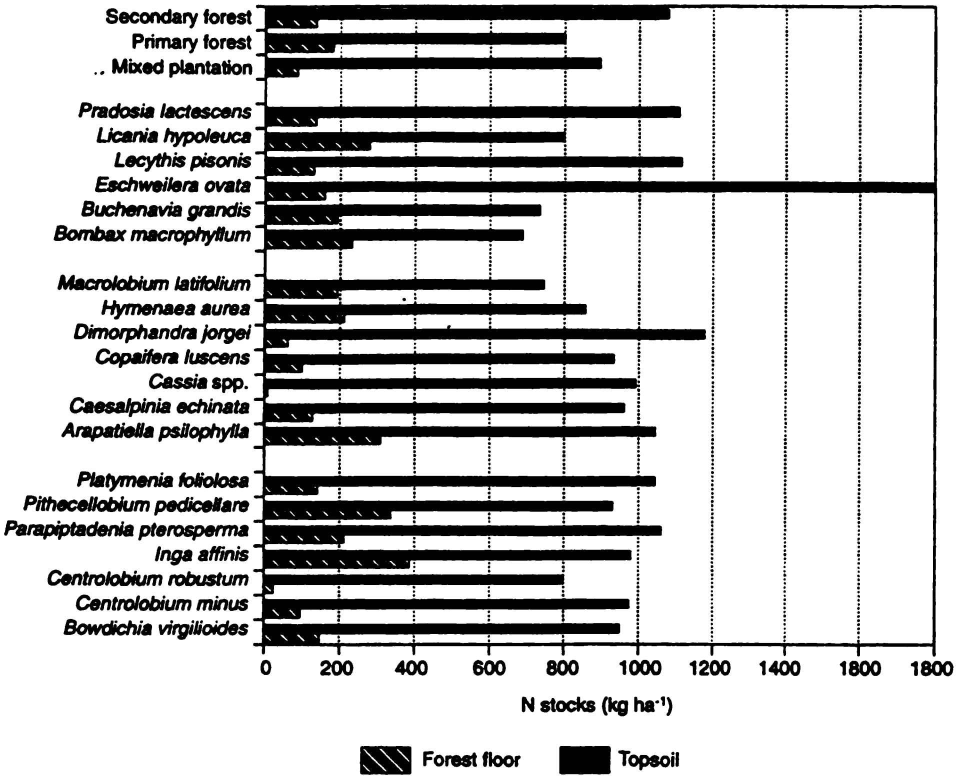

Fig. 2. Nitrogen stocks in topsoil (0–5 cm depth) and in total forest-floor litter under 20 tree species in the arboretum, secondary forest, primary forest and mixed-species plantation at the Pau Brasil Ecological station. The species are grouped taxonomically, as in Table 1.

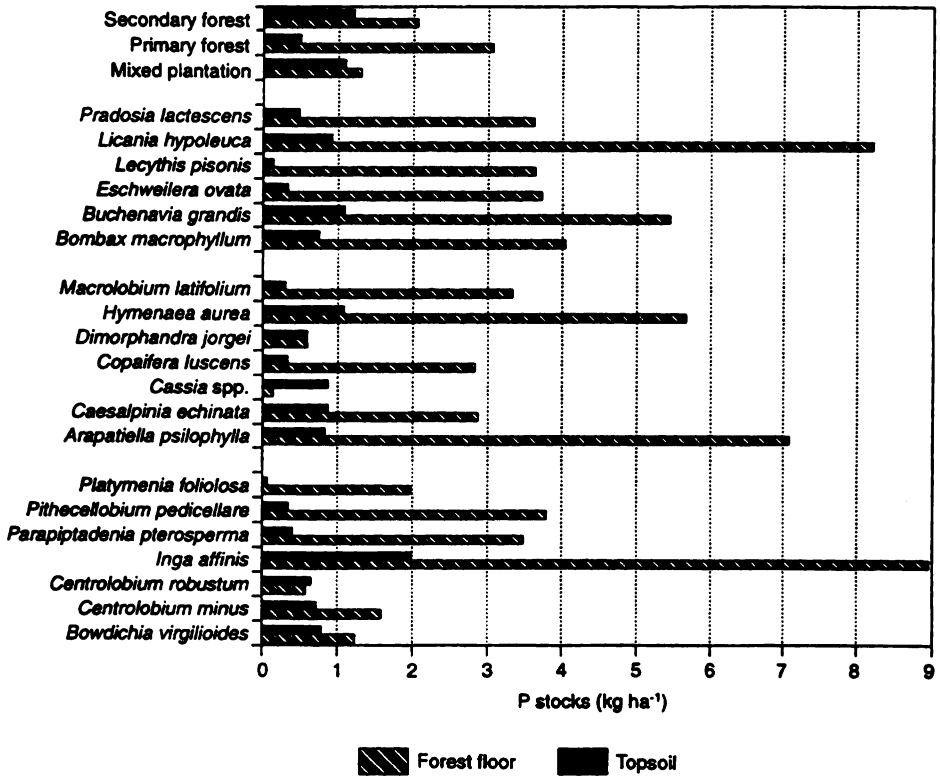

Fig. 3. Phosphorus stocks in topsoil (0–5 cm depth) and in total forest-floor litter under 20 tree species in the arboretum, secondary forest, primary forest and mixed-species plantation at the Pau Brasil Ecological station. The species are grouped taxonomically, as in Table 1.

Table 6. K, Ca and Mg stores (kg ha^{-1}) in topsoil (0–5 cm depth) and in total forest-floor (F.floor) litter. Bulk density (g cm^{-3}) also shown

	K		Ca		Mg		
Species/sites	Topsoil	F. floor	Topsoil	F. floor	Topsoil	F. floor	Bulk density
N-fixing leguminous species							
Bowdichia vigilioides	13·9	7·5	161	101	27·8	12·0	1·19
Centrolobium minus	11·9	18·3	64·7	83·4	15·4	12·6	1·22
C. robustum	12·0	1·4	49·2	21·4	11·8	3·7	1·23
Inga affinis	14·9	21·4	82·8	313	32·0	31·4	1·09
Parapiptadenia pterosperma	16·5	7·7	148	218	38·2	26·6	1·06
Pithecellobium pedicellare	12·1	10·1	98·0	127	29·8	25·2	1·24
Platymenia foliolosa	11·3	4·0	122	61·4	29·2	5·4	1·16
Non-N fixing leguminous species							
Arapatiella psilophylla	13·6	23·6	44·1	247	25·8	25·0	1·16
Caesalpinia echinata	15·4	5·6	132	195	26·4	1·5	1·24
Cassia spp.	16·9	0·4	69·4	6·0	25·3	9·1	1·13
Copaifera luscens	12·9	6·8	127	102	22·4	9·0	1·1
Dimorphandra jorgei	7·3	1·3	122	24·0	23·8	3·2	1·24
Hymenaea aurea	12·5	14·8	27·8	153	15·4	21·9	1·07
Macrolobium latifolium	7·3	10·0	33·5	237	14·0	45·5	0·93
Of other families							
Bombax macrophyllum	12·4	11·0	89·0	431	21·0	92·7	1·06
Buchenavia grandis	12·3	13·9	84·0	241	20·8	23·0	1·05
Eschweilera ovata	24·9	18·2	160	248	36·9	32·8	1·16
Lecythis pisonis	9·7	6·7	181	140	23·8	11·7	1·24
Licania hypoleuca	15·6	43·6	149	474	23·9	55·3	1·14
Pradosia lactescens	12·0	14·1	103	240	17·7	30·1	1·23
Secondary forest	13·4	10·3	216	169	36·5	23·9	0·98
Primary forest	16·7	6·5	132	134	23·1	14·5	1·07
Mixed plantation	8·7	2·8	66·1	62·7	22·2	9·4	1·12

Discussion

AMELIORATIVE EFFECTS OF TREES ON SOILS

The ranges of values for the soil variables measured in this research were comparable to those generally found in acid, infertile areas of tropical humid forest regions (Young 1989; van Wambeke 1992). The soil bulk density values were relatively high, similar to earlier reports for soils at the station, attributable to the high sand and silt content of these soils (Cadima Zeballos *et al.* 1982; da Vinha & Lobão 1989; Leão & Melo 1990).

Soil pH, C, N, P, Ca and Mg were higher under secondary than under primary forest. The values shown here for secondary forest were similar to those reported earlier by Cadima Zeballos *et al.* (1982) for secondary forest at the station, except that they found higher extractable P at 0–5 cm depth; and they did not measure soil total N. As in the present study, Silva (1990a) found higher soil pH and higher exchangeable Ca and Mg in a 20-year-old forest than in primary forest on Ultisols (argillic horizon of low base saturation) in Barrolandia, Bahia, near Porto Seguro. Soil conditions in the secondary forest of the present study may have improved as a result of the impacts of the dominant plant species in the regrowth. In other research at the station, *Eschweilera ovata, Inga affinis* and *Pithecellobium pedicellare* were found in the pioneer phase (first year) of forest regeneration (da Vinha, Cadima & Santos 1983). *Bowdichia virgilioides* grows as a pioneer in abandoned fields in other environments in the neotropics, with a broad range of natural occurrence from Venezuela and the Guianas to SE Brazil (Chudnoff 1984). These species tended to have positive effects on soil properties, as shown by the present study.

When the soil variables, and topsoil and forest-floor nutrient stocks are compared between secondary forest and the tree species in the arboretum, several species appear to have positive impacts on soils and ecosystem nutrients. Some were leguminous, e.g. *Inga affinis, Parapiptadenia pterosperma*; others were leguminous but have not been reported to fix N (*Arapatiella psilophylla, Caesalpinia echinata*); while some of the most outstanding effects were found under species of other families, such as *Bombax macrophyllum, Eschweilera ovata, Lecythis pisonis* and *Licania hypoleuca*. Except for *Cassia* spp. and *Parapiptadenia pterosperma*, the species with more positive effects on soils were medium or small in size. This may be related to crown shape: shorter trees may have broadly spread branching with more leaves and small branches, i.e. a larger proportion of potentially recyclable biomass in comparison with taller trees with more straight boles and less branching.

The mixed plantation had similar soil pH, total C, total N and exchangeable Mg, but slightly higher extractable P.

and lower K and Ca than the primary forest. Thus, this system apparently represents an intermediate situation with respect to the pure stands of the arboretum. However, the plantation also included some exotics such as *Pinus* spp. and *Eucalyptus* spp., whose presence may have created a different situation with respect to the native species, i.e. these species with their fast growth may have been more nutrient demanding than the indigenous trees, possibly resulting in lower soil nutrient concentrations than in a mixture comprising native species only.

The importance of specific effects of trees on soil properties depends on the particular objectives of land rehabilitation projects. If it is desired to rehabilitate soils for future tree or crop production, the results of standard soil fertility tests such as those used in this study may not always reveal the soil's productive potential, because they do not include all chemical forms of nutrients available for plant uptake (Lugo, Cuevas & Sánchez 1990). It is generally difficult to evaluate the direct effects of trees on soil nutrient availability (especially N and P). Experiments with test plants can indicate impacts on soils in an indirect manner, e.g. by measuring plant growth and N and P uptake following the addition of the species' tree litter or mulch (Montagnini, Ramstad & Sancho 1993). Experiments of this kind may reveal important influences by the trees in this study on soil properties other than those shown by the results of the present research. Especially for the species which exerted the most important effects, additional studies with appropriate site replication would be needed to confirm the impacts of the species on soils or on associated trees or crops.

NUTRIENT RECYCLING MECHANISMS

The impacts of trees on soil fertility depend on their nutrient recycling characteristics such as litter chemistry and decomposition. Leaf nutrient concentrations can give an indication of tree nutrient uptake as well as nutrient recycling potential. The ranges of values of leaf N, P and K concentrations for the species of this research were within those reported for tree species in Amazon forests growing on poor, upland (never flooded) soils (Medina & Cuevas 1994). All the N-fixing species in this study had leaf N concentration exceeding 2%, comparable to other tropical N-fixing tree species (Young 1989; Montagnini & Sancho 1993). Two non-N-fixing species also showed values greater than 2%, namely *Dimorphandra jorgei* and *Hymenaea aurea*. These species may also be capable of fixing atmospheric N, although nodulation was not seen at the time their roots were examined and no reference was found to the N-fixing ability of these species. The other leaf nutrients studied were within ranges reported elsewhere for other tropical trees (Young 1989; Montagnini & Sancho 1993). Some species showed high leaf concentrations for a few of the nutrients examined. For example, *Parapiptadenia pterosperma* had high leaf N and Ca, *Centrolobium robustum* had high P and K, *Dimorphandra jorgei* had high N and P, *Bombax macrophyllum* and *Licania hypoleuca* had high K and Mg, and *Buchenavia grandis* had high leaf N, However, no particular set of nutrients was co high in any group of species.

In agreement with their positive effects on soil (Tables 5 and 6), *Inga affinis* and *Parapiptadenia pterosperma* gave high leaf N concentrations (Table 3). However, leaf nutrient concentration was not always a good indicator of the species' effects on soils. For example, no beneficial effects on soils were noted under *Centrolobium robustum* or *C. minus*, although these two species showed high P and cation concentrations in leaves and forest-floor litter. Litter turnover data would be needed to clarify these trends. Although *Arapatiella psilophylla* had the highest leaf Al, the concentration was not as high as has been found in other species considered to be Al-accumulators (Goodland 1971). Our ability to interpret these results is limited because leaf nutrient concentrations can vary with the season, canopy position and leaf age; however, trends in differences among species tend to be consistent throughout the year (de Oliveira Garrido & Poggiani 1981/1982; F. Montagnini & F. Sancho, unpublished data).

Tree litter can act as mulch and be used for differing objectives: a fast mulch decomposition rate may accelerate the growth of associated crops on poor soils, while in other cases a more persistent litter may be desired. High rates of litterfall and slower decomposition result in high litter accumulation and high soil organic matter, while a less abundant litter with relatively faster decomposition and high nutrient content may promote fast nutrient recycling (Lugo *et al.* 1990; Montagnini *et al.* 1993). Litter accumulation on the forest-floor was greater in secondary than in primary forest, similar to findings by Silva (1990a) from Barrolandia. Litter nutrients were also higher than in primary forest suggesting that, in secondary forest, forest-floor litter is an important source of nutrients to the soil. However, litter turnover rates would be needed to confirm these findings.

Among the 20 species in the arboretum, the highest dry weights of forest-floor litter were found under *Arapatiella psilophylla*, *Bombax macrophyllum*, *Inga affinis*, *Licania hypoleuca* and *Pithecellobium pedicellare*; positive effects on soils were found under all these species, with *P. pedicellare* having the least influence. This suggests that forest-floor nutrients were incorporated into the soil via decomposition under these species. da Vinha & Pereira (1983) reported high rates of litterfall under *Bombax macrophyllum*, *Buchenavia grandis*, *Caesalpinia echinata*, *Hymenaea aurea*, *Lecythis pisonis* and *Plathymenia foliolosa* in the same arboretum. Of this group of species, leaf-litter decomposition was faster under *Buchenavia grandis*, *Hymenaea aurea* and *Bombax macrophyllum*, in that order (da Vinha *et al.* 1985). The forest-floor litter and topsoil nutrient stores presented in Figs 2 and 3, and Table 6 contribute to interpreting some of these results: for example, litter under *Licania hypoleuca* had low nutrient concentrations, but because of its relatively high mass it resulted in large nutrient stores, and positive effects on soils, as shown by the present study. Under the species with high litter nutrient concentrations and slower decomposition, forest-floor litter may serve as a nutrient reservoir, as well as to protect the soil against erosion.

In previous paragraphs we have summarized the potential impacts of species on soils and pointed to some mechanisms related to the observed responses. It must be noted again that these results are limited because measurements were taken at one point in time only and several variables may change throughout the year. Additionally, in order to make generalizations about species performance, the study should be replicated on different sites, which was impossible at the time this research was conducted, because of the limited availability of pure species stands for sampling. However, individual-tree sampling, similar to our approach, is often used to study impacts of trees on soils in agroforestry systems and in other situations such as savanna ecosystems where trees are found in isolation (Young 1989; Lugo *et al.* 1990; Belsky *et al.* 1993). In spite of such limitations, these results offer a contribution to knowledge of the ecology of the species studied in conjunction with the existing body of information on soils and nutrient cycling for the region. The results should be applicable under similar ecological conditions. For example, with regard to species choices for sustainable systems in the region, Silva (1990b) suggested favouring those with high nutrient recycling capacity (e.g. species with high rates of litterfall and fast decomposition rates, such as *Gmelina arborea*), as well as those adapted to low soil fertility (e.g. *Bowdichia virgilioides*). Mixed-tree plantations can offer ecological advantages to monospecific plantations. For example, in mixed-species systems, litterfall and litter decomposition are more evenly distributed throughout the year because of the different timing of the associated species (de Oliviera Garrido & Poggiani 1981/1982). For soil rehabilitation purposes, species should be chosen with regard to their nutrient requirements and recycling capabilities (Montagnini & Sancho 1993; Montagnini *et al.* 1993). Experiences in Hawaii have shown that greater nutrient cycling rates by one tree species (in this case, *Albizia falcataria*, a N-fixing legume) coupled with greater nutrient-use efficiency by another (*Eucalyptus saligna*) allowed for higher stand productivity in mixed stands than in pure stands of either species (Binkley *et al.* 1992). From the results of our study, it appears that species that contribute to increased C and N such as *Caesalpinia echinata*, *Inga affinis*, *Parapiptadenia pterosperma* and *Plathymenia foliolosa*, could be combined with those that increase soil pH and/or certain cations, such as *Copaifera luscens*, *Eschweilera ovata*, *Lecythis pisonis* and *Licania hypoleuca*. The inclusion of *Arapatiella psilophylla*, *Bombax macrophyllum*, *Buchenavia grandis*, *Caesalpinia echinata*, *Cassia* spp., *Hymenaea aurea* and *Inga affinis* could contribute to increases, however small, in levels of extractable P in the surface soil. In addition to their potential effects on soil fertility, species choices must be guided by seed and seedling availability, as well as by farmers' preferences, the species' local uses, and economic aspects (cost of establishment and market potential). Multi-species systems are a promising land-use alternative for poor soils if information is available on the species' soil improving capacity, economic viability and management needs (Silva 1990b; Montagnini 1992).

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References

Allen, O.N. & Allen, E.K. (1981) The *Leguminosae: a Source Book of Characteristics, Uses, and Nodulation*. University of Wisconsin Press, Madison, Wisconsin.

Anderson, J.M. & Ingram, J.S.I. (eds) (1989) *Tropical Soil Biology and Fertility: a Handbook of Methods*. CAB International, Wallingford, Oxon, UK.

Anonymous (1980) *Reference Methods for Soil Testing*. Council on Soil Testing and Plant Analysis, University of Georgia Athens.

Belsky, A.J., Mwonga, S.M, Amundson, R.G., Duxbury, J.M. & Ali, A.R. (1993) Comparative effects of isolated trees on their undercanopy environments in high- and low-rainfall savannas. *Journal of Applied Ecology*, **30**, 143–155.

Binkley, D., Dunkin, K.A., DeBell, D. & Ryan, M.G. (1992) Production and nutrient cycling in mixed plantations of *Eucalyptus* and *Albizia* in Hawaii. *Forest Science*, **38**, 393–408.

Briceño, J.A. & Pacheco, R. (eds) (1984) *Métodos Analíticos para el Estudio de Suelos y Plantas*. Editorial de la Universidad de Costa Rica. San José.

Brooke, J. (1993) Brazilian rain forest yields most diversity for species of trees. *The New York Times, New York*, 30 March 1993, p. C4.

Cadima Zeballos, A., da Silva, L.F. & Lobão, D.E. (1982) Alterações edáficas provocadas por um sistema de agricultura itinerante em solos deTabuleiros do Sul da Bahia. *Theobroma (Brazil)*, **12**, 267–272.

Chudnoff, M. (1984) *Tropical Timbers of the World*. USDA Forest Service, Agricultural Handbook 605, Washington, DC.

da Vinha, S.G., Cadima Z., A. & Santos, O.M. (1983) A fase pionera dc uma sucessão vegetal secundária no sul da Bahia: estrutura e composição química da vegetação. *Theobroma (Brazil)*, **13**, 27–34.

da Vinha, S.G., de Carvalho, A.M. & Silva, L.A.M. (1985) Taxa de decomposição do folhedo de dez espécies de árvores nativas no Sul da Bahia, Brasil. *Theobroma (Brazil)*, **15**, 207–212.

da Vinha, S.G. & Lobão, D.E.V.P. (1989) *Estação Ecológica Pau Brasil – Porto Seguro, Bahia.* Centro de Pesquisas do Cacau, Itabuna, Bahia.

da Vinha, S.G. & Pereira, R.C. (1983) Produção de folhedo e sua sazonalidade em 10 especies arbóreas nativas no Sul da Bahia. *Theobroma (Brazil)*, **13**, 327–341.

da Vinha, S.G., Ramos do J.S., T. & Hori, M. (1976) Inventário Florestal. *Comissão Executiva do Plano da Lavoura*

Cacaueira, Recursos Florestais. Ilhéus, BA, Brasil. CEPLAC/IICA. pp. 20–212. (Diagnóstico Socioeconômico da Região Cacaueira, 7)

de Oliveira Garrido, M.A. & Poggiani, F. (1981/1982) Avaliação da quantidade e do conteúdo de nutrientes do folhedo de alguns povoamentos puros e mistos de espécies indígenas. *Silvicultura em São Paulo*, **15/16**, 1–22.

Evans, J. (1987) Site and species selection: changing perspectives. *Forest Ecology and Management*, **21**, 299–310.

Gladstone, W.T. & Ledig, F.T. (1990) Reducing pressure on natural forests through high-yield forestry. *Forest Ecology and Management*, **35**, 69–78.

Goodland, R. (1971) Oligotrofismo e aluminio no cerrado. *III Simposio Sobre o Cerrado* (ed. M.G. Ferri), pp. 44–60. Universidade Sao Paulo, Editora Edgar Blucher, São Paulo.

Hurlbert, S.T. (1984) Pseudoreplication and the design of ecological field experiments. *Ecological Monographs*, **54**, 187–211.

Jacobs, M. (1988) *The Tropical Rainforest: a First Encounter*. Springer-Verlag, New York.

Leao, A.C. & de Melo, A.A.O. (1990) *Características Morfológicas, Físico-químicas e Mineralógicas dos Solos da Estação Ecológica Pau-Brasil, Porto Seguro, Bahia*. CEPLAC, Itabuna, Bahia.

Lugo, A.E., Cuevas, E. & Sánchez, M. J. (1990) Nutrients and mass in litter and topsoil of ten tropical tree plantations. *Plant and Soil*, **125**, 263–280.

McNeely, J.A., Miller, K.R., Reid, W.V., Mittermeier, R.A. & Werner, T.B. (1990) *Conserving the World's Biological Diversity*. World Wildlife Fund, Gland, Switzerland.

Medina, E. & Cuevas, E. (1994) Mineral nutrition: humid tropical forests. *Progress in Botany*, **55**, 115–129.

Montagnini, F. (1990) Ecology applied to agroforestry in the humid tropics. *Race to Save the Tropics. Ecology and Economics for a Sustainable Future* (ed. R.A. Goodland), pp. 49–58. Island Press, Washington, D.C.

Montagnini, F. (1992) Mixed-tree plantations with native trees: land-use systems for economic returns and soil restoration. Experiments in Costa Rica and Argentina. *Agroforestry Today*, **4**, 4–6.

Montagnini, F., Fanzeres, A. & da Vinha, S.G. (1994) Estudios de restauración en la región del bosque Atlántico de Bahía, Brasil. *Yvyraretá (Argentina)*, **5**, 9–23.

Montagnini, F., Ramstad, K. & Sancho, F. (1993) Litterfall, litter decomposition and the use of mulch of four indigenous tree species in the Atlantic lowlands of Costa Rica. *Agroforestry Systems*, **23**, 39–61.

Montagnini, F. & Sancho, F. (1990) Impacts of native trees on tropical soils: a study in the Atlantic lowlands of Costa Rica. *Ambio*, **19**, 386–390.

Montagnini, F. & Sancho, F. (1993) Aboveground biomass and nutrients in young plantations of indigenous trees on infertile soils in Costa Rica: implications for site nutrient conservation. *Journal of Sustainable Forestry*, **1**, 115–139.

Mori, A.S. & Silva, L.A.M. (1980) *O herbario do Centro de Pesquisas do Cacau em Itabuna, Brasil, Ilheus, BA*. CEPLAC/CEPEC, Boletim Tecnico No. 78. Itabuna, Bahia, Brazil.

Nair, P.K.R. (1989) The role of trees in soil productivity and protection. *Agroforestry systems in the tropics* (ed. P.K.R. Nair), pp. 567–589. Kluwer, Dordrecht.

Parrotta, J.A. (1992) The role of plantation forests in rehabilitating degraded tropical ecosystems. *Agriculture, Ecosystems and Environment*, **41**, 115–133.

Quintela, C.E. (1990) An SOS for Brazil's beleaguered Atlantic forest. *Nature Conservancy Magazine*, **40**, 14–19.

Sánchez, P.A., Palm, C.A., Davey, C.B., Szott, L.T. & Russell, C.E. (1985) Tree crops as soil improvers in the humid tropics? *Atributes of Trees as Crop Plants* (eds M.G.R. Cannell & J.E. Jackson), pp. 327–350. Institute of Terrestrial Ecology, Abbots Ripton, Huntingdon.

Santana, M.B.M., Pereira, G.C. & Morais, F.I. (1977) *Métodos de Análise de Solos, Plantas e Água Utilizados no Laboratório do Setor de Fertilidade do CEPEC*. Centro de Pesquisas do Cacau, CEPLAC, Itabuna, Bahia, Brazil.

Silva, L.F. (1981) Alterações edaficás em 'Solos de tabuleiro' (Haplorthox) por influencia do desmatamento, queima e sistemas de manejo. *Theobroma (Brazil)*, **11**, 5–19.

Silva, L.F. (1983) Influência de cultivos e sistemas de manejo nas modificações edáficas dos oxisols de tabuleiro (Haplorthox) do sul da Bahia. *CEPLAC*, Departamento Especial da Amazônia. Belém.

Silva, L.F. (1988) Alterações edáficas provocadas por essências florestais implantadas em solos de tabuleiro no Sul da Bahia. *Theobroma (Brazil)*, **18**, 259–267.

Silva, L.F. (1990a) Interação solo-vegetação em floresta primária e capoeira do ecossistema de tabuleiro do sul da Bahia. *CEPLAC*, Itabuna, Bahia.

Silva, L.F. (1990b) Manejo dos recursos naturais dos trópicos e suas consequências, contradições e perspectivas de uso em agricultura sustentável. Seminario Internacional sobre Investigación en Recursos Naturales para la Producción Agropecuaria, Bogotá, Colombia, 19–23 Noviembre, 1990. *CEPLAC*, Itabuna, Bahia.

van Wambeke, A. (1992) Vegetation, soil organic matter, and crops. *Soils of the Tropics. Properties and Appraisal* (ed. A. van Wambeke), pp. 69–95. McGraw-Hill, New York.

Young, A. (1989) *Agroforestry for Soil Conservation. Science and Practice of Agroforestry*. C.A.B. International and International Council for research in Agroforestry, Wallingford.

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STUDIES ON RESTORATION ECOLOGY IN THE ATLANTIC FOREST REGION OF BAHIA, BRAZIL

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Four hundred years ago the forest of the Atlantic coast of Brazil was approximately 100 million hectares. Today, it has been reduced to <5% of its original size (McNeely *et al.* 1990). In the south of Bahia, the site of the present study, the primary forest is cleared primarily for agriculture. Following timber extraction, the area is slashed, burned, and planted with subsistence crops or grazed by cattle. Within a few years, the results are visible signs of erosion, low crop yields and non-economic grazing carrying capacities. To decrease pressure on the remaining natural forest, it is necessary to increase the productivity of the degraded areas making food, wood and fodder available to the groups exerting pressure on the primary forest. Tree plantations are feasible alternatives for the recovery of degraded lands to productive use in areas with poor natural forest regeneration (Evans 1987, Gladstone and Ledig 1990, Montagnini 1990, 1992). The presence of certain tree species in a production system can result in better soil structure and increases in soil nutrient availability (Sanchez *et al.* 1985, Nair 1989, Young 1989, Montagnini and Sancho 1990). In southern Bahia, previous research has shown the potential of certain tree species for their incorporation in productive land use systems. For example, increases in Ca, Mg and K were found in soils under plantations of *Cordia trichotoma* and *Caesalpina echinata* (Silva 1983). In another location, increases in soil pH and cations were found in 7-year-old *Gmelina arborea* stands, while the other species studied had improved general site conditions to varying degrees (Silva 1988). In 1990, we examined species/site relationships of twenty native tree species growing in pure stands on the same soils, in an arboretum at the Pau Brasil Ecological Station in Porto Seguro, Bahia. The goals were to identify those species with a positive influence on soil fertility. Each soil parameter was compared among the species and among primary and secondary forest. Additionally, a mixed-tree plantation was evaluated to obtain a heterogeneous pattern contrasting with the pure species plots.

Study site

The Pau Brasil (Brazil's national tree, *Caesalpinia echinata*) Ecological Station is 16 km from Porto Seguro, Bahia (16°23'S, 39°11'W). The 1,145 ha station has an arboretum with approximately 40 indigenous species, other experimental plantings, and a reserve with areas in primary and secondary forest (da Vinha and Lobão 1989). The climate is classified as Af in the Köeppen system. The annual rainfall is 1,696 mm, there is no defined dry period, and the daily temperature averages 23°C (with a 30°C maximum and a 20°C minimum). The topography is flat, and the soils are Oxisols (Haplorthoxes) originating from Tertiary sediments; they are acid and infertile (Cadima Zeballos *et al.* 1982, da Vinha *et al.* 1976, da Vinha and Lobão 1989).

Our study focused on 20 native tree species chosen for their good growth and economic potential (da Vinha and Pereira, 1983, da Vinha *et al.* 1985) (Table I). All the species can be found in the natural forest at the Station. The trees were in pure stands of 36 individuals spaced 2 m by 2 m, all on the same soils. Seedlings were produced at the Station's nursery, from seeds collected from the reserve. All the stands were part of the arboretum and were planted in 1974-75; thus all the trees were approximately the same age, 14-15 years old, at the time this research was conducted. Sampling took place in June, 1990.

/ KEY WORDS / Restoration ecology / Native species / Soil fertility restoration / Brazil /

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Methods

Superficial roots (0-15 cm depth) of the leguminous species of this study (Table I) were excavated and examined for the presence of root nodules. At least five trees were examined for each species. Soils for chemical analysis and bulk density were sampled under the 20 species in the arboretum, a mixed-species plantation, a 20-year-old secondary forest, and the native forest. Composite soil samples were taken beneath five individuals (randomly selected) of each species in the arboretum. In the other three sites, samples were taken at locations randomly selected and within one meter of a tree stem. For soil general chemical characteristics, composite samples were taken at 0-5, 0-15, 15-30 and 30-60 cm depth. The pH, the extractable Ca, Mg, K, Al and P, and total C and N were measured following standard procedures for tropical soils (Santana *et al.* 1977, Reference Methods for Soil Testing 1980, Anderson and Ingram 1989). The forest-floor litter was collected in the area demarcated by a 16 mm diameter plastic frame. The samples were dried at approximately 60°C until constant weight and were sorted into branches, whole leaves and fragments. Leaf samples were collected from the same trees using a pole pruner to cut two fully-grown branches from opposite sides of the trees. The total height and the diameter at breast height of each sampled tree were also measured. All tissue material (litter and leaves) was analyzed for N, P, Ca, Mg, K and Al using similar procedures as for soils. All chemical analyses were conducted in laboratories at Yale School of Forestry and Environmental Studies, CT, USA.

Results and discussion

The presence of root nodules was evident in all trees examined for the mimosoid and papilionoid leguminous species; these were apparently active N-fixing nodules, as suggested by their reddish coloration in laboratory observations. No nodules were found in any of the caesalpinoid tree roots examined; these species have not been reported to nodulate (Allen and Allen 1981). Although diameters at breast height ranged from a mean of 9.3 cm in *Centrolobium robustum* to 24.1 cm in *Inga affinis* stands, these differences were not statistically significant (Table II). Mean total tree height ranged from 7.5 m to 14.2 m: the highest trees were in *Bombax macrophyllum, Cassia spp.* and *Parapiptadenia pterosperma* stands (Table II).

TABLE I
SPECIES STUDIED IN MONOCULTURE STANDS AT THE ARBORETUM IN THE PAU BRAZIL ECOLOGICAL STATION, PORTO SEGURO, BAHIA

Common Name	*Scientific Name*	*Family*	*Sub-Family*
		Nitrogen-Fixing Leguminous Species	
Sucupira	*Bowdichia virgilioides*	Leguminosae	Papilionoideae
Putumuju Castanho	*Centrolobium minus*	Leguminosae	Papilionoideae
Putumuju Gigante	*Centrolobium robustum*	Leguminosae	Papilionoideae
Inga Cipó	*Inga affinis*	Leguminosae	Mimosoideae
Viola	*Parapiptadenia pterosperma*	Leguminosae	Mimosoideae
Juerana Branca	*Pithecelobium elegans*	Leguminosae	Mimosoideae
Vinhático	*Plathymenia foliolosa*	Leguminosae	Mimosoideae
		Non-Nitrogen-Fixing Leguminous Species	
Arapati	*Arapatiella psilophylla*	Leguminosae	Caesalpinioideae
Pau Brasil	*Caesalpinia echinata*	Leguminosae	Caesalpinioideae
Faveira	*Cassia sp.*	Leguminosae	Caesalpinioideae
Pau Oleo	*Copaifera lucens*	Leguminosae	Caesalpinioideae
Angelim	*Dimorphandra jorgei*	Leguminosae	Caesalpinioideae
Jatobá	*Hymenaea aurea*	Leguminosae	Caesalpinioideae
Oleo Cumumbá	*Macrolobium latifolium*	Leguminosae	Caesalpinioideae
		Other Families	
Imbiruçu	*Bombax macrophyllum*	Bombacaceae	
Pequi Doce	*Buchenavia grandis*	Combretaceae	
Biriba	*Eschweilera ovata*	Lecythidaceae	
Sapucaia	*Lecythis pisonis*	Lecythidaceae	
Oiti	*Licania hypoleuca*	Chrysobalanaceae	
Buranhém	*Pradosia lactescens*	Sapotaceae	

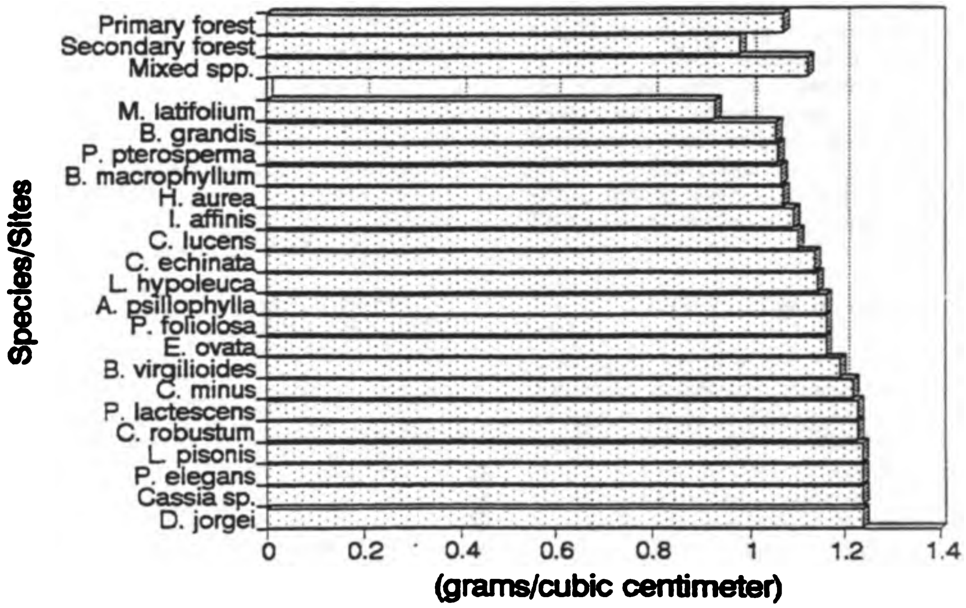

Fig. 1. Soil Bulk Density

Ameliorative effects on soils

Values of soil parameters under the native species and forests of this study (Figs. 1, 2 and 3, Table III) were in the same ranges as those reported by Leao and Melo (199?) and Cadima *et al.* (1982) for the Station. In our study, soil pH, C, N, P, Ca and Mg were higher under secondary than under primary forest (Table III). Silva (1990a) also found higher soil pH and exchangeable Ca and Mg in 20-year-old forest than in primary forest in Barrolandia, near Porto Seguro. Probably the nutrient recycling mechanisms of the secondary species (rapid growth, shorter life span and consequently faster incorporation of nutrients to the soil), contribute to higher fertility.

The effects of the 20 tree species of the arboretum on soil properties, in reference to primary forest, are summarized in Table IV. The values for each parameter were ranked as negative, similar or better than in primary forest. Positive or similar effects on at least five parameters were detected under 15 species. Positive effects on at least three parameters were noted under *I. affinis*, *P. pterosperma* (N-fixing species); *A. psilophylla*, *C. echinata*, (leguminous, non-N-fixing); *E. ovata*, *L. pisonis*, *L. hypoleuca* (of other families). The results confirm previous findings with respect to positive effects on soils under *C. echinata* (Silva 1983); no background information was found for the other species. Except for *P. pterosperma*, the species with greatest positive effects on soils were medium or small in size. This may be related to crown shape: smaller trees may have spreaded branching with more leaves and small branches, *i.e.* a larger proportion of potentially recyclable biomass, in comparison with taller trees with more straight boles and less branching. The mixed plantation had similar soil pH, C, N, Mg, slightly higher P and lower K and Mg than the primary forest (Table III): thus, this system apparently represents an intermediate situation with respect to the pure stands. This mixed plantation also included some exotic trees such as *Pinus spp*. and *Eucalyptus spp*., whose presence may have created a different situation with respect to the native species.

Nutrient recycling mechanisms

All N-fixing species, except for *P. elegans*, had leaf N concentration >2%, comparable to other tropical N-fixing tree species (Young 1989, Montagnini and Sancho 1992) (Table V). Two non-N-fixing species had values >2%: *D. jorgei* and *H. aurea*; possibly these species also fix N, although nodulation was not seen at the time these trees were examined; no reference was found on the N fixing ability of these species. The other leaf nutrients studied were within ranges reported elsewhere for other tropical trees (Young 1989, Montagnini and Sancho 1992) (Table V), with differences among species. Some species had high leaf concentrations of a few of the nutrients examined: for example, *P. pterosperma* had high N and Ca, *C. robustum* had high P and K, *D. jorgei* had high N and P, *B. macrophyllum* and *L. hypoleuca* had high

TABLE II

DIAMETER AT BREAST HEIGHT AND TOTAL HEIGHT OF THE TREES INTHE ARBORETUM AND IN THE MIXED-SPECIES STAND

Species	*Diameter at breast height (cm)*	*Height (m)*
N-FIXING LEGUMINOUS SPECIES		
Bowdichia virgilioides	11.4^{a}	9.4^{def}
Centrolobium minus	14.5^{a}	10.3^{bcde}
Centrolobium robustum	9.3^{a}	7.9^{def}
Inga affinis	24.1^{a}	9.5^{cdef}
Parapiptadenia pterosperma	16.6^{a}	2.4^{abc}
Pithecelobium elegans	10.4^{a}	7.7^{de}
Plathymenia foliolosa	15.8^{a}	7.3^{ef}
NON N-FIXING LEGUMINOUS SPECIES		
Arapatiella psilophylla	11.1^{a}	7.5^{ef}
Caesalpinia echinata	9.7^{a}	8.0^{def}
Cassia spp.	21.4^{a}	13.2^{ab}
Copaifera lucens	10.6^{a}	7.7^{ef}
Dimorphandra jorgei	14.0^{a}	8.8^{def}
Hymenaea aurea	10.8^{a}	8.5^{def}
Macrolobium latifolium	14.3^{a}	9.7^{cdef}
OTHER FAMILIES		
Bombax macrophyllum	22.8^{a}	14.2^{a}
Buchenavia grandis	12.3^{a}	8.6^{def}
Eschweilera ovata	11.1^{a}	9.4^{def}
Lecythis pisonis	12.9^{a}	7.5^{ef}
Licania hypoleuca	9.5^{a}	7.9^{ef}
Pradosia lactescens	10.9^{a}	8.1^{def}
MIXED-SPECIES PLANTATION	11.8^{a}	10.9^{bcd}

Note: In this and in the following tables, differences among means for a given parameter are statistically significant ($P<0.05$) when followed by different letters.

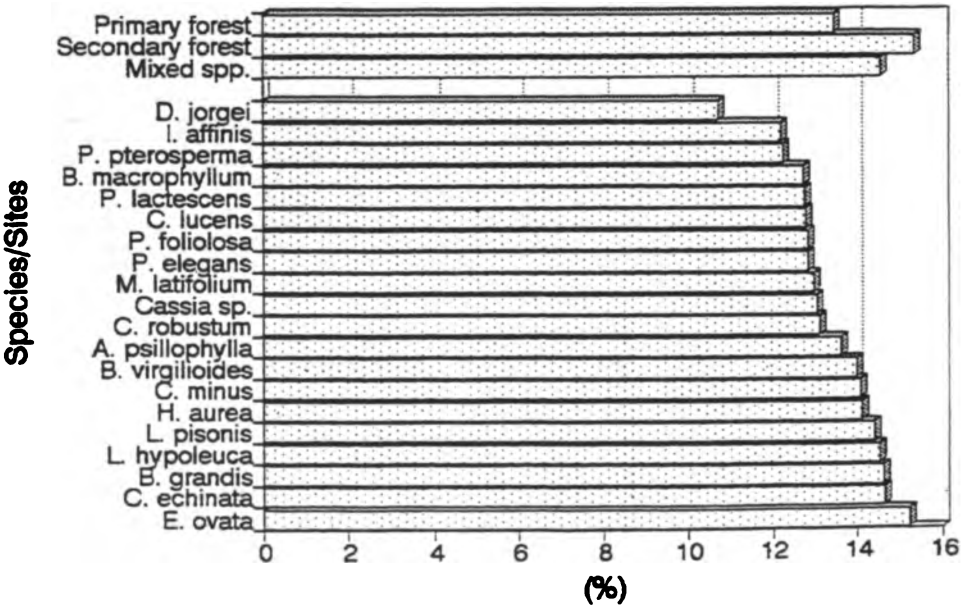

Fig. 2. Soil Water Content

TABLE III
SOIL CHEMICAL CHARACTERISTICS UNDER THE 20 MONOSPECIFIC STANDS IN THE ARBORETUM, PRIMARY AND SECONDARY FOREST AND MIXED PLANTATION.

N-FIXING LEGUMINOUS SPECIES	DEPTH (cm)	pH	C (%)	N (%)	P (mg/kg)	K (umol/kg)	Ca (umol/kg)	Mg (umol/kg)
Bowdichia virgilioides	0-5	4.98	1.98^{defg}	0.16^{def}	1.32^{defg}	0.06^{cdefg}	1.35^{bc}	0.39^{de}
	5-15	5.07	1.52^{hijk}	0.17^{abc}	1.14^{efgh}	0.06^{bcd}	1.08^{abcd}	0.35^{cd}
	15-30	5.04	1.14^{efghi}	0.12^{bcd}	0.43^{def}	0.03^{cdefg}	1.04^{ab}	0.36^{bc}
	30-45	4.97	0.89^{defg}	0.09^{fghi}	0.03^{d}	0.02^{cdef}	0.92^{ab}	0.32^{b}
Centrolobium minus	0-5	4.65	1.87^{efghi}	0.16^{def}	1.19^{efgh}	$0.05^{defghij}$	0.53^{hi}	0.21^{i}
	5-15	4.59	1.57^{ghij}	0.15^{cdef}	1.00^{ghij}	0.04^{efg}	0.35^{hijkl}	0.16^{efg}
	15-30	4.54	0.94^{jk}	0.10^{fg}	0.07^{ij}	0.02^{gh}	0.32^{ijk}	0.17^{ghij}
	30-45	4.54	0.76^{g}	0.09^{i}	0.00^{d}	0.02^{defg}	0.34^{ghij}	0.16^{fg}
Centrolobium robustum	0-5	4.55	1.65^{ij}	0.13^{f}	1.07^{fghi}	0.05^{fghij}	0.40^{i}	0.16^{i}
	5-15	4.49	1.39^{kl}	0.13^{gh}	0.92^{hijk}	0.04^{efg}	0.31^{jkl}	0.14^{j}
	15-30	4.45	1.02^{hijk}	0.09^{g}	0.35^{ef}	0.03^{efgh}	0.22^{k}	0.09^{l}
	30-45	4.51	0.89^{defg}	0.08^{i}	0.13^{cd}	0.02^{cdef}	0.24^{ijk}	0.08^{i}
Inga affinis	0-5	4.91	2.10^{cde}	0.18^{cd}	3.64^{a}	0.07^{bcde}	0.76^{gh}	0.49^{bc}
	5-15	4.89	1.85^{bcd}	0.17^{abc}	3.48^{a}	0.06^{abcd}	0.59^{ghi}	0.43^{efg}
	15-30	4.90	1.46^{a}	0.14^{ab}	1.41^{b}	0.05^{a}	0.54^{fghi}	0.33^{bc}
	30-45	4.88	1.01^{bcd}	0.12^{bcd}	0.29^{c}	0.03^{ab}	0.51^{efgh}	0.25^{cd}
Parapiptadenia pterosperma	0-5	4.97	2.38^{ab}	0.20^{bc}	0.78^{ijk}	0.08^{b}	1.40^{bc}	0.60^{a}
	5-15	4.92	1.76^{cdef}	0.18^{a}	0.63^{jkl}	0.06^{bcd}	1.01^{bcde}	0.49^{a}
	15-30	4.91	1.29^{bcde}	0.14^{ab}	0.12^{ghij}	0.03^{cdefg}	0.81^{cd}	0.42^{a}
	30-45	4.86	1.09^{b}	0.11^{def}	0.00^{d}	0.02^{bcd}	0.79^{bc}	0.39^{a}
Pithecelobium elegans	0-5	4.84	1.67^{hij}	0.15^{ef}	0.59^{kl}	0.05^{efghij}	0.79^{gh}	0.40^{de}
	5-15	4.86	1.48^{ijkl}	0.13^{fgh}	1.41^{def}	0.04^{fgh}	0.73^{fg}	0.28^{bc}
	15-30	4.73	1.10^{fghij}	0.12^{bcd}	1.98^{a}	0.02^{gh}	0.56^{efgh}	0.17^{ghij}
	30-45	4.69	0.79^{fg}	0.11^{defg}	0.93^{a}	0.02^{cdefg}	0.44^{fghi}	0.12^{ghi}
Plathymenia foliolosa	0-5	4.68	2.08^{cde}	0.18^{bcd}	0.13^{m}	0.05^{efghij}	1.05^{cdefg}	0.42^{cd}
	5-15	4.81	2.17^{a}	0.17^{ab}	0.10^{m}	0.05^{def}	1.19^{ab}	0.40^{hi}
	15-30	4.84	1.35^{abc}	0.12^{cde}	0.01^{ij}	0.03^{efgh}	0.95^{abc}	0.32^{c}
	30-45	4.66	1.08^{bc}	0.11^{def}	0.00^{d}	0.02^{bcd}	0.67^{cd}	0.24^{cde}

Note: In this and following tables, differences among means for a given parameter and depth are statistically significant ($P<0.05$) when followed by different letters.
Cont'...

K and Mg, and *B. grandis* had high leaf N, P and Ca; however, no particular set of nutrients was consistently high in any group of species.

In line with their positive effects on soil N, *I. affinis* and *P. pterosperma* had high leaf N concentrations. However, leaf nutrient concentration of the species was not always a good indicator of their effects on soils. For example, no beneficial effects on soils were noted under *C. robustum* or *C. minus*, although these two species had high P and cation concentrations in leaves (Table V) and forest-floor litter (Table VI). The interpretation of these results is limited because leaf nutrient concentrations can vary with time of sampling; however, trends of differences among species tend to be consistent throughout the year (Garrido and Poggiani 1981/2, Montagnini and Sancho, unpub. data).

Litter accumulation on the floor (Fig. 3) was larger in secondary than in primary forest, similar to findings by Silva (1990a) in Barrolandia; litter nutrients were also higher than in primary forest (Table VI), suggesting that in secondary forest, forest-floor litter is an important source of nutrients to the soil.

Among the 20 species in the arboretum, the highest amounts of

TABLE III cont'

NON N-FIXING LEGUMINOUS SPECIES	DEPTH (cm)	pH	C (%)	N (%)	P(mg/kg)	K (umol/kg)	Ca (umol/kg)	Mg (umol/kg)
Arapatiella psilophylla	0-5	4.68	1.94defg	0.18bcd	1.45de	0.06bcdef	0.38i	0.37de
	5-15	4.67	1.76^{cdef}	0.17^{abc}	1.31^{efg}	0.05^{def}	0.35^{ijkl}	0.30^{b}
	15-30	4.70	1.18^{defgh}	0.12^{cde}	0.63^{d}	0.03^{efgh}	0.36^{ghijk}	0.23^{def}
	30-45	4.71	1.00^{bcde}	0.11^{def}	0.14^{cd}	0.02^{cdefg}	0.39^{fghij}	0.16^{fg}
Caesalpinia echinata	0-5	5.08	2.41^{a}	0.17^{cdef}	1.54^{de}	0.72^{bcd}	1.17^{bcde}	0.39^{de}
	5-15	5.08	1.97^{b}	0.18^{a}	2.04^{b}	0.07^{a}	0.77^{efg}	0.43^{ab}
	15-30	5.05	1.36^{abc}	0.15^{a}	1.16^{c}	0.04^{ab}	0.42^{ghij}	0.39^{ab}
	30-45	5.16	1.89^{a}	0.16^{a}	0.56^{b}	0.04^{a}	0.56^{de}	0.29^{bc}
Cassia sp.	0-5	4.73	1.94^{defg}	0.16^{def}	1.40^{def}	0.07^{bcde}	0.56^{hi}	0.34^{de}
	5-15	4.74	1.79^{bcde}	0.16^{bcde}	1.12^{fghi}	0.06^{abcd}	0.47^{hijk}	0.28^{ij}
	15-30	4.69	1.23^{cdef}	0.13^{bcd}	0.34^{fg}	0.03^{cdef}	0.41^{ghij}	0.20^{efgh}
	30-45	4.66	0.90^{cdefg}	0.10^{efgh}	0.09^{d}	0.02^{bcd}	0.39^{fghij}	0.15^{fgh}
Copaifera lucens	0-5	5.03	2.02^{cdef}	0.17^{cdef}	0.63^{jkl}	0.06^{cdefgh}	1.15^{bcdef}	0.34^{de}
	5-15	5.03	1.88^{bc}	0.14^{efg}	0.38^{lm}	0.04^{efg}	0.94^{cdef}	0.27^{efg}
	15-30	5.09	0.89^{k}	0.06^{h}	0.00^{j}	0.02^{gh}	1.06^{a}	0.26^{d}
	30-45	4.92	0.80^{fg}	0.05^{j}	0.00^{d}	0.01^{fg}	1.01^{a}	0.23^{de}
Dimorphandra jorgei	0-5	4.98	1.97^{defg}	0.19^{bc}	0.97^{ghij}	0.03^{j}	0.98^{defg}	0.32^{efgh}
	5-15	5.02	1.74^{cdefg}	0.16^{bcde}	0.74^{ijkl}	0.03^{h}	0.92^{def}	0.26^{ij}
	15-30	4.97	1.15^{efghi}	0.13^{bc}	0.10^{hij}	0.02^{h}	0.75^{cdef}	0.20^{efgh}
	30-45	4.86	0.84^{defg}	0.11^{cde}	0.00^{d}	0.01^{g}	0.54^{def}	0.15^{fgh}
Hymenaea aurea	0-5	4.44	2.00^{defg}	0.16^{def}	2.03^{c}	0.06^{cdefgh}	0.26^{i}	0.24^{hi}
	5-15	4.40	1.60^{fghi}	0.15^{cdef}	1.28^{efgh}	0.05^{def}	0.17^{l}	0.15^{efgh}
	15-30	4.11	1.15^{efghi}	0.12^{cde}	0.56^{d}	0.04^{bcd}	0.13^{k}	0.12^{ijkl}
	30-45	4.40	0.89^{defg}	0.13^{b}	0.00^{d}	0.02^{bcd}	0.11^{k}	0.10^{fgh}
Macrolobium latifolium	0-5	4.76	1.90^{efgh}	0.16^{def}	0.67^{jk}	0.04^{hij}	0.36^{i}	0.25^{fghi}
	5-15	4.73	1.59^{fghij}	0.15^{cdef}	0.59^{kl}	0.03^{h}	0.28^{kl}	0.15^{efg}
	15-30	4.70	1.34^{abcd}	0.12^{cd}	0.23^{fghi}	0.02^{h}	0.30^{jk}	0.11^{kl}
	30-45	4.62	0.97^{bcdef}	0.11^{defg}	0.06^{d}	0.02^{cdefg}	0.24^{ijk}	0.09^{i}

Cont...

forest-floor litter were found under *L. hypoleuca*, *A. psilophylla*. *I. affinis*. *B. macrophyllum* and *P. elegans* (Fig. 3): positive effects on soils were found under all these species, with *B. macrophyllum* and *P. elegans* having the least influence. This suggests that forest-floor nutrients were incorporated to the soil via decomposition, while probably litter decomposed more slowly under the other species and thus their contribution to soil nutrients was relatively smaller. Da Vinha and Pereira (1983) reported high rates of litterfall under *B. grandis*. *B. macrophyllum*. *C. echinata*. *P. foliolosa*. *H. aurea* and *L. pisonis* in the same arboretum. Of this group of species leaf-litter decomposition was faster under *B. grandis* (da Vinha et al. 1985). Although it had positive effects on soils, litter under *L. hypoleuca* did not have high nutrient concentrations in our study. Forest-floor litter may act as a reservoir under the other species with high nutrient content and slower decomposition.

In previous paragraphs we have listed the species potentially useful for their restorative effects on soils, and pointed to some mechanisms related to the observed responses. It should be noted again that these results are limited because measurements were taken at one point in time only, and several parameters may change throughout the year. Additionally, in order to make generalizations about species performance, the study should be replicated on different sites. However, individual-tree sampling is often used to study their impacts on soils in agroforestry systems and in other situations where trees are found in isolation (Young 1989). These results can offer a contribution to the knowledge of the ecology of the species studied, in conjunction with the existing body of information on soils and nutrient cycling for the region. The results should be applicable under similar ecological conditions. For example, with regards to species choices for sustainable systems in the region, Silva (1990b) suggested to fa-

TABLE III cont'.

OTHER FAMILIES	DEPTH (cm)	pH	C (%)	N (%)	P (mg/kg)	K (umol/kg)	Ca (umol/kg)	Mg (umol/kg)
Bombax macrophyllum	0-5	4.81	1.78^{ghij}	0.13^{f}	1.42^{de}	$0.06^{cdefghi}$	0.84^{efgh}	0.33^{ef}
	5-15	4.69	1.68^{defgh}	0.13^{gh}	1.24^{efgh}	0.06^{abc}	0.57^{ghi}	0.24^{gh}
	15-30	4.58	1.41^{ab}	0.09^{g}	0.59^{d}	0.04^{abcd}	0.34^{hijk}	0.13^{ijkl}
	30-45	4.55	1.09^{b}	0.08^{i}	0.05^{d}	0.03^{bc}	0.34^{ghij}	0.10^{hi}
Buchenavia grandis	0-5	4.60	2.06^{cdef}	0.14^{f}	2.09^{c}	0.06^{bcdef}	0.80^{fgh}	0.33^{ef}
	5-15	4.54	1.90^{bc}	0.15^{defg}	1.89^{bc}	0.05^{de}	0.42^{hijkl}	0.25^{fgh}
	15-30	4.46	1.18^{defgh}	0.12^{cdef}	1.01^{c}	0.03^{efgh}	0.22^{k}	0.18^{fghi}
	30-45	4.46	0.89^{defg}	0.09^{hi}	0.12^{cd}	0.02^{bcde}	0.21^{jk}	0.16^{fg}
Eschweilera ovata	0-5	5.32	1.82^{fghij}	0.31^{a}	0.58^{kl}	0.11^{a}	1.38^{bc}	0.53^{ab}
	5-15	5.16	1.65^{efghi}	0.15^{cdef}	0.42^{lm}	0.06^{ab}	1.18^{abc}	0.39^{bc}
	15-30	4.99	1.18^{defg}	0.09^{g}	0.10^{hij}	0.04^{abcd}	0.81^{bc}	0.22^{defg}
	30-45	4.60	0.79^{fg}	0.09^{ghi}	0.00^{d}	0.02^{cdef}	0.37^{fghij}	0.09^{i}
Lecythis pisonis	0-5	5.27	1.99^{defg}	0.18^{bcd}	0.23^{lm}	0.04^{ghij}	1.46^{b}	0.32^{efgh}
	5-15	5.25	1.61^{efghi}	0.17^{ab}	0.08^{m}	0.03^{gh}	1.31^{a}	0.29^{defg}
	15-30	5.87	1.00^{ijk}	0.13^{bcd}	0.00^{j}	0.02^{h}	1.12^{a}	0.25^{de}
	30-45	4.92	0.84^{defg}	0.12^{bc}	0.00^{d}	0.01^{fg}	0.79^{abc}	0.20^{ef}
Licania hypoleuca	0-5	5.02	1.63^{j}	0.14^{f}	1.61^{d}	0.07^{bcd}	1.31^{bcd}	0.35^{de}
	5-15	4.96	1.33^{l}	0.12^{h}	1.34^{defg}	0.05^{cde}	1.08^{abcd}	0.27^{def}
	15-30	4.92	0.93^{k}	0.09^{g}	0.32^{fgh}	0.02^{fgh}	0.78^{cde}	0.24^{de}
	30-45	4.85	0.82^{efg}	0.09^{i}	0.04^{d}	0.01^{efg}	0.70^{bcd}	0.24^{cde}
Pradosia lactescens	0-5	4.91	2.15^{bcd}	0.18^{bcd}	0.81^{ijk}	0.05^{fghij}	0.84^{efgh}	0.24^{ghi}
	5-15	4.83	1.76^{cdef}	0.11^{efg}	0.51^{l}	0.04^{fgh}	0.60^{gh}	0.17^{ij}
	15-30	4.73	1.23^{cdef}	0.10^{efg}	0.02^{ij}	0.03^{efgh}	0.58^{defg}	0.14^{ijkl}
	30-45	4.67	0.91^{cdefg}	0.10^{efgh}	0.00^{d}	0.01^{defg}	0.45^{fghi}	0.12^{ghi}
CONTROL SITES								
Primary forest	0-5	4.69^{cde}	1.99^{defg}	0.15^{ef}	0.96^{hij}	0.08^{bc}	1.23^{bcd}	0.36^{de}
	5-15	4.67^{def}	1.42^{jkl}	0.12^{h}	0.43^{lm}	0.05^{bcd}	0.54^{ghij}	0.21^{de}
	15-30	4.72^{bcdefg}	1.02^{hijk}	0.10^{fg}	0.06^{ij}	0.05^{ab}	0.34^{hijk}	0.12^{jkl}
	30-45	4.66^{e}	0.77^{g}	0.09^{hi}	0.00^{d}	0.03^{ab}	0.25^{ijk}	0.10^{hi}
Secondary forest	0-5	5.15^{jkl}	2.25^{abc}	0.22^{b}	2.46^{b}	0.07^{bcde}	2.20^{a}	0.62^{a}
	5-15	5.04^{lmno}	1.68^{defgh}	0.16^{abcd}	1.71^{bcd}	0.05^{cde}	0.93^{def}	0.32^{de}
	15-30	4.82^{defg}	1.03^{ghijk}	0.11^{def}	0.60^{d}	0.03^{defgh}	0.52^{fghij}	0.21^{defg}
	30-45	4.62^{de}	0.78^{g}	0.11^{def}	0.03^{d}	0.02^{cdef}	0.32^{hijk}	0.20^{ef}
Mixed-species plantation	0-5	4.67^{cde}	1.74^{hij}	0.16^{def}	1.97^{c}	0.04^{ij}	0.59^{hi}	0.33^{efg}
	5-15	4.62^{de}	1.69^{defgh}	0.17^{ab}	1.52^{cde}	0.03^{gh}	0.40^{hijkl}	0.25^{fgh}
	15-30	4.64^{bcdef}	0.97^{jk}	0.13^{bc}	0.34^{f}	0.02^{h}	0.28^{k}	0.15^{hijk}
	30-45	4.60^{de}	0.79^{fg}	0.11^{def}	0.00^{d}	0.01^{fg}	0.25^{ijk}	0.11^{ghi}

vor those with high nutrient recycling capacity (e.g., *Gmelina arborea*), as well as those adapted to low soil fertility (e.g., *Bowdichia virgilioides*). Mixed-tree plantations can offer ecological advantages to mono-specific plantations: for example, recent experiences in Hawaii have shown that greater nutrient cycling rates by one tree species (in this case, *Albizia falcataria*, a nitrogen-fixing legume) coupled with greater nutrient-use efficiency by another (*Eucalyptus saligna*) allowed for higher stand productivity in mixed stands than in pure stands of either species (Binkley *et al.* 1992). In mixed-species systems, litterfall and litter decomposition are more evenly distributed along the year because of the different timing of the associated species (Garrido and Poggiani 1981/2). Multi-species systems are a promising land-use alternative for poor soils, if information is available on the species' soil improving capacity, economic viability and management needs (Silva 1990b, Montagnini 1992).

TABLE IV
RANKING OF THE TWENTY SPECIES OF THE ARBORETUM BY THEIR INFLUENCE ON SOIL PARAMETERS IN REFERENCE TO PRIMARY FOREST

SPECIES	*EFFECTS ON SOIL PARAMETERS*									
	BD	H_2O	FF	pH	C	N	P	Ca	Mg	K
N-Fixing Species										
Bowdichia virgilioides	-	0	-	-	0	0	0	0	0	0
Centrolobium minus	-	0	-	0	-	0	0	-	-	-
Centrolobium robustum	-	0	-	0	-	-	0	-	-	-
Inga affinis	-	-	+	-	+	+	+	-	+	0
Parapiptadenia pterosperma	0	-	+	-	+	+	-	0	+	0
Pithecelobium elegans	-	-	-	0	0	-	-	-	0	-
Plathymenia foliolosa	-	-	-	0	+	+	-	-	0	-
Non N-Fixing Leguminous Species										
Arapatiella psilophylla	-	0	-	0	0	+	-	-	0	0
Caesalpinia echinata	-	-	0	-	+	-	+	0	0	0
Cassia sp.		0	-	0	0	0	+	-	0	0
Copaifera lucens	-	-	-	-	0	0	-	0	0	0
Dimorphandra jorgei	-	-	-	-	0	+	0	-	0	-
Hymenaea aurea	0	0	-	-	0	0	+	-	-	0
Macrolobium latifolium	+	-	-	0	0	0	-	-	-	-
Other Families										
Bombax macrophyllum	0	-	-	0	-	-	+	-	0	0
Buchenavia grandis	0	+	0	-	0	-	+	-	0	0
Eschweilera ovata	-	+	0	+	-	+	-	0	+	+
Lecythis pisonis	-	+	0	+	0	+	-	0	0	-
Licania hypoleuca	-	+	+	-	-	-	+	0	0	0
Pradosia lactescens	-	-	+	0	0	+	0	-	-	-

Note: BD= bulk density, FF= forest floor accumulation; H_2O= soil moisture.
(-) = less than in forest; 0 = similar to forest; (+) = better than in forest.

TABLE V
N, P, K, CA, MG AND AL CONCENTRATIONS IN LIVE LEAVES OF THE TWENTY SPECIES OF THE ARBORETUM

SPECIES/SITES	NITROGEN (%)	PHOSPHORUS (%)	POTASSIUM (%)	CALCIUM (%)	MAGNESIUM (%)	ALUMINIUM (mg/kg)
Nitrogen-Fixing Leguminous Species						
Bowdichia virgilioides	2.18^{b}	0.07^{cdefgh}	0.62^{def}	0.72^{efg}	0.16^{g}	100^{fg}
Centrolobium minus	2.05^{bc}	0.10^{b}	0.90^{bcd}	1.08^{d}	0.30^{bc}	100^{fg}
Centrolobium robustum	2.16^{b}	0.14^{a}	1.46^{a}	0.50^{ghi}	0.24^{bdef}	40^{g}
Inga affinis	2.61^{a}	0.12^{a}	0.67^{def}	1.11^{cd}	0.19^{efg}	280^{b}
Parapiptadenia pterosperma	2.46^{a}	0.05^{h}	0.58^{efgh}	1.67^{a}	0.35^{b}	120^{ef}
Pithecelobium elegans	1.76^{c}	0.05^{gh}	0.32^{h}	0.48^{ghi}	0.18^{fg}	180^{de}
Plathymenia foliolosa	2.17^{b}	$0.07^{bcdefgh}$	0.64^{def}	0.24^{i}	0.14^{g}	80^{fg}
Non Nitrogen-Fixing Leguminous Species						
Arapatiella psilophylla	1.42^{f}	0.08^{bcd}	1.02^{b}	0.36^{hi}	0.15^{g}	420^{a}
Caesalpinia echinata	1.88^{cde}	0.08^{bcde}	0.67^{def}	1.38^{bc}	0.16^{g}	260^{bc}
Cassia sp.	1.80^{de}	0.07^{cdefgh}	0.33^{gh}	0.90^{def}	0.25^{cde}	200^{cd}
Copaifera lucens	1.99^{bcd}	0.08^{bcdefg}	0.71^{cde}	1.04^{d}	0.14^{g}	120^{ef}
Dimorphandra jorgei	2.16^{b}	0.09^{bc}	0.56^{efgh}	0.36^{hi}	0.14^{g}	100^{fg}
Hymenaea aurea	2.02^{bc}	0.09^{bc}	0.62^{def}	0.61^{gh}	0.21^{defg}	100^{fg}
Macrolobium latifolium	1.50^{f}	0.08^{bcd}	0.52^{efgh}	0.69^{fg}	0.31^{bc}	80^{fg}
Other Families						
Bombax macrophyllum	1.52^{f}	0.06^{defgh}	1.31^{a}	1.02^{d}	0.54^{a}	120^{ef}
Buchenavia grandis	2.02^{bc}	0.09^{b}	0.79^{bcde}	1.56^{ab}	0.25^{cde}	100^{fg}
Eschweilera ovata	1.42^{f}	0.06^{fgh}	0.40^{fgh}	1.01^{d}	0.28^{cd}	200^{cd}
Lecythis pisonis	1.73^{c}	0.08^{bcdef}	0.59^{efg}	1.03^{d}	0.26^{cde}	140^{def}
Licania hypoleuca	1.42^{f}	0.06^{efgh}	0.95^{bc}	0.98^{de}	0.31^{bc}	100^{fg}
Pradosia lactescens	1.19^{g}	0.08^{bcd}	0.67^{def}	0.66^{fg}	0.15^{g}	300^{b}

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REFERENCES

Allen, O. N. and Allen, E. K. (1981): *The leguminosae: A source book of characteristics, uses, and nodulation*. University of Wisconsin Press, Madison, Wisconsin. 812 pp.

Anderson, J. M. and Ingram, J. S. I. (eds.). (1989): *Tropical soil biology and fertility: a handbook of methods*. CAB International. Wallingford, Oxon, UK. 171 pp.

Binkley, D.; Dunkin, K. A.; DeBell, D. and Ryan, M. G. (1992): *Production and nutrient cycling in mixed plantations of* Eucalyptus *and* Albizia *in Hawaii. Forest Science*. 38(2): 393-408.

Briceño, J. A. and Pacheco, R. (eds.). (1984): *Métodos analíticos para el estudio de suelos y plantas*. Editorial de la Universidad de Costa Rica. San José, Costa Rica. 152 pp.

Cadima Zeballos, A.; da Silva, L. F. and Lobão, D. E. (1982): Alterações edáficas provocadas por um sistema de agricultura itinerante em solos de Tabuleiros do Sul de Bahia. *Theobroma*, 12(4):267-272.

Evans, J.; (1987): Site and species selection: Changing perspectives. *Forest Ecology and Management*, 21:299-310.

Garrido, M. A. de Oliveira and Poggiani, F. (1981/82): *Avaliação da quantidade e do conteúdo de nutrientes do folhedo de alguns povoamentos puros e misto de espécies indígenas*. Silvicultura em São Paulo 15/16:1-22.

Gladstone, W. T., and Ledig, F. T. (1990): Reducing pressure on natural forests through high-yield forestry. *Forest Ecology and Management*, 35:69-78.

Leao, A. C. and de Melo, A. A. O. (199?): *Caracteristicas morfológicas, fisico quimicas e mineralógicas dos solos da Estaçao Ecológica Pau-Brasil, Porto Seguro, Bahia*. Theobroma, CEPLAC, Itabuna, Bahia, Brasil.

TABLE VI
PERCENT N, P, K, CA AND MG IN FOREST-FLOOR LITTER LEAVESFOR THE TWENTY SPECIES
OF THE ARBORETUM, PRIMARY AND SECONDARY FOREST, AND MIXED-PLANTATION

Species/sites	Nitrogen	Phosphorus	Potassium	Calcium	Magnesium
Nitrogen-Fixing Leguminous Species					
Bowdichia virgilioides	1.84^{ab}	0.01^{h}	0.08^{fghijk}	1.06^{j}	0.13^{ik}
Centrolobium minus	1.89^{a}	0.04^{a}	0.41^{a}	1.20^{hij}	0.21^{cd}
Centrolobium robustum	1.51^{efgh}	0.04^{a}	$0.08^{fghijklm}$	1.31^{fgh}	0.19^{de}
Inga affinis	1.86^{ab}	0.04^{ab}	0.11^{defi}	1.58^{c}	0.15^{ghi}
Parapiptadenia pterosperma	1.65^{cdef}	0.03^{bc}	0.05^{mn}	1.23^{ghi}	0.17^{efg}
Pithecelobium elegans	1.54^{defg}	0.02^{d}	0.04^{mn}	0.45^{n}	0.10^{jkl}
Plathymenia foliolosa	1.81^{abc}	0.03^{bc}	0.04^{n}	0.41^{n}	0.02^{m}
Non Nitrogen-Fixing Leguminous Species					
Arapatiella psilophylla	1.18^{jlm}	0.02^{de}	0.08^{ghijkl}	0.85^{lm}	0.10^{l}
Caesalpinia echinata	1.49^{gh}	0.03^{bc}	0.07^{hijklm}	2.05^{a}	0.10^{jkl}
Cassia sp.	1.10^{lmno}	0.02^{defg}	0.06^{ijklmn}	0.74^{lm}	0.10^{kl}
Copaifera lucens	1.37^{hil}	0.04^{a}	0.20^{b}	1.16^{hij}	0.17^{efg}
Dimorphandra jorgei	1.69^{bcde}	0.01^{gh}	0.05^{mno}	0.68^{m}	0.16^{kl}
Hymenaea aurea	1.35^{hil}	0.04^{a}	0.12^{de}	0.87^{l}	0.17^{efg}
Macrolobium latifolium	1.04^{mn}	0.02^{fg}	0.05^{mno}	1.21^{ghij}	0.27^{b}
Other Families					
Bombax macrophyllum	1.15^{jlm}	0.02^{efg}	0.02^{efg}	2.08^{a}	0.47^{a}
Buchenavia grandis	1.50^{fgh}	0.04^{ab}	0.10^{defgi}	1.77^{b}	0.18^{e}
Eschweilera ovata	0.97^{no}	0.02^{efg}	0.12^{de}	1.09^{ij}	0.26^{b}
Lecythis pisonis	1.23^{ijl}	0.04^{ab}	0.09^{fghij}	1.31^{efg}	0.16^{efg}
Licania hypoleuca	0.82^{op}	0.02^{d}	0.15^{c}	1.36^{defg}	0.16^{fgh}
Pradosia lactescens	0.71^{p}	0.02^{def}	0.11^{defgi}	0.81^{lm}	0.14^{hi}
Control Sites					
Primary forest	1.71^{bce}	0.02^{d}	0.09^{efghi}	1.49^{cdf}	0.18^{ef}
Secondary forest	1.78^{abc}	0.03^{c}	0.13^{cd}	1.53^{c}	0.23^{c}
Mixed-species plantation	1.15^{jlm}	0.02^{def}	0.06^{jklmn}	0.82^{lm}	0.17^{efg}

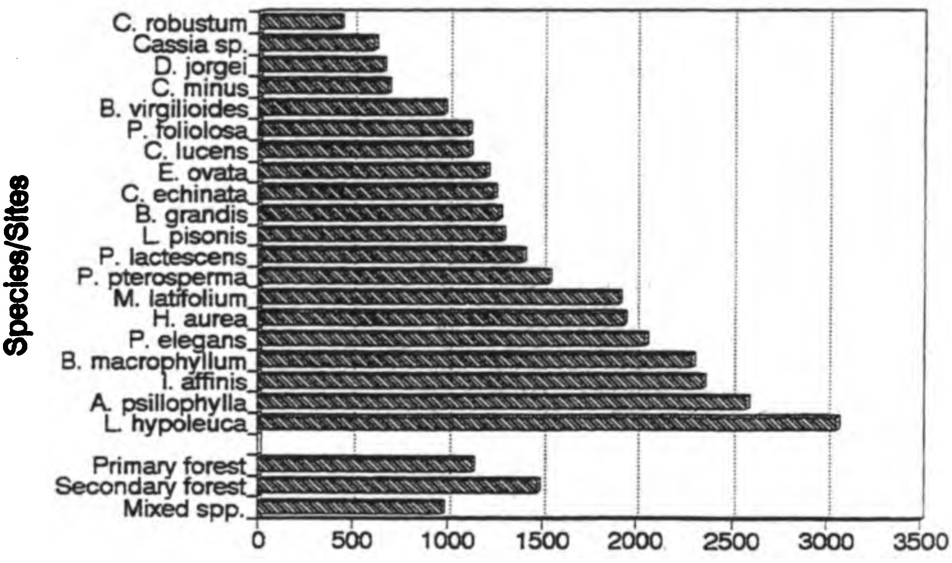

Fig. 3. Total Forest Floor Litter

McNeely, J. A.; Miller, K. R.; Reid, W. V.; Mittermeier, R. A. and Werner, T. B. (1990): *Conserving the World's Biological Diversity*. The World Bank, World Resources Institute, International Union for the Conservation of Nature, Conservation International and World Wildlife Fund. Gland, Switzerland. 193 pp.

Montagnini, F. (1990): Ecology applied to agroforestry in the humid tropics. pp. 49-58. In: R.A. Goodland (ed.) *Race to Save the Tropics. Ecology and Economics for a sustainable future*. Island press, Washington, D.C.

Montagnini, F. (1992): *Mixed-tree plantations with native trees: land-use systems for economic returns and soil restoration.* Experiments in Costa Rica and Argentina. *Agroforestry Today*, 4(3): 4-6.

Montagnini, F. and Sancho, F. (1990): Impacts of native trees on tropical soils: a study in the Atlantic lowlands of Costa Rica. *Ambio.* 19(8):386-390.

Montagnini, F. and Sancho, F. (1992): Nutrient budgets of young plantations with native trees: strategies for sustained management. In: W. Bentley and M. Gowen (eds.). *Forests and wood-based biomass energy as rural development assets.* Proceedings of a workshop held in Old Saybrok (CT, USA), February 23-27, 1992. Winrock International Institute for Agricultural Development. Morrilton, Arkansas, USA. In press.

Nair, P. K. R. (1989): The role of trees in soil productivity and protection. pp. 567-589 In Nair, P. K. R. (ed.). *Agroforestry systems in the tropics.* Kluwer Academic Publishers/International Council for Research in Agroforestry. Dordrecht, The Netherlands.

Reference Methods for Soil Testing. (1980): *Council on soil testing and plant analysis.* 1111 Plant Science Building. University of Georgia. Athens, Georgia. 130 pp.

Sánchez, P. A.; Palm, C. A.; Davey, C. B.; Szott, L. T. and Russell, C. E. (1985): Tree crops as soil improvers in the humid tropics? Pp. 327-350. In M .G. R. Cannell and J. E. Jackson (eds.). *Atributes of trees as crop plants.* Institute of Terrestrial Ecology. Natural Environmental Research Council. Abbots Ripton, Huntingdon, England.

Santana, M. B. M.; Pereira, G. C. and Morais, F. I. (1977): *Métodos de análise de solos, plantas e água utilizados no laboratório do setor de fertilidade do CEPEC.* Centro de Pesquisas do Cacau, CEPLAC, Ilheus-Itabuna, Bahia, Brasil. 28 pp.

Silva, L. F. (1983): *Influencia de cultivos e sistemas de manejo nas modificações edáficas dos oxisols de tabuleiro (Haplorthox) do sul da Bahia.* Belem (Brazil): CEPLAC, Departamento Especial da Amazônia.

Silva, L. F. (1988): Alterações edáficas provocadas por essencias florestais implantadas em solos de tabuleiro no Sul da Bahia. *Theobroma.* 18(4):259-267.

Silva, L. F. (1990a): *Interação solo-vegetação em floresta primária e capoeira do ecossistema de tabuleiro do sul da Bahia.* Agrotrópica. CEPLAC, Itabuna, Bahia, Brasil.

Silva, L. F. (1990b): *Manejo dos recursos naturais dos trópicos e suas consequencias, contradições e perspectivas de uso em agricultura sustentavel.* Seminario Internacional sobre Investigacion en Recursos Naturales para la Producción Agropecuaria. Bogotá, Colombia, 19-23 Noviembre, 1990.

da Vinha, S. G.; Ramos do T., J. S. and Hori, M. (1976): Inventario Florestal. In: Comissão Executiva do Plano da Lavoura Cacaueira, *Recursos Florestais.* Ilheus, BA. Brasil. CEPLAC/IICA. pp. 20-212. (Diagnóstico Socioeconómico da Região Cacaueira. v. 7).

da Vinha, S. G. and Pereira, R. C. (1983): *Produção de folhedo e sua sazonalidade em 10 especies arbóreas nativas no Sul da Bahia. Theobroma.* 13(4):327-341.

da Vinha, S. G., Carbalho A. M. de e Luiz Silva, A.M. (1985): Taxa de decomposição do folhedo de dez especies de árvores nativas no sul da Bahia. Brasil. *Theobroma* 15(4): 207-212.

da Vinha, S. G. e Lobão, D. E. V. P. (1989): *Estação Ecológica Pau Brasil - Porto Seguro, Bahia.* Centro de Pesquisas do Cacau. Itabuna. Bahia. Brazil. 41 pp.

Young, A. (1989): *Agroforestry for soil conservation.* Science and Practice of Agroforestry. C.A.B. International and International Council for research in Agroforestry. Wallingford. UK. 276 pp.

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EVOLUCION DE LA REGENERACION NATURAL EN DOS SISTEMAS DE APROVECHAMIENTO Y BOSQUE NATIVO NO PERTURBADO EN LA PROVINCIA DE MISIONES - REPUBLICA ARGENTINA.

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RESUMEN

La Provincia de Misiones cuenta con superficies cubiertas por bosques nativos en diferentes estados de degradación cuya recuperación aún no ha sido evaluada. En este trabajo se examina la regeneración de especies forestales nativas en un bosque aprovechado bajo dos sistemas de corta: diámetros mínimos de corta y espaciamiento uniforme, con respecto a la situación original. Se releva la regeneración en 5 clases de tamaños, desde su germinación hasta un máximo de 10 cm de diámetro a la altura del pecho (dap), utilizando parcelas permanentes de 5, 15 y 30 m^2. Considerando el total de renuevos en todas las clases de tamaños y especies, se encontraron 22.266 renuevos/ha en el bosque que había sido sometido a corte basado en diámetros mínimos y 54.333 renuevos/ha bajo sistema de corte por espaciamiento uniforme, a los 3 años de la intervención. En un bosque sometido al sistema de diámetros mínimos de corte 30 años atrás, la cantidad de renuevos por ha fue de 49.999 renuevos/ha. En bosque nativo no explotado se hallaron 32.833 renuevos/ha. Estos resultados se comparan con otro muestreo más intensivo para sistema de corte por diámetros mínimos y bosque sin explotar, llegándose a valores similares. Se evaluó la cobertura de copas y el tipo de sotobosque en cada tratamiento. Las aperturas del dosel como resultado de los aprovechamientos no siempre benefician a la regeneración arbórea, ya que el aumento de la luminosidad favorece el predominio de bambúseas, las cuales a su vez compiten fuertemente con los renovales. El tratamiento silvicultural a largo plazo tendiente a la regeneración de la masa arbórea debe contemplar el manejo del sotobosque.

Palabras clave: selva subtropical oriental, Misiones, sistemas de aprovechamiento, regeneración natural

SUMMARY

A uniform spacing method of selective cutting was recently implemented in the 5,340 ha Guaraní Reserve, Misiones, Argentina, to mantain species diversity and enhance forest productivity. In this article we compare tree regeneration in forests cut by diameter limit and by uniform spacing. Five size classes were considered up to 10 cm d.b.h. (diameter at breast height) using 5, 15 and 30 m^2 plots. Three years after cutting, 22,266 seedlings/ha were found in the forest cut by diameter limits, 54,333 seedlings/ha in the forest cut by uniform spacing, and 32,833 seedlings/ha in undisturbed forest. In another forest cut by diameter limits 30 years ago, a total of 49,999 seedlings/ ha were found. Similar trends were found for saplings of commercial value. The species composition of the understory was more heterogeneous in the forest cut by uniform spacing than by diameter limits. These results suggest that the uniform spacing method contributes to higer tree and understory species diversity.

Key words: eastern subtropical forest, Misiones, selective cutting systems, natural regeneration

INTRODUCCION

La Selva Misionera es un bosque subtropical húmedo localizado en la Provincia de Misiones, Noreste de la República Argentina (25° lat.S, 45° long.O). Esta Provincia cubre una superficie de 30.000 km^2, que representa aproximadamente el

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Los ensayos en estudio se encuentran instalados en la región de la Selva Subtropical Oriental (Provincia Paranaense) ubicada al Noreste de la Provincia de Misiones en la República Argentina. La Selva Misionera comprende la extensión más austral del bosque pluvial amazónico (PERTICARARI,1992). El clima de la región corresponde al tipo Cfa, según Koppen, mesotérmico, constantemente húmedo y subtropical, con precipitaciones anuales de 1700 a 2400 mm, distribuídas en todos los meses del año. La temperatura media del mes más cálido (enero) es de 25°C con máximas de 39°C, y la temperatura media del mes más frío (julio) es de 14°C con mínimas absolutas de -6°C (EIBL y col., 1994).

El área demostrativa y experimental de Guaraní - Departamento Guaraní - Misiones, 26°15'lat.S; 54°15'long.O y 267 a 574 msnm, se encuentra situada al este de la provincia, cerca de la frontera con Brasil, entre las localidades de San Pedro y El Soberbio, y a 170 km de Eldorado. La Reserva fue establecida en 1975 cuando el Gobierno Provincial le cedió el área a la UNaM, (Universidad Nacional de Misiones) que a su vez delegó la administración a la Facultad de Ciencias Forestales. Debido a su composición florística y condiciones físicas, los bosques de la reserva son representativos de una gran parte de los bosque nativos de la provincia (UNaM 1992). La Facultad dedicó la Reserva como sitio experimental para el estudio de métodos de manejo y utilización del bosque de manera económicamente atractiva que al mismo tiempo mantengan la integridad del ecosistema. La mayor parte de la reserva permanece inexplotada, ya que sólo un 20% ha sido dedicada a uso experimental. Una pequeña población indígena (Guaraní) se encuentra aún viviendo en una porción de la reserva. Los indígenas utilizan métodos de cultivo tradicionales, los cuales luego de su abandono han dado lugar a campos en diferentes estados de sucesión natural.

Como referencia se comparó la regeneración en un bosque situado en Eldorado- Departamento Eldorado, 26o23'lat.S, 54o40' long.O y 160 msnm, de clima semejante al de Guaraní, en el cual se han realizado estudios de dinámica de la regeneración en parcelas permanentes (EIBL y col. 1993). En este sitio la explotación de las mejores especies de importancia comercial data la década de 1960.

En ambos sitios los suelos predominantes son Ultisoles, del gran grupo kandiudultes (US Soil Taxonomy), conocidos regionalmente como tierra colorada o suelo rojo profundo (LASERRE,1968/69). Son arcillosos, con predominancia de sesquióxidos y caolinita, ácidos (pH en agua 5 - 5.5, bien drenados, bien estructurados, profundos, con materia orgánica en superficie generalmente superior a 3% CIP (Capacidad de intercambio catiónico) entre 10 - 20 cmol/kg y porcentaje de saturación de bases mayores del 50%

MATERIALES Y METODOS

Se instalaron parcelas permanentes en cuatro sitios con diferentes tratamientos silviculturales. **SITIO 1**: Reserva Guaraní, tratamiento de la masa por diámetros mínimos de cortas, aproximadamente 60 ha, realizado en 1990 (GRANCE y MAIOCCO,1993); **SITIO 2**: Reserva Guaraní, cortas selectivas por espaciamiento uniforme, 100 ha, realizado en 1991 (GRANCE y MAIOCCO,1993); **SITIO 3**: Reserva Guaraní, situación de bosque no perturbado, 100 ha; **SITIO 4** : Eldorado, diámetros mínimos de cortas, 4,5 ha, realizado en la década del 60 (EIBL y col., 1993). En todos los casos los aprovechamientos se realizaron extrayendo únicamente ejemplares de especies de importancia comercial (Tabla 1).

Al comenzar los estudios de la regeneración, en el SITIO 1, el área basal de la masa fue de 10 m^2/ha, con 105 árboles/ha. En el SITIO 2 el área basal fue de 22 m^2/ha con 280 árboles/ha. En el SITIO 3 el área basal fue de 28 m^2/ha con 300 árboles/ha (GRANCE y MAIOCCO 1993). En el SITIO 4 el área basal fue de 21 m^2/ha con 304 árboles/ha.

Las unidades de muestreo se establecieron como parcelas permanentes para estudios de regeneración a largo plazo sobre 2 (dos) hectáreas en cada sitio. Se utilizaron parcelas de 5m^2 para la clase de renuevos más pequeñas (CLASE 1 <10 cm de altura), 15 m^2 para las clases intermedias (CLASE 2, de 10 a 49 cm de altura y CLASE 3 de 50 a 149 cm de altura) y 30 m^2 para las clases superiores (CLASE 4 de 150 a 299 cm de altura y CLASE 5 >300 cm de altura). Los ejemplares son considerados renuevos cuando el dap es inferior a los 10 cm. Estos tamaños de parcelas se escogieron a partir de experiencias anteriores en las cuales se comparó la variabilidad encontrada en el número de individuos para cada clase de altura de renuevos, en parcelas de diferentes tamaños (EIBL y col. 1993). Estos métodos son similares a los utilizados en estudios de regeneración natural de bosques aprovechados en los trópicos húmedos (SCHMITT y BARITEAU 1989, ASHTON 1990, GONZALEZ Y CHAVEZ, 1994).

blanco (9.18%) y la más frecuente grapia (100%) y guatambú blanco (80%). Mientras que en el SITIO 2 (Tabla 7), además de las anteriores se encontró incienso (Grupo A) y anchico colorado (Grupo B1). Las especies más abundantes para este Sitio fueron grapia (31.77%) y anchico colorado (7.27%) y las más frecuentes grapia (100%) y laurel guaicá (71%).

En el SITIO 3 (Tabla 8) se encontró guatambú, laurel guaicá, incienso (Grupo A) y anchico colorado y grapia en el grupo B1. En este Sitio no se encontró cedro ni cacheta, dos especies de importancia comercial que se registraron en SITIOS 1 y 2. La especie más abundante para este Sitio fué laurel negro (26.73%) esta última del grupo comercial B2 y las más frecuentes grapia (100%), laurel negro (100%) y guatambú blanco (50%).

En el SITIO 4 (Tabla 9) se encontró incienso, laurel guiacá, guatambú y cedro (Grupo A), y anchico colorado, grapia y caña fístola (Grupo B1), lo cual lo hace similar al SITIO 2. Para este Sitio las especies más abundantes fueron laurel guaicá (10.24%) y laurel amarillo (9.31%) esta última del grupo comercial B2 y las más frecuentes laurel amarillo (83%), cancharana (75%) esta última del grupo comercial B2, laurel guaicá (58%), incienso (50%), guatambú blanco (50%) y cedro (42%).

Regeneración de especies arbóreas en Guaraní: parcelas circulares

Los resultados obtenidos con parcelas circulares de 5 y 25 m^2 mostraron que para el SITIO 1 los totales generales de renuevos por ha para los tres grupos comerciales fueron similares a aquéllos encontrados en muestreos de parcelas permanentes rectangulares (estos valores no incluyen la Clase 5 de tamaño) (Tabla 10). Comparando los valores encontrados para la Clase 4 solamente, los totales para cada grupo también fueron similares a los encontrados con parcelas rectangulares. Tabla 12.

En el caso del SITIO 3 (Tabla 11) el número total de individuos para todas las clases y grupos de especies comerciales es similar para ambos métodos empleados.

Tipos de sotobosque y cobertura

En el SITIO 1, en todas las parcelas se encontraron bambúseas: *Bambusa guadua* Humb.& Bonpl. (tacuaruzú), *Chusquea ramosisima* Lind. (tacuarembó), *Guadua trinii* (Nees) Ruprecht. (yatebó), *Merostachys clausseni* Munro (tacuapí). En el 73% de los casos se encontraron helechos arborescentes tales como *Alsophilla* spp., *Diksonia* spp. (Fig. 4)(Tabla 13). En el SITIO 2 la composición del sotobosque fue más heterogénea, también con predominio de bambúseas pero con presencia de latifoliadas, principalmente de arbustos tales como *Actinostemun concolor*, *Bahuinia* spp, *Piper* spp., *Solanum* spp, *Trichilia* spp. y enredaderas tales como *Bahuinia* spp. En el SITIO 3 únicamente se encontraron bambúseas y en el SITIO 4 se halló una distribución casi proporcional entre bambúseas, helechos, latifoliadas y enredaderas, como así también una pequeña proporción de pastos: *Eragrostis* spp., *Paspalum* spp., *Setaria* spp., *Sporobolus* spp., *Trichloris* spp., lo cual lo asemeja más al SITIO 2. (Fig. 4)(Tabla 13).

En cuanto a la frecuencia de los tipos de cobertura (Fig. 5)(Tabla 14) en el SITIO 1 predominaron parcelas abiertas y en segundo lugar cobertura media. En el SITIO 2 predominaron parcelas de cobertura cerrada, en menor proporción media y muy pocas parcelas abiertas. En el SITIO 3 predominaron las parcelas abiertas y se encontró una proporción similar de parcelas de cobertura media y cerrada. En el SITIO 4 predominó la cobertura media y en iguales proporciones la abierta y cerrada.

DISCUSION

La mayor abundancia de renovales en la Clase de tamaño 2 en todos los sitios estudiados (Fig. 1)(Tabla 2) se podría explicar por la diferente estacionalidad en la germinación de las especies más abundantes, lo cual produce un gran número de individuos de ciertas especies en un momento dado. Estos individuos al cabo de varios meses con su crecimiento pasan a la clase superior, siendo reemplazados en las clases inferiores por aquellos individuos que germinen en su momento. Esta característica se vio menos marcada en el Sitio 1 (Fig. 1), posiblemente debido a la mayor apertura del dosel provocado por la extracción de madera más intensa con el sistema de diámetros mínimos de corta. La mayor luminosidad estimularía una germinación masiva de semillas de la reserva del suelo. En esta situación pueden germinar gran cantidad de semillas de especies pioneras que se encontraban en la reserva del suelo en estado latente (BAZZAZ, 1990).

La menor cantidad de renovales en las Clases de tamaño 3, 4 y 5 (Fig. 1) se debería a la acción de depredadores de renovales, enfermedades, la permanencia del recurso.

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BIBLIOGRAFIA

* Ashton, P. M. S, Gunatilleke,C.V.S., and Gunatilleke, I.A.U.N., 1995. Seedling survival and growth of four Shorea species in a Sri Lankan rainforest. *Journal of Tropical Ecology*, **11**, 263-279.

* Bazzaz, F. A. 1990. Regeneration of tropical forests: physiological responses of pioneer and secondary species. *In*: Gomez-Pompa, A., Whitmore,T.C., and Hadley,M. (Eds.), *Rainforest Regeneration and Management*, MAB Series, UNESCO. Paris. pp.91-118.

* Brown, N. 1993. The implications of climate and gap microclimate for seedling growth conditions in a Bornean lowland rain forest. ***Journal of Tropical Ecology***. 9, 153-168.

* Buschbacher, R. J. 1990. Natural forest management in the humid tropics: Ecological, social, and economic considerations. ***Ambio*** **19**(5): 253-258.

* Clark, D. and Clark, D. 1984. Spacing dynamics of a tropical forest tree: evaluation of the Janzen-Connell model. ***American Naturalist***. 124 (6): 769-709.

* Clark, D. and Clark,D. 1992. Life history diversity of canopy and emergent trees in a neotropical rain forest. ***Ecological Monographs*** 62(3): 315-344.

* Deschamps, J. R. y Ferreira, M. O. 1987. Estudios sobre las comunidades postclimáxicas de Misiones, I: Los campos abandonados o «capueras». En: Instituto Subtropical de Investigaciones Forestales (ISIF) (Ed.)*IV Jornadas Técnicas:Bosques Nativos Degradados. Tomo II*. Universidad Nacional de Misiones. Facultad de Ciencias Forestales. Eldorado. Misiones. Argentina. pp.36-45.

* Eibl,B; Szczipanski,L;Rios,R & Vera,N. 1993. Regeneración de especies forestales nativas de la selva Misionera. En:Instituto Subtropical de Investigaciones Forestales (ISIF)(Ed.). *VII Jornadas Técnicas: Bosque Nativo:uso, manejo y conservación.*. Universidad Nacional de Misiones. Facultad de Ciencias Forestales. Eldorado . Misiones. Argentina. pp.100-122.

* Eibl, B; Silva, F; Bobadilla, A; Weber, E & Gonseski,D. 1994 . *Boletín Meteorológico Aeródromo Eldorado. Período 1985/1994*. Instituto Subtropical de Investigaciones Forestales (Ed.). Facultad de Ciencias Forestales. Universidad Nacional de Misiones. Eldorado, Misiones, Argentina.

* Fahler, J. C. 1989. Estado actual de la tecnología y manejo de las forestaciones en el NE Argentino. *IV Jornadas Forestales de Entre Ríos (Argentina,.)*, 3, 1-23.

* Finegan, B. and Sabogal, C. 1988. El desarrollo de sistemas de producción sostenible en bosques tropicales húmedos de bajura: un estudio de caso en Costa Rica. ***El Chasqui (Costa Rica)*** 17:3-24.

* Gonzalez, E. and Chavez, E. 1994. Estructura y composición de un bosque húmedo tropical explotado en la región norte de Costa Rica. *Yvyraretá (Argentina)* 5,57-69.

* Gotz,I. 1987. Estudio de la masa de un bosque nativo de Misiones. Espesura, área basimétrica y volúmenes. Instituto Subtropical de Investigaciones Forestales (ISIF)(Ed.)*IV Jornadas Técnicas:Bosques Nativos Degradados. Tomo II.* Universidad Nacional de Misiones. Facultad de Ciencias Forestales. Eldorado. Misiones. p.46-61.

* Graaf, N. R. and Poels, R. L. H. 1990. The Celos management system: A polycyclic method for sustained timber production in South American rain forest. En: Anderson, A.B. (Ed.) *Alternatives to Deforestation: Steps Toward Sustainable Use of the Amazon Rain Forest.* Columbia University Press. New York. pp.116-127.

* Grance,L & Maiocco,D. 1993. Comparación de dos criterios de entresaca en el bosque subtropical Misionero. En:Instituto Subtropical de Investigaciones Forestales (Ed.) ***VII Jornadas Técnicas sobre Bosque Nativo:uso, manejo y conservación.*** Facultad de Ciencias Forestales. Universidad Nacional de Misiones. Eldorado.Misiones. Argentina. pp.284-299.

* Grance, L. y Maiocco, D. 1995. Enriquecimiento del bosque nativo con *Bastardiopsis densiflora* (Hook et Arn) Hassl, cortas de mejora y estímulo a la regeneración natural *Yvyraretá (Argentina)*.N° 6 (en imprenta).

FIGURA 1: Total de renuevos por hectárea para todas las clases de altura en todos los sitios.

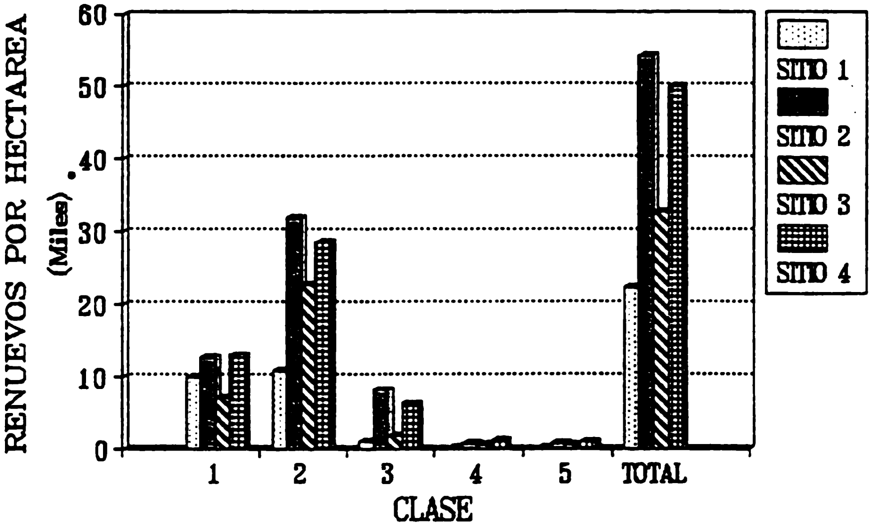


FIGURA 2: Renuevos por hectárea para especies comerciales según sitio

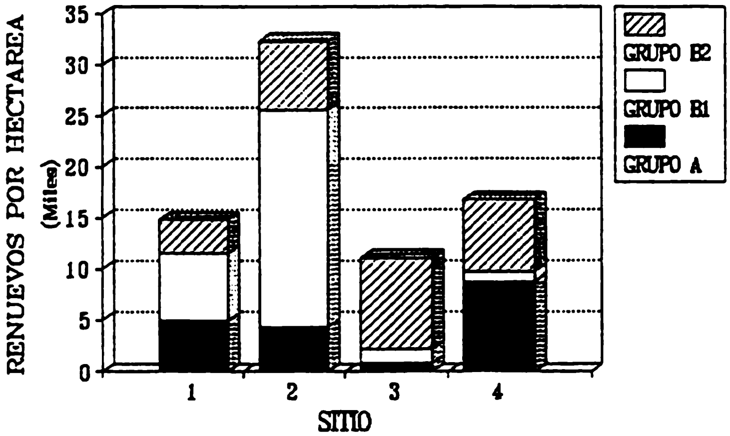
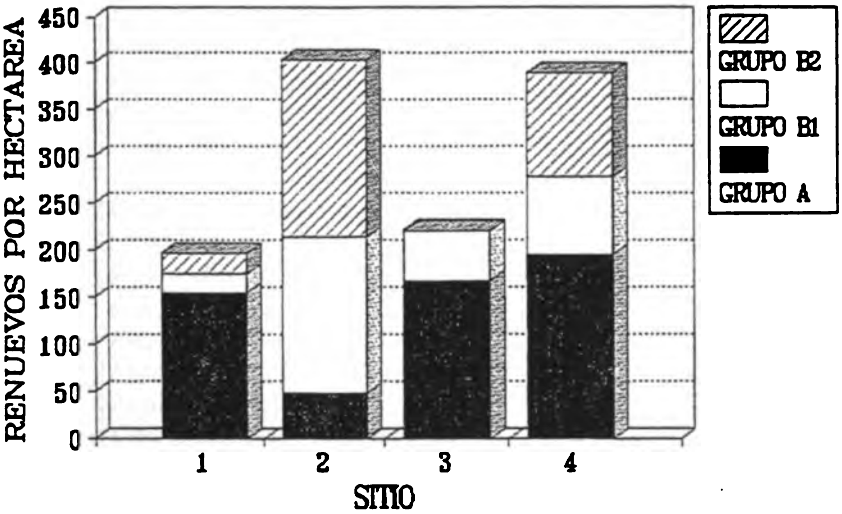


Figura 3: Renuevos por hectárea de especies de clase 4 y 5, según sitio.



SITIO 1	SITIO 2	SITIO 3	SITIO 4
OTRAS ESPECIES	OTRAS ESPECIES	OTRAS ESPECIES	OTRAS ESPECIES
YUQUERI GUAZU	CANELA DE VENADO	YUQUERI GUAZU	COLITA
FAGARA	FAGARA	JABORANDI	JABORANDI
	ISAPUHY	PATA DE VACA	ISAPUHY
	BURRO CAA	SAMOHU	BURRO CAA
	RABO MACACO	RABO MACACO	RABO MACACO
	RESINOSO	RESINOSO	MANDIOCA BRAVA
	COCU	NO IDENT	COCU
	ANONACEA	INGA	ANONACEA
	TIMBO BLANCO	TALA	TALA
	YERBA MATE	VASURIÑA	YERBA MATE
	TARUMA	ALECRIN	ALECRIN
			NIÑO RUPA
			GUATAMBU AMARILLO
			MOLLE
			HORQUETERO
			LECHERON
			FUMO BRAVO
			ÑANDIPA
			LAURACEA

ANEXO II
LISTADO DE ESPECIES RELEVADAS COMO RENUEVOS EN LOS CUATRO SITIOS

	NOMBRE CIENTIFICO	FAMILIA
Aguay	*Chrysophyllum gonocarpum*	Sapotáceas
Alecrín	*Holocalyx balansae*	Leguminosas
Ambay	*Cecropia adenopus*	Moráceas
Anchico blanco	*Albizzia hassleri*	Leguminosas
Anchico colorado	*Parapíptadenia rígida*	Leguminosas
No identif.	*No identif.*	Anonáceas
Burro caá	*Casearia sylvestris*	Flacurtiaceas
Cacheta	*Didymopanax morototoni*	Araliaceas
Camboatá blanco	*Matayba eleagnoides*	Sapindáceas
Camboatá colorado	*Cupania vernalis*	Sapindáceas
Cañafístula	*Peltophorum dubium*	Leguminosas
Cancharana	*Cabralea canjerana*	Meliaceas
Canela de Venado	*Helietta apiculata*	Rutáceas
Caroba	*Jacarandá spp.*	Bignoniaceas
Catiguá	*Trichilia spp.*	Meliaceas
Cedro	*Cedrela fissilis*	Meliaceas
Ceibo	*Erythrina falcata*	Leguminosas
Cocú	*Allophylus edulis*	Sapindáceas
Colita	*Cordia ecalyculata*	Borragináceas
Fagara	*Fagara spp.*	Rutáceas
Fumo bravo	*Solanum verbascifolium*	Solanáceas
Grapia	*Apuleia leiocarpa*	Leguminosas
Guabirá	*Campomanesia xanthocarpa*	Mirtáceas
Guatambú amarillo	*Aspidosperma australe*	Apocináceas
Guatambú blanco	*Balfourodendron ridelianum*	Rutáceas

Nombre común	Nombre científico	Familia
Anchico colorado	*Parapiptadenia rigida* (Benth.)Brenan	Leguminosae (Mimosoidea)
Timbó	*Enterolobium contortisiliquum* (Vell)Morang	Leguminosae (Mimosoidea)
Grupo B2		
Laurel amarillo	*Nectandra lanceolata* Nees	Lauraceae
Laurel ayuí	*Ocotea diospirifolia* (Meissn.)Mez.Emend.Hassl	Lauraceae
Laurel negro	*Nectandra saligna* Nees.et Mart	Lauraceae
Seibo	*Erythrina falcata*	Leguminosae (Papilionoidea)
Mora amarilla	*Chlorophora tinctoria* (L.)Gaudich	Moraceae
Carne de vaca	*Styrax leprosus* Hook et Arn	Styracaceae
Rabo molle	*Lonchocarpus muehlbergianus* Hassl.	Leguminosae (Papilionoidea)
Persiguero	*Prunus subcoriacea* (Chod.et Hassl.)Koehn	Rosaceae
Marmelero	*Ruprechtia laxiflora* Meissn	Poligonaceae
Cancharana	*Cabralea canjerana* C.D.C	Meliaceae
Azota caballo	*Luehea divaricata* Mart	Tiliaceae
Loro blanco	*Bastardiopsis densiflora*(Hook et Arn.)Hass	Malvaceae
Rabo itá	*Lonchocarpus leucanthus* Burk	Leguminosae (Papilionoidea)
Guayubira	*Patagonula americana* Linné	Boraginaceae

TABLA 2: Renuevos por hectárea por clases de altura para todas las especies según sitio

CLASE	SITIO 1	SITIO 2	SITIO 3	SITIO 4
1	9999	12714	7053	13026
2	10891	31808	22780	28470
3	1022	8238	1778	6389
4	199	810	556	1084
5	155	762	666	1030
TOTAL	22266	54333	32833	49999

TABLA 3: Renuevos por hectárea en tres grupos de especies comerciales, para todas las clases de altura según sitios.

GRUPO	SITIO 1	SITIO 2	SITIO 3	SITIO 4
A	4956	4333	833	8760
B 1	6600	21214	1389	1030
B 2	3355	6810	9000	7043
TOTAL ESP.COM.	14911	32357	11222	16833

TABLA 4: Renuevos por hectárea de especies comerciales de las clases de altura 4 y 5, según sitio.

GRUPO	SITIO 1	SITIO 2	SITIO 3	SITIO 4
A	155	48	167	196
B 1	22	167	56	84
B 2	22	191	0	112
TOTAL ESP.COM.	199	406	223	392

TABLA 5: Análisis de variancia (LSD) para numeros de renuevos entre sitios y clases de altura.

RENUEVOS POR HECTAREA	NIVEL DE SIGNIFICANCIA	
	TODOS LOS SITIOS	SITIOS 1 y 2
TOTAL	0.0183	0.0005
COMERCIALES	0.0593	0.0450
COMERCIALES PARA CLASES 4 y 5	0.4608	0.1521

SITIO 1: Explotación según diámetro mínimo de corta.
SITIO 2: Explotación por entresaca selectiva por espaciamiento uniforme.
SITIO 3: Sin explotación. Suelo pedregoso.
SITIO 4: Explotación intensiva por diámetros mínimos, hace 30 años.

TABLA 8: SITIO 3. Número de renovales por clase de altura por grupos comerciales y Otras y Totales. Abundancia y Frecuencia.

ESPECIES por GRUPOS	CLASES I	II	III	IV	V	TOTAL	ABUNDANCIA RELATIVA	FRECUENCIA
GRUPO A								
GUATAMBU BLANCO		333	111		111	555	1.69	50
LAUREL GUAICA		111				111	0.34	17
INCIENSO			111		55	167	0.51	33
TOTAL A		444	222		166	833	2.54	67
GRUPO B1								
GRAPIA		889	111	56		1056	3.21	100
ANCHICO COLORADO		333				333	1.02	33
TOTAL B1		1222	111	56		1389	4.23	100
GRUPO B2								
LAUREL NEGRO	5000	3556	222			8778	26.73	100
LAUREL AYUI		111				111	0.34	17
PERSIGUERO			111			111	0.34	17
TOTAL B2	5000	3667	333			9000	27.41	100
TOTAL COMERCIaA.	5000	5333	667	56	166	11222	34.18	100
OTRAS ESPECIES	2053	17447	1111	500	500	21611	65.82	100
TOTAL/ha.	7053	22780	1778	556	666	32833	100	100

TABLA 9: SITIO 4. Número de renovales por clase de altura por grupos comerciales y Otras y Totales. Abundancia .

ESPECIES por GRUPOS	CLASES I	II	III	IV	V	TOTAL	ABUNDANCIA RELATIVA	FRECUENCIA
GRUPO A								
INCIENSO		889	56			945	1.89	50
LAUREL GUAICA	3173	1833		28	84	5118	10.24	58
GUATAMBU BLANCO		1167	278	28	56	1529	3.06	50
CEDRO	501	667				1168	2.34	42
TOTAL A	3674	4556	334	56	140	8760	17.52	83
GRUPO B1								
ANCHICO COLORADO		556	167	56	28	807	1.61	25
GRAPIA		167				167	0.33	25
CAÑAFISTOLA		56				56	0.11	8
TOTAL B1		779	167	56	28	1030	2.06	58
GRUPO B2								
LAUREL AMARILLO	668	3874	111			4653	9.31	83
RABO MOLLE	167	500	111			778	1.56	25
PERSIGUERO		167				167	0.33	17
MARMELERO				28		28	0.06	8
LAUREL NEGRO		444				444	0.89	33
CANCHARANA		667	222		56	945	1.89	75
LAUREL AYUI					28	28	0.06	17
TOTAL GRUPO B2	835	5652	444	28	84	7043	14.09	100
TOTAL COMERC.	4509	10987	945	140	252	16833	33.67	100
OTRAS ESPECIES	8517	17483	5444	944	778	33166	66.33	100
TOTAL/ha	13026	28470	6389	1084	1030	49999	100	100

Otras Especies : Ver Anexo I

THE INFLUENCE OF NATIVE TREE SPECIES ON SOIL CHEMISTRY IN A SUBTROPICAL HUMID FOREST REGION OF ARGENTINA

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Fernández, R., Montagnini, F., and Hamilton, H. 1997. The influence of native tree species on soil chemistry in a subtropical humid forest region of Argentina. *Journal of Tropical Forest Science*. **In Press.**

Abstract

The effects of native tree species on the chemical characteristics of soil were studied under five native species from Misiones Province, Argentina: *Balfourodendron riedelianum* (Engler) Engler, *Cordia trichotoma* (Vell.) Johnst, *Bastardiopsis densiflora* (Hook et Arn) Hass, *Enterolobium contortisiliquum* (Vell) Morang, and *Ocotea puberula* (Nees et Mart.) Nees, using adjacent areas free of trees as controls.

Results from the two-way ANOVAs showed the importance of C, N and Ca as key elements that may be influenced by soil cover and depth. The highest total soil carbon and nitrogen contents were found under the crowns of *B. densiflora*, *C. trichotoma*, and *E. contortisiliquum*. The pH values were highest under *B. densiflora* and *C. trichotoma* in the first 15 cm of soil depth while *B. riedelianum* had the lowest pH, including that of the control site. *B. densiflora*, *C. trichotoma* and *E. contortisiliquum* had the highest sum of bases in the first 15 cm of soil depth. Extractable calcium under the canopy of *B. densiflora* and *C. trichotoma* was significantly different from that of control plots for up to 30 cm in soil depth. Soil magnesium content under the crowns of *E. contortisiliquum* was significantly different from that of the control up to 30 cm depth. Significant differences for potassium were found up to 15 cm in depth below *B. densiflora*, *C. trichotoma* and *E. contortisiliquum*. Of the species studied, *B. densiflora* showed the greatest promise for use in rehabilitation of degraded lands.

Key words: plant-soil relationships- nutrient cyling- native species- Misiones- Argentina- subtropical.

Introduction

In northeast Argentina, the Province of Misiones has an area of 30,000 km^2, about 1% of the country total (Margalot 1985); however its forests provide an estimated 66% of sawnwood and over 85% of plywood to Argentina (Ministerio de Ecología y Recursos Naturales Renovables 1993). Most of Misiones' timber production comes from plantations of Pinus spp., Araucaria angustifolia Bert. O. Kze., Eucalyptus spp., and Melia azedarach (L.) var. gigantea. Although Misiones contains approximately 200,000 ha of planted forest, the area cultivated with native species constitutes less than 10% of this figure and, with the exception of Araucaria angustifolia, is practically insignificant. This situation is partially due to insufficient information regarding adequate silvicultural methods for the establishment and management of native species. Yet alternatives for land use are clearly necessary to support current economic and ecological needs: inappropriate land use and management often has led to soil degradation (Fernández 1984) and to subsequent abandonment of lands in the region.

Pure and mixed planting of certain tree species, such as Gmelina arborea Roxb. (Sánchez et al. 1985), Cordia trichotoma (Vell) Johnst (Silva 1983), and other species from tropical and sub-tropical regions, can result in improved soil fertility by increasing soil nutrient content (Montagnini et al. 1994; Montagnini & Sancho 1994, 1993, 1990; Montagnini et al. 1991; Young 1989). Knowledge of native tree species that are both economically valuable and that restore fertility is especially relevant because, in addition to the eventual improvement of edaphic conditions, planting these species provides a source of income for farmers.

In the Misiones Province, studies have been conducted to determine plant-soil relationships with exotic species, such as Pinus spp. (Fernández & Imbach 1988, Fernández 1987), but to date no studies have been published involving native species. This article presents the effects of five native tree species from forests in Misiones on the chemical characteristics of soil. The results reported here are complemented by a related study of the chemical composition of biomass of the same native species (Montagnini et al. 1995).

Materials and methods

Sampling sites were located in the humid forests of Eldorado and Montecarlo, Misiones Province (25-28° S, 53-56° W; 160 m a.s.l.). According to the Köppen classification, the climate is of the Cfa type (Ometto 1981), continually humid and sub-tropical with average annual precipitation from 1700 to 2400 mm, distributed proportionally over all months of the year. The average temperature of the hottest month (January) is 25° C, with absolute highs of 39° C; the average temperature for the coldest month (July) is 14° C, with absolute lows of -6° C.

The five native species used for this study were typical of forests in Misiones Province: Balfourodendron riedelianum (Engler) Engler, Cordia trichotoma (Vell)Johnst, Bastardiopsis densiflora Hook et Arn, Enterolobium contortisiliquum (Vell) Morang and Ocotea puberula (Nees et Mart.) Nees. Species were selected for their economic value and to complement on-going studies that are evaluating tree species' growth on degraded sites.

Three sites were chosen in areas with varying species and land use histories (Table 1). Site 1 was located in a pasture with interspersed trees that is currently still in use. Site 2 was located in a yerba mate or South American holly (Ilex paraguariensis Saint Hilaire) plantation where some regeneration of original forest was observed, and Site 3 was located in a plantation of O. puberula that had been established in an old pasture.

According to the USDA Soil Taxonomy system, the soils in Site 2 belong to the great group kandiumult known locally as red soil, and soils in Sites 1 and 3 belong to the hapludalf group (gray-brown soils). They are soils of medium fertility and good drainage generally used in the Province for perennial crops and plantation forestry.

Five circular plots, each 80 m^2 in size, were delimited to sample soils under five randomly selected trees of each species. Five soil sub-samples were taken approximately 1 meter from the trunk of the trees, making up one composite sample. In addition, five samples composited in the same manner as for the tree plots, were taken from areas outside the influence of the tree crowns, at five randomly selected sites. Samples were collected at the following depths: 0-5, 5-15, 15-30, and 30-45 cm.

These control plots had similar area and similar edaphic and topographic conditions as the areas covered with the tree species. In Site 1 soils under B. riedelianum were compared with soils from the control area free of trees. In Site 2 the same control area was used to compare with soils under B. riedelianum, B. densiflora, C. trichotoma and E. contortisiliqum. In Site 3, similar to Site 1, soils under O. puberula were compared with soils in the control area free of trees.

Soils were air dried and passed through a 2 mm sieve. Analysis for pH, extractable Ca, Mg, K and P were performed at Yale School of Forestry and Environmental Studies in New Haven, Connecticut, following standard procedures for tropical soils (Anderson & Ingram 1989, Council on Soil Testing and Plant Analysis 1980). The pH was measured in a 1:2.5 mixture of soil and deionized water using a combination electrode and a Fisher Accumet 915 digital pH meter. Ca, Mg, K, and P were extracted with Melich's solution (0.025 N H_2SO_4 and 0.05 N HCl) using a 1:5 proportion of soil-solution.

Cations were measured using a Thermo Jarrel Ash Inductively Coupled Atom Scan Spectrometer (Thermo Jarrell Ash, Franklin, Massachusetts). Extractable phosphorus was measured colorimetrically at 880 nm wavelength using a Perstorp Analytical Flow Solution Analyzer (Perstorp Analytical, Wilsonville, Oregon) after extraction in Melich's solution and reaction with ascorbic acid and a molybdate reagent. Total carbon and nitrogen were measured by dry combustion using a Leco CNH-600 Carbon Nitrogen Determinator (Leco Corp., St. Joseph, Michigan).

All variables were compared among soils for each site and depth under each tree species and the respective area of control free of trees. The results were processed using two-way and one-way analysis of variance, using LSD as tests for means (n=5, P<0.05).

Results and discussion

Results from the two-way ANOVAs showed that for Site 1 (B. riedelianum and control) there were significant differences among covers for N and Mg, and among soil depths for all elements, with no significant cover x depth interactions. For Site 2 (B. riedelianum, B. densiflora, C. trichotoma, E. contortisiliqum, and control) significant differences were found among covers and depths for all elements; in addition, significant cover x depth interactions were detected for C, N and Ca. Finally, in Site 3 (Q. puberula and control) significant differences among covers were found for Ca and K, and among depths for Ca, Mg and P, with no significant cover x depth interactions. Results of this analysis highlight the importance of C, N and Ca as key elements that may be influenced by treatment, potentially including significant effects with depth, in the soils of the study area.

Data in Tables 2, 3 and 4 correspond to the concentrations of elements in the four soil depths under the crowns of each of the five species and three control areas free of trees. Concentrations of all nutrients and carbon were high in comparison to values for the region (INTA 1993). However, the soil chemical methods used in this study differ from those typically employed in the region.

The greatest differences for soil total carbon content among covers were found in the first 15 cm of soil depth for all three sites (Tables 2, 3 and 4). Significant differences in soil carbon content were observed under the crowns of B. densiflora, where carbon concentrations were approximately twice those found in areas free of trees (Table 3). The carbon content under the canopies of C. trichotoma and E. contortisiliquum, though not significantly different from each other, was higher than that in the open area (Table 3).

Findings for soil total nitrogen were similar to those of carbon, with N concentrations under B. densiflora being double those in the control area. For Site 1, total N content in the topsoil under B. riedelianum was significantly higher than in the control (Table 2). Concentrations of N in tree tissue for the five species of this study were all relatively high in comparison with other forest species (Montagnini et al. 1995). In particular, N foliar concentration of B. densiflora was 2.87%, and that of B. riedelianum was 3.29%. However, the positive influence of these two species on soil N also depends on their rates of biomass production and recycling characteristics. Future studies of biomass production and decomposition and nutrient release by these species would help to clarify this topic.

Extractable phosphorus was detected only at Site 3, although there were no significant differences between P content under O. puberula and that of the control area (Table 4). The detection limit of the chemical method used in this study is about 2 mg/kg of soil P. Generally, the extractable P content of soil of the region lies below the detection limit (INTA 1993). A more sensitive method would help to detect potential differences among treatments.

Soil pH under B .densiflora canopy was highest followed by those under C. trichotoma and E. contortisiliquum canopies in Site 2 (Table 3). The soil under B. riedelianum canopy, in Sites 1 and 2, had the lowest pH, with values lower than those found in the control area (Tables 2 and 3).

Differences in soil pH relate to the distinct cation content found under the treatments. Thus, significant differences in soil extractable calcium concentrations up to 30 cm in depth were found under the canopies of C. trichotoma and B. densiflora (the highest) in comparison with B. riedelianum, E. contortisiliquum and the control (the lowest) (Table 3). The highest concentrations of extractable magnesium were found under E. contortisiliquum, B. densiflora and C. trichotoma, with significant differences up to 15 cm in depth, in comparison with B. riedelianum and the control. Potassium showed significant differences below B. densiflora, C. trichotoma, and E. contortisiliquum, where it was higher than below B. riedelianum and the control, up to 15 cm in depth.

In addition, values for the sum of bases (Ca + Mg + K) in the first 15 cm for *E. contortisiliquum*, *C. trichotoma*, and *B. densiflora* were much higher below their crowns than in the control, especially for *B. densiflora*. In contrast, values were similar both inside and outside the area of crown influence for *B. riedelianum* (Site 1 and 2) and *O. puberula* (Site 3). The higher value for *B. densiflora* is probably due to higher levels of soil carbon below this species.

Values of extractable bases under the canopy of *C. trichotoma* reported in the present study coincide with the findings by Silva (1983), who detected levels between two and three times higher in soil calcium, magnesium and potassium in plantations of this species in comparison with native forest soils in southern Bahia, Brazil.

It is interesting to note that similar values for extractable bases under *B. densiflora* canopies have also been found other tropical forest species of the same family, Malvaceae. For example, higher soil concentrations of exchangeable Ca and higher pH under *Gmelina arborea* plantations at Jari (Brazil) have been reported by Jordan and Russell (1983) and Sanchez *et al*. (1985). Likewise, higher extractable Ca under *G. arborea* plantations in Nigeria in comparison with native forest were reported by Adejunwon and Ekanade (1988). Other studies have reported similar findings for *G. arborea* plantations in Malaysia (Halenda 1993). In a comparison of soil properties under four plantation species in Darjeeling, India, the highest exchangeable Ca and K was found under *Tectona grandis* L., another Malvaceae species (Singh *et al*. 1985). Possibly species of the Malvaceae family tend to accumulate and recycle high amounts of bases in their aerial biomass, as already mentioned above for *B. densiflora* (Montagnini *et al*. 1995).

Of the five species studied, it is worth emphasizing the potential of *B. densiflora* to restore soil fertility, given its high values of the variables examined. B. densiflora is a pioneer species that frequently colonizes abandoned areas and has performed well in enrichment planting of degraded forests within the region (Eibl et al. 1994, Grance & Maiocco 1995). In addition, its wood is considered to be of good commercial value.

It is important to note that, because of differences in land use on the three study sites and a lack of other sites for comparison, interpretation of these results is limited. It would be advisable to confirm results, especially those that are most striking, with similar studies at other sites. However, the results presented here do suggest that certain indicated species hold great potential for use in the rehabilitation of soils.

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References

ADEJUWON, J. O. & EKANADE, O. 1988. Soil changes consequent upon the replacement of tropical rain forest by plantations of Gmelina arborea, Tectona grandis and Terminalia superba. Journal of World Forest Resource Management 3: 47-49.

ANDERSON, J. M. & INGRAM, S. I. (Eds.). 1989. Tropical Soil Biology and Fertility: A Handbook of Methods. CAB International, Wallingford, England. 171 pp.

COUNCIL ON SOIL TESTING AND PLANT ANALYSIS. 1980. Reference methods for soil testing. 1111 Plant Science Building, University of Georgia, Athens, Georgia. 130 pp.

EIBL, B., GRANCE, L., MAIOCO., D & SZCZIPANCKI, L. 1994. Técnicas de enriquecimiento y conducción de la regeneración natural en áreas de bosques nativos degradado, provincia de Misiones, República Argentina. Pp. 419-428 in Actas I Sinpósio Sul Americano "Recuperacao de áreas degradadas". Foz de Iguacu, Parana, Brasil. 6-10 November 1994. FUPEF, Curitiba.

FERNÁNDEZ, R. 1984. La habilitación de las tierras en la selva misionera y consecuencias sobre la degradación de los suelos. Pp. 71-99 in Actas Segundas Jornadas Técnicas, Facultad de Ciencias Forestales. UNaM, Eldorado, Argentina.

FERNÁNDEZ, R. 1987. Influencia del sistema desmonte-reforestación con *Pinus spp.* sobre algunas características químicas de los suelos. Ciencia del Suelo 52: 123 - 129.

FERNÁNDEZ, R.& IMBACH, A. 1988. Alteraciones en características químicas de ultisoles destinados al cultivo de *Pinus spp* respecto de su condición original bajo bosque nativo. Pp. 345 - 347 in Actas VI Congreso Forestal Argentino. Tomo II:. Santiago del Estero.

GRANCE, L.& MAIOCO, D. 1995. Enriquecimiento del bosque nativo con Bastardiopsis densiflora (Hook et Arn) Hassl, cortas de mejora y estímulo a la regeneración natural en Guaraní, Misiones, Argentina. Yvyraretá (Argentina) 6: 29-44.

HALENDA, C. J. 1993. Aboveground biomass production and nutrient accumulation of a Gmelina arborea plantation in Sarawak, Malaysia. Journal of Tropical Forest Science 5: 429-439.

I.N.T.A., INSTITUTO NACIONAL TECNOLOGÍA AGROPECUARIA. 1993. Características químicas de los suelos de la Provincia de Misiones. Unpublished. E.E.A. Montecarlo, Montecarlo, Misiones, Argentina.

JORDAN, C. F. & RUSSELL, C. E. 1983. Jarí: productividad de las plantaciones y pérdida de nutrientes debida al corte y a la quema. Interciencia 8: 294-297.

MARGALOT, J.A. 1985. Geografía de Misiones. Industria Gráfica del Libro. Buenos Aires.

MINISTERIO DE ECOLOGÍA Y RECURSOS NATURALES RENOVABLES. 1993. Censo de la Industria de Transformación Mecánica de la Madera de la Provincia de Misiones, Septiembre 1992-Julio 1993. Ministerio de Ecología y Recursos Naturales Renovables, Posadas, Misiones, Argentina.

MONTAGNINI, F. & SANCHO, F. 1990. Impacts of native trees on tropical soils: A study in the Atlantic lowlands of Costa Rica. Ambio 19 (8): 386 - 390.

MONTAGNINI, F., SANCHO, F., RAMSTAD, K. &. STIJFHOORN, E. 1991. Multipurpose trees for soil restoration in the humid lowlands of Costa Rica. Pp. 41- 58 in Taylor, D.A. & Mc Dicken, K.G. (Eds.). Research on Multipurpose Tree Species in Asia. Winrock International Institute for Agricultural Development, Bangkok, Thailand.

MONTAGNINI, F.& SANCHO, F. 1993. Reciclaje de nutrientes en plantaciones jóvenes con árboles nativos: Estrategias para un manejo sustentable. Yvyraretá (Argentina) 4: 9 - 23.

MONTAGNINI, F.& SANCHO, F. 1994. Aboveground biomass and nutrients in young plantations of indigenous trees on infertile soils in Costa Rica: Implications for site nutrient conservation. Journal of Sustainable Forestry 1 (4): 115 - 139.

MONTAGNINI, F., FANZERES, A. & GUIMARAES DA VINHA, S. 1994. Studies on restoration ecology in the Atlantic forest region of Bahia, Brazil. Interciencia 19 (6): 323-330.

MONTAGNINI, F., FERNÁNDEZ, R. & HAMILTON, H. 1995. Relaciones entre especies nativas y la fertilidad de los suelos. Parte 1: Contenido de elementos en la biomasa. Yvyrareta (Argentina) 6: 5 - 12.

OMETTO, J.C. (Ed.). 1981. Bioclimatología Vegetal. Agronómica Ceres Ltda, Sao Paulo, Brasil.

SANCHEZ, P. A., PALM, C. A., DAVEY, C. B., SZOTT, L. T.& RUSSELL, C. E. 1985. Tree crops as soil improvers in the humid tropics? Pp. 327-350 in Cannell, M. G. R. and Jackson, J. E. (Eds.). Attributes of trees as crop plants. Institute of terrestrial Ecology. Abbots Ripton, Huntingdon, England.

SILVA, L. F. 1983. Influencia de cultivos e sistemas de manejo nas modificacoes edáficas dos Oxisols de tabuleiro (Haplortox) do sul da Bahía. CEPLAC, Departamento Especial da Amazonia, Belém, Brasil.

SINGH, S. B., NATH, S., PAL, D. K. & BANERJEE, S. K. 1985. Changes in soil properties under different plantations of the Darjeeling forest division. Indian Forester 111: 90-98.

YOUNG, A. 1989. Agroforestry for soil conservation. ICRAF, CAB International, Wallingford, Inglaterra. 276 pp.

Table 1. General characteristics of the three study sites.

Table 2. Concentrations of elements at four different soil depths under the canopy of *B. riedelianum* and in the open at Site 1. For each soil variable and depth, differences among means are statistically significant when followed by different letters (n=5, P<0.05).

Table 3. Concentrations of elements at four different soil depths under the canopy of four tree species and in the open at Site 2. For each soil variable and depth, differences among means are statistically significant when followed by different letters (n=5, P<0.05).

Table 4. Concentrations of elements at four different soil depths under the canopy of *O. puberula* and in the open at Site 3. For each soil variable and depth, differences among means are statistically significant when followed by different letters (n=5, P<0.05).

Table 1.

Site	Location	Species	Soil Type	Land Use
1	Municipality of Sgo. Liniers	*Balfourodendron riedelianum*	Hapludalf	Pasture with interspersed trees
2	Municipality of Victoria	*Balfourodendron riedelianum* *Cordia trichotoma* *Bastardiopsis densiflora* *Enterolobium contortisiliquum*	Kandiumult	*Ilex paraguariensis* plantation
3	Municipality of Montecarlo	*Ocotea puberula*	Hapludalf	*Ocotea puberula* plantation on an old pasture site

Table 2.

Areas Sampled	Depth (cm)	C	N	P	pH	Ca	Mg	K	S(1)
		%		ppm		cmol/kg			
B.riedelianum canopy	0-5	4.0a	0.56a	-	6.0	11.9a	2.5a	0.78a	15.2
	5-15	2.6a	0.43a	-	5.7	8.8a	1.7a	0.50a	11.0
	15-30	1.9a	0.33a	-	5.6	7.5a	1.3a	0.47a	6.3
	30-45	1.2a	0.23a	-	5.4	6.2a	1.3a	0.32a	7.8
Control (open area)	0-5	3.4a	0.43b	-	5.8	9.9a	1.6b	0.72a	12.2
	5-15	2.6a	0.38a	-	5.7	9.0a	1.2a	0.54a	10.7
	15-30	1.8a	0.26a	-	5.8	7.6a	0.9a	0.40a	8.9
	30-45	1.1a	0.19a	-	5.8	6.9a	0.9a	0.26a	8.1

(1) Sum of the Bases: Ca + Mg + K

Table 3.

	Depth	C	N	P	pH	Ca	Mg	K	S(1)
Areas Sampled	(cm)	%		ppm		cmol/kg			
B.riedelianum canopy	0-5	2.6b	0.34ab	-	5.8	7.1bc	1.7c	0.55bc	9.4
	5-15	2.0ab	0.28ab	-	5.6	5.9b	1.6c	0.49bc	8.0
	15-30	1.5bc	0.23ab	-	5.1	3.8d	1.1c	0.36b	5.3
	30-45	1.0ab	0.16a	-	4.8	3.0b	0.5b	0.29b	3.8
B. densiflora canopy	0-5	6.3a	0.65a	-	7.1	20.4a	3.4ab	1.28a	25.1
	5-15	3.2a	0.38a	-	6.7	12.8a	2.7ab	0.95a	16.5
	15-30	2.1ab	0.29a	-	6.0	8.9a	2.4ab	0.83a	12.1
	30-45	1.2ab	0.17a	-	6.3	5.9a	2.1a	0.72a	8.7
C. trichotoma canopy	0-5	4.0ab	0.46ab	-	6.4	13.6ab	2.6abc	0.79b	17.0
	5-15	2.6ab	0.33ab	-	6.3	10.3a	1.9bc	0.63b	12.8
	15-30	2.0ab	0.26ab	-	6.2	8.0ab	1.6bc	0.52ab	10.1
	30-45	1.3a	0.20a	-	5.9	5.9a	1.2ab	0.45ab	7.6
E.contortisiliquum canopy	0-5	3.4ab	0.39ab	-	6.1	8.7bc	3.5a	0.67b	12.9
	5-15	2.3ab	0.29ab	-	5.7	6.4b	3.0a	0.49b	9.9
	15-30	2.3a	0.27ab	-	5.9	6.3bc	3.0a	0.5ab	9.8
	30-45	2.3ab	0.21a	-	5.6	4.4ab	2.4a	0.38ab	7.2
Control (open area)	0-5	2.2b	0.27b	-	5.8	6.3c	2.4bc	0.26c	9.0
	5-15	1.9b	0.23b	-	5.8	6.6b	1.6c	0.25c	8.5
	15-30	1.3c	0.20b	-	5.9	5.5cd	1.2dc	0.23b	6.9
	30-45	0.9b	0.16a	-	5.5	4.8a	1.0ab	0.23b	6.0

(1) Sum of the Bases: Ca + Mg + K

Table 4.

	Depth	C	N	P	pH	Ca	Mg	K	S(1)
Areas Sampled	(cm)	%		ppm		cmol/kg			
O. puberula canopy	0-5	4.4a	0.59a	6.09a	6.1	17.3a	4.7a	1.11a	23.1
	5-15	3.7a	0.45a	5.11a	6.2	16.7a	4.4a	1.08a	22.2
	15-30	2.7a	0.34a	3.04a	6.3	15.4a	3.4a	1.01a	18.8
	30-45	1.5a	0.33a	2.20a	6.3	13.1a	1.9a	1.03a	16.0
Control (open area)	0-5	4.3a	0.48a	5.19a	6.3	18.6a	5.5a	1.05a	25.2
	5-15	3.0a	0.39a	3.39a	6.3	17.5a	4.3a	0.88b	22.7
	15-30	2.2a	0.30a	2.87a	6.5	17.1a	3.3a	0.88a	21.3
	30-45	1.4a	0.31a	2.46a	6.6	15.9b	2.3a	1.00a	19.2

(1) Sum of the Bases: Ca + Mg + K

Running head:

Montagnini, Eibl, Szczipanski, and Ríos

Regeneration and Diversity Following Selective Cutting

Tree Regeneration and Species Diversity Following Conventional and Uniform Spacing Methods of Selective Cutting in a Subtropical Humid Forest Reserve[1]

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ABSTRACT

There are a variety of ways to diminish the negative impacts of forest management for timber on biodiversity. A pilot project using a uniform spacing method of selective cutting was recently implemented in the 5,340 ha Guaraní Reserve, Misiones, Argentina, to design adequate management schemes for the subtropical forests of the region. Uniform spacing involves moderate timber harvesting and careful selection of remnant trees. In this article we compare tree regeneration in forests experimentally cut by diameter limit and uniform spacing methods. Seedlings of five size classes from 10 cm to 3 m height were sampled using rectangular nested plots. Three years after cutting, an average of 54,330 and 22,270 seedlings /ha (all height classes combined) of commercial and non-commercial species were found in the forest cut by uniform spacing and by minimum diameter, respectively. In an adjacent uncut forest there were 34,900 seedlings /ha, and in another forest cut by minimum diameters 30 years ago there were 50,000 seedlings /ha. The forest cut by uniform spacing had the highest numbers of commercial seedlings/ha, with three times as many as the forest cut by minimum diameter three years ago and twice as many as the forest treated by minimum diameters 30 years ago. The forest cut by uniform spacing and the forest treated by minimum diameters 30 years ago had the highest diversity of understory plants other than trees, as well as heterogeneous canopy cover, while the other two forests had a predominance of bamboo in the understory and more open canopy conditions. Although lack of site replication limits interpretation of the results, these early findings suggest that the uniform spacing method can be an ecologically sound forest management option for the region.

Key words: biodiversity; forest regeneration; logging methods; minimum diameter; Misiones; subtropical; uniform spacing

RESUMEN

Existen una variedad de maneras de disminuir los impactos negativos del manejo de bosques sobre la biodiversidad. Recientemente se implementó un proyecto piloto que utilizó un método de espaciamiento uniforme de corte selectivo, en la Reserva Guaraní, de 5.340 ha, en Misiones, Argentina, con el objetivo de diseñar esquemas de manejo para los bosques subtropicales de la región. El método de espaciamiento uniforme implica niveles de explotación moderados y selección cuidadosa de árboles residuales. En este artículo se compara la regeneración arbórea en bosques explotados experimentalmente por diámetro mínimo y por espaciamiento uniforme. Se muestrearon los renovales en cinco clases de altura de 10 cm a 3 m (< 10 cm d.a.p.) usando parcelas rectangulares, se examinó la composición de especies no arbóreas del sotobosque y se midió el grado de apertura del dosel. Tres años después del corte, se encontró un promedio de 54.330 renuevos/ha (combinando todas las clases de altura) de especies comerciales y no-comerciales en el bosque cortado por espaciamiento uniforme, mientras que se hallaron solamente 22.270 renuevos/ha en el bosque cortado por diámetro mínimo. En un bosque sin cortar se encontraron 34.800 renuevos/ha, y en otro bosque cortado por diámetro mínimo 30 años atrás se encontraron 50.000 renuevos/ha. La mayor cantidad de renuevos de importancia comercial se encontraron en el bosque cortado por espaciamiento uiforme, con el triple de la cantidad encontrada en el bosque cortado por diámetro mínimo, y el doble de la cantidad encontrada en el bosque cortado por diámetro mínimo 30 años atrás. La composición de especies del sotobosque y la apertura del dosel fueron más heterogéneas en espaciamineto uniforme y diámetro mínimo 30 años atrás, mientras que en los otros dos sitios predominaron bambúseas en el sotobosque y se encontraron mayores aperturas del dosel. A pesar de que la falta de repeticiones limita la interpretación de estos resultados preliminares, éstos sugieren que el método de espaciamiento uniforme puede proveer una opción de manejo adecuada para los bosques de la región.

Palabras clave: biodiversidad; diámetro mínimo; espaciamiento uniforme; métodos de corta; Misiones; regeneración natural; subtropical.

Many tropical and subtropical humid forests have been subject to human intervention for centuries, but with the low intensity of management usually employed, environmental functions and species biodiversity were generally well preserved (Gómez-Pompa 1991). In contrast, most current management schemes for the production of timber result in much greater physical disruption of the forests. Management for timber carries with it an unavoidable risk of extinction of local endemics and other species vulnerable to disruption of their habitat (Sayer & Whitmore 1991). However, a variety of practices can greatly diminish the impacts of forest management on biodiversity. For example, it has been suggested that selective logging should strive for minimal canopy opening and minimal soil disturbance (Cheah 1991, Vanclay 1992). Damage to the forest structure can be reduced by decreasing the intensity of timber harvesting and by improving logging practices (Bertault & Sist 1995, Sayer *et al.* 1995).

Many tropical countries have recently changed forest management regulations to make them compatible with the principle of sustained yield and maintenance of biodiversity (Boyle & Sayer 1995). These regulations tend to be very broad and are generally appropriate for application to large tracts of forest (generally >10,000 ha) (Silva 1992, Boyle & Sayer 1995). Specific guidelines are needed to cover a vast array of forest conditions at both large and small scales. These guidelines should be adjusted to suit the scale and objectives of management as well as the light requirements of the species involved. In addition, methods are needed to evaluate ecological indicators that can serve to verify effects of management on long-term forest productivity and maintenance of biodiversity (Lowe 1995). Evaluation of tree regeneration following timber extraction is needed to design treatments that favor the growth of desired individuals. In the context of other ecological, economic and social criteria and indicators, forest regeneration can also serve as an indicator of the performance of a particular management system (Dawkins 1958, Cheah 1978, Schmitt & Bariteau 1989, Lamprecht 1990, Bertault & Sist 1995).

The extent of subtropical forest in Misiones, Argentina, is currently about 1,100,000 ha, about half of which is in national and state parks, leaving the other half for management (Ministerio de Ecología y Recursos Naturales Renovables 1985, 1993). Under the minimum diameter cutting method prevalent in Argentina, commercial species are extracted if they have a minimum stipulated diameter that ranges from 40 to 55 cm d.b.h. (diameter at breast height) depending on the species (Ministerio de Ecología y Recursos Naturales Renovables 1987). This method was set by the government to allow for the extraction of timber and to make forest cutting economically attractive, but it was established without substantial knowledge of the biology and regeneration dynamics of the species involved (Mangieri 1965, Ministerio de Ecología y Recursos Naturales Renovables 1987). When no other regulations are used to complement this method, such as leaving enough residual trees, avoiding excessive canopy opening, or tending of natural regeneration, a number of undesirable effects may follow its application. For example, most of the healthy adults that could serve as future seed sources are extracted, hampering regeneration, especially if important dispersal mechanisms are also absent or diminished. Additionally, extensive canopy openings tend to favor growth of heliophilous understory species such as bamboos and grasses that compete strongly with regeneration of several commercial tree species (Lamprecht 1990, Cheah 1992, Grance & Maiocco 1993).

In the present study, tree regeneration was examined following timber extraction by the conventional minimum diameter method practiced in the region and by a low-intensity, "uniform spacing" method designed for a subtropical forest reserve. Regeneration of commercial and non-commercial species following both methods of selective cutting was compared to that of an uncut forest. The species composition of understory plants other than trees and the degree of canopy closure were also examined. The study was part of a larger program to design techniques for management and rehabilitation of logged forests and abandoned agricultural lands in the region.

STUDY SITE

The Province of Misiones, in northeast Argentina (25-28°S, 53-56°W, 100-800 m elevation), has an area of about 30,000 km^2, less than 1% of the country total (Margalot 1985); however, it produces over 75% of the country's timber (Ministerio de Ecología y Recursos Naturales Renovables 1993). In 1993, Misiones' total production of sawn timber was 831,500 m^3, of which about 30% came from natural forests and 70% from plantations of *Pinus* spp., *Melia azederach* L. and *Araucaria angustifolia* (Bert.) O.K. (Ministerio de Ecología y Recursos Naturales Renovables 1993). In the Köppen system the climate of Misiones is classified as Cfa, where C = a mesothermic climate, f = lack of a defined dry season, and a = subtropical (Eibl *et al.* 1994). Annual precipitation ranges from 1700 to 2400 mm per year. The mean temperature of the hottest month (January) is 25°C with a maximum of 39°C, and the mean temperature of the coldest month (July) is 14°C with a minimum of -6°C (Eibl *et al.* 1994).

The Misiones forest is part of the Paranaense province of the eastern subtropical forest region, and its natural range extends over most of the province (Dimitri 1979). The mixed Paranaense forest formerly covered more than 100,000 km^2 in regions of Argentina, Paraguay and Brazil, but has been reduced to less than 10% of its original size (Chévez & Gil 1995). The Paranaense forest is one of the most diverse ecosystems of both Argentina and Paraguay (Dimitri 1979). In its mature form, the Misiones forest contains an average of about 100 tree species per hectare. The species composition varies with geographical location: for example, the presence of *Araucaria angustifolia* (Bert.)O.K. (pino Paraná) is restricted in the NE part of the province, while *Aspidosperma polyneuron* Müll. Arg. (palo rosa) only occurs in the NW. The complex forest structure includes trees attaining heights of up to 40 m, with no single species reaching importance values (average of relative abundance and relative frequency) >8%, as well as a dense understory of lianas, tree ferns, palms and bamboos, small shrubs, and herbs (Dimitri 1979).

The Guaraní Reserve (26°15' S, 54°15'W, 267-574 m elevation) is a 5,340 ha forest reserve located east of Misiones, near the Brazilian border. The floristic composition and physical conditions of the Guaraní Reserve are similar to those of large areas of Misiones (Universidad Nacional de Misiones 1992). The Guaraní Reserve remains largely unexploited: only 20% of its area has been used for experimental purposes, including the experimental forest cuttings which served as study sites for the present research. No past history of fire disturbance has been recorded for the Guaraní Reserve (Universidad Nacional de Misiones 1992). A small indigenous population (Guaraní) still lives in an area of the Reserve. They use traditional cultivation methods, leaving abandoned fields in different stages of natural succession. Except for the small areas (< 10 ha total) used by the Guaraní Indians, the Guaraní forest was never clear cut; it was kept as a reserve for future exploitation by private and state-owned companies until 1974. The Guaraní Reserve was established in 1975 when the Government of Misiones transferred the area to the National University of Misiones (Universidad Nacional de Misiones, UNaM), who in turn delegated its administration to the School of Forest Science in Eldorado.

The Guaraní forest is part of the 250,000 ha Yabotí Reserve, which was designated a Biosphere Reserve in 1994 (Chévez & Gil 1995). A number of relatively small farms (< 100 ha on average) are scattered throughout the Yabotí Reserve, the majority of which practice some form of subsistence agriculture (generally growing cassava, yams, maize, and a variety of horticultural crops in small home gardens) and small scale timber extraction.

The predominant soils in Guaraní are Ultisols, great group kandiudults (US Soil Taxonomy), regionally known as "red soils" (Laserre 1980). They are deep, clayey, with a predominance of sesquioxide and kaolinite, well drained and well structured, with topsoil organic matter ranging between 3 and 8%, cation exchange capacity of 10-20 cmol/kg, pH in water 5.0-5.5, and base saturation of 50-60%. The relief is rolling hills with slopes ranging from about 5 to 15%.

One of the forests chosen for regeneration studies was on a private farm in Eldorado (26°23'S, 54°40'W, 160 m average elevation). Eldorado is about 200 km from Guaraní and has similar climate and soils (Eibl *et al.* 1993).

METHODS

Site selection.--The present study was conducted in areas of the Guaraní reserve that were subjected to experimental timber cuttings three years ago, using the standard minimum diameter method (MD3) and a uniform spacing method (US3), as described in the next section. The uniform spacing method was applied for the first time in the region and there was just one site available for regeneration studies. The protected status of the Guaraní forest also prevented replication of the method elsewhere in the reserve. An uncut forest (UC) also in Guaraní, and a forest cut by diameter limits 30 years ago (MD30) on a private farm in Eldorado were also used for comparison (Table 1). Only commercially valuable species were extracted in the three logged forests. In the 1960s fewer species had commercial value than in the 1990s, but in Eldorado the timber harvest had been particularly intensive, with extraction of a timber volume similar to the experimental minimum diameter cut in Guaraní (Eibl *et al.* 1993) (Table 1). The study was conducted in 1994-1995.

Experimental logging methods.--Logging intensity in Guaraní was based on results of a pre-felling inventory that was described by Grance & Maiocco (1990, 1993). For the inventory, a total of eight 5,000 m^2 (50 m x 100 m) plots were set randomly throughout the area to be subjected to the experimental cuttings. All trees (>10 cm d.b.h.) of commercial and non-commercial species were censused in the plots and categorized by commercial value and diameter class. For the forest to be cut by minimum diameters, the results of the inventory yielded a potential cutting intensity of 6% of the total number of trees, or 12% of the commercial trees, which corresponded to 21% of the total and 39% of the commercial basal area, respectively (Grance & Maiocco 1990, 1993). These figures may suggest a relatively low cutting intensity, but the impacts of extraction using this method were particularly detrimental for species that grow in patches, such as *Ocotea puberula*, whose density ranged from 0 to 30 trees/ha. In one of the eight plots censused, 90% of *Ocotea puberula* trees had diameters larger than the minimum, thus when using the minimum diameter cutting method, such areas of forest were almost cleared of mature individuals of this species that could serve as seed sources (Grance & Maiocco 1993).

In contrast, in the uniform spacing method, many commercially important trees with diameters large enough to be cut under the diameter limit method were left uncut. In the pre-felling inventory, trees were selected for extraction or marked as residuals for retention according to the following criteria: 1- Species scarcity: exploitation was less intense for the scarcest species; 2- Species horizontal distribution: for the species with a patchy distribution, exploitation was lower in the less dense areas, where only 1-4 trees of commercial size/ha were found; 3- The remaining trees displayed adequate timber characteristics (straight, healthy bole) as well as healthy crowns; 4- The remaining trees were mature individuals, but they did not look too old (i.e., they did not show evidence of senescence: damaged crowns, dead branches or signs of decomposition at the base of the trunk), so that they would produce seeds for a prolonged period of time.

By combining these four criteria, a more homogeneous spatial distribution of residual trees was expected. For example, based on their scarcity (first criterium), a proportion of individuals of each species was left uncut. No individuals of the scarcest species, i.e., those with less than one tree of commercial size/ha, as determined in the pre-felling inventory (such as *Enterolobium contortisiliquum, Parapiptadenia rigida, Peltophorum dubium, Pentapanax warmingiana*), were extracted at all. For the most common species (e.g., *Apuleia leiocarpa, Nectandra* spp., *Ocotea puberula*) only ¼ to ½ of the individuals were extracted, leaving at least 5-8 trees of each species per ha to serve as seed trees. For the species with a patchy distribution (second criterium), cutting intensity was lower in the less dense areas. For example, for the patchily distributed *Ocotea puberula*, only a total of 5 m^3/ ha were extracted using uniform spacing, while 10.7 m^3 /ha were extracted using minimum diameters. In contrast, for *Myrocarpus frondosus*, a more evenly distributed species (0-4 trees of commercial size/ha), extraction was light with both methods (< 1 m^3/ha) (Grance & Maiocco 1993). Finally, use of the maturity and good-health criteria for residual trees was expected to ensure adequate seed sources for natural regeneration following logging.

In both cutting methods, logging roads were opened prior to logging, following prescribed specifications to avoid as much damage as possible during mechanized felling and skidding. Lianas and bamboos were cut with a machete about a month before felling. Directional felling was done whenever possible.

Under the minimum diameter method, a volume of timber comparable to the average for the region (about 37 m^3/ha) was extracted (Table 1). Use of the uniform spacing method resulted in a cutting intensity of about half that by minimum diameter. Likewise, the uniform spacing method resulted in about half as much damage to the remaining trees than in the adjacent forest cut by diameter limits (Grance & Maiocco 1990, 1993).

Tree regeneration studies.--Permanent plots were established at random in each of the three logged forests and the uncut forest. A total of 14, 15, 20 and 12 plots were sampled for each height class in US3, MD3, UC and MD30, respectively. The number of plots in each site is currently being increased to reach 25 plots per site for long term studies of regeneration. The plots were rectangular, with their size varying according to the categories of seedlings/saplings sampled (Fig. 1). Each plot was comprised of four nested subplots. The smallest nested subplots, 1 m x 5 m (5 m^2), were used to sample the smallest seedlings (Class I, <10 cm height). With a set width of 1 m, the subplot length was increased to 15 m to have 15 m^2 subplots for the intermediate size classes (Class II, 10-49 cm height and Class III, 50-149 cm height). Two 15 m^2 subplots side by side formed a 2 m x 15 m (30 m^2) plot for the saplings (Class IV, 150-299 cm height and Class V, >300 cm height but <10 cm d.b.h.).

Seedlings and saplings of commercial and non-commercial species were identified, and their height and number per plot were recorded. The relative density and the relative frequency of commercial species were calculated for each site. Importance values (IV) were calculated as the average of relative density and relative frequency for each commercial species and site. Limitations in site replication at Guaraní, as explained before, resulted in "pseudo-replication" as described by Hurlbert (1984); therefore a conventional analysis of variance could not be used. Instead, means and standard errors were used to graphically compare numbers of tree seedlings among treatments.

Plot sizes and height classes were based on previous research in the same forests: for the smallest height class, 5 m^2 plots gave similar numbers of seedlings/ ha and with a comparable standard deviation to those of 10 m^2 or 15 m^2 plots (Eibl *et al.* 1993). For the intermediate height classes, the number of seedlings/ ha leveled off when plot size was 15 m^2, while the number of saplings only levelled off when using 30 m^2 plots. The use of nested subplots with sizes varying according to seedling size class is common in studies of regeneration following logging of tropical forests (e.g. Schmitt & Bariteau 1989, Ashton 1990).

Characterization of the understory (plants other than trees) and canopy closure.--Frequency of understory species other than trees was calculated as the proportion of the total number of plots which contained a given type of understory plant (bamboos, ferns, grasses, small shrubs). Canopy cover at the center of each 30 m^2 plot was classified as open when the distance between tree crowns was greater than the average horizontal crown diameter; medium, if the distance between crowns was less than their average diameter; and closed, when the crowns overlapped. Plots were classified as having no cover when lying at or near the center of a forest gap whose diameter was larger than the average tree height. Frequency of canopy closure was calculated as the proportion of plots that had each category of canopy cover.

RESULTS

Tree regeneration in the logged and uncut forests.--Comparing the mean number of tree seedlings/saplings of both commercial and non-commercial species, more than twice as many were found in the forest cut by uniform spacing three years ago (US3) (mean = 54,330/ha, standard error = 6870), than in the forest cut by minimum diameter 3 years ago (MD3) (mean = 22,270/ha, s.e. = 4620) (Fig. 2). In the uncut forest (UC) an intermediate number (mean

= 32,830/ha, s.e. = 13,550) seedlings/saplings were found. In the forest cut by the minimum diameter method 30 years ago (MD30) the mean (50,000/ha, s.e. = 11,170) was similar to that found in US3. The greatest differences were found between MD3 and US3, and between MD3 and MD30.

When sorted according to their commercial value, the highest numbers of seedlings of commercial species were again found in US3, and the lowest in UC (Fig. 2). In contrast, the highest numbers of seedlings of non-commercial species were found in MD30, and the lowest in MD3. US3 had about three times as many seedlings of non-commercial species as MD3. UC had a similar number to US3.

UC and MD30 had the highest total (commercial + non-commercial) species richness with 46 species, followed by MD3, which had 34 species, and by US3, which had 28 species (Tables 2 and 3). The uncut forest had the highest richness of commercial species with 18 species, while MD3 had the least richness in this category with 13 species (Table 2). Ten tree/shrub species of no current commercial value were shared by the four forests (Table 3). The highest species richness in this category was found in MD30 with 32 species, followed by UC.

Apuleia leiocarpa was the species of highest relative Importance Value (IV) in US3 and MD3 (34.8% and 31.7%, respectively) (Table 2), while this species ranked second in UC with 14.4%, and ranked one of the lowest in MD30. The Lauraceae (*Nectandra* spp. and *Ocotea* spp.) was the best represented family in all four sites with almost half of the total IV in UC and MD30, but with a relatively smaller value in both recently cut forests, MD3 and US3. - Four commercial species in UC were absent in the other three forests: *Bastardiopsis* *densiflora, Cordia trichotoma, Erythrina falcata* and *Lonchocarpus leucanthus*. *Cedrela fissilis* was the only commercial species found in US3 and MD3 that was not found in UC. Two species were only found in MD30 and were absent in the other three forests: these were *Peltophorum dubium* and *Ruprechtia laxiflora*, although they had relatively low IVs. MD30 had a more evenly distributed range of IVs than the other forests, with a maximum value of 21.9% for *Ocotea diospirifolia*.

In the forest cut by minimum diameter method 3 years ago (MD3), the number of seedlings in the two smallest height classes (< 10 cm and 10-49 cm) were similar to each other, while in the other three forests, the highest number of seedlings were found in the 10-49 cm height class II (Fig. 3). In all four forests, there were only a few individuals in the two larger size categories, 150-299 cm and >300 cm (< 10 cm d.b.h.), which comprised 1% and 4% of the total seedlings, respectively.

Types of understory vegetation and canopy cover.--US3 and MD30 had the highest heterogeneity in understory species composition (plants other than trees). In US3, the species composition of the understory was very heterogenous, with a predominance of bamboos but also with shrubs such as *Solanum* spp. and *Trichilia* spp., and vines such as *Bauhinia* spp. (Fig. 4). In MD3, four species of bamboo were present in all sampled plots: *Bambusa guadua* Humb.& Bonpl. (tacuaruzú), *Chusquea ramosissima* Lind. (tacuarembó), *Guadua trinii* (Nees) Ruprecht. (yatebó), and *Merostachys clausseni* Munro (tacuapí). The arborescent ferns *Alsophila* spp. and *Dicksonia* spp. were found in 73% of the plots (Fig. 4). MD30 was similar to US3 in that there was an almost equal distribution of bamboos, ferns, shrubs and vines, as well as a few grasses, such as *Eragrostis* spp., *Paspalum* spp., *Setaria* spp., *Sporobolus* spp. and *Trichloris* spp. In UC there were only bamboos (Fig. 4).

The more heterogeneous understory found in US3 and MD30 was related to a greater assortment of canopy cover conditions, with varying proportions of plots with open, medium and closed cover found in these forests (Fig. 5). In contrast, the predominance of bamboos in MD3 and UC corresponded to a greater proportion of open plots in these sites.

DISCUSSION

Tree regeneration following timber extraction.--The forest cut by uniform spacing had the highest density of seedlings and saplings of total as well as commercial species, and it also exhibited high diversity of understory plants other than trees. In contrast, the uncut forest had the lowest density of seedlings of commercial species and a predominance of bamboos in the understory. Due to its relatively higher diversity of canopy cover types and more varied understory conditions (Figs. 4 and 5), the forest treated by uniform spacing may have appropriate conditions for growth of a higher number of species than undisturbed forest. Differences in the size of canopy openings created by natural disturbance, or in this case by timber extraction, promote differentiation of regeneration, survival, and growth among tree species (Bazzaz 1990, Brown 1993). Therefore, application of low-intensity logging methods with selection of remnant trees, such as with the uniform spacing system described here, may in the long term result in changes in forest composition, with presumably a larger proportion of desired species than in uncut forests.

In the present research it is probably too early to attribute differences in seedling species composition between US3 and MD3 to either the overall lower cutting intensity or to differential cutting of trees according to their scarcity, spatial distribution, and good health. However, the impact of US3 could be assessed by examining the spatial distribution of seedlings and saplings of species that tend to occur in patches such as *Ocotea puberula*. For this species, higher relative densities and frequencies of seedlings and saplings were found in US3 than in MD3 (Table 2). In absolute terms, *O. puberula* seedlings and saplings were found in 71% of the sampled plots in US3, while in MD3 their frequency was just 40%. In other words, three years after cutting, *O. puberula* seedlings and saplings seemed to have a more uniform spatial distribution in US3 than in MD3. The lower frequency of seedlings and saplings of *O. puberula* in MD3 could be attributed to the extraction of most of the mature individuals, which left almost no mature trees of this species standing in several areas of forest. (As mentioned before, in some areas up to 90% of the trees of this species had diameters above the cutting limits.) (Grance & Maiocco 1993).

It should be pointed out that both the preliminary nature of these results and the lack of replication of the treatments limit further interpretation and extrapolation to other situations. In the long term, species composition of each forest will depend on resulting light conditions from the degree of canopy opening in each method, apart from immigrant seeds from nearby forests. Additionally, seed germination and seedling survival may be affected by different impacts on soil characteristics associated with each logging method. In the uniform spacing method the residual trees are expected to provide adequate seed sources of preferred species. In the forest cut by minimum diameter 30 years ago, the higher abundance and richness of species of non-commercial value was probably due to large canopy openings that allowed colonization by several pioneer and early successional species. However, some species of high commercial value may require large gaps for their successful regeneration, as with *Swietenia macrophylla* G. King (mahogany) in other tropical forests (Lamb 1966). The availability of resources other than light, as well as intra- and inter-specific competition may also influence species distribution and growth.

Applicability of the uniform spacing method in forest reserve management.--In other research in the same forests, a separate analysis was done for the commercial species > 150 cm height (Classes IV and V), which have a greater possibility of reaching harvestable size: there were means of 400 saplings/ ha in US3, 200 in MD3, 220 in UC, and 390 in MD30 (Montagnini *et al.* 1995; Eibl *et al.* 1996). In some methods of selective cutting that include management of natural regeneration such as the tropical shelterwood system, a minimum of approximately 100 saplings/ha of commercial value is expected to ensure a good future timber harvest (Lamprecht 1990). For humid tropical forests on good soils, a minimum safe standard of about 200 saplings/ha of commercial species has been suggested (Bruenig 1996). The values reported by Eibl *et al.* (1996) suggest that the uniform spacing method can provide an adequate stock of saplings of commercial species for the forests of the Guaraní reserve and other similar forests throughout the region.

Results of previous experiences in the region suggest that competition by aggressive understory plants is a major constraint to growth of regenerating seedlings in these forests

(Schultz 1967, Eibl *et al.* 1993). In a separate study in the same forest cut by diameter limits, González (1993) found that, two years after forest exploitation, an increase in light availability to the forest floor from the diameter-limit harvest favored growth of bamboo (48% of ground cover) and pioneer trees such as *Solanum verbascifolium* L. (fumo bravo; 32% cover), as well as tree ferns (*Alsophila atrovirens* Langsd. et Fich; 23% cover). Additionally, Woodward (1995) found a negative correlation between bamboo abundance and seedling abundance, confirming the assumptions expressed above, although there were some exceptions. Bamboo apparently outcompetes seedlings for light and physically obstructs growth by forming patches of dense overhanging vegetation. Without adequate seed sources and with competition from bamboo growth, natural regeneration of commercially valuable species was low (González 1993). In Peninsular Malaysia forest management guidelines indicate that excessive canopy openings should be avoided to prevent the growth of bamboo (*Dendrocalamus* spp.; Cheah 1991).

The minimum diameter method is currently the predominant cutting method because of the larger extractable volume and consequently greater short-term financial benefits it renders. However, the uniform spacing method may be more economically sensible in the long term because it may allow for an earlier second harvest. In evaluating the two methods, consideration should be given to the financial profits as well as to the environmental benefits associated with maintenance of species diversity. The uniform spacing method uses detailed guidelines for selection of remaining trees, and requires careful pre- and post-harvest evaluations. The uniform spacing method should be applicable in the small farms in the Yabotí Biosphere Reserve and other forests in the region. In spite of their preliminary nature, the results suggest that if the minimum diameter method is modified to decrease harvest intensity and to include selection of residual trees, it also could contribute to maintaining tree species diversity in these forests.

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LITERATURE CITED

Ashton, P. M. S. 1990. Method for the evaluation of advanced regeneration in forest types of south and southeast Asia. For. Ecol. Manage. 36: 163-175.

Bazzaz, F. A. 1990. Regeneration of tropical forests: physiological responses of pioneer and secondary species. *In* A. Gómez-Pompa, T. C. Whitmore, and M. Hadley (Eds.). Rainforest Regeneration and Management, pp. 91-118. MAB Series, UNESCO, Paris.

Bertault, J. C., and P. Sist. 1995. Impact de l'exploitation en forêt naturelle. Bois et Forêts des Tropiques 245: 5-20.

Boyle, T. J. B., and J. A. Sayer. 1995. Measuring, monitoring and conserving biodiversity in managed tropical forests. Comm. For. Rev. 74: 20-25.

Brown, N. 1993. The implications of climate and gap microclimate for seedling growth conditions in a Bornean lowland rain forest. J. Trop. Ecol. 9: 153-168.

Bruenig, E. F. 1996. Conservation and Management of Tropical Rainforests. An Integrated Approach to Sustainability. CAB International, Wallinford, Oxon, UK.

Cheah, L. C. 1978. Forest regeneration and development options in Peninsular Malaysia today. Malay. For. 41: 171-175.

———. 1991. Letter to the editor. J. Trop. For. Sci. 4: 96-99.

Chévez, J. C., and G. Gil. 1995. Misiones hoy al rescate de la selva. Nuestras Aves (Argentina): 5-9.

Dawkins, H. C. 1958. The Management of Natural High Forest with Special Reference to Uganda. Comm. For. Inst. Paper No. 34. 155 pp.

Dimitri, M. J. 1979. Las áreas argentinas de bosques espontáneos. *In* D. Cozzo. Enciclopedia Argentina de Agricultura y Ganadería, 2da. Ed., Tomo II, pp. 6-17. Ed. ACME, Buenos Aires.

Eibl, B., L. Szczipanski, R. Ríos, and N. Vera. 1993. Regeneración de especies forestales nativas de la selva Misionera. *In* Instituto Subtropical Investigaciones Forestales (Ed.). VII Jornadas Técnicas: Bosque Nativo: Uso, Manejo y Conservación, pp.100-122. UNaM, Facultad Ciencias Forestales, Eldorado, Misiones, Argentina.

———, F. Silva, A. Bobadilla, E. Weber, and D. Gonseski. 1994. Boletín Meteorológico Aeródromo Eldorado. Período 1985/1994. UNaM, Facultad Ciencias Forestales, Eldorado, Misiones, Argentina.

———, F. Montagnini, C. Woodward, L. Szczipanski, and R. Ríos, R. 1996. Evolución de la regeneración natural en dos sistemas de aprovechamiento y bosque nativo no perturbado en la Provincia de Misiones - República Argentina. Yvyraretá (Argentina) 7(7): 63-78.

Gómez-Pompa, A. 1991. Learning from traditional ecological knowledge: insights from Mayan silviculture. *In* A. Gómez-Pompa, T. C. Whitmore, and M. Hadley (Eds.). Rainforest Regeneration and Management, pp. 335-342. MAB Series, UNESCO, Paris.

González, A. E. 1993. Evaluation of the early growth dynamics of four native timber species in enrichment planting in Argentina's subtropical forests. TRI News (Spring): 7-10.

Grance, L. and D. Maiocco. 1990. Informe cuatrimestral presentado a la Dirección General de Bosques, Pcia. de Misiones, sobre el Plan de Ordenación de Guaraní. Ministerio de Ecología y Recursos Naturales Renovables Posadas, Misiones, Argentina.

———. 1993. Comparación de dos criterios de entresaca en el bosque subtropical Misionero. *In* Instituto Subtropical Investigaciones Forestales (Ed.). VII Jornadas Técnicas: Bosque Nativo: Uso, Manejo y Conservación, pp. 284-299. UNaM, Facultad Ciencias Forestales, Eldorado, Misiones, Argentina.

Hurlbert, S. T. 1984. Pseudoreplication and the design of ecological field experiments. Ecol. Mono. 54: 187-211.

Lamb, F. B. 1966. Mahogany of Tropical America: Its Ecology and Management. University of Michigan Press, Ann Arbor.

Lamprecht, H. 1990. Silvicultura en los Trópicos, pp.129-133. GTZ, Eschborn.

Laserre, S. 1980. Los Suelos Misioneros y su Capacidad de Uso para Plantaciones Forestales. Asoc. Plantad. For. Mis., Bol. No. 10. Posadas, Misiones, Argentina.

Lowe, P.D. 1995. The limits to the use of criteria and indicators for sustainable forest management. Comm. For. Rev. 74: 343-349.

Mangieri, H. R. 1965. Reconstitución de los bosques misioneros y características biológicas de las principales especies. Primeras Jornadas de Trabajo del CEBS, pp.141-145. Eldorado, Misiones, Argentina.

Margalot, J. A. 1985. Geografía de Misiones. Industria Gráfica del Libro, Buenos Aires.

Ministerio de Ecología y Recursos Naturales Renovables. 1985. Programa Mapa Forestal. Minist. Ecol. y Rec. Nat. Renov./UNaM. Posadas, Misiones, Argentina.

———. 1987. Diámetros Mínimos de Corta. Decreto 1617/87. Posadas, Misiones, Argentina.

———. 1993. Censo de la Industria de Transformación Mecánica de la Madera de la Provincia de Misiones, Sept. 1992- Julio 1993. Posadas, Misiones, Argentina.

Montagnini, F., B. Eibl, C. Woodward, L. Szczipanski, and R. Ríos. 1995. Natural regeneration under two systems of selective cutting and undisturbed forest in Misiones, Argentina. XXth IUFRO World Congress, Tampere, Finland. 6-8 August 1995. Available from the Internet: http//iufro.boku.ac.at/procee/s107/s10700.htm.

Sayer, J. A., and T. C. Whitmore. 1991. Tropical moist forests: destruction and species extinction. Biological Conservation 55: 199-214.

———, P. A. Zuidema, and M. H. Rijks. 1995. Managing for biodiversity in humid tropical forests. Comm. For. Rev. 74: 282-287.

Schmitt, L., and M. Bariteau. 1989. Gestion de l'écosystème forestier guyanais. Etude de la croissance et de la régénération naturelle. Dispositif de paracou. Bois et Forêts des Tropiques 220: 3-23.

Shultz, J. P. 1967. La regeneración natural de la selva mesofítica tropical de Surinam después de su aprovechamiento. Bol. Inst. For. Latinoamer. Invest. Capacit. (Mérida, Venezuela) 23: 3-27.

Silva, J. N. M. 1992. A note on Brazil's tropical rain forests under new forest management regulations. J. Trop. For. Sci. 4: 355-356.

Universidad Nacional de Misiones. 1992. Centro Forestal Guaraní. Facultad de Ciencias Forestales, Eldorado, Misiones, Argentina.

Vanclay, J. K. 1992. Species richness and productive forest management. *In* F. R. Miller, and K. L. Adam (Eds.). Wise Management of Tropical Forests, pp. 1-9. Oxford For. Inst., Oxford.

Woodward, C. 1995. Relationships Between Forest Management Practices, Light Conditions and Regeneration of Tree Species in Misiones, Argentina. Trop. Res. Inst. Working Paper #85, Yale Univ. School For. Environ. Stud., New Haven, Connecticut.

Table 1. Characteristics of the four sites used for comparisons of tree regeneration.

	Treatment			
	US3	MD3	UC	MD30
Treatment	Uniform spacing	Minimum diameter	Uncut	Minimum diameter
Years since cutting	3	3	--	30
Timber volume extracted* (m^3/ha)	16	37	--	about 40
Basal area after cutting* (m^2/ha)	22	10	28	about 10
Number of trees/ha after cutting*	280	105	300	304
Size (ha)	100	60	100	4.5
Location	Guaraní	Guaraní	Guaraní	Eldorado

Note: US3: Forest cut by Uniform Spacing 3 years ago, MD3: forest cut by Minimum Diameter 3 years ago, UC: uncut forest, MD30: forest cut by Minimum Diameter 30 years ago.

*Data based on tree inventories using censuses of all trees (> 1cm d.b.h.) in eight 5,000 m^2 plots randomly located in each site.

Table 2. Abundance, frequency and importance values of seedlings and saplings (all size classes together) of commercial species in the four forests under study.

	TREATMENT											
	Uniform Spacing (US3)			Minimum Diameter (MD3)			Uncut Forest (UC)			Minimum Diameter (MD30)		
SPECIES	Relative abundance (%)	Relative frequency (%)	Importance value (%)	Relative abundance (%)	Relative frequency (%)	Importance value (%)	Relative abundance (%)	Relative frequency (%)	Importance value (%)	Relative abundance (%)	Relative frequency (%)	Importance value (%)
Apuleia leiocarpa (Vog.)J. Macbr.	53.3	16.3	34.8	44.3	19.2	31.7	12.8	15.9	14.4	1.0	4.8	2.9
Balfourodendron riedelianum (Engl.)Engl.	1.2	5.9	3.5	13.7	15.3	14.5	4.7	7.2	6.0	9.1	9.7	9.4
Bastardiopsis densiflora (Hook et Arn.)Hassl.	--	--	--	--	--	--	0.2	1.4	0.8	--	--	--
Cabralea canjerana (Vell.)Mart.	1.5	9.3	5.4	9.5	12.8	11.2	2.1	2.9	2.5	5.6	14.5	10.1
Cedrela fissilis Vell.	0.3	2.3	1.3	13.7	9.0	11.4	3.2	2.9	3.1	6.9	8.1	7.5
Cordia trichotoma (Vell.)Johnst.	--	--	--	--	--	--	0.2	1.4	0.8	--	--	--
Didymopanax morototoni (Aubl.)Dec. et Planch.	0.3	1.1	0.7	0.1	1.3	0.7	--	--	--	--	--	--
Erythrina falcata Benth.	--	--	--	--	--	--	0.2	1.4	0.8	--	--	--
Lonchocarpus leucanthus Burk.	--	--	--	--	--	--	5.9	7.2	6.6	--	--	--
Lonchocarpus muelhlbergianum Hassl.	--	--	--	--	--	--	0.5	1.5	1.0	4.6	4.8	4.7
Luehea divaricata Mart.	--	--	--	0.3	1.3	0.8	0.3	1.5	0.9	--	--	--
Myrocarpus frondosus Allemao	0.4	3.4	1.9	--	--	--	0.7	4.5	2.6	5.6	9.7	7.7
Nectandra lanceolata Nees et Mart. ex Nees	5.7	11.6	8.7	4.5	12.8	8.7	0.6	1.6	1.1	0.2	3.3	1.7
Nectandra saligna Nees et Mart. ex Nees	2.4	5.9	4.1	1.8	2.5	2.1	56.5	26.0	41.3	2.6	6.4	4.5
Ocotea diospirifolia (Meisn.)Mez.Emd.Hass.	2.5	11.6	7.0	5.2	12.8	9.0	3.5	5.8	4.7	27.6	16.1	21.9
Ocotea puberula (Nees et Mart.)Nees	11.2	11.6	11.4	5.7	7.7	6.7	0.5	2.9	1.7	30.4	11.2	20.8
Parapiptadenia rigida (Benth.)Brenan	12.2	7.0	9.6	--	--	--	3.9	8.7	6.3	4.8	4.8	4.8
Patagonula americana L.	0.1	1.1	0.6	--	--	--	2.1	2.9	2.5	--	--	--
Peltophorum dubium (Sprengel)Taub.	--	--	--	--	--	--	--	--	--	0.3	1.6	0.9
Prunus subcoriacea (Chod.et Hassl.)Koehn	8.8	12.9	10.8	1.2	5.2	3.2	2.2	4.3	3.3	1.0	3.3	2.1
Ruprechtia laxiflora Meisn.	--	--	--	--	--	--	--	--	--	0.2	1.6	0.9

Table 3. Non-commercial species found in the four studied forests. (+) = present, (-)= absent.

Species	**TREATMENT**			
	US3	**MD3**	**UC**	**MD30**
Acacia tucumanensis Gris.	+	-	+	-
Albizia hassleri (Chod)Burk.	+	+	+	+
Alchornea iricurana Cas.	+	-	-	-
Allophilus edulis (St. -Hil.)Radlk.	-	+	-	+
Aloysia virgata (Ruiz et Parm.)Juss.	-	-	-	+
Arecastrum rommanzofianum (Chom.)Beccari	+	+	+	+
Aspidosperma australe M.Argov.	-	-	-	+
Ateleia glazyoyeana Baill.	-	+	-	-
Bauhinia candicans Benth.	-	-	+	-
Campomanesia xanthocarpa Berg.	-	-	-	+
Casearia syslvestris Swartz	-	+	-	+
Celtis tala Gill.	-	-	+	+
Chorisia speciosa St.-Hil.	-	+	-	-
Chrysophyllum gonocarpum (Mart et Eich)	+	+	+	+
Chrysophyllum marginatum (Hook.et Am.)Radlk.	-	-	+	-
Cordia ecalyculata Vell.	-	-	-	+
Cupania vernalis Cambess	+	+	+	+
Diatenopteryx sorbifolia Radlk.	+	+	+	+
Fagara naranjillo (Gris.)Engl.	-	-	+	-
Fagara spp.	+	+	-	-
Helettia apiculata Benth.	-	+	-	-
Holocalyx balansae Micheli.	-	-	+	+
Ilex paraguariensis St.-Hil.	-	+	-	+
Inga affinis DeCand.	-	-	+	-
Inga urugüensis Hook et Am.	-	-	+	+
Jacaranda spp.	+	+	-	-
Lonchocarpus nitidus (Vog.)Benth.	-	+	+	+
Machaerium spp.	+	+	+	+
Manihot grahamii Hook.	-	-	-	+
*Matayba eleagnoides*Radlk.	+	+	+	+
Peschiera australis (M.Argov.)Miers.	-	-	-	+
Pilocarpus pennatifolius Lemaire	-	-	+	+
Rapanea spp.	+	+	-	+
Schinus molle L.	-	-	-	+
Sebaetiana brasiliensis Sprenfel	-	-	-	+
Solanum vervascifolium Jacq.	-	-	-	+
Sorocea bonplandii (Baill.)Burg.Lanj.&Boer	-	-	-	+
Strychnos brasiliensis (Spreng.)Mart.	+	+	+	+
Trichilia spp.	+	+	+	+
Unidentified Anonaceae	-	-	-	+
Unidentified Euphorbiaceae	-	+	+	-
Unidentified Lauraceae	-	-	-	+
Unidentified Myrtaceae	+	+	+	+
Vitex megapotamica	-	+	-	-

Figure legends:

Figure 1. Schematic representation of nested permanent plots used to monitor seedlings and saplings.

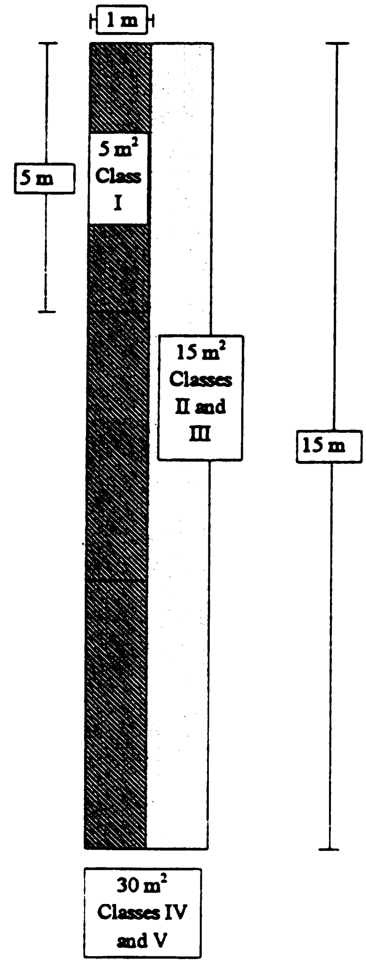
Figure 2. Average numbers of seedlings/saplings of commercial and non-commercial species in three forests following timber extraction and in an uncut forest. US3: Uniform Spacing method applied three years ago (n=14), MD3: Minimum Diameter method applied three years ago (n=15), UC: uncut forest (n=20), MD30: Minimum Diameter method applied 30 years ago (n=12). The bars are standard errors as calculated for the totals (commercial + non-commercial species).

Figure 3. Total number of seedlings/saplings by height class and treatment. Treatment codes as in Fig. 2 (see also Table 1).

Figure 4. Frequency of understory plant species other than trees. Treatment codes as in Fig. 2.

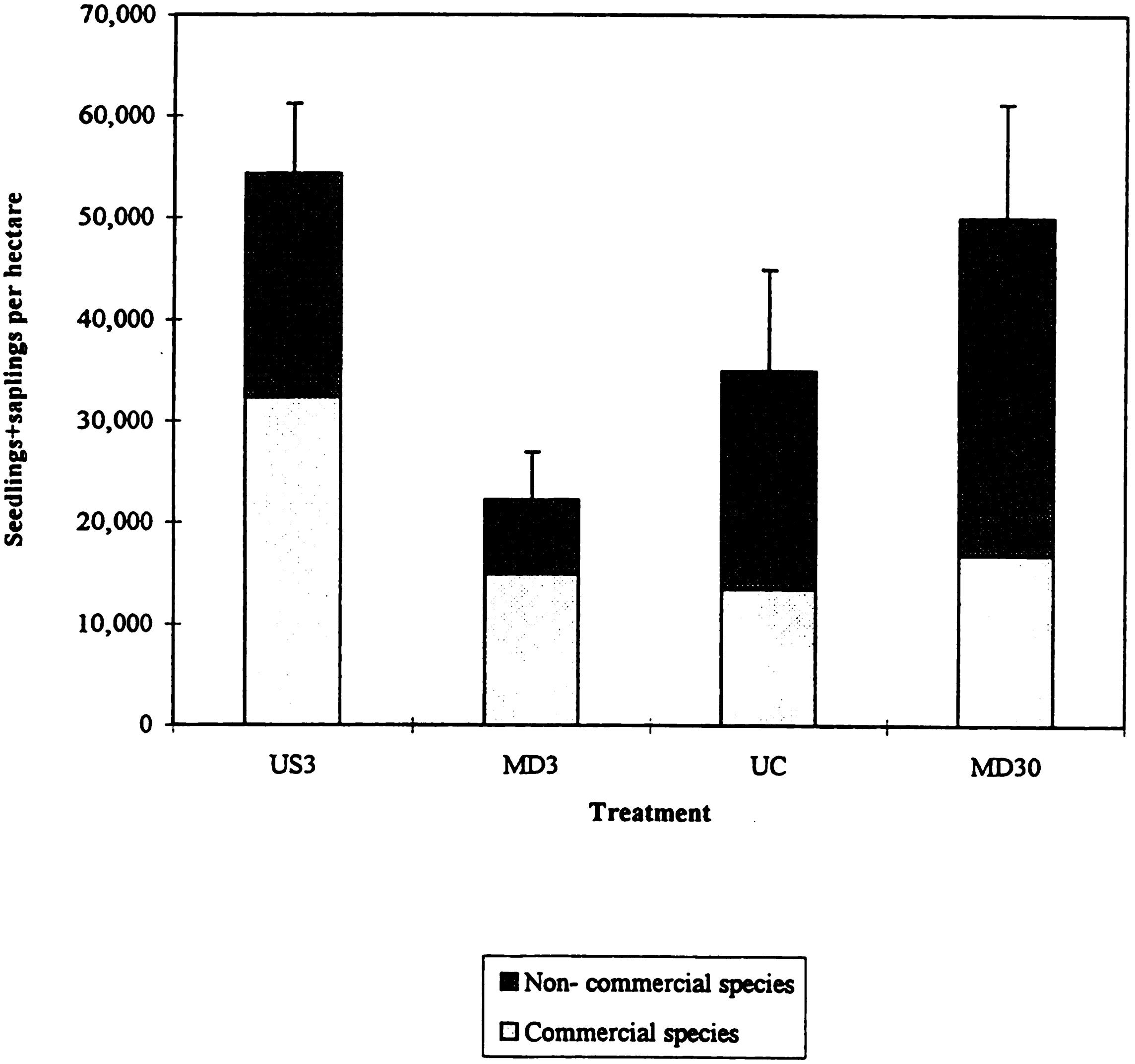
Figure 5. Frequency of canopy cover categories. Open: distance between tree crowns > average horizontal crown diameter. Medium: crowns do not touch but distance between crowns < average crown diameter. Closed: crowns touch or overlap. No cover: plot at or near center of forest gap of diameter > average tree height. Treatment codes as in Fig. 2.

Fig. 1



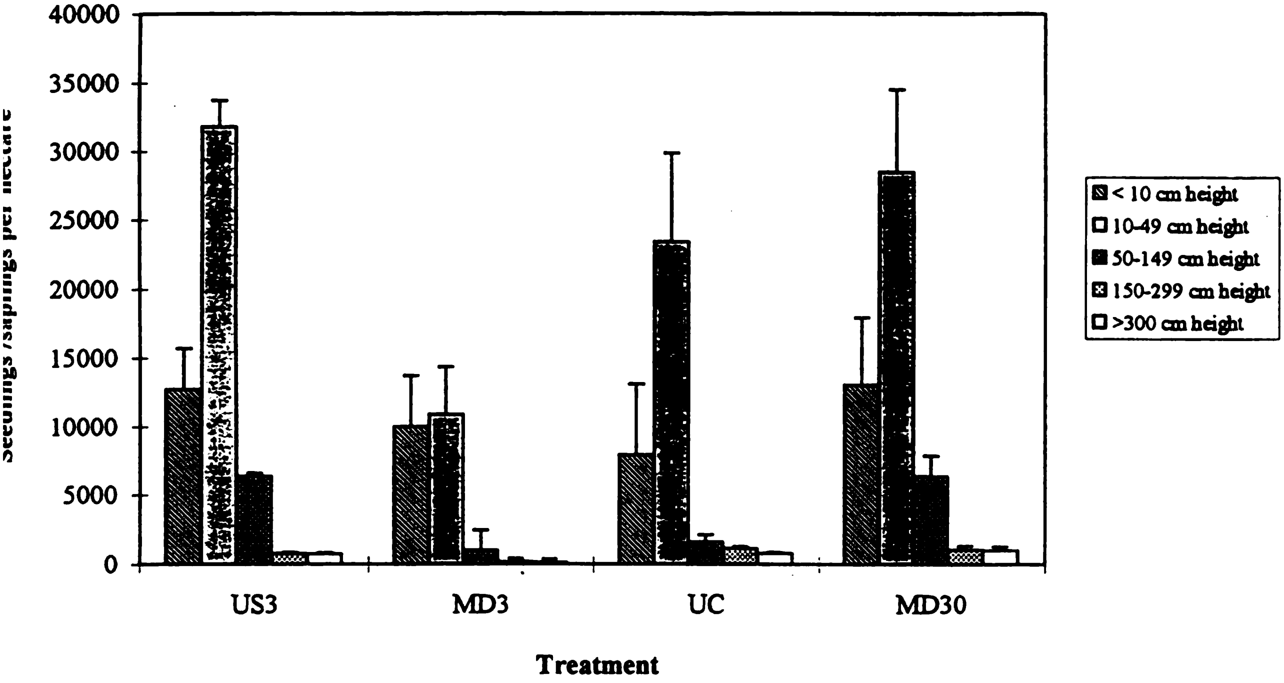
Height Classes	
I	< 10 cm
II	10 - 49 cm
III	50 - 149 cm
IV	150 - 299 cm
V	> 300 cm and < 10 cm dbh

Fig -

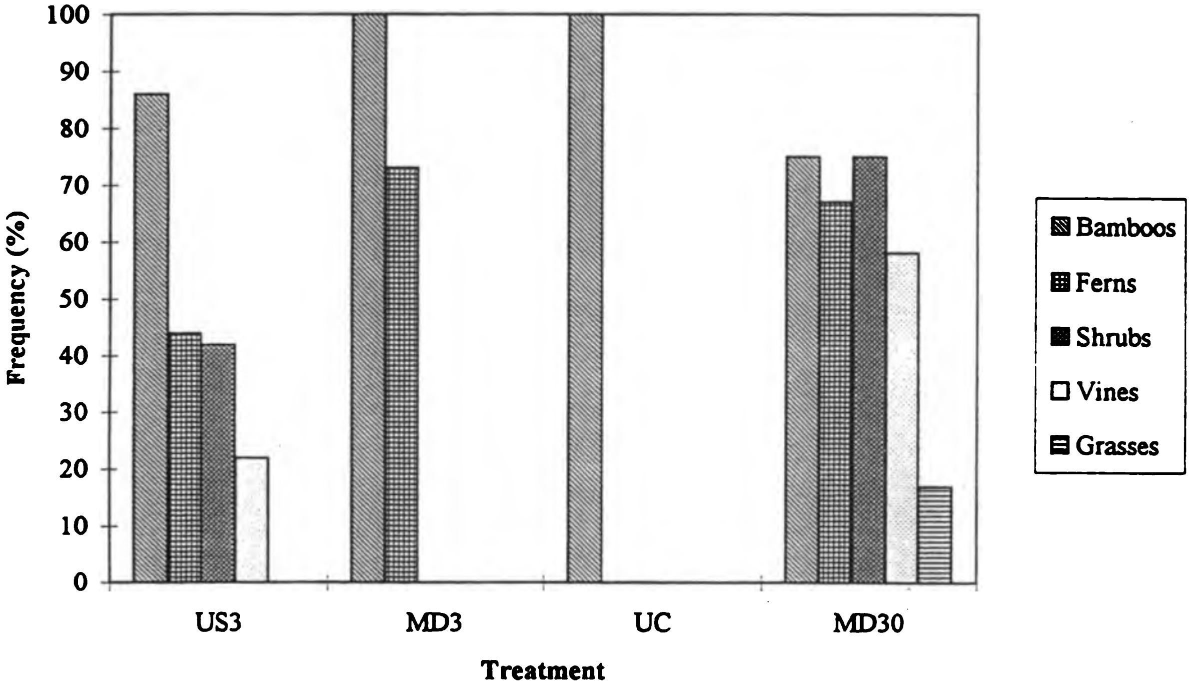


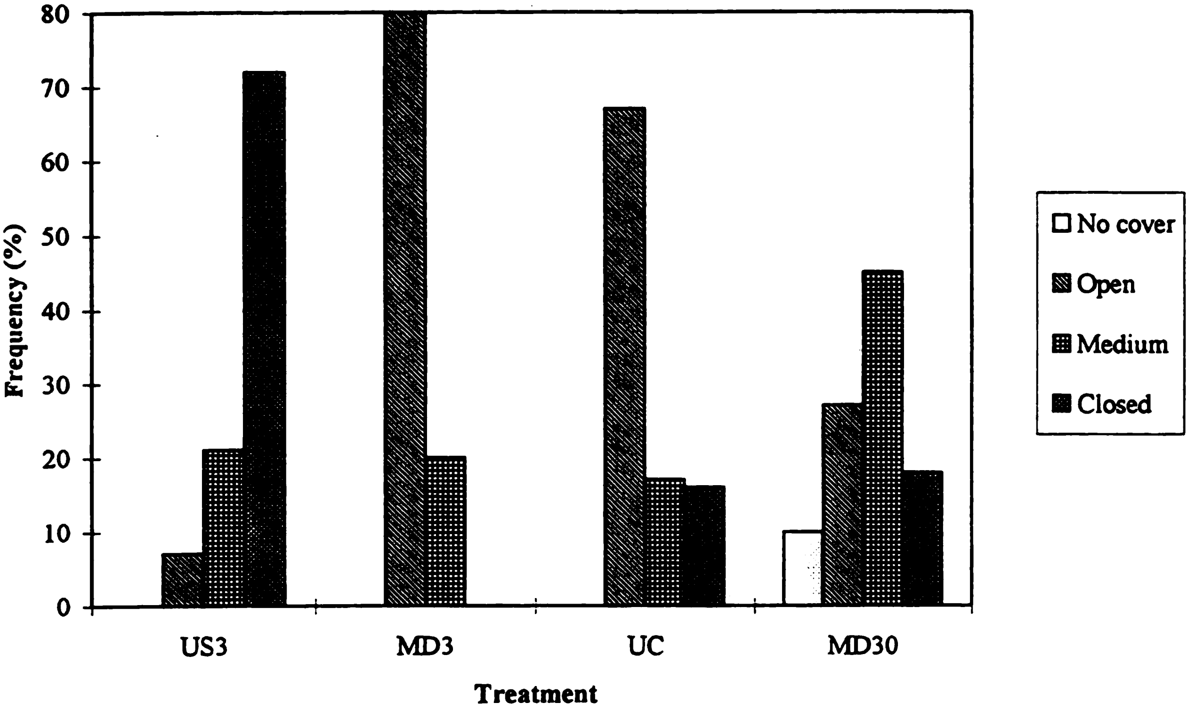
70,000
60,000
50,000
40,000
30,000
20,000
10,000
0
Seedlings+saplings per hectare
US3
MD3
UC
MD30
Treatment
■ Non- commercial species
□ Commercial species

Fig 3



Seedlings /saplings per hectare
40000
35000
30000
25000
20000
15000
10000
5000
0
US3
MD3
UC
MD30
Treatment
▨ < 10 cm height
☐ 10-49 cm height
■ 50-149 cm height
▩ 150-299 cm height
☐ >300 cm height


100
90
80
70
60
50
40
30
20
10
0
Frequency (%)
US3
MD3
UC
MD30
Treatment
Bamboos
Ferns
Shrubs
Vines
Grasses


80
70
60
50
40
30
20
10
0
Frequency (%)
US3
MD3
UC
MD30
Treatment
☐ No cover
▨ Open
▦ Medium
■ Closed

Evaluating the Role of Plantations as Carbon Sinks:
an Example of an Integrative Approach from the Humid Tropics

Running Head: Role of Plantations as Carbon Sinks

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ABSTRACT

Despite their fast growth, tropical plantations are a small sink of atmospheric carbon because they occupy only a small area in relation to other land uses worldwide. Proper design and management of plantations can increase biomass accumulation rates, making them more effective C sinks. However, fast-growing plantations can extract large amounts of nutrients from the soil, and site fertility declines may limit sustained plantation forestry after a few rotations. We measured aboveground biomass accumulation, carbon sequestration, and soil chemistry in three young plantations of twelve indigenous tree species in pure and mixed designs in the humid lowlands of Costa Rica. Annual biomass increments for the three mixed plantations ranged from 10-13 Mg/ha. The mixtures of four species gave higher biomass per hectare than that obtained by the sum of ¼ hectare of each species in pure plots. At this early age of the plantations, estimated annual C sequestration values were comparable to other reports from young plantations of exotic species commonly grown in the tropics.

Four years after planting, decreases in soil nutrients were apparent in pure plots of some of the fastest growing species, while beneficial effects on soils were noted under other species. The mixed plots showed intermediate values for the nutrients examined, and sometimes improved soil conditions. A mixture of fast and slower growing species yields products at different times, with the slower growing species constituting a longer term sink for fixed carbon. Examination of the role of tropical plantations as C sinks necessitates integrative approaches that consider rates of C sequestration, potential deleterious effects on ecosystem nutrients, and economic, social and environmental constraints.

key words: native trees, aboveground biomass, stem increments, rotation length, soil nutrients, ecomomics.

INTRODUCTION

It is generally accepted that forests can play a critical role in capturing and storing large amounts of carbon from the atmosphere and can thus contribute to reducing the buildup of atmospheric carbon dioxide. Despite their relatively fast growth, it has been suggested that tropical plantations are a small sink of atmospheric carbon because they occupy a relatively small area in relation to other vegetation types and land uses worldwide (Brown et al. 1986). The area of plantations annually planted in the tropics is currently <10% of the simultaneously deforested area, and tree planting currently compensates for 0.3% (at most) of the carbon released by deforestation (Bruenig 1996). To have a significant impact as a global C sink, plantations would need to be established on an unprecedented scale (Sedjo 1989, Myers and Goreau 1991, Houghton 1996). However, rates of reforestation and afforestation worldwide are likely to grow over the next decades as many countries seek to compensate for the loss of natural forests, and thus the role of plantations in sequestering C may also increase (Gladstone and Ledig 1990, Rotmans and Swart 1991, Houghton 1996). Several exotic and indigenous tree species growing in a variety of tropical environments should be tested with respect to their rates of growth and biomass accumulation, especially those that produce good quality timber, which results in longer-term storage of the fixed carbon.

Afforestation and other forest management options to sequester C in tropical latitudes may fail unless they address local economic, social, environmental, and political needs of people in the developing world (Cairns and Meganck 1994, Houghton 1996). Tree plantations are a source of cash, savings and insurance for the individual farmers (Chambers and Leach 1990). On the other hand, fast growing tropical tree plantations incorporate considerable amounts of nutrients in their biomass over a relatively short period of time. Site fertility declines can limit sustained plantation forestry in tropical regions: soil fertility can be decreased through excessive removal of living biomass, particularly if nutrients in tree crowns are lost through harvest or site preparation (Jorgensen and Wells 1986, Perry and Maghembe 1989). This can be particularly serious when plantations are established on soils that are inherently poor. Therefore, examination of the role of tropical plantations as C sinks necessitates integrative approaches to evaluate not only the rates of C sequestration by different tree species, but also their design and management to minimize potential deleterious effects on ecosystem nutrients, and to make plantations economically, socially and environmentally sound land use options.

Mixed plantations yield more diverse forest products than monospecific stands, helping to diminish farmers' risks in unstable markets. If planned with consideration for each species' response to mixed conditions, mixed designs can be more productive than monospecific systems (Smith 1986, Burkhart and Tham 1992, Kelty 1992, Wormald 1992). In this article we report results of biomass accumulation and soil nutrients from three young experimental plantations with native trees in mixed and pure stands in the Atlantic humid lowlands of Costa Rica. In previous reports we have shown that the growth of dominant species was faster in mixed than in pure conditions, and that total volume per hectare in mixed plantations ranked first or second in comparison with pure stands of the fastest growing species (Montagnini et al. 1994, 1995). We expected that total aboveground biomass production, stem biomass increments and C sequestration rates were higher in mixed than in pure plantations. In addition, we hypothesized that soil nutrient depletion had occurred in the pure plantations, while soils in the the mixed plantations maintained more consistent nutrient levels. Although the young age of the plantations precludes proper extrapolation over a whole rotation, the results do suggest design and management options that can enhance the value of tropical plantations as C sinks, diminish their potential negative influences on ecosystem nutrients, and make them economically attractive to the local farmers.

STUDY SITE

The experiments were established on abandoned pasture at the Guaira Annex of La Selva Biological Station in the Atlantic humid lowlands of Costa Rica (10°26'N, 86°59'W, 50 meters mean altitude, 24°C mean annual temperature, 4000 mm mean annual rainfall). Soils are Fluventic Dystropepts derived from volcanic alluvium; they are deep, well drained, stone-free, acid, with low or medium organic matter, low nutrient content and moderately heavy texture (Sancho and Mata 1987). The area had been cleared in the mid-1950s and grazed until 1981, a sequence of land uses common in the region at the time (Montagnini 1994). The area is on flat, uniform terrain. By the time of clearing for the plantations, the area was covered with shrubs and early successional trees, interspersed with patches of grass and ferns. Soil conditions at the time of clearing were too poor for cultivation of bananas or other commercial crops commonly grown in the region (Berstch 1986, Sancho and Mata 1987). The site was cleared manually and no burning was done. The slash was left on the floor, to protect against soil erosion and to delay the growth of weeds.

Experimental Setting

A total of twelve native tree species of economic value were tested in three plantations, each with four species: Plantation 1: *Jacaranda copaia* (Aubl.)D.Don, *Vochysia guatemalensis*

.Sm., *Callophylum brasiliense* Cambess and *Stryphnodendrom microstachyum* Poepp. et Endl.; lantation 2: *Terminalia amazonia* (Gmell.)Exell., *Dipteryx panamensis* (Pittier) Record&Mell, *irola koschnyi* Warb and *Albizia guachapele* (H.B.K.) Little; and Plantation 3: *Hyeronima lchorneoides* Fr. Allemao, *Pithecellobium elegans* D.C.Benth., *Genipa americana* L. and *ochysia ferruginea* Mart. In each plantation of four tree species there was at least one nitrogen-fixing tree, a relatively fast growing species, and a slower growing species. The criteria for species selection were: growth rate and economic value, potential impacts on soils and nutrient cycling, and seedling availability (Montagnini et al. 1995). The plantations were in randomized blocks, with four replicates and six treatments: four pure plantation plots of each species, a mixed-species plot (with the four species), and a fallow (natural regrowth) plot. Each plot was 32 m x 32 m. Initial planting distance was 2 m x 2 m to speed canopy closure and obtain early impacts on soils, with 50% thinning planned after canopy closure. Within each mixed-tree plot, trees of the four species were planted alternating two species per row. The sequential order of the species within rows was systematically reversed every other row. In that manner, each column contained the four species of the mixture in a sequence.

METHODS

Aboveground Tree Biomass and Carbon Accumulation

The plantations were thinned after canopy closure, which occurred approximately 2.5-3 years after planting, although some species such as *Jacaranda copaia* closed canopies within a year. For consistency, the three plantations were thinned three years after planting. With thinning, the initial 2 m x 2 m planting distance was widened to 2 m x 4 m (1,250 trees per ha).

This plantation density is similar to the prevalent 3 m x 3 m (1,111 trees per ha) and thus it would allow for comparison with other experiences in the region. Thinning was performed in one half of each plot, leaving the other non-thinned half for comparison. For thinning, all trees were cut in alternate rows. From every thinned row, two trees were randomly selected for biomass determinations, giving a total of 16 sampled trees per plot. The material from each tree was separated into its parts (stem, branches and leaves) and weighed fresh at the site using a field scale. Subsamples of all materials, including stems (lower, middle and top parts) were taken to the laboratory and dried at 70°C to constant weight. Dry:wet weight ratios from felled trees were used to correct the field weight determinations and obtain biomass on a per tree basis. Data from the 16 sampled trees were averaged to obtain values per plot. The average biomass per tree was multiplied by the number of trees per plot, corrected for tree mortality, and extrapolated to a hectare. Analysis of variance and LSD tests were run to compare mean biomass (n=4) of tree parts among species. Comparisons were made among species in pure and mixed conditions on a per tree basis, and also among pure and mixed plots on a per hectare basis.

For calculation of carbon accumulation by each plantation species, only stem biomass values were used, because most leaves and a great portion of the branches are expected to turnover every year, i.e., they represent only a short term carbon storage. In addition, C sequestration by harvestable timber can be compared with other values from the literature. Stem biomass was divided by plantation age (3 years) to calculate average annual increments. Average stem biomass increments were converted to total carbon content by assuming that biomass is approximately 50% carbon (Brown and Lugo 1982).

Soil Chemistry

Soils were sampled before clearing the land, and annually thereafter. Soil conditions before clearing (1991) have been reported elsewhere (Montagnini et al. 1993, 1994), and only results of sampling from 1992 to 1995 are reported here. Composite samples were taken in each of the four replicate plots per treatment, at 0-5, 5-15, 15-30 and 30-60 cm depth. The pH was measured in a 1:2.5 mixture of soil:deionized water. The exchangeable Ca and Mg were extracted with a 1 N KCl solution, while the exchangeable P and K were extracted with a modified Olsen solution, which is a mixture of 0.5 N $NaHCO_3$, 0.01 N bi-sodium EDTA and Superfloc 127 (a commercial flocculant) (Diaz Romeu and Hunter 1978). A 1:5 proportion of soil:extractant was used in all cases. Cations were measured using an Atomic Absorption Spectrophotometer. Extractable P was measured colorimetrically after reaction with $(NH_4)_2MoO_4$ and $SnCl_2$, using a spectrophotometer. Organic matter was measured with the Walkley-Black technique (Allison 1975) and total N was measured using a semi-Micro-Kjeldahl technique (Bremner and Mulvaney 1982). Analysis of variance and LSD tests were run to compare the means for each variable and soil depth ($n=4$, $P<0.05$) among sites.

RESULTS

Aboveground Tree Biomass

a- Comparisons among species in pure and mixed conditions on a per tree basis

In Plantation 1, *Jacaranda copaia* and *Vochysia guatemalensis* had the highest total aboveground biomass per tree when grown in mixture (Figure 1a). These differences were statistically significant ($P<0.05$). In contrast, for *C. brasiliense*, biomass of each plant part and the total were higher in pure than in mixed plots. For *S. microstachyum* there were no statistically significant differences in biomass between pure and mixed plots.

In Plantation 2, the highest total biomass per tree was found in *Terminalia amazonia* and *Dipteryx panamensis* growing in mixed conditions (Figure 1b). In *T. amazonia*, total biomass in mixed plots was more than twice that in pure plots. In the other three species of this plantation, biomass of tree parts was always higher in mixed than in pure plots although the differences were not as pronounced as for *T. amazonia*.

In Plantation 3, total biomass was similar for *Hyeronima alchorneoides, Pithecellobium elegans* and *Vochysia ferruginea* (Figure 1c), while the total biomass in *Genipa americana* plots was about half that of the other three species. Biomass of plant parts was higher in mixed than in pure stands of *H. alchorneoides* and *P. elegans*, while the opposite was true for the other two species.

b- Biomass per hectare in pure plots of the twelve species and in mixtures of four species

Annual biomass increments for the three mixtures were 10.8 Mg/ha for Plantation 1, 13.0 Mg/ha for Plantation 2, and 10.3 Mg/ha for Plantation 3. In the three plantations, the biomass of one hectare of the mixture was higher than the sum of ¼ of a ha of each of the four species in pure stands (Table 1). In Plantation 1 the total biomass was higher in *J. copaia* pure plots, followed by the mixture; in Plantation 2, the highest total biomass per hectare was found in the mixed plots, followed by *T. amazonia*; and in Plantation 3, the three leading species in pure plots shared similar amounts of total biomass per hectare (Table 1).

Carbon Sequestration in Pure and Mixed Plantations

As for biomass, in Plantation 1 the mixture of four species ranked second after *J. copaia* in average annual carbon sequestration (Table 2). In Plantation 2 the mixture of four species had the highest value, close to that of the mixture in Plantation 1. In Plantation 3, the two leading species were *P. elegans* and *H. alchorneoides*, and the mixture ranked third, again with a value close to those of the mixtures in the other two plantations.

Soil Chemistry

In Plantation 1, statistically significant differences in soil nutrients between treatments were found only for K and P four years after planting (Table 3). The natural regrowth plots had the highest and the *V. guatemalensis* plots had the lowest concentrations of soil K at all depths. Similarly, the natural regrowth had the highest and *V. guatemalensis* the lowest concentration of soil P, although significant differences for P only occurred in the top soil (0-5 cm depth). A general trend of slightly decreasing amounts of K over time was seen in all treatments, with the largest declines occurring in the *J. copaia*, mixed, and *V. guatemalensis* treatments (Figure 2). Soil P increased only slightly from 1992 to 1995, especially in the mixed and natural regrowth plots (Figure 3).

In Plantation 2, four years after planting the highest values of soil K were found in *D. panamensis* and *A. guachapele,* and the lowest in *T. amazonia* and *V. koschnyi*, with intermediate values in the natural regrowth and mixed plots (Table 4). A similar trend was found for Ca and Mg, although statistically significant differences were only found for Mg at 5-15 cm depth. There were no statistically significant differences in P among treatments in the top soil. Increases in cation content under *D. panamensis* and *A. guachapele* had only occurred in the current year, following a decline in cations from 1992 to 1994 (data not shown).

In Plantation 3, three years after planting, the highest values of soil K, Ca and Mg were found in the regrowth plots and the lowest in the *H. alchorneoides* plots (Table 5). *P. elegans* plots had the second highest values of soil K. The reverse was true for P: *H. alchorneoides* plots had the highest soil P values at 0-5 cm depth, significantly different from those in the mixed and natural regrowth plots (Table 5). *G. americana* plots followed with the second highest values. There was a small trend of an increase in most nutrients at all depths over time, especially for the natural regrowth and mixed plots (data not shown).

DISCUSSION

Aboveground Tree Biomass in Pure and Mixed Plantations

The most successful mixed plantings are stratified mixtures composed of faster-growing, shade-intolerant species above slower-starting tolerants (Smith 1986). If the trees in the upper canopy are not too dense, they grow more rapidly in diameter than if crowded into the single canopy of a pure plantation; lower-stratum species can influence stem form and self pruning of upper-stratum species in ways similar to that of a pure stand (Burkart and Tham 1992). In the present research, the dominant species of each plantation grew larger when grown with other species compared to single species plantation. Apparently in the mixtures the dominant species, with less intra-specific competition, can attain larger diameters, as reported in earlier research (Montagnini et al. 1995). Only two out of the twelve species tested were seemingly suppressed by the dominant species and thus grew better in pure plots: *C. brasiliense* (Plantation 1) and *G.*

americana (Plantation 3). Except in the two cases noted, the other species associated with the faster growing dominants apparently shared resources with the dominant species and had higher biomass of plant parts in mixed than in pure plots.

Farmers may prefer species diversification for financial reasons, or because of uncertainties about species' performance, scarcity of seedlings, or risks from potential pest damage. Species diversification could be achieved by planting species mixtures or planting a set of monospecific plots. In the three plantations tested the mixtures always had greater biomass accumulation rates than the sum of each of the component species in pure plots. These results suggest that mixed designs, if planned with consideration for each species' response to mixed conditions, may result in greater production than using the same area of land for pure species stands.

The inclusion of faster and relatively slower growing species in a mixture has the additional advantage of providing harvestable products at different rotation times, with the slower growing species (e.g., *C. brasiliense, V. ferruginea*) producing relatively more valuable wood. This product constitutes a longer term sink for fixed carbon (e.g., construction timber, furniture, wood crafts), than timber of less value, whose uses may be relatively shorter-lived (e.g., boxes, poles, fuelwood). Additionally, because the different species of the mixture have different rotation lengths, the land is in use for a longer period than if planted with just one fast-growing, short rotation species (such as *J. copaia*). This diminishes incentives for changing to other land uses, keeps a vegetative cover that protects the soil, and serves other environmental purposes as well.

The values of mean annual aboveground biomass production and stem biomass increments for the three mixtures lie within the ranges reported elsewhere for fast-growing, monospecific plantations of commonly used exotics in the humid tropics (Table 6). The values in Table 6 were for plantations of relatively young age; values will also vary with climate and site fertility (Lugo et al. 1988). Values for the two slower growing trees in pure plots, *C. brasiliense* and *G. americana*, are similar to ranges reported for relatively slower-growing species (Table 6). Thus, the species of the present research had acceptable growth rates in pure and mixed conditions, and were adequate for their incorporation as timber species in forestry/agroforestry systems in the region.

Carbon Sequestration in Pure and Mixed Plantations

Values of mean carbon storage over a whole rotation have been recenlty reported for several tree species commonly grown in tropical regions (Shroeder 1992). The plantations of the present research were too young for proper extrapolation of initial growth data over a whole rotation. Calculations based on data obtained at an early age of the plantations can overestimate C sequestration, since most of the carbon uptake occurs in the youngest age classes (0-10 yr) (Brown et al. 1986).

Rotation length is a key factor in the ability of plantations to remove carbon from the atmosphere over the long-term (Shroeder 1992). Rotation times of 12-15 years are expected for the fastest growing species and 20 years for the slower growing species of these experiments (Table 2) (Montagnini et al. 1995, Montagnini and Mendelsohn 1996). The longer the rotation time, the larger the error associated with extrapolating annual C sequestration calculated at an early age.

Several assumptions are commonly used when calculating C storage by tree plantations:

for example, stem biomass is calculated using data on volume yield and wood density, because stem biomass is not generally measured at the time of harvest. We expect to obtain additional biomass measurements at intermediate and mature ages of each species of these experiments to obtain accurate estimations of C storage over a full rotation.

Live trees generally comprise the greatest portion of the aboveground biomass of a plantation. For example, in a 6.6 year old *Gmelina arborea* plantation in Sarawak, total aboveground biomass (92.1 Mg/ha) was comprised of 92% overstory, 3.5% undergrowth, and 4.2% litter (Halenda 1993). The undergrowth is expected to be a small component of aboveground biomass in managed plantations, although this may vary with the weeding intensity, site characteristics and planting distance. In another plantation at La Selva that included some of the species of the present research, with the same planting distance, and on similar soils, the undergrowth was <2% of the total aboveground biomass (Montagnini and Sancho 1994).

Our current estimates of C sequestration only include aboveground tree parts. Roots of tropical trees appear to decay at slower rates than leaf tissue (Bloomfield et al. 1993), which means that they may function as a longer-term C storage mechanism. However, tropical plantations have a smaller fraction of total tree biomass in roots than natural forests (Vogt et al. 1997). To date, estimates of root biomass density have been made only in the top soil (0-15 cm) of these plantations, data by far too incomplete to deserve consideration here. Accurate measurements of root biomass, especially coarse roots with longer residence time, could aid in a more precise evaluation of C sequestration by plantation ecosystems.

Soil Chemical Characteristics in Pure and Mixed Plantations

K and P, the two nutrients more likely to be depleted from plantation soils (Wadsworth 1983, Bowen and Nambiar 1984), were most depleted in the soils under faster growing species, such as *V. guatemalensis*, while depletion of these nutrients was less pronounced in the plots of the slower growing species of this plantation (*C. brasiliense*). This suggests that rapid uptake and accumulation of nutrients in tree biomass served as the main mechanism responsible for this decrease. In contrast, the natural regrowth plots seemingly functioned as "fallows" and contributed to the recovery of soil nutrients from initial pre-plantation levels, presumably through biomass turnover and nutrient release.

In other cases, beneficial effects on some of the same soil nutrients were noted: increases in cations, especially K were found under *D. panamensis* and *A. guachapele*. These increases had occured only recently, following initial declines, thereby pointing to a recovery presumably caused by nutrient cycling mechanisms. Plantation 3 exhibited both types of results, with P enrichment in two treatments (*H. alchorneoides* and *G. americana*), in comparison with natural regeneration plots; and the reverse pattern found for K. On the other hand, the mixed plots showed intermediate values for the nutrients examined, and even improved soil conditions, as in Plantation 3. This suggests that in mixed conditions it may take longer to deplete soil nutrients than in monospecific stands of fast-growing species.

Ameliorating effects of plantation forests on soils generally occur during the period immediately following canopy closure (the "fallow enrichment phase"), while during the maximum-production phase a deterioration of site quality may occur, as mineral nutrients are taken up by the trees and litter accumulates on the floor due to unfavorable conditions for organic matter decomposition (Sánchez et al. 1985). Results of continued sampling will be needed to assess the long term effects of plantation treatments on soil chemistry. Additionally, the examination of whole stand nutrient budgets, including soil and biomass nutrients, and litter decomposition studies, may help sort out the relative roles of nutrient uptake by trees and nutrient inputs from weeding and from litterfall for the five treatments.

Potential of Tropical Tree Plantations as Carbon Sinks

Tropical forests harbor more carbon than most other ecosystems and roughly 44 times more than agricultural lands; therefore, although young plantation forests sequester C at a higher rate than mature forests, primary forests conserve much more C per hectare (Cairns and Meganck 1994, Bruenig 1996). Carbon loss associated with deforestation occurs more rapidly than reforestation can sequester C, thus it may be less effective to focus on plantations, except as an alternative to cutting more primary forest (Brown and Adger 1994, Cairns and Meganck 1994).

Fearnside (1995) assessed the monetary carbon costs and benefits for the Brazilian Amazon, and showed that reduction of deforestation has a potential C benefit about four times that of plantation establishment for pulp and sawlogs. In a survey from 94 nations from tropical and temperate regions, mean initial cost of soil rehabilitation and revegetation has been estimated from $500 to $3000/ha (Dixon et al. 1994). These authors estimated that natural regeneration of woody vegetation or agro-afforestation establishment costs were <$1000/ha in temperate and tropical regions. These values are similar to our own estimates of establishment costs for tree plantations in the humid lowlands of Costa Rica (Montagnini et al. 1995, Montagnini and Mendelsohn 1996). Establishment costs were lower for the slower growing species in mixture than alone. In comparison with pure stands of the fastest growing species, mixtures had the advantage of including other species of high economic value.

Tropical plantations can serve diverse productive, economic, social, political and ecological functions. With their relatively high yields, tropical and subtropical plantations can make substantial contributions to world timber and pulp production (Wadsworth 1983, Evans 1992). Plantations may help stabilize rural populations in regions where shifting agriculture is the predominant land use. In combination with subsistence and commercial crops (agroforestry) or cattle (agrosilvopastoral systems), plantations have been used as tools in rural development projects worldwide. In Indonesia, policy efforts aimed at reducing deforestation and biomass burning include the development of plantation forests, the integration of transmigration policies with these new forest plantations, and the reduction of shifting cultivation (Murdiyarso 1993). Industrial plantations can make developing countries producers of wood-based commodities and at the same time bring about net reductions of atmospheric carbon (Dabas and Bhatia 1996). If put in context with their other economic, social and environmental functions, well designed and managed tropical plantations can provide viable alternatives to help reduce levels of atmospheric carbon.

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LITERATURE CITED

Allison, L.E. 1975. Organic carbon. Pages 1367-1378 *in* C.A. Black (ed.). Methods of soil analysis, Part 2. American Society of Agronomy, Inc., Madison, Wisconsin.

Bertsch, F. H. 1986. Manual para interpretar la fertilidad de los suelos en Costa Rica. Universidad de Costa Rica. Escuela de Fitotecnia, San José, Costa Rica, 76 pp.

Bloomfield, J., K. A. Vogt, and D. J.Vogt. 1993. Decay rate and substrate quality of fine roots and foliage of two tropical tree species in the Luquillo Experimental Forest, Puerto Rico. *Plant and Soil* 150: 233-245.

Bowen, G. D., and E.K.S. Nambiar. 1984. Nutrition of plantation forests. Academic Press, New York, 516 pp.

Bremner, J. M., and C.S. Mulvaney. 1982. Nitrogen-total. Pages 595-624 *in* A. L. Page, R. H. Miller and R.R. Keeney (eds.). Methods of soil analysis, Part 2, 2nd. ed. American Society of Agronomy, Madison, Wisconsin.

Brown, K., and W. N. Adger. 1994. Economic and political feasibility of international carbon offsets. *Forest Ecology and Management* 68: 217-229.

Brown, S., and A. E. Lugo. 1982. The storage and production of organic matter in tropical forests and their role in the global carbon cycle. *Biotropica* 14:161-187.

Brown, S., A.E. Lugo, and J. Chapman. 1986. Biomass of tropical tree plantations and its implications for the global carbon budget. *Canadian Journal of Forest Research* 16(2):390-394.

Bruenig, E. F. 1996. Conservation and management of tropical rainforests. An integrated approach to sustainability. CAB International, Wallingford, Oxon, UK, 339 pp.

Burkhart, H.E., and Å. Tham. 1992. Predictions from growth and yield models of the performance of mixed-species stands. Pages 21-34 *in* M.G.R. Cannell, D.C. Malcolm and P.A. Robertson (eds.). The ecology of mixed-species stands of trees. Blackwell Scientific, Boston.

Cairns, M.A., and R.A. Meganck. 1994. Carbon sequestration, biological diversity, and sustainable development: integrated forest management. *Environmental Management* 18(1):13-22.

Chambers, R., and M. Leach. 1990. Trees as savings and security for the rural poor. *Unasylva* 41:39-52.

Dabas, M., and S. Bhatia. 1996. Carbon sequestration through afforestation: role of tropical industrial plantations. *Ambio* 25:327-330.

Díaz-Romeu, R., and A. Hunter. 1978. Método para el muestro de suelos, análisis químico de suelos y tejido vegetal e investigación en invernaderos. CATIE, Turrialba, Costa Rica.

Dixon, R.K., J.K. Winjum, K.J. Andrasko, J.J. Lee, and P.E. Schroeder. 1994. Integrated land-use systems: assessment of promising agroforest and alternative land-use practices to enhance carbon conservation and sequestration. *Climatic Change* 27(1): 71-92.

Evans, J. 1992. Plantation forestry in the tropics. Tree planting for industrial, social, environmental, and agroforestry purposes. 2nd. ed. Clarendon Press, Oxford, England, 403 pp.

Fearnside, P.M. 1995. Global warming response options in Brazil's forest sector: comparison of project-level costs and benefits. *Biomass and Bioenergy* 8: 309-322.

Gladstone, W.T., and F.T. Ledig. 1990. Reducing pressure on natural forests through high-yield forestry. *Forest Ecology and Management* 35:69-78.

Halenda, C.J. 1993. Aboveground biomass production and nutrient accumulation of a *Gmelina arborea* plantation in Sarawak, Malaysia. *Journal of Tropical Forest Science* 5(4): 429-439.

Houghton, R. A. 1996. Converting terrestrial ecosystems from sources to sinks of carbon. *Ambio* 25(4):267-272.

Jorgensen, J.R., and C.G. Wells. 1986. Tree nutrition and fast-growing plantations in developing countries. *International Tree Crops Journal* 3:225-244.

Kelty, M.J. 1992. Comparative productivity of monocultures and mixed-species stands. Pages 125-141 *in* M. J. Kelty, B. C. Larson and C. D. Oliver (eds.). The ecology and silviculture of mixed-species forests. Kluwer Academic Publishers, Dordrecht.

Lugo, A. E., S. Brown, and C. G. Chapman. 1988. An analytical review of production rates and stemwood biomass of tropical forest plantations. *Forest Ecology and Management* 23:179-200.

Montagnini, F. 1994. Agricultural systems in the La Selva region. Pages 307-316 *in* L. A. McDade, K. Bawa, H. A. Hespenheide and G. S. Hartshorn (eds.). La Selva: ecology and natural history of a neotropical rainforest. University of Chicago Press, Chicago.

Montagnini, F., and F. Sancho. 1994. Aboveground biomass and nutrients in young plantations of four indigenous tree species: implications for site nutrient conservation. *Journal of Sustainable Forestry* 1:115-139.

Montagnini, F., F. Sancho, E. González, and A. Moulaert. 1993. Mixed-tree plantations with indigenous trees in the Atlantic lowlands of Costa Rica. Pages 161-169 *in* J. A. Parrotta and M. Kanashiro (eds.). Management and rehabilitation of degraded lands and secondary forests in Amazonia. Proceedings of an International Symposium. Santarem, Pará, Brazil. 18-22 April, 1993. IITF,USDA Forest Service, Puerto Rico.

Montagnini, F., E. González, C. Porras, R. Rheingans, and F. Sancho. 1994. Mixed-tree plantations in the humid tropics: Growth, litterfall and economics of experimental systems in Latin America. Pages 125-135 *in* Proceedings from IUFRO International Symposium on Growth and Yield of Tropical Forests. Sept. 26-Oct. 1, 1994. Tokyo University of Agriculture and Technology, Fuchu, Tokyo, Japan.

Montagnini, F., E. González, R. Rheingans, and C. Porras. 1995. Mixed and pure forest plantations in the humid neotropics: a comparison of early growth, pest damage and establishment costs. *Commonwealth Forestry Review* 74(4): 306-314.

Montagnini, F., and R. Mendelsohn. 1996. Managing forest fallows: improving the economics of swidden agriculture. *Ambio* 26(2): 118-123.

Murdiyarso, D. 1993. Policy options to reduce CO_2 release resulting from deforestation and biomass burning in Indonesia. *Chemosphere* 27(6): 1109-1121.

Myers, N., and T. J. Goreau. 1991. A management response to the greenhouse effect. *Climatic Change* 19: 215-225.

Perry, D.A., and J. Maghembe. 1989. Ecosystem concepts and current trends in forest management: time for reappraisal. *Forest Ecology and Management* 26: 123-140.

Rotmans, J., and R. S. Swart. 1991. Modeling tropical deforestation and its consequences for global climate. *Ecological Modelling* 58: 217-247.

Sánchez, P. A., C. A. Palm, C. B. Davey, L. T. Szott, and E. C. Russell. 1985. Tree crops as soil improvers in the humid tropics? Pages 327-350 *in* M. G. R. Cannell and J. E. Jackson (eds.). Attributes of trees as crop plants. Institute of Terrestrial Ecology, Natural Environmental Research Council, Abbots Ripton, Huntingdon, England.

Sancho, F., and R. Mata. 1987. Estudio detallado de suelos. Estación Biológica La Selva. Organización Estudios Tropicales, San José, Costa Rica, 162 pp.

Schroeder, P. 1992. Carbon storage potential of short rotation tropical tree plantations. *Forest Ecology and Management* 50: 31-41.

Sedjo, R. A. 1989. Forests: a tool to moderate global warming? *Environment* 31(1): 14-21.

Smith, D. M. 1986. *The Practice of Silviculture*. (8th ed.). John Wiley and Sons, New York, 527 pp.

Vogt, K., H. Asbjornsen, A. Ercelawn, F. Montagnini, and M. Valdes. 1997. Roots and mycorrhizas in plantation ecosystems. *in* E. K. S. Nambiar and A. G. Brown (eds.). Better management of soil, water and nutrients in tropical plantation forests. In press.

Wadsworth, F. H. 1983. Production of usable wood from tropical forests. Pages 279-288 *in* F. B. Golley (ed.). Tropical Rain forest ecosystems: structure and function. Ecosystems of the World 14A. Elsevier, New York.

Wang, D., F. H. Bormann, A. E. Lugo, and R. D. Bowden. 1991. Comparison of nutrient-use efficiency and biomass production in five tropical tree taxa. *Forest Ecology and Management* 46: 1-21.

Wormald, T.J. 1992. Mixed and pure forest plantations in the tropics and subtropics. FAO Forestry Paper 103. FAO, Rome, 152 pp.

Table 1. Aboveground biomass per hectare of tree species in pure plots and in mixtures of four species each (means, standard errors and statistical significance).

Treatment	Aboveground biomass (Mg/ha)							
	Stems		Branches		Foliage		Total	
Plantation 1:								
Jacaranda copaia	40.9	0.84 a	3.48	0.13 b	2.23	0.13 c	46.6	0.94 a
Vochysia guatemalensis	19.0	0.89 c	4.25	0.22 b	4.03	0.38 b	27.3	1.38 b
Calophyllum brasiliense	7.2	1.46 d	5.71	0.71 a	5.89	0.52 a	18.8	2.67 c
Stryphnodendron microstachyum	1.7	1.26 e	0.56	0.42 c	0.20	0.14 d	2.5	1.82 d
FOUR SPS. MIXTURE	25.3	1.38 b	3.86	0.24 b	3.13	0.23 bc	32.3	1.53 b
Plantation 2:								
Terminalia amazonia	22.4	3.46 a	5.96	0.47 b	4.19	0.38 a	32.5	4.23 ab
Dypterix panamensis	19.1	2.21 a	6.84	0.83 ab	3.22	0.49 a	29.1	3.05 ab
Virola koschnyi	17.8	2.39 a	4.28	1.00 bc	3.61	0.75 a	25.7	3.54 b
Albizia guachapele	7.9	0.85 b	1.92	0.24 c	0.54	0.14 b	10.3	1.10 c
FOUR SPS. MIXTURE	24.8	2.58 a	9.66	1.72 a	4.68	0.63 a	39.1	4.41 a
Plantation 3:								
Pithecellobium elegans	28.8	3.83 a	3.17	0.77 b	1.21	0.23 c	33.2	4.20 a
Hyeronima alchorneoides	26.3	4.99 a	6.74	0.97 a	2.87	0.27 ab	35.9	6.09 a
Vochysia ferruginea	20.3	1.07 a	7.25	1.11 a	3.62	0.44 a	31.1	2.36 a
Genipa americana	13.9	2.85 b	3.06	0.74 b	1.26	0.23 c	18.2	3.70 b
FOUR SPS. MIXTURE	23.1	2.58 ab	5.55	0.36 ab	2.32	0.18 b	31.0	3.06 ab

Note: For each plantation and tree parts, differences among means are statistically significant when standard errors are followed by different letters (n = 4, $P<0.05$).

Table 2. Stem biomass and carbon sequestration by twelve tree species in pure plots and in mixtures of four species each.

Treatment	Mean annual stem increment (Mg/ha)	Mean annual C sequestr. (Mg/ha)	Estimated rotation length (years)
Plantation 1:			
Jacaranda copaia	13.6	6.82	12
Vochysia guatemalensis	6.3	3.17	15
Calophyllum brasiliense	2.4	1.20	25
Stryphnodendron microstachyum	0.6	0.28	20
FOUR SPS. MIXTURE	8.4	4.21	18
Plantation 2:			
Terminalia amazonia	7.5	3.73	20
Dypterix panamensis	6.4	3.18	20
Virola koschnyi	5.9	2.96	15
Albizia guachapele	2.6	1.31	20
FOUR SPS. MIXTURE	8.3	4.13	18.75
Plantation 3:			
Pithecellobium elegans	9.6	4.80	20
Hyeronima alchorneoides	8.8	4.39	20
Vochysia ferruginea	6.8	3.38	15
Genipa americana	4.6	2.32	20
FOUR SPS. MIXTURE	7.7	3.85	18.75

able 3. Soil chemical characteristics in Plantation 1, four years after planting. Means, standard errors (SE), and statistical significance (Sig.)*.

REATMENT	DEPTH (cm)	pH			Extractable cations									Extractable P			Organic matter			Total N		
					Ca cmol/kg			Mg			K			mg/kg			%					
		mean	SE	Sig.	mean	SE	Sig	mean	SE	Sig	mean	SE	Sig.	mean	SE	Sig.	mean	SE	Sig.	mean	SE	Sig.
ıcaranda copaia																						
	0-5	4.43	0.09	ab	1.60	1.13	a	0.48	0.09	a	0.12	0.02	c	9.55	3.07	ab	6.04	2.19	a	0.39	0.05	a
	5-15	4.45	0.10	a	1.00	0.73	a	0.33	0.07	a	0.12	0.03	b	8.30	2.26	a	6.22	1.11	a	0.30	0.05	a
	15-30	4.43	0.08	a	0.67	0.50	ab	0.26	0.06	a	0.13	0.03	ab	7.08	2.17	a	4.52	1.04	a	0.24	0.03	a
	30-60	4.53	0.11	a	0.41	0.32	a	0.17	0.04	a	0.11	0.03	abc	5.38	1.85	a	3.32	0.61	a	0.18	0.02	a
alophyllum brasiliense																						
	0-5	4.30	0.04	b	0.75	0.47	a	0.46	0.07	a	0.19	0.05	bc	15.08	4.85	ab	7.23	0.47	a	0.38	0.03	a
	5-15	4.45	0.05	a	0.47	0.33	a	0.31	0.04	a	0.17	0.06	b	10.33	2.61	a	4.54	0.74	a	0.26	0.02	a
	15-30	4.43	0.03	a	0.23	0.14	b	0.44	0.15	a	0.19	0.06	ab	11.58	3.75	a	3.48	0.50	a	0.22	0.01	a
	30-60	4.53	0.05	a	0.15	0.05	a	0.21	0.04	a	0.20	0.06	ab	10.00	1.73	a	2.60	0.46	a	0.15	0.01	ab
ryphnodendron microstachyum																						
	0-5	4.45	0.03	ab	0.75	0.11	a	0.86	0.14	a	0.24	0.05	b	9.83	2.41	ab	8.17	0.50	a	0.37	0.02	a
	5-15	4.50	0.00	a	0.39	0.13	a	0.40	0.07	a	0.13	0.02	b	6.43	1.73	a	5.41	0.56	a	0.25	0.01	a
	15-30	4.48	0.05	a	0.22	0.10	b	0.28	0.04	a	0.11	0.04	ab	6.63	2.21	a	3.34	0.69	a	0.19	0.02	a
	30-60	4.55	0.10	a	0.46	0.26	a	0.17	0.03	a	0.11	0.04	abc	5.58	1.93	a	2.34	0.45	a	0.12	0.01	b
ochysia guatemalensis																						
	0-5	4.55	0.09	a	1.50	1.03	a	0.88	0.36	a	0.11	0.01	c	6.70	0.76	b	7.98	1.13	a	0.41	0.04	a
	5-15	4.43	0.05	a	0.69	0.62	a	0.30	0.09	a	0.09	0.02	b	5.80	0.88	a	5.64	1.28	a	0.29	0.05	a
	15-30	4.45	0.06	a	2.16	1.17	a	0.70	0.25	a	0.09	0.03	b	7.58	1.21	a	4.36	1.24	a	0.23	0.05	a
	30-60	4.50	0.04	a	1.06	0.70	a	0.29	0.07	a	0.08	0.03	bc	5.25	1.96	a	1.90	0.25	a	0.14	0.01	b
lixed																						
	0-5	4.45	0.09	ab	1.07	0.24	a	0.57	0.17	a	0.14	0.01	bc	10.18	3.88	ab	6.99	0.37	a	0.37	0.20	a
	5-15	4.38	0.10	a	0.44	0.14	a	0.30	0.06	a	0.10	0.01	b	8.43	4.14	a	4.68	0.37	a	0.26	0.02	a
	15-30	4.50	0.00	a	0.40	0.08	b	0.32	0.08	a	0.11	0.02	ab	9.23	2.69	a	3.68	0.42	a	0.22	0.02	a
	30-60	4.55	0.05	a	0.12	0.03	a	0.15	0.03	a	0.07	0.01	c	5.83	1.39	a	2.61	0.27	a	0.14	0.01	b
egeneration																						
	0-5	4.60	0.12	a	1.02	0.46	a	0.88	0.23	a	0.36	0.05	a	17.70	3.87	a	6.61	0.68	a	0.36	0.03	a
	5-15	4.53	0.08	a	0.52	0.20	a	0.37	0.03	a	0.31	0.06	a	11.35	2.88	a	5.32	0.74	a	0.28	0.02	a
	15-30	4.50	0.12	a	0.49	0.22	b	0.71	0.42	a	0.22	0.07	a	11.50	2.90	a	3.76	0.63	a	0.23	0.02	a
	30-60	4.53	0.08	a	0.17	0.04	a	0.29	0.07	a	0.21	0.07	a	7.60	1.71	a	3.40	0.82	a	0.15	0.01	ab

In the present and following tables, differences between sites for a given depth and soil variable are statistically significant when standard errors are followed y different letters (n=4, $P<0.05$).

able 4. Soil chemical characteristics in Plantation 2, four years after planting. Means, standard errors (SE), and statistical significance (Sig.).

REATMENT/DEPTH (cm)	pH			Extractable cations									Extractable P			Organic matter			Total N		
				Ca cmol/kg			Mg			K			mg/kg			%					
	mean	SE	Sig.	mean	SE	Sig.	mean	SE	Sig.	mean	SE	Sig.	mean	SE	Sig.	mean	SE	Sig.	mean	SE	Sig.
lbizia guachapele																					
0-5	4.38	0.10	a	1.03	0.34	a	0.88	0.24	a	0.43	0.10	a	13.45	2.17	a	6.86	0.97	a	0.41	0.01	a
5-15	4.50	0.00	a	0.68	0.14	a	0.50	0.07	ab	0.26	0.06	ab	8.35	0.74	a	4.66	0.54	a	0.27	0.02	ab
15-30	4.60	0.00	ab	0.55	0.12	a	0.40	0.07	a	0.22	0.06	a	7.03	0.75	a	3.66	0.28	b	0.20	0.02	b
30-60	4.73	0.05	a	0.38	0.05	a	0.23	0.03	a	0.20	0.04	ab	5.60	1.26	b	2.69	0.23	ab	0.14	0.02	ab
ipteryx panamensis																					
0-5	4.48	0.13	a	1.13	0.23	a	0.75	0.28	a	0.42	0.06	a	9.93	0.16	a	7.06	0.67	a	0.40	0.02	a
5-15	4.58	0.16	a	0.63	0.07	a	0.78	0.29	a	0.33	0.06	a	7.98	1.27	a	4.48	0.16	a	0.26	0.01	ab
15-30	4.65	0.60	a	0.43	0.05	a	0.38	0.09	a	0.28	0.07	a	5.93	0.89	a	3.29	0.24	b	0.19	0.01	b
30-60	4.58	0.06	ab	0.28	0.05	a	0.23	0.03	a	0.24	0.03	a	4.40	0.23	b	2.68	0.21	ab	0.16	0.01	ab
erminalia amazonia																					
0-5	4.28	0.05	a	0.75	0.05	a	0.55	0.09	a	0.23	0.04	b	13.26	0.64	a	7.18	0.62	a	0.38	0.03	a
5-15	4.43	0.09	a	0.45	0.07	a	0.33	0.05	b	0.13	0.02	c	8.45	1.00	a	4.94	0.59	a	0.25	0.02	b
15-30	4.58	0.09	ab	0.38	0.03	a	0.28	0.03	a	0.15	0.04	a	7.70	1.48	a	3.37	0.12	b	0.20	0.01	b
30-60	4.60	0.07	ab	0.25	0.03	a	0.18	0.03	a	0.10	0.02	c	5.78	1.00	ab	2.23	0.51	b	0.15	0.01	ab
irola koschnyi																					
0-5	4.28	0.05	a	1.00	0.26	a	0.55	0.16	a	0.21	0.02	b	13.05	1.72	a	6.70	1.39	a	0.41	0.03	a
5-15	4.35	0.03	a	0.53	0.09	a	0.30	0.04	b	0.16	0.01	bc	10.60	1.68	a	4.33	0.44	a	0.28	0.02	ab
15-30	4.45	0.06	b	0.43	0.11	a	0.28	0.05	a	0.16	0.02	a	9.60	1.85	a	3.61	0.28	b	0.22	0.00	ab
30-60	4.58	0.08	ab	0.35	0.10	a	0.23	0.05	a	0.13	0.02	bc	7.53	1.47	ab	2.52	0.39	ab	0.14	0.01	b
lixed																					
0-5	4.33	0.05	a	0.68	0.21	a	0.43	0.06	a	0.27	0.05	ab	10.78	2.16	a	6.61	0.38	a	0.38	0.02	a
5-15	4.45	0.03	a	0.50	0.12	a	0.38	0.09	b	0.22	0.05	abc	8.40	2.08	a	4.72	0.26	a	0.27	0.02	ab
15-30	4.55	0.05	ab	0.43	0.11	a	0.30	0.06	a	0.16	0.03	a	6.98	1.44	a	3.54	0.15	b	0.23	0.02	ab
30-60	4.60	0.04	ab	0.30	0.04	a	0.20	0.00	a	0.12	0.02	bc	5.50	1.12	b	2.57	0.09	ab	0.14	0.00	ab
egeneration																					
0-5	4.33	0.05	a	1.00	0.12	a	0.58	0.03	a	0.34	0.05	ab	11.80	2.50	a	8.29	0.74	a	0.43	0.02	a
5-15	4.38	0.06	a	0.58	0.11	a	0.43	0.03	ab	0.22	0.04	abc	8.43	1.96	a	5.76	0.76	a	0.32	0.04	a
15-30	4.48	0.06	ab	0.45	0.06	a	0.35	0.05	a	0.23	0.04	a	8.13	1.45	a	4.85	0.70	a	0.27	0.04	a
30-60	4.53	0.08	b	0.35	0.07	a	0.25	0.05	a	0.21	0.05	ab	10.55	3.14	a	3.42	0.30	a	0.18	0.01	a

able 5. Soil chemical characteristics in Plantation 3, four years after planting. Means, standard errors (SE), and statistical significance (Sig.).

				Extractable cations																	
REATMENT/DEPTH (cm)	pH			Ca cmol/kg			Mg			K			Extractable P mg/kg			Organic matter %			Total N		
	mean	SE	Sig.	mean	SE	Sig	mean	SE	Sig.	mean	SE	Sig.	mean	SE	Sig.	mean	SE	Sig.	mean	SE	Sig
enipa americana																					
0-5	4.50	0.06	b	0.57	0.21	b	0.64	0.35	b	0.34	0.10	bc	6.28	1.31	ab	6.77	0.33	ab	0.33	0.02	a
5-15	4.60	0.08	a	0.27	0.08	b	0.31	0.17	ab	0.24	0.10	bc	4.30	0.65	a	4.30	0.63	a	0.23	0.02	a
15-30	4.63	0.09	a	0.26	0.11	b	0.27	0.13	ab	0.22	0.09	bc	4.30	0.62	a	3.23	0.42	a	0.20	0.02	a
30-60	4.53	0.05	a	0.10	0.04	b	0.13	0.07	a	0.12	0.07	a	3.50	0.82	a	1.67	0.38	a	0.13	0.01	a
ieronyma alchorneoides																					
0-5	4.33	0.05	b	0.44	0.06	b	0.39	0.04	b	0.14	0.02	c	8.30	1.30	a	5.90	0.59	b	0.34	0.01	a
5-15	4.43	0.09	a	0.17	0.05	b	0.21	0.02	b	0.10	0.01	c	4.43	0.99	a	4.49	0.85	a	0.24	0.01	a
15-30	4.43	0.05	a	0.19	0.06	b	0.19	0.04	b	0.10	0.02	c	4.38	1.12	a	3.68	0.29	a	0.22	0.02	a
30-60	4.50	0.06	a	0.06	0.02	b	0.10	0.02	a	0.09	0.02	a	3.83	0.78	a	1.85	0.30	a	0.13	0.01	a
ithecellobium elegans																					
0-5	4.50	0.13	b	1.19	0.44	b	0.67	0.28	ab	0.32	0.03	bc	4.75	1.03	ab	8.15	0.15	a	0.32	0.06	a
5-15	4.48	0.14	a	0.88	0.35	a	0.52	0.15	ab	0.25	0.06	bc	3.73	0.24	a	5.10	0.29	a	0.26	0.02	a
15-30	4.50	0.09	a	0.52	0.11	ab	0.29	0.06	ab	0.19	0.04	bc	3.33	0.60	a	3.69	0.87	a	0.16	0.03	a
30-60	4.50	0.06	a	0.80	0.53	a	0.43	0.30	a	0.17	0.07	a	3.13	1.00	a	3.32	0.87	a	0.20	0.07	a
ochysia ferruginea																					
0-5	4.55	0.10	b	1.06	0.46	b	0.97	0.27	ab	0.52	0.19	b	4.90	0.53	ab	6.64	0.62	ab	0.38	0.01	a
5-15	4.58	0.09	a	0.49	0.19	ab	0.49	0.08	ab	0.39	0.12	ab	2.85	0.40	a	4.81	0.63	a	0.27	0.01	a
15-30	4.63	0.09	a	0.36	0.19	ab	0.33	0.10	ab	0.30	0.09	ab	2.25	0.44	a	3.69	0.46	a	0.19	0.01	a
30-60	4.55	0.10	a	0.19	0.05	ab	0.16	0.03	a	0.19	0.05	a	2.35	1.01	a	1.85	0.15	a	0.12	0.00	a
Mixed																					
0-5	4.38	0.06	b	0.65	0.13	b	0.63	0.13	b	0.22	0.03	bc	3.88	1.00	b	7.05	0.18	ab	0.38	0.01	a
5-15	4.48	0.08	a	0.34	0.13	b	0.37	0.07	ab	0.17	0.03	bc	2.45	0.78	a	5.00	0.43	a	0.27	0.03	a
15-30	4.60	0.17	a	0.30	0.11	b	0.26	0.07	ab	0.12	0.02	bc	2.38	0.71	a	3.75	0.31	a	0.20	0.01	a
30-60	4.55	0.10	a	0.27	0.12	ab	0.17	0.06	a	0.11	0.02	a	1.90	0.66	a	1.89	0.43	a	0.13	0.00	a
Regeneration																					
0-5	4.90	0.18	a	2.49	0.59	a	1.38	0.28	a	0.96	0.21	a	3.93	1.83	b	8.30	1.21	a	0.38	0.02	a
5-15	4.68	0.16	a	0.90	0.12	a	0.57	0.09	a	0.58	0.12	a	3.20	0.75	a	5.09	0.34	a	0.25	0.01	a
15-30	4.65	0.12	a	0.70	0.13	a	0.43	0.07	a	0.41	0.07	a	3.80	0.93	a	2.91	0.20	a	0.20	0.01	a
30-60	4.55	0.06	a	0.30	0.10	ab	0.17	0.02	a	0.18	0.03	a	2.00	0.65	a	2.83	1.42	a	0.13	0.01	a

Table 6. Aboveground biomass and stemwood production in tropical plantations.

Species	Age (years)	Aboveground biomasss production (Mg $ha^{-1}yr.^{-1}$)	Stemwood biomass production (Mg $ha^{-1}yr.^{-1}$)	Country	Source
Eucalyptus citridiora	9	11.8	7.2	Brazil	Lugo et al. (1988)
Eucalyptus deglupta	8	13.1	11.9	Costa Rica	Lugo et al. (1988)
Gmelina arborea	5	12.9	11.8	Costa Rica	Lugo et al. (1988)
Gmelina arborea	6.6	13.9	10	Sarawak	Halenda (1993)
Albizia lebbek	3	9.8	8.4	Puerto Rico	Wang et al. (1991)
Leucaena leucocephala	5.5	11	9	Puerto Rico	Wang et al. (1991)
Swietenia spp.	9-13	NA	1-4	Nicaragua	Wadsworth (1983)
Tectona grandis	14	NA	7-11	Cuba	Wadsworth (1983)

NA: not available.

CAPTIONS FOR FIGURES

Figure 1.

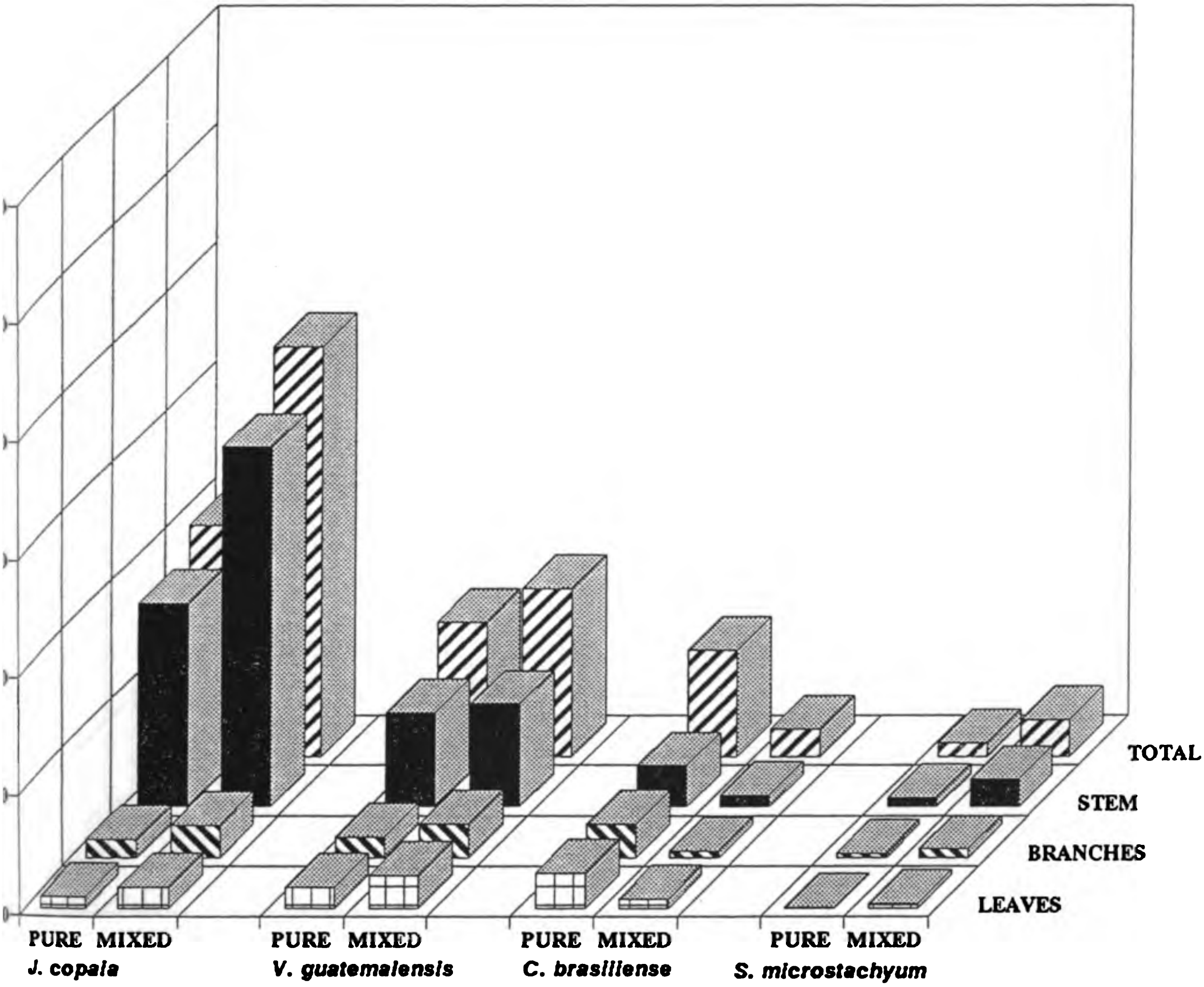
a- Aboveground tree biomass (leaves, branches, stem, and total) of *Jacaranda copaia*, *Vochysia guatemalensis*, *Calophyllum grasiliense* and *Stryphnodendron microstachyum* in pure and mixed plots.

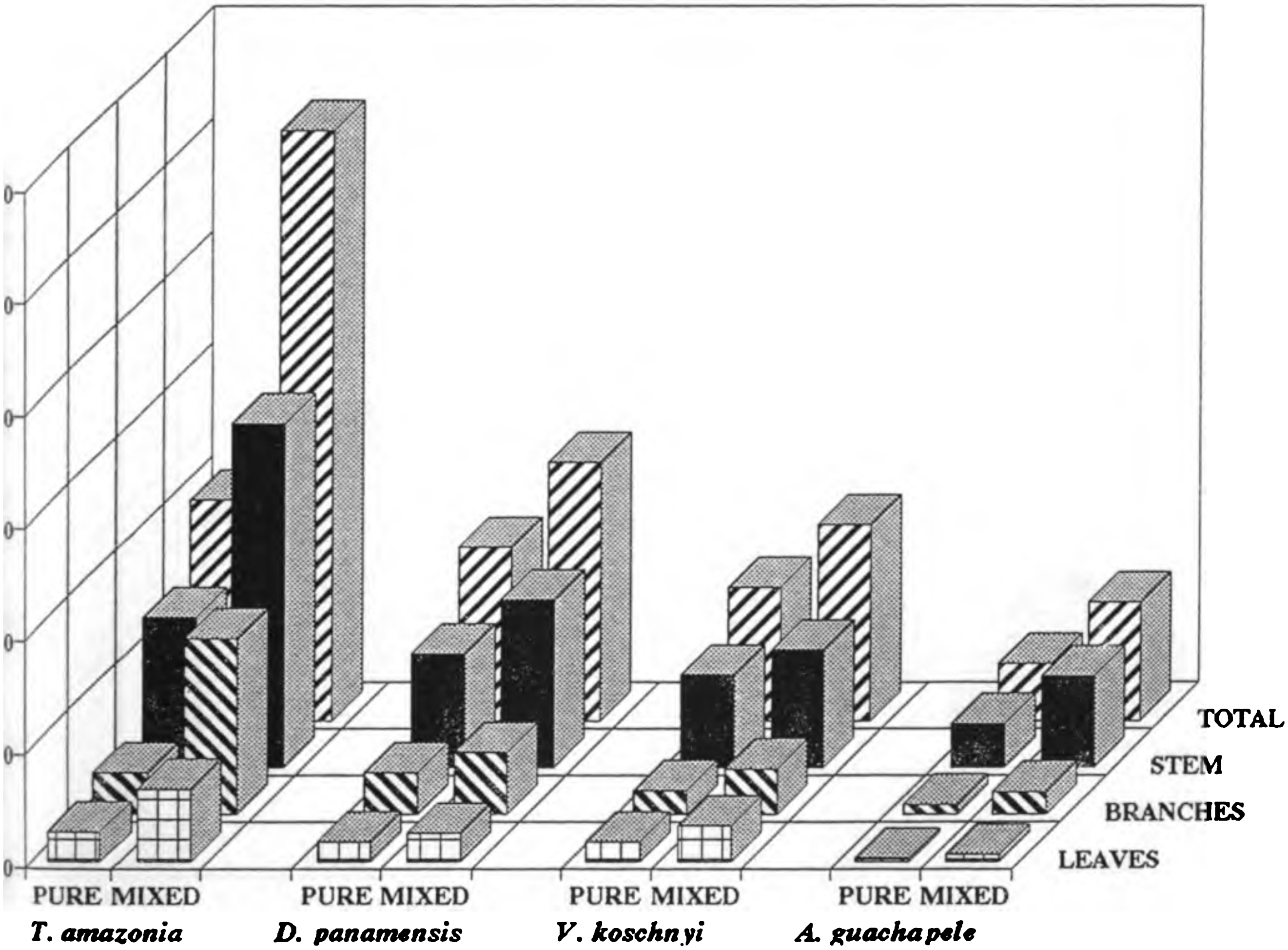
b- Aboveground tree biomass (leaves, branches, stem, and total) of *Terminalia amazonia*, *Dipteryx panamensis*, *Virola koschnyi* and *Albizia guachapele* in pure and mixed plots.

c- Aboveground tree biomass (leaves, branches, stem, and total) of *Hyeronima alchorneoides*, *Pithecellobium elegans*, *Vochysia ferruginea* and *Genipa americana* in pure and mixed plots.

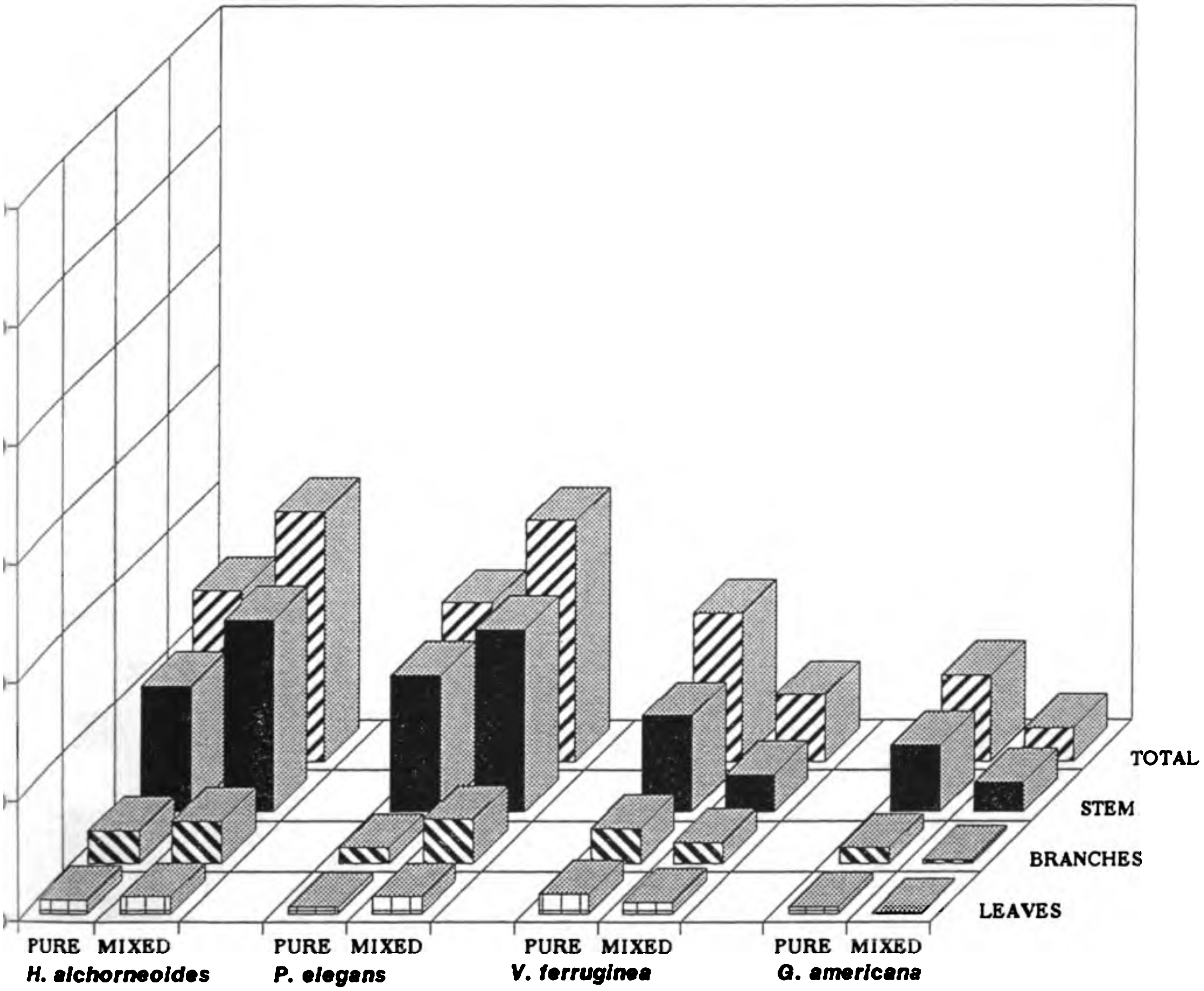
Figure 2. Soil potassium in Plantation 1 at 0-5 cm and 5-15 cm depths, in sampling done from 1992 to 1995 (one to four years after planting), under *Stryphnodendron microstachyum*, *Vochysia guatemalensis*, *Jacaranda copia*, *Calophyllum brasiliense*, mixture of four species, and regeneration plots (natural regrowth). See text for statistical significances

Figure 3. Soil phosphorus in Plantation 1 at 0-5 cm and 5-15 cm depths, in sampling done from 1992 to 1995 (one to four years after planting), under *Stryphnodendron microstachyum*, *Vochysia guatemalensis*, *Jacaranda copia*, *Calophyllum brasiliense*, mixture of four species, and regeneration plots (natural regrowth). See text for statistical significances.


TOTAL
STEM
BRANCHES
LEAVES
PURE
MIXED
J. copala
PURE
MIXED
V. guatemalensis
PURE
MIXED
C. brasiliense
PURE
MIXED
S. microstachyum



PURE MIXED
PURE MIXED
PURE MIXED
PURE MIXED
T. amazonia
D. panamensis
V. koschnyi
A. guachapele
TOTAL
STEM
BRANCHES
LEAVES


TOTAL
STEM
BRANCHES
LEAVES
PURE
MIXED
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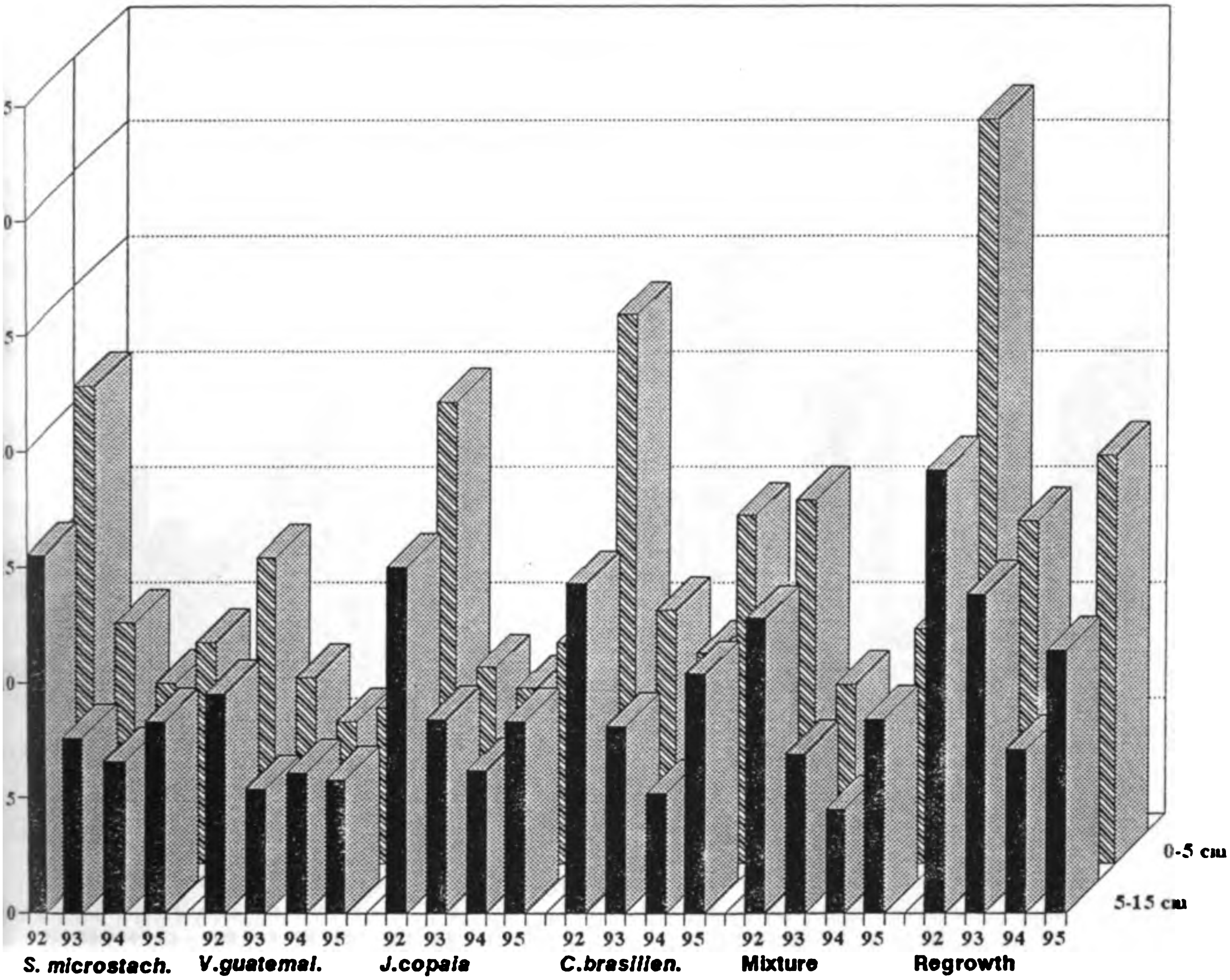
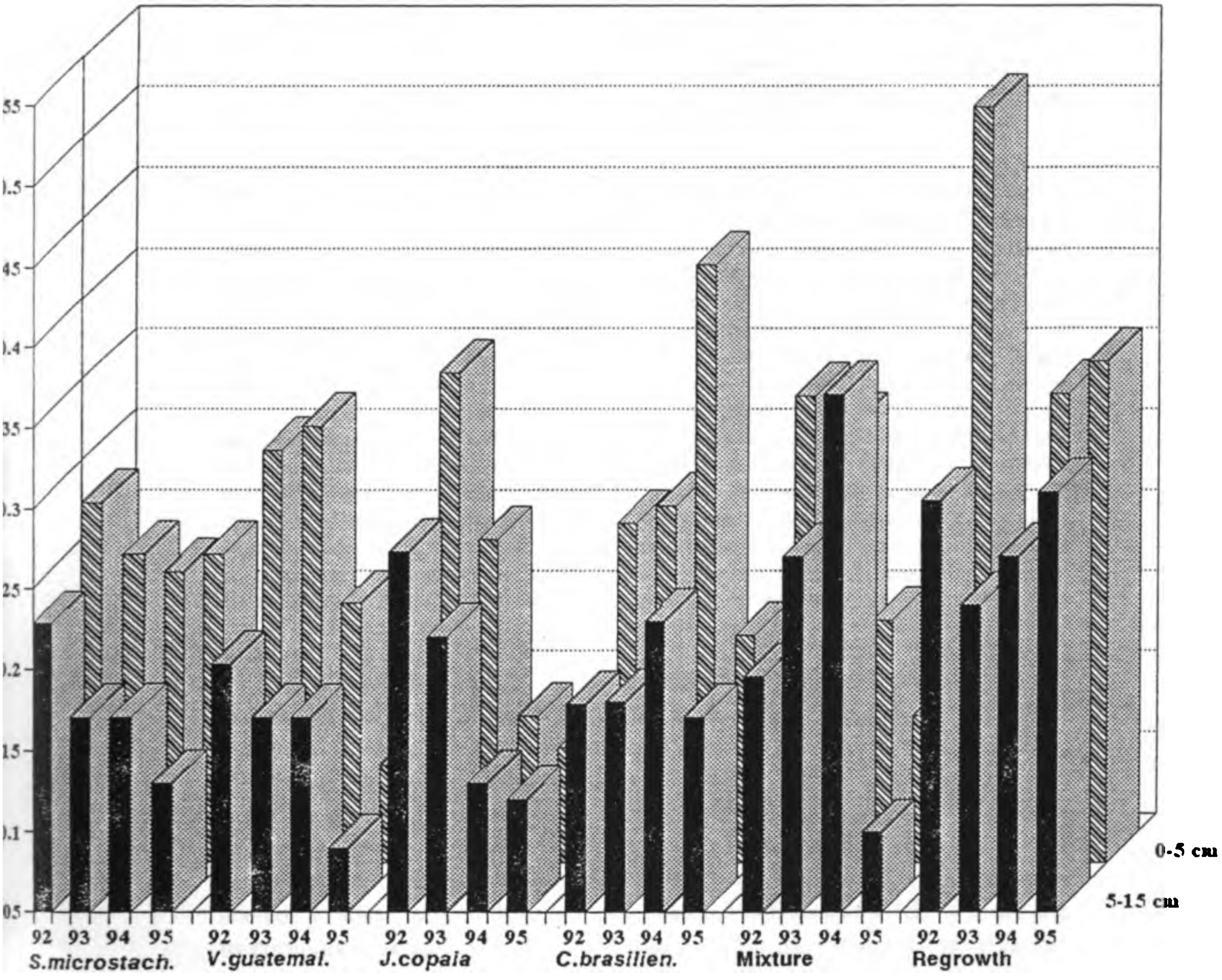
PURE
MIXED
P. elegans
PURE
MIXED
V. ferruginea
PURE
MIXED
G. americana



5
0
5
0
5
0
5
0
0-5 cm
5-15 cm
92 93 94 95
92 93 94 95
92 93 94 95
92 93 94 95
92 93 94 95
92 93 94 95
S. microstach.
V.guatemal.
J.copaia
C.brasilien.
Mixture
Regrowth


55
.5
45
.4
35
.3
25
.2
15
.1
05
92 93 94 95
S.microstach.
92 93 94 95
V.guatemal.
92 93 94 95
J.copaia
92 93 94 95
C.brasilien.
92 93 94 95
Mixture
92 93 94 95
Regrowth
0-5 cm
5-15 cm

Author -
Acc p. 252, 256, 259, 260, 266
268, 270, 271, 272, 273
275, 277, 278, 284, 287,
289, 291, 294

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8

Roots and Mycorrhizas in Plantation Ecosystems

K. Vogt,
H. Asbjornsen, A. Ercelawn,
F. Montagnini and M. Valdés

Abstract

The role of roots and mycorrhizas in natural and plantation forests in the tropics is reviewed. To illustrate key issues that need to be considered when trying to assess the role of roots and mycorrhizas in tropical forest plantations, literature from the temperate zone is used when information is not available from the tropics. The following characteristics of roots and mycorrhizas are reviewed: root ~~above~~ diameters and their function, root density and nutrient uptake, rooting depth, fine root seasonality, root adaptations, types and distribution of mycorrhizal associations, mycorrhizal attributes, and variability in host plant and fungus relationships. Other topics reviewed are: 1) tree productivity, carbon allocation within trees and what controls allocation to roots plus mycorrhizas and shoots, 2) how the importance of roots and mycorrhizas vary with stand development and succession, 3) the relationships between roots and mycorrhizal associations and nutrient cycling, and 4) how roots and mycorrhizal associations need to be considered in forest management (specifically focusing on fungal pathogens and insect pests, heavy metal toxicity and several management activities). Research topics that are important to pursue to better understand the role of roots and mycorrhizas in forest plantations are presented throughout the text. The rationale is presented for using an ecosystem approach, rather than isolated studies, when examining roots and mycorrhizas.

MOST RESEARCH on tropical plantations has emphasised those factors that would assist survival of seedlings planted at a site, those parts of the ecosystem that were thought to have the strongest influence on the wood growth of trees, or the effects of harvesting trees on environmental site conditions. These studies have been very useful for developing management tools to increase wood growth of plantation species, for producing techniques that guarantee the regeneration of the desired species and for minimising erosion and nutrient losses from sites after harvesting. In addition to these factors, there is a real need to understand the role of roots and mycorrhizas in acquiring nutrients and water in plantations since the latter factors control carbon allocation patterns within plants and the achievable productivity on the site. Frequently roots and mycorrhizas have not been included in studies because of the difficulties of collecting and processing data on something that is not visible. The emphasis in the ecological literature has been to identify surrogate ecological parameters that can be measured aboveground or to model carbon allocation to root growth (Vogt et al. 1986; Raich and Nadelhoffer 1989; Santantonio 1990; Landsberg et al. 1991; Cannell and Dewar 1994). The database on fine roots and mycorrhizas for plantation ecosystems in any climatic zone is small (Nambiar 1983; Gholz et al. 1986; Vogt 1987; Fabiao et al. 1990/91) and few data are available from tropical and subtropical plantations (see Tables 8.1–8.4 on pages 266–278; Cuenca et al. 1983; Singh and Srivastava 1984; Santantonio and Santantonio 1987; Cuevas et al. 1991; Montagnini et al. 1991; Lugo 1992; Parrotta 1992; Parrotta and Singh 1992; Montagnini 1995). Most research on plantations has focused on aboveground parts.

We are beginning to understand the role of fine roots and mycorrhizas in the ecosystem-level response of forests to a changing environment (Allen 1991; Vogt et al. 1993). Since intensive management of plantations has the goal of increasing the growth of specific parts of a plant as the desired product, we need to understand the implications of a management activity imposed on part of the system and how this affects plant carbon allocation between the shoots and roots in both the short and long terms.

Improved understanding of belowground response to management requires studies with a holistic approach that considers roots and mycorrhizas as an integral part of the ecosystem. We frequently do not know the feedbacks in ecosystems, so it is wise not to ignore a large part of a system. It is equally critical that studies of belowground parts of ecosystems do not ignore the rest of the ecosystem. The consequences of not taking a holistic approach are often severe: ecosystems may become more susceptible to insects and disease, to moisture and/or nutrient stress, and ultimately have decreased production. Since management practices are intended to accelerate aboveground growth, we have to understand how the same practices influence the resistance of plants to disturbance.

Whether the major concern is carbon and nutrient cycling rates, net primary production or plant response to and their rate of recovery (i.e. resilience) after a disturbance, there are certain fundamental issues of the belowground environment which should be considered. For example, the contribution of roots to controlling/regulating carbon and nutrient cycling rates and stand production must be understood because roots acquire nutrients from the soil and they may contribute significantly upon their senescence to decomposition and nutrient mineralisation (Vogt et al. 1986). Symbionts (mycorrhizal associations) are particularly important to studies of plant responses to disturbance (Vogt et al. 1993) since seedlings without the interface that mycorrhizae provide between the plant and the soil grow poorly (Harley and Smith 1983; Perry et al. 1987).

This chapter addresses the role of the belowground ecosystem in maintaining the productivity and health of plantations, focusing on roots and mycorrhizae. In particular, we explore the following questions: What do we presently understand about the belowground ecosystem in tropical plantations? How may belowground

The amount of carbon allocated to roots appears to vary with the plant spacing (Puri et al. 1994). In a desert region in India, Puri et al. (1994) recorded that the proportion of total root biomass in fine roots increased from 30 to 75% when the spacing of *Populus deltoides* trees increased from a 2 × 2 m to 6 × 6 m, respectively. Furthermore, trees growing under wider spacing allocated more total carbon to their roots compared to those with the narrower spacing.

Coarse roots have been effectively incorporated in biomass studies because this biomass can be predicted from allometric regressions incorporating tree diameter at breast height (Santantonio 1990). Even though fine roots and mycorrhizal associations are maintained by carbohydrate fixed in leaves, it has been difficult to identify aboveground parameters that can be used to predict how much carbon is allocated to root growth and maintenance. Fine roots and mycorrhizal associations respond at the microsite scale that is very different from the response of the whole root system (Friend et al. 1990; Pregitzer et al. 1993; Roy and Singh 1995). The overall position is further complicated by the fact that while the presence of the symbionts on root systems may be costly (~15% of total Net Primary Production, NPP, is allocated to symbiotic associations), since the symbionts increase the longevity of the fine roots the actual cost of maintaining these roots may be much reduced when amortised over annual time scales (Vogt et al. 1982). It is critical that we understand the dynamics of fine root mycorrhizas since they respond to a plant's changing resource availability.

There is no relationship between the measured mean annual fine root biomass and annual fine root NPP. These differences are strongly highlighted in a comparison of a secondary wet tropical forest with adjacent *Pinus caribaea* plantations in Puerto Rico (Cuevas et al. 1991). In the plantation less than 1% of the total biomass was in fine roots compared to 6% of NPP in fine roots (Cuevas et al. 1991). The secondary forest had an even more dramatic difference between biomass and NPP—9% of total biomass and 44% of total NPP was in fine roots.These comparisons were made in forests that were both 11 years of age. They exemplify the substantial differences which may occur between species in allocation of resources to fine roots to acquire the nutrients required for growth. [cf. authors' conclusion].

Root density and nutrient uptake

Since nutrient uptake by plants is more a function of the root surface area than root weight, root weights by themselves are difficult to convert to a useful index of plant ability to take up nutrients (Nambiar 1985). Root density (i.e., root length per given volume of soil) measurements are a more useful indication of plant ability to access soil nutrients. For example, Barley (1970) originally developed soil nutrient depletion curves that related rooting density to the mobility of soil nutrients (e.g., highly, poorly or non-mobile). This type of analysis makes it possible to determine whether the rooting density is adequate to access the nutrients required for growth. As part of the nutrient depletion curves, the optimal rooting densities had to be greater than 2 cm cm^{-3} for taking up the highly mobile elements nitrate and sulfate, while a rooting density greater than 4 cm cm^{-3} was required for the poorly mobile elements (Barley 1970; Nambiar 1985). Actual rooting density measurements for *Pinus radiata* were 0.13–0.18 cm cm^{-3} when seedlings were 3–4 years old, 1.1–2.9 cm cm^{-3} when 8 years old and 2 cm cm^{-3} at 14–16 years of age (Bowen 1984; Nambiar 1985). It is obvious that these values are much lower than those desirable for accessing poorly mobile and non-mobile elements, and therefore the role of mycorrhizae in facilitating nutrient uptake must be considered. In other cases, mycorrhizas may not be as important in contributing to increasing root densities since plant root densities are effective at acquiring even the most non-mobile nutrients. For example, 11-year-old *Eucalyptus marginata* had a rooting density of up to 7 cm cm^{-3} (Carbon et al. 1980) which based on Barley's (1970) nutrient depletion curves would be very effective in absorbing poorly mobile nutrients such as P from the soil.

Under field conditions, mycorrhizal hyphae or rhizomorphs significantly increase the surface area of plant root systems accessible to poorly or immobile elements like ammonium, phosphate, copper and zinc. However, as measurements of the extent of hyphal development in the field have not been well documented the significance of the contribution by hyphae to nutrient uptake cannot be quantified. Interestingly, in subalpine *Abies amabilis* ecosystems in Washington, USA, extensive hyphal networks were observed when soil fluxes of poorly mobile nutrients were greatest and when fine root growth was the most active (Vogt et al. 1982). Roy and Singh (1995) observed a similar direct correlation between root growth and mineral nitrogen in a dry tropical forest. These studies suggest that the timing of N mineralisation and growth of roots and associated fungi is synchronous—an effective adaptive mechanism for conserving nutrients in forest ecosystems.

Rooting depth

Many studies of the success of mixed-species plantings have collected information on rooting depth for each species (Alpizar et al. 1986; Jonsson et al. 1988; Young 1989; Dhyani et al. 1990; Fassbender et al. 1991; Opakunle 1991). In addition to revealing how much of the soil space is occupied by roots, rooting depth information is particularly useful in the tropics since large areas of the those forests experience short- to long-term seasonal droughts. Growth of plantations in areas with dry periods is facilitated if deep-rooted tree species are selected to use deeper sources of water. It has been shown that deep-rooted plants may bring up water from deep sources and make it available to other plants growing in their space (Richards and Caldwell 1987; Caldwell and Richards 1989). This ability may be a useful criterion to use when selecting the combination of trees to grow together in a mixed plantation, but one has to careful that these species do not over-utilise water resources.

Stone and Kalisz (1991) have synthesised information on the maximum rooting depths for tree species—mostly for the temperate zone. Most plants appear to have rooting depths that average 1–2 m. Bowen (1984) reported *Eucalyptus marginata* rooting to 1.6 m while Dhyani et al. (1990) reported values of 4.2 m for *Eucalyptus tereticornis* and 2.8 m for 28-month-old *Leucaena leucocephala*. Deep-rooted Amazonian semi-evergreen forests have been reported to have maximum rooting depths of 12 m (Stone and Kalisz 1991), while the greatest root depths (consistently exceeding 35 m) were reported for several eucalypt species, *Acacia raddiana* and *Prosopis juliflora* (a desert shrub). The maximum rooting depth reported for any plant species was for *Eucalyptus* sp. which had roots going to 60 m.

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Fine root seasonality

There are seasonal patterns of root growth in coniferous and deciduous forests in the temperate zone (Harris et al. 1977; Vogt et al. 1982; Aber et al. 1985; Vogt et al. 1986; Santantonio and Santantonio 1987). In the cold temperate zone, seasonal peaks of higher root biomass occur immediately before or after the period of high shoot growth—typically drawing on stored carbohydrate in early spring and current photosynthate and stored carbohydrate in the autumn. For example, 40-year-old *Pseudotsuga menziesii* growing in the temperate zone had fine root production directly correlated to the starch content of phloem tissues in the bole (Vogt et al. 1985).

Similar seasonal cycles (i.e. modal or bimodal) of fine root growth have been reported in the tropics. In seasonally-dry tropical forests in India, fine root biomass varied seasonally from about 700 to >2000 kg ha^{-1} at 20–40 cm depth (Singh and Srivastava 1985) and from 1740 to 3740 kg ha^{-1} (Roy and Singh 1995). In wet humid tropical forests in Puerto Rico, fine root biomass ranged from 200 to 8000 kg ha^{-1} (Cuevas et al. 1991; Kangas 1992; Vogt et al. 1995a).

Disturbance may reduce the seasonal peak of fine root biomass. For example, following hurricanes with several year drought cycles in the Caribbean (Scatena, International Institute of Tropical Resources, Puerto Rico), the standing crop of fine root biomass was 2400 kg ha^{-1} (Vogt et al. 1995a) compared to previously reported values exceeding 8000 kg ha^{-1}. In the same forest, Kangas (1992) recorded a fine root biomass (<5 mm) of 8186 kg ha^{-1} during a non-hurricane period. Because fine roots turn over at least once annually (Vogt and Bloomfield 1991), the data presented by Cuevas et al. (1991) also suggest that it is not unrealistic to have a difference of 8000 kg ha^{-1} in seasonal fine root biomass in the humid tropics which is comparable to reported values in the cold temperate zone (Vogt 1991).

In the wet and dry tropical forests, short-term (i.e. weeks) dry periods appear to have strong influences on the timing of root turnover and periods of fine root growth. In tropical dry forests, moisture availability controls the timing of fine root growth (Singh and Srivastava 1985; Kavanagh and Kellman 1992). Singh and Srivastava (1985) reported a bimodal pattern of root tip growth of *Tectona grandis* plantations in seasonally dry areas that was regulated by moisture availability. This is similar to a dry tropical forest studied by Roy and Singh (1995) which also showed a modal pattern of fine root growth. Even in humid tropical forests, fine root growth is controlled by short periods of low or no precipitation. In a humid tropical secondary forest in Puerto Rico, a modal cycle of root growth occurred where the seasonality was controlled by annual dry periods several weeks long (Vogt et al. 1995a). It is therefore critical to determine the periodicity of root growth so that sampling can effectively detect this variability.

Most of the studies in the tropics on plant species for agroforestry or multiple-tree species systems have used a one-time sampling period to determine differences between the root biomass of species (Table 1). Because there are seasonal patterns of fine root growth, variation between species in the timing and cessation of fine root growth, and variation in root growth by depth in the soil profile (Ford and Deans 1977; Vogt et al. 1995a), one-time sampling without information on temporal changes should be avoided. The lack of significant differences in fine root biomass (531–780 kg ha^{-1}) between four tree species grown in combination with an agricultural crop (Jonsson et al. 1988) could be related to the time period in which root cores were collected. In this case, seasonal data on root biomass might have shown differences in fine root biomass of the species.

Root adaptations

In addition to the climatic variables that strongly control shoot growth, roots and symbionts exist in an environment where the soil chemical and physical environment may significantly modify their growth dynamics. For example, while the shoot of a tree can be defined as an individual that is competing with other trees for light resources, this distinction is frequently not so clear belowground where fine roots of many plants intermingle extensively. For example, trees of many species are capable of root grafting with one another or with those of other species (Graham and Bormann 1966) or potentially have mycorrhizal hyphal connections between different plants (Ritz and Newman 1984; Finlay and Read 1986) so that the entire belowground part of a forest may have to be considered as one responding unit instead of many individuals forming a stand (Vogt et al. 1993). The importance of root grafting was observed in the 1960s when systemic chemicals were used to kill trees and many adjacent trees that were not treated also died because of the transfer of the chemical through root grafts (Bormann and Graham 1960). On the positive side, there is the potential that a plant may increase its ability to acquire nutrients limiting plant growth, or carbohydrate, if the plant is able to acquire these compounds from neighbours through root and/or mycelial connections (Finlay and Read 1986). These characteristics make it very difficult to compare the competitive environment of the shoot with that of the root at an individual plant level.

Plant roots are capable of modifying their morphology in response to edaphic conditions. One example relevant to wet tropical ecosystems, because of high precipitation rates, is the morphological adaptation of fine roots to high water levels. This adaptation is typically observed on stems and roots, where tissues are modified to contain internal gas spaces that function in transport and storage of oxygen in structures called aerenchyma, under conditions of low oxygen availability (Drew and Stolzy 1991; Waisel and Agami 1991). How common aerenchyma is in tropical systems is not known; its presence has been predominantly studied in areas with excess water (i.e. epiphytes in cloud forests with aerial roots, Benzing 1991). In secondary tropical forests in Puerto Rico, several tree species—even on ridge slopes, where water accumulated in small depressions after storms—have aerenchyma (Vogt unpublished). This adaptation is therefore relevant not only in riparian zones but in areas where soils may have a high clay content and surface water accumulates for short time periods.

Characteristics of mycorrhizal associations

Types and distribution of mycorrhizal associations

Two main types of mycorrhizal associations are relevant to plantation management: ectomycorrhizas and vesicular-arbuscular (VA) mycorrhizas. Less common mycorrhizas which will not be considered here include ericoid, arbutoid, monotropoid, orchid and E-strain (Harley and Smith 1983).

Ectomycorrhizal roots are characterised by a change in their morphology which causes an increase in the surface area of the root. The fungi expand the fine roots to an extensive network of short, multi-branched root systems which are larger in diameter than roots not colonised by fungi. Ectomycorrhizas can be recognised because of the distinct root branching pattern and the formation of an external mantle of fungal tissue which surrounds each root tip and can be quite colourful (ranging from white to purple to fluorescent green). In addition, ectomycorrhizas produce an internal hyphal network (the 'Hartig net') which separates cortical cells from one another and where nutrient exchange occurs between the fungus and the plant root.

Vesicular-arbuscular mycorrhizas do not structurally modify the root exterior and are primarily located inside root cortical cells. The distinguishing features of VA mycorrhizas are vesicles and arbuscules produced within root tissue. These can be observed only under a microscope after sectioning and staining root samples. These structures are believed to play a role in carbohydrate storage and phosphorus transfer.

In general, ectomycorrhizas are found in environments where the soils are low in nitrogen (N) or where N is sequestered in detrital material and unavailable to plants because of slow decay, while VA mycorrhizas are found colonising plants when phosphorus (P) availability is low (Harley and Smith 1983; Allen 1991). Furthermore, ectomycorrhizal fungi are commonly found in mesic climatic zones and where soil organic matter is abundant, while VA fungi are more common in arid and semi-arid climatic zones and where soils have low content of organic matter (Allen et al. 1995). However, both mycorrhizal types are frequently found on the same site since plant growth may be limited by insufficiency of both N and P.

Plant families which are ectomycorrhizal include Fagaceae, Dipterocarpaceae, Pinaceae, Myrtaceae, Salicaceae and Betulaceae, as well as a few species in Leguminosae, Rosaceae and Euphorbiaceae (Newman and Reddell 1987). VA mycorrhizas are more ubiquitous and are found in most non-ectomycorrhizal plants with the exception of rushes and sedges (Powell 1980; Allen 1991). VA mycorrhizas may also form dual or tripartite associations with ectomycorrhizas and/or nitrogen fixing plants in some trees such as *Alnus* and *Eucalyptus* (Trappe 1962; Chilvers et al. 1987; Allen 1991). Only about 1% of the total number of vascular plant species in the world have been surveyed for their mycorrhizal status (Newman and Reddell 1987), and only an estimated 5–10% of mycorrhizal fungal species have been described (Allen et al. 1995).

Mycorrhizal attributes

In a mycorrhizal association, the fungi increase uptake of nutrients by the plant and protect plant roots against soil pathogens, while the plant supplies the growth and maintenance requirements of the fungus by translocating assimilate to the fungus (Harley and Smith 1983). In cold temperate coniferous ecosystems, the presence of fungi increases the longevity of the root from several weeks to many years (Vogt and Bloomfield 1991). Clearly factors that reduce photosynthetic capacity of the plant will limit the ability of the plant to sustain this relationship. For example, shading a seedling stopped the development of fruiting bodies of mycorrhizal fungi associated with its roots (Harley and Smith 1983).

Many benefits, mainly identified in greenhouse and laboratory studies, have been attributed to the mycorrhizal association. It is important to test these benefits in the field if these associations are to be used in practical management. It has been hypothesised that mycorrhizal associations assist a plant to survive and grow by minimising the plant's exposure to toxic chemicals in the soil, increasing nutrient uptake under low soil nutrient availabilities and reducing mortality of root tissues due to pathogens in the soil (Vogt et al. 1991a). Mycorrhizae can be thought of as an interface between the plant and the soil environment that increases a plant's ability to occupy a site by ameliorating or filtering out negative factors in the soil that could reduce plant growth (Marx 1969, 1973; Harley and Smith 1983; Burgess and Malajczuk 1989; Vogt et al. 1991a).

Mycorrhizas are reported to have improved uptake of N, P and K by a range of plant species in greenhouse experiments (Fitter 1977; Alexander 1981; Hall et al. 1984; Bolan 1991). Enhanced uptake of N and/or P by ectomycorrhizas may be due to two mechanisms: 1) increasing the surface area of roots in a given unit of soil; and 2) solubilising P from poorly soluble sources in the soil by the production of phosphatases and utilising N from organic sources (Alexander 1981; Harley and Smith 1983; Bolan 1991). Outcomes from studies of potential enhancement of water relations by mycorrhizas have been inconclusive (Allen et al. 1981; Allen and Allen 1986). It is not clear if the increased uptake of water by mycorrhizal plants is a direct effect of the fungus or the fact that improved P nutrition indirectly affects plant water relations. Further research is needed to determine more definitively how mycorrhizas benefit the host plant under field conditions in the tropics and under what conditions these benefits are realised.

The ability of mycorrhizas to support plants to grow in environments with high and/or toxic levels of heavy metals has been shown in the field for cold and warm temperate conifers, and the mechanisms involved have been analysed (Allen and Allen 1980; Dahlgren et al. 1991; Wilkins 1991). Mycorrhizas can act as a selective membrane that reduces a plant root's exposure to toxic metals such as aluminium (Al) by decreasing the amount of Al that gets into the biologically active portions of plant tissues by selectively excluding or sequestering these metals in their own tissues (Danielson 1985; Vogt et al. 1987, 1991a; Dahlgren et al. 1991; Wilkins 1991). Reclamation and restoration of minespoil and other disturbed lands can be assisted by inoculation of plants with mycorrhizal fungi (Daft and Hacskaylo 1976; Allen 1989; Miller and Jastrow 1992).

a, b

Variability in host plant and fungus relationships

Host plants display a high degree of variability in their 'mycorrhizal dependency', defined as their ability to grow without mycorrhizas. Plants range from obligate (high dependency) mycotrophs which are unable to survive without mycorrhizas, to facultative (low dependency) mycotrophs which can survive under some conditions without mycorrhizas, to non-mycorrhizal plants which do not generally form mycorrhizal associations (Janos 1980; Malloch et al. 1980). Obligately mycotrophic plants commonly grow in very stressed environments (i.e. low temperatures, low nutrient availability), facultative mycotrophic plants grow in low-stress environments while non-mycorrhizal plants are found under low-stress conditions where nutrient availability is high but disturbance frequent. The degree of dependency of a plant on mycorrhizas is relevant to the importance of managing mycorrhizas in plantations. Experience with *Pinus caribaea* in the American tropics demonstrated that this tree was unable to grow in a healthy manner without mycorrhizas—seedlings were stunted and nutrient-deficient until they were inoculated with appropriate mycorrhizal species (Marks and Kozlowski 1973).

VA and ectomycorrhizal fungi have different capacity to improve plant growth and nutritional status, have different optimum soil fertility and pH ranges at which they are capable of maintaining the mycorrhizal association and have different temperature ranges at which they are able to survive and grow (Harley and Smith 1983; Hung and Trappe 1983; Abbott and Robson 1991; Allen 1991). Furthermore, within the mycorrhizal types, individual species of symbiotic fungi vary in their capacity to colonise different host plant species — there typically exists greater specificity between the plant and ectomycorrhizal fungi while VA fungi have less specificity and form associations with many different plant families (Trappe 1962; Harley and Smith 1983). It is only recently that new molecular techniques have allowed researchers to begin identifying mycorrhizal fungi to the species level in the field (Gardes et al. 1991), a valuable development. Certain isolates of mycorrhizas are more effective than others in improving plant growth and P or N uptake in glasshouse experiments (Marks and Kozlowski 1973; Alexander 1981; Harley and Smith 1983; Schubert and Hayman 1986; Allen 1991).

Tree productivity, carbon allocation and abiotic controls

Roots

Several studies on cold temperate conifers have shown decreased carbon allocation to fine roots when water and/or nutrient availability was increased (Keyes and Grier 1981; Kurz 1989; Vogt et al. 1990; Gower et al. 1992, 1994, 1995). In a *Pseudotsuga menziesii* forest in Washington, Keyes and Grier (1981) determined that at a high-quality site a 40-year-old stand allocated 8% of its total net primary production to fine roots in contrast to a stand of similar age on a low-quality site that allocated 36% of its NPP to fine roots. Analogous allocation patterns to the Keyes and Grier (1981) study were obtained by Kurz (1989) for *P. menziesii* growing in British Columbia, Canada. Similarly, a montane *P. menziesii* forest in New Mexico allocated 34% less total NPP to fine roots when it was fertilised with N (Gower et al. 1992).

The pattern of increased allocation of carbon to roots with decreasing availability of nutrients found in temperate zones should be applicable to the tropics. Results of one tropical study in 5.6-year-old *Eucalyptus grandis* plantations in the State of Sao Paulo, Brazil, (Goncalves 1994) do parallel those obtained for *P.*

menziesii: sites with high productive capacity had low fine root biomass (1584 kg ha^{-1}) while sites with low productive capacity had high root biomass (2844 kg ha^{-1}).

What controls the amount of root biomass maintained, and its rate of turnover, is not clear when comparing different vegetation communities across climatic zones. For example, Nadelhoffer et al. (1985) hypothesised that in hardwood-dominated forests in Wisconsin fine root NPP should increase as the amount of N increased—opposite the pattern obtained for P. *menziesii*. They suggested that fine root biomass would be lower in nutrient-poor sites but that total allocation to maintaining fine root production would be higher because of a faster turnover of fine root tissues. Using mini-rhizotron technology in hardwood-dominated sites in Michigan, USA, however, Pregitzer et al. (1993) showed that with higher levels of nutrients and water root longevity was increased, rather than decreased as suggested by Nadelhoffer et al. (1985).

It is premature to generalise how water and nutrients change fine root NPP and turnover in forests. Many factors may influence the direction of these relationships, such as: 1) differences in individual tree species efficiency in resource (i.e., nutrients and water) acquisition from the soil and their use within the tree; 2) the ability of trees to utilise organic and inorganic forms of N (i.e., nitrate and ammonium); and 3) species differences in within-tree carbon allocation to above- and belowground biomass and secondary compounds. Field experimental manipulations of water and nutrients have been confounded by the difficulty of determining when nutrients and when water controls tree root growth. If water availability limits tree growth on a site, it may override the effect of a nutrient limitation (Gower et al. 1994). In the *P. menziesii* site in New Mexico where some stands were irrigated, others received N fertilizer applications and others were both irrigated and fertilised, both water and nutrients limited tree growth but at different times during the year (Gower et al. 1992). The limitation of water availability on root growth is difficult to separate from nutrient limitations since irrigation concurrently increases nutrient availability by speeding decomposition (Vogt et al. 1990).

The different relationship reported between N and fine root growth for *P. menziesii* and the hardwood sites in Wisconsin may be partially explained by what is the dominant inorganic N form in the soil. For example, *P. menziesii* sites have N available in the ammonium form (Vogt 1987) while the sites in Wisconsin had a high nitrate-N availability (Nadelhoffer et al. 1985). It has been shown that nitrate nitrogen changes root development by resulting in roots with less branching and fewer fine root tips (Vogt et al. 1990). A field study of (manipulated) forms of inorganic N is necessary to determine how they affect root growth and maintenance costs.

In the tropical pine and mahogany plantations and secondary forests studied by Lugo (1992) in Puerto Rico, differences in carbon allocation to above and belowground biomass were reported for trees of the same age but different species growing adjacent to one another. While both plantations and secondary forests achieved similar total NPP, there were significant differences in how much carbon was allocated to above and belowground biomass. A summary of the studies conducted in the tropics (Table 8.1) does show a general pattern of lower (4–11%) total living biomass allocated to roots in plantations compared to natural forests (6–33%). However, these differences are not distinctive characteristics of plantations compared to secondary forests but are attributes of the species grown in the plantations (Lugo 1992; Vogt et al. 1995b). The impact of different carbon allocation patterns by species on ecosystem-level carbon and nutrient cycling needs to be examined. If trees in plantations allocate less carbon to fine root mass and associated mycorrhizas, will it affect their susceptibility to insects and pests, and their ability to recover after disturbance?

Symbiotic associations

Ectomycorrhizal and VA mycorrhizal associations require different amounts of assimilate from the host plant to maintain the relationship. Ectomycorrhizas, with their greater biomasses and more extensive sheath and hyphal networks, require a greater carbohydrate investment by the host plant than do VA mycorrhizas.

Field studies that estimated the cost to the plant of maintaining ectomycorrhizal associations have been conducted in the temperate forests, but the findings are underestimates since not all contributions of symbionts to the carbon cycle were included. For example, Rommell (1939) estimated that 10% of the potential timber production in a spruce *(Picea abies* L. Karst.) forest was used to produce ectomycorrhizal sporocarps. In a study of an *A. amabilis* ecosystem by Vogt et al. (1982), 15% of the total net primary production was allocated to the ectomycorrhizal fungal symbiont (including sporocarps, fungal sheaths and Hartig nets). Neither study included respiratory carbon losses or losses of carbon as exudates from ectomycorrhizas (Vogt et al. 1991a). Although losses of carbon dioxide from mycorrhizal roots as a proportion of total carbon fixed by a plant have not been ~~measured in~~ the field, laboratory and greenhouse estimates range from 10 to 30% ~~(Harley 1969;~~ Harley and Smith 1983; Reid et al. 1983; Rygiewicz and Andersen 1994).

As well as the carbon cost, mycorrhizal associations modify the physiology of the plant and change the rate at which carbon is cycled within the plant. Using *P. menziesii* seedlings growing in controlled conditions, Rygiewicz and Andersen (1994) showed that even though only 5% of the total seedling dry weight was in fungal tissue the presence of the symbionts increased carbon allocation belowground by 23% compared to non-mycorrhizal plants. In this study, the mycorrhizal plants accumulated less total biomass compared to non-mycorrhizal plants since carbon was being allocated to the development of the mycorrhizal association and the hyphal network extending from the roots. Reid et al. (1983) reported that

Pinus taeda inoculated with mycorrhizal fungi assimilated more CO_2^{-14}, allocated a greater percentage of assimilated C^{-14} to root systems, and lost a greater percentage of C^{-14} by root respiration than did non-mycorrhizal plants. Allen et al. (1981) reported a 68% increase in the photosynthetic rate of mycorrhizal compared to non-mycorrhizal plants.

Stand development and succession

Fine roots

Several studies have examined the development of fine root biomass along successional sequences in temperate forests (Gholz et al. 1986; Vogt 1987; Vogt et al. 1987). These studies generally show fine root biomass peaking at canopy closure and levelling off after this time (Vogt et al. 1987). The main effect of nutrient availability on this relationship was that a *P. menziesii* stand at a lower quality site reached canopy closure after 40 years of age while a higher site quality stand reached canopy closure 10–15 years earlier (Vogt et al. 1987). Even though the fine root biomass may not increase with increasing stand age, a greater proportion of total carbon fixed by a plant appears to be allocated to roots. For example, in subalpine *A. amabilis* stands, 36% of total NPP was allocated to fine roots (<2 mm) in a 23-year-old stand, but this fraction increased to 66% by 180 years (Vogt et al. 1982).

c

~~a or b~~

c

The relative importance of root biomass and surface area in the different root diameter classes will vary with the developmental stage of the plant (Vogt et al. 1989). During the first year of seedling growth most of the roots are in the fine root category, in contrast to mature trees that may have <5% of total roots in this category. For example, a 30-year-old *A. amabilis* tree with a stem diameter of 2.0 cm at 15 cm stem height had 14% of total root weight and 56% of the total surface area in the <2 mm root diameter class, while a plant with a stem diameter of 6.5 cm at 15 cm stem height had 4% of the total root weight and 15% of the total root surface area in the <2 mm class (Vogt et al. 1989).

Symbiotic associations

Successional changes in mycorrhizal fungi within the same ecosystem have been observed in both relatively undisturbed forests (Schenck et al. 1989; Vogt et al. 1981, 1992) and plantations in the temperate zone (Chilvers et al. 1987; Termorshulzen and Schaffers 1989; Richter and Bruhn 1993). In *Eucalyptus* plantations (a genus capable of forming concurrent associations with VA and ectomycorrhizal fungi), mycorrhizal colonisation progresses from a VA-dominated system during early stages of plantation growth to ectomycorrhizal fungi in later stages (Lapeyrie and Chilvers 1985; Chilvers et al. 1987; Mendonca Bellei et al. 1992). Pine species also show successional change in mycorrhizal colonisation of root tips, generally having an increase in species richness and abundance of colonised root tips with increasing tree age following transplanting to the field (Chu-Chou 1979; Chu-Chou and Grace 1982, 1987, 1988; Richter and Bruhn 1993). However, in another study comparing young (5–13 year) and older (50–80 year) plantations, Termorshulzen and Schaffers (1989) observed that the number of mycorrhizal species was greatest for the younger trees and the number of unique species (i.e., not occurring on other stands) was also greatest during the early stages of plant growth. Such successional change in the mycorrhizal species on roots needs to be considered in understanding how propagules of different fungal species are able to reach plantations at different stand ages.

Management activities that affect surface organic horizons or the soil may influence mycorrhizal fungal succession. For example, *Coriaria* (Coriariaceae) will have ectomycorrhizas, VA fungi and *Frankia* nodules on the same root system when growing in a pine-oak forest but it loses the ectomycorrhizal associations when the soil is disturbed (Cruz-Cisneros and Valdés 1990). *Eucalyptus marginata* will form symbiotic associations with VA fungi when the roots are located in the mineral soil but roots restricted to the surface organic horizons have only ectomycorrhizal associations (Reddell and Malajczuk 1984).

We know from laboratory and greenhouse studies that many symbionts are capable of colonising one tree species (Trappe 1962, Brundrett 1991) but we do not have a good understanding of what determines the diversity found in the field. For example, Trappe (1962) noted that over 2000 different species of fungi were capable of forming a symbiotic relationship with one tree species while field measurements typically recorded only 7 species of symbionts in a mature forest (Vogt et al. 1981). It is not clear how many different species can be maintained on the root system of a tree growing in a plantation, what level of diversity is desirable or what the effects of management activities are on species diversity. Despite this, researchers have attempted to increase the diversity of mycorrhizas in plantations. For example, Ikram et al. (1992) introduced a high-diversity inoculum of VA mycorrhizas (eight VA species) for rubber *(Hevea brasiliensis)* seedlings in Malaysia. There appears to be some limitation on how many different species will be found on the root systems of trees in forests. For example, a study in pine plantations in Sweden showed that the original composition of mycorrhizas introduced 13 years earlier had been totally replaced even though the degree of colonisation was undiminished (Arnebrant et al.1990). Since different nutrients are unevenly distributed in the soil, the existence of diverse mycorrhizal fungi on tree roots may assist a plant to effectively access this heterogeneous resource.

Nutrient cycling, roots and mycorrhizal associations

Fine roots and mycorrhizas have an important role in modifying the cycling of nutrients in ecosystems because they: 1) contribute to nutrient uptake; 2) change the rate at which nutrients and heavy metals are recycled and stored; and 3) contribute significantly to nutrient cycling rates when they die and decompose (Vogt et al. 1986; Vogt et al. 1991b; Bloomfield et al. 1993). These are discussed further below.

Nutrients and plant carbon allocation

Nitrogen has a significant effect on plant carbon allocation patterns in temperate zone forest ecosystems. Nitrogen uptake from the soil influences the source-sink relationships of photosynthetically-fixed carbon in trees in temperate forests (Waring and Schlesinger 1985; Lechowicz 1987; Vogt et al. 1987b). Its effects on tree growth and carbon allocation in tropical plantations have yet to be determined. In addition to N, it is also important to understand the effects of K, Ca and P fertilisation on trees in the tropics because deficiencies of these nutrients limit growth of tropical trees (Wadsworth 1983; Jorgensen and Wells 1986). How scarcity of these nutrients might affect carbon allocation patterns in trees needs to be determined. In temperate zones, nitrogen fertilisation and/or irrigation (which increases the availability of N in the soil) of forests increased carbon allocation to coarse roots but decreased that allocated to fine roots, thus effectively decreasing the nutrient- and moisture-acquiring area of the plants (Vogt et al. 1990; Gower et al. 1992).

In general, as N availability increases, plants decrease carbon allocation (as a proportion of the total carbon fixed) to root biomass, to mycorrhizal fungi and to secondary defensive chemicals, and increase allocation to aboveground tissues (foliage and stems) (Waring et al. 1985). Decreases in fine root and mycorrhizal biomass due to excessive addition of one nutrient with strong effects on carbon allocation can result in deficiencies in other nutrients (Vogt et al. 1990). The negative consequences of excessive nutrient additions have been shown in several experimental studies in forests in Sweden (Persson 1980; Axelsson 1984). The shift in carbon allocation to the aboveground from belowground biomass in plantations has to be analysed from the perspective that roots have a role in maintaining tree health by increasing nutrient uptake by plants under conditions of low decomposition rates (Vogt et al. 1986; Vogt et al. 1991b), that they are a supporting mechanism for avoiding Al toxicity (Vogt et al. 1987b) and that the starch stored in them can be utilised to prevent fungal pathogens entering the plant (Wargo 1972).

Recently there has been interest in developing total nutrient cycling budgets (which include above- and belowground biomass plus soils data) for tree plantations and secondary or primary forests to assess the potential impact of fast-growing tree species on soil nutrient levels and long-term sustainability of plantations (Table 8.3;

Russell 1987; Cuevas et al. 1991; Montagnini et al. 1991; Lugo 1992). These budgets show that plantations maintain a smaller fraction of the total N in the living biomass in roots (typically <15%), while natural forests store a larger fraction of their N in roots (17–35%, Table 8.3). Similarly plantations had less than 10% of total P in living roots while natural forests had 11–41% in roots (Table 8.3). Somewhat similar patterns occurred for K but the differences between forests and plantations were not as large (Table 8.3). A greater proportion of nutrients in living biomass are potentially removed during harvesting in plantations than in natural forest. The soil reserves of all three nutrients, however, were quite high in the cases reported in Table 8.3, suggesting a high capacity of the soil to replenish nutrients removed during harvesting.

Roots, mycorrhizas and nutrient availability

Fine roots and mycorrhizas may affect soil nutrient availability through the secretion of organic acids, soluble sugars and carbon dioxide produced from respiration (Johnson et al. 1977; Schwab et al. 1983), and upon senescence of fine root and mycorrhizal tissues. In two subalpine *A. amabilis* stands in Washington, USA, an estimated 15% of the total organic material returned to the soil was derived from mycorrhizal tissues despite the fact that they accounted for less than 3% of the total living biomass (Vogt et al. 1982). Furthermore, in a *P. menziesii* stand in Oregon, USA, mycorrhizal roots comprised an estimated 6% of the living biomass while contributing 48% of the organic matter to the soil (Fogel and Hunt 1983). These inputs by mycorrhizal fungi consist of tissues that have high nutrient contents and should decay rapidly.

Decomposing fine roots may also increase the nutrient storage capacity of tropical forests. In secondary tropical forests in Puerto Rico, fine roots decayed and released minerals at a slower rate than foliage in the same site (Bloomfield et al. 1993). This means that dead roots potentially act as a longer-term store for nutrients and may be important in minimising nutrient losses. Questions related to the role of roots and mycorrhizas in nutrient cycling and conservation are critical areas needing research since many tropical plantations are located on nutrient-poor soils and some of the failures of tropical plantations have been attributed to low nutrient availability (Fearnside and Rankin 1985; Moran 1986; Lugo et al. 1990).

Mycorrhizas also directly respond to microsites of higher nutrient availability in the soil. The length of VA mycorrhizal hyphae involved in nutrient transport increased with decreasing organic matter content and total soil mineral content (McNaughton and Oesterheld 1990). Fine roots and mycorrhizal hyphae have also been shown to concentrate in areas of high organic matter content (St. John et al. 1983). By contributing directly to carbon and nutrient stores in the soil and by selectively exploiting pockets of high nutrient availability, fine roots and mycorrhizal fungi affect the cycling of these materials within the system.

Results from laboratory and greenhouse studies suggests that trees may transfer metabolites and nutrients through belowground connections to neighbouring individuals via intra- and inter-specific mycorrhizal hyphal connections or through root grafts (Brownlee et al. 1983; Read et al. 1985; Newman 1988). Under more controlled conditions, Newman and Eason (1989) reported that P-32 was transferred from dying to living roots of two VA mycorrhizal plants *(Lollium perenne–L. perenne* and *L. perenne–Plantago lanceolata)* but not between a mycorrhizal and a non-mycorrhizal plant *(Lollium perenne-Brassica oleracea).* More experiments are needed to determine whether the amount of nutrients transferred is large enough to play a significant role in nutrient cycling processes and the potential for managing for mycorrhizal hyphal interactions in plantations.

Because of the role mycorrhizas play in P uptake, the degree of mycorrhizal colonisation of root systems has been shown to be inversely related to soil P concentrations (Johnson et al. 1991). Therefore P fertilisation may have direct effects on mycorrhizal associations. Similarly N fertilisation produces a fast-growing root that eliminates the symbiont from the root. Studies on effects of fertilizer on plantation performance rarely consider the implications for the symbiont component under field conditions. A study by Johnson (1993) of VA mycorrhizal communities in fertilised and unfertilised agricultural fields in Minnesota found that fertilisation altered the species composition of the mycorrhizae, resulting in dominance of mycorrhizal species which had lower effectiveness in improving plant performance. The fungi from the fertilised soil produced fewer hyphae and arbuscules and the same number of vesicles as fungi from unfertilised soil, and were therefore considered to be 'inferior mutualists' (Johnson 1993).

Theoretically it should be possible to determine what level of P fertilisation is optimal for enhancing plantation crop production while minimising the suppression of the mycorrhizal association, but this will require field experiments which monitor mycorrhizal–plant interactions at various levels of P fertilisation. This would also depend on tree species differences and the diversity of symbionts located on the root systems. Laboratory and greenhouse experiments have found differences in tree species responses to fertilizer with and without mycorrhizas. For example, Browning and Whitney (1992) found that inoculated *Picea mariana* seedlings had significantly greater dry weight biomass (44%) than uninoculated controls at low soil P levels, while inoculated *Pinus banksiana* seedlings had greater dry weight biomass than uninoculated seedlings at both high and low levels of soil P (26% and 33%, respectively). These results suggested that *P. banksiana* may tolerate higher levels of P fertilisation if mycorrhizal colonisation can be maintained by inoculation, while inoculation of *P. mariana* will be beneficial only under low P applications. Conversely, another approach would be to select for strains of mycorrhizas that are more effective at the soil P levels desired with the fertilisation regime. Schubert and

Hayman (1986) demonstrated that different VA mycorrhizal species varied in their capacity to improve plant growth under different levels of soil P, suggesting that selection of field inoculants may be made based on mycorrhizal behaviour under conditions of elevated soil P. The applicability of these observations under field conditions, however, is not yet clear.

Most studies on mycorrhizae focus on P (Table 8.4). This ignores the fact that other abiotic variables may be limiting plant growth or that soil chemical attributes may be having a stronger influence on modifying P availability in the field. For example, P may be strongly controlled by Al cycling in the soil (Dahlgren et al. 1991), which means that the forms of Al in the soil may determine what levels of P the plants plus associated mycorrhizas will have access to. Since potential Al toxicity is considered to exist over 60% of the soils in the tropics (Moran 1986), it is important to also examine the role of Al in affecting P availability.

Pot experiments have suggested that mycorrhizas may enhance heavy metal tolerance in the host plant (Brown and Wilkins 1985; Wilkinson and Dickinson 1995) but this characteristic varies by both fungal and plant species and cannot be generalised. The differential tolerance of plants to heavy metals may be strongly driven by which symbionts are on the root systems, how well developed are the relationships between plant and fungus, and also whether the plant is a metal accumulator. For example, in an ecosystem in Washington state, USA, *A. amabilis* had well developed mycorrhizas which appeared to reduce the uptake of Al at the root level. The associated tree species (*Tsuga mertensiana*, an Al accumulator) had the same symbionts on its root systems but the mutualism was poorly developed between the fungus and root and the trees accumulated high levels of Al in their leaves (Vogt et al. 1987a).

Roots and Mycorrhizas in Management

The following section will attempt to summarise how roots and symbionts are affected by different management activities. Data used to develop the discussion are in Tables 8.1–8.4. Of the many stresses impinging upon ecosystems, the following can have strong effects on ecosystem health and total productivity: 1) insect pests and fungal pathogens; 2) management activities (i.e., fertilisation, pruning/thinning, herbicides, pesticides etc.); 3) heavy metal toxicity; 4) air pollution; and 5) stochastic factors (i.e., climatic variations, droughts, hurricanes).

The information presented in this chapter highlights some of the limitations in our current knowledge: 1) most mycorrhizal studies have used seedlings grown in pots in nurseries or greenhouses conditions, and do not explain processes in the field or for mature trees; 2) those root studies conducted in the field are few in number and represent only a few tree species; 3) most studies focused on examining one factor in isolation (e.g., P uptake by plants, or one mycorrhizae inoculated on a seedling) thus precluding many interacting factors that could modify their expression in the field (i.e. soil aluminium levels which immobilise P in the field); 4) the short duration of the studies (especially with mycorrhizal fungi which typically were of several months duration) which is not relevant to long-term processes; and 5) studies concentrated on exotic species without understanding if and how they differed from native species, and on using 'superior' trees and mycorrhizal symbionts based on their ability to extract nutrients or protect seedlings from pathogens under laboratory conditions.

Fungal pathogens and insect pests

Many large-scale plantation projects (see Gonçales et al., this volume) have been successful so far in obtaining high yields from fast-growing tree species but their long-term sustainability have not yet been assessed. The fact that plantation trials do not always result in the successful establishment of the desired plant species (due to either serious fungal disease or insect pest outbreaks and/or inherent abiotic site factors reducing or eliminating productivity) suggests the importance of having a better understanding of what controls the health and growth of these systems at a holistic level and in the long term (Trappe et al. 1984; Jorgensen and Wells 1986; Waring 1987). For example, one large plantation project in the tropics (the Jari project in Para, Brazil), started more than 20 years ago, had to dramatically change the plant species and management strategies used due to pest and disease problems (Fearnside and Rankin 1985; Russel 1987; Fearnside 1988).

Tropical plantations may be highly susceptible to fungal pathogens and insect pests (Perry and Maghembe 1989; Wormald 1992). However, many of the data are observational and good documentation of cause-and-effect relationships is difficult to find for the tropics. The temperate zone studies suggest some possible explanations for the susceptibility of tropical plantations to diseases and pests, and also to help identify variables that might be sensitive indicators of stand health. For example, there may be a legacy of fungal diseases (coarse root fragments infected with root rot fungi, Chavez et al. 1980) that remain on a site which are capable of eliminating young trees planted after harvesting. The use of more genetically-uniform trees in a plantation may result in a greater proportion of the trees being susceptible to introduced insect pests or diseases. Seedlings may have been out planted with an introduced mycorrhizal fungus which was ineffective in protecting the plants against native disease organisms. Nitrogen fertilisation can cause shifts in carbon allocation away from plant secondary defensive chemicals and at the same time increase the palatability of leaves to herbivores. The structure of plantations often does not maintain the population of predatory insects that could help protect plants by containing pests (Schowalter and Means 1989).

Some studies have shown mycorrhizal fungi to be very effective at preventing the infection of plant roots by pathogenic fungi (Marx 1973). In laboratory experiments using agar plate tests, mycorrhizal fungi were shown to inhibit the growth of certain root pathogenic fungi and soil bacteria (Marx 1969). In pot experiments, mycorrhizal plants exhibited greater disease resistance and survival, once infected by pathogenic fungi, than non-mycorrhizal plants (Table 8.4). Thomas (1988) reported an inverse relationship between the degree of VA mycorrhizal colonisation of coconut palm roots *(Cocos nucifera)* and the population of VA spores in the soil, and the degree of root rot on palm roots. Maintaining healthy VA mycorrhizal populations in the soil may be critical in mixed planting situations. Plants maintaining healthy mycorrhizal populations should be used to identify which plant to intercrop in a plantation as a means of maintaining mycorrhizal inoculum potential over long-term plantation cycles (Waidyanatha 1980; Thomas 1988).

Research should also determine how much of the effect of mycorrhizal fungi is a nutrient effect and whether appropriate fertilisation can result in similar plant responses. Enhanced resistance of mycorrhizal plants to disease may be largely due to indirect effects of improving plant nutrition and health which would confer decreased susceptibility to attack by pathogens. Little is known about the effectiveness of different mycorrhizal species in protecting plants against many types of pathogens. However, since the contribution of a mycorrhizal species to plant performance probably varies with the physical and biotic environment (Perry et al. 1987), it is also likely that mycorrhizal species will have varying effects on plant responses to different pathogens.

Heavy metal toxicity

Heavy metals, particularly zinc, nickel, aluminium and copper, have detrimental effects on plant growth when present beyond critical levels (Kabata-Pendias and

Pendias 1984). Since some soils in the wet tropical zones have Al present at levels at which plant growth may be impaired (see Lal this volume; Marcar and Khanna this volume), the mechanisms by which plants are able to avoid Al toxicity becomes relevant. Many native plants are well adapted to these metals and are accumulators of some of them (Goodland 1971) but exotic species may not have the same tolerance. This has been observed in the Amazon where the conversion of secondary forests to agricultural fields has required indigenous people to select agricultural crops tolerant of Al after initial crop failures (Pinedo-Vasquez, unpublished).

Some plants (tea, western and mountain hemlock) (Antonovics et al. 1971; Vogt et al. 1987a) are able to tolerate and accumulate heavy metals by sequestering them in non-biologically active tissues (Kabata-Pendias and Pendias 1984) while other plants are protected because the mycorrhizal associations on their roots either exclude metals or accumulate them within their mantle sheaths (Vogt et al. 1987a; Wilkins 1991). In the latter case, the plant shoots have significantly lower concentrations of the metals than non-tolerant species (Wilkins 1991). This is not unusual since fungi are known to be accumulators of many heavy metals and their reproductive structures (mushrooms) have been collected for chemical analyses to use as an indicator of pollution (Cromack et al. 1979; Vogt et al. 1992). There is evidence of a high degree of specificity between different mycorrhizal fungal species and their effect on plant tolerance against different metals (Jones and Hutchinson 1988). The high acidity of many tropical soils make them often prone to Al and Mn toxicity and low P availability, so that mycorrhizas may be particularly important for plant growth in these environments.

Limited information is available on the effects of, and the response to, heavy metals in plantation ecosystems. Even in natural ecosystems (mainly in the temperate zone), the focus has been primarily on herbaceous species (Brown and Wilkins 1985), understanding the effect of increased Al cycling due to acid rain on vegetative communities or the links between vegetation and soil forming processes (Dahlgren et al. 1991). Preliminary studies suggest the importance of studying how Al toxicity varies by tree provenances since the tolerance of *Picea abies* to Al varied by provenances (Hodson and Wilkins 1989; Wilkins and Hodson 1989). No information is available on the effect of VA mycorrhizas on heavy metal tolerance (Wilkins 1991).

Management activities

In assessing the role of disturbance in natural and managed systems, it is important to consider the impact on both increasing and decreasing various types of environmental heterogeneity. If the imposed disturbance or management regime reduces belowground heterogeneity, this would have strong implications for the maintenance of healthy belowground ecosystems.

Fertilizers

Fertilizers are often an important input in plantation systems—not only is their application often required to increase and sustain production, but they are often applied at higher levels in order to enhance productivity (see Gonçales et al. this volume). Excessive application of N or P fertilizers may alter mycorrhizal relationships between plant roots and microorganisms due to direct effects of high nutrient concentrations on microbial populations, or as a result of changes in the species composition or extent of colonisation of mycorrhizas caused by host regulation of the symbiosis in response to changed nutrient availability (see earlier section). Mycorrhizal colonisation on roots may decrease and their presence could ultimately be reduced or eliminated from the site as the capacity to maintain viable inoculum is reduced. Ikram et al. (1987, 1992) found that seedlings of *Calopogonium caeruleum* and *Hevea brasilensis* inoculated with VA mycorrhizas in the nursery exhibited less mycorrhizal root colonisation when soils were fertilised with P. The effect of P fertilisation on mycorrhizas is not simple and will vary with the original P content of the soil itself (Johnson 1993). For management purposes, it is important to know how the gradients of soil nutrients affect the degree of mycorrhizal colonisation of fine root systems and to identify threshold levels at which mycorrhizas are finally eliminated from root systems. The end result could be a plant that may have decreased growth due to metal toxicities or increased susceptibility to root pathogens (Marx 1969; Vogt et al. 1991a). How much of ecosystem resilience is directly linked to processes requiring strong root-microflora-soil interactions should be determined.

Pesticides and herbicides

Relatively few studies have been conducted on the potential effects of pesticides on roots or their associated microflora (Table 8.4). This could be important because pesticides can have unforeseen effects on non-target organisms which may influence productivity as much as or more so than the pests they are intended to control (Trappe et al. 1984). Effects of pesticides on mycorrhizal–plant interactions is one potential source of declining health and productivity of plantations which requires greater attention.

The few studies which have been conducted on pesticide–mycorrhizal interactions focus on isolated mycorrhizal species under highly controlled conditions and over short periods (Table 8.4). They indicate a high degree of variability in the effect of different pesticides and herbicides on different mycorrhizal species (Screenivasa and Bagyaraj 1989; Rouillon et al. 1989; Thapar and Uniyal 1990). Thapar and Uniyal (1990) studied the effect of four different pesticides (Aldrin, BHC, Furadon and Hexanema) on the growth of four species of ectomycorrhizal fungi, and reported that although all inhibited mycorrhizal formation in seedlings, they varied in their degree of toxicity and in the concentration required for toxic effects to occur. Screenivasa and Bagyaraj (1989) examined the effect of 9 fungicides, 3 nematicides and 5 insecticides at the recommended and at half the recommended levels on the growth of VA fungi in pot cultures and the effectiveness of the symbionts in reducing contaminant uptake. All were found to have a deleterious effect on VAM fungi at the recommended level. Interestingly, two of the chemicals, when given at half the recommended level, not only suppressed the contaminants but also improved VA mycorrhizal colonisation of roots, which Screenivasa and Bagyaraj (1989) attributed to reduced competition for space and nutrients between VA fungi and the contaminants. Similar mixed stimulatory/inhibitory effects have been reported in other studies (Iloba 1976).

Results of a few studies also indicate variable effects of herbicides on mycorrhizas. Sidhu and Chakravarty (1990) and Chakravarty and Chatarpaul (1988) indicated that with increasing seedling age, toxicity of herbicides was reduced. Increased degradation of herbicides in the field by soil microorganisms reduced the toxicity of herbicides compared to lab and greenhouse conditions. In-vitro studies by Rouillon et al. (1989) also indicate the ability of some mycorrhizas to degrade herbicides. The effect of herbicides on roots also directly affects mycorrhizal health. Herbicides have been reported to inhibit short root growth (more so than shoot growth) along with mycorrhizal formation and it is speculated that seedling production of glucose and belowground allocation is directly affected by herbicides. The complexity of interactions and herbicidal effects on the system is also indicated by Kassaby and Hepworth's study (1987) on the fungal root disease *Phytophthora cinnamomi* where the disease was found to be reduced or stimulated by different herbicides.

Thinning

Canopy architecture is known to affect dry matter partitioning among aboveground components (Linder and Rook 1984; Cannell 1985; Ford 1985), and provides an important justification for thinning practices in forest management. Very little is understood about the potential effects of thinning on carbon allocation between above and belowground sinks. Santantonio and Santantonio (1987) showed that thinning reduced fine-root longevity and increased the relative turnover rate by a factor of 2.4, and did not appear to provide a means for shifting production to another component, such as stem wood.

Soil disturbance

Most of the research on the effects of management-induced soil disturbance on the belowground system has focused on quantifying losses of organic matter and nutrients from erosion and leaching processes, and the risks associated with landslides under different management practices. There exists a good data base for this from temperate ecosystems (Edmonds et al. 1989). Most of the research in the tropics has concentrated on examining postharvest effects on the system (Nykvist et al. 1988; see also Bruijnzeel this volume; Fölster and Khanna this volume). In general, roots are less likely to be affected than the forest floor during manual timber harvest operations, while mechanical site operations may seriously affect the root system and its nutrient storing and recycling capacity.

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Studies in temperate regions have suggested that soil disturbance can reduce mycorrhizal populations by breaking up hyphal connections, eliminating inoculum and consequently affecting vegetation recovery (Perry et al. 1987). Loss of organic matter may also reduce mycorrhizal populations since hyphae are usually concentrated in areas of high organic matter, and lack of organic matter may reduce the availability of microsites suitable for sustaining mycorrhizas (St. John et al. 1983; Vogt et al. 1995a). Studies in temperate regions have also specifically assessed the impact of soil compaction, nutrient leaching, organic matter loss, root strength and slope stability on root growth, generally showing a clear relationship between soil disturbance and decreased root growth (Ziemer and Swanston 1977; Ziemer 1981; Ruark et al. 1982; ~~Petersson~~ and Messing 1987). Roots have been found to positively affect soil physical conditions (decrease soil compaction, decrease soil erosion) when plantations were planted on abandoned pastures (Montagnini et al. 1991; McGroddy 1995). Similarly, VA mycorrhizas are usually reduced by various forms of soil disturbance, including strip mining (Allen and Allen 1980), soil erosion (Powell 1980) and mechanical disruption (Moorman and Reeves 1979; Reeves et al. 1979; Doerr et al. 1984; Cuenca and Lovera 1991). Species diversity of mycorrhizal populations may also be reduced and/or altered (Cuenca and Lovera 1991) and should be examined in greater detail.

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Synthesis

A survey of research conducted on mycorrhizas in plantations suggests that much of the research was aimed at finding a 'super-symbiont' for inoculating plantation species (Table 8.4). The research sought to identify those symbionts which resulted in the greatest increases in seedling growth and to compare the ability of exotic and native fungal inoculants to increase plant growth (Lapeyrie and Chilvers 1985; Martinez-Amores et al. 1991; Ikram et al. 1992). Since many plantation tree species are exotic (Table 8.4), the focus on testing exotic symbiotic fungi is obvious—frequently areas being planted to exotic species do not have any of the appropriate mycorrhizal fungi present although seedling survival depends on these associations (Valdés 1986; Michelsen 1992). Most inoculation studies have concentrated on determining the effect of a single symbiont on seedling establishment and growth within the first 6–12 months following the outplanting (Table 8.4; Ikram et al. 1987).

Several studies have examined the replacement of nursery inoculum with indigenous mycorrhizal species following outplanting to the field (Lapeyrie and Chilvers 1985; Chilvers et al. 1987; Mendonca Bellei et al. 1992; Richter and Bruhn 1993) and the successional replacement of VA fungi by ectomycorrhizal fungi on roots (Table 8.4). How relevant these studies are for changes in fungal species in plantations over longer time scales is not known. More information is needed on interaction—both synergistic and antagonistic—between mixed-species communities of microorganisms, and on successional change within these communities in response to environmental change in plantations.

Inoculation of seedlings with ectomycorrhizas or VA mycorrhizas in the nursery has been shown to enhance initial seedling establishment and growth in the field, probably through the advantage conferred to seedlings by enhanced nutrition during this critical period (Janos 1980; Marx 1980). The positive effects of inoculation may also be explained by the often-low inoculum potential of nursery soils due to fumigation practices, collection of soil from areas depleted of mycorrhizas, or, in the case of exotic ectomycorrhizal species, the lack of colonising fungi in native soils (Marks and Kozlowski 1973). It is clear that inoculation trials with pure cultures of different fungal species can yield positive results in identifying fungi which have particular superior performance in the field (Valdés 1986; Ikram et al. 1987; Sieverding and Toro 1987; Burgess and Malajczuk 1989). Under natural conditions, however, trees are typically colonised by a wide array of different mycorrhizal species, and often by different types of mycorrhizas as well. This high diversity in the mycosphere may be crucial in buffering the system against disturbances or even fluctuations in the environment. However, only a few studies have assessed the performance of inoculation with mixtures of known species of mycorrhizas (Azizah and Martin 1992) or mycorrhizas in combination with other symbionts (Ramirez-Saad et al. 1992), and generally have not compared mixed with pure cultures, or different combinations of species. More common has been inoculation with field mixtures of indigenous mycorrhizas found in soil collected from suitable areas (Table 8.4; Sidhu and Behl 1992) and the identification of field mixtures with the greatest inoculum potential and most effect on plant growth (Asbjornsen and Montagnini 1994).

Most research on root–mycorrhizal–plant relations in tropical plantations has focused on seedlings in laboratory or shadehouse conditions with short time scales (6–12 months) and rarely includes follow-up studies or comparisons with mature trees. Although seedling establishment and growth are critical in terms of overall plant development, and stress due to transplanting shock may be high (Nambiar 1983), the belowground system continues to have an important function throughout the life of the plantation. Furthermore, since the life of a plantation may be 20–40 years or longer, plants will be exposed to a dynamic and changing environment over extended periods.

More recent studies have begun to address other belowground aspects, for example, the processes of shifting carbon allocation, and improving techniques for isolating and testing effective mycorrhizal fungal species (Table 8.1–8.4). Research should address several issues: 1) multiple species interactions; 2) differences between seedling and adult tree responses; 3) exotic vs. indigenous species (both for trees and mycorrhizas) and their ecosystem attributes; 4) diversity and ecosystem resilience and the role of roots and mycorrhizas in contributing to these; 5) carbon allocation and implications for ecosystem function, and how exotic and native species vary in the allocation of carbon to belowground components; 6) implications for agroforestry systems when plants are selected to maximise the use of nutrients in deeper soil horizons; 7) effects of nitrogen-fixing tree species on soil organic matter storage in addition to the nutrient effects; 8) identification of situations in which management practices are unable to compensate for abiotic or biotic changes in the environment and how belowground processes may compensate for these changes; and 9) how belowground elements contribute to ecosystem carbon and nutrient cycles.

Management practices are a key facet of the plantation environment through their effects on disturbance regimes, nutrient cycling, stand structure and diversity, and concentration of metals and chemicals in the soil, to name a few. Although intensive human activities may unavoidably increase the level of stress in the ecosystem, management can also help to enhance ecosystem resilience and resistance to stress through judicious manipulation. These approaches need to be expanded to include techniques which create conditions to favour a healthy belowground system in the long term. For example, techniques that enhance belowground heterogeneity, thus creating a more diverse mycorrhizal community, and which use fertilizers and pesticides wisely based on sound knowledge about the indirect effects on symbiotic associations, can contribute to the long-term productivity of the ecosystem.

In order to achieve this, we need to learn how natural systems maintain their resistance and resilience to disturbances. Many of the disturbances that a plant will be exposed to will be detected and responded to by roots and mycorrhizas before any symptoms become apparent aboveground (Vogt et al. 1993). Mycorrhizas may buffer the ecosystem against environmental stress and greatly enhance resiliency by, for example, increasing uptake of nutrients when available and releasing them from storage when they are scarce, or by preventing infection by root pathogens during times when the plant is susceptible to stresses (Marks and Kozlowski 1973; Vogt et al. 1991a). It is important to increase our understanding of when and how roots and mycorrhizas functions in ecosystems to sustain plant growth over longer time scales. This type of information can then be used to determine the trade-offs between management options.

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References

Abbott, L.K. and Robson, A.D. 1991. Factors influencing the occurrence of vesicular-arbuscular mycorrhizas. Agriculture, Ecosystems Environment 35, 121–150.

Aber, J.D., Melillo, J.M., Nadelhoffer, K.J., McClaugherty, C.A. and Pastor, J. 1985. Fine root turnover in forest ecosystems in relation to quantity and form of nitrogen availability: a comparison of two methods. Oecologia (Berlin) 66, 317–321.

Allen, E.B. 1989. The restoration of disturbed arid landscapes with special reference to mycorrhizal fungi. Journal of Arid Environments 17, 279–286.

Allen, E.B. and Allen, M.F. 1980. Natural re-establishment of vesicular-arbuscular mycorrhizae following strip-mine reclamation in Wyoming. Journal of Applied Ecology 17, 139–147.

— 1986. Water relations of xeric grasses in the field: interactions of mycorrhizas and competitions. New Phytologist 104, 559–571.

Allen, E.B., Allen, M.F., Helm, D.J., Trappe, J.H., Molina, R. and Rincon, E. 1995. Patterns and regulation of arbuscular and ectomycorrhizal plant and fungal diversity: a hypothesis. Plant and Soil (in press)

Allen, M.F. 1991. The Ecology of Mycorrhizae. Cambridge University Press. Cambridge.

Allen, M.F., Smith, W.K., Moore, T.S. and Christensen, A.M. 1981. Comparative water relations and photosynthesis of mycorrhizal and non-mycorrhizal *Bouteloua gracilis* H.B.K. Lag ex Steud. New Phytologist 88, 683–693.

Alexander, I.J. 1981. The significance of ectomycorrhizas in the nitrogen cycle. In: Lee, J.A., McNeill, S. and Rorison, I.H., ed. Nitrogen as an Ecological Factor. Blackwell Scientific. Oxford, Boston. 69–93.

Alpizar, L., Fassbender, H.W., Heuveldop, J., Folster, H. and Enriquez, G. 1986. Modelling agroforestry systems of cacao *(Theobroma cacao)* with laurel *(Cordia alliodora)* and poro *(Erythrina poeppigiana)* in Costa Rica. Agroforestry Systems 4, 175–189.

Antonovics, J., Bradshaw, A.D. and Turner, R.G. 1971. Heavy metal tolerance in plants. Advances in Ecological Research 7, 1–85.

Arnebrant, K., Baath, E. and Soderstrom, B. 1990. Changes in microfungal community structure after fertilization of Scots pine forest soil with ammonium nitrate or urea. Soil Biology and Biochemistry 22, 309–312.

Asbjornsen, H. and Montagnini, F. 1994. Vesicular-arbuscular mycorrhizal inoculum potential affects the growth of *Stryphnodendrum microstachium* seedlings in a Costa Rican humid tropical lowland. Mycorrhiza 5, 45–51.

Axelsson, B. 1984. Increasing forest productivity and value by manipulating nutrient availability. In: Ballard, R., Farnum, P., Richie, G. A. and Winjum, J. K., ed. Forest Potentials. Productivity and Value. Tacoma, Washington, Weyerhaeuser Science Symposium #4, 5–27.

Azizah Chulan, H. and Martin, K. 1992. The vesicular-arbuscular (VA) mycorrhiza and its effects on growth of vegetatively propagated *Theobroma cacao* L. Plant and Soil 144, 227–233.

Barley, K.P. 1970. The configuration of the root system in relation to nutrient uptake. Advances in Agronomy 22, 159–201.

Benzing, D.H. 1991. Aerial roots and their environments. In: Waisel, Y., Eshel, A. and Kafkafi, U. ed. Plant Roots. The Hidden Half. Marcel Dekker, Inc. 867–886.

Bloomfield, J., Vogt, K.A. and Vogt, D.J. 1993. Decay rate and substrate quality of fine roots and foliage of two tropical tree species in the Luquillo Experimental Forest, Puerto Rico. Plant and Soil 150, 233–245.

Bolan, N. S. 1991. A critical review of the role of mycorrhizal fungi in the uptake of phosphorus by plants. Plant and Soil 134, 189–207.

Bormann, F.H. and Graham, B.F. Jr. 1960. Translocation of silvicides through root grafts. Journal of Forestry 58, 402–403.

Bowen, G.D. 1984. Tree roots and the use of soil nutrients. In: Bowen, G.D. and Nambiar, E.K.S. ed. Nutrition of Plantation Forests. Academic Press. 147–179.

Brown, M.T. and Wilkins, D.A. 1985. Zinc tolerance of mycorrhizal *Betula*. New Phytologist 99, 101–106.

Browning, M.H.R. and Whitney, R.D. 1992. The influence of phosphorus concentration and frequency of fertilization on ectomycorrhizal development in containerized black spruce and jack pine seedlings. Canadian Journal of Forest Research 22, 1263–1270.

Brownlee, C., Duddridge, J.A., Malibari, A. and Read, D.J. 1983. The structure and function of mycelial systems of

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ectomycorrhizal roots with special reference to their role in forming interplant connections and providing pathways for assimilate and water transport. Plant and Soil 82, 433–443.

Brundrett, M. 1991. Mycorrhizas in natural ecosystems. Advances in Ecological Research 21, 171–313.

Burgess, T. and Malajczuk, N. 1989. The effect of ectomycorrhizal fungi on reducing the variation of seedling growth of *Eucalyptus globulus*. Agriculture, Ecosystems and Environment 28, 41–46.

Caldwell, M.M. and Richards, J.H. 1989. Hydraulic lift: water efflux from upper roots improves effectiveness of water uptake by deep roots. Oecologia 19, 1–5.

Cannell, M.G.R. 1985. Dry matter partitioning in tree crops. In: Cannell, M.G.R. and Jackson, J.E. ed. Attributes of Trees as Crop Plants. Huntington, England, Institute of Terrestrial Ecology, 160–193.

Cannell, M.G.R. and Dewar, R.C. 1994. Carbon allocation in trees: a review of concepts for modelling. Advances in Ecological Research 25, 59–105.

Carbon, B.A., Bartle, G.A., Murray, A.M. and MacPherson, D.K. 1980. The distribution of root length, and the limits to flow of soil water to roots in a dry sclerophyll forest. Forest Science, 26, 656–664.

Chakravarty, P. and Chatarpaul, L. 1988. The effects of velpar L (hexazinone) on seedling growth and ectomycorrhizal symbiosis of *Pinus resinosa*. Canadian Journal of Forest Research 18, 917–921.

Chavez, T.D. Jr., Edmonds, R.L. and Driver, C.H. 1980. Young-growth western hemlock stand infection by *Heterobasidion annosum* 11 years after precommercial thinning. Canadian Journal of Forest Research 10, 389–394.

Chilvers, G.A., Lapeyrie, F.F. and Horan, D.P. 1987. Ectomycorrhizal vs. endomycorrhizal fungi within the same root system. New Phytologist 107, 441–448.

Chu-Chou, M. 1979. Mycorrhizal fungi of *Pinus radiata* in New Zealand. Soil Biology and Biochemistry 11, 557–562.

Chu-Chou, M. and Grace, L.J. 1982. Mycorrhizal fungi of *Eucalyptus* in the North Island of New Zealand. Soil Biology and Biochemistry 14, 133–137.

— 1987. Mycorrhizal fungi of *Pseudotsuga menziesii* in the South Island of New Zealand. Soil Biology and Biochemistry 19, 243–246.

— 1988. Mycorrhizal fungi of radiata pine in different forests of the North and South Islands in New Zealand. Soil Biology and Biochemistry 20, 883–886.

Cromack, K. Jr., Sollins, P., Graustein, W.C., Speidel, K., Todd, W.A., Spycher, G., Li, C.Y. and Todd, R.L. 1979. Calcium oxalate accumulation and soil weathering in mats of the hypogeous fungus *Hysterangium crassum*. Soil Biology and Biochemistry 11, 463–468.

Cruz-Cisneros, R. and Valdés, M. 1990. Ecological aspects of the actinorhizal plants growing in the Basin of Mexico. Nitrogen Fixing Tree Association Research Report 8, 42–47.

Cuenca, G., Aranguren, J. and Herrera, R. 1983. Root growth and litter decomposition in a coffee plantation under shade trees. Plant and Soil 71, 477–486.

Cuenca, G. and Lovera, M. 1991. Vesicular-arbuscular mycorrhizae in disturbed and revegetated sites from La Gran Sabana, Venezuela. Canadian Journal of Botany 70, 73–79.

Cuevas, E., Brown, S. and Lugo, A.E. 1991. Above- and belowground organic matter storage and production in a tropical pine plantation and a paired broadleaf secondary forest. Plant and Soil 135, 257–268.

Daft, M.J. and Hacskaylo, E. 1976. Arbuscular mycorrhizas in the anthracite and bituminous coal wastes of Pennsylvania. Journal of Applied Ecology 13, 523–531.

Dahlgren, R.A., Vogt, K.A. and Ugolini, F.C. 1991. The influence of soil chemistry on fine root aluminum concentrations and root dynamics in a subalpine Spodosol, Washington State, USA. Plant and Soil 133, 117–129.

Danielson, R.M. 1985. Mycorrhizae and reclamation of stressed terrestrial environments. In: Tate, R.L. and Klein, I. and D.A. ed. Soil Reclamation Processes: Microbial Analyses and Applications. New York, Dekker, 173–201.

Dhyani, S.K., Narain, P. and Singh, R.K. 1990. Studies on root distribution of five multipurpose tree species in Doon Valley, India. Agroforestry Systems 12, 149–161.

Doerr, T.B., Redente, E.F. and Reeves, F.B. 1984. Effects of soil disturbance on plant succession and levels of mycorrhizal fungi in a sagebrush-grassland community. Journal of Range Management 37, 135–139.

Drew, M.C. and Stolzy, L.H. 1991. Growth under oxygen stress. In: Waisel, Y., Eshel, A., and

Kafkafi, U. ed. Plant Roots. The Hidden Half. Marcel Dekker, Inc. 331–350.

Edmonds, R.L., Binkley, D., Feller, M.C., Sollins, P., Abee, A. and Myrold, D.D. 1989. Nutrient cycling: effects on productivity of Northwest forests. In: Perry, D.A., Meurisse, R., Thomas, B., Miller, R., Boyle, J., Means, J., Perry, C.R. and Powers, R.F. ed. Maintaining the Long-term Productivity of Pacific Northwest Forest Ecosystems. Timber Press, Portland, Oregon. 17–35.

Ewel, J. 1971. Biomass changes in early tropical succession. Turrialba 21, 110–112.

Fabiao, A., Madeira, M. and Steen, E. 1990/91. Effect of water and nutrient supply on root distribution in an *Eucalyptus globulus* plantation. Water, Air and Soil Pollution 54, 635–640.

Fassbender, H.W., Beer, J., Heuveldop, J., Imbach, A., Enriquez, G. and Bonnemann, A. 1991. Ten-year balances of organic matter and nutrients in agroforestry systems at CATIE, Costa Rica. Forest Ecology and Management 45, 173–183.

Fearnside, P.M. 1988. Jari at age 19: lessons for Brazil's silvicultural plans at Carjas. Interciencia 13, 12–24.

Fearnside, P.M. and Rankin, J.M. 1985. Jari revisited: changes and the outlook for sustainability in Amazonia's largest silvicultural estate. Interciencia 10, 121–129.

Finlay, R.D. and Read, D.J. 1986. The structure and function of the vegetative mycelium of ectomycorrhizal plants. II. The uptake and distribution of phosphorus by mycelial strands interconnecting host plants. New Phytologist 103, 157–165.

Fitter, A.H. 1977. Influence of mycorrhizal infection on competition for phosphorus and potassium by two grasses. New Phytologist 79, 119–125.

Fogel, R. and Hunt, G. 1983. Contribution of mycorrhizae and soil fungi to nutrient cycling in a Douglas-fir ecosystem. Canadian Journal of Forest Research 13, 219–232.

Ford, E.D. 1985. Branching, crown structure and control of timber production. In: Cannell, M.G.R. and Jackson., J. E. ed. Attributes of Trees as Crop Plants. Huntington, England, Institute of Terrestrial Ecology, 228–252.

Ford, E.D. and Deans, J.D. 1977. Growth of a sitka spruce plantation: spatial distribution and seasonal fluctuations of lengths, weights and carbohydrate concentrations of fine roots. Plant and Soil 47, 463–485.

Friend, A.L., Eide, M.R. and Hinckley, T.M. 1990. Nitrogen stress alters root proliferation in Douglas-fir seedlings. Canadian Journal of Forest Research 20, 1524–1529.

Gardes, M., White, T.J., Fortin, J.A., Bruns, T.D. and Taylor, J.W. 1991. Identification of indigenous and introduced symbiotic fungi in ectomycorrhizae by amplification of nuclear and mitochondrial ribosomal DNA. Canadian Journal of Botany 69, 180–190.

Gholz, H.L., Hendry, L.C. and Cropper, W.P. Jr. 1986. Organic matter dynamics of fine roots in plantations of slash pine *(Pinus elliottii)* in north Florida. Canadian Journal of Forestry Research 16, 529–538.

Goncalves, J.L.M. 1994. Caracteristicas do sistema radicular de absorcao do *Eucalyptus grandis* sob diferentes condicoes edaficas. Dissertation. Escola Superior de Agricultura 'Luiz de Queiroz', University of Sao Paulo, Brasil.

Goodland, R. 1971. Oligotrofismo e aluminio no cerrado. In: Ferri, M.G., ed. III. Simposio sobre o Cerrado. Universidade Sao Paulo. 44–60.

Gower, S.T., Gholz, H.L., Nakane, K. and Baldwin, V.C. 1994. Production and carbon allocation patterns of pine forests. In: Gholz, H.L., Linder, S. and McMurtrie, R.E. ed. Environmental Constraints on the Structure and Productivity of Pine Forest Ecosystems: a Comparative Analysis. Ecological Bulletins (Copenhagen) 43, 115–135.

Gower, S.T., Running, S.W., Gholz, H.L., Haynes, B.E., Hunt, E.R. Jr., Ryan, M.G., Waring, R.H. and Wendell P.C. Jr. 1995. Influence of climate and nutrition on carbon allocation and net primary production of four conifer forests. Tree Physiol. (in press)

⑥ [illegible]

Gower, S.T., Vogt, K.A. and Grier, C.C. 1992. Carbon dynamics of Rocky Mountain Douglas-fir: influence of water and nutrient availability. Ecological Monographs 62, 42–65.

Graham, B.F.Jr. and Bormann, F.H. 1966. Natural root grafts. The Botanical Review 32, 255–292.

Hall, I.R., Johnstone, P.D. and Dolby, R. 1984. Interactions between endomycorrhizas and soil nitrogen and phosphorus on the growth of ryegrass. New Phytologist 97, 447–453.

Harley, J.L. and Smith, S.E. 1983. Mycorrhizal Symbiosis. Academic Press. London.

Harris, W.F., Kinerson, R.S. and Edwards, N.T. 1977. Comparison of belowground biomass of natural deciduous forests and loblolly pine plantations. Pedobiologia 17, 369–381.

Hodson, M.J. and Wilkins, D.A. 1989. Factors affecting aluminum tolerance in *Picea abies* (L.) Karst. American Journal of Botany Supplement 76, 180.

Hung, L.L. and Trappe, J.M. 1983. Growth variation between and within species of ectomycorrhizal fungi in response to pH in vitro. Mycologia 75, 234–241.

Ikram, A., Mahmud, A.W., Ghani, M.N., Ibrahim, M.T. and Zainal, A.B. 1992. Field nursery inoculation of *Hevea brasilensis* Muell. Arg. seedling rootstock with vesicular-arbuscular mycorrhizal (VAM) fungi. Plant and Soil 145, 231–236.

Ikram, A., Mahmud, A.W. and Napi, D. 1987. Effects of P-fertilization and inoculation by two vesicular-arbuscular mycorrhizal fungi on growth and nodulation of *Calopogonium caeruleum*. Plant and Soil 104, 195–207.

Iloba, C. 1976. The effect of some herbicides on the development of ectotrophic mycorrhiza of *Pinus sylvestris*. European Journal of Forest Pathology 5, 339–343.

Janos, D.P. 1980. Vesicular-arbuscular mycorrhizae affect a lowland tropical rain forest plant growth. Ecology 61, 151–162.

Johnson, D.W., Cole, D.W., Gessel, S.P. and Minden, R.V. 1977. Carbonic acid leaching in a tropical, temperate, subalpine and northern forest soil. Arctic and Alpine Research 9, 329–343.

Johnson, N.C. 1993. Can fertilization of soil select less mutualistic mycorrhizae? Ecological Applications 3, 749–757.

Johnson, N.C., Zak, D.R., Tilman, D. and Pfleger, F.L. 1991. Dynamics of vesicular-arbuscular mycorrhizae during old-field succession. Oecologia 86, 349–358.

Jones, M.D. and Hutchinson, T.C. 1988. Nickel toxicity in mycorrhizal birch seedlings infected with *Lactarius rufus* or *Scleroderma flavidum*. I. Effects on growth, photosynthesis, respiration and transpiration. New Phytologist 108, 451–459.

Jonsson, K., Fidjeland, L., Maghembe, J.A. and Hogberg, P. 1988. The vertical distribution of fine roots of five tree species and maize in Morogoro, Tanzania. Agroforestry Systems 6, 63–69.

Jorgensen, J.R. and Wells, C.G. 1986. Tree nutrition and fast-growing plantations in developing countries. The International Tree Crops Journal 3, 225–244.

Kabata-Pendias, A. and Pendias, K. 1984. Trace Elements in Soils and Plants. CRC Press, Inc. Boca Raton, Florida.

Kangas, P. 1992. Root regrowth in a subtropical wet forest in Puerto Rico. Biotropica 24, 463–465.

Kassaby, F.Y. and Hepworth, G. 1987. *Phytophthora cinnamomi*: effects of herbicides on radial growth, sporangial production, inoculum potential and root disease in *Pinus radiata*. Soil Biology and Biochemistry 19, 437–441.

Kavanagh, T. and Kellman, M. 1992. Seasonal pattern of fine root proliferation in a tropical dry forest. Biotropica 24, 157–165.

Keyes, M.R. and Grier, C.C. 1981. Above- and below-ground net production in 40-year-old Douglas-fir stands on low and high productivity sites. Canadian Journal of Forestry Research 11, 599–605.

Kurz, W.A. 1989. Net primary production, production allocation and foliage efficiency in second growth Douglas-fir stands with differing site quality. Ph.D. dissertation. University of British Columbia, Vancouver, B.C. Canada.

Landsberg, J.J. 1986. Physiological Ecology of Forest Production. Academic Press, London.

Landsberg, J.J., Kaufmann, M.R., Binkley, D., Isebrands, J. and Jarvis, P.G. 1991. Evaluating progress towards closed forest models based on fluxes of carbon, water and nutrients. Tree Physiology 9, 1–15.

Lapeyrie, F.F. and Chilvers, G.A. 1985. An endomycorrhiza-ectomycorrhiza succession associated with enhanced growth of *Eucalyptus dumosa* seedlings planted in a calcareous soil. New Phytolologist 100, 93–104.

Lechowicz, M.J. 1987. Resource allocation by plants under air pollution stress: implications for plant-pest-pathogen interactions. The Botanical Review 53, 281–300.

Linder, S. and Rook, D.A. 1984. Effects of mineral nutrition on carbon dioxide exchange and partitioning of carbon in trees. In: Bowen, G. D. and Nambiar, E. K. S. ed. Nutrition of Plantation Forests. New York, Academic Press, 211–236.

Lugo, A.E. 1992. Comparison of tropical tree plantations with secondary forests of similar age. Ecological Monographs 62, 1–41.

Lugo, A.E., Wang, D. and Bormann, F.H. 1990. A comparative analysis of biomass production in five tropical tree species. Forest Ecology and Management 31, 153–166.

Malloch, D.W., Pirozynski, K.A. and Raven, P.H. 1980. Ecological and evolutionary significance of mycorrhizal symbioses in vascular plants (a review). Proceedings National Academy Science (USA) 77, 2113–2118.

Marks, G.C. and Kozlowski, T.T. ed. 1973. Ectomycorrhizae: Their Ecology and Physiology. Academic Press, London. 444 p.

Martinez-Amores, E., Valdes, M. and Quintos, M. 1991. Seedling growth and ectomycorrhizal colonization of *Pinus patula* and *P. radiata* inoculated with spores of *Helvella lacunosa, Russula brevipes* or *Lycoperdon perlatum*. New Forests 4, 237–245.

Marx, D.H. 1969. The influence of ectotrophic mycorrhizal fungi on the resistance of pine roots to pathogenic infections. I. Antagonism of mycorrhizal fungi to root pathogenic fungi and soil bacteria. Phytopathology 59, 153–163.

— 1973. Mycorrhizae and feeder root disease. In: Marks, G.C. and Kozlowski, T.T., ed. Ectomycorrhizae: Their Ecology and Physiology. Academic Press, New York. 351–389.

— 1980. Ectomycorrhiza fungus inoculations: a tool for improving forestation practices. In: Mikola, P. ed. Tropical Mycorrhiza Research. Oxford, Oxford University Press, 13–71.

McGroddy, M. 1994. Impacts of native tree species in mixed and pure plantations on soil structure at La Selva, Costa Rica. TRI Working Paper #81. Yale School of Forestry and Environmental Studies, New Haven, Connecticut, USA. 38 p.

McNaughton, S.J. and Oesterfeld, M. 1990. Extramatrical mycorrhizal abundance and grass nutrition in a tropical grazing ecosystem, the Serengeti National Park, Tanzania. Oikos 59, 92–96.

Mendonca Bellei, M., Garbaye, J. and Gil, M. 1992. Mycorrhizal succession in young *Eucalyptus viminalis* plantations in Santa Catarina (southern Brazil). Forest Ecology and Management 54, 205–213.

Michelsen, A. 1992. Mycorrhiza and root nodulation in tree seedlings from five nurseries in Ethiopia and Somalia. Forest Ecology and Management 48, 335–344.

Miller, R.M. and Jastrow, J.D. 1992. The application of Va mycorrhizae to ecosystem restoration and reclamation. In: Allen, M.F. ed. Mycorrhizal Functioning. Routledge, Chapman and Hall, New York. 438–467.

Mo, J., Brown, S., Lenart, M. and Kong, G. In press. Nutrient dynamics of a human-impacted pine forest in a MAB reserve of subtropical China. Biotropica.

Montagnini, F. 1995. Rehabilitating forest ecosystems in the humid tropics: recent experiences from Latin America. IUFRO International Symposium on Growth and Yield of Tropical Forests. Sept. 27–Oct. 1, 1994. Fuchu, Tokyo, Japan. In press.

Montagnini, F., Gonzalez, E., Porras, C., Rheingans, R. and Sancho, F. 1995. Mixed-tree plantations in the humid tropics: Growth, litterfall and economics of experimental systems in Latin America. IUFRO International Symposium on Growth and Yield of Tropical Forests. Sept. 27–Oct. 1, 1994. Fuchu, Tokyo, Japan. In press.

Montagnini, F. and Sancho, F. 1994. Above-ground biomass and nutrients in young plantations of four indigenous tree species: implications for site nutrient conservation. Journal of Sustainable Forestry 1, 115–139.

Montagnini, F., Sancho, F., Ramstad, K. and Stijfhoorn, E. 1991. Multipurpose trees for soil restoration in the humid lowlands of Costa Rica. In: Taylor, D.A. and McDicken, K.G. ed. Research on Multipurpose Trees in Asia. Winrock International Institute for Agricultural Development, Bangkok, 41–58.

Moorman, T. and Reeves, F.B. 1979. The role of endomycorrhizae in revegetation practices in the semi-arid west. II. A bioassay to determine the effect of land disturbance on endomycorrhizal populations. American Journal of Botany 66, 14–18.

Moran, E.F. 1986. Monitoring fertility degradation of agricultural lands in the lowland tropics. In: Little, P. D., Horowitz, M. M. and Nyerges, A. E. ed. Lands at Risk in the Third World: Local-Level Perspectives. Boulder, CO, Westview Press.

Nadelhoffer, K.J., Aber, J.D. and Melillo, J.M. 1985. Fine roots, net primary production and soil nitrogen availability: a new hypothesis. Ecology 66, 1377–1390.

Nambiar, E.K.S. 1983. Root development and configuration in intensively managed radiata pine plantations. Plant and Soil 71, 37–47.

— 1985. Increasing forest productivity through genetic improvement of nutritional characteristics. In: Ballard, R., Farnum, P., Ritchie, G. A. and Winjum, J. K. ed. Forest Potentials. Productivity and Value. Tacoma, Washington, Weyerhaeuser Science Symposium No. 4, 191–216.

Newman, E.I. 1988. Mycorrhizal links between plants: their functioning and ecological significance. Advances in Ecological Research 18, 243–270.

Newman, E.I. and Eason, W.R. 1989. Cycling of nutrients from dying roots to living plants including the role of mycorrhizas. In: Clarholm, M. and Bergstrom, L. ed. Ecology of Arable Land. Kluwer, Dordrecht. 133–137.

Newman, E.I. and Reddell, P. 1987. The distribution of mycorrhizas among families of vascular plants. New Phytologist 106, 745–751.

Opakunle, J. S. 1991. The cycling of micro-nutrients (Fe, Cu and Zn) in a cacao agro-ecosystem. Tropical Ecology 32, 223–230.

Parrotta, J.A. 1992. The role of plantation forests in rehabilitating degraded tropical ecosystems. Agriculture, Ecosystems and Environment 41, 115–133.

Parrotta, J.A. and Singh, I.P. 1992. Vertical distribution of fine roots in mono-specific and mixed-species tree plantations in Puerto Rico. Nitrogen Fixing Tree Research Reports 10, 89–90.

Perry, D.A. and Maghembe, J. 1989. Ecosystem concepts and current trends in forest management: time for reappraisal. Forest Ecology and Management 26, 123–140.

Perry, D.A., Molina, R. and Amaranthus, M.P. 1987. Mycorrhizae, mycorrhizospheres and reforestation: current knowledge and research needs. Canadian Journal of Forest Research 7, 929–940.

Persson, H. 1980. Fine-root dynamics in a Scots pine stand with and without near-optimum nutrient and water regimes. Acta Phytogeographica, Suecica 68, 101–110.

Petersson, H. and Messing, I. 1987. Influence of root mass on saturated hydraulic conductivity in arid soils of central Tunisia. Arid Soil Research and Rehabilitation 1, 149–160.

Powell, C.L. 1980. Effect of phosphate fertilizers on the production of mycorrhizal inoculum in soil. New Zealand Journal of Agricultural Research 23, 219–223.

Pregitzer, K. S., Hendrick, R.L. and Fogel, R. 1993. The demography of fine roots in response to patches of water and nitrogen. New Phytologist 125, 575–580.

Priess, J. and Folster, H. 1994. Carbon cycle dynamics and soil respiration of forests under natural degradation in the Gran Sabana. Interciencia 19, 317–322.

Puri, S., Singh, V., Bhushan, B. and Singh S. 1994. Biomass production and distribution of roots in three stands of *Populus deltoides*. Forest Ecology and Management 65, 135–147.

Raich, J.W. and Nadelhoffer, K.J. 1989. Belowground carbon allocation in forest ecosystems: global trends. Ecology 70, 1346–1354.

Ramirez-Saad, H., Valdes, M. and Cruz, R.C. 1992. Inoculacion y riego con aguas residuales de *Casuarina* en vivero. Turrialba 42, 476–481.

Read, D.J., Francis, R. and Finlay, R.D. 1985. Mycorrhizal mycelia and nutrient cycling in plant communities. In: Fitter, A.H. ed. Ecological Interactions in Soil. Blackwell Scientific Publication, Boston, Massachusetts, USA. 193–217.

Reddell, P. and Malajczuk, N. 1984. Formation of ectomycorrhizae by jarrah (*Eucalyptus marginata* Donn ex Smith) in litter and soil. Australian Journal of Botany 32, 435–444.

Reeves, F.B., Wagner, D., Moorman, T. and Kiel, J. 1979. The role of endomycorrhizae in revegetation practices in the semi-arid west. I. A comparison of incidence of mycorrhizae in severely disturbed vs. natural environments. American Journal of Botany, 66, 6–13.

Reid, C.P.P., Kidd, F.A. and Ekwebelam, S.A. 1983. Nitrogen nutrition, photosynthesis and carbon allocation in ectomycorrhizal pine. Plant and Soil 71, 415–432.

Richards, J.H. and Caldwell, M.M. 1987. Hydraulic lift: substantial nocturnal water transport between soil layers by *Artemisia tridentata* roots. Oecologia (Berlin) 73, 486–489.

Richter, D.L. and Bruhn, J.N. 1993. Mycorrhizal fungus colonization of *Pinus resinosa* Ait. transplanted on northern hardwood clearcuts. Soil Biology and Biochemistry 25, 355–369.

Ritz, K. and Newman, E.I. 1984. Movement of 32-P between intact grassland plants of the same age. Oikos 43, 138–142.

Rommell, L.-G. 1939. Barrskogens marksvampar och deras roll i skogens liv. Swenska Skogsvaardsforen Tidskr 37, 348–375.

Rouillon, R., Poulian, C., Bastide, J. and Coste, C.M. 1989. Degradation of the herbicide chlorpropham by some ectomycorrhizal fungi in pure culture. Agriculture Ecosystems and Environment 28, 421–424.

Roy, S. and Singh, J. S. 1995. Seasonal and spatial dynamics of plant-available N and P pools and N-mineralization in relation to fine roots in a dry tropical forest habitat. Soil Biology and Biochemistry 27, 33–40.

Ruark, G.Z., Mader, D.L. and Tattar, T.A. 1982. The influence of soil compaction and aeration on the root growth and vigour of trees – a literature review. Part 1. Aboricultural Journal 6, 251 265.

Russell, C.E. 1987. Plantation forestry: the Jari Project, Para, Brazil. In: Jordan, C. F. ed. Amazonian Rainforests, Ecosystem Disturbance and Recovery. Ecological Studies 60. New York, Springer-Verlag, 76–89.

Ryglewicz, P.T. and Andersen, C.P. 1994. Mycorrhizae alter quality and quantity of carbon allocated below ground. Nature 369, 58–60.

Saldarriaga, J.G., West, D.C., Tjarp, M.L. and Uhl, C. 1988. Long-term chronosequence of forest succession in the upper Rio Negro of Colombia and Venezuela. Journal of Ecology 76, 938–958.

Sanford, R.L. Jr. 1989. Root systems of three adjacent, old growth Amazon forests and associated transition zones. Journal of Tropical Forest Science 3, 268–279.

Santantonio, D. 1990. Modeling growth and production of tree roots. In: Dixon, R.K., Meldahl, R.S., Ruark, G.A. and Warren, W.G. ed. Process Modeling of Forest Growth Responses to Environmental Stress. Portland, Oregon, Timber Press. 124–141.

Santantonio, D. and Santantonio, E. 1987. Effect of thinning on production and mortality of fine roots in a *Pinus radiata* plantation on a fertile site in New Zealand. Canadian Journal of Forestry Research 17, 919–928.

Scatena, F.N., Silver, W., Siccama, T., Johnson, A. and Sanchez, M.J. 1993. Biomass and nutrient content of the Bisley Experimental Watersheds, Luquillo Experimental Forest, Puerto Rico, before and after Hurricane Hugo, 1989. Biotropica 25, 15–27.

Schenck, N.C., Siqueira, J.O. and Oliveira, E. 1989. Changes in the incidence of VA mycorrhizal fungi with changes in ecosystems. In: Vancura, V., Kunc, E. ed. Interrelationships between Micro organisms and Plants in Soil. New York, Elsevier, 125–129.

Schowalter, T.D. and Means, J.E. 1989. Pests link site productivity to the landscape. In: Perry, D.A., Meurisse, R., Thomas, B., Miller, R., Boyle, J., Means, J., Perry, C.R. and Powers, R.F. ed. Maintaining the Long-term Productivity of Pacific Northwest Forest Ecosystems. Timber Press, Portland, Oregon. 248–250.

Schubert, A. and Hayman, D. S. 1986. Plant growth responses to vesicular-arbuscular mycorrhiza. XVI. Effectiveness of different endophytes at different levels of soil phosphate. New Phytologist 103, 79–90.

Schwab, S.M., Menge, J.A. and Leonard, R.T. 1983. Quantitative and qualitative effects of phosphorus on extracts and exudates of sudangrass in relation to vesicular-arbuscular mycorrhiza formation. Plant Physiology 73, 761–765.

Screenivasa, M.N. and Bagyaraj, D.J. 1989. Use of pesticides for mass production of vesicular-arbuscular mycorrhizal inoculum. Plant and Soil 119, 127–132.

Sidhu, O.P. and Behl, H.M. 1992. Infectivity and effectiveness of VAM fungi in *Casuarina obesa* for alkaline soil sites. Nitrogen Fixing Tree Research Reports 10, 150–154.

Sidhu, S.S. and Chakravarty, P. 1990. Effect of selected forestry herbicides on ectomycorrhizal development and seedling growth of lodgepole pine and white spruce under controlled and field environment. European Journal of Forest Pathology 20, 77–94.

Sieverding, E. and Toro, S.T. 1987. Growth of coffee and tea plants in nurseries inoculated with different VAM fungal species. In: Sylvia, D. M., Hung, L. L. and Graham, J. H. ed. Mycorrhizae in the Next Decade: Practical Applications and Research Priorities. Gainesville, FL, IFAS, 58.

Singh, K.P. and Srivastava, S.K. 1984. Spatial distribution of fine root mass in young trees *(Tectona grandis)* of varying girth sizes. Pedobiologia 27, 161–170.

— 1985. Seasonal variations in the spatial distribution of root tips in teak *(Tectonia grandis* Linn. f.) plantations in the Varaseni Forest Division, India. Plant and Soil 84, 93–104.

Singh, L. and Singh, J. S. 1991. Species structure, dry matter dynamics and carbon flux of a dry tropical forest in India. Annals of Botany 68, 263–273.

St John, T.V., Coleman, D.C. and Reid, C.P.P. 1983. Growth and spatial distribution of nutrient-absorbing organs: selective exploitation of soil heterogeneity. Plant and Soil 82, 487–493.

Stone, E.L. and Kalisz, P.J. 1991. On the maximum extent of tree roots. Forest Ecology and Management 46, 59–102.

Termorshuizen, A.J. and Schaffers, A.P. 1989. Succession of mycorrhizal fungi in stands of *Pinus sylvestris* in The Netherlands. Agriculture, Ecosystems and Environment 28, 503–507.

Thapar, H. S. and Uniyal, K. 1990. Effect of pesticides on the growth of ectomycorrhizal fungi in-vitro. Indian Forester 116, 791–794.

Thomas, G.V. 1988. Vesicular-arbuscular mycorrhizal symbiosis in coconut *(Cocos nucifera)* in relation to the root (wilt) disease and intercropping or mixed cropping. Journal of Agricultural Sciences 7, 145–7.

Trappe, J.M. 1962. Fungus associates of ectotrophic mycorrhizae. Botanical Review 28, 538–606.

Trappe, J.M., Molina, R. and Castellano, M. 1984. Reactions of mycorrhizal fungi and mycorrhiza formation to pesticides. Annual Review of Phytopathology 22, 331–359.

Valdés, M. 1986. Survival and growth of pines with specific ectomycorrhizae after 3 years on a highly eroded site. Canadian Journal of Botany 64, 885–888.

Vogt, D.J. 1987. Douglas-fir Ecosystems in Western Washington: Biomass and Production as Related to Site Quality and Stand Age. Dissertation. University of Washington, Seattle, Washington, USA.

Vogt, K.A. 1991. Carbon budgets of temperate forest ecosystems. Tree Physiology 9, 69–86.

Vogt, K.A. and Bloomfield, J. 1991. Tree root turnover and senescence. In: Waisel, Y., Eshel, A. and Kafkafi, U. ed. Plant Roots: the hidden half. Marcel Dekker, Inc., New York. 287–306.

Vogt, K.A., Bloomfield, J., Ammirati, J.F. and Ammirati, S.R. 1992. Sporocarp production by basidiomycetes, with emphasis on forest ecosystems. In: Carroll, G.C. and Wicklow, D.T. ed. The Fungal Community. Its Organization and Role in the Ecosystem. 2nd ed. 563–581.

Vogt, K.A., Bloomfield, J., Perez, J.M., Vogt, D.J. and Silver, W.L. 1993. Belowground responses as indicators of environmental change. Environmental Experimental Botany 33, 189–205.

Vogt, K.A., Dahlgren, R., Ugolini, F., Zabowski, D., Moore, E.E. and Zasoski, R. 1987a. Aluminum, Fe, Ca, Mg, K, Mn, Cu, Zn and P in above- and belowground biomasss. I. *Abies amabalis* and *Tsuga mertensiana*. Biogeochemistry 4, 277–294.

— 1987b. Aluminum, Fe, Ca, Mg, K, Mn, Cu, Zn and P in above– and belowground biomasss. II. Pools and circulation in a subalpine *Abies amabalis* stand. Biogeochemistry 4, 295–311.

Vogt, K.A., Edmonds, R.L. and Grier, C.C. 1981. Dynamics of ectomycorrhizae in *Abies amabilis* stands: the role of *Cenococcum graniforme*. Holarctic Ecology 4, 167–173.

Vogt, K.A., Grier, C.C., Gower, S.T., Sprugel D.G. and Vogt, D.J. 1985. Overestimation of net root production: A real or imaginary problem? Ecology 67, 577–579.

Vogt, K., Grier, C.C., Meier, C.E. and Edmonds, R.L. 1982. Mycorrhizal role in net primary production and nutrient cycling in *Abies amabilis* ecosystems in western Washington. Ecology 63, 370–380.

Vogt, K.A., Grier, C.C. and Vogt, D.J. 1986. Production, turnover and nutrient dynamics of above- and belowground detritus of world forests. Advances in Ecological Research 15, 303–377.

Vogt, K.A., Publicover, D.A. and Vogt, D.J. 1991a. A critique of the role of ectomycorrhizas in forest ecology. Agriculture Ecosystems and Environment 35, 171–190.

Vogt, K.A., Vogt, D.J., Asbjornsen, H. and Dahlgren, R.A. 1995a. Roots, nutrients and their relationship to spatial patterns. Plant and Soil 168–169, 113–123.

Vogt, K.A., Vogt, D.J. and Bloomfield, J. 1991b. Input of organic matter to the soil by tree roots. In: McMichael, B.L. and Persson, H. ed. Plant Roots and Their Environment. Elsevier Science Publishers B.V. 171–190.

Vogt, K.A., Vogt, D., Brown, S., Tilley, J., Edmonds, R., Silver, W. and Siccama, T. 1995b. Forest floor and soil organic matter contents and factors controlling their accumulation in boreal, temperate and tropical forests. Advances in Soil Science 62, 159–178.

Vogt, K.A., Vogt, D.J., Moore, E.E., Fatuga, B.A., Redlin, M.R. and Edmonds, R.L. 1987 c Douglas-fir overstory and understory live

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fine root biomass in relation to stand age and productivity. Journal of Ecology 75, 857–870.

Vogt, K.A., Vogt, D.J., Gower, S.T. and Grier, C.C. 1990. Carbon and nitrogen interactions for forest ecosystems. In: Persson, H. ed. Above- and Belowground Interactions in Forest Trees in Acidified Soils. Air Pollution. Environmental Research Programme, Commission of the European Community 32, 203–235.

Vogt, K.A., Vogt, D.J., Moore, E.E. and Sprugel, D.G. 1989. Methodological considerations in measuring biomass, production, respiration and nutrient resorption for tree roots in natural ecosystems. In: Torrey, J.G. and Winship, L.J. ed. Applications of Continuous and Steady-State Methods to Root Biology. Kluwer Academic Publishers, Dordrecht, Boston. 197–232.

Wadsworth, F.H. 1983. Production of usable wood from tropical forests. In: Golley, F. B. ed. Tropical Rain Forest Ecosystems. Structure and Function. Ecosystems of the World 14A. New York, Elsevier. 279–288.

Waidyanatha, U.P.de S. 1980. Mycorrhizae of *Hevea* and leguminous ground cover in rubber plantations. In: Mikola, P. ed. Tropical Mycorrhiza Research. New York, Oxford University Press. 238–241.

Waisel, Y. and Agami, M. 1991. Ecophysiology of roots of submerged aquatic plants. In: Waisel, Y., Eshel, A., and Kafkafi, U. ed. Plant Roots. The Hidden Half. Marcel Dekker, Inc. 887–905.

Wargo, P.M. 1972. Defoliation-induced chemical changes in sugar maple roots stimulate growth of *Armillaria mellea*. Phytopathology 62, 1278–1283.

Waring, R.H. and Schlesinger, W.H. 1985. Forest Ecosystems: Concepts and Management. Orlando, Florida, Academic Press. 340 p.

Waring, R.H. 1987. Nitrogen pollution: a particular danger to boreal and subalpine coniferous forests. In: Fujimori, T. and Kimura, M. ed. Human Impacts and Management of Mountain Forests. Ibaraki, Japan, Forestry and Forest Products Research Institute. 93–105.

Waring, R.H., McDonald, A.J.S., Larsson, S., Ericsson, T., Wiren, A., Arwidsson, E., Ericsson, A. and Lohammer, T. 1985. Differences in chemical composition of plants grown at constant relative growth rates with stable mineral nutrition. Oecologia (Berlin) 66, 157–160.

Wilkins, D.A. 1991. The influence of sheathing (ecto-) mycorrhizas of trees on the uptake and toxicity of metals. Agriculture, Ecosystems and Environment 35, 81–87.

Wilkins, D.A. and Hodson, M.J. 1989. The effects of aluminium and *Paxillus involutus* on the growth of Norway spruce *(Picea abies)*. New Phytologist 113, 225–232.

Wilkinson, D.M. and Dickinson, N.M. 1995. Metal resistance in trees: the role of mycorrhizae. Oikos 72, 298–300.

Wormald, T.J. 1992. Mixed and Pure Forest Plantations in the Tropics and Subtropics. FAO Forestry Paper 103. FAO Technical Papers. Food and Agriculture Organization of the United Nations, Rome, Italy. 152 p.

Young, A. 1989. The Role of Roots. In: Agroforestry for Soil Conservation. C.A.B. International—International Council for Research in Agroforestry. 151–156.

Ziemer, R.R. 1981. Roots and the stability of forested slopes. Erosion and Sediment Transport in Pacific Rim Steeplands. I.A.H.S. publ. No. 132, 343–357.

Ziemer, R.R. and Swanston, D.N. 1977. Root strength changes after logging in Southeast Alaska. United Sates Department Agriculture; Forest Service Technical Report 306, 1–10.

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Table 8.1. Total and root biomass of tropical and subtropical forests and plantations

Species	Root sampling frequency #	Stand age (yr)	Above- and belowground living biomass (Mg ha^{-1})	Biomass of fine or small roots (Mg ha^{-1})	Fraction of total living biomass in total roots (%)	Source
Plantations						
Theobroma cacao + *Cordia alliodora*	1	5	45.9^{a}	4.2^{b}	9	Alpizar et al. 1986, Fassbender et al. 1991
Theobroma cacao + *Cordia alliodora*	1	10	95.4^{a}	9.8^{b}	10	Alpizar et al. 1986, Fassbender et al. 1991
Pinus caribaea	1	4	40.8	1.6^{b}	7	Lugo 1992
Pinus caribaea	4	11	95.6^{a}	0.7^{b}	–	Cuevas et al. 1991
Pinus caribaea	1	18.5	186.0	4.6^{b}	11	Lugo 1992
Swietenia macrophylla	1	17	102.0	3.0^{c}	8	Lugo 1992
Swietenia macrophylla	1	49	127.0	3.2^{c}	4	Lugo 1992
Stryphnodendron microstachyum	1	4	54.9^{a}	5.5^{i}	10	Montagnini et al. 1991, 1994
Vochysia guatemalensis	1	4	55.5^{a}	2.8^{i}	5	Montagnini et al. 1991, 1994
Vochysia ferruginea	1	4	49.9^{a}	4.9^{i}	11	Montagnini et al. 1991, 1994
Hyeronima alchorneoides	1	4	43.9^{a}	4.6^{i}	11	Montagnini et al. 1991, 1994
Jacaranda copaia	1	3^{a}	50.1^{a}	1.3^{g}	3	McGroddy 1994, Montagnini et al. 1995
Vochysia guatemalensis	1	3	28.4^{a}	2.3^{g}	8	McGroddy 1994, Montagnini et al. 1995
Mixed plantation	1	3^{a}	33.6^{a}	1.1^{g}	3	McGroddy 1994, Montagnini et al. 1995

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Table 8.1. (cont'd) Total and root biomass of tropical and subtropical forests and plantations

Species	Root sampling frequency	Stand age (yr)	Above- and belowground living biomass (Mg ha^{-1})	Biomass of fine or small roots (Mg ha^{-1})	Fraction of total living biomass in total roots (%)	Source
Natural forests						
Bana	1	Mature	92.0^{a}	16.2^{f}	–	Sanford 1989
Caatinga	1	Mature	246.0^{a}	18.7^{f}	–	Sanford 1989
Tierra firme	1	Mature	396.0^{a}	14.3^{f}	–	Sanford 1989
Tierra firme	1	11	61.0^{d}	n.d.	13	Saldarriaga et al. 1988
Tierra firme	1	20	73.0^{d}	n.d.	16	Saldarriaga et al. 1988
Tierra firme	1	35	130.0^{d}	n.d.	16	Saldarriaga et al. 1988
Tierra firme	1	60	244.0^{d}	n.d.	19	Saldarriaga et al. 1988
Tierra firme	1	80	170.0^{d}	n.d.	16	Saldarriaga et al. 1988
Tierra firme	1	Mature	268.0^{d}	n.d.	17	Saldarriaga et al. 1988
Primary forest	5	Mature	178.0^{a}	7.4^{h}	–	Priess and Folster 1994
Secondary forest	5	Young	79.0^{a}	11.4^{h}	–	Priess and Folster 1994
Secondary forest	5	50	190.0^{a}	10.3^{h}	–	Priess and Folster 1994
Secondary forest	4	Mature	23.0^{a}	5.3^{c}	–	Cuevas et al. 1991
Dry forest	12		28.0^{a}	1.6^{c}	–	Singh and Singh 1991
Secondary forest — evergreen	1	4	33.0	4.5^{c}	33	Lugo 1992
Secondary forest — evergreen	1	17	81.0	5.4^{c}	16	Lugo 1992
Secondary forest— evergreen	1	18.5	111.0	4.9^{c}	19	Lugo 1992
Secondary forest — evergreen	1	49	99.0	4.3^{c}	21	Lugo 1992
Secondary forest — evergreen	1	Mature	302.0^{i}	8.2^{d}	27	Scatena et al.1993, Kangas 1992

Table 8.1. (cont'd) Total and root biomass of tropical and subtropical forests and plantations

Species	Root sampling frequency	Stand age (yr)	Above- and belowground living biomass (Mg ha^{-1})	Biomass of fine or small roots (Mg ha^{-1})	Fraction of total living biomass in total roots (%)	Source
Pinus massoniana	1	30	92.0[a]	9.3[fc]	10	Mo et al. in press 1995
Secondary forest	1	2	2.0[d]	n.d.	10–22	Ewel 1971
Secondary forest	1	4	4.0[d]	n.d.	6–7	Ewel 1971
Secondary forest	1	6	5–7[d]	n.d.	25–26	Ewel 1971
Broadleaf semi-deciduous	1	50	359.0[d]	n.d.	15	Vogt et al. 1995a
Secondary forest	1	16	237.0[d]	n.d.	14	Vogt et al. 1995a
Secondary forest	1	10	n.d.[a]	15.9[ed]	-	McGroddy 1994
Secondary forest	1		n.d.[a]	7.9[id]	-	Montagnini et al. 1991

[a]Does not include coarse structural roots; [b]fine roots classified = <5 mm–20mm; [c]fine roots equal to or less than 2mm; [d]coarse roots only; [e]fine roots < 5mm; [f]roots sampled to 10 cm soil depth; [g]roots sampled to 15 cm depth; [h]roots sampled to 20 cm depth; [i]roots sampled to 60 cm depth. [j]used fine root data <5mm (8.2 Mg/ha) from Kangas (1992) instead of Scatena et al. 1993 (2.2 Mg/ha) since that reported in the latter article was hurricane impacted and too low for an undisturbed forest.

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Table 8.2 Above- and belowground net primary production of tropical forests and plantations

Species	Age (years)	Aboveground NPP ($Mg\ ha^{-1}\ yr^{-1}$)	Belowground NPP ($Mg\ ha^{-1}\ yr^{-1}$)	Total NPP ($Mg\ ha^{-1}\ yr^{-1}$)	Source
Plantation					
Pinus caribaea	4	7.9	–	–	Lugo 1992
Pinus caribaea	11	18.1	1.1	19.2	Cuevas et al. 1991
Pinus caribaea	18.5	15.1	–	–	Lugo 1992
Swietenia macrophylla	17	16.6	–	–	Lugo 1992
Swietenia macrophylla	49	19.1	–	–	Lugo 1992
Theobroma cacao + *Cordia alliodora*	5–10	22.7	5.5	28.2	Fassbender et al. 1991
Natural forest					
Secondary	4	7.9	–	–	Lugo 1992
Secondary	11	11.0	8.5	19.4	Lugo 1992
Secondary	17	8.5	–	–	Lugo 1992
Secondary	18.5	10.0	–	–	Lugo 1992
Secondary	49	12.3	–	–	Lugo 1992
Primary	Mature	3.8	3.7	7.5	Priess and Folster 1994
Secondary	Young	2.7	5.7	8.4	Priess and Folster 1994
Secondary	50	2.6	5.2	7.8	Priess and Folster 1994

Table 8.3 Nitrogen, phosphorus and potassium storage in roots compared to the remaining living biomass and in relationship to soil content of these nutrients in plantations and naturally regenerating forests

Species	Age (years)	Nitrogen		Phosphorus		Potassium		Source
		Total living tree N (kg ha^{-1}) (% of total living tree N in roots)	Soil N (kg ha^{-1}) (% of total ecosystem N in the soil)	Total living tree P (kg ha^{-1}) (% of total living tree P in roots)	Soil P (kg ha^{-1}) (% of total ecosystem P in the soil)	Total living tree K (kg ha^{-1}) (% of total living tree K in roots)	Soil K (kg ha^{-1}) (% of total ecosystem K in the soil)	
Plantation								
Pinus caribaea	4	359 (4)	8920 (96)	12.4 (7)	1710 (99)	50(22)	31480 (>99)	Lugo 1992
Pinus caribaea	18.5	1443 (5)	11630 (89)	54.8 (7)	1690 (97)	509 (13)	26250 (98)	Lugo 1992
Swietenia macrophylla	17	560 (8)	8110 (94)	28.5 (9)	1350 (98)	361 (7)	30010 (99)	Lugo 1992
Swietenia macrophylla	49	998 (4)	5480 (85)	37.1 (10)	1410 (97)	412 (3)	18120 (98)	Lugo 1992
Theobroma cacao + *Cordia alliodora*	5	370 (10)^a	7991 (96)	45.4 (9)^a	3594 (99)	364 (6)^a	577 (61)	Alpizar et al. 1986
Stryphnodendron microstachyum	4	467 (11)^a	12925 (96)	37 (33)^a	-	79 (10)^a		Montagnini and Sancho 1994, Montagnini 1995
Vochysia guatemalensis	4	263 (10)^a	13958 (98)	43 (13)^a	-	177 (1)^a		Montagnini and Sancho 1994, Montagnini 1995
Vochysia ferruginea	4	223 (20)^a	13578 (98)	35 (36)^a	-	77 (26)^a		Montagnini and Sancho 1994, Montagnini 1995
Hyeronimo alchorneoides	4	294 (15)^a	11520 (97)	55 (14)^a	-	256 (2)^a		Montagnini and Sancho 1994, Montagnini 1995
Eucalyptus grandis	25	1117 (15)	3682 (77)	-	-			Drechsel and Zech 1993

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Table 8.3 (cont'd) Nitrogen, phosphorus and potassium storage in roots compared to the remaining living biomass and in relationship to soil content of these nutrients in plantations and naturally regenerating forests

Species	Age (years)	Nitrogen		Phosphorus		Potassium		Source
		Total living tree N (kg ha⁻¹) (% of total living tree N in roots)	Soil N (kg ha⁻¹) (% of total ecosystem N in the soil)	Total living tree P (kg ha⁻¹) (% of total living tree P in roots)	Soil P (kg ha⁻¹) (% of total ecosystem P in the soil)	Total living tree K (kg ha⁻¹) (% of total living tree K in roots)	Soil K (kg ha⁻¹) (% of total ecosystem K in the soil)	
Natural forests								
Secondary forest	4	218 (25)	5180 (96)	7.2 (41)	970 (99)	160 (36)	25040 (99)	Lugo 1992
Secondary forest	17	495 (24)	8440 (95)	35.9 (24)	2780 (99)	466 (13)	18720 (98)	Lugo 1992
Secondary forest	18.5	610 (17)	8020 (93)	34.4 (11)	1190 (97)	479 (12)	26990 (98)	Lugo 1992
Secondary forest	49	478 (21)	8880 (95)	29 (13)	2230 (99)	367 (9)	21090 (98)	Lugo 1992
Secondary forest	Mature	946 (35)[b]	7522 (89)	49 (32)[b]	-	602 (15)[b]		Scatena et al. 1993; Kangas 1992.
Secondary forest	16	820 (17)	5500 (87)	-	-			Vogt et al. 1995
Pinus massoniana	30	219 (32)	-	11.5(39)	-	80 (40)		Mo et al. (~~in press~~)

Note: See Table 1 for diameter size and depth of sampling for roots; [a]Does not include coarse roots; [b]Adjusted fine root data < 5mm using Kangas's (1992) biomass of 8.2 Mg ha⁻¹ instead using the 2.2 Mg ha⁻¹ reported in Scatena et al. 1993 since this value reflected a hurricane-impacted number.

1995

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b

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Table 8.4 Studies on mycorrhizas in tropical plantations and forests

Tree species	Native/exotic	Mycorrhizas species	Location	Age	Setting	Study time	Focus of study	Source
Mycorrhizas—Inoculation								
Theobroma cacao	Native	*Scutellospora calospora* *Glomus mosseae*	Sabah, Malaysia	3-6 months	Pot experiment	6 months	Improved growth and nutrient uptake of vegetative propagules with VAM[a] inoculation; inoculated VAM more effective than indigenous soil mycorrhizae.	Azizah Chulan and Martin 1992
Oil Palm	n/a +	n/a	Ivory Coast	5 months	Pot experiment	5 months	Improved growth and nutrient uptake with inoculation by indigenous species. Effectiveness varied with mycorrhizal species.	Blal and Gianinazzi-Pearson 1989
Eucalyptus globulus	Native	*Laccaria laccata* *Scleroderma verrucosum* *Setchelliogaster* sp.	Australia	5 months	Pot experiment	5 months	Improved growth with inoculation; mycorrhizas reduced phenotypic variability of seedlings.	Burgess and Malajczuk 1989
Eucalyptus urophylla × *E. kirtoniana*	Exotic	*Pisolithus tinctorius* *Scleroderma texense* *S. dictyosporum* *S. aurantium* *S. cylindrosporum*	Congo	50 months	Plantation	50 months	Inoculation with exotic EM[b] improved growth but mycorrhizas varied in sustainability of effect and competed poorly with native mycorrhizas over long term.	Garbaye et al. 1988.
Acacia nilotica *Leucaena leucocephala*	n/a Exotic	*Glomus etunicatum* *G. mossae* *G. occultum*	Somalia	3 months	Pot experiment	3 months	Improved growth with indigenous VAM inoculation. Improved drought resistance of *L. leucocephala*, no change for *A. nilotica*.	Michelsen and Rosendahl 1990

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Table 8.4 (cont'd) Studies on mycorrhizas in tropical plantations and forests

Tree species	Native/exotic	Mycorrhizas species	Location	Age	Setting	Study time	Focus of study	Source
Pinus caribaea *Pinus oocarpa*	Exotic	*Pisolithus tinctorius*	Nigeria	0–3 years	Experimental plantation	3 years	Successful survival of exotic mycorrhiza, *P. tinctorius* compared to indigenous soil inoculant. Improved growth and survival with inoculation.	Momoh and Gbadegesin 1980
Pinus caribaea	Exotic	*Pisolithus tinctorius* *R. luteolus* *T. terrestris*	Kumasi and Takoradi, Ghana	1 year	Nursery	1 year	Growth and survival varied with exotic inoculant species.	Ofosu-Asiedu 1980
Citrus volkameriana	n/a	*Glomus intraradices*	Florida, USA	3 months	Pot experiment	3 months	Analysis of carbon costs: growth depression in mycorrhizal citrus at high P^c supply.	Peng et al. 1993
Casuarina obesa	Exotic	*Glomus fasciculatum*	Lucknow, India	3 months	Greenhouse	3 months	Improved growth in alkaline soil with inoculation by indigenous mycorrhizas. Reduced root/shoot ratio in mycorrhizal seedlings.	Sidhu and Behl 1992
Pinus michoacana *Pinus pseudostrobus*	Native	*Pisolithus tinctorius* *Laccaria laccata*	Tepetlaoxtoc, Mexico	18 months–3 years	Experimental plantation	3 years	Improved growth and survival with inoculation; higher survival with *P. tinctorius* inoculant, higher mycorrhizal colonisation of *P. Pseudostrobus*.	Valdés 1986

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Table 8.4 (cont'd) Studies on mycorrhizas in tropical plantations and forests

Tree species	Native/exotic	Mycorrhizas species	Location	Age	Setting	Study time	Focus of study	Source
Hevea brasiliensis	Exotic	*Glomus* spp. *Sclerocytis* spp. *Acaulospora* spp. *Gigaspora* spp.	Sri Lanka	1–5 years	Industrial plantation	n/a	Improved P uptake with mycorrhizal infection. No effect of mycorrhizas on *Hevea*'s growth. Greater mycorrhizal infection under legume ground cover; stimulation of nitrogen fixing activity by mycorrhizas.	Waidyanatha 1980.
Mycorrhizae — presence documentation studies								
Stryphnodendron microstachium	Native	n/a	La Selva, C.Rica	20 years	Pot experiment	160 days	VAM inoculum potential of three vegetation types in abandoned pasture; seedling establishment.	Asbjornsen, and Montagnini 1994.
Pinus radiata	Exotic	*Scleroderma* spp. *Endogone flammicorona* *Amanita muscaria* *Tuber* spp. *Rhizopogon rubescens* *Suillus* spp. *Hebeloma crustuliniforme* *Laccaria laccata* *Thelephora terrestris*	New Zealand	2–17 years	Plantation and nursery	5 years	Mycorrhizal diversity varied with forest and soil type. Greater diversity in older forests.	Chu-Chou and Grace 1988
Psuedotsuga menziesii	Exotic	*Hebeloma crustuliniforme* *Laccaria laccata* *Rhizopogon parksii* *Suillus lakei*	South Island, New Zealand	2–40 years	Nursery and forest	6 years	Different mycorrhizal associations in forests of different ages.	Chu-Chou and Grace 1987.

Table 8.4 (cont'd) Studies on mycorrhizas in tropical plantations and forests

Tree species	Native/exotic	Mycorrhizas species	Location	Age	Setting	Study time	Focus of study	Source
Eucalyptus spp.	Exotic	*Hydnangium carneum* and others	North Island, New Zealand	Seedling –50 years	Plantation	2 years	Different mycorrhizal associations in forests of different ages.	Chu-Chou and Grace 1982.
Coffee arabica	Exotic	n/a	Miranda State, Venezuela	25 years	Industrial plantation	1 years	High VAM infection of coffee roots; study of root biomass distribution, seasonal fine root growth, and litter decomposition. VAM infection did not affect decomposition rate of litter.	Cuenca et al. 1983.
Shorea bracteolata *S. leprosula* *S. curtisii*	Native	n/a	Forest Research Institute of Malaysia, Kepong	n/a	Plantation and logged forest	1 month	High mycorrhizal infection of seedlings in 61-year-old plantation and logged forest. Suggest that mycorrhizas have positive effect on P uptake.	Lee and Lim 1989
Citrus aurantifolia	n/a	n/a	Colima, Mexico	6–7 years	Plantation and family garden	6 months	Indigenous VAM colonisation of plants was lower in high-input (irrigation, fertilised) agroecosystems vs. low-input systems.	Michel-Rosales and Valdés (in press)

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Table 8.4 (con'd) Studies on mycorrhizas in tropical plantations and forests

Tree species	Native/exotic	Mycorrhizas species	Location	Age	Setting	Study time	Focus of study	Source
Acacia spp. *Callistemon lanceolatus* *Casuarina equisetifolia* *Chamlaecytisus* sp. *Cordia africana* *Croton macrostachys* *Cupressus* spp. *Eucalyptus* spp. *Euphorbia pulcherrima* *Grevillea robusta* *Juniperus procera* *Leucaena leucocephala* *Olea africana* *Pinus patula*	11 native, 30 exotic, (not all species listed)	n/a	Somalia, Ethiopa	2–14 months	Nursery	4 years	Mycorrhizal and root nodulation documented in tree seedlings. Degree of mycorrhizal colonisation varied by tree species.	Michelsen 1992
Cocos nucifera	n/a	n/a	Kasaragod, Kerala	25–30 years	Experimental plantation	n/a	Reduced VAM on root (wilt) diseased plants. Higher VAM in intercropped system.	Thomas 1988
			Mycorrhizas—fertilisation					
Hevea brasiliensis	Exotic	*Glomus manihot* *Glomus clarum* *Entrophospora colombiana* *Glomus macrocarpum* *Scutellispora calospora* *Glomus intraradix*	Kota Tinggi, Malaysia	26 weeks	Experimental plantation	26 weeks	Multi-species inoculant of indigenous VAM species used on seedling rootstock. Fertilisation with P decreased mycorrhizal root colonisation, improved growth and nutrient uptake with inoculation when P limiting.	Ikram et al. 1992

Table 8.4 (cont'd) Studies on mycorrhizas in tropical plantations and forests

Tree species	Native/exotic	Mycorrhizas species	Location	Age	Setting	Study time	Focus of study	Source
Alnus nepalensis	Native	*Glomus mosseae*	Sillong, India	6 months	Pot experiment	6 months	Fertilisation w/P reduced VAM infection. Improved growth with inoculation when P limiting. VAM infection of N-fixing *Alnus* increased with successful nodulation and vice versa.	Jha et al. 1993
			Mycorrhizas—pesticides/herbicides					
In-vitro only	n/a	*Cenococcum geophilum* *Corticium bicolor* *Laccaria laccata* *Pisolithus tinctorius*	Dehra Dun, India	6 weeks	Lab experiment/ flasks	12weeks	Inhibition of EM by 4 different pesticides.	Thapar and Unlyal 1990
Pinus radiata	Native Exotic	n/a	Victoria, Australia	3 and 6 months	Pot experiment	6 months	Herbicides (propazine and chlorthal dimethyl) affected mycorrhizal composition. Impact of herbicide varied with mycorrhizal species and concentration. High concentrations reduced mycorrhizal development and root growth. Low concentrations of chlorthal had positive impact.	Marks and Becker 1990.

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Table 8.4 (cont'd) Studies on mycorrhizas in tropical plantations and forests

Tree species	Native/exotic	Mycorrhizas species	Location	Age	Setting	Study time	Focus of study	Source
			Mycorrhizas—succession					
Pinus radiata	Exotic	*Suillus* spp. *Tuber* spp.	New Zealand	0–4 years	Nursery and forest	4 years	Mycorrhizal composition sometimes changed after transplanting seedlings from nursery to forest. Related to soil type and fertility.	Chu-Chou and Grace 1990 88
Eucalyptus dumosa	Native	*Glomus* sp.	New South Wales, Australia	2–5 months	Pot experiment	5 months	Succession of VAM to EM in calcium carbonate soils. Improved growth and P uptake with inoculation	Lapeyrie and Chilvers 1985 and Chilvers et al. 1987.
Eucalyptus marginata *E. diversicolor* *Acacia pulchella* *Banksia grandis*	Native	*Glomus fasciculatus*	Western Australia	4 months	Pot experiment	4 months	Succession of VAM to EM. VAM infection favoured over EM after fire.	Malajczuk et al. 1981
Eucalyptus viminalis	~~Native~~ Exotic	*Pisolithus tinctorius* *Scleroderma* spp.	Santa Catarina, Brazil	2–15 months	Plantation	9 months	Succession of VAM to EM	Mendonca Bellei et al. 1992

[a]VAM = vesicular arbuscular mycorrhizas; [b]EM = ectomycorrhizas; [c]P = phosphorus; n/a = not available.

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Table 8.4 (cont'd) Studies on mycorrhizas in tropical plantations and forests

Tree species	Native/exotic	Mycorrhizas species	Location	Age	Setting	Study time	Focus of study	Source
Pinus caribaea *Pinus oocarpa*	Exotic	*Pisolithus tinctorius*	Nigeria	0–3 years	Experimental plantation	3 years	Successful survival of exotic mycorrhiza, *P.tinctorius* compared to indigenous soil inoculant. Improved growth and survival with inoculation.	Momoh and Gbadegesin 1980
Pinus caribaea	Exotic	*Pisolithus tinctorius* *R. luteolus* *T. terrestris*	Kumasi and Takoradi, Ghana	1 year	Nursery	1 year	Growth and survival varied with exotic inoculant species.	Ofosu-Asiedu 1980
Citrus volkameriana	n/a	*Glomus intraradices*	Florida, USA	3 months	Pot experiment	3 months	Analysis of carbon costs: growth depression in mycorrhizal citrus at high P^c supply.	Peng et al. 1993
Casuarina obesa	Exotic	*Glomus fasciculatum*	Lucknow, India	3 months	Greenhouse	3 months	Improved growth in alkaline soil with inoculation by indigenous mycorrhizas. Reduced root/shoot ratio in mycorrhizal seedlings.	Sidhu and Behl 1992
Pinus michoacana *Pinus pseudostrobus*	Native	*Pisolithus tinctorius* *Laccaria laccata*	Tepetlaoxtoc, Mexico	18 months–3 years	Experimental plantation	3 years	Improved growth and survival with inoculation; higher survival with *P.tinctorius* inoculant, higher mycorrhizal colonisation of *P. Pseudostrobus*.	Valdés 1986

added

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add to references

Garbaye J, Delwaulle JC, Dingane D (1988) Growth response of *Eucalypts* in the Congo to ectomycorrhizal inoculation. For. Ecol. Manage. 24: 151-15

Momoh ZO, Gbadegesin RA (1980) Field performance of Pisolith tinctorius as a mycorrhizal fungus of pines in Nigeria In: Tropical Mycorrhiza Research (P. Mikola, ed). Oxford University Press, Oxford, U.K.

Michelsen, A. and Rosendahl, S. 1990. The effect of VA mycorrhizal fungi phosphorus and drought stress on the growth of acacia-nilotica and leucoena - leucocephala seedlings. Plant Soil 124: 1. 7-14

Drechsel, P and Zech, W. 1994. DRIS evaluation of teak (Tectona grandis L.f.) mineral nutrition and site quality on teak growth in West Africa. Forest Ecology and Management 70 (1-3) 121-133.

Add to references –

Marks, G.C. and Becker, S.L. 1990. Influence of Propozine and chlorathal-dimethyl on mycorrbizal development in pinus-radiata seedlings. Australian Journal of Botony 38 (4) 341-350.

Jha, D.K, Sharma, G.D., Mishra, R.R. 1993. Mineral Nutrition in the trapartite interaction between frankia glomus and alnus at different soil phosphorus regimes. New Phytol. 123 (2). 307-311

Lee, S.S., Lim, K.L. 1989. Mycorrhizal infection and foliar phosphorus content of seedlings of three dipterocarp species growing in a selectively logged forest and a forest plantation. Plant Soil 117 (2). 1237-242.

Blal, B. and Gianinazzi-Pearson, V. 1990. Interest of endomycorrhizae for the production of micropropagated oil palm clones. Meeting on ecological and applied aspects of ecto- and endomycorrhizal associations held at the 2nd European symposium on mycorrhizae, Pregue, Czchoslovakia, Aug. 5-9, 1988. Agric. Ecosyst. Environ. 29 (1-4). 1990. 39-44.

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TITLE:          THE EFFECT OF VA MYCORRHIZAL FUNGI PHOSPHORUS AND DROUGHT
                  STRESS ON THE GROWTH OF ACACIA-NILOTICA AND LEUCAENA-
                  LEUCOCEPHALA SEEDLINGS
SOURCE:         PLANT AND SOIL 124 (1). 1990. 7-14.
ABBR. SOURCE:   PLANT SOIL

AUTHOR(S):      MICHELSEN A; ROSENDAHL S
ADDRESS:        INST. PLANT ECOL., UNIV. COPENHAGEN, O. FARIMAGSGADE 2 D, DK-
                  1353 K, DENMARK.

ABSTRACT:       The effect of vesicular-arbuscular mycorrhizal (VAM) fungi on
                  growth and drought resistance of Acacia nilotica and
                  Leucaena leucocephala seedlings was studied in a glasshouse
                  experiment. The experimental design was a
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TITLE:          DRIS evaluation of teak (Tectona grandis L.f.) mineral
                  nutrition and effects of nutrition and site quality on teak
                  growth in West Africa.
SOURCE:         Forest Ecology and Management 70 (1-3). 1994. 121-133.

AUTHOR(S):      Drechsel P; Zech W
ADDRESS:        Inst. Soil Sci., Univ. Bayreuth, 95440 Bayreuth, Germany

ABSTRACT:       The objective of the investigation was to study the site
                  variables controlling teak yield (Tectona grandis Linn.
                  fil.) and to establish guidelines for the selection of high
                  productivity sites in Benin, Cote d'Ivoire, Liberia, Nigeria
                  and Togo. Depending on stand age, soil and region, between
                  70 and 90% of the variation in tree growth (site index, SI)
                  could be explained by the supply of nitrogen, the root-
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TITLE:          INFLUENCE OF PROPAZINE AND CHLORTHAL-DIMETHYL ON MYCORRHIZAL
                  DEVELOPMENT IN PINUS-RADIATA SEEDLINGS
SOURCE:         AUSTRALIAN JOURNAL OF BOTANY 38 (4). 1990. 341-350.
ABBR. SOURCE:   AUST J BOT

AUTHOR(S):      MARKS G C; BECKER S L
ADDRESS:        DEP. CONSERVATION, FORESTS AND LANDS, DIV. FOREST, 378 COTHAM
                  RD., KEW, VIC. 3101, AUST.

ABSTRACT:       In an investigation into the side effects of herbicides on
                  mycorrhizal formation in Pinus radiata nurseries, propazine
                  and chlorthal dimethyl were added at concentrations that
                  approximated to normal (2 .cntdot.20 and 1 .cntdot. 88 g
                  a.i-1 L) and half-normal (1 .cntdot. 10 and 0 .cntdot. 94 g
                  a.i.-1L) field application rates respectively to P. radiata
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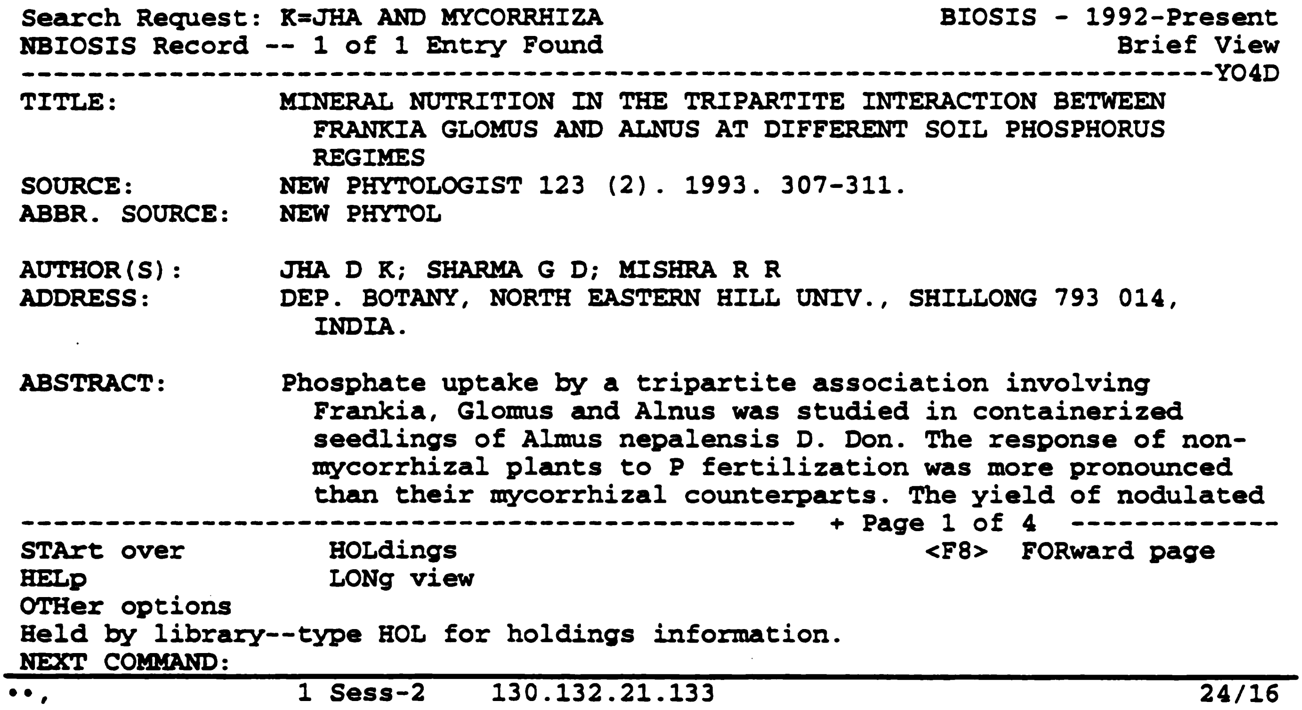

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                  FRANKIA GLOMUS AND ALNUS AT DIFFERENT SOIL PHOSPHORUS
                  REGIMES
SOURCE:         NEW PHYTOLOGIST 123 (2). 1993. 307-311.
ABBR. SOURCE:   NEW PHYTOL

AUTHOR(S):      JHA D K; SHARMA G D; MISHRA R R
ADDRESS:        DEP. BOTANY, NORTH EASTERN HILL UNIV., SHILLONG 793 014,
                  INDIA.

ABSTRACT:       Phosphate uptake by a tripartite association involving
                  Frankia, Glomus and Alnus was studied in containerized
                  seedlings of Almus nepalensis D. Don. The response of non-
                  mycorrhizal plants to P fertilization was more pronounced
                  than their mycorrhizal counterparts. The yield of nodulated
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                   SEEDLINGS OF THREE DIPTEROCARP SPECIES GROWING IN A
                   SELECTIVELY LOGGED FOREST AND A FOREST PLANTATION
SOURCE:          PLANT AND SOIL 117 (2). 1989. 237-242.
ABBR. SOURCE:    PLANT SOIL

AUTHOR(S):       LEE S S; LIM K L
ADDRESS:         FAC. FORESTRY, UNIV. PERTANIAN MALAYSIA, 43400 SERDANG,
                   SELANGOR, MALAYSIA.

ABSTRACT:        Foliar phosphorus content and mycorrhizal infection of
                   dipterocarp seedlings growing in a 61-year-old forest
                   plantation (site A) and a selectively logged forest (site B)
                   were determined. Mycorrhizal infection levels were
                   high.sbd.83.7% for Shorea bracteolata and 95.0% for S.
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TITLE:          INTEREST OF ENDOMYCORRHIZAE FOR THE PRODUCTION OF
                  MICROPROPAGATED OIL PALM CLONES
SOURCE:         MEETING ON ECOLOGICAL AND APPLIED ASPECTS OF ECTO- AND
                  ENDOMYCORRHIZAL ASSOCIATIONS HELD AT THE 2ND EUROPEAN
                  SYMPOSIUM ON MYCORRHIZAE, PRAGUE, CZECHOSLOVAKIA, AUGUST 5-
                  9, 1988. AGRIC ECOSYST ENVIRON 29 (1-4). 1990. 39-44.

AUTHOR(S):      BLAL B; GIANINAZZI-PEARSON V
ADDRESS:        INRA, LAB. PHYTOPARASITOL., STN. D'AMELIORATION DES PLANTES,
                  BV 1540, 21034 DIJON CEDEX, FR.

ADDED KEYWORDS: GROWTH MINERAL NUTRITION
MAJOR CONCEPT CODES:
                51504; 51510; 53004

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Chapter 14

Silvicultural plantations

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email: floren@minerva.cis.yale.edu

In: M. E. McClain, L. A. Martinelli and J. E. Richey (eds).

The Biogeochemistry of the Amazon Basin

and its Role in a Changing World

Oxford University Press

Montagnini, F. 1997. Silvicultural plantations. In: McClain, M. E., Martinelli, L. A. and Richey, J. E (Eds.). *The Biogeochemistry of the Amazon Basin and its Role in a Changing World.* Oxford University Press. In Press.

1- Introduction

Tropical plantations can serve diverse economic, social, political and ecological functions. With considerably higher yields than managed native forests, tropical and subtropical plantations can make substantial contributions to world timber and pulp production (Wadsworth 1983, Evans 1992). Tree plantations can also be a source of cash, savings and insurance for individual farmers. Plantations may help stabilize rural populations in regions where shifting agriculture is the predominant land use. In combination with subsistence and commercial crops (agroforestry) or cattle (agrosilvopastoral systems), plantations have been used as tools in rural development projects worldwide. Plantations are often seen as alternatives to deforestation as they can provide products that otherwise would be taken from natural forests (Fearnside 1983, Mc Nabb et al. 1994).

Nutrient cycling characteristics of tropical plantations differ from those of natural forests in a number of ways. Natural forests are adapted to ecological niches by intricate and effective physiological adaptations of growth in the environment (see Jordan, Chapter 4, this volume). Instead, tropical plantations are simplified, generally monospecific ecosystems that occupy the site for a limited period of time that can range from 4-12 years (for biomass, pulpwood or fuelwood) up to 20-40 years (timber). In many instances plantations are composed of species that are exotic to the region, or even when indigenous, are new to the particular plantation site. Since plantation tree species have been generally selected for production of timber or other aboveground tree parts, they tend to maintain a smaller fraction of total tree biomass nutrients in roots than natural forests (Vogt et al. 1997). In rain forests growing on poor soils, high tree productivity is in part due to the existence of important nutrient conserving mechanisms mediated by the root system (Chapter 4). The smaller biomass of plantation root systems may thus make them more susceptible to nutrient and water stress. Smaller root systems may also make plantation forests more susceptible to disturbances from strong winds, pathogens that attack aerial parts (Vogt et al. 1997).

Nutrient demands by plantation trees vary from season to season and with the developmental age of the stand (Drechsel and Zech 1993). During the life of the plantation, large quantities of nutrients are returned to the soil by above and below ground litter, harvest residues, stem flow and throughfall. These elements are mineralized in the soil and may be used by the trees or by associated crops. Deposition of certain mineral elements from the atmosphere can also be important, sometimes even compensating from losses in stemwood removal at harvest (Bruijnzeel 1989). Retranslocation of absorbed nutrients can be also of considerable magnitude, often being able to support sustained growth in the short and long term (Nambiar 1984).

Plantations are frequently managed intensively, with silvicultural inputs, for maximum wood or biomass production in the shortest time. Plantation management (e.g., thinning, pruning, coppicing, fertilizing) profoundly affects stand structure, crown characteristics, and plantation micro environment, all of which in turn can affect nutrient cycling processes. Other forestry operations, especially during harvest and those associated with the establishment of the following crop (biomass removal, soil disturbance, residue disposal by burning, intense site preparation such as ploughing, discing or blading, weed control and fertilization) have profound influences on the productivity of a site (Lundgren 1980, Sánchez et al. 1985). The effects of perturbation on nutrient losses are greatly accelerated in short rotations of intensively managed plantations, and these considerations have often led to the concept of economic vs. ecological rotations (Nambiar 1984, Drechsel and Zech 1993).

Fast growing tropical tree plantations can incorporate considerable amounts of nutrients in their biomass over a relatively short period of time. Site fertility declines can limit sustained plantation forestry in tropical regions: soil fertility can be decreased through excessive removal of nutrients in living biomass, particularly if nutrients in tree crowns are lost through harvest or site preparation (Jorgensen and Wells 1986, Perry and Maghembe 1989). Site fertility declines can be more serious if the trees are harvested in short rotation schemes, and if whole-tree harvesting is applied. This can be particularly serious when plantations are established on soils that are inherently poor, as occurs over vast areas of the Amazon basin (Chapter 4, this volume).

If plantation species are chosen with knowledge of their nutrient-use efficiencies and recycling capacities, they can be highly productive and even serve a function in ecosystem restoration projects. In particular, mixed-species designs can offer product diversification and can complement nutrient resource use with positive impacts on soil nutrients (Alvim 1989, Silva and Uhl 1992, Montagnini et al. 1995). In addition, rotation length and harvest techniques can be adjusted to minimize nutrient losses and maintain site productivity in the long term.

This chapter considers large scale industrial tree plantations, as well as small and medium scale plantations for timber and land rehabilitation. Aspects that influence plantation sustainability are emphasized, and suggestions are given regarding plantation design and management.

2- Plantations in the Amazon

Tree plantations in the Amazon are used at small, medium, and large scales, each of which serves different functions, such as rural development, land rehabilitation, or industrial purposes. The first major entrepreneurial effort in Amazonian tree plantations was the establishment of native rubber (*Hevea brasiliensis*) in 1928 at the Fordlândia Estate owned by Henry Ford on the lower Tapajós river in the state of Pará, Brazil. These plantations were abandoned in the late 1940s due to low latex productivity that resulted from a high incidence of the south American leaf blight (Rankin 1985). After this failure, large scale tree plantations were not undertaken again in the region until 1968 when Jarí Forestal e Agropecuaria was established, also in Pará. Other early attempts at plantation establishment in the Amazon include small plantations of Brazil nut (*Bertholletia excelsa*) near Manaus in 1931, which had generally low nut yield but good tree growth, and scattered efforts to cultivate the valuable Meliaceae. Of the Meliaceae, *Swietenia macrophylla* (mahogany) and *Cedrela odorata* (cedar), were planted most often, but neither these nor other species were successful, as all were stricken by the shoot borer *Hypsipyla grandella* (Palmer 1977).

Plantations have been sometimes recommended as a potentially viable land use for the Amazon region (Alvim 1989, Hoyos et al. 1992, McNabb et al. 1994). Silvicultural plantations have also been promoted as an alternative means of supplying wood and paper needs while also reducing pressure for additional rain forest clearing (Fearnside 1983). However, as in other tropical humid regions of the world, many authors have raised concerns about the ecological and economic sustainability of large scale plantations in the Amazon basin: fast-growing exotics planted in monospecific stands deplete soil nutrients in a few rotations and often suffer from pest and disease problems (Johnson 1976, Fearnside and Rankin 1980, Rankin 1985, Palmer 1977, Russell 1987). In the Brazilian Amazon, hardwood species have been restricted to experimental settings, but fast-growing species for pulp, plywood and sawlogs have been planted in an increasing number of commercial plantations that are partially or fully owned by foreign investors. Examples include 20,000 ha of Caribbean pine (*Pinus caribaea*) in the Amapá territory; 500,000 ha of Caribbean pine near Portel in the state of Pará; and the highly publicized Jarí project, also in Pará.

3- Nutrient cycling in industrial plantations of fast growing exotics: the Jarí project

Located along the Jarí River (a tributary 300 km from the mouth of the Amazon), the 1.6 million ha Jarí estate was originally purchased by the American multimillionaire Daniel Ludwig in 1967 (see also Jordan, Chapter 18, this volume). In the first fifteen years of the project, more than 100,000 ha of forest were cleared and planted with exotic species, mostly *Gmelina arborea*, *Pinus caribaea var. hondurensis,* and *Eucalyptus* spp. (McNabb et al. 1994). In 1982 Ludwig sold the forestry operation to a consortium of Brazilian businesses, taking a substantial loss on the original investment (Chapter 18). Now called the Monte Dourado Forestry Company, this estate has become a modern forestry enterprise similar to those established in southeastern Brazil. Current forestry, agricultural, and mining uses encompass about 28% of the property, while the remaining 72% is still relatively undisturbed rain forest (McNabb et al. 1994).

Controversy has surrounded the capacity of the soils to support long-term plantation productivity at Jarí. For example, Irion (1981) suggested that the soil would be completely exhausted after the second generation (14-20 years) even though the *Gmelina arborea* plantations had reached a height of 20 m in seven years in the first generation, and the other species (*Pinus caribaea* and *Eucalyptus deglupta*) had shown few signs of nutrient deficiency at the time. Other authors have suggested that soil fertility could be improving under the forest plantations at Jarí; for example, company researchers showed that in the plantations there was no economic response to the application of mineral fertilizers in the early years (Palmer 1977). Likewise, Greaves (1979) stated that the fertility and moisture retention of the soils was apparently improving under the forest plantations, making reference to the thicker organic layer that had developed under both pine and *Gmelina* species.

Russell (1987) examined whole ecosystem nutrients within a native forest, a 6-month pine plantation, a 9.5-year pine plantation, an 8.5-year *Gmelina* plantation, and a 1.5-year second generation pine plantation that was established on a previous 8.5-year *Gmelina* plantation. A synthesis of the changes in nutrient stocks during the course of plantation establishment and growth is presented in Figure 1. At the end of the first rotation of *Gmelina* (8.5 years) or *Pinus caribaea* (9.5 years), total plant biomass was about 40-60% of that in the virgin forest. Most of the losses were accounted for by the dry matter extracted by harvest, as well as by the disturbance caused by site preparation. The plantations of all ages contained about 60% of the total N stock of the rain forest. Most losses occurred shortly after rain forest clearing, but thereafter the plantations maintained a relatively constant level of N. The ecosystem, therefore, lost 40% of its N, and then reached a new equilibrium level. Stocks of P ranged from 76% to 116% of the rain forest values, with the decrease in P at the start of the rotation largely accounted for by the P removed in the first rotation harvest. Significant losses of K occurred after rain forest clearing, with a decrease to about 32% of that in the forest before clearing. Most of the losses were accounted for by the removal at harvest, as well as by rapid leaching losses recorded during this period, an expected result since K is a highly mobile ion and it is readily lost through leaching. Afterwards, there were slight increases, to about 40% of the rain forest values. Ca stocks decreased to about 56% of the rain forest values upon planting of the first pine rotation. Losses were again accounted for by Ca removal at forest harvest and small amounts that were leached. This reduced level of Ca remained relatively stable with *Pinus*, but increased to above pre-clearing levels with *Gmelina*. Magnesium stocks decreased with age in *Pinus*, but mature *Gmelina* plantations maintained a steady level of about 75% of that in the rain forest.

Most of the ecosystem nutrient losses occurred during the plantation establishment phase because of the removal of forest debris at clearing and soil disturbance during mechanized operations. Despite the potential improvement in Ca levels and maintenance of Mg levels as mentioned for *Gmelina*, both the extraction of nutrients during harvesting, and leaching losses prior to canopy closure, lead to a depletion of key nutrients, particularly potassium, that must be replaced by fertilization if yields are to be maintained (Sánchez et al. 1985, Russell 1987).

Likewise, Spangerberg (1994) reported on nutrient removal by eucalyptus at Jarí and stressed the need for fertilization after the first rotation. Studies were made on first rotation, 4½-year-old plantations of *Eucalyptus urograndis* (a hybrid of *E. urophylla* and *E. grandis*) in order to calculate nutrient losses due to the removal of wood and bark during harvesting for pulpwood. Plantation trees exhibited no nutrient deficiencies, although foliar concentrations of Ca seemed to be rather low. Average nutrient losses due to removal of wood and bark amounted to 64.6% for N, 54.2% for P, 76.3% for Ca, 57.2% for K, and 60.7% for Mg, of the whole tree biomass. If the same nutrient removal was assumed in the next rotation, there would be a deficiency of Ca, and compensations of up to 250 kg Ca/ha would be necessary.

Results of experimental research on nutrient dynamics in industrial plantations elsewhere in the Amazon also point to the need for supplemental fertilization to sustain yields in the medium to long term. In experimental plantations at the National Institute for Amazonian Research (INPA) in Manaus results of studies by Magalhaes et al. (1986a, 1986b) showed how height of several tree species growing in 3-year-old plantations correlated strongly with soil fertility parameters (exchangeable bases, organic matter, exchangeable Al, total Zn and Mn). However, nutrient requirements vary among plantation species and with plantation age. For example, in experiments using four doses of lime (calcium carbonate) during establishment of plantations on acid soils at La Selva, Costa Rica, only one third of the species exhibited a significant response in growth (Soto et al. 1996). The species tested were all native to the region, and they were probably adapted to growing on the acid soil conditions of the experimental area. In addition, responses to fertilizer also vary with plantation age. In the early stages of stand development prior to canopy closure, the annual rate of nutrient accumulation increases rapidly and tree growth is very dependent on current nutrient uptake. Mineral deficiencies are frequently observed and responses to fertilizer application are common during this stage. Once the canopy has closed, the reduction in rate of nutrient uptake is associated with attaining maximum foliage biomass, high internal retranslocation of mobile nutrients as well as increasing nutrient recycling via litter fall. This decreases the nutrient contribution by the soil, thus fertilizer responses are unlikely during this stage (Drechsel and Zech 1993). The type, amounts and timing of fertilization used in plantations needs to be adjusted according to species requirements, ideally using results of field fertilization experiments.

In summary, in high-yield, short-rotation plantation forestry in rain forest sites such as Jarí, and other locations with similar ecological conditions, nutrients are likely to become limiting after the second or third rotation; therefore, yields will not be maintained without extra fertilizer inputs. Repeated fertilization can upset soil nutrient balances and alter microbial populations, and it would also pose problems for the economics of producing low-value commodity timbers (see also Chapter 18).

In spite of the lessons from Jarí, other large scale plantation development plans continue in the Brazilian Amazon. If developed, the Grande Carajás Program would consume large areas of tropical forest in the eastern Amazon in order to obtain charcoal for the smelting of pig-iron from the Carajás' mines. The area of *Eucalyptus* plantation to produce the required amount of charcoal would be over 700,000 ha — more than 10 times the area of *E. deglupta* already cultivated in the Jarí Project (Fearnside 1989).

4- Small scale plantations for timber

Nutrient cycling in timber plantations in the Amazon has not been studied as much as industrial plantations, yet these systems have great potential to provide a more sound land-use option for the region: they can produce high quality timber, help to restore degraded lands and contribute to rural development. Because there are still large areas of native forest available for management and extraction of valuable timber species, plantations of exotic and native hardwoods remain small and mostly experimental.

A lack of information on the silvicultural management for some of the most preferred timber species, which are often difficult to grow in open plantations, also limits the current expansion of timber plantations in the Amazon. For example, in recent experiences in the Peruvian Amazon, populations of *Hypsipyla grandella* (the mahogany shoot borer) grew rapidly in the rainy season as food availability increased from new growth sprouted on the host trees (*Cedrela odorata, C. fissilis* and *Swietenia macrophylla*). *C. odorata* was more susceptible to the pest than *S. macrophylla* (Yamazaki et al. 1990). It was suggested that planting trees in small cleared areas and avoiding clean weeding may reduce the ease with which the pest finds its host species.

Several other native species have been tried with success in plantations in the Peruvian Amazon. Results of 20 years' experience with plantations of 9 exotic and 104 native species at Jenaro Herrera, near the Ucayali river 200 km upstream from Iquitos, were summarized by Claussi et al. (1992). As a result of the failure of some exotics and attacks by *Hypsipyla* on the Meliaceae, the plantation work concentrated on non- Meliaceae native species. *Cedrelinga catenaeformis* and *Simarouba amara [Quassia simarouba]* were the two best timber species, with mean annual increments of over 1.5 cm in diameter and 1.5 m in height at ten years of age. Two species suitable for rural construction work, *Guatteria elata* and *G. hyposericea*, had mean annual increments of over 1.5 cm in diameter and 1.5 m in height. Other suitable timber species recommended by these authors include *Parkia multijuga, Ormosia* spp., and *Sclerolobium aff. tinctorium.* Recommendations on plantation establishment included species mixtures, such as *C. catenaeformis* with *Q. simarouba* and *Guatteria elata*, and agroforestry combinations with agricultural crops.

In the Brazilian Amazon, the earliest experiences reported are those from timber plantations at EMBRAPA's Curuá-Una station in Santarem, Pará (Pedroso 1973a, 1973b, SUDAM 1979). These experiences provided data on species trials established since 1959, as well as information on silvicultural methods and regeneration techniques developed for establishing plantations of indigenous and exotic species in the Amazon region. Fourteen to eighteen years after planting, tree growth of 47 native and 18 exotic species showed that promising native species included *Anacardium giganteum, Bagassa guianensis, Bertholletia excelsa, Buchenavia huberi, Didymopanax morototoni, Goupia glabra, Jacaranda copaia, Parkia multijuga, Simarouba amara, Vatairea guianensis, Virola cuspidata*, and *Vochysia maxima* (SUDAM 1979). Performance of *Pinus caribaea var. hondurensis* and *Eucalyptus* spp. were also good. Other species recommended for their inclusion in tree improvement programs were the natives *Carapa guianensis, Platonia insignis, Schizolobium amazonicum* and *Virola surinamensis,* and exotics such as *Gmelina arborea* and *Terminalia ivorensis* (Pitcher 1976). *Cordia alliodora* has also been recommended as a good prospect for commercial, large-scale plantations (Carpanezzi et al. 1982).

Important lessons regarding plantation management strategies have been learned from the results of pioneer studies in the eastern Amazon. From their experiences in Paragominas (in Pará), Nepstad et at. (1990) and Uhl et al. (1991) suggested that burning before planting would decrease competition by grass. In trials with 27 native species, they concluded that the addition of fertilizer or manure was not essential for establishment. They also suggested planting trees in patches of already established shrubs, such as *Cordia multispicata* which presumably will offer a more favorable microclimate for tree establishment. Among the best performers in these trials were fruit trees such as *Anacardium occidentale* (caju), *Bixa orellana*, as well as timber trees such as *Swietenia macrophylla.*

As seen, a considerable number of valuable timber species can be grown in plantations with relative success in the Amazon region, and a few silvicultural guidelines are available to aid in their establishment and management. Tree plantations, especially with indigenous species, can contribute to soil restoration and facilitate natural forest regeneration (Guariguata et al. 1995). Plantations of exotics can also be beneficial on many degraded sites, and can facilitate natural regeneration in some circumstances, as explained in the next section. Over large areas of the tropics, with pressing human needs for land, the restorative effects of tree plantations can be realized if local people are willing to plant trees for their products such as timber. Overall, in the Amazon basin this is probably the most important role of silvicultural plantations, the most unrealized one, and the one in need of greater research and promotion.

5- Plantations as a tool for land rehabilitation and rural development

Plantations for land rehabilitation are generally grown at a small to medium scale because they usually require intensive initial care, often including external inputs (mycorrhiza inoculation, use of fertilizers or herbicides). In some cases, initial intercropping with annual plants can help to offset costs, as described in Section 6. The experiences in Paragominas, Pará, Brazil mentioned in the previous section and experiments at EMBRAPA stations constitute isolated, pioneer examples of this type of silvicultural plantation in the Amazon.

Keys to success of these systems are correct species choice and design. Choice of species should be based on the nutrient use efficiency and growth rate of each species. Recent studies on the natural impact of native trees on soil fertility and nutrient cycling in the Atlantic forest region of Bahia, and in the Atlantic humid lowlands of Costa Rica, help to illustrate these points. During trials in Bahia, Brazil, 15 out of 20 tree species planted in monospecific stands had positive effects on at least five soil fertility parameters, 13-15 years after planting. Several species contributed to increased soil carbon and nitrogen levels in the topsoil: *Inga affinis, Parapiptadenia pterosperma, Plathymenia foliolosa* (leguminous, N-fixing species), *Caesalpinia echinata, Copaifera luscens* (leguminous, non-N-fixing), *Eschweilera ovata,* and *Pradosia lactescens* (Montagnini et al. 1994). In experiments at La Selva Biological Station in Costa Rica, improved soil conditions were found just after tree canopy closure in pure plantations of timber trees compared to pasture lands. The highest values for soil carbon, total nitrogen and phosphorus were found under *Vochysia ferruginea*, a valuable timber species native to Central America. After three years the soils under pure stands of native species had soil fertility values similar to those found in 20-year-old natural secondary forests originated after abandonment from cattle pastures (Montagnini and Sancho 1994).

In the same region of Costa Rica, the use of improved fallow systems yielded land values of $5-12 thousand per hectare at a 5% real interest rate, after inflation (Montagnini and

Mendelsohn 1996). This system involved planting native tree species to replenish soil and provide economically valuable timber. Although the experiences are site specific, the species used have broad distribution in Latin America. Therefore, the systems would be transferable in other areas with similar ecological and economic conditions.

Reforestation of mine spoils

Under the highly degraded conditions present in mine spoils, serious nutrient deficiencies limit tree growth and require heavy use of external inputs to ensure success of restoration projects. In experiences on reforestation of bauxite mining sites at Porto Trombetas (western Pará), low levels of soil organic matter, N, P, K, Ca and Mg were found to be the principal factors for reduced growth of planted trees (Ferraz 1993). The plantations present great variability in growth and degree of vegetation cover, even in areas of apparently homogeneous soils. The restored areas receive surface soil as an amendment before reforestation. This topsoil is stored after removing it to allow for bauxite mining, thus the length and conditions of soil storage may affect its suitability to serve as bed for the newly planted seedlings. Additions of mycorrhizae and supplemental nutrients are often necessary. This increases the per hectare cost of reforestation although at levels still reasonable for the mining company (Knowles, pers. comm.).

In the past, reforestation relied on the establishment of monospecific plantations, often with exotics (e.g., *Eucalyptus, Pinus, Acacia* spp.), or a limited number of native tree taxa for which seeds are readily available and silvicultural practices have been developed (Knowles and Parrotta 1995). Also at Porto Trombetas, about 160 native forest species in mixed plantings were evaluated for their suitability for forest restoration on bauxite mine land over a 14 year period. Observations over 600 ha of plantings have yielded information on ecological characteristics of the species and cost-effective propagation methods. The plantations of exotics and natives are expected to catalyze natural forest succession in the understory and thus accelerate the rate at which species-rich native forest stands develop on severely degraded lands.

6- Nutrient cycling and plantation design and management

The impacts of trees on soil fertility depend on nutrient recycling characteristics such as litter chemistry and decomposition rates. Tree litter can be used as mulch with different outcomes: a fast mulch decomposition rate may accelerate the growth of associated crops on poor soils, while in other cases a more persistent litter may provide a steady source of nutrients and a better soil cover year round. In the experiments in Costa Rica described in the previous section, high rates of litter fall and slower decomposition resulted in high litter accumulation and high soil organic matter under *V. ferruginea*, making this species well suited for protecting soils against erosion. In contrast, litter from another species of *Vochysia*, *V. guatemalensis,* may be especially important for Ca and Mg recycling (Montagnini et al. 1993). Although in this experiment the litter of *Hieronyma alchorneoides* was less abundant than the other three species, it had a relatively faster decomposition rate and higher nutrient content. These characteristics promoted fast nutrient recycling, especially of N, Ca, Mg, K and P.

The ability of a species to produce large amounts of biomass with less nutrients may be an important consideration in choosing species for degraded, nutrient-poor sites. When put in context with nutrient recycling characteristics of a species, Nutrient Use Efficiency (NUE) values, calculated as the annual biomass increments per nutrients in annual leaf litter fall, can indicate appropriate system design and management to maintain productivity and recover or conserve nutrients over the long term. Results from experiments in Bahia, Brazil suggest that *Bombax macrophyllum* and *Plathymenia foliolosa*, with overall high NUE values, would grow well on relatively nutrient-poor soils, and thus could be good alternatives for reforestation of degraded sites following the abandonment from agriculture and pasture that is frequent in the region (Montagnini 1994). *B. macrophyllum* stands tended to accumulate high amounts of litter under its canopy while *P. foliolosa* stands had relatively high amounts of organic matter and total N in the topsoil in comparison with adjacent areas of secondary forest (Montagnini et al. 1994). These features indicate that these species may be well suited for soil rehabilitation, including increasing soil organic matter content and protecting against soil erosion. Also at Bahia, species such as *Buchenavia grandis* and *Hymenaea aurea*, with overall lower NUE values, would be most appropriate for agroforestry combinations where crops could benefit from nutrient recycling from litter. Species choices and designs should be suited to the kind of soil rehabilitation desired, a goal that should be tightly connected with the future use expected from the rehabilitated land.

At La Selva, *Vochysia ferruginea* showed comparatively low efficiency values for N and P (Fig. 2), confirming the beneficial role of this species in recycling organic matter and positively impacting soil fertility as shown above, while the higher NUE values shown for *V. guatemalensis* illustrate the relatively large allocation of nutrients to stem biomass and comparatively low recycling in leaf litter. The relatively low efficiency (high recycling) of N and P found for *Stryphnodendron microstachyum* and *Hyeronima alchorneoides* (Fig. 2) was also shown in experiments where maize grown with mulch of these species grew better and absorbed more N and P than with mulch of other species (Montagnini et al. 1993).

Nutrient allocation in trees can impact soil nutrients in plantations when different parts of the trees are harvested and removed. When biomass nutrient allocation was compared among species at La Selva, the forest floor appeared to be an important compartment for long-term recycling of N, with marked differences among species (Fig. 3a). Similar results were obtained with respect to Ca and Mg, which also had relatively low use efficiency values (Montagnini 1994). If the forest floor is burned or collected for fuelwood, a substantial loss of organic matter and nutrients may occur, while if the litter is left after harvest, it represents a significant reservoir for the next tree rotation. In contrast, most species had higher use efficiency of P, and this nutrient was found in higher proportion in live tree biomass (Fig. 3b); a similar pattern was found for K (Montagnini 1994). Roots were also important for P, in comparison with forest-floor P. Roots of tropical trees appear to decay at slower rates than leaf tissue, which means that they may function as a longer-term storage mechanism for nutrients (Bloomfield et al. 1993). The biomass of fine roots in tropical plantations is generally two to four times lower than in adjacent secondary forest of similar age (Lugo 1992, Vogt et al. 1997). Certain indigenous species that tend to maintain a relatively large proportion of living tree biomass nutrients in roots, while still producing high stem biomass increments (such as *V. ferruginea* and *H. alchorneoides*), would be preferred in sites where nutrient losses are a major concern. This can be especially critical for P and K, often mentioned as the nutrients which are most likely to be depleted from soils with subsequent rotations (Wadsworth 1983, Bowen and Nambiar 1984, Bruijnzeel 1984).

Altering the rate of nutrient removal in products is probably one of the most important design considerations in planning sustainable plantations (Wang et al. 1991). Variation between species in nutrient allocation and the parts of the tree removed from the site will determine the extent to which the nutrients are removed during harvesting. For example, whole tree harvests of *V. guatemalensis* would result in substantial nutrient removals, especially of Ca and Mg, while the harvest of *H. alchorneoides* would result in large removals of P and K (Montagnini and Sancho 1994). This can be assessed through nutrient and biomass sampling and estimation, and harvesting guidelines can be developed that reduce the extent of nutrient losses. The degree to which harvest losses will impact on forest production will depend on the amount of nutrients stored in remaining pools and the rate at which they are mineralized from these pools.

Finally, a key issue in nutrient management of tree plantations is to find the best compromise between ecological requirements and rotation length so as to ensure adequate nutrient supply in the long term. Due to increasing nutrient use efficiency in the stands with time, lengthening the rotation age of fast growing species will reduce net nutrient uptake from soil reserves (Drechsel and Zech 1993).

Other considerations for management and design

The recovery of the productive capacity of soils is frequently expensive, thus the techniques involved must produce financial returns to ensure they are adopted by local farmers. In soil rehabilitation projects, species such as *B. macrophyllum* and *P. foliolosa* (Bahia) or *V. guatemalensis* (Costa Rica) should be grown first as they can generally tolerate more impoverished conditions than other species while producing valuable timber and protecting soils against erosion. Other species, such as *B. grandis* and *H. aurea* (Bahia), or *H. alchorneoides* (Costa Rica), with lower nutrient use efficiency and potentially producing higher nutrient cycling, might be planted at the same time, or underplanted later. The calculation of NUE and its interpretation in context with the recycling capacities of the species could contribute to species selection and system design focusing on the potential role of each species on productivity and soil rehabilitation.

Mixed-species designs can be more advantageous than tree monocultures for site nutrient rehabilitation if systems are planned to complement each species' nutrient demands and effects. For the fastest-growing, light demanding species included in a mixture, tree productivity can be higher than in monospecific stands, while for the slower-growing, shade-tolerant species of generally more valuable timber, the mixture offers a more adequate growth environment than a single-stratum, open plantation (Montagnini et al. 1995). In experiments with mixed and pure species plantations at La Selva, Costa Rica, mixed stands of four indigenous species ranked first or second in terms of above ground biomass, in comparison with pure stands of each species (Fig. 4). The data for roots in Fig. 4 were only for the top 15 cm layer of mineral soil; it would be interesting to see if roots explore the soils in a more efficient way in mixed than in pure stands. The advantages to mixed forest designs in terms of long-term effects on ecosystem nutrients have yet to be demonstrated, but mixed systems show promise as they may be preferred to diversify product outputs, decrease risks of failure, and contribute to species and landscape diversity.

7- Combinations of plantation trees with agricultural crops or cattle (agroforestry)

In plantations for timber, with relatively slower growth and longer rotations than pulp or energy species, the first years of plantation establishment can be costly, and combinations with agricultural crops or cattle in agroforestry or agrosilvopastoral systems often can help to defray these costs. Based on available information on the agroecological characteristics of humid tropical regions, Alvim (1989) recommended agroforestry systems that include black pepper, cacao, rubber, and some successful silvopastoral systems similar to those in the cacao region of Bahia and in the Amazon region of Brazil. Likewise, Sombroek (1992) pointed to timber plantations and agroforestry systems as approaches for the reclamation of degraded and abandoned areas. The potential of agroforestry as an ecologically and economically sound land use alternative in the Amazon is also discussed by Jordan (Chapter 18, this volume).

A variety of experimental settings involving forestry and agroforestry practices have been established by EMBRAPA over the last 10-15 years in uplands (terra firme) near Santarem, on the Tapajós river, a tributary of the Amazon. For example, along the Santarem/Cuiabá road, research has been initiated to help smallholder adopt more environmentally sustainable farming practices and to obtain additional sources of capital. Fast growing species with high economic value have been introduced into farming areas. Systems include combinations of corn, banana, freijo (*Cordia goeldiana*) and mahogany (*Swietenia macrophylla*) (Brienza Junior and Yared 1991).

Other agroforestry models involve combinations of crops, fruit trees and timber tree species designed to provide immediate returns and longer-term investment for the small holders. Food crops associated with tree establishment reduced tree plantation costs and decreased the frequency of crop weeding. For example, the trees tatajuba (*Bagassa guianensis*), parapará (*Jacaranda copaia*) and freijo were planted in a mixture with cowpea (*Vigna unguiculata*) with good results in terms of crop yields and tree growth.

The use of agrosilvopastoral systems is an alternative to the ranching system operated over large areas of Amazonia, which results in progressive loss of soil fertility. Such agrosilvopastoral systems have been introduced to the Paragominas region of eastern Pará using the forestry species *Eucalyptus tereticornis, B. guianensis* and *Schizolobium amazonicum*, the crop *Zea mays*, and the forage species *Brachiaria brizantha, B. humidicola* and *Panicum maximum*. Performance of the forestry and forage species has been satisfactory and the maize yield was greater than the regional average. The cattle, at a low stocking rate, grazed normally on the site and caused no harm to the planted trees (Brienza Junior and Jared 1991).

The sustained management of tree plantations and tree-crop combinations (agroforestry) are potentially biologically and socially feasible alternatives for soils unsuitable for local agriculture because of severe degradation. Tree plantations or agroforestry also represent productive uses of lands that have poor regeneration due to a lack of nearby sources of forest propagules. As the area of degraded land expands, there is an increasing emphasis on the planting of tree species which can grow in such conditions and still yield potentially profitable products (such as timber and fuelwood) as well as environmental benefits (such as soil conservation and watershed protection).

The choice of appropriate species is the key to success of such systems. Ideally, species should be indigenous to the region, have fast growth, good economic value, and positive impacts on soil fertility. Additionally, management systems must be compatible with local farming and cultural practices and avoid increasing labor requirements beyond acceptable levels. These conditions should aid the adoption of these systems by local farmers. Because of the importance of nutrients in soils of humid tropical regions, nutrient cycling studies in timber plantations and agroforestry systems, including those using valuable timber species, are needed to determine appropriate designs and management so that systems and practices can be promoted throughout the Amazon basin.

CONCLUSIONS

Though the total area in the Amazon Basin dedicated to plantation silviculture is relatively small compared to other managed systems, plantations have been encouraged as an alternative land use for the region, and their area has been increasing steadily over the last decade. Large scale plantations with fast-growing exotics planted in monospecific stands can deplete soil nutrients in a few rotations and often suffer from pest and disease problems. Most of the ecosystem nutrient losses occur during plantation establishment because of the removal of forest debris at clearing and soil disturbance during mechanized operation. Long-term productivity of short rotation plantations can generally be sustained with the application of fertilizers, in heavily subsidized systems much like those in southern Brazil and in several industrialized countries of the temperate region.

In comparison with natural forests, plantations tend to have a smaller standing biomass, and a smaller proportion of their biomass in the root system. Therefore, belowground nutrient cycling in plantations is potentially diminished compared with natural forests. Management guidelines generally focus on the aboveground component of plantations since the ultimate goal is the production of wood and other aboveground tree products. There is an important need to understand the role of roots and root symbionts in acquiring nutrients and water in plantations since they control carbon allocation patterns within plants.

Nutrient cycling in small-scale timber plantations in the Amazon has not been the subject of extensive study. However, using longer rotations of native species, or trees in combination with agriculture, these systems are a potentially more sound land use option for the region, as they can produce high quality timber, contribute to the restoration of degraded lands, and serve a rural development purpose. A considerable number of valuable timber species can be grown in plantations in the Amazon region, and a few silvicultural guidelines are available to aid in their establishment and management. Further information on the silvicultural management of preferred timber species would enhance the successful establishment of these plantations.

Choice of species for land rehabilitation should be based on their nutrient use efficiencies (NUE) and growth rates. Recent studies show the recycling abilities and ameliorating effects of indigenous species on soils and suggest guidelines for their use in economically and ecologically sound land use systems. Species with high NUE values can produce high biomass on poor sites, while species with low efficiencies would be preferred for nutrient recycling. Mixed-species designs can be more advantageous than tree monocultures for site nutrient rehabilitation if systems are planned to complement each species' nutrient demands and effects.

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Figure legends.

Fig 1. Total nutrient stocks and in plant biomass plus the soil in rain forest, newly planted *Pinus caribaea* (6 months old), *P. caribaea* and *Gmelina arborea* plantations at the end of the first rotation (9.5 and 8.5 years old, respectively), and second rotation *P. caribaea* (1.5 years old) at Jarí loss (Sanchez et al 1985). H = harvest loss from trees taken when clearing the rain forest for the plantations; L = leaching. Total nutrient stock is defined as the sum of all the nutrients in plant biomass (above-ground, litter, detritus, roots) plus total N, available P (extracted by the Mehlich method), and exchangeable K, Ca, and Mg in the top meter of the soil.

Fig. 2. Nitrogen and phosphorus use efficiency of 4-year-old stands of four indigenous timber species grown in pure plantation at La Selva Biological Station, Costa Rica.

Fig. 3. Nitrogen and phosphorus stocks in above ground biomass, forest-floor litter and roots of 4-year-old stands of four indigenous timber species grown in pure plantation at La Selva Biological Station, Costa Rica.

Fig. 4. Above-ground biomass and roots (0-15 cm soil depth) of 3-year-old stands of four

indigenous tree species: *Terminalia amazonia, Hieronyma alchorneoides, Albizia guachapele* and *Virola koschnyi*, grown in pure plots, and a mixture of the four species at La Selva Biological Station, Costa Rica.

Literature Cited

Alvim, P. 1989. Tecnologias appropriadas para a agricultura nos tropicos umidos. Agrotropica **1**:1, 5-26.

Bloomfield, J., K. A. Vogt, and D. J.Vogt. 1993. Decay rate and substrate quality of fine roots and foliage of two tropical tree species in the Luquillo Experimental Forest, Puerto Rico. Plant and Soil **150**:233-245.

Brienza-Junior, S., and J. A. G. Yared. 1991. Agroforestry systems as an ecological approach in the Brazilian Amazon development. Forest Ecology and Management **45**:319-323.

Bowen, G. D., and E. K. S. Nambiar. 1984. Nutrition of plantation forests. Academic Press, New York. 516 pp.

Bruenig, E. F. 1996. Conservation and Management of Tropical Rainforests. An IntegratedApproach to Sustainability. CAB International, Wallinford, Oxon, UK.

Bruijnzeel, L. A. 1984. Immobilization of nutrients in plantation forests of *Pinus merkusii* and *Agathis dammara* growing in volcanic soils in central Java, Indonesia. Pages 19-29 *in* A. Tajib and E. Pushparajah, editors. Proceedings of International Conference on Soils and Nutrition of Perennial Crops. Malaysian Soil Science Society, Kuala

Lumpur, Malaysia.

Bruijnzeel, L. A. 1989. Nutrient content of bulk precipitation in south-central Java, Indonesia. Journal of Tropical Ecology **5**: 187-202.

Carpanezzi, A. A., M. Kanashiro, I. A. Rodrigues, S. Brienza-Junior, and L. C. T. Marques. 1982. Informacoes sobre *Cordia alliodora* (R. & P.) Oken na Amazonia Brasileira. Unidade Regional de Pesquisa Florestal Centro Sul, EMBRAPA, Brazil. No. **10**:105-115.

Claussi, A., D. Marmillod, and J. Blaser. 1992. Descripción silvicultural de las plantaciones forestales de Jenaro Herrera. Instituto de Investigaciones de la Amazonia Peruana, Iquitos, Perú. 334 pp.

Drechsel, P. and W. Zech. 1993. Mineral nutrition of tropical trees. Pages 516-567 *in* L. Pancel, editor. Tropical Forestry Handbook, Volume 1. Springer-Verlag, New York.

Evans, J. 1992. Plantation forestry in the tropics. Tree planting for industrial, social, environmental, and agroforestry purposes. 2nd. ed. Clarendon Press. Oxford. England. 403 pp.

Fearnside, P. M., and J. M. Rankin. 1980. Jarí and development in the Brazilian Amazon. Interciencia **5**:146-156.

Fearnside, P. M. 1989. The charcoal of Carajas: a threat to the forests of Brazil's eastern Amazon region. Ambio **18**:141-143.

Fearnside, P. M. 1990. Predominant land uses in Brazilian Amazonia. Pages 233-251 *in* A. B. Anderson, editor. Alternatives to Deforestation: Steps Towards Sustainable Use of the

Amazon Rain Forest. Columbia University Press, New York, USA.

Fearnside, P. M. 1995. Global warming response options in Brazil's forest sector: comparison of project-level costs and benefits. Biomass and Bioenergy **8**: 309-322.

Ferraz, J. B. S. 1993. Soil factors influencing the reforestation on mining sites in Amazonia. Pages 47-52 *in* H. Lieth and M. Lohman, editors. Restoration of tropical Forest Ecosystems. Kluwer Academic Publishers, The Netherlands.

Greaves, A. 1979. *Gmelina*: large scale planting, Jarilandia, Amazon basin. Commonwealth Forestry Review. **58**:267-269.

Groulez, J. 1975. Conversion to plantation forestry in tropical rain forest. Bois et Forets des Tropiques 162:3-24

Guariguata, M. R., Rheingans, R., and Montagnini, F. 1995. Early woody invasion under tree plantations in Costa Rica: implications for forest restoration. *Restoration Ecology* **3**:252-260.

Hoyos, J. B, F. J. Bruseke, A. K. O. Homma, J. B. Veiga, N. M. Silva, and W. L. Overal. 1992. Desenvolvimento sustentavel: um novo caminho? J. B. Hoyos, editor. Serie Universidade e Meio Ambiente. Universidade Federal do Para, Nucleo de Meio Ambiente, Belém, Brazil. 119 pp.

Irion, G. 1981. Holzplantage im Urwald?. Naturwissnschaften **68**:133-138.

Johnson, N. E. 1976. Biological opportunities and risks associated with fast-growing plantations in the tropics. Journal of Forestry **74**:206-211.

Jorgensen, J. R., and C. G. Wells. 1986. Tree nutrition and fast-growing plantations in developing countries. International Tree Crops Journal **3**:225-244.

Knowles, O. H., and J. A. Parrotta. 1995. Amazonian forest restoration: an innovative system for native species selection based on phenological data and field performance indices. Commonwealth Forestry Review **74**:230-243.

Lugo, A. E. 1992. Comparison of tropical tree plantations with secondary forests of similiar age. Ecological Monographs **62**: 1-41.

Lundgren, B. 1980. Plantation forestry in tropical countries--physical and biological potentials and risks. Swedish University of Agricultural Sciences. International Rural Development Centre. Rural Development Studies 8. Uppsala. 134 pp.

Magalhaes, L. M. S., W. E. H. Blum, and N. P. Fernandes. 1986. Crescimento de *Eucalyptus deglupta* Blume em solos de diferentes texturas. Características edáfico-nutricionais de plantios florestais na regiao de Manaus. 1. Acta Amazonica. **16-17**:509-521.

McNabb, K., J. Borges, and J. Welker. 1994. Jarí at 25. An investment in the Amazon. Journal of Forestry **92**:21-26.

Montagnini, F., K. Ramstad, and F. Sancho. 1993. Litterfall, litter decomposition and the use of mulch of four indigenous tree species in the Atlantic lowlands of Costa Rica. Agroforestry Systems **23**:39-61.

Montagnini, F. 1994. Rehabilitating forest ecosystems in the humid tropics: Recent experiences from Latin America. Pages 224-234 *in* Proceedings from IUFRO International Symposium on Growth and Yield of Tropical Forests. Sept. 26-Oct. 1,

1994. Tokyo University of Agriculture and Technology. Fuchu, Tokyo, Japan.

Montagnini, F., and F. Sancho. 1994. Above-ground biomass and nutrients in young plantations of four indigenous tree species: implications for site nutrient conservation. Journal of Sustainable Forestry 1:115-139.

Montagnini, F., A. Fanzeres, and S. G. da Vinha. 1994. Studies on restoration ecology in the Atlantic Forest region of Bahia, Brazil. Interciencia **19**:323-330.

Montagnini, F., and R. Mendelsohn. 1996. Managing forest fallows: improving the economics of swidden agriculture. Ambio **26**(2): 118-123.

Montagnini, F., E. González, R. Rheingans, and C. Porras. 1995. Mixed and pure forest plantations in the humid neotropics: a comparison of early growth, pest damage and establishment costs. Commonwealth Forestry Review **74**:306-314.

Nambiar, E. K. S. 1984. Plantation forests: their scope and perspective on plantation nutrition. Pages 1-15 *in* G. D. Bowen and E. K. S. Nambiar, editors. Nutrition of Plantation Forests. Academic Press, New York.

Nepstad, D., C. Uhl and E. A. S. Serrao. 1991. Recuperation of a degraded Amazonian landscape: forest recovery and agricultural restoration. Ambio **20**:248-255.

Palmer, J. R. 1977. Forestry in Brazil-Amazonia. Commonwealth Forestry Review **56**:115-130.

Pedroso, L. M. 1973a. Informacoes sobre o atual comportamento de especies exoticas na regiao do Medio Amazonas. SUDAM-Document **5**:21-31. Superintendencia do Desenvolvimento da Amazonia (SUDAM), Belém, Pará, Brazil.

Pedroso, L. M. 1973b. Alguns aspectos sobre o florestamento e reflorestamento na Amazonia. SUDAM Document **5**:35-49. Superintendencia do Desenvolvimento da Amazonia (SUDAM), Belém, Pará, Brazil.

Perry, D.A., and J. Maghembe. 1989. Ecosystem concepts and current trends in forest management: time for reappraisal. Forest Ecology and Management **26**:123-140.

Pitcher, J. A. 1976. Forestry development and research. Brazil. A tree improvement programme for Amazonia. FAO-Report. 1976., No. FO: DP/BRA/71/545 Technical Report 3. 42 pp.

Rankin, J. M. 1985. Plantations. Pages 379-387 *in* G. T. Prance and T. E. Lovejoy, editors. Key Environments. Amazonia. Pergamon Press, New York.

Russell, C. E. 1987. Plantation forestry. Case study No. 9: The Jarí project, Pará, Brazil. Pages 76-89 *in* C. F. Jordan, editor. Amazonian Rain Forests. Ecosystem Disturbance and Recovery. Ecological Studies 60. Springer-Verlag, New York.

Sánchez, P. A., C. A. Palm, C. B. Davey, L. T. Szott, and E. C. Russell. 1985. Tree crops as soil improvers in the humid tropics? Pages 327-350 *in* M.G.R. Cannell and J.E. Jackson, editors. Attributes of trees as crop plants. Institute of Terrestrial Ecology, Natural Environmental Research Council, Abbots Ripton, Huntingdon, England.

Silva, N. M, and Uhl, C. 1992. Forest management for timber production: A sustainable use for the Brazilian Amazon. Anais da Academia Brasileira de Ciencias **64** (suppl. 1):89-95.

Sombroek, W. G. 1992. Strategies for protection of soil fertility in the Amazon Region.

Pages 43-46 *in* H. Jaenicke and P. Flynn, editors. Sustainable land use systems and human living conditions in the Amazon region: proceedings of a meeting held in Bonn, Germany, 1- 2 November 1991. Commission of the European Communities, Luxembourg.

Soto, G., Alvarado, A. y Montagnini, F. 1996. Encalado de especies forestales nativas. p. 144 *in*: F. Bertsch, W. Badilla, y E. Bornemisza, editors. Suelos: ¿Puede la Agricultura Sostenible ser Competitiva?. Memorias, X Congreso Nacional Agronómico y de Recursos Naturales/II Congreso de Suelos. Volumen III. Ed. Universidad Estatal a Distancia/Ed. de la Universidad Nacional. San José, Costa Rica.

Spangenberg, A. 1994. Nahrstoffvorrate und exporte von *Eucalyptus urograndis*, Plantagen in Ostamazonien (Jari), Brasilien. Gottingen Beitrage zur Land und Forstwirtschaft in den Tropen und Subtropen No.93. Gottingen, Germany; Institut fur Pflanzenbau und Tierhygiene in den Tropen und Subtropen.

SUDAM. 1979. Caracteristicas silviculturais de especies nativas e exoticas dos plantios do Centro de Technologia Madeireira - Estaçâo Experimental de Curua-Una. Superintendencia do Desenvolvimento da Amazonia, Belém, Brazil. 351 pp.

Uhl, C., D. Nepstad, J. M. Cardoso da Silva, and I. Vieira. 19991. Restauraçâo da floresta em pastagems degadadas. Ciencia Hoje 13:22-31.

Vogt, K., H. Asbjornsen, A. Ercelawn, F. Montagnini, and M. Valdes. 1997. Roots and mycorrhizas in plantation ecosystems. *in* E. K. S. Nambiar and A. G. Brown, editors. Better Management of Soil, Water and Nutrients in Tropical Plantation Forests. In press.

Wadsworth, F.H., 1983. Production of usable wood from tropical forests. Pages 279-288 *in*: F.B. Golley, editor. Tropical Rain Forest Ecosystems. Structure and Function. Ecosystems of the World 14A. Elsevier, New York,

Wang, D., Bormann, F. H., Lugo, A. E. and Bowden, R. D. 1991. Comparison of nutrient-use efficiency and biomass production in five tropical tree taxa. Forest Ecology and Management **46**:1-21.

Yamazaki, S., Taketani, A., Fujita, K., Vasques, C. P., Ikeda, T. 1990. Ecology of *Hypsipyla grandella* and its seasonal changes in population density in Peruvian Amazon forest. Japan Agricultural Research Quarterly **24**:2, 149-155.

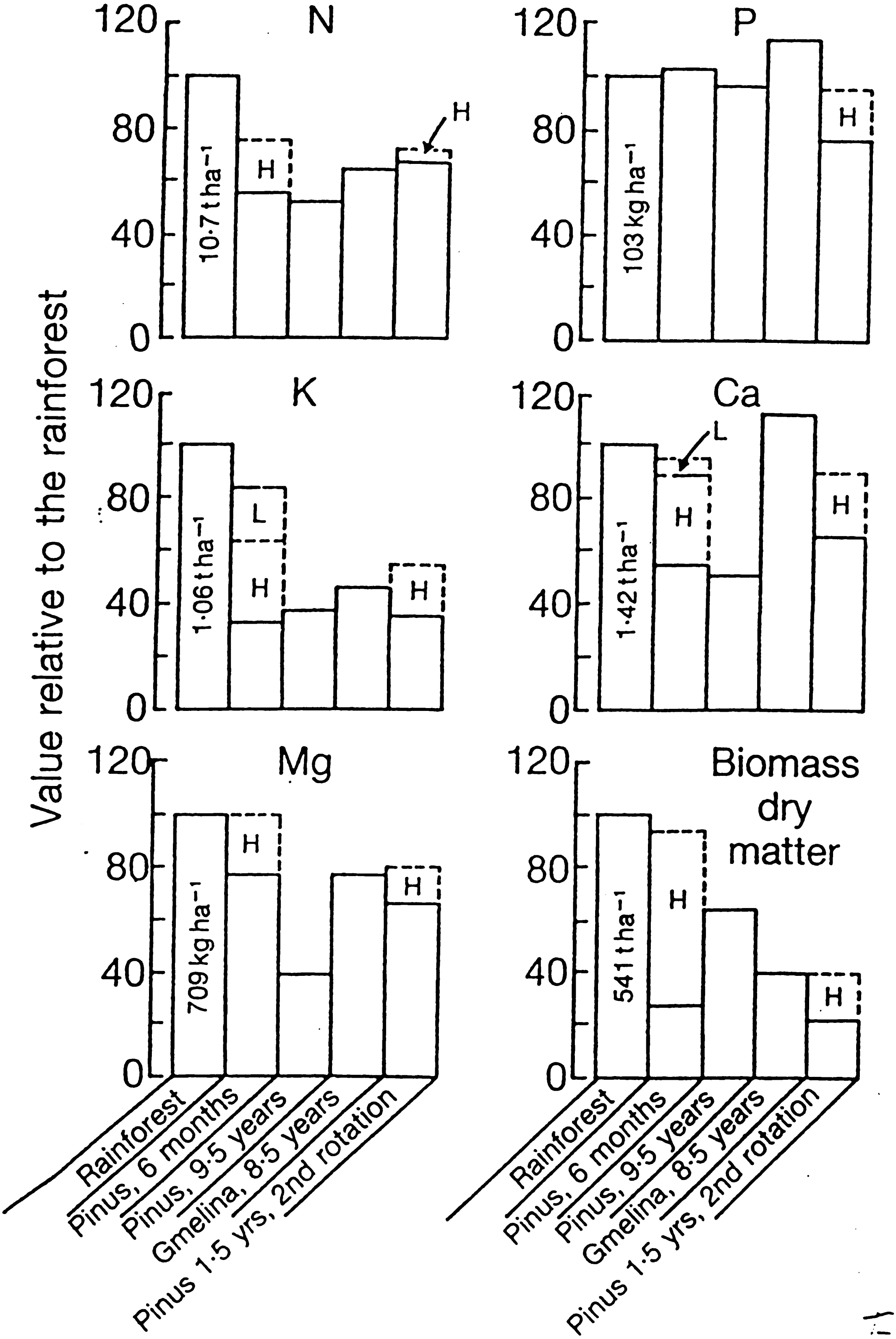
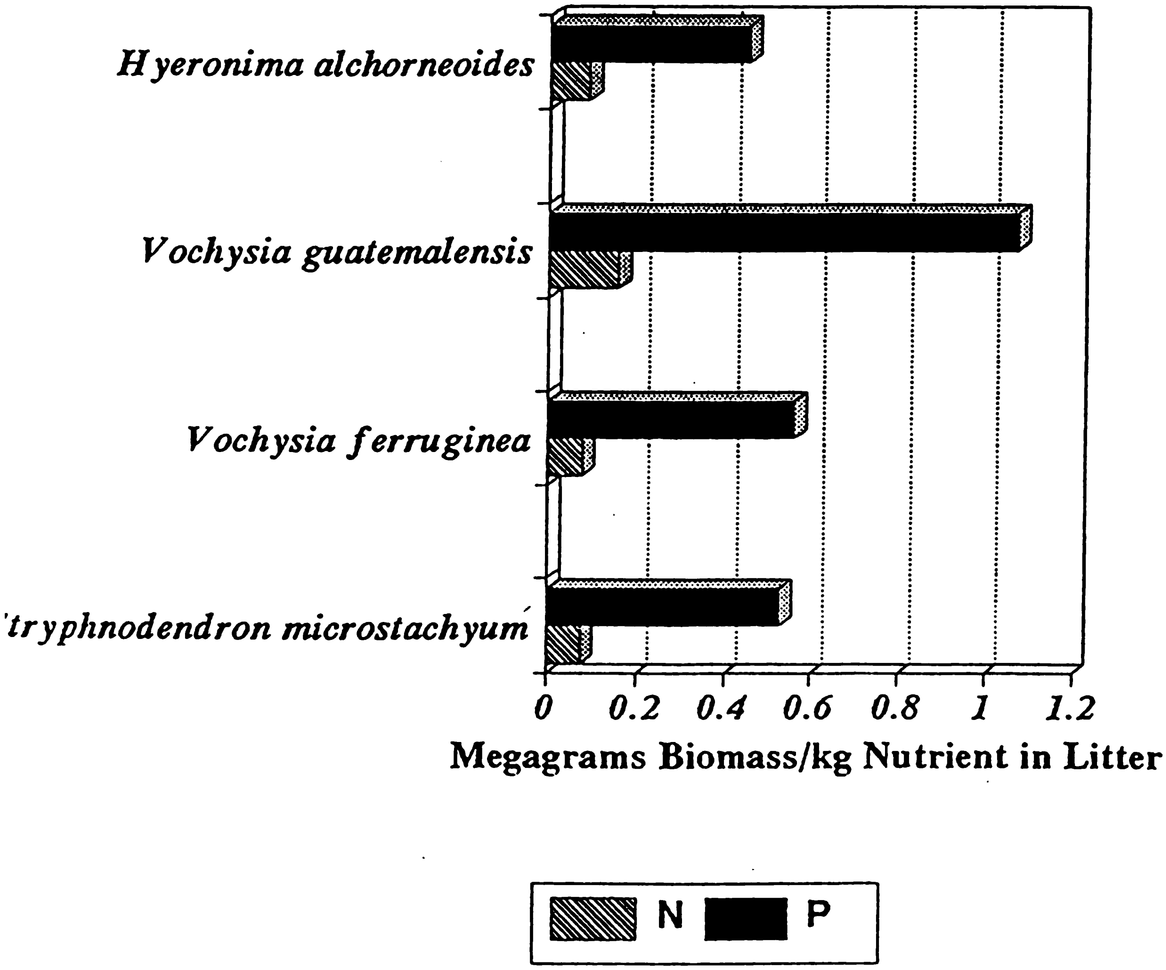

Value relative to the rainforest
N
10·7 t ha⁻¹
H
H
P
103 kg ha⁻¹
H
K
1·06 t ha⁻¹
L
H
H
Ca
1·42 t ha⁻¹
L
H
H
Mg
709 kg ha⁻¹
H
H
Biomass dry matter
541 t ha⁻¹
H
H
0
40
80
120
Rainforest
Pinus, 6 months
Pinus, 9·5 years
Gmelina, 8·5 years
Pinus 1·5 yrs, 2nd rotation

Fig 1

Phosphorus and Nitrogen Use Efficiency



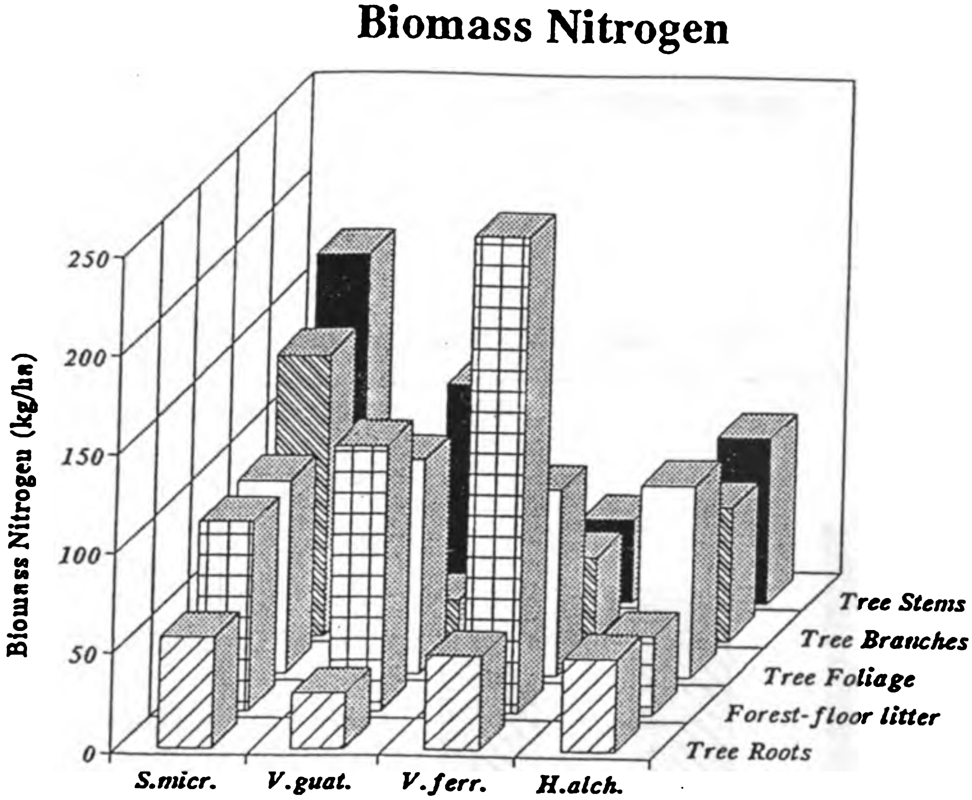
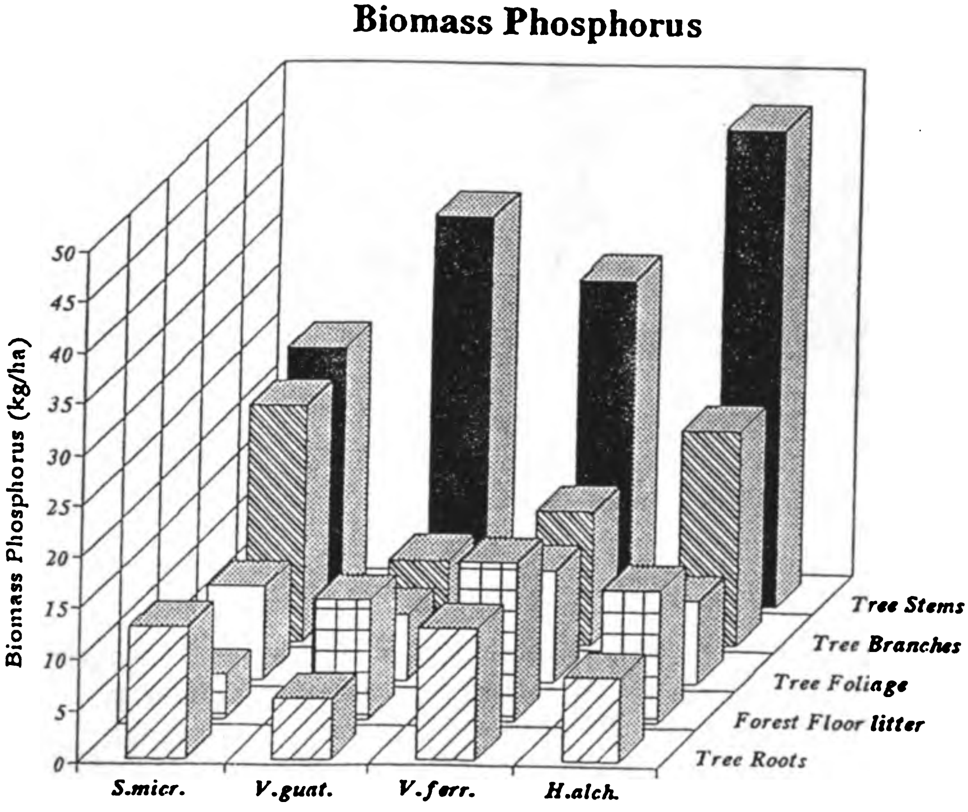

Biomass Nitrogen
Biomass Nitrogen (kg/ha)
250
200
150
100
50
0
S.micr.
V.guat.
V.ferr.
H.alch.
Tree Stems
Tree Branches
Tree Foliage
Forest-floor litter
Tree Roots

Fig 3


Biomass Phosphorus
Biomass Phosphorus (kg/ha)
50
45
40
35
30
25
20
15
10
5
0
S.micr.
V.guat.
V.ferr.
H.alch.
Tree Stems
Tree Branches
Tree Foliage
Forest Floor litter
Tree Roots

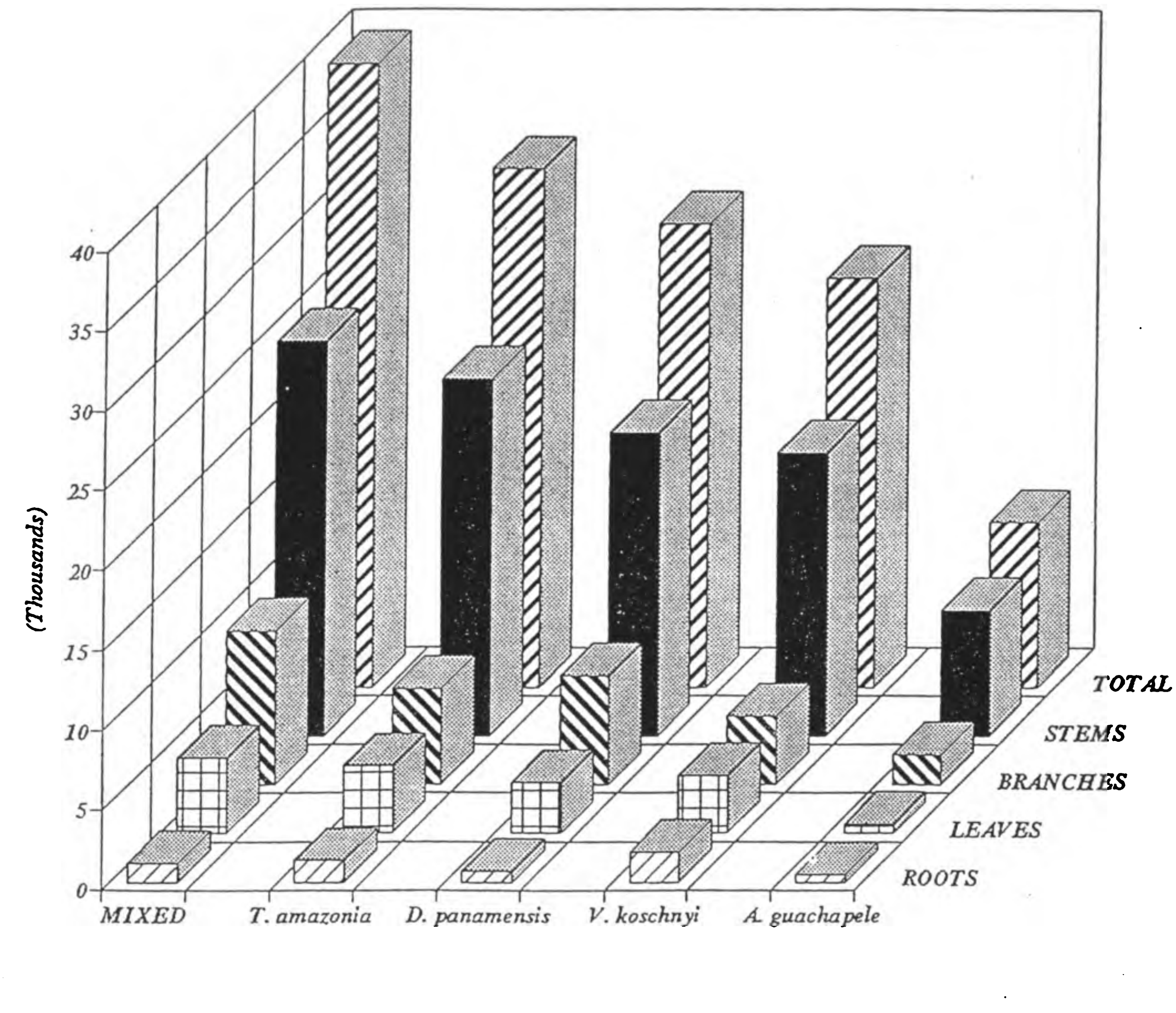

(Thousands)
40
35
30
25
20
15
10
5
0
MIXED
T. amazonia
D. panamensis
V. koschnyi
A. guachapele
TOTAL
STEMS
BRANCHES
LEAVES
ROOTS

Fig 4

Nutrient cycling and nutrient use efficiency in agroforestry systems

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INTRODUCTION

In humid tropical regions, soil nutrients are key factors influencing plant productivity and long-term sustainability of a production system. It has long been maintained that nutrient losses and increased weed invasion are the principal contributors to abandonment of fields of annual grains or root crops after 2-4 years of use (Watters 1971, Van Wambeke 1992, Bandy et al. 1993). Increased weed infestation of agricultural fields after nutrient loss results from the greater ability of weeds to take up scarce nutrients relative to most annual or root crops, thus out-competing these plants in the use of nutrients and other resources.

Many "weed" species are perennials and woody species, whose ability to compete depends on a variety of mechanisms associated with roots, woody stems, and litter production. A key to increasing the sustainability of agricultural systems is to incorporate species that have these nutrient-conserving capabilities, while at the same time producing a crop that has economic and/or subsistence value. Many indigenous peoples have devised such systems through trial and error, and this chapter presents examples from the Kayapó in Brazil, and from other traditional systems from Asia and Africa.

The importance of nitrogen fixing species in agroforestry systems is widely recognized. In this chapter, we discuss this and other effects of woody species on soil fertility, the interactions between species of woody plants, and the significance for design of agroforestry systems. The concept of nutrient use efficiency by plants is brought forward as a potential tool to aid in system design and management. Finally, we stress the need for initial economic incentives to allow for system establishment and to increase the adoptability of sound agroforestry techniques by local farmers.

NUTRIENT DYNAMICS IN AGROFORESTRY SYSTEMS

Examples of Traditional Sustainable Agroforestry

Shifting agriculture has been practiced in the tropics for many centuries. Today, shifting (also called "swidden", "slash-and-burn") agriculture is the predominant land-use practice on about 30% of the arable soils of the world and provides sustenance for an estimated 300 million of the world's poorest people (Andriesse and Schelhaas 1987). Traditional shifting agriculture uses long forest fallows between short periods of farming. Long fallows make the traditional technique sustainable but also require extensive amounts of land. When land is scarce, farmers shorten forest fallows and lengthen agricultural periods, resulting in soil nutrient depletion, reduced crop yields and increased weed invasion.

Similar patterns are reported in the tropics worldwide, in spite of differences in ecological and socioeconomic conditions. For example, the "jhum" cycle is a system of shifting agriculture widely practiced by about 30 million people in the hilly, subtropical region of northeast India (Ramakrishnan 1992). A variety of versions of jhum agriculture are practiced by the different tribes in cycles that range from 10 to 30 years. However the shortening of the jhum cycle to 4-5 years during recent times has led to concerns about the resulting soil degradation and yield declines in a pattern much like that experienced in lowland humid regions of Latin America and Africa.

An Example from the Kayapó in Brazil

There are numerous examples of agricultural practices of indigenous peoples, or of pioneers such as the Amazonian caboclos, that use trees to maintain or restore soil fertility without hemical fertilizers (Anderson 1990, Gómez-Pompa and Kaus 1990, Subler and Uhl 1990, Balée 992, Lescure et al. 1992, Nations 1992, Jordan 1995). One well-documented example is that of ıe Kayapó in Brazil (Posey 1982). The Kayapó live today on a 2.5 million hectare reserve in the ingú River Basin in the Amazon region. Although the Kayapó are nomads for part of the year, ultivation of plants for food and medicine is an important part of their culture. Cultivation begins vith the clearing of a circular field. Trees are felled so that the fallen stems radiate outward, and he bulk of the forest canopy biomass ends up near the perimeter of the circle. Root crops such as weet potatoes or yams (*Dioscorea* spp.), taro (*Colocasia esculenta*) and manioc (*Manihot sculenta*) are planted in open corridors left between the fallen trees. The crops are already ooted and growing before burning occurs.

Burning is carefully managed. Tribal elders agree upon an appropriate day when winds are ninimal and the fields will burn thoroughly but not too quickly. The farmers begin burning the iles of dried debris one at a time. A protracted burn minimizes the heat, so that the root crops will lose their green tops but not their viability. These pre-burn crops are given a head start on weeds that will establish in the ash.

Papaya, bananas, cotton, urucú (*Bixa orellana*), and tobacco, which require a high quantity of nutrients, are planted on the outer margins of the field, where ash concentrations are highest. A few weeks after the burn, the farmers gather up unburned sticks and limbs for a second fire. In the resulting piles of ash, other high-nutrient requiring plants like beans, squash, and melons are planted.

The fields of the Kayapó last for many years. Sweet potato and yam bear in fields that are four or five years old. Bananas and urucú, and domesticated varieties of a large vine-like plant called "kupa" commonly continue to bear edible leaves and stalks for 8 to 12 years, and some fields that are 40 years old still yield edible kupa.

Many plants useful to the Kayapó establish naturally in the old fields. Some of these spontaneously colonizing plants have important medicinal values, and others provide seeds, berries, and roots for food. Some of the colonizing plants bear fruits that make excellent fish bait. Others attract animals or birds. The animals drawn to the leafy and bushy plants in these sites are easier to hunt than those inhabiting the canopy of the high forest.

Because the Kayapó understand this process and take advantage of the species that sequentially occupy a site, they do not need to continually seek new forest to cut and burn. After many years, when an old site develops into a closed forest, it can be cut and used again, with no long term degradation of the site.

Kayapó practices contrast with the shifting cultivation in the Amazon carried out by colonists from southern and northeastern Brazil. The latter depend mainly upon crops such as corn, rice, and cassava which grow well for only two or three years. When yields decline, the colonists abandon the fields and clear new forest.

Homegardens: Traditional Low- Scale, Low-Input Agroforestry

Homegardens are systems for the production of subsistence crops for the gardener and family, with or without the addition of cash crops. They can be located immediately surrounding the home or slightly further away, but still near the residential area. It is claimed that homegardens originated in prehistoric times when hunters and gatherers accidentlaly dispersed seed of highly valued fruit trees close to their homes (Soemarwoto 1987). In the near east, homegardens are documented in paintings dated 3,000 years BC, and the practice continues in modern times. There are several well documented examples from Java, and they are also common in other parts of Indonesia, and in Malaysia, India, and in countries of Africa and Latin America. They hold great species diversity with many life forms varying from climbers to tall trees and vines, creating a forest-like, multistorey canopy structure. The canopies of most homegardens consist of 2-5 layers. Usually there are no rows, blocks or definite planting distances among components. Chemical fertilizers are generally not used; dung, household wastes and pruning residues are used instead. The use of species with anti-pest properties is also a widespread practice that decreases the need for chemical pesticides (Fernandes et al. 1989, Michon et al. 1989). They generally have stable yields and great variety of products, allowing continuous or repeated harvests during the year under a low-input system.

In west Java, the average size of homegardens is <0.1 ha, with an average of 19.0 and 24 species per garden in the dry and wet seasons, respectively. Size of homegardens decreases with altitude with highest number of species occurring at 500-1000 m. Poor people tend to grow more staples, vegetables and fruits, well-off people tend to grow more ornamentals and high-economic value cash crops. More subsistence crops are grown in remote areas, more cash crops are grown near cities. Culture and tradition influence composition: e.g., more medicinal plants are found in west Java, while tobacco and coffee are more commonly grown in Muslim districts of southern Ethiopia; animals are found in most gardens but pigs are not found in Muslim homegardens; in west Java with intense rains fishponds are usually present (Soemarwoto 1987).

Homegardens can be sustainable production systems, however this is true under low-input and low-yield conditions. For example, the homegardens of the Chagga, in Mt. Kilimanjaro

(Tanzania) represent ecologically sustainable land-use systems, but their productivity is relatively low and needs to be increased if they are expected to support larger populations (Fernandes et al. 1989). Migration of youngsters to urban areas has disrupted the traditional transmission of the knowledge and experience required for the successful management and perpetuation of the complex multicropping system. Availability of fertilizers has decreased the need for organic manures, thus greatly reducing labor inputs in homegardens and therefore reducing nutrient recyling processes. If homegardens are to be used for raising the standard of living of people to satisfactory levels, the question arises whether the yield and the income can be significantly increased without sacrificing their sustainability.

Nutrient Mobilization and Losses in Shifting Agriculture

Scientists have long believed that sharp decreases in growth of annuals like corn and rice after two or three years of shifting cultivation were due to nutrient losses such as leaching of calcium and potassium and volatilization of N. However, results from the Man and the Biosphere project at San Carlos de Río Negro in Venezuela (Jordan 1989) suggested that during the first 2-3 years of cultivation of a cleared forest, only a very small proportion of the nutrient stocks was actually lost through leaching (Figs. 1, 2). The decrease in production was instead due to binding of formerly labile phosphorus by iron and aluminum in the mineral soil, thus rendering the P unavailable to crop plants.

In undisturbed forests of the region, P appears to be readily available to the trees (Jordan 1989). Even after cutting and burning the forest, and during the first few years of cultivation, most of the soil P was kept mobile because it was chelated to Fe and Al by organic acids leached from decomposing organic matter on the soil surface. After the site was cut and burned, and as the humus and litter gradually disappeared during the three years of cultivation, liberation of organic acids decreased and an increasing proportion of P was bound in the soil. By the end of the third year, all of the humus, and most of the tree trunks were gone. The study concluded that ack of labile P caused diminishing crop productivity, and that the conversion of P from labile to bound states was due to the disappearance of humus and organic matter on the soil surface.

Despite binding of P in the soil, secondary successional vegetation invaded the site, and by the fifth year stocks of Ca, K, Mg, and N began to decline (Figs. 1, 2). There were no detectable changes in total ecosystem stocks of P during the experiment. However, there was an increase in P in biomass as the successional forest became established. Apparently, successional plant species were able to take up bound P from the soil. This P was probably in Fe- and Al-bound fractions that were unavailable to the crop plants.

What is the mechanism through which woody vegetation is able to take up the P unavailable to crops? One possibility is excretion of piscidic acid[1] from the roots (Ae et al. 1990), or leaching of citric and malic acids from the decomposing leaf litter of the trees (Han 1989). These organic acids can replace the P bound by Fe and Al the clay, liberating the P and rendering it soluble and readily available for uptake. Annual plants may not have these P recycling mechanisms, or crop plants bred for productivity may have lost the capability of taking up these forms of P (Chapin 1980, 1983).

Mobilization of bound P by woody plants accounts for sustainability of agroforestry systems such as those of the Kayapó. The tree crops are established soon after clearing and burning,

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[1] Piscidic acid = (p-hydroxy benzyl) tartaric acid

before the tree trunks, branches, and organic matter in the upper soil horizons are completely decomposed. Because the new trees are already producing litter before the remains of the old ones disappear, the production of organic acids is not interrupted, and the P is kept in a labile state.

This suggests that it would be desirable to start an agroforestry system immediately after clearing a fallow or primary forest. For example, establishment of rubber trees (*Hevea brasiliensis*) in the Brazilian Amazon region has been highly successful under the partially opened canopy of a secondary forest (Mesquita 1995). At the time of planting, a thick layer of litter and humus on the forest floor supplied nutrients, improved the microclimate, prevented erosion, and was an energy source for soil microorganisms that improved the physical and chemical properties of the soil.

Unfortunately, many agroforestry systems are established on sites that have been cropped or kept in pasture for many years. In such sites, nutrient status of the soils is low. Figs. 1 and 2 show that in the experimental plots at San Carlos de Río Negro, nutrient loss continued even after cultivation was abandoned after three years, and nutrient recovery did not begin until year five. Apparently in this system with high rainfall (3600 mm/year) and low cation exchange capacity, it took a couple of years for fallow vegetation to cover the site and reestablish nutrient cycling mechanisms that lead to recovery. By the time the reversal began, nutrient stocks were only a fraction of those in the ecosystem when cultivation started.

Managed Forest Fallows

Improved fallows have been proposed as a management alternative to shifting cultivation in he tropics (Nair 1990, Kass et al. 1993). Traditionally shifting cultivators have encouraged the resence of certain tree or herb species in fallows to restore site fertility, suppress weeds and ncrease economic yields. Several types of traditional "enriched" fallows have been described, ncluding those techniques involving planting or tending selective species for fruit, fuelwood or imber in fallow fields or secondary forests which are maintained by local populations over long eriods of time, for local consumption, for markets or both (Kass et al. 1993, Denevan at al. 1984, Padoch et al. 1985, Padoch and De Jong 1987, Raintree and Warner 1986, Unruh 1990, Deal Amo and Ramos 1993, Sips 1993). Some of these systems produce crops for local onsumption and for a regional market, providing substantial cash income for many farmers (Padoch et al. 1985).

The use of managed fallows based on a single species is quite widespread in the Americas, ccurring from subtropical areas of Brazil to highland regions of Central America (Kass et al. 1993, Sips 1993). These systems include both biologically and economically enriched fallows. Some of the economically enriched fallows of the Amazon require more intensive management by which certain trees are protected during clearing or planted during the cropping period and maintained during the fallow (Padoch and De Jong 1987). In the planted fallows, one or more species with biological or economic value are introduced to shorten the fallow regeneration period or increase its economic value (Szott et al. 1991, Vergara 1987).

For example, in an experimental fallow system in the Peruvian Amazon, selected soil-improving tree species were planted in abandoned shifting agriculture fields (Szott et al 1991). The species planted were acid-tolerant woody legumes, *Cajanus cajan* and *Inga edulis*. Two years after planting, the total ecosystem levels of Mg and Ca declined, while total N and K increased, and the levels of P increased after 4.5 years. In these experiences, weed control was achieved more rapidly with herbaceous species (*Pueraria phaseoloides, Desmodium ovalifolium*), however good suppression of weeds was also eventually obtained by the woody legumes.

Experiences such as those described by Szott et al. (1991) are relevant in tropical regions worldwide where land becomes scarce and the fallows are not long enough to restore soils to their productive capacity. For example, *Gliricidia sepium*, a N-fixing tree native from the Neotropics and broadly used there as shade for coffee, for living fences and as a common component of homegardes, is currently a popular fallow tree in some parts of lowland rainforest regions of western Nigeria (Adejuwon and Adesina 1990). Its poles are staked as support for training yam vines, and as the species propagates vegetatively, the staked poles coppice within a short time and at the end of the cropping cycle they become part of the fallow vegetation. Compared to natural fallows in which the development of trees is random, the progress of the cultivated fallows of *G. sepium* leads to greater organic matter build up and increases in nitrate-nitrogen and potassium concentrations in the soils. Other leguminous trees that are also becoming popular in the region such as *Leucaena leucocephala* or *Derris indica* could also be used with similar results (Adejuwon and Adesina 1990).

Other improved fallow systems rely more on the introduction of valuable species in the fallow period, in combination with other species that have soil restoring capacity. For example, in a traditional shifting cultivation system in the lowlands of Papua New Guinea, the cropping cycle is usually 18 months, consisting on mixed food crop gardens with yams, bananas, taro, sugar cane and some fruit trees. The fallow cycles last up to 30 years. Robusta coffee, a cash crop component, has been added to the fallows in some areas since the 1950s. The coffee is terplanted with *Leucaena leucocephala* as shade, and food crops are planted in the stablishment phase. This seems to be a promising enriched fallow alternative, and the local llow gardeners appear to be willing to take on such innovations (Allen 1985).

utrient Dynamics in More Recent Agroforestry: Alley Cropping

In the mid-1980s, considerable research focused on the development of low-input echnologies for sustainable food production by small-hold farmers. Results from this research uggest that in situations where planted fallows are not feasible because land is scarce, techniques uch as alley cropping and the application of mulch (green covers) may become practical lternatives (Kang and Wilson 1987, Kang et al. 1990). In alley cropping, annual crops are grown etween hedgerows of preferably N-fixing leguminous shrubs and trees, which are periodically runed to prevent shading of companion crops. The prunings can then be used as mulch and reen manure to improve soil fertility and produce high-quality fodder. Alley cropping is egarded as an improved bush-fallow system with the following potential advantages: 1) Cropping nd fallow phases are combined; 2) Cropping periods are longer, and land is used more ntensively; 3) Soil fertility is effectively maintained with the use of species selected for that purpose; and 4) The need for external inputs is reduced (Kang and Wilson 1987).

In areas of Nigeria and in other forest-savanna transition regions of Africa with non-acid soils, results of field and on-farm trials have shown that alley cropping with corn, cowpea, rice and cassava between hedgerows of *Leucaena leuocephala* and *Gliricidia sepium* allowed higher levels of crop production than monocultures (Kang and Wilson 1987). Cowpea and rice showed no significant increase in yield in comparison with monocultures, but when planted in alley cropping with *Leucaena*, they did not respond to N fertilization, indicating that the N supply from prunings was adequate, and additional fertilizers were not necessary.

When used in regions of low soil fertility, the addition of green manure from the trees grown in the hedgerows can significantly increase the yield of the crops grown in the alleys. For example, in western Kenya, experiments carried on red, acid soils showed that maize and bean yields were higher when grown in alley cropping with *Leucaena leucocephala*, *Cajanus cajan* and *Sesbania sesban.* These responses were still significant in the third testing season (Onim et al. 1990).

However, in some instances although the tree prunings can add substantial amounts of nutrients and organic matter to the soil, these quantities may not be enough to reach the levels required by the associated crops. For example in experiments conducted in Ibadan, Nigeria, prunings from *Gliricidia sepium* hedgerows yielded the highest N while prunings from *Cassia* spp. yielded the highest organic matter. N supplementation was needed to optimize the yield of maize, with higher amounts required in *Flemingia* alleys than in *Gliricidia* or *Cassia* alleys (Yamoha et al. 1986).

Agroforestry techniques such as alley cropping are better able to increase available stocks of nutrients than monocultures. The following examples illustrate the contributions of this agroforestry system to P and N dynamics. Fig. 3 compares total labile P in a replicated alley-cropping system (*Albizia julibrissin* as the hedge, *Sorghum bicolor* as the grain crop) on an Ultisol in the state of Georgia, U.S.A., with plots without alleys that otherwise had received the same treatment. Both alley-cropped and monocultured sorghum were previously green-manured in summer with velvet bean (*Mucuna deeringiana*) and in winter with crimson clover (*Trifolium* *incarnatum*). There was a gradual increase in labile P between the two systems, but even by the third year, sorghum production in the agroforestry system was not greater than that in the monoculture (Matta-Machado and Jordan 1995).

This study was carried out on soil degraded by a century of cotton and soybean farming. While agroforestry can increase nutrient stocks compared to non-agroforestry plots, this increase comes slowly. A better strategy, if it is affordable, might be to initially fertilize the agroforestry system to enable faster production. An even better strategy, if a suitable site is available, is to start the system following a fallow. When an agroforestry system begins with high levels of nutrients, the system has a higher chance of maintaining itself.

Research at the Center for Tropical Agriculture Research and Training (CATIE) in Turrialba, Costa Rica has addressed the role of N in alley cropping annual crops with trees used in agroforestry throughout the humid tropics. Results of long term experiments with maize grown with *Erythrina poeppigiana* and *Gliricidia sepium* hedgerows showed that after seven years, maize productivity and N uptake were more than twice as high in alley cropping with either species than in monoculture (Haggar et al. 1993). Higher rates of soil N mineralization in the alley cropping systems led to faster maize establishment in comparison with the single crop. These higher rates of soil N mineralization resulted from the build up of readily mineralizable organic N compounds in the soil after seven years of tree mulch application. The long term accumulation of mineralizable N was more important than the synchrony of mulch N release and crop uptake in determining the higher yields and N uptake by maize in the alley cropping system compared with the sole crop. In spite of higher yields, total recovery of mulch N by the maize in a single year was only about 10 kg/ha, with most of it taken up during the first two months following planting; however this initial effect led to faster establishment of maize in the alley crop. This again points to the need for long-term studies that assess the benefits of alley cropping to crop yields. This also serves to stress that early results may not be outstanding, and that other external inputs may be necessary initially to ensure the system's successful establishment.

The use of alley cropping can also help ameliorate the detrimental effects caused by certain soil management practices. For example, experiments in Ibadan, Nigeria have shown overall nutrient declines in soils through a four year cropping cycle, with the highest depletion of soil nutrients in plow-till systems and the least severe in *Leucaena* based systems (Lal 1989).

In alley cropping systems sometimes competition between trees and crops can significantly reduce yields by the crop (Haggar 1994). Other research on non-acid, alluvial soils in Yurimaguas, in the Peruvian Amazon, showed that rice yield reductions from light competition were evident up to 1.5 meters from the hedgerows of all tree species tried (*Inga* spp., *Leucaena* spp. and *Erythrina* spp.), with the greatest decrease in yield found with *Leucaena* hedgerows (Salazar et al. 1993). Weed control was better achieved with the slowly decomposing *Inga* mulch, but rice yields (at a distance >1.5 m from the hedgerows) were higher with *Leucaena* and *Erythrina*.

Species choice strongly influences the success and overall applicability of alley cropping techniques. For example, many plant species contain allelochemicals that suppress weeds and other plants. Allelopathic interactions are useful when the suppressed plants are considered weeds, but care must be exercised when the mulch is applied to crop plants (Regnier and Janke 1990). Finally, on very acid soils with high aluminum saturation, some of the tree species preferred for alley cropping, such as *Leucaena* spp. and *Gliricidia* spp., do not grow well, and hey have to be replaced by other species more adapted to those conditions (e.g., *Calliandra* spp., *assia* spp., *Inga* spp., *Flemingea* spp., or *Paraserianthes* spp.).

Iodified Traditional Systems: Trees Used for Shade of Perennial Crops

At CATIE, Costa Rica, research has long intended to modify the predominant traditional ystems of the region--coffee or cacao with shade trees--to improve their productivity and ustainability. This research started with examination of nutrient cycling variables in the existing ystems in the region and was followed by experimental systems where nutrient cycling could be xamined in controlled experiments. For example, on a farm near CATIE, Beer (1988) compared he annual nutrient return in litter fall and prunings in systems of coffee with *Erythrina oeppigiana* (poró), and coffee with poró and *Cordia alliodora* (laurel). Both trees are common n agroforestry systems with perennial crops in Latin America. The total annual input of litter fall lus pruning residues was similar in both systems. Total annual litter fall input from poró was less han half in association with laurel than without laurel, but litter fall from laurel compensated for he reduced litter fall from poró. In addition, the inclusion of laurel with poró and coffee resulted n a more even distribution of annual nutrient input. Annual inputs of Ca and Mg in litter fall and runings were larger in the system including laurel than in the system with poró alone. There vere no differences in the total input of N or P between the two systems, and the system including aurel had a smaller annual input of K. In spite of these differences among the two systems, the mounts of nutrients recycled by the associated trees reached the recommended levels of fertilizer equired for coffee production in both cases.

Which system to choose will depend on the most limiting nutrients in each case. In the previous example, the system with laurel was preferred by many farmers because, apart from a more even nutrient input throughout the year, the value of the laurel timber added an economic incentive. In addition, laurel is a self pruning species while poró has to be pruned to increase biomass recycling; the system including laurel is therefore less costly than the system with poró alone. Results of experiments at CATIE confirmed these findings. Recommendations were also drawn to modify the traditional systems in order to take advantage of the nutrient cycling benefits from the shade trees and to consider labor availability and timber value (Fassbender et al. 1991).

Other research on similar traditional systems have also demonstrated the importance of nutrient cycling by shade trees and perennial crops. In Ocumare de la Costa, Venezuela, Aranguren et al. (1982) concluded that shade trees of cacao plantations contributed about half of the total annual litter fall. The rate of N transfer to the soil via litter fall was 321 kg/ha. N output with the harvest of cacao pods was 45 kg/ha, with approximately 20 kg returned to the field after processing from pod shells. The authors concluded that the net harvest output of N could be compensated by inputs of N in shade-tree leaf litter from species of *Inga* and *Erythrina*.

Agroforestry in Semi-arid Environments

The semi-arid tropics cover an area of about 20 million km^2 and are inhabited by about 700 million people, nearly half of them in India (Vandenbeldt 1990). It covers most of western, eastern, and south-central Africa; most of India, northeastern Burma, northeastern Thailand, and northern Australia; large parts of eastern and central south America, and western parts of Central America. In all, about 34% of the land area of 48 countries is included in the semi-arid tropics. They are characterized by low standards of living and low and erratic crop yields due to defficient nd strongly seasonal and undependable precipitation (Swindale 1982, in Vandenbeldt 1990). he climate is characterized by high atmospheric water demand; high mean anual temperatures >18°C); and low, variable annual rainfall (400-1900mm). The climate of most of the semi-arid opics is monsoonal, with over 90% of the rainfall occurring in the period of April-October in the orthern hemisphere and October-April in the southern hemisphere.

In arid and semi-arid environments, agroforestry systems help to provide greater insurance gainst weather abnormalities (Swaminathan 1987). Some multiple purpose trees commonly used agroforestry such as species of *Acacia*, *Prosopis*, and *Casuarina*, can grow well in arid areas nd can be conbined with grain crops. Perennial shrubs such as *Sesbania grandiflora* and *ajanus cajan* are also promising for producing food, fodder and fuelwood. In semi-arid regions, rowsing from shrubs and trees, more resistant to dry periods than herbaceous forage, can epresent as much of 20-25% of the total intake for livestock (Le Houérou 1987). This provides tability and productivity to livestock and is a main source of income to farmers.

In Africa, shrubland, woodland (open dry forest with more than 50% canopy cover) and avanna (annual or perennnnial grass or herb cover with <50% canopy cover) cover about 10 nillion km^2, or about 35% of the continent (Le Houérou 1987). Trees, shrubs and palms have lways played important ecological and economic roles semi-arid Africa. In ancient Egypt, ertain species of trees and palms (e.g., *Balanites aegyptica*, *Phoenix dactylifera*) were worshiped as sacred trees (von Maydell 1987). The baobab (*Adansonia digitata*) and *Acacia albida* are other trees of great significance to people in Saharan, Sahelian, and Sudan savannas. *A. albida,* a N-fixing tree widespread in arid and semi-arid Africa, keeps its foliage through the dry season and only sheds its leaves at the beginning of the growing season, therefore there is no competition for water or nutrients with the associated crops. In fields where *A. albida* grows naturally at densities of 20-40 trees/ha, the most common intercrops are with millet, sorghum, maize, and peanuts. The pods of *A. albida* are good fodder during the dry season, and the tree also produces good firewood, thorny fencing material, tannins, gum, and bee forage (von Maydell 1987).

In India, the extent of the arid and semi-arid region is about 300,000 km^2, mostly in the northwest (Shankarnarayan 1989). The *Prosopis cineraria* based systems of semi-arid India are similar to the *A. albida* systems of semi-arid Africa. *P. cineraria*, also a N-fixer, is an important source of animal feed, fuel and timber. As *A. albida*, *P. cineraria* has a very deep tap root and it can be lopped at a young age (about 8 years) with yields of 40-70 kg of fuelwood, 20-30 kg of leaves and 5 kg of pods per year (Singh 1987). In fields with relatively low densities of *P. cineraria* (about 120 trees per ha, depending on soil type and rainfall), it is usually intercropped with millet and legumes. Improved soil fertility and higher moisture content have been found in *P. cineraria* intercropped systems, along with higher grain yield and forage biomass production (Singh 1987).

In semi-arid ecosystems, soils under tree canopies apparently have greater levels of organic matter, calcium, magnesium, potassium and phosphorus than those in open grass (Belsky *et al.* 1993, Campbell *et al.* 1994, Isichei and Moughalu 1992, Kellman 1989). However, in these systems the direct effects of trees cannot be easily distinguished from other, indirect effects, because higher fertility underneath the trees is often associated with a more favorable microenvironment (Belsky *et al.* 1993). Additionally, because the trees in savanna ecosystems have generally been in place for a relatively long time before crops are interplanted and soils are ampled, it is hard to determine cause and effect relationships between the presence of the trees nd improved soil conditions under their canopies.

he Role of Animals: Agrosilvopastoral Systems

Agrosilvopastoral systems--the combination of timber, fuelwood or fruit trees with animals, ith or without crops--are practiced at many scales. A large scale system may include timber lantations with grazing to control weeds and to obtain a more immediate return from the sale of nimal products. Cattle raising can also complement subsistence agriculture, with animals ntegrated in home gardens or in systems of fodder production to feed animals in stables. In farms vhere alley cropping is practiced, animal manure can be added to mulch to contribute rapidly vailable nutrients to crops. Mulches of manure can also serve as a nutrient source for microbial ecomposers, speeding up the decomposition of plant materials. In some regions, the ncorporation of trees--especially MPTS--can change cattle raising from an inefficient use of land o a more ecologically and economically feasible activity. The incorporation of trees can improve ystem productivity either by increasing pasture yields or through the production of tree fodder rom leaves and fruits (Gill et al. 1990, Cobbina 1994/1995).

Though the presence of animals in a tree plantation may accelerate nutrient cycling, if the nimal load is too high, soil compaction may affect tree growth (Montagnini 1992). It is often ifficult to separate the effects of soil compaction and nutrient recycling by animals from the npacts of trees and forage grasses or legumes. In experimental systems in the Atlantic region of Costa Rica, a fast-growing leguminous tree species (*Erythrina berteroana*) was introduced in ative grass pastures. Over a three-year study period, soil organic C increased in two non-grazing treatments, and soil bulk density decreased in the control areas with no grazing and no trees (Cooperband and Logan 1993). Changes in soil pH, exchangeable cations, Al and P levels were not clearly a result of the impacts associated with grazing, or of changes associated with site preparation.

Other experiments on eroded marginal lands in subtropical India compared soil erosion in agrosilvopastoral systems with *Leucaena leucocephala* (used for fuelwood and fodder) and *Pennisetum purpureum* (used for fodder) with the traditional rainfed crop sequence of *Sesamum indicum* followed by *Brassica napus* (Grewal et al. 1994). Results suggested that the agrosilvopastoral systems were more effective in conserving soil than the traditional cropping system. However, animal grazing did not have an influence on soil variables because the animals were kept outside of the system.

Agrosilvopastoral systems require careful management to take advantage of nutrient cycling and to avoid soil compaction and trampling by cattle. This can be achieved at a small scale where manual recycling of manure, managing and rotating pastures and hauling fodder to feed animals in stables or enclosures are more feasible. However, these practices are labor intensive and will only be adopted when the benefits and returns are attractive to the farmers.

THE EFFECTS OF TREES ON SOIL FERTILITY

Agroforestry systems have often been regarded as having protecting functions on soil physical and chemical properties. It can be argued that erosion control can be achieved through the use of soil covers, independently of the presence of trees. A number of herbaceous species were used in early attempts to improve fallows in tropical areas, but in the more seasonal climates, he herbaceous crops with their shallow roots were not able to sustain the dry season very well. ome herbaceous, leguminous species such as *Pueraria phaseoloides* and *Centrosema pubescens* re still used with success as green covers of commercial tree plantations (rubber, cacao) in everal tropical humid regions. In the 1970s and 1980s, as selective herbicides became more ccessible and the "minimun tillage" practices became popular in tropical regions, the use of cover rops such as *Pueraria phaseoloides* and *Mucuna utilis* became widespread as in-situ mulches. However, small shrubs such as *Crotalaria* spp. and *Cajanus cajan* were found to be more dequate than herbaceous species because they could stand drier periods and competed less with the associated herbaceous crops. Tree or shrub species that stand pruning, have high rates of organic matter production and good nutrient cycling abilities can be combined in agroforestry systems with agricultural crops or cattle, with the added advantage of yielding products such as fuelwood, timber, fruits or fodder.

In addition, in agroforestry all system components including trees, crops, and their litter can contribute to nutrient cycling and soil protection. For example, a summary of erosion rates under tropical forest, tree crops and some agroforestry systems is given in Table 1. If the rates of soil loss shown are considered low (<2tons/ha/yr), moderate (2-10 tons/ha/yr) and high (>10 tons/ha/yr), then the lowest erosion rates correspond to natural rain forest, forest fallows, multistorey tree gardens, and undisturbed forest plantations; intermediate or moderate to high rates are found for cropping periods of shifting agriculture and taungya systems; and the highest rates are recorded for tree plantation crops and for forest plantations, both under intense management. The wide ranges shown by the data indicate the importance of management rather than the intrinsic nature of the systems. Additionally, it can be seen that the highest erosion rates were recorded for the two intensively managed systems in which there was no surface cover (Young 1989).

A key to the success of agroforestry systems is the choice of fast-growing woody components with positive impacts on soil properties (Sanchez et al. 1985, Nair 1989, Young 1989, Montagnini 1992). A number of publications compile characteristics, uses, and properties of Multiple-Purpose Tree Species (MPTS) for their application worldwide (e.g., NAS 1979, NAS 1980, Glover and Adams 1990, Lantican and Taylor 1991). The majority of the MPTS lists and data- bases include information on the role of trees on soil fertility or nutrient cycling. These guides emphasize the N-fixing ability and nodulating status of leguminous trees and actynorrhizal plants with few statements on their potential effect on other ecosystem nutrients.

Several indigenous and exotic tree species show potential for improving soil chemical, biological and physical characteristics, and could be advantageous in agroforestry combinations. For example, out of about 30 economically valuable tree species tested in experimental conditions in humid lowland regions of Costa Rica, Brazil and Argentina, nearly half had a positive influence on soil total N, organic matter, and/or exchangeable cations and P, in comparison with nearby pasture (Table 2). In several cases the values of the parameters tested under the tree canopies were close to those found in adjacent young secondary forests. Most of the other species tested did not appear to change soil conditions substantially, and they could be used on non-degraded soils (Table 2).

A number of constraints limit the broad utilization of results, such as those shown in Table 2, as a single criterion for species selection for agroforestry. Primarily, the results of standard soil fertility tests used in agriculture may not always reveal the soil's productive potential because they o not include all chemical forms of nutrients available for plant uptake. For example, although ineral N (NO_3^- and NH_4^+) makes up less than 10% of the total soil N pool, it is the form of N vailable to plants. Data on N mineralization rates under tree species are frequently not available ecause their estimation requires time-consuming laboratory or field incubation of soil samples. :valuating the effects of trees on soil P availability is even more difficult, although P release from tter and its uptake by test crops can give an indirect indication of impacts on soil P availability.

The impacts of trees on soil fertility depend on nutrient recycling characteristics such as itter chemistry and decomposition rates. Tree litter can be used as mulch with different outcomes: a fast mulch decomposition rate may accelerate the growth of associated crops on poor soils, while in other cases a more persistent litter may provide a steady source of nutrients and a etter soil cover year round. In the example shown in Table 2, high rates of litter fall and slower lecomposition resulted in high litter accumulation and high soil organic matter under V. *ferruginea*, making this species well suited for protecting soils against erosion. In contrast, itter from *V. guatemalensis* may be especially important for Ca and Mg recycling (Montagnini et al. 1993). Although the litter of *H. alchorneoides* was less abundant than the other three species, it had a relatively faster decomposition rate and higher nutrient content. These characteristics promoted fast nutrient recycling, especially of N, Ca, Mg, K and P.

Additional factors influencing nutrient release from litter are its polyphenol and lignin content, as both compounds lower the quality of plant materials. The polyphenol to N ratio, for example, may serve as an index for short-term immobilization patterns observed for legumes with relatively high polyphenol content, and the lignin plus polyphenol to N ratio may serve as an index for longer-term release patterns (Palm 1995). The timing of nutrient release by trees is also important so that nutrients will be supplied in synchrony with crop needs (Palm 1995). Yet as discussed in the previous section, synchronizing nutrient supply may not be as important as the long-term build up of tree litter mulch and soil organic matter in influencing crop yields and, equally important, in maintaining soil productivity.

It has been argued that the ability of agroforestry systems to enhance nutrient availability is very limited on infertile soils compared to systems on fertile soils, although they can indeed play an important role in reducing nutrient losses in both situations (Szott et al. 1991). Litter production and quantities of nutrients recycled in litter are greater on fertile than infertile soils; however, use of prunings to accelerate nutrient fluxes may increase plant productivity on infertile soils (Szott et al. 1991).

Inclusion of woody components in a production system can provide benefits from the tree products themselves (timber, fuelwood, leaf mulches, and other tree products) and from their potential ecological advantages, especially their nutrient cycling abilities. The choice of a tree species will often depend on whether both productive and ecological advantages can be achieved in the same system, and in some cases one prevailing function may be desired.

NUTRIENT USE EFFICIENCY AND SPECIES CHOICE

The nutrient use efficiency (NUE) concept has been employed to describe the differential ability of tree species to accumulate organic matter in relation to nutrients taken up from the soil. NUE has been defined on different scales of space and time. At the plant population and community levels, NUE is generally defined as the amount of biomass produced per unit of nutrient taken up (Grubb 1989, Binkley et al. 1992, Medina 1995). Since direct measurements of nutrient absorption are not usually made for mature tree stands, leaf litter fall nutrients are generally used as an estimate of annual nutrient uptake (Vitousek 1984, Grubb 1989, Binkley et al. 1992). Ideally, efforts should be made to measure total production by stems, branches and roots and to consider nutrient uptake plus losses to herbivory and leaching of nutrients (Grubb 1989). Differences in nutrient cycling and efficiency of use may result from an ability to use various nutrient conserving mechanisms, from physiological to mutualistic interactions (Chapin 1980, 1983).

It is also important to consider the relationship between the recycling ability of the species and its potential short and long-term impacts on soil nutrient amelioration. A "nutrient cycling index" (NCI), taken as the inverse of NUE, i.e., the amount of nutrients in annual litterfall/annual tree biomass production, has been used to assess suitability of tree species for agroforestry combinations. For example, Fassbender et al. (1991) found that the P recycling index was about six times higher in combinations of cacao with *Erythrina poeppigiana* than with *Cordia alliodora* in agroforestry systems in Turrialba, Costa Rica. *Cordia*, a timber species, accumulated much P in stem biomass, while *Erythrina*, a shade tree with good nutrient cycling properties, produced large amounts of leaves and branches resulting in greater P recycling.

When put in context with nutrient recycling characteristics of a species, NUE can indicate appropriate system design and management to maintain productivity and recover or conserve nutrients over the long term. The ability of a species to produce large amounts of biomass with less nutrients may be an important consideration in choosing species for degraded, nutrient-poor sites.

into account the objectives that the change is seeking to achieve, thus species selection for agroforestry must be based on several factors apart from their positive influence on soils and crop yields (Wood 1990). Furthermore, species choices for forestry and agroforestry systems are mandated by local people's preferences, which in turn depend on seedling availability, official incentives, and markets.

Choice of suitable crop species is also important for the success of alley cropping systems. Maize and rice, for example, are more light demanding than beans or cassava and thus more affected by shading by trees. The height of pruning and the width of alleys can be adjusted to avoid excessive competition between crops and trees: in experiments at CATIE, for example, Kass (1989) found that maize yield was higher when planted farther away from *Gliricidia* hedgerows. Results of economic analyses for the same systems indicated that the alley cropping system was not as profitable for N, with a lower market cost for fertilizer, as for K and P, with relatively higher market fertilizer prizes.

The adoption of alley cropping systems appears widespread in low income areas of eastern Indonesia, southern Philippines, and Sri Lanka (Kang and Wilson 1987). In Nigeria, researchers from the International Institute of Tropical Agriculture (IITA) have found that although labor for pruning hedges is a major constraint, alley cropping with *Calliandra* spp. has given good results (Plucknett 1990). However the application of alley cropping techniques has its limitations: sometimes crop monocultures are preferred for practical reasons, and sometimes the value of prunings from the hedgerows is higher than the value of crops. Planting the hedgerow trees at high density favors biomass production by trees, but may result in lower crop yields because of competition with trees for light and nutrient resources. On highly weathered soils, successful alley ropping may require the use of external inputs (e.g., liming to increase soil pH) to maintain levels f soil fertility adequate for the desired crop yields (Evensen et al. 1995).

he Need for Initial Economic Incentives to Facilitate System Establishment

When nutrient stocks are low, it may take a number of years for an agroforestry system to uild up nutrients and soil carbon to the point where the system is profitable compared with nonocultures. For example, three years after the establishment of the *Albizia*-sorghum alley ropping system previously discussed, production of the grain crop was still less than the control, lespite the slow but continuous rise in available soil P in the agroforestry system. Because of the low initial productivity of agroforestry systems established on degraded soil, sometimes it is not economically feasible for a farmer to begin agroforestry systems.

Since the adoption of agroforestry systems involves the planting of selected trees, some initial capital will be needed to cover the first 2-3 years of establishment costs. This requirement can be a problem if farmers have no access to capital. In the Atlantic lowlands of Costa Rica, enriched fallow systems are more profitable than conventional agriculture or cattle; however, some assistance may be required to help farmers make the initial expenditures needed to plant the trees (Montagnini and Mendelsohn 1996). Small subsistence farmers often have no access to loans and so cannot afford to make even profitable investments. In Costa Rica, programs such as the Forestry Development Fund (FDF) provide loans for planting trees to small farmers. The farmers repay the loan by giving 30% of the income from harvesting the trees at maturity. Such programs could make sustainable development a reality by allowing small farmers to make sound long-term investments in their land.

CONCLUSIONS

One of the most important reasons for adoption of agroforestry systems in regions where commercial fertilizers are expensive or unavailable is the ability of such systems to recover, recycle, or efficiently utilize nutrients. This ability is often linked to mechanisms associated with woody or perennial species. While agroforestry systems can be profitable if established immediately after forest clearing, they often require a number of years to become profitable when established on degraded lands. For this reason, capital-limited farmers on poor soils may require subsidies to encourage establishment of agroforestry systems.

LITERATURE CITED

Adejuwon, J. O. And Adesina, F. A. 1990. Organic matter and nutrient status of soils under cultivated fallows: an example of *Gliricidia sepium* fallows from South Western Nigeria. Agroforestry Systems 10: 23-32.

Ae, N., J. Arihara, K. Okada, T. Yoshihara, and C. Johansen. 1990. Phosphorus uptake by pigeon pea and its role in cropping systems of the Indian subcontinent. Science 248: 477-480.

Allen, B. J. 1985. Dynamics of fallow successions and introduction of robusta coffee in shifting cultivation in the lowlands of papua New Guinea. Agroforestry Systems 3: 227-238.

Anderson, A.B. 1990. Extraction and forest management by rural inhabitants in the Amazon estuary. pp. 65-85 In: Anderson, A.B. (Ed.). Alternatives to Deforestation: Steps Toward Sustainable Use of the Amazon Rain Forest. Columbia Univ. Press, N.Y.

Andreiesse, J.P. and Schelhaas, R.M. 1987. A monitoring study of nutrient cycles in soils used for shifting cultivation under various climatic conditions in tropical Asia. III. The effects of land clearing through burning on the fertility level. Agriculture, Ecosystems and Environment 19: 311-332.

Aranguren, J., Escalante, G. and Herrera, H. 1982. Nitrogen cycle of tropical perennial crops under shade trees II. Cacao. Plant and Soil 67: 259-269.

Balée, W. 1992. People of the fallow: a historical ecology of foraging in lowland South America. pp. 35-57 In: Redford, K. H. and Padoch, C. (Eds.). Conservation of Neotropical Forests. Columbia Univ. Press, N.Y.

Bandy, D. E., Garrity, D. P. and Sanchez, P. A. 1993. The worldwide problem of slash and burn agriculture. Agroforestry Today 5: 2-9.

Beer, J. 1988. Litter production and nutrient cycling in coffee (*Coffea arabica*) or cacao (*Theobroma cacao*) plantations with shade trees. Agroforestry Systems 7: 33-45.

Belsky A J, Mwonga S M, Amundson R G, Duxbury J M and Ali A R 1993 Comparative effects of isolated trees on their undercanopy environments in high- and low-rainfall savannas. J. Appl. Ecol. 30, 143-155.

Binkley, D., Dunkin, K. A., DeBell, D. and Ryan, M. G. 1992. Production and nutrient cycling in mixed plantations of *Eucalyptus* and *Albizia* in Hawaii. Forest Science 38: 393-408.

Campbell B M, Frost P, King J A, Mawanza M and Mhlanga L 1994 The influence of trees on soil fertility on two contrasting semi-arid soil types at Matopos, Zimbabwe. Agrofor. Sys. 28, 159-172.

Chapin, F.S. 1980. The mineral nutrition of wild plants. Annual Review of Ecology and Systematics 11: 233-260.

Chapin, F.S. 1983. Patterns of nutrient absorption and use by plants from natural and man-modified environments. pp. 175-187 In: Mooney, H. A. and Godron, M.(Eds.). Disturbance and Ecosystems. Ecological Studies Vol. 44. Springer Verlag, Berlin.

Cobbina, J. 1994/1995. Growth and herbage productivity of gliricidia in *Panicum maximum* pasture as influenced by seed preparation, planting and weed control techniques. Agroforestry Systems 28: 193-201.

Cooperband, L. R. and Logan, T. J. 1993. Baseline soil characteristics of a humid tropical lvopastoral system and changes in selected soil properties. Turrialba **43**: 22-36.

el Amo, R.S. and Ramos, P.J. 1993. Use and management of secondary vegetation in a humid-opical area. *Agrofor. Sys. 21*, 27-42.

enevan, W.D, Treacy, J.M., Alcorn, J.B., Padoch, C., Denslow, J. and Paitan, S.F. 1984. ıdigenous forestry in the Peruvian Amazon: Bora Indian management of forest fallows. *ıterciencia 9*, 346-357.

vensen, C. I., Dierolf, T. S. and Yost, R. S. 1995. Decreasing rice and cowpea yields in alley ropping on a highly weathered Oxisol in West Sumatra, Indonesia. Agroforestry Systems **31**: 1-9.

assbender, H. W., Beer, J., Heuveldop J., Imbach, A., Enriquez, G. and Bonnemann, A. 1991. en year balances of organic matter and nutrients in agroforestry systems at CATIE, Costa Rica. orest Ecology and Management **45**: 173-183.

emandes, E.C.M., A. O'Kting'ati, and J. Maghembe. 1989. The Chagga homegardens: a nultistoreyed agroforestry cropping system on Mount Kilimanjaro (northern Tanzania), in Nair, .K.R. (ed.) Agroforestry systems in the tropics. Kluwer Academic Publishers. Dordrecht. pp. 309-332.

Fernández, R., Montagnini, F., and Hamilton, H. 1997. The Influence of native tree species on soil chemistry in a subtropical humid forest region of Argentina. Journal of Tropical Forest Science. In Press.

Gill, A. S., Gangwar, K. S. and Sinsinwar, B. S. 1990. Productivity of perennial grasses in association with *Acacia albida* under different cutting schedules in dryland conditions. Indian Journal of Dryland Agricultural Research and Development 5: 68-71.

Glover, N. and Adams, N. (Eds.). 1990. Tree Improvement of Multipurpose Species. Multipurpose Tree Species Network Technical Series, vol. 2. Winrock International Institute for Agricultural Development. Arlington, VA.

Gómez-Pompa, A., and Kaus, A. 1990. Traditional management of tropical forests in Mexico. pp. 45-64 In: Anderson, A.B. (Ed.). Alternatives to Deforestation: Steps Toward Sustainable Use of the Amazon Rain Forest. Columbia Univ. Press, N.Y.

Grewal, S., Juneja, J. M., Singh, K. and Singh, S. 1994. A comparison of two agroforestry systems for soil, water and nutrient conservation on degraded land. Soil Technology 7: 145-153.

Grubb, P. J. 1989. The role of mineral nutrients in the tropics: a plant ecologist view. pp. 417-440 In: Proctor, J. (Ed.). Mineral Nutrients in Tropical Forest and Savanna Ecosystems. Blackwell Scientific Publications, Boston.

laggar, J. P. 1994. Trees in alley cropping: competitors or soil improvers? Outlook on griculture 23: 27-32.

laggar, J. P., Tanner, E. V. J., Beer, J. W. and Kass, D. C. L. 1993. Nitrogen dynamics of opical agroforestry and annual cropping systems. Soil Biology and Biochemistry 25: 1363-378.

lan, X. 1989. The mobilization of aluminum- and iron- bound phosphorus by organic matter ecomposition in highly weathered soils. Ph.D. Dissertation. Univ. of Georgia, Athens, GA.

sichei A O and Muoghalu J I 1992 The effects of tree canopy cover on soil fertility in a Nigerian avanna. J. Trop. Ecol. 8, 329-338.

ordan, C.F. 1989. An Amazonian Rain Forest. UNESCO and The Parthenon Group. Carnforth, .K.

ordan, C.F. 1995. Conservation: Replacing Quality with Quantity as a Goal for Global anagement. Wiley, N.Y.

ang, B. T. and Wilson, G. F. 1987. The development of alley cropping as a promising groforestry technology. pp. 227-244 In: Steppler, H. A. and Nair, P. K. R. (Eds.). groforestry. A Decade of Development. ICRAF, Nairobi.

Kang, B. T., Reynolds, L. And Atta-Krah, A. N. 1990. Alley farming. Advances in Agronomy 43: 315-359.

Kass, D. L. 1989. Resultados de seis años de investigación de cultivos en callejones (alley cropping) en "La Montaña", Turrialba, Costa Rica. El Chasqui (Costa Rica) 19: 5-24.

Kass, D. C. L., Foletti, C., Szott, L. T., Landaverde, R. and Nolasco, R. 1993. Traditional fallow systems of the Americas. Agroforestry Systems 23: 207-218.

Kellman M 1989 Mineral nutrient dynamics during savanna-forest transformation in Central America. *In* Mineral Nutrients in Tropical Forest and Savanna Ecosystems. Ed. J. Proctor. pp. 137-151. Blackwell Scientific Publications. Boston.

Lal, R. 1989. Agroforestry systems and soil surface management of a tropical alfisol: III: Changes in soil chemical properties. Agroforestry Systems 8: 113-132.

Lantican, C. B. and Taylor, D. A. (Eds.). 1991. Compendium of National Research on Multipurpose Tree Species 1976-1990. Winrock International Institute for Agricultural Development, Arlington, VA.

Le Houérou, H.N. 1987. Indigenous shrubs and trees in the silvopastoral systems of Africa, in Steppler and Nair (eds) Agroforestry: A decade of development. ICRAF. Nairobi, pp. 141-156.

,escure, J., Emperaire, L., Pinton, F. and Renault-Lescure, O. 1992. Non-timber forest ıroducts and extractive activities in the middle Rio Negro Region, Brazil. pp. 151-172 In: 'lotkin, M. and Famolare, L. (Eds.). Sustainable Harvest and Marketing of Rain Forest Products. sland Press, Washington, D.C.

/latta-Machado, R. and Jordan, C. F. 1995. Nutrient dynamics during the first three years of an lley cropping agroecosystem in southeastern USA. Agroforestry Systems 30: 351-362.

/ledina, E. 1995. Physiological ecology of trees and application to forest management. pp. 289-07 In: Lugo, A.E. and Lowe, C. (Eds). Tropical Forests: Management and Ecology. Ecological tudies 112. Springer- Verlag, New York.

/lesquita, R. 1995. The effect of different proportions of canopy opening on the carbon cycle of 'entral Amazonian secondary forest. Ph.D. Dissertation, Univ. of Georgia, Athens, GA.

/lichon, G., F. Mary and J. Bompard. 1989. Multistoreyed agroforestry garden system in West umatra, Indonesia, in Nair, P.K.R. (ed.) Agroforestry systems in the tropics. Kluwer Academic ublishers. Dordrecht. The Netherlands. pp. 243-268.

/lontagnini, F. 1992. Sistemas Agroforestales. Principios y Aplicaciones en los Trópicos. 2da. d. OTS/CATIE, San José, Costa Rica. 622 pp.

Montagnini, F., Ramstad, K. and Sancho, F. 1993. Litterfall, litter decomposition and the use of mulch of four indigenous tree species in the Atlantic lowlands of Costa Rica. Agroforestry Systems 23: 39-61.

Montagnini, F., Fanzeres, A. and da Vinha, S. G. 1994. Studies on restoration ecology in the Atlantic forest region of Bahia, Brazil. Interciencia 19: 323-330.

Montagnini, F. 1995. Recuperación de Áreas Degradadas con la Utilización de Árboles Nativos: Experiencias en Tres Regiones de Latinoamérica. III Congreso Latinoamericano de Ecología, Mérida, Venezuela. October 19-21, 1995.

Montagnini, F. and Mendelsohn, R. 1996. Managing forest fallows: improving the economics of swidden agriculture. Ambio. In press.

Nair, P. K. R. 1989. The role of trees in soil productivity and protection. pp. 567-589 In: Nair, P. K. R. (Ed.). Agroforestry Systems in the Tropics. Kluwer Academic Publishers/International Council for Research in Agroforestry, Dordrecht, The Netherlands.

Nair, P. K. R. 1990. The Prospects and Promise of Agroforestry in the Tropics, a Review of Technical and Socioeconomic Information with Special Emphasis to Africa. Report to the World Bank, Washington, DC. 121 pp.

ational Academy of Sciences. 1979. Tropical Legumes: Resources for the Future. Board of cience and Technology for International Development. National Research Council, ashington, DC.

ational Academy of Sciences. 1980. Firewood Crops. Shrubs and Tree Species for Energy roduction. Board of Science and Technology for International Development. National Research ouncil, Washington, DC.

ations, J.D. 1992. Xateros, chicleros, and pimenteros: Harvesting renewable tropical forest esources in the Guatemalan Petén. pp. 208-219 In: Redford K.H. and Padoch, C. (Eds.). onservation of Neotropical Forests. Columbia Univ. Press, N.Y.

nim, J. F. M., Mathuva, M., Otieno, K. And Fitzhugh, H. A. 1990. Soil fertility changes and esponse of maize and beans to green manures of leucaena, sesbania and pigeonpea. Agroforestry Systems 12: 197-215.

Padoch, C., Chota Inuma, J., De Jong, W. and Unruh, J. 1985. Amazonian agroforestry: a market-oriented system in Peru. *Agrofor. Sys. 3,* 47-58.

Padoch, C. and De Jong, W. 1987. Traditional agroforestry practices of native and ribereno farmers in the lowland Peruvian Amazon. In *Agroforestry, Realities, Possibilities and Potentials,* Gholz, H.(ed.). Martinus Nijhoff, Dordrecht, The Netherlands, p.179-194.

Palm, C. A. 1995. Contribution of agroforestry trees to nutrient requirements of intercropped plants. Agroforestry Systems 30: 105-124.

Plucknett, D. L. 1990. International goals and the role of the international research centers. pp. 32-49 In: Edwards, C.A., Lal, R., Madden, P. Miller, G. and House, G. (Eds.). Sustainable Agricultural Systems. St. Lucie Press, Delray Beach, Florida.

Posey, D.A. 1982. The keepers of the forest. Garden 6: 18-24.

Raintree, J.B. and Warner, K. 1986. Agroforestry pathways for intensification of shifting agriculture. *Agrofor. Sys. 4*, 39-54.

Ramakrishnan, P. S. 1992. Shifting agriculture and sustainable development. Man and the Biosphere Series. Volume 10. Parthenon, New Jersey. 424 pp.

Regnier, E. and Janke, R. 1990. Evolving strategies for managing weeds. pp. 174-202 In: Edwards, C.A., Lal, R., Madden, P. Miller, G. and House, G. (Eds.). Sustainable Agricultural Systems. St. Lucie Press, Delray Beach, Florida.

Salazar, A., Szott, L. T. and Palm, C. A. 1993. Crop-tree interactions in alley cropping systems on alluvial soils in the Upper Amazon basin. Agroforestry Systems 22: 67-82.

Sanchez, P.A., Palm, C.A., Davey, C.B., Szott, L.T. and Russell, E.C. 1985. Tree crops as soil mprovers in the humid tropics? pp. 327-350 In: Cannell, M.G.R. and Jackson, J.E. (Eds.). Attributes of Trees as Crop Plants. Inst. of Terr. Ecol., Nat. Environ. Res. Council, Abbots Ripton, Huntingdon, England.

Sanchez, P. A. 1995. Science in agroforestry. Agroforestry Systems 30: 5-55.

Singh, G. B. 1987. Agroforestry in the Indian subcontinent: past, present and future. Pp. 117-138 in H. A. Steppler and P. K. R. Nair (eds) Agroforestry: A decade of development. ICRAF. Nairobi.

Sips, P. 1993. Management of Tropical Secondary Rain Forests in Latin America. Today's Challenge, Tomorrow's Accomplished Fact!? National Reference Center for Nature, Forests and Landscape, Ministry of Agriculture, Nature Management and Fisheries, Wageningen, The Netherlands. 72 pp.

Soemarwoto, O. 1987. Homegardens: a traditional agroforestry system with a promising future. in H. A. Steppler and P. K. R. Nair (eds) Agroforestry: A decade of development. ICRAF. Nairobi, pp. 157-171.

Subler, S. and Uhl, C. 1990. Japanese agroforestry in Amazonia: a case study in Tomé-Açu, Brazil. pp. 152-166 In: Anderson, A.B. (Ed.). Alternatives to Deforestation: Steps Toward Sustainable Use of the Amazon Rain Forest. Columbia Univ. Press, N.Y.

Szott, L. T., Palm, C. A. and Sanchez, P. A. 1991. Agroforestry in acid soils of the humid tropics. Advances in Agronomy 45: 275-300.

Unruh, J.D. 1990. Iterative increases of economic tree species in managed swidden-fallows of the Amazon. *Agrofor. Sys. 11*, 175-197.

Vandenbeldt, R. J. 1990. Agroforestry in the semiarid tropics, in MacDicken, K. and N. Vergara (eds). Agroforestry: Classification and management. Wiley. New York, pp. 150-194.

Van Wambeke, A. 1992. Soils of the Tropics. Properties and Appraisal. McGraw-Hill, New York.

Vergara, N.T. 1987. Agroforestry: a suitable land use for fragile ecosystems in the humid tropics. In *Agroforestry, Realities, Possibilities and Potentials*. Gholz, H. (ed.). Martinus Nijhoff, Dordrecht, The Netherlands, p. 7-20.

Vitousek, P. M . 1984. Litterfall, nutrient cycling, and nutrient limitation in tropical forests. Ecology 65: 285-298.

Von Maydell, H. J. 1987. Agroforestry in the dry zones of Africa: past, present and future. Pp. 89-116 in in H. A. Steppler and P. K. R. Nair (eds) Agroforestry: A decade of development. ICRAF. Nairobi.

Watters, R. F. 1971. Shifting Cultivation in Latin America. FAO Forestry Development Paper No. 17. Food and Agriculture Organization of the United Nations, Rome. 305 pp.

Wood, P. J. 1990. Principles of species selection for agroforestry. pp. 290-309 In: MacDicken, K. G. and Vergara, N. T. (Eds.). Agroforestry: Classification and Management. Wiley, New York.

Yamoha, C. F., Abgoola, A. A. And Wilson, G. F. 1986. Nutrient contribution and maize performance in alley cropping systems. Agroforestry Systems 4: 247-254.

Young, A., 1989. Agroforestry for Soil Conservation. C.A.B. International and International Council for Research in Agroforestry, Wallingford, UK, 276 pp.

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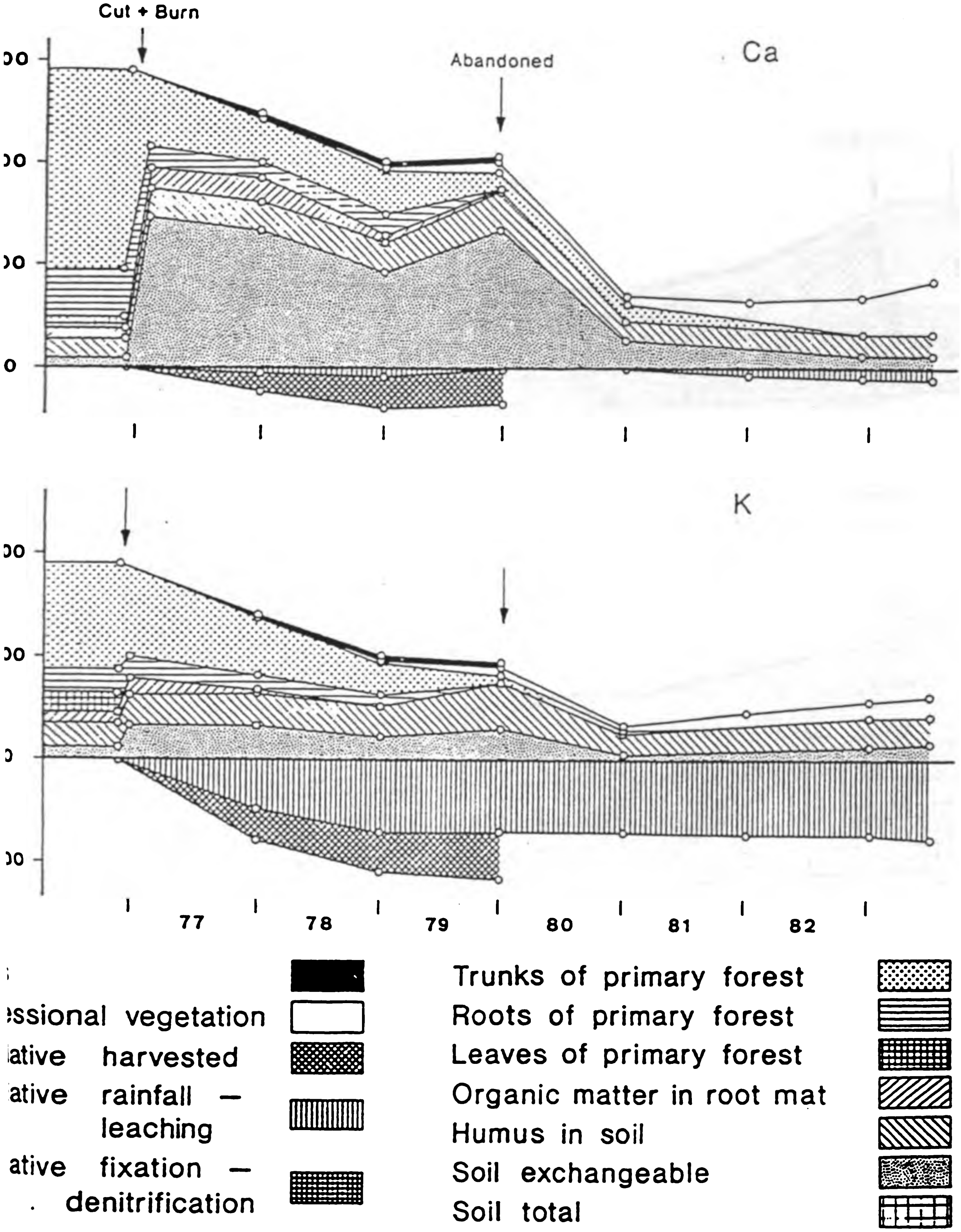
Figure Legends

Fig. 1. Stocks and cumulative losses of calcium and potassium as a function of time in the experimental plot at San Carlos de Rio Negro, Venezuela.

Fig. 2. Stocks and cumulative losses of magnesium and nitrogen as a function of time in the experimental plot at San Carlos de Rio Negro, Venezuela. Keys as for Fig. 1

Fig. 3. Labile phosphorus stocks in fractions of the upper 75 cm of soil and in the aboveground biomass in an experimental alley cropping system (AC), and in a monoculture control of sorghum (NA). There is a trend of gradually increasing differences between the two systems throughout the three-year experimental period. Due to large variability, differences were not significant except between those fractions labeled "a" and "b". PO is organic phosphorus, PI is inorganic phosphorus, NaOH and NaHCO3 are the extractants. ABOVEBIO is aboveground biomass.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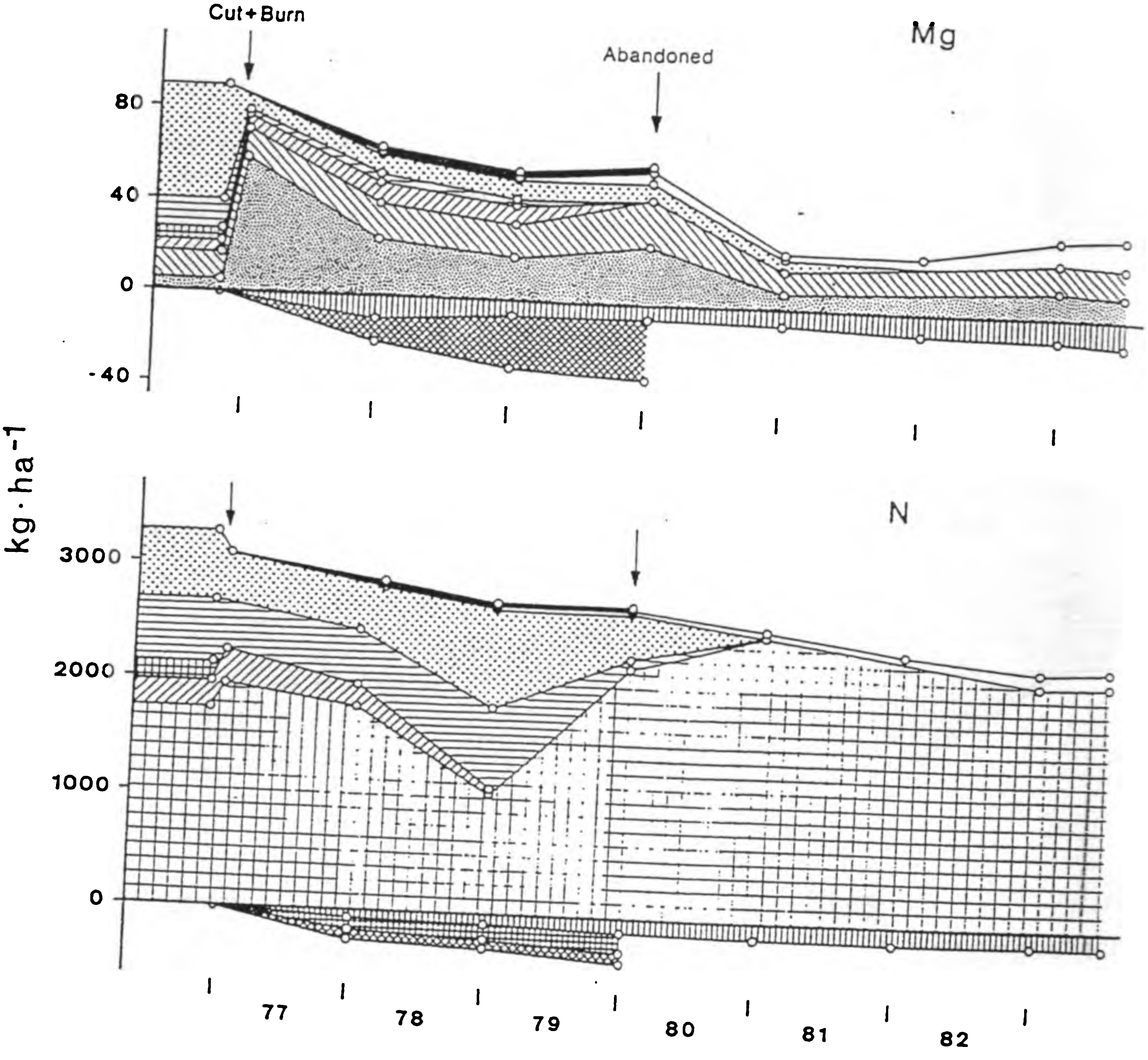
Leaves of primary forest
Organic matter in root mat
Humus in soil
Soil exchangeable
Soil total

Fig 2



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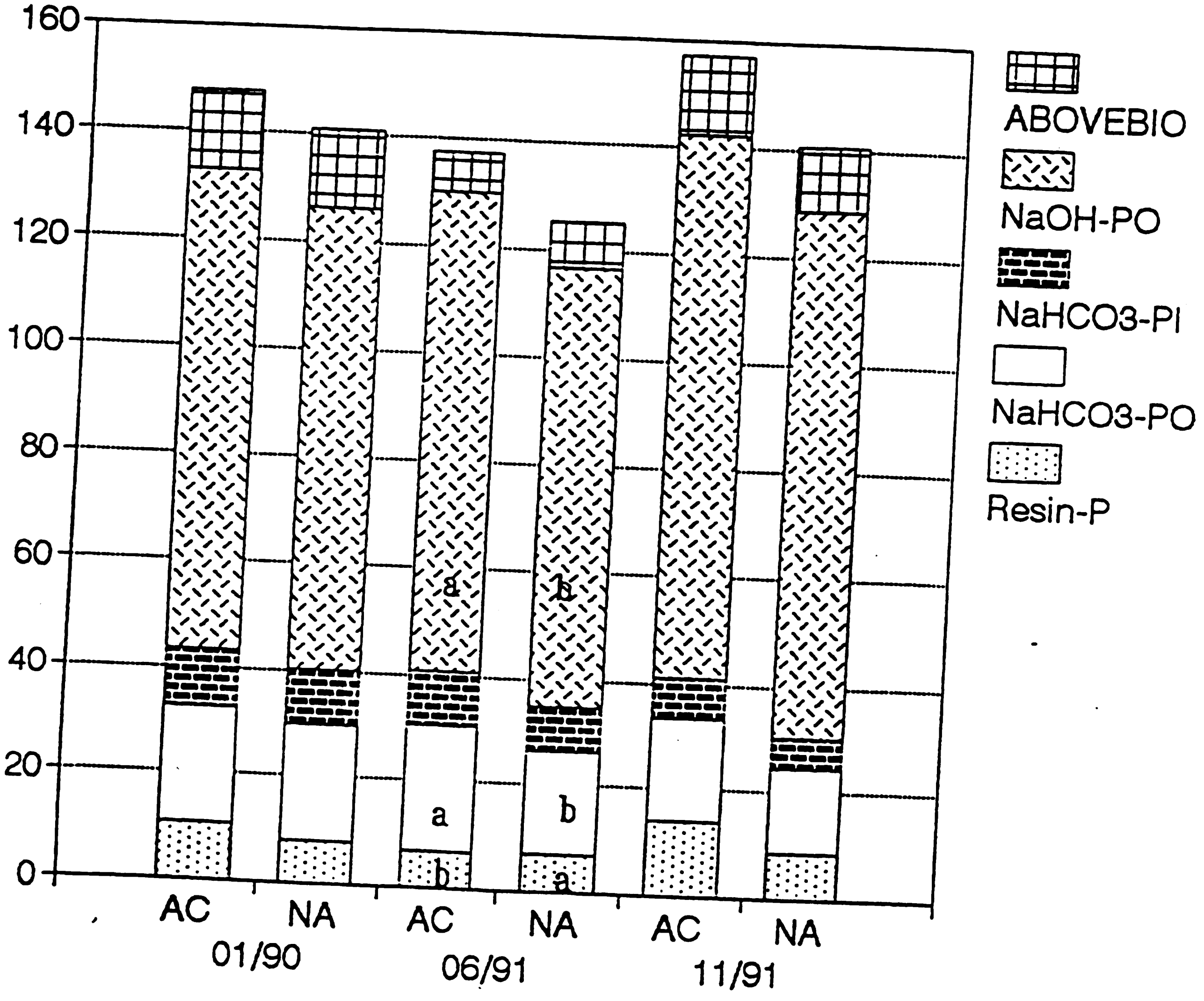
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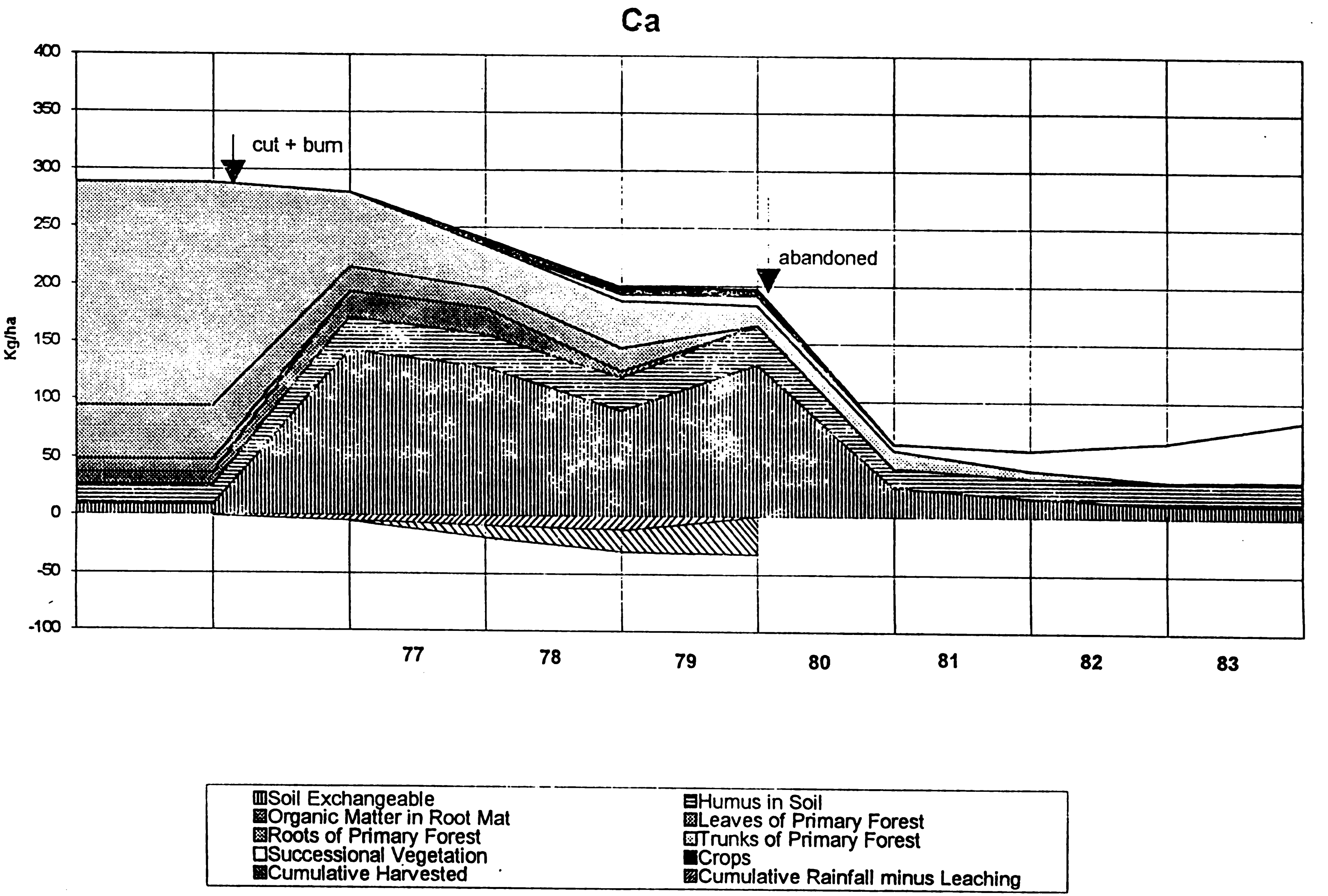
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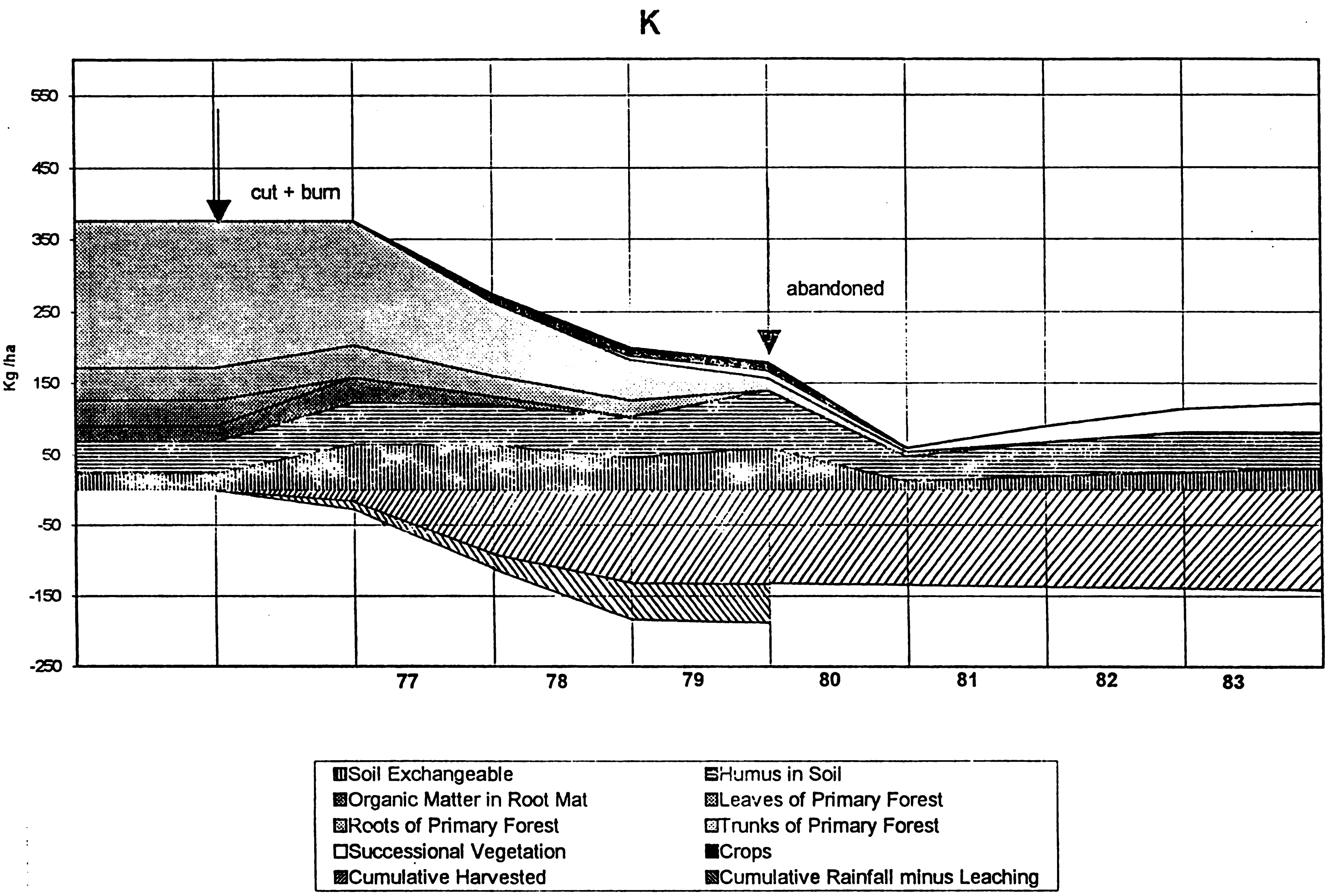
▥Soil Exchangeable
▨Organic Matter in Root Mat
▨Roots of Primary Forest
☐Successional Vegetation
▨Cumulative Harvested
⊟Humus in Soil
▨Leaves of Primary Forest
▨Trunks of Primary Forest
■Crops
▨Cumulative Rainfall minus Leaching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Soil Exchangeable
Humus in Soil
Organic Matter in Root Mat
Leaves of Primary Forest
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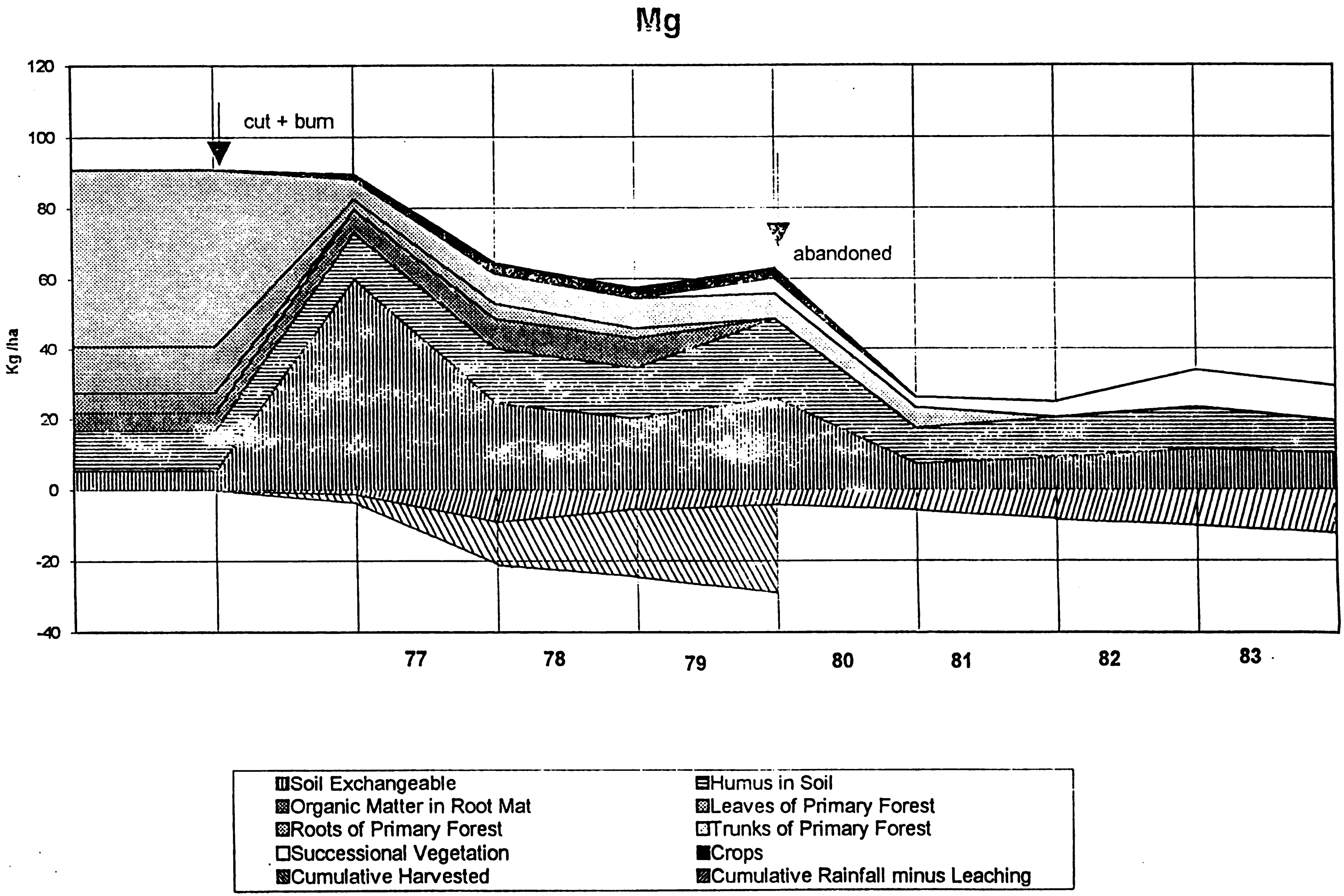
Trunks of Primary Forest
Successional Vegetation
Crops
Cumulative Harvested
Cumulative Rainfall minus Leaching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▤Humus in Soil
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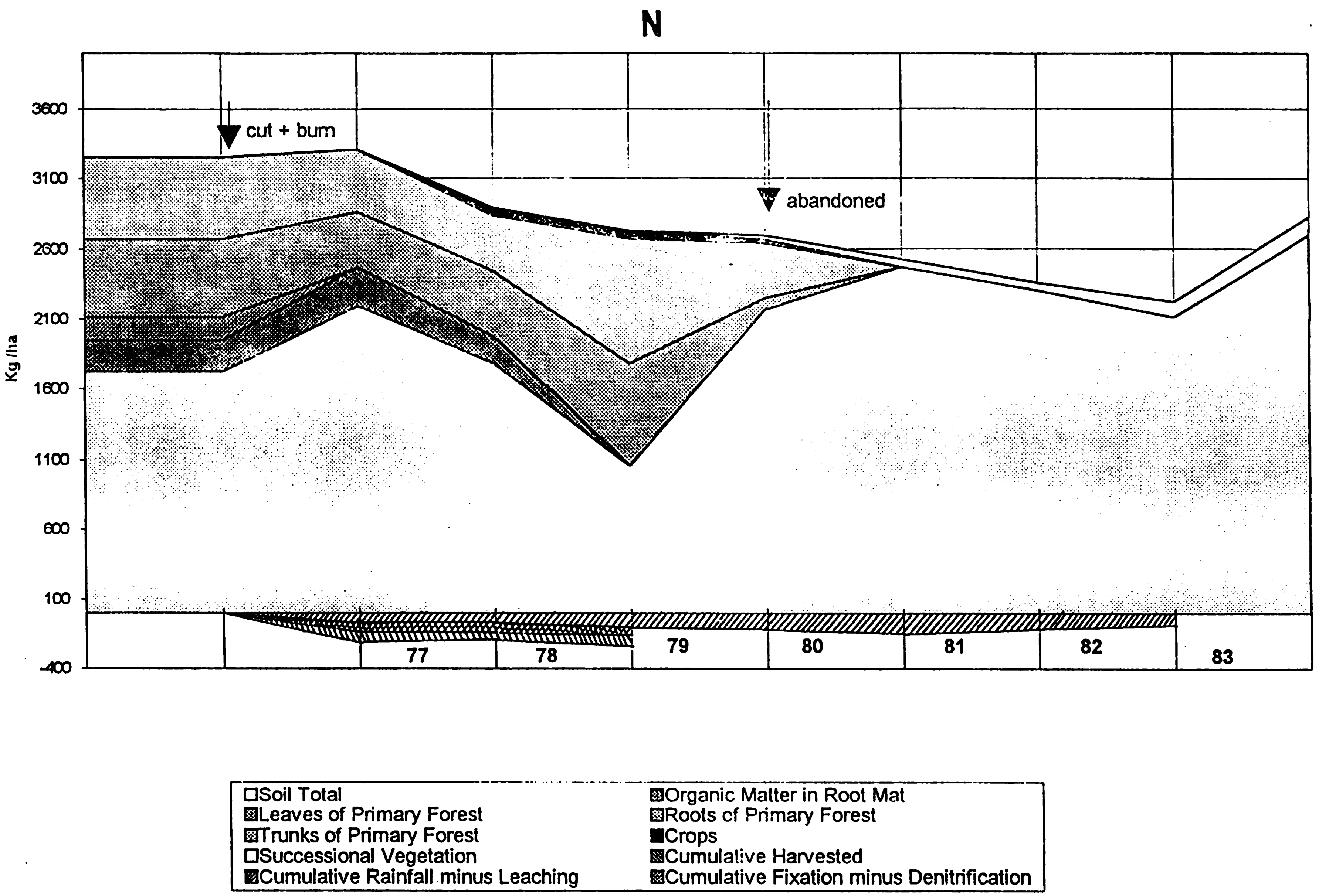
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▨Leaves of Primary Forest
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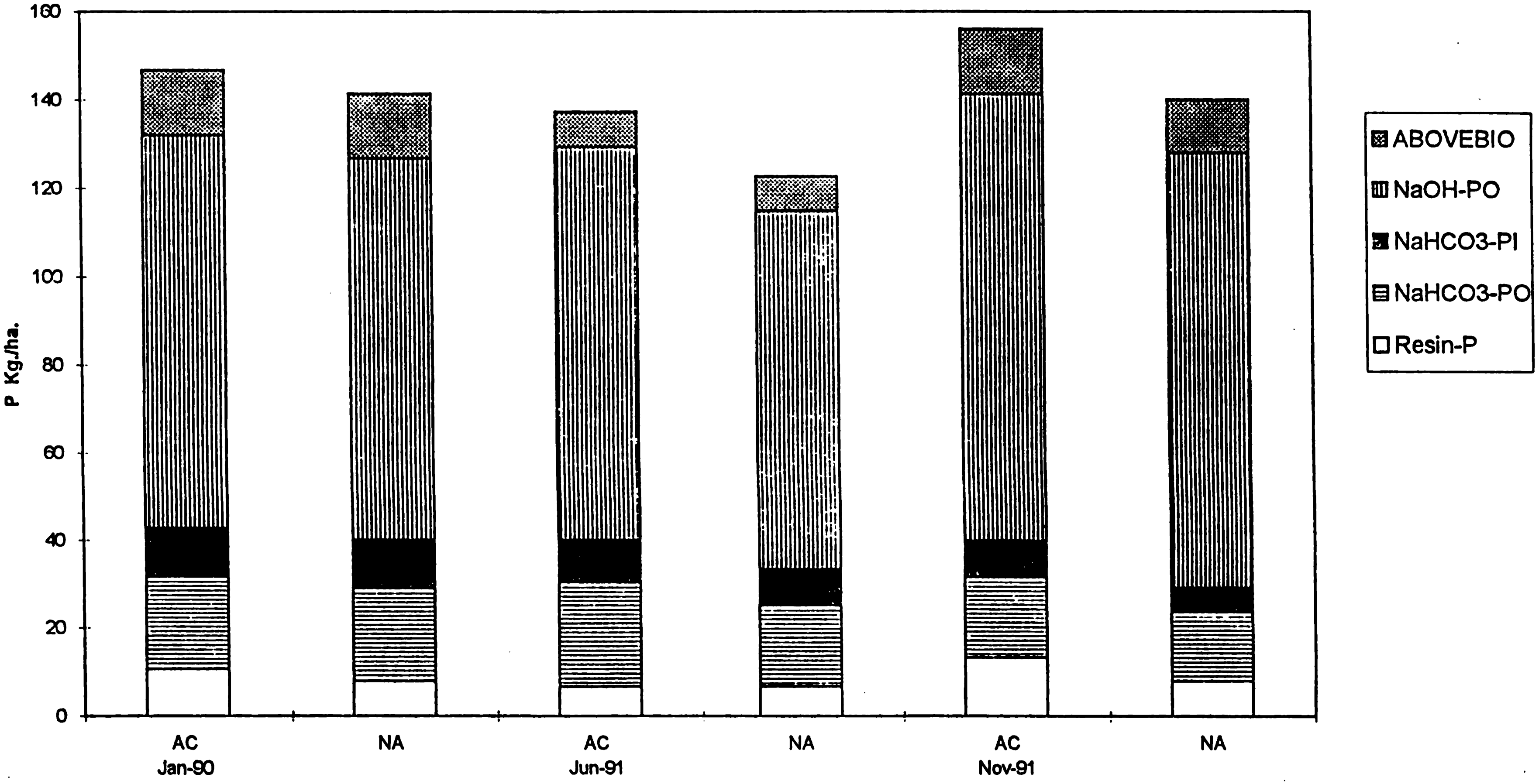
☐Successional Vegetation
▨Cumulative Rainfall minus Leaching
▨Organic Matter in Root Mat
▨Roots of Primary Forest
■Crops
▨Cumulative Harvested
▨Cumulative Fixation minus Denitrification

Labile Phosphorus Stocks in Fractions of the Upper 75 cm. of Soil and in the Aboveground Biomass in an Experimental Alley Cropping System (AC) and in a Monoculture Control of Sorghum (NA)



Aboveground Biomass and Nutrients in Young Plantations of Indigenous Trees on Infertile Soils in Costa Rica: Implications for Site Nutrient Conservation

Florencia Montagnini
Freddy Sancho

ABSTRACT. Aboveground-tree biomass and nutrient content (nitrogen, phosphorus, calcium, magnesium and potassium) were measured in 4-year-old stands of four indigenous tree species: *Stryphnodendron microstachyum* Poepp. et Endl. (ex *S. excelsum* Harms), *Vochysia guatemalensis* Donn. Smith (ex *V. hondurensis* Sprague), *Vochysia ferruginea* Mart and *Hyeronima alchorneoides* (O), growing on infertile soils in an experimental plantation in the Atlantic humid lowlands of Costa Rica. Biomass and nutrient content among the species, and among aboveground tree parts, forest-floor litter and understory vegetation were compared, as key factors that can be manipulated with different effects on site nutrient conservation. Biomass and stemwood annual increments of the four species were similar to those reported for other

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tropical tree plantations in the humid tropics. *S. microstachyum* had the highest accumulation of N in stem, branch and total aboveground tree biomass. *V. guatemalensis* had the highest accumulation of Ca and Mg in the biomass, while *H. alchorneoides* had the highest stem K and P. In spite of their relatively lower N tissue concentrations, *V. ferruginea* and *H. alchorneoides* showed a high potential for N recycling due to its more even distribution in stems, branches and leaves. Nutrient accumulation by the understory in *S. microstachyum* and *H. alchorneoides* plots was 0.8-7.7% of aboveground tree biomass nutrients. The forest-floor litter represented a major compartment for nutrient accumulation and recycling under the four species, especially for N, Ca, Mg and P.

INTRODUCTION

The sustained management of tree plantations becomes a biologically and socially feasible alternative on soils that are unsuitable for the continuous practice of agriculture that uses prevailing local technologies (Gladstone and Ledig 1990). In particular, tree plantations and tree-crop combinations represent productive alternatives for uses of deforested lands that have poor regeneration of natural forests due to long distance to sources of propagules or intense site degradation. As the area of degraded lands expands, there is increasing emphasis on the planting of tree species which can grow in such conditions and yield potentially profitable products (timber, fuelwood and other) as well as environmental benefits (soil conservation, watershed protection) (Evans 1987). On the other hand, young tropical tree plantations are rapidly aggrading ecosystems which incorporate considerable amounts of nutrients in their biomass over a relatively short period of time (Bruijnzeel 1991). Site fertility declines can be a serious limitation to sustained plantation forestry in tropical regions; soil fertility can be decreased through excessive removal of living biomass, particularly if nutrients in tree crowns are lost through harvest or site preparation (Jorgensen and Wells 1986; Perry and Maghembe 1989). However, tree species vary in their nutrient uptake rates and capacity for nutrient recycling. Data on different tree species' nutrient acquisition rates and recycling capabilities will help in the design of management strategies that either can take advantage of the ameliorating effects of trees on soil fertility or avoid site deterioration at harvest.

In the present article we report on aboveground biomass and nutrient content (nitrogen, phosphorus, calcium, magnesium and potassium) for 4-year-old stands of four indigenous tree species: *Stryphnodendron microstachyum* Poepp. et Endl. (ex *S. excelsum* Harms), *Vochysia guatemalensis* Donn. Smith (ex *V. hondurensis* Sprague), *Vochysia ferruginea* Mart, and *Hyeronima alchorneoides* (O), growing on infertile soils in an experimental plantation in the Atlantic humid lowlands of Costa Rica. Results from earlier studies had shown that, after 2.5 years, soils under these species had higher organic matter, N, K and Mg than adjacent areas of abandoned pastures (Montagnini and Sancho 1990a, 1990b; Montagnini et al. 1991). Here we compare biomass and nutrient content among the species, and among aboveground tree parts, forest-floor litter and understory vegetation, as key factors that can be manipulated with different effects on site nutrient conservation. These strategies should be useful for promoting the use of these species in production systems (mixed or pure plantations, agroforestry) in the area as well as in other tropical lowland regions with similar ecological characteristics.

STUDY SITE

The experimental plantation was established in December 1985 on abandoned pasture at the La Selva Biological Station of the Organization for Tropical Studies (10°26'N, 86°59'W; 50 m mean altitude; 24°C mean annual temperature; 4000 mm mean annual rainfall, with maximum in July and minimum in March–La Selva Biological Station weather reports). Soils in the experimental area are Fluventic Dystropepts derived from volcanic alluvium; they are deep, well drained, stone-free, with low or medium organic matter content, moderately heavy texture, and are generally acid and infertile (Sancho and Mata 1987). The area had been cleared in the mid-1950s and grazed until 1981 (Pierce 1991). The site was cleaned manually before planting. The experimental area was on flat, uniform terrain. The design consisted on complete blocks, with five replicates, and tree plots (14 m × 14 m each) were set at random within the blocks. The tree species plots contained seven rows of seven trees, with 2 m between trees. Five 14 m × 14 m plots were also established in an adjacent open area with grass, and in a nearby patch of secondary forest. During the first year, weeds were manually cut four times; weeding was done mechanically thereafter until canopy closure made it no longer necessary. The grass was weeded simultaneously to keep it free of trees, with comparable treatments.

The Tree Species

The criteria for species selection for this study were: growth rate during the first 3-4 years of the plantation (Espinoza Camacho and Butterfield 1989; Gonzalez et al. 1990); presence of root nodules in the leguminous species (field observations); and economic value (Chudnoff 1984; Gonzalez et al. 1990). *S. microstachyum* (Leguminosae, sub-family Mimosoidae) ("vainillo") is found only in Costa Rica, although representatives of this genus are native to tropical South America (Brazil, Costa Rica, Guyana) (Allen and Allen 1981). It grows in low altitude with very humid climates and apparently adapts to alluvial soils as well as to slopes and abandoned pastures with poor soils (Gonzalez et al. 1990). Its timber is primarily used for general construction, and also small furniture and turnery (Allen and Allen, 1981). *V. ferruginea* (Vochysiaceae) ("botarrama") grows in lowland forests from Nicaragua to Brazil (Whitmore and Hartshorn 1969); it is found on well-drained, acidic, infertile soils, but it can adapt to a variety of soils (Gonzalez et al. 1990). It is a self-pruning pioneer species that forms uniform, even-aged stands in abandoned fields, and its wood is used for plywood and construction. *V. guatemalensis* (Vochysiaceae) ("mayo") is found from Mexico to Panama, at up to 900 m altitude (Whitmore and Hartshorn, 1969); it usually grows on humid, low altitude areas, on either rich alluvial or poor soils; its timber is used for carpentry, plywood, and furniture, and has been considered a substitute for mahogany. *H. alchorneoides* (Euphorbiaceae) ("pilon") ranges from southern Mexico to southern Brazil (Chudnoff 1984); it grows well on hills and on abandoned pastures, but not much is known about its edaphic requirements. Its timber is used for heavy construction, furniture, cabinet work, decorative veneers and turnery (Chudnoff 1984).

METHODS

Tree Aboveground Biomass and Nutrients

Taking advantage of plot thinning performed in December 1989, we chose two trees per plot of *S. microstachyum*, *V. ferruginea* and

V. guatemalensis for biomass determinations and chemical analysis. *H. alchorneoides* plots were thinned in July 1990, at which time we also chose trees for the same purpose. From each plot, we selected trees of diameter close to the average for each respective plot, as calculated by the foresters in charge of tree measurements and thinning. The material was separated into its parts (stem, branches and leaves) and weighed fresh at the site using a field scale. Subsamples of all materials, including stems (lower, medium and top parts) were taken to the laboratory and dried at 70°C until a constant weight was obtained. Dry:wet weight ratios from felled trees were used to correct the field weight determinations. The stem samples were used for chemical analysis. In order to obtain a broader sample of other tissue, leaves and branches were obtained from five more trees per species, using a pole pruner. Three whole branches of opposite orientation from the upper portion of the canopy of each tree were sampled. Leaves from the tip, medium, and lower portions of each branch were pooled to obtain one sample per tree. Portions of tip, medium and bottom parts of branches of the sampled trees were cut and pooled in the same manner. The material was oven-dried at 70°C and then ground for chemical analysis. The total N, P, Ca, Mg and K were measured on nitroperchloric digests (Diaz-Romeu and Hunter 1978); N and P were measured using a Flow Injection Analyzer, while cations were measured using an Atomic Absorption Spectrophotometer. Analysis of variance and LSD tests were run to compare mean biomass ($n = 5$) and nutrient content of tree parts ($n = 5$ for each tree part) among species. Total biomass nutrient content for each species was calculated by multiplying the mean biomass of each species' plant part (leaves, branches or stems) times the mean nutrient concentration of the respective plant parts.

Biomass and Nutrient Concentration of Understory Vegetation

Biomass and nutrient concentrations of herbaceous vegetation growing under the four tree species were measured in August (time of peak understory growth) 1989. Grass and other herbaceous vegetation from the five replicate plots of each species were cut at ground level by hand using 50 cm × 50 cm iron frames to define the sample area. One sample per plot was taken, because both the understory and forest-floor litter were very homogeneous in these mono-specific plots. The material was oven-dried and sub-samples were analyzed in the same manner as tree tissue. Statistical analyses (analysis of variance and LSD tests) were done to compare biomass (n = 5) and nutrient concentrations of understory vegetation among the tree species.

Forest Floor Litter

The amount of litter accumulating on the ground under the five replicate plots of the four species was measured in August 1989, December 1989, and in March, May and August 1990, as part of another study on litter dynamics (Montagnini et al. 1993). A 50 cm × 50 cm iron frame (one per plot) was used to demarcate an area in which all material to the top of the mineral soil was collected. The material was oven-dried, sorted (whole leaves, fragments and branches), and weighed. Chemical analysis was performed as described above for other tissue. Analysis of variance and LSD tests were used to compare the amounts of forest-floor litter among species, for each collection. The average amounts of each litter portion for each species (n = 5) was multiplied times the mean of nutrient concentration of each portion (n = 5), for the results obtained in August 1989; August results were used because the understory had also been sampled on that date. Then the nutrient contents (kg/ha) of all forest-floor litter fractions were summed to get the total nutrient accumulation in forest-floor litter.

Soil Fertility

For general chemical characteristics of the soils, samples were taken with a "Dutch type" auger at 0-15, 15-30, and 30-60 cm depths. Composite samples were taken in each of the five replicate plots for each species. Soils were sampled in May (end of dry season) of 1989, 1990 and 1991. Chemical analyses were performed at the Soils Laboratory of the College of Agriculture, University of Costa Rica, following standard methods currently used by soil testing laboratories in the country. The pH was measured in a

1:2.5 mixture of soil:deionized water. Ca and Mg were extracted with a 1N KCl solution, while P, K and micronutrients were extracted with a modified Olsen solution (Diaz Romeu and Hunter 1978). Cations were measured using an Atomic Absorption Spectrophotometer. P was measured colorimetrically after reaction with acid $(NH_4)_2MoO_4$ and $SnCl_2$, using a Spectrophotometer. Organic matter was measured with the Walkley-Black technique (Allison 1975) and total N was measured using a semi-Micro-Kjeldahl technique (Bremmer and Mulvaney 1982). Analysis of variance and LSD tests were run to compare the means for each parameter and soil depth ($n = 5$) among sites.

RESULTS

Aboveground Biomass and Nutrient Concentrations

Trees

V. guatemalensis and *S. microstachyum* had the highest stem and total aboveground biomass; these differences were statistically significant ($P < 0.05$) (Table 1). *V. guatemalensis* had the lowest branch biomass; no significant differences were found among the other three species ($P < 0.05$). There were no statistically significant differences ($P < 0.05$) in leaf biomass among the species, although values ranged from 4.3 tons/ha for *S. microstachyum* to 7.2 tons/ha for *V. guatemalensis* (Table 1).

The leguminous, N-fixing *S. microstachyum* had the highest N concentrations in leaf tissue (Table 2). *V. ferruginea* and *V. guatemalensis* had the lowest leaf N concentrations, but they had relatively high leaf Ca concentrations. *H. alchorneoides* had low or intermediate concentrations of most nutrients in leaves. *S. microstachyum* had relatively low Ca, K and Mg leaf concentrations. Similar trends of differences in nutrient concentrations among species held for branch tissue, with lower general values than those for leaves (Table 2). Stems had lower N concentrations than either leaves or branches (10-20% of leaf values), with the highest value found in *S. microstachyum*. The Ca values in stems were similar or greater than those of leaves, with the highest in *V. guatemalensis*; this species

TABLE 1. Means of tree diameter at breast height (dbh), height, aboveground biomass and annual increments[1].

Tree species	Dbh, cm	Height, m	Aboveground live biomass, kg/ha				Mean annual increment, $t\ ha^{-1}yr^{-1}$	
			Stem	Branches	Leaves	Total	Total	Stems
S. microstachyum	12.0a	8.9b	35,250a	15,250a	4,325a	54,825	13.7a	8.8a
V. ferruginea	10.3	8.1b	24,750b	14,250a	5,925a	44,925	11.2b	6.2b
V. guatemalensis	10.8a	12.0a	41,750a	6,500b	7,250a	55,500	13.9a	10.4a
H. alchorneoides	10.8a	9.0b	26,250b	12,250a	5,350a	43,850	12.0b	6.5b

[1] Differences between sites for a given parameter are statiscally significant ($P < 0.05$) when means are followed by different letters.

TABLE 2. Nutrient content in tissues of four indigenous trees grown in plantation at La Selva Biological Station, Costa Rica.[1]

Tissue/species	Nutrient content, %				
	N	P	Ca	Mg	K
Leaves					
S. microstachyum	2.25a	0.20ab	0.47c	0.22b	0.76a
V. ferruginea	1.58c	0.18ab	1.06ab	0.25b	0.41b
V. guatemalensis	1.49c	0.09c	1.22a	0.41a	0.29b
H. alchorneoides	1.81b	0.15b	1.02ab	0.41a	0.71a
Branches					
S. microstachyum	0.93a	0.15ab	0.44ab	0.15a	0.70bc
V. ferruginea	0.29c	0.09b	0.36b	0.10a	0.56bc
V. guatemalensis	0.29c	0.12b	0.44ab	0.16a	0.49c
H. alchorneoides	0.55b	0.17ab	0.59ab	0.15a	1.14a
Stems					
S. microstachyum	0.49a	0.07b	0.81b	0.04b	0.20c
V. ferruginea	0.17b	0.09b	1.12b	0.10a	0.23c
V. guatemalensis	0.26b	0.09b	1.46a	0.12a	0.42b
H. alchorneoides	0.32b	0.18ab	0.28c	0.10a	0.96a

[1] Differences between species for a given nutrient and tissue are statistically significant ($p < 0.05$) when means are followed by different letters.

also had high stem K and Mg. *H. alchorneoides* had the highest stem K and P, but it had low Ca and Mg.

Understory

There was no understory vegetation in either *V. ferruginea* or *V. guatemalensis* plots, probably because these two species had completely closed canopies at the time of sampling and light levels underneath were very low. Abundant growth was found under *S. microstachyum* (Table 3), whose small leaves and open crown allowed considerable light penetration. In understory vegetation, the highest N concentrations were found under *S. microstachyum* and

TABLE 3. Nutrient concentrations, biomass and nutrient content of understory vegetation of indigenous tree species growing in plantation.

(a) Nutrient concentrations of understory:[1]

Species plots	N	P	Ca	Mg	K
			(%)		
S. microstachyum	1.70a	0.13a	0.33ab	0.41b	1.01a
H. alchomeoides	1.35ab	0.73a	0.77a	0.45ab	0.79a

[1] For a given nutrient, means followed by a different letter are significantly different ($P < 0.05$).

(b) Biomass and nutrients of understory:

Species plots	Biomass (kg/ha)	N	P	Ca	Mg	K
				(kg/ha)		
S. microstachyum	874	14.9	1.1	2.9	3.6	8.8
H. alchomeoides	425	5.7	3.1	3.3	1.9	3.3

the highest Ca was found under *H. alchorneoides*; differences in Mg, K and P were not statistically significant (Table 3).

Forest-Floor Litter

Results of August 1989 showed that overall forest-floor biomass and nutrient accumulation was highest under *V. ferruginea* and *V. guatemalensis* (Table 4). Similar patterns of differences among species were observed from August 1989 to August 1990 (Montagnini et al. 1991, 1993). Nutrient concentrations in forest-floor material revealed a pattern similar to that of living tissue: in whole leaves, N was higher beneath *S. microstachyum*; Ca was higher beneath *V. guatemalensis*; K was higher beneath *H. alchorneoides*; Mg was higher beneath *V. guatemalensis* and *H. alchorneoides*; there were no statistically significant differences in P (Table 5). Branch and fragments in forest-floor litter showed similar trends of differences in nutrient content among species as whole leaves (Table 5).

TABLE 4. Biomass and nutrients of forest-floor litter; Totals include leaves, fragments and branches.

Species	Total Biomass (kg/ha)	Total nutrients N	P	Ca (kg/ha)	Mg	K
S. microstachyum	5612	95.1	4.3	41.6	8.2	6.6
V. ferruginea	17215	240.3	15.5	187.6	19.1	12.1
V. guatemalensis	11084	134.0	11.6	170.0	26.4	9.7
H. alchorneoides	4238	39.2	12.9	55.0	11.9	6.8

TABLE 5. Nutrient concentrations of forest-floor litter under four indigenous tree species in plantation.[1]

Tissue/species	N	Ca	K	Mg	P
			%		
Leaves					
S. microstachyum	2.10a	0.82c	0.12bc	0.16b	0.02a
V. ferruginea	1.79ab	1.34b	0.05c	0.09c	0.04a
V. guatemalensis	1.56b	1.92a	0.13bc	0.39a	0.10a
H. alchorneoides	1.05c	1.40b	0.25a	0.37a	0.08a
Fragments					
S. microstachyum	1.93a	0.89d	0.15ab	0.21cd	0.10a
V. ferruginea	1.41a	1.07cd	0.06c	0.12e	0.09a
V. *guatemalensis*	1.33a	1.59a	0.06c	0.24bc	0.10a
H. alchorneoides	1.19a	1.44ab	0.15ab	0.31a	0.08a
S. microstachyum	1.61abc	0.71d	0.12bc	0.12cd	0.05a
V. ferruginea	1.18c	0.92bc	0.08c	0.10d	0.11a
V. guatemalensis	1.29bc	1.19abc	0.10c	0.20bc	0.14a
H. alchorneoides	0.60d	1.12c	0.18a	0.24ab	1.04ab

[1] For a given nutrient and tissue, means followed by a different letter are significantly different ($P < 0.05$).

Soil Fertility

Analysis of samples collected in 1989 showed similar trends of differences in organic matter and N among sites as in 1988 (Montagnini and Sancho 1990a, 1990b), but unlike 1988, these differences were not statistically significant (P < 0.05) (Table 6). Soils under secondary forest had almost twice as much Ca as under *V. guatemalensis*, *V. ferruginea* or *H. alchorneoides*. Within the tree plantation, these were no significant differences among species in soil cation content. Results of similar soil measurements done in

TABLE 6. Organic matter (OM), total N, P, pH, Ca, Mg, and K in soils under the four native tree species in plantation, grass and secondary forest[1].

Site	Depth (cm)	OM (%)	N (%)	P (mg/kg)	pH	Ca (cmol/kg)	Mg (cmol/kg)	K (cmol/kg)
S. microstachyum	0-15	4.50a	0.278a	2.4a	5.1a	0.68b	0.44a	0.13a
	15-30	3.29a	0.224a	2.1a	5.1ab	0.52bc	0.22bc	0.14a
	30-60	1.88a	0.196a	1.8b	5.1a	0.54a	0.16a	0.14a
V. ferruginea	0-15	5.08a	0.320a	3.24a	5.0a	0.63bc	0.53a	0.16a
	15-30	3.66a	0.248a	2.48a	5.0c	0.35d	0.20c	0.10a
	30-60	2.94a	0.200a	2.50b	5.1a	0.33a	0.16a	0.15a
V. guatemalensis	0-15	4.30a	0.304a	2.30a	5.2a	0.47bc	0.50a	0.10a
	15-30	3.16a	0.232a	1.82a	5.1ab	0.38cd	0.22bc	0.07a
	30-60	2.42a	0.232a	2.00b	5.1a	0.38a	0.15a	0.08a
H. alchorneoides	0-15	5.16a	0.282a	1.5a	5.1a	0.31c	0.21b	0.88a
	15-30	2.77a	0.248a	1.5a	5.1ab	0.45bcd	0.19c	0.10a
	30-60	1.21a	0.158a	1.7b	5.2a	0.46a	0.20a	0.10a
Grass	0-15	3.98a	0.200a	4.1a	5.2a	0.57bc	0.38a	0.22a
	15-30	2.94a	0.236a	3.4a	5.1ab	0.51bcd	0.27bc	0.17a
	30-60	2.46a	0.194a	8.9a	5.2a	0.47a	0.20a	0.13a
Forest	0-15	5.11a	0.248a	2.3a	5.2a	1.16a	0.49a	0.21a
	15-30	3.83a	0.244a	2.0a	5.2a	0.92a	0.45a	0.17a
	30-60	2.46a	0.206a	1.4b	5.2a	0.92a	0.27a	0.12a

[1] Differences between sites for a given depth and parameter are statistically significant (p<0.05) when means are followed by different letters.

1990 and 1991 showed trends similar to those found in 1988 and 1989. When examining data from 1988 to 1991, no increasing or decreasing trends with time were apparent for any individual nutrient (Montagnini and Sancho, unpublished data).

DISCUSSION

Annual diameter increment (calculated by dividing diameter at breast height at time of measurement by tree age) was 3 cm/yr for *S. microstachyum* and just over 2.5 cm for the other species. These rates are within the expected range for tropical tree plantations (Lugo et al., 1990). Our values are consistent with reports by Espinoza Camacho and Butterfield (1989) and Gonzalez et al. (1990), who measured tree diameters periodically and calculated increments based on differences between consecutive measurements.

Aboveground Tree Biomass

The values of aboveground tree biomass reported here are greater than those reported for 4-year-old *Albizia lebbek* (Parrotta 1989), and for 5.5-year-old *Leucaena leucocephala* (Wang et al. 1991), both growing in dense plantations for biomass production in Puerto Rico. Mean annual increments for aboveground biomass (Table 1) lie within the ranges reported elsewhere for monospecific plantations in the humid tropics; for example, *Eucalyptus citridiora* (11.8 tons/year) in Brazil, *E. deglupta* (13.1) in Costa Rica, and *Gmelina arborea* (12.9) in Costa Rica (Lugo et al. 1988). Our values are similar to those reported for *E. robusta* (12.2), but less than *Albizia procera* (22.5) and *Casuarina equisetifolia* (36.2) planted at 2m × 2m distance in Puerto Rico; growth rates in this Puerto Rican site were higher than those reported for other tropical sites (Lugo et al. 1990). However, the increments shown here (Table 1) are lower than those reported for some of the fastest growing trees in the humid tropics such as *Acacia mangium* and *Leucaena leucocephala* (Young 1989).

Annual increments of stemwood biomass for broadleafs ranges from 1 to 28 tons/ha/yr (Wadsworth 1983). Fast growing species such as *Gmelina arborea* and *E. saligna* range from 10-20 and 8-28 tons/ha, respectively, and relatively slower growing species such as *Swietenia* spp. and *Tectona grandis* range from 1-4 and 3-12 tons/ha, respectively (Wadsworth 1983). Thus, the mean annual stemwood biomass increments for the species of this study (Table 1) also fall within the ranges reported for other fast-growing tree species in the humid tropics.

These comparisons are useful to put our data in perspective; however, to assert real differences in growth rates of tree species, data should be compared among species grown under similar conditions, including life zone and characteristics of site and management. Investigations to assess the growth rates of the species of this study on different sites are under way. The relatively fast growth rates reported here tend to confirm predictions by Lugo et al. (1988), who suggested that tree plantations increase biomass production with increasing water availability, provided the climate is not excessively wet. High annual rainfall, such as that registered at La Selva, may decrease soil cation availability, which can in turn affect tree growth. For example, a substantial decrease in extractable cations, with a corresponding increase in soil acidity occurred during the month of peak rainfall (Montagnini and Sancho 1990a). However, we do not know if these changes in soil nutrient content have any negative effects on tree productivity.

Nutrient Concentrations in Tree Tissue

Nitrogen content of *S. microstachyum* leaves was similar to values reported for many N-fixing trees; values summarized by Young (1989) range from 1.63% for *Acacia auriculiformis* to 4.4% for *Gliricidia sepium*, with a majority of N-fixing trees in the 2-3% N range. The same can be said for *S. microstachyum*'s leaf P content, which was similar to other N-fixing species (Young 1989). Leaf Ca and K content of *S. microstachyum* was approximately half of most values reported for N-fixing trees (Young 1989); Mg was also relatively low, about half the values reported for *Albizia procera* and *Leucaena leucocephala* in Puerto Rico (Wang et al. 1991). The leaf N value reported here for *S. microstachyum* was similar, while P and cations were higher than in another species of the same genus, *S. adstringens* Harms, growing in a drier region in San Pablo, Brasil (Pagano et al. 1982). The two *Vochysia* species and *H. alchor-*

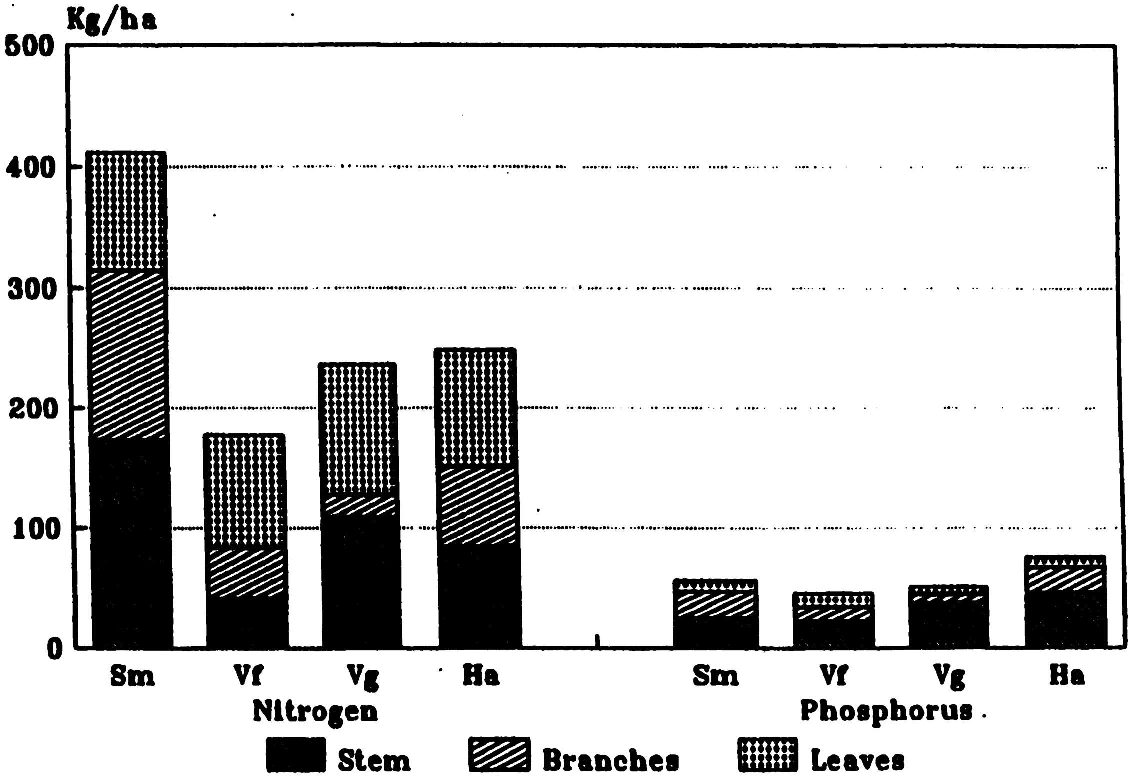
neoides had higher leaf Ca, similar to values reported in the literature for non-N-fixing tropical trees. The two *Vochysia* species' higher leaf Mg was not comparable to other reports in the literature (Young, 1989; Wang et al. 1991). The leaf nutrient values reported here for *S. microstachyum*, *V. guatemalensis* and *V. ferruginea* were similar to those found in August 1990 when leaves from a total of seventeen tree species growing in 2-4 year-old mixed-stands were sampled as part of another research project at La Selva (Montagnini and Sancho, unpublished data). *H. alchorneoides* was not included in such study.

S. microstachyum's stem N was greater than values reported for other N-fixing trees, including *Leucaena* spp. (Young, 1989; Wang et al. 1991), but it was lower than that of *S. adstringens* (Pagano et al., 1982). The other three species had lower N stem contents, with values comparable to those reported for other non-N-fixing tree species, including *E. robusta* in Puerto Rico (Wang et al. 1991), and *Gmelina arborea* in Nigeria (Chijiocke 1980, in Young 1989). *S. microstachyum* had similar stem P and K, higher Ca and lower Mg than *S. adstringens* (Pagano et al. 1982). With respect to stem cation content, the most outstanding finding was the high values of stem Ca found in the two *Vochysia* species and the high stem K found in *H. alchorneoides*, which are all above those reported in the literature (Wadsworth 1983; Young 1989; Wang et al. 1991). Stem Mg was similar to other species reported in the literature.

Nutrient Accumulation in Aboveground Tree Biomass

Consistent with trends found in N tissue concentrations, *S. microstachyum* had the highest accumulation of N in stem and branch biomass (Figure 1). Taking leaves and branches together, approximately 200 kg/ha, or 60% of *S. microstachyum*'s aboveground biomass N would be left on the site at time of harvest if only stems were removed. *V. ferruginea* and *H. alchorneoides* showed a higher potential for N recycling than *V. guatemalensis*, due to their more even distribution of N in stems, branches and leaves. *H. alchorneoides* had the highest aboveground tree biomass P; the other species had all similar values, equivalent to 60-70% those of *H. alchorneoides* (Figure 1).

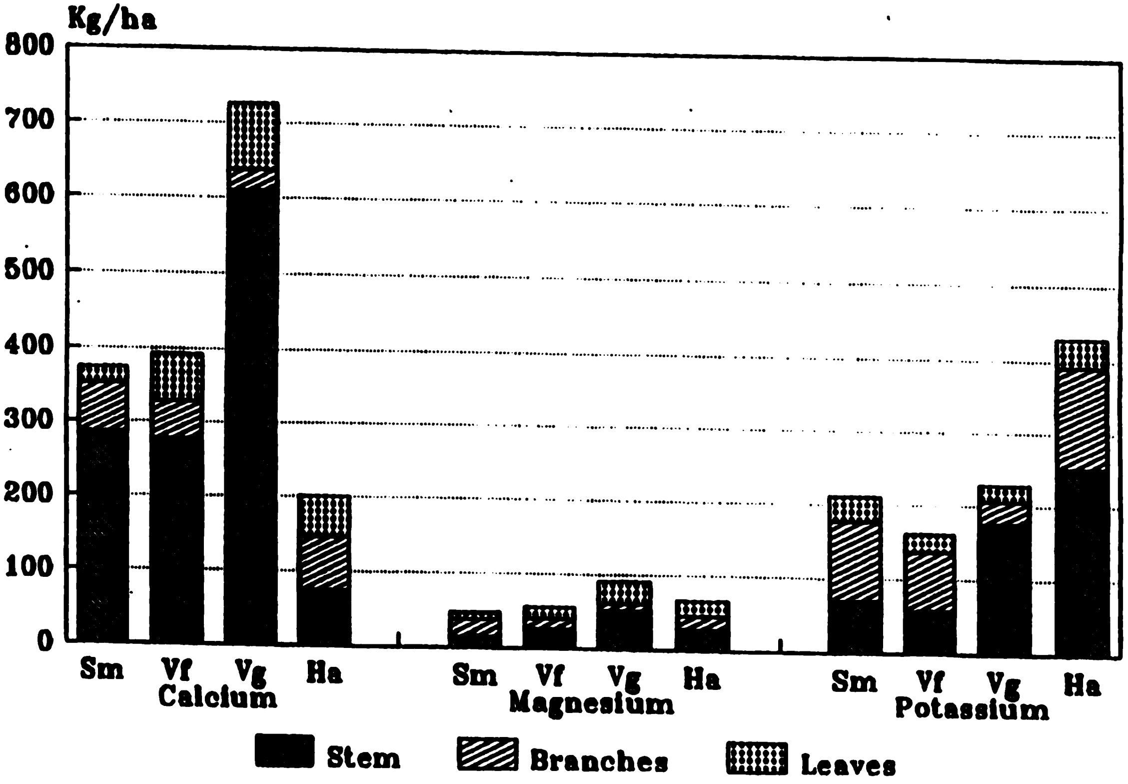
FIGURE 1. Aboveground tree nutrients in a 4-yr-old plantation of indigenous trees at La Selva Biological Station, Costa Rica: nitrogen and phosphorus.
Sm: *S. microstachyum*, Vf: *V. ferruginea*, Vg: *V. guatemalensis*, Ha: *H. alchorneoides*



V. guatemalensis, with the highest stem biomass and Ca concentration, also had the highest stemwood Ca (over 600 kg/ha, or 84% of aboveground tree biomass Ca), approximately twice as much as either *S. microstachyum* or *V. ferruginea*, and several times more than *H. alchorneoides* (Figure 2). Therefore, the harvest of *V. guatemalensis* trees could substantially reduce the amount of Ca in the site. However, the potentially recyclable portion (leaves+ branches) for this species was relatively large (over 100 kg/ha), although it represented just 16% of aboveground tree biomass. The proportion of Ca in stems relative to aboveground tree biomass was similar for *S. microstachyum* and *V. ferruginea*, but the absolute amounts were less than half those of *V. guatemalensis*. *H. alchorneoides* again showed a more even distribution of Ca in stems, leaves and branches, with aboveground tree biomass Ca slightly over half those of *S. microstachyum* and *V. ferruginea*. Similar to Ca levels, *V. guatemalensis*, with its high stem biomass and high Mg concentration also had the highest Mg in stemwood (Figure 2). Again, removal of *V. guatemalensis* stems would affect the sites's Mg budget more dramatically than would the other species, especially if the whole tree was harvested. The other species showed lower proportions of aboveground tree biomass Mg in their stems (Figure 2). For K the picture changed; the highest accumulation of K in stems was found in *H. alchorneoides* (Figure 2), followed by *V. guatemalensis*. Thus, whole-tree harvest of *H. alchorneoides* and *V. guatemalensis* may have the greatest affects on the site's K budget. *S. microstachyum* and *V. ferruginea* had proportionally more K (over 65%) in the leaves + branches portion; however, *H. alchorneoides*'s absolute amounts of K in the recyclable tree parts was the largest of the four (over 180 kg/ha).

These results confirm previous reports on the negative effects of whole-tree harvest on site nutrient pools; for example, Bruijnzeel and Wiersum (1985) calculated that total tree harvest of a 40-year-old plantation of *Agathis dammara* in upland Java would remove the entire input of K and Ca, almost half of the Mg input and twice as much the input of P. Our results suggest that leaving tree residues in the site could greatly decrease the negative impacts of nutrient removal at harvest, with different consequences depending on the species. For example, slash from *V. guatemalensis* will be more rich

FIGURE 2. Aboveground tree nutrients in a 4-yr-old plantation of indigenous trees at La Selva Biological Station, Costa Rica: calcium, magnesium and potassium.
Sm: *S. microstachyum*, Vf: *V. ferruginea*, Vg: *V. guatemalensis*, Ha: *H. alchorneoides*



in Ca and Mg, residues from *S. microstachyum* will return appreciable amounts of N, and so on.

Our results are based on nutrient concentrations for a young plantation; the conclusions may change if younger trees had higher nutrient concentrations than older trees. However, Bruijnzeel and Wiersum (1985) found that stemwood P concentrations of 35-year-old *Agathis dammara* were lower than those of younger trees, whereas no such differences were found for other nutrients. Altering the rate of nutrient removal in products is probably one of the most important design considerations in planning sustainable plantations (Wang et al. 1991). The tree species and parts of the tree removed from the site will determine the nutrient "cost" of removal. This can be assessed before hand with nutrient and biomass sampling and estimation.

Nutrient Accumulation in Understory Vegetation

Nitrogen accumulation in the total understory biomass was higher under *S. microstachyum* (14.9 kg/ha), although this amount represented only 3.6% of aboveground tree biomass N (Table 3). For *H. alchorneoides*, understory biomass N was 5.7 kg/ha or 2.3% of aboveground tree biomass N. For the other nutrients, accumulation in understory biomass under *S. microstachyum* ranged from 0.8 to 7.7%, and under *H. alchorneoides* it ranged from 0.8 to 4.1% of aboveground tree biomass nutrients (Table 3). Since vegetation in the understory apparently accounts for a relatively small proportion of nutrients, as compared to the whole tree, manipulations of the understory should have little effect on nutrient cycling at the site. For example, weeding should have a relatively minor effect on nutrient recycling, unless the understory is removed or turned over many times per year. This also suggests that intercropping with annual, herbaceous species that attain similar biomass as the understory found under *S. microstachyum* or *H. alchorneoides* may not have a substantially negative effect on the balance of nutrients at the site. Since samplings of understory biomass were taken at a time when the quantity of biomass was at its peak, the amounts reported here are considered to approximate those that could be attained by crops. However, an accurate assessment of the influence of intercropping should involve measurements of the crop's nutrient requirements and parts removed at harvest. Bruijnzeel and Wiersum (1985) also concluded that the use of controlled intercropping in tree plantations in upland Java, with care to minimize soil erosion, was acceptable from a nutrient conservation point of view. Additionally, they argue that farmers may be willing to use fertilizers for the crops, and the residual effects of the nutrients applied may even increase the growth of the trees in early stages.

Nutrient Accumulation in Forest-Floor Litter

Forest-floor biomass and nutrient accumulation were highest under *V. ferruginea*; N in forest-floor litter under this species was greater than its aboveground tree biomass N (Table 4 and Figure 1). As noted above, *V. ferruginea*'s leaf and branch biomass account for a large proportion of aboveground tree biomass. This species is self-pruning, a characteristic that enhances shedding of branches and leaves, and occasional prunings may have added even more tree litter to the forest floor. Litter decomposes relatively slowly under *V. ferruginea*, contributing to the high accumulation noted above (Montagnini et al. 1991, 1993). Forest-floor litter Ca, Mg and P were also considerable under *V. ferruginea* (Table 4), a finding especially relevant for P, because of the potential site deficiencies in this element mentioned earlier. Forest-floor biomass nutrients were also high under *V. guatemalensis*, and again this was more important for N, Ca, Mg and P. Thus, in spite of this species' fast growth rate, nutrient recycling from litter may at least partially compensate for soil nutrient depletion. Forest-floor litter N was more than double under *S. microstachyum* than under *H. alchorneoides*, although both species had similar forest-floor litter biomass (Table 4); the reverse was true for P.

These results show that the forest floor is an important compartment for nutrient accumulation and recycling, particularly for N, Ca, Mg and P, but less for K, with marked differences among tree species. If the forest floor is burned or collected for fuelwood, a substantial loss of organic matter and nutrients may occur. Wang et al. (1991) also found that with the exception of K, nutrients in forest-floor litter were equivalent to a large proportion (16-50%) of the nutrients contained in the aboveground tree biomass, and they concluded that if the litter were left on the floor after harvest, it would represent a substantial reservoir for the next rotation.

Impacts of Trees on Soil Nutrients

The impacts of plantation trees on soil nutrients depend on: (1) the annual nutrient uptake by the trees in relation to the nutrient supplying capacity of the soil, (2) nutrient recycling, (3) the parts of the tree removed, whether the whole tree or stemwood, and their biomass and nutrient content at harvest, and (4) the total/available soil nutrient pools. A look at these relationships for *V. guatemalensis*, the fastest-growing, and seemingly the most nutrient-demanding species of this study, will illustrate this point. Nutrient retention by *V. guatemalensis* (calculated by dividing biomass nutrients by plantation age) averaged 58 kg of N, 181 kg of Ca, 57 kg of K, 22 kg of Mg and 13 kg of P/ha/yr. The N, Ca, Mg and K values are all twice those reported by Wadsworth (1983) for teak plantations; the P value is similar. Although these nutrient values are high, they should be compared with the nutrient-supplying capacity of the soil. For example, Wadsworth (1983) compared data from the rates of annual nutrient uptake of various agricultural crops on upland Ultisols and Oxisols in Puerto Rico (N = 90-120 kg/ha/year, K = 50-90, Ca = 86-109, Mg = 68-98), with the mean rates of annual nutrient retention for fast-growing teak and pine plantations. He concluded that the capacity of the soils to supply nutrients was enough for the needs of the plantations and that plantation trees could be harvested without creating soil deficiencies, except maybe for P.

At present, no data are available on the nutrient-supplying capacity of the soils of this study. Long-term soil fertility measurements, as well as comparisons of vegetation and soil nutrient pools (Montagnini and Sancho 1993) may show specific trends of soil nutrient accumulation or deficiencies. Our results show that following the initial site improvement which was found in 1988, approximately one year after canopy closure (Montagnini and Sancho 1990a, 1990b), no further positive or negative changes in soil chemistry were detected. Lundgren (1980) proposed that ameliorating effects of plantation forests on soils occur only during the 5-10 year period immediately following canopy closure (the "fallow enrichment phase"). During the maximum-production phase an actual deterioration of site quality would occur, as mineral nutrients are taken up by the trees and litter accumulates on the floor due to unfavorable conditions for organic matter decomposition (Lundgren 1980). However, Sanchez et al. (1985) reviewed the information available at the time to test Lundgren's model, and concluded that deleterious effects on soils occur only during plantation establishment. Continued soil measurements at the La Selva site will be needed to confirm the trends reported for 1988-1991.

To obtain a more realistic picture on soil nutrient budgets, other components and transfers should be considered. Weathering inputs are unlikely to be of major importance in these soils; atmospheric deposition is expected to be small in magnitude, although it may be important over long spans of time (Szott et al. 1991). Additionally, we are not considering the ability of the trees to absorb nutrients from below 60 cm soil depth; or leaching losses, which may be considerable under the high rainfall conditions at La Selva. However, our results so far tend to agree overall with the conclusions of Wadsworth (1983), and Bruijnzeel and Wiersum (1985), pointing to P as the most critical element with a potential for depletion from soils following cultivation and harvest of relatively fast-growing trees in monospecific plantations. Finally, as tree species differ in their nutrient demands, as well as in their effects on soils, mixed-species designs can be more advantageous for site nutrient conservation if designs are planned so as to complement each species' nutrient demands and effects.

CONCLUSIONS

Biomass and stemwood annual increments in young stands of the indigenous tree species *S. microstachyum*, *V. guatemalensis*, *V. ferruginea* and *H. alchorneoides*, growing on infertile soils in the Atlantic humid lowlands of Costa Rica, were comparable to those reported for other tree species in the humid tropics. The four species differed in their tissue nutrient content and nutrient accumulation in aboveground biomass. *S. microstachyum* had the highest accumulation of N in stem, branch and total aboveground tree biomass. *V. guatemalensis* had the highest accumulation of Ca and Mg in the biomass, while *H. alchorneoides* had the highest stem K and P.

Whole-tree harvest will have more negative effects on site nutrients than stem harvest only; although the effects will vary according to the species and tree parts removed. Nutrient accumulation by the understory had a relatively small role on the site's nutrient budget. The forest-floor litter was a major compartment for nutrient accumulation and recycling.

REFERENCES

Allen, O.N. and Allen, E.K. 1981. The leguminosae: A source book of characteristics, uses, and nodulation. University of Wisconsin Press, Madison, Wisconsin, 812 pp.

Allison, L.E. 1975. Organic carbon. In: C.A. Black (Editor), Methods of Soil Analysis, Part 2. Amer. Soc. Agron., Inc., Madison, Wisconsin, pp. 1367-1378.

Bremmer, J.M. and Mulvaney, C.S., 1982. Nitrogen-total. In: A.L. Page, R.H. Miller and R.R. Keeney (Editors), Methods of Soil Analysis, Part 2, 2nd. ed. Amer. Soc. Agron., Inc., Madison, Wisconsin, pp. 595-624.

Bruijnzeel, L.A. and Wiersum, K.F. 1985. A nutrient balance sheet for *Agathis dammara* Warb. plantation forest under various management conditions. For. Ecol. Manage. 10:195-208.

Bruijnzeel, L.A. 1991. Nutrient input-output budgets of tropical forest ecosystems: a review. J. Trop. Ecol. 7:1-24.

Chudnoff, M. 1984. Tropical timbers of the world. USDA Forest Service, Agricultural Handbook 605, Washington, DC.

Diaz-Romeu, R. and Hunter, A. 1978. Metodo para el muestro de suelos, analisis quimico de suelos y tejido vegetal e investigacion en invernaderos. CATIE, Turrialba, Costa Rica, pp. 9-11, 15-27.

Espinoza Camacho, M. and Butterfield, R. 1989. Adaptabilidad de 13 especies nativas maderables bajo condiciones de plantacion en las tierras bajas humedas del Atlantico, Costa Rica. In: R. Salazar (Editor), Manejo y aprovechamiento de plantaciones forestales con especies de uso multiple. Actas Reunion IUFRO, Guatemala, 3-7 de Abril 1989. CATIE, Turrialba, Costa Rica, pp. 159-172.

Evans, J. 1987. Site and species selection–Changing perspectives. For. Ecol. Manage. 21:299-310.

Gladstone, W.T. and Ledig, F.T. 1990. Reducing pressure on natural forests through high-yield forestry. For. Ecol. Manage. 35:69-78.

Gonzalez, E., Butterfield, R., Segleau, J. and Espinoza, M. 1990. Primer Encuentro Regional sobre Especies Forestales Nativas de la Zona Norte y Atlantica. Memoria, 28-29 Julio 1989, Chilamate, Costa Rica. Instituto Tecnologico de Costa Rica, Cartago, Costa Rica, 46 pp.

Jorgensen, J.R. and Wells, C.G. 1986. Tree nutrition and fast-growing plantations in developing countries. Int. Tree Crops J. 3:225-244.

Lugo, A.E., Brown, S. and Chapman, J. 1988. An analytical review of production rates and stemwood biomass of tropical forest plantations. For. Ecol. Manage. 23:179-200.

Lugo, A.E., Wang, D. and Bormann, F. 1990. A comparative analysis of biomass production in five tropical tree species. For. Ecol. Manage. 31:153-166.

Lundgren, B. 1980. Plantation forestry in tropical countries–physical and biological potentials and risks. Swedish University of Agricultural Sciences. International Rural Development Centre. Rural Development Studies 8. Uppsala.134 pp.

Montagnini, F. and Sancho, F. 1990a. Influencia de seis especies de arboles nativos sobre la fertilidad del suelo en una plantacion experimental en la llanura del Atlantico de Costa Rica. Yvyrareta (Argentina), 1(1):29-49.

Montagnini, F. and Sancho, F. 1990b. Impacts of native trees on tropical soils: a study in the Atlantic lowlands of Costa Rica. Ambio, 19(8):386-390.

Montagnini, F., Sancho, F., Ramstad, K. and Stijfhoorn, E. 1991. Multipurpose trees for soil restoration in the humid lowlands of Costa Rica. In: D.A. Taylor and K.G.Mc Dicken (Editors), Research en multipurpose trees in Asia. Proceedings of an International Symposium, November 19-23, 1990, Los Banos, Philippines. Winrock Int. Inst. Agric. Develop., Bangkok, pp. 41-58.

Montagnini, F. and Sancho, F. 1993. Nutrient budgets of young plantations with native trees: strategies for sustained management. In: W. Bentley and M. Gowen (Eds.). Forests and Wood-Based Biomass Energy as Rural Development Assets. Proceedings of a workshop held in Old Saybrook, CT, USA, February 23-27, 1992. Winrock Int. Inst. Agric. Develop. (in press).

Montagnini, F., Ramstad, K. and Sancho, F. 1993. Litterfall, litter decomposition and the use of mulch of four native tree species in the Atlantic lowlands of Costa Rica. Agrofor. Sys. (in press).

Pagano, S.N., Cesar, O. and Santos, P.S. 1982. Compartimentacao em orgaos vegetativos aereos em tres especies de leguminosas num sistema de cerrado. Silvicultura on Sao Paulo. Edicao Especies. Vol. 16A. Parte 1. pp. 536-544. Instituto Florestal Coordenador da Pesquisa de Recursos Naturais. Secretaria de Agricultura e Abastecimento. Sao Paulo, Brasil.

Parrotta, J.A. 1989. The influence of management practices on the biogeochemical stability of tropical fuelwood plantations. Trop. Ecol. 30:1-12.

Perry, D.A. and Maghembe, J. 1989. Ecosystem concepts and current trends in forest management: time for reappraisal. For. Ecol. Manage. 26:123-140.

Pierce, S.M. 1991. Environmental history of the La Selva Biological Station: how colonization and deforestation of Sarapiqui canton, Costa Rica have altered the ecological context of the station. In: H.K. Steen and R.P. Tucker (Editors), Changing tropical forests: Historical perspectives in today's challenges in Central and South America. Forest History Society, Durham, NC, USA. (in press).

Sanchez, P.A., Palm, C.A., Davey, C.B., Szott, L.T. and Russell, E.C. 1985. Tree crops as soil improvers in the humid tropics? In: M.G.R. Cannell and J.E. Jackson (Editors), Attributes of trees as crop plants. Institute of Terrestrial Ecology, Natural Environmental Research Council, Abbots Ripton, Huntingdon, England, pp. 327-350.

Sancho, F. and Mata, R. 1987. Estudio detallado de suelos. Estacion Biologica La Selva. Organizacion para Estudios Tropicales, San Jose, Costa Rica, 162 pp.

Szott, L.T., Fernandes, E.C.M. and Sanchez, P.A. 1991. Soil-plant interactions in agroforestry systems. For. Ecol. Manage., 45:127-152.

Wadsworth, F.H. 1983. Production of usable wood from tropical forests. In: F.B. Golley (Editor), Tropical Rain Forest Ecosystems. Structure and Function. Ecosystems of the World 14A. Elsevier, New York, pp. 279-288.

Wang, D., Bormann, F.H., Lugo, A.E. and Bowden, R.D. 1991. Comparison of nutrient-use efficiency and biomass production in five tropical tree taxa. For. Ecol. Manage., 46:1-21.

Whitmore, J.L. and Hartshorn, G.S. 1969. Literature review of common tropical trees. Tropical Forestry Series, Contribution No. 8. Institute of Forest Products, College of Forest Resources, University of Washington, Seattle, 113 pp.

Young, A. 1989. Agroforestry for soil conservation. ICRAF, Science and Practice of Agroforestry. C.A.B. International and International Council for Research in Agroforestry, Wallingford, UK, 276 pp.

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Multipurpose Trees for Soil Restoration in the Humid Lowlands of Costa Rica

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Summary

This paper describes impacts of seven native species of economic value (*Stryphnodendron excelsum, Dalbergia tucurensis, Dipteryx panamensis, Vochysia ferruginea, Vochysia hondurensis, Tabebuia rosea* and *Hyeronima oblonga*) on soil fertility and nutrient cycling in the humid lowlands of Costa Rica. Results of a three-year study of pure plantation stands revealed that soil conditions were improved: in the top 15 cm, soil nitrogen and organic matter were higher under the trees than under grass, with values close to those found in an adjacent 20-year-old forest. Highest values for soil organic matter, total N, Ca and P were found under *V. ferruginea*. Soil nitrate and increased soil N mineralization were higher under the two leguminous species, *S. excelsum* and *D. tucurensis*.

Litterfall was higher under *V. ferruginea, V. hondurensis* and *S. excelsum*. *D. tucurensis* had the highest concentrations of N, P, Ca, Mg and K in living leaf and in litter tissue, but there was greater accumulation of forest floor litter under *V. ferruginea* and *V. hondurensis*. Greatest understory biomass was found under *T. rosea, S. excelsum* and *D. tucurensis*. The highest nutrient concentrations in understory biomass were found under *S. excelsum* and *D. tucurensis*.

Other investigations used the four best-growing species of this experiment: *S. excelsum, V. ferruginea, V. hondurensis* and *H. oblonga*. *H. oblonga* and *V. ferruginea* had the highest biomass of fine roots (< 1 mm) in the 0-15 cm soil depth, while *S. excelsum* and *V. hondurensis* had a more even root distribution in the soil profile. In a study of leaf litter decomposition, *V. ferruginea* showed the slowest rate of weight loss. When leaves of these four species were mixed with soil as mulches for a maize crop, initial maize growth was better with *S. excelsum* and *H. oblonga*.

Introduction

Agroforestry systems and tree plantations can help restore soil fertility of locations that have been abandoned after extensive use for agriculture or cattle raising. Information on native species that can be used for soil restoration in the tropics is scarce. Native trees can be more appropriate than exotics because (1) they are better adapted to local environmental conditions, (2) seeds and other propagules are locally available, and (3) farmers are familiar with them and their uses.

In the Atlantic lowlands of Costa Rica, the Costa Rican Forest Service, Direccion General Forestal (DGF) is conducting experiments on the growth performance of tree species for plantation. Among the species currently recommended by DGF to farmers (*Gmelina arborea, Pinus caribaea, Eucalyptus deglupta* and *Cordia alliodora*), only *C. alliodora* is native to the region. In 1985, DGF established a plantation of 13 native tree species at the La Selva Biological Station of the Organization for Tropical Studies (OTS). After three years, four of these species (*Stryphnodendron excelsum, Vochysia hondurensis, Vochysia ferruginea* and *Hyeronima oblonga*) exhibited growth rates equal to or greater than those reported for

Montagnini, F., Sancho, F., Ramstad, K. and Stijfhoorn, E. 1991. Multipurpose trees for soil restoration in the humid lowlands of Costa Rica. pp. 41-58 In Taylor, D. A. & Mc Dicken, K. G. (eds.). *Research on multipurpose trees in Asia*. Winrock International Institute for Agricultural Development. Bangkok. 259 pp.

the officially recommended species (Espinoza and Butterfield 1989). In 1988, we initiated an independent study on the impacts of seven species in this experiment on soil fertility and mechanisms of nutrient recycling (Montagnini and Sancho 1990a, 1990b). Here we report on the impacts of trees on soil fertility, rates of litterfall and litter decomposition, root biomass, and nutrient recycling. The results are being used to design tree-based productive systems such as agroforestry combinations and mixed tree plantations. The results may also apply to other humid tropical areas with similar soils.

Study site

The experimental plantation was established in December 1985 on abandoned pasture at the OTS La Selva Biological Station. Soils are Fluventic Dystropepts derived from alluvially deposited volcanic materials; they are deep, well drained, stone-free, with low or medium organic matter content, moderately heavy texture, and generally acid and unfertile (Sancho and Mata 1987). The area had been cleared in the 1950s and grazed until 1984. The dominant species in the pastures were grasses (*Olyra latifolia, Melinis minutiflora*), ferns (*Pteridium* sp.), and bushes (*Psidium guajava* and *Piper culebranum*). In the pastures there were patches of approximately 20-year-old forest with: *Pentachlethra macroloba*, a mimosoid, N-fixing legume dominant in the primary forest at La Selva; *Piper culebranum*, and species of the Melastomataceae family; and ferns (*Pteridium* spp.) and tree seedlings in the understory. The site was cleaned manually before planting. The tree species were planted in a randomized block design with five replicates, each plot containing seven rows of seven trees (14 m x 14 m each), with two meters between trees. Five 14 m x 14 m plots were also established in an adjacent open area with grass, and in a nearby patch of secondary forest. During the first year, weeds were manually cut four times; weeding was done mechanically thereafter until canopy closure made it no longer necessary. The grass was weeded simultaneously to keep it free of trees and with comparable treatments.

The seven species used for our compariso of soil fertility and nutrient recycling are presented in Table 1. The criteria for species selection were: (1) good growth, (2) presence of root nodules in the leguminous species, and (3) other potentially important effects on soils. Although it does not fix nitrogen, the leguminous *D. panamensis* was included because it has wide distribution in tropical Latin America (Holdridge and Poveda 1975). *V. ferruginea* is a self-pruning pioneer species that forms uniform, even-aged stands in abandoned fields; its wood is used for plywood and construction. Botanical characteristics and general uses of all the species are described by Holdridge and Poveda (1975), Hartshorn (1983), Standley (1937-38), and Hartshorn and Hammel (unpublished). All the species have economi uses (timber of medium to high quality) and seeds are available from natural forests at

Table 1. Species studied for their effects on soils and nutrient cycling.

Scientific name	Common name	Family
Stryphnodendron excelsum	vainillo	Leguminosae (mimosoid)
Vochysia ferruginea	botarrama	Vochysiaceae
Vochysia hondurensis	mayo	Vochysiaceae
Hyeronima oblonga	pilon	Euphorbiaceae
Dalbergia tucurensis	granadillo	Leguminosae (papilionoid
Dipteryx panamensis	almendro	Leguminosae (papilionoid
Tabebuia rosea	roble sabana	Bignoniaceae

*Does not fix nitrogen.

La Selva and elsewhere in the region. Detailed studies on seed and germination characteristics are presented by Gonzalez (in press).

Initial selection of species for studies of impacts on soils was made in 1987, when the plantation was 2.5 years old. In 1988, *H. oblonga* was added due to its better growth that year; *T. rosea* was dropped due to stunted growth. In 1989 and 1990, detailed studies on root biomass and litter decomposition concentrated on the four most promising species (i.e., best growth): *S. excelsum, V. ferruginea, V. hondurensis* and *H. oblonga.*

Materials and Methods

Soil fertility

For general chemical characteristics of the soil, samples were taken with a "Dutch type" corer at 0-15, 15-30, and 30-60 cm depth. During the first year, soils were sampled in April (dry season) and August (rainy season); in 1989 and 1990, soils were sampled in May only (end of dry season). Chemical analyses were performed at the Soils Laboratory of the College of Agriculture, University of Costa Rica, following standard methods currently used by soil testing laboratories in the country. The pH was measured in a 1:2.5 mixture of soil: de-ionized water using a Corning 7 pH meter. Ca and Mg were extracted with a 1 N KCl solution, while P, K, and micronutrients were extracted with a modified Olsen solution (Diaz Romeu and Hunter 1978). Cations were measured using a Perkin Elmer 2380 Atomic Absorption Spectrophotometer. P was measured colorimetrically after reaction with acid $(NH_4)_2MoO_4$ and $SnCl_2$, using a Perkin Elmer-Coleman 295 Spectrophotometer. Organic matter was measured with the Walkley-Black technique (Allison 1975) and total N was measured using a semi-Micro-Kjeldahl technique (Bremmer and Mulvaney 1982).

Soil nitrogen mineralization

For N mineralization and nitrification studies, soils were sampled at 0-15 cm with a 2.5 cm diameter soil corer, using the same plots as for soil general chemistry. These measurements were taken quarterly, starting in May 1989. NO_3-N and NH_4-N were extracted on field moist soils with 2 NKCl, and measured using a Lachat Flow Injection Analyzer. One subset of samples was extracted immediately after sampling; another subset was incubated in plastic cups in the laboratory (Keeney 1982) for seven days. The difference between final (after incubation) and initial NO_3-N concentration or NO_3-N + NH_4-N concentration gave the net nitrification or net N mineralization potential rates, respectively. These measure soil N availability (Keeney 1982).

Nutrient concentration in living biomass

To obtain an indication of nutrient requirements and potential effects on nutrient cycling, living tree tissue was sampled in August 1989. Using a pole pruner, leaves and branches were harvested from one tree per plot for the seven species. At least two whole branches of opposite orientation on the upper portion of the canopy were sampled. Leaves from the tip, medium, and lower portions of each branch were pooled to obtain one sample per tree. Portions of tip, medium, and bottom parts of branches were cut and pooled in the same manner. Taking advantage of plot thinning performed in August 1989, we were able to obtain stem samples (lower, medium, and bottom parts) of *S. excelsum, V. ferruginea* and *V. hondurensis* for chemical analysis. *H. oblonga* plots were thinned in July 1990, at which time we also obtained stem samples for chemical analysis. Roots were sampled as described below; subsamples were also analyzed for their nutrient content. The material was oven-dried at 70°C and ground for chemical analysis. The total N, P, Ca, K, Mg, Cu, Fe, Zn, and Mn were measured on nitro-perchloric digests: N and P were measured using a Lachat Flow Injection Analyzer, while cations were measured using an Atomic Absorption Spectrophotometer.

Biomass and nutrient concentration of understory vegetation

Biomass and nutrient concentration of herbaceous vegetation growing under the seven species were measured in August 1989 to assess the contribution of the trees to nutrient redistribution. Grass and other herbaceous vegetation were cut at ground level by hand using 50 x 50 cm iron frames to define the sample area. The material was oven-dried and analyzed in the same manner as tree tissue.

Root biomass and chemistry

Roots were sampled in May-June 1989 in *S. excelsum*, *V. ferruginea*, *V. hondurensis*, *H. oblonga*, grass, and secondary forest using an 80 mm diameter x 150 mm length root auger (Stijfhoorn 1989). Sampling sites within each plot were chosen randomly in areas within 1 m from the trees. Two root cores from 0-15, 15-30, and 30-60 cm depth were obtained per plot. The roots were separated from the soil by manual wet sieving, and divided into four size classes: fine (< 1mm), medium fine (1-2mm), medium coarse (2-5mm), and coarse roots (> 5mm). Roots in all categories were oven-dried and weighed. For chemical analysis, roots from 1-5 mm were pooled together, thus having three categories: < 1, 1-5, and > 5mm. Chemical analysis was performed as described above.

Litter fall

Litter was collected from 90 x 55.5 cm litterfall traps made of a wooden frame with fiberglass screen bottoms (1 mm mesh size), set at 50 cm above the ground. There was one trap per plot for the seven species of the study, 35 traps total. The traps were emptied every two weeks, their contents oven-dried (70°C), sorted (leaves and branches), and weighed. Collections began in April 1988 and continued through 1989-90. Chemical analyses, as described above, were performed on samples of leaf and branch litter collected in April, July, and October 1989.

The amount of litter accumulating on the ground under the seven species was measured in August 1989, December 1989, and in March, May, and August 1990. A 50 x 50 cm iron frame (one per plot) was used to demarcate an area in which all material to the top of the mineral soil was collected. The material was oven-dried, sorted (whole leaves, fragments, branches, and dry grass of understory vegetation), and weighed. Chemical analysis was performed on the material collected in August 1989.

Litter decomposition

Litter bags were weighed and sampled every two weeks for seven weeks. Approximately 2,500 g of whole leaves were collected from each species plot for *V. ferruginea*, *V. hondurensis*, and *H. oblonga*. Only leaves with complete or almost complete margins were chosen. Leaves from *S. excelsum*, leaflets and rachis of which are difficult to collect from the ground, were collected fresh. All leaves were dried at 70°C prior to filling litter bags.

Litter bags (50cm x 50cm) were constructed out of plastic mesh (average mesh size 2mm x 2mm). Each bag was filled with 100 g of dried leaves, weighed to 0.1 g.

The subplots were designated randomly in each of the four species plots, which were replicated five times. An area slightly larger than the litter bags was cleared of leaf litter; once the bags were in place they were covered with most of the displaced litter. The soil under the bags was exposed but not entirely bare of decomposing leaves. Within each plot, each subplot represented a different treatment of its corresponding litter bag. These treatments were: (1) Undisturbed throughout the duration of the experiment; (2) Weighed, but not subsampled; (3) Subsampled and weighed at two-week intervals.

Subsampling consisted of removing 30-60 ; of the field weight of the leaves, which were then dried at 70°C to determine a field weight:dry weight ratio. After subsampling, the bags were returned to the field. The experiment ran from 6 June to 25 July, 1990. On the final pick-up, the bags were destructively sampled and residual mud was cleaned off the leaves before drying and weighing.

For the sampled bags, weight loss due to decomposition was calculated by comparing the expected weight loss (loss due to sample removed) with the actual weight loss. The actual weight loss was determined by the wet:dry ratio of the sample from each bag. For each species, the weight loss due to decomposition was calculated from its 100 g initial weight (for the sampled bags) and from the final dry weight of the leaves when the bags were destructively sampled at the end of the experiment (for all treatments).

Mulch experiment

In the mulch experiment, maize seedlings were grown for 40 days in small plots mulched with the litter of the four species used in the litter decomposition study mentioned above. In preparation, a small amount of pasture on the north side of the tree trials (7m x 7m) was cleared to soil level . In this clearing, 25 plots measuring 50 x 50 cm each and spaced 30 cm apart were laid out in a square, five plots on each side. Grass was cleared within 1-2 m of the plots, shade and sun patterns were consistent over the plots, and a chicken-wire fence was erected around the entire experiment area. For each treatment, including the control with no mulch, there were five replicates; all were set at random.

For mulch, 100 g of dried leaves of each species were "scrunched" and incorporated into the top 10-15 cm of soil in an appropriate plot with a trowel. After a week, each plot was planted with 25 maize seeds. The maize was a local, non-hybrid variety that had been cleaned and culled beforehand. After cleaning it exhibited a 96% germination rate in the lab. The seed was planted at 3 cm depth, 8-12 cm apart, using a planting dibble. Ten days after planting (approximately one week after germination), 100 g scrunched leaves were again laid on the soil in the maize plots. All but two plots experienced an initial germination rate of at least 92%.

Maize seedlings were measured at 10-day intervals, beginning 10 days after sowing. The height of each seedling was recorded according to the "reach" of the entire plant along a meter stick held parallel to it. Forty days after planting, the maize seedlings were carefully dug up. Shoots and roots from the top 10-15 cm of soil were washed, separated (shoots from roots), oven-dried, and weighed.

Results and Discussion

Soil fertility

Results from April 1988, revealed that organic matter and total N were higher in the tree plantation than in grass, with values close to those of secondary forest (Montagnini and Sancho 1990a, 1990b). In just 2.5 years, there was an increase in soil organic matter in the upper 15cm, from a mean of 4.83% in grass to 5.31-6.60% in the plantation. The highest mean value in the plantation (for *Vochysia ferruginea*), was close to the mean in the secondary forest (7.58%); a similar trend was found at 15-30 and at 30-60 cm. Total N in the tree plantation was 0.26-0.32%; these values are again higher than in grass, with the highest, under *V. ferruginea*, close to the mean in the forest (0.33%).

The soil P concentrations were higher in the plantation than in grass, and lowest in the forest (Montagnini and Sancho 1990a, 1990b). This is probably due to immobilization of P in plant biomass and in soil organic matter in the forest. Cu concentrations exhibited a similar trend (higher in the tree plantation, lower in grass and forest). The pattern for Zn, Mn and Fe was similar to that of Ca and Mg. Soil Ca and Mg content were higher in the plantation than in grass, with values close to those in the forest. Within the tree plantation, there were no significant differences among species in soil cation content. However, there was a trend of higher Ca under *D. panamensis* and *V. ferruginea*, higher Mg under *S. excelsum and D. panamensis*, and higher K under *S. excelsum*, *D. tucurensis*, *D. panamensis* and *V. ferruginea*. Based on levels determined by the Ministry of Agriculture of Costa Rica for soil fertility assessments (Bersth 1986), these higher cation values were close to those acceptable for agricultural crops. Under the species mentioned above, soil Mg and K were at or above the critical levels for agriculture, representing an improvement over the grass in only 2.5 years (Montagnini and Sancho 1990a, 1990b).

Results of measurements taken in August 1988 showed similar trends of differences among sites (Montagnini and Sancho 1990a), but the soil base content was lower. This was accompanied by higher soil exchangeable acidity, possibly resulting from leaching of bases during the time of peak precipitation (457 mm in August, in comparison with only 43.6 mm in April 1988, data from La Selva weather station). Results of similar measurements done in May 1989 and May 1990 showed trends similar to those found in 1988 (Montagnini and Sancho, unpublished data).

A close relation between organic matter content and sum of bases was found (Montagnii and Sancho 1990a, 1990b), indicating that organic matter was responsible for much of the cation retention capacity. Thus, poor management practices of repeated burning, lack of good soil cover, over-grazing, and compaction – all of which tend to decrease organic matter content (Sanchez 1976) – could significantly lower soil fertility to a point from which recovery is very difficult. By contrast, tree planting with species that tend to increase organic matter content (like some tested in this project), would tend to increase and maintain soil fertility. For example, a 1-2% increase in soil organic matter in the range of 4-6% would more than double base content (Montagnini and Sancho 1990a, 1990b), reaching values in the range recommended for agriculture (Bertsch 1986).

Soil N mineralization

Measurements taken in May 1989 (Montagnini and Sancho 1990b) showed that soil NO_3-N concentrations at 0-15 cm depth were higher in grass (Table 2), possibly due to the presence of leguminous herbs which were invading the area. Within the plantation, NO_3-N was higher under *S. excelsum*, with values similar to those under forest, and there was a trend of higher concentration under *D. tucurensis*. There were no statistically significant differences in NH_4-N or in total N mineralization potential rates. The highest net nitrification was under *S. excelsum*, followed by grass, forest and *D. tucurensis*. There appeared to be a trend of higher NO_3-N production under N-fixing species in the plantation, although rates of N fixation in the young plantation possibly were still too low to result in significant changes in soil N availability and total N content. Current analysis of data from 1989 and 1990 measurements is revealing trends similar to those found in May 1989 (Montagnini and Sancho, unpublished data).

The results above suggest a potential ameliorating effect of these native tree species on soil fertility, especially with respect to organic matter and base content. It is emphasized that these effects were occurring at an early stage, during the first 2-4 years of plantation establishment. This should be stressed as a great advantage where pressure exists to produce timber or fuelwood quickly and improve soil fertility in degraded areas. This relatively quick, positive impact on soil fertility will greatly facilitate demonstration of the potential benefits of using these species in plantations or tree-crop combinations.

Developing recommendations for farmers requires understanding of the mechanisms potentially responsible for these responses. The following sections suggest several possible causes and help toward an understanding of the role of each species.

Nutrient concentrations in living tree biomass

The N, Ca, K, Mg, P, Fe, Cu, Zn and Mn concentrations in leaves and branches of the seven species of this study are shown in Table 3. There were significant differences in nutrient concentrations in leaf tissue, except for Fe and Cu ($p = 0.05$). The two N-fixing species (*D. tucurensis* and *S. excelsum*) had the highest N concentrations in leaf tissue. *V.*

Table 2. Soil nitrate and ammonium concentrations, net nitrification, and net N-mineralization potential rates (0-15 cm depth, May 1989).

	NO_3-N (mg/kg)	NH_4-N (mg/kg)	Nitrification (mg NO_3-N $kg^{-1}d^{-1}$)	N mineralization (mg NO_3-N + NH_4-N $kg^{-1}d^{-1}$)
S. excelsum	2.52^{bc}	7.30^{a}	4.75^{a}	5.01^{a}
D. ucurensis	1.99^{c}	6.83^{a}	2.96^{bc}	2.96^{a}
V. ferruginea	0.81^{c}	7.05^{a}	0.88^{d}	0.49^{a}
V. hondurensis	0.76^{c}	4.36^{a}	1.24^{d}	0.60^{a}
T. rosea	0.34^{d}	6.34^{a}	1.46^{cd}	1.96^{a}
D. panamensis	0.53^{d}	5.84^{a}	1.26^{d}	0.53^{a}
Grass	5.62^{a}	7.77^{a}	3.80^{ab}	4.00^{a}
Forest	2.82^{b}	6.73^{a}	3.49^{ab}	2.79^{a}

Values followed by the same letter do not differ significantly at $p = 0.05$.

Table 3. Tree tissue composition (August 1989).

	N	Ca	K	Mg	P	Fe	Cu	Zn	Mn
	(%)					(mg/kg)			
Leaves									
S. excelsum	2.25^{b}	0.47^{d}	0.76^{c}	0.22^{c}	0.20^{ab}	91.8^{b}	21.0^{b}	1.8^{bc}	53.0^{ef}
D. tucurensis	2.52^{a}	1.01^{b}	1.20^{ab}	0.49^{a}	0.23^{a}	172^{b}	36.0^{ab}	73.2^{a}	1149^{a}
V. ferruginea	1.58^{d}	1.06^{ab}	0.41^{d}	0.25^{c}	0.18^{ab}	450^{a}	42.5^{a}	15.5^{cd}	321^{bc}
V. hondurensis	1.49^{d}	1.22^{a}	0.29^{d}	0.41^{b}	0.09^{c}	189^{b}	25.0^{b}	11.4^{d}	181^{de}
T. rosea	1.78^{c}	0.71^{c}	1.22^{a}	0.52^{a}	0.19^{ab}	94.2^{b}	27.0^{bc}	17.0^{cd}	40.4^{f}
D. panamensis	1.78^{c}	0.67^{c}	0.99^{b}	0.20^{c}	0.18^{ab}	140^{b}	26.8^{bc}	25.4^{b}	233^{cd}
H. oblonga	1.81^{c}	1.02^{ab}	0.71^{c}	0.41^{b}	0.15^{b}	252^{ab}	31.4^{ab}	29.0^{b}	372^{b}
Branches									
S. excelsum	0.93^{b}	0.44^{bc}	0.70^{cd}	0.15^{c}	0.15^{ab}	76.4^{b}	22.6^{bc}	33.2^{a}	31.4^{c}
D. tucurensis	1.17^{a}	0.70^{a}	0.77^{c}	0.25^{b}	0.22^{a}	155^{a}	49.4^{a}	37.2^{a}	276^{b}
V. ferruginea	0.29^{d}	0.36^{c}	0.56^{de}	0.10^{c}	0.09^{b}	58.4^{b}	22.6^{bc}	15.8b	411^{a}
V. hondurensis	0.29^{d}	0.44^{bc}	0.49^{e}	0.16^{c}	0.12^{b}	54.8^{b}	22.0^{c}	13.2^{b}	490^{a}
T. rosea	0.54^{c}	0.60^{ab}	0.97^{b}	0.35^{a}	0.22^{a}	58.6b	34.0^{b}	37.6^{a}	28.6^{c}
D. panamensis	0.52^{c}	0.56^{ab}	0.59^{de}	0.10^{c}	0.15^{ab}	45.2^{b}	23.4^{bc}	12.8^{b}	81.0^{c}
H. oblonga	0.55^{c}	0.59^{ab}	1.14^{a}	0.15^{c}	0.17^{ab}	66.0^{b}	24.2^{bc}	13.4^{b}	91.0^{c}
Stems									
S. excelsum	0.49^{a}	0.81^{b}	0.20^{b}	0.04^{b}	0.07^{a}	172^{a}	5.8^{a}	15.4^{a}	18.6^{b}
V. ferruginea	0.17^{b}	1.12^{b}	0.23^{b}	0.10^{a}	0.09^{a}	125^{a}	4.0^{a}	11.3^{a}	1040^{a}
V. hondurensis	0.26^{b}	1.46^{a}	0.42^{a}	0.12^{a}	0.09^{a}	249^{a}	4.4^{a}	11.4^{a}	641^{a}

Values followed by the same letter do not differ significantly at $p = 0.05$.

ferruginea and *V. hondurensis* had the lowest N concentrations, but they had relatively high Ca concentrations. *D. tucurensis* also had high Ca concentrations in leaf tissue, as well as high Mg, K, P, Cu, Zn and Mn concentrations. *T. rosea* also had high K and Mg concentrations. *H. oblonga* had relatively lower or intermediate concentrations of most nutrients. *S. excelsum* had relatively low Ca, K and Mg concentrations. Similar trends held for branch tissue, with lower general values than those for leaves.

Data for comparison of stem nutrients was available for only three species. Stems had lower N concentrations than either leaves or branches (10-20% of leaf values), with the highest value found in *S. excelsum* (Table 3). Stems also had relatively low P, but differences among species were not statistically significant. The Ca values in stems were similar or greater than those of leaves, with the highest in *V. hondurensis*, which also had the highest stem K and Mg.

Table 4 shows that fine roots had higher nutrient concentrations than medium and coarse roots. Of the four species compared, *S. excelsum* had the highest N, Ca and Zn concentrations in the fine root fraction. *H. oblonga* had the highest Mg and Mn concentrations, while *V. ferruginea* and *V. hondurensis* had the highest P and Cu.

These data suggest that the two N-fixing species have the greatest potential for recycling N from their tissue as leaf, branch, or root litter, while *V. ferruginea*, *V. hondurensis* and *T. rosea* may recycle more cations or P. However, this should be examined in conjunction with litter production and decomposition rates. Data on stem nutrient concentrations will be useful in calculating total tree biomass and nutrient content for estimates of total nutrient loss from the site at harvest.

Biomass and nutrient concentration of understory vegetation

There was no understory vegetation in either *V. ferruginea* or *V. hondurensis* plots, probably because these two species had completely closed canopies at the time of sampling and light levels underneath were very low. The largest biomass of understory vegetation was found in *T. rosea* plots, which performed most poorly and thus allowed more light and growth of grasses. Abundant understory growth was found also in *S. excelsum* and *D. tucurensis* plots (Table 5).

In understory vegetation, the highest N concentrations were found under *S. excelsum* and *D. tucurensis*, the highest Ca was found under *D. tucurensis* and *H. oblonga*, and the highest K and Mg were found under *D. tucurensis*. Differences among other nutrients were not statistically significant.

When biomass of understory vegetation was multiplied by nutrient concentrations, differences in nutrients on a g/m^2 basis were not statistically significant, but there was a trend of higher nutrient content under *T. rosea* and *D. tucurensis* (Table 5a and b).

The two N-fixing species appear to have indeed recycled N from their tissues, with the increased N being used by the associated vegetation. Consistent with findings of higher Ca and Mg in *D. tucurensis* tissue, recycling of these cations appears greater under this species. Data on litterfall and decomposition should clarify these mechanisms.

Root biomass

Overall, the forest area had the highest total root biomass (all size classes) in the top horizon. Within root-size classes, however, the plantation as a whole had greater fine-root biomass than the grass, with values similar to that of the forest (Figure 1). Among the four species compared, *H. oblonga* and *V. ferruginea* had the highest fine-root biomass in the top soil horizon. *H. oblonga* also had the highest medium-fine and medium-coarse root biomass. The forest had the highest coarse root biomass in the top soil, followed by *S. excelsum*.

In the intermediate and lower horizons, *V. ferruginea* and the forest plots again had more fine (> 2mm) and medium-fine (> 5mm)

Table 4. Root tissue composition (August 1989).

	N	Ca	K	Mg	P	Fe	Cu	Zn	Mn
	(%)					(mg/kg)			
Root diameter									
<1 mm									
S. excelsum	1.68^{a}	0.42^{b}	0.08^{bc}	0.16^{b}	0.07^{c}	4135^{c}	177^{bc}	440^{a}	318^{d}
V. ferruginea	1.33^{b}	0.34^{b}	0.12^{ab}	0.19^{b}	0.29^{a}	4731^{c}	430^{a}	318^{ab}	585^{bc}
V. hondurensis	1.39^{b}	0.34^{b}	0.04^{d}	0.17^{b}	0.20^{b}	7858^{a}	469^{a}	441^{a}	632^{b}
H. oblonga	1.14^{c}	0.35^{b}	0.06^{cd}	0.52^{a}	0.17^{c}	5920^{b}	216^{b}	266^{bc}	1419^{a}
Grass	1.07^{c}	0.65^{a}	0.14^{a}	0.18^{b}	0.18^{b}	8022^{a}	151^{c}	170^{c}	411^{cd}
Forest	1.82^{a}	0.47^{b}	0.14^{a}	0.17^{b}	0.10^{d}	3870^{c}	128^{c}	140^{c}	252^{d}
1-5mm									
S. excelsum	0.92^{ab}	0.55^{ab}	0.19^{ab}	0.16^{b}	0.27^{ab}	4741^{b}	80.0^{a}	98^{b}	173^{c}
V. ferruginea	0.61^{c}	0.40^{b}	0.22^{a}	0.14^{b}	0.27^{a}	5482^{ab}	42.2^{b}	123^{b}	602^{b}
V. hondurensis	0.67^{c}	0.39^{b}	0.04^{c}	0.09^{b}	0.25^{ab}	5150^{b}	37.2^{bc}	224^{a}	1349^{a}
H. oblonga	0.76^{bc}	0.63^{a}	0.13^{b}	0.49^{a}	0.18^{ab}	6749^{a}	57.6^{ab}	93^{b}	779^{b}
Grass	-	-	-	-	-	-	-	-	-
Forest	1.07^{a}	0.42^{ab}	0.23^{a}	0.14^{b}	0.09^{b}	3042^{c}	17.0^{c}	75^{b}	224^{c}
>5mm									
S. excelsum	0.63	0.39	0.19	0.12	0.11	3615	45.0	37.0	180
V. ferruginea	0.29	1.06	2.09	0.22	0.27	1821	6.0	15.0	275
V. hondurensis	0.32	0.16	0.03	0.06	0.14	1432	13.0	27.0	351
H. oblonga	0.28	1.76	0.32	0.48	0.32	4432	8.0	40.0	256
Grass	0.79	0.80	0.20	0.20	0.16	2388	12.0	72.0	256
Forest	0.60	0.34	0.26	0.12	0.08	1913	8.0	26.0	220

roots than the rest. *S. excelsum* had more roots >2mm and >5mm below 15 cm depth.

Distribution of root biomass among soil horizons is a consideration when choosing species of trees or crops for mixed plantings. Especially in the upper horizons, there would seem to be greater root competition in mixtures that included *V. ferruginea* and *H. oblonga*. These species would serve better where the need is to protect against soil erosion. On the other hand, *S. excelsum's* more uniform distribution of roots at various depths would present less competition with other trees or crops in the upper soil horizons. Roots of *V. ferruginea* and *H. oblonga* show great potential for nutrient recycling; this could be clarified with root decomposition studies.

Litterfall

Figure 2 shows that total annual leaf litterfall for April 1989 through March 1990 was highest under *V. ferruginea* (1101 g/m^2). This was followed by *V. hondurensis*

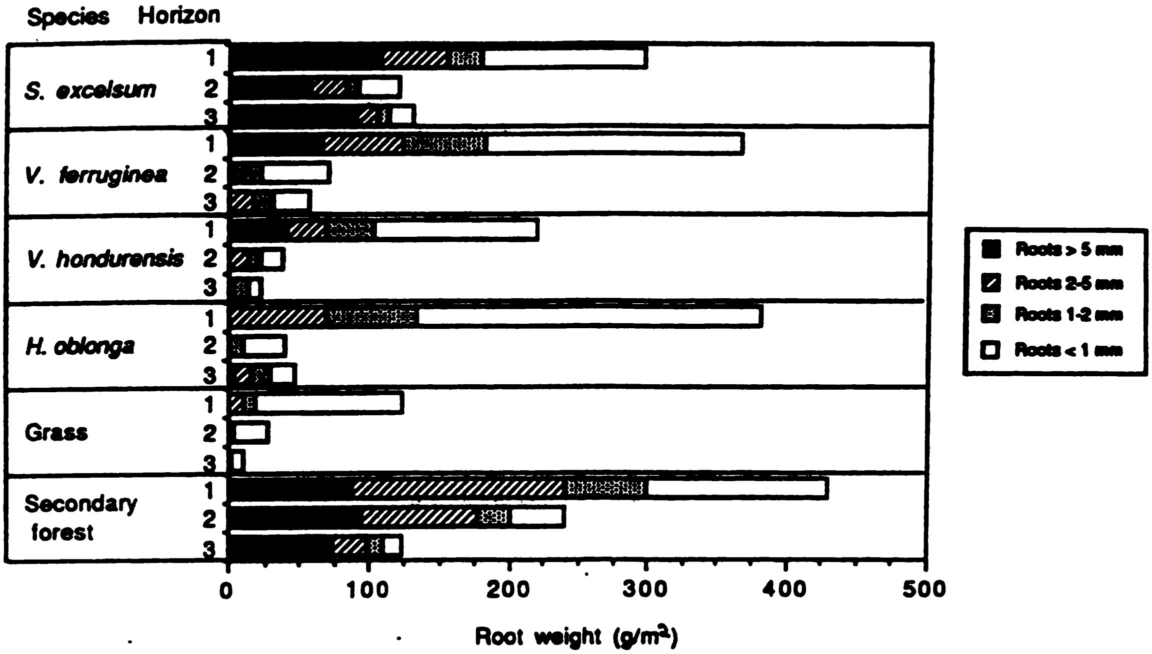

Figure 1. Mean root biomass, by class and horizon.

(885 g/m^2), *S. excelsum* (827 g/m^2) and *H. oblonga* (802 g/m^2). Other species ranged between 125 and 363 g/m^2. Branch litterfall was higher under *S. excelsum* and *V. ferruginea*. Monthly means for leaf litterfall, calculated from biweekly collections, are plotted in Figure 3 to show the seasonal pattern. Annual totals were calculated as the sum of all collections and not as the sum of these means. *V. ferruginea* and *V. hondurensis* exhibited peaks in leaf fall in June and September-October (beginning and end of rainy season, respectively). *S. excelsum* peaked in November; *H. oblonga* showed a more even pattern. Results of current data collection may clarify these trends.

Leaf and branch litter chemistry for October 1989 was chosen for comparison because data were more complete and differences in nutrient concentrations among species were similar to those of April and July 1989. *D. tucurensis* had the highest N concentration, followed by *T. rosea* and *S. excelsum* (Table 6). *H. oblonga*, *V. hondurensis* and *D. tucurensis* had the highest Ca and Mg, while *D. tucurensis* and *H. oblonga* had the highest K and P. There were no significant differences in Fe litter concentrations. *D. tucurensis* had the highest Cu, Zn and Mn concentrations.

Nutrient concentrations of branch litter were lower than those of leaf litter (Table 6). Although differences were not statistically significant, N concentrations were higher in *D. tucurensis*, *S. excelsum* and *T. rosea*, the same pattern found for leaf litter. *V.*

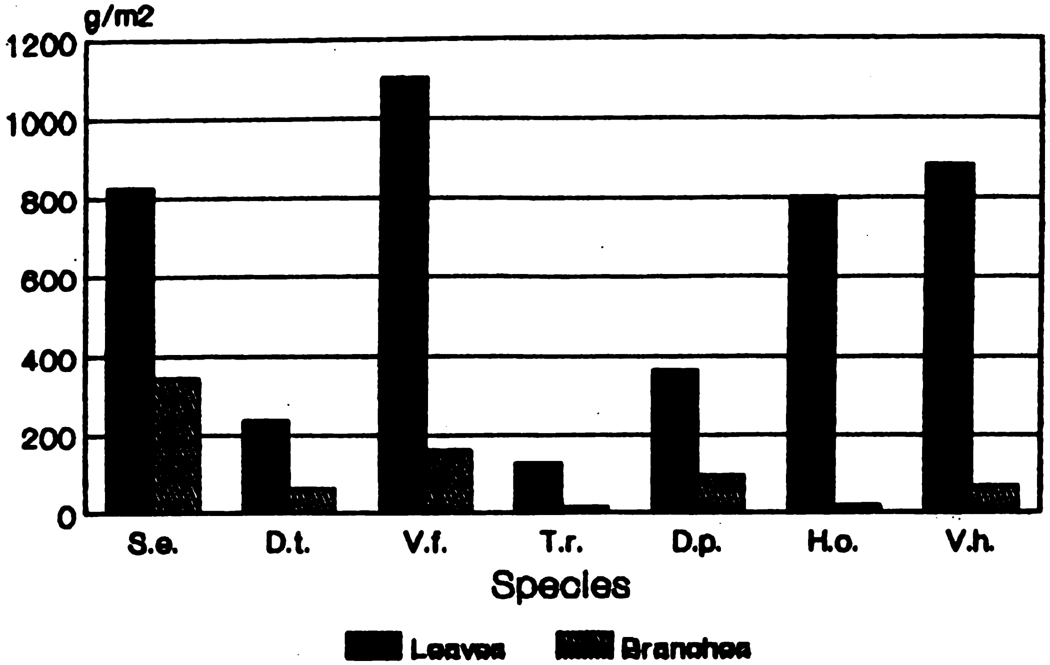

Figure 2. Litterfall for April 1989 - March 1990, leaf and branch annual totals. S.e. = *Stryphnodendron excelsum*; D.t. = *Dalbergia tucurensis*; D.p. = *Dipteryx panamensis*, V.f. = *Vochysia ferruginea*; V.h. = *V. hondurensis*; T.r. = *Tabebuia rosea*; H.o. = *Hyeronima oblonga*.

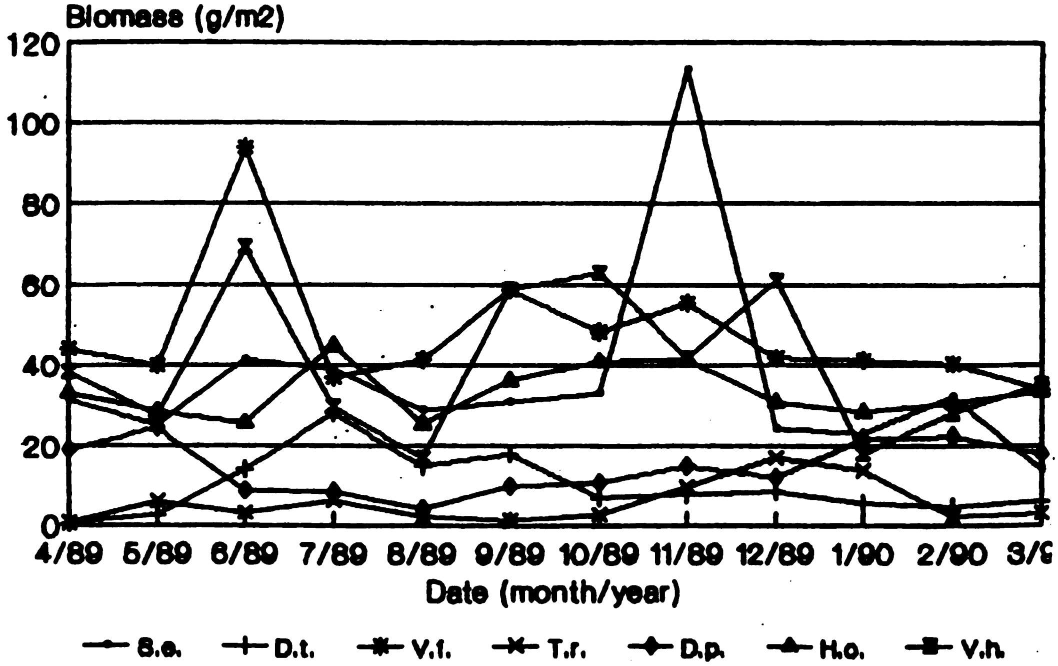

Figure 3. Litterfall for April 1989 - March 1990, monthly means for leaf biomass.

hondurensis and *D. tucurensis* had the highest Ca in branch litter. *H. oblonga* had the highest K; *V. ferruginea* had the highest Mg; *V. hondurensis* had the highest P and Fe. *D. tucurensis* had the highest Cu; *S. excelsum* the highest Zn and *V. hondurensis* the highest Mn in branch litter.

The high organic matter accumulation under *V. ferruginea* may be related to this species' high rates of litterfall; high Mg recycling could also be expected. Recycling of Ca and Mg should be high under *V. hondurensis*; K and P recycling could be high under *H. oblonga*. *S. excelsum*'s high rates of litterfall and litter N concentration suggest high N recycling under these species. Although *D. tucurensis* litter showed high concentrations of most nutrients, its capacity for recycling maybe limited by low rates of litterfall.

Comparison of forest floor litter accumulation at five dates between August 1989 and August 1990 (Figure 4) reveals that overall leaf litter accumulation tends to be greatest under *V. ferruginea*, followed by *S. excelsum*. This ranking is reversed starting in May 1990, with higher accumulation under *S. excelsum*. Leaf litter under *V. hondurensis* increased thoroughout the sampling period, the largest accumulation occurring in August 1990. A similar pattern was found for *H. oblonga*; accumulation under this species, though, was less than under *V. ferruginea*. For leaf fragments, *V. ferruginea* and *V. hondurensis* showed the highest values in August and May 1989 and in August 1990 (Figure 5).

Nutrient concentrations in forest floor material revealed a pattern similar to that of litterfall: N was higher in *S. excelsum; D. tucurensis* and *T. rosea*; Ca was higher in *D. tucurensis* and *V. hondurensis;* K was higher in *D. tucurensis*; Mg was higher in *D. tucurensis*, *V. hondurensis* , *H. oblonga* and *T. rosea* (Montagnini and Sancho, unpublished data).

The high litter accumulation recorded under *V. ferruginea* makes it well suited for protecting soil against erosion. On the other hand, an approximate indication of litter decomposition rates (given by the proportion of litter accummulation with respect to total litterfall) indicates that *V. ferruginea* litter would decompose slower than that of the other species. More detailed decomposition studies shed some light on these interactions.

Litter decomposition

Although the difference among decomposition rates (weight loss) was not significant (Table 7), the trends between them stayed fairly consistent throughout the experiment, based on initial and final leaf weights. The variance within the treatments was larger than expected; this was attributed to the unanticipated accumulation of mud in the litter bags and problems removing it completely from leaf fragments. Overall, however, the data suggest that *V. ferruginea* litter decomposes more slowly than the litter of other species, and that the fresh-dried, N-rich litter of *S. excelsum* does not decompose significantly faster than the other species, as we had expected.

Mulch experiment

Differences in seedling heights between treatments were significant at $p = 0.05$ and consistent throughout the experiment (Table 8). Within treatments there was very little variance. Initially, maize growing in plots with *H. oblonga* and *S. excelsum* showed greatest growth, while seedlings in the unmulched control plots showed significantly inferior growth. After 20 days, maize growth in the *H. oblonga* plots began to slow relative to *S. excelsum* plots, but plants in those plots remained larger and stronger than the maize seedlings in either of the *Vochysia* treatments. The control plots were slow-growing throughout the experiment and the seedlings in these plots were noticeably weaker and yellower than the plants in the other plots.

Differences in dry shoot weights were significant at $p = 0.05$ as well. The primary difference was between the shoots of the maize grown in *S. excelsum* mulch and all the others (Table 8a and b). Shoot weight of the maize grown in *S. excelsum* plots averaged

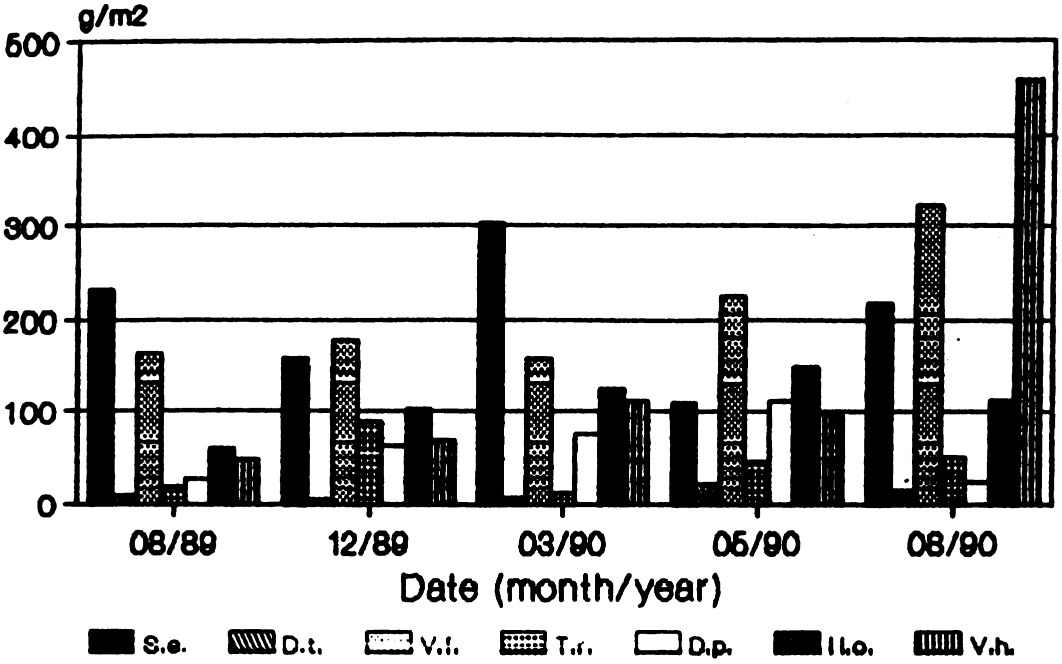

Figure 4. Overall forest-floor accumulation of leaf litter, August 1989 - August 1990. S.e. = *Stryphnodendron excelsum*; D.t. = *Dalbergia tucurensis*; D.p. = *Dipteryx panamensis*, V.f. = *Vochysia ferruginea*; V.h. = *V. hondurensis*; T.r. = *Tabebuia rosea*; H.o. = *Hyeronima oblonga*.

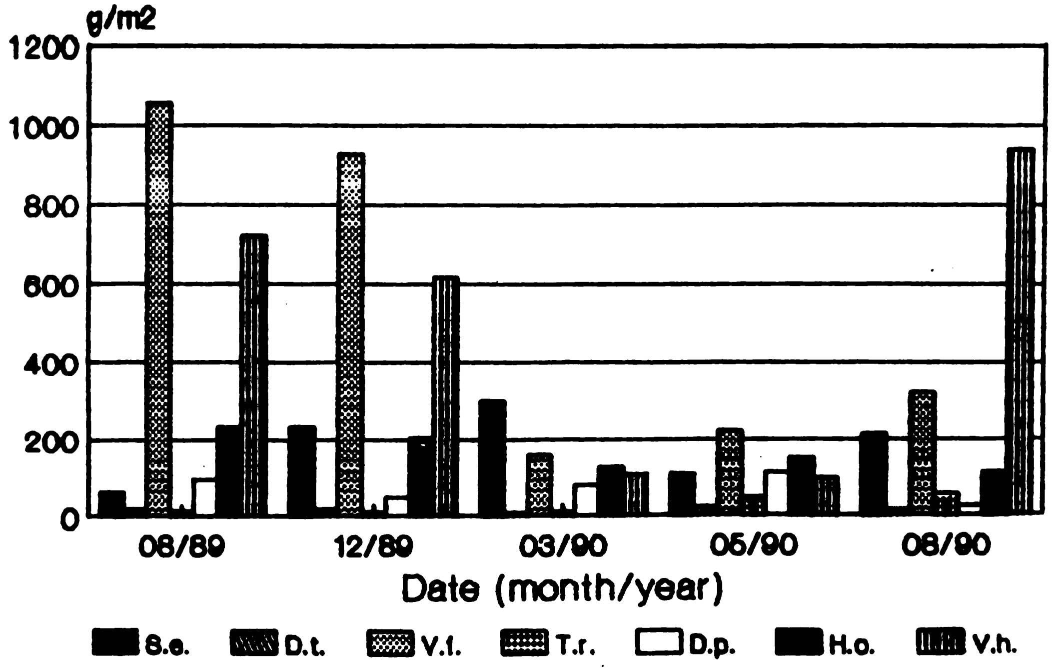

Figure 5. Leaf fragment accumulation on the forest floor, August 1989 - August 1990.

Table 7a. Leaf litter decomposition: percentage of initial weight (June-July 1990).

	Date of collection			
	6/18	6/28	7/10	7/25
S excelsum	96.94^{a}	78.92^{a}	77.13^{a}	74.98^{a}
V. ferruginea	96.25^{a}	87.64^{a}	81.67^{a}	83.59^{a}
V. hondurensis	92.31^{ab}	81.82^{a}	76.06^{a}	77.63^{a}
H. oblonga	86.61^{b}	81.05^{a}	78.91^{a}	77.80^{a}
p =	.2669	.5874	.8157	.5206

Table 7b. Leaf litter decomposition percentage of initial weight (means pooled from all treatments, sampled, undisturbed, and weighed).

	7/25
S excelsum	95.42^{a}
V. ferruginea	96.93^{a}
V. hondurensis	85.27^{a}
H. oblonga	84.43^{a}

Values followed by the same letter do not differ significantly at $p = 0.0455$.

Table 8a. Growth of maize seedlings in plots with mulch of four tree species (cm).

	Date			
	6/28	7/7	7/17	7/28
S. excelsum	17.9^{a}	36.8^{a}	48.9^{a}	53.7^{a}
V. ferruginea	15.2^{b}	24.2^{c}	29.6^{c}	35.7^{c}
V. hondurensis	15.1^{b}	25.2^{b}	30.8^{c}	39.5^{bc}
H. oblonga	17.9^{a}	30.9^{b}	38.1^{c}	44.6^{b}
Control	12.7^{c}	19.8^{d}	23.8^{b}	25.2^{d}
p =	.0002	.0000	.0006	.0021

Table 8b. Shoot and root biomass growth of maize in mulch plots.

	Shoots	Roots
S. excelsum	16.5	5.1
V. ferruginea	5.1	2.3
V. hondurensis	5.7	2.7
H. oblonga	8.2	3.3
Control	2.8	1.6
p =	.0465	.0004

two to eight times greater than that grown in other plots. Root biomass of maize grown in *S. excelsum* mulch also had the greatest biomass.

These results suggest that (1) tree leaf mulches played a significant role in maize seedling growth, and (2) some species had more important effects on initial maize growth. In particular, maize seedlings grown with the *Stryphnodendron* mulch were taller and visibly healthier looking than the other seedlings. This may be due in part to the fact that these leaves were dried fresh, instead of as litter; it also may be due to the higher levels of N they contain. The lackluster growth of the seedlings grown in both *Vochysia* treatments may be due to a variety of factors, including the prevalence of Al + ions released from the litter in the upper strata of soil, or the immobilization of N in the process of breaking down the fibrous litter. Although it was not reflected in the decomposition experiment, stands of *H. oblonga* showed low accumulation of leaf litter on the floor. This suggests that litter from this species decomposes relatively quickly, and perhaps explains the strong initial growth of maize in plots mulched with *Hyeronima* leaves.

Conclusions

S. excelsum, V. ferruginea, V. hondurensis and *H. oblonga* were the most promising species studied, for both growth and nutrient recycling capabilities.

V. ferruginea performed best for organic matter accumulation in soil, protection against erosion, and recycling of certain nutrients such as Ca. However, it may not be the best species for N recycling. Its effects on Al in soils should be further investigated. Strong competition with roots of nearby crops or trees should also be considered when planning species mixtures.

S. excelsum and *D. tucurensis* showed greater potential for N recycling. Of the two, *S. excelsum*'s high rates of litterfall make it more capable of high N recycling. This species' effects on understory growth and the effects of its mulch on maize seedling growth suggest that indeed it has a positive effect on associated crops. High rates of litterfall make the potential for using this litter as mulch practical. More studies with *Stryphnodendron* mulch and litter (for example, in alley-cropping systems) would be worthwhile. Its relatively uniform root distribution in the soil may present fewer problems of root competition with nearby trees or crops.

V. hondurensis and *H. oblonga* ranked intermediate in rates of litterfall and potential for nutrient recycling. These two species may enhance recyling of cations and P.

In spite of ranking the highest in terms of tissue and litter nutrient content, *D. tucurensis* has low potential for nutrient recycling due to low litterfall under present plantation conditions. This species should be further explored, however. With appropriate pruning practices, it could probably be managed to encourage leaf production and litter recycling.

We expect that the results of these studies will be disseminated to farmers of the region through local institutions. This may take place through collaboration with DGF, for example, which is already promoting native trees among local farmers. We are continuing measurements of soil fertility to assess the long-term impacts of the tree species on soil amelioration. We are also starting more detailed studies with the most promising species and with more native species in the region, designing tree species mixtures and agroforestry combinations.

Acknowledgements

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References

Allison, L.E. 1975. Organic carbon. In *Methods of soil analysis*, Part 2, 1367-1378; Black, C.A., ed. Madison, Wisconsin: American Society of Agronomy.

Bertsch, F.H. 1986. *Manual para interpretar la fertilidad de los suelos en Costa Rica*. Universidad de Costa Rica, Escuela de Fitotecnia.

Bremmer, J.M. and C.S. Mulvaney. 1982. Nitrogen-total. In *Methods of Soil Analysis*, Second edition, Part 2, 595-624. A.L. Page, R.H. Miller, and R.R. Keeney, eds. Madison, Wisconsin: American Society of Agronomy.

Diaz-Romeu, R. y A. Hunter. 1978. *Metodo para el muestro de suelos, analisis quimico de suelos y tejido vegetal e investigacion en invernaderos*, 9-11 and 15-27. Turrialba, Costa Rica: CATIE.

Espinoza Camacho, M. and R. Butterfield. 1989. Adaptabilidad de 13 especies nativas maderables bajo condiciones de plantacion en las tierras bajas humedas del Atlantico, Costa Rica. Reunion de IUFRO, IV Grupo, S1-07-09, Silvicultura de Plantaciones en America Latina. Guatemala, 3-7 de abril 1989.

Gonzalez, E. In press. *Preliminary seed trials for 36 native tree species*. Costa Rica: Revista de Biologia Tropical.

Hartshorn, G. 1983. Plants. In: *Costa Rican Natural History*, 118-157, D. Janzen, ed. Chicago, Illinois: University of Chicago Press.

Hartshorn, G. and B. Hammel. Trees of La Selva. Unpublished manuscript. La Selva Biological Station, OTS: Apdo 676, 2050 San Pedro, Costa Rica.

Holdridge, L.R., and L.J. Poveda. 1975. *Arboles de Costa Rica*. San Jose, Costa Rica: Centro Cientifico Tropical.

Keeney, D. R. 1982. Nitrogen-availability indexes. In *Methods of soil analysis*. Part 2. 2nd. ed., p. 711-730. Page, A.L., R.H. Miller and R.R. Keeney, eds. Madison, Wisconsin: American Society of Agronomy.

Montagnini, F. 1990. Ecology applied to agroforestry in the humid tropics. In: *Race to save the tropics: Ecology and economics for a sustainable future*, 49-58; Goodland, R.A., ed. Washington, D.C.: Island Press.

Montagnini, F. and F. Sancho. 1990a. Influencia de seis especies de arboles nativos asobre la fertilidad del suelo en una plantacion experimental en la llanura del Atlantico de Costa Rica. *Yvyrareta* (Argentina) 1(1):29-49.

________. 1990b. Impacts of native trees on tropical soils: A study in the Atlantic lowlands of Costa Rica. *Ambio* 19(8):386-390.

Rundel, P.W. Unpublished data, Laboratory of Biomedical and Environmental Sciences. Los Angeles, California: University of California.

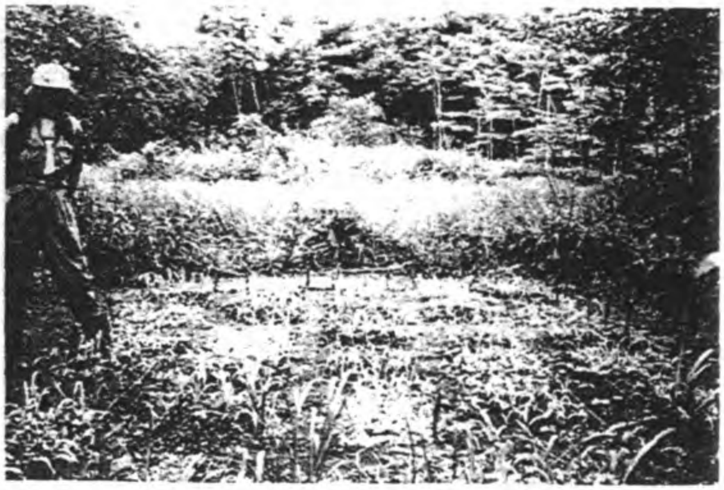
Sanchez, P.A. 1976. *Properties and management of soils in the tropics*. New York: Wiley and Sons.

Sancho, F., and R. Mata. 1987. Estudio detallado de suelos. Estacion Biologica La Selva. San Jose, Costa Rica: Organizacion para Estudios Tropicales.

Standley, P.C. 1937-38. *Flora of Costa Rica*. Chicago: Field Museum of Natural History.

Stijfhoorn, E. 1989. Root biomass and distribution under plantations of native tree species, grass and secondary forest vegetation in the Atlantic lowlands of Costa Rica. MS Special Project. New Haven, Connecticut: Yale University, School of Forestry and Environmental Studies.

Left: *Vochysia ferruginea* Mart. (Vochysiaceae) at 3.5 years.
Right: *V. hondurensis* Sprague (Vochysiaceae) at 3.5 years.



Maize seedlings in mulch experiment at OTS La Selva Biological Station. *Photos: F. Montagnini.*

CHAPTER 10

NUTRIENT BUDGETS OF YOUNG PLANTATIONS WITH NATIVE TREES: STRATEGIES FOR SUSTAINED MANAGEMENT

Florencia Montagnini
Freddy Sancho

INTRODUCTION

Our research focuses on a specific area in the humid lowland tropics of Central America in Costa Rica where banana plantations are predominant. Deforestation and the consequent degradation of land from mismanagement—shifting agriculture and cattle grazing—are common problems. Unpalatable native grasses and ferns reclaim abandoned land. A 4000 mm/yr rainfall hastens erosion of soil that has been depleted of nutrients from repeated harvesting.

Restoration of the soil to its former productivity and ecological balance has become a predominant concern of the government. There are local low- to medium-income farmers who are willing to risk some part of their land to raise trees, for they consider trees as a form of savings or investment under conditions of high inflation. They may reserve 10% to 15% of their land for trees as a future cash value. Regional forest services encourage farmers to plant exotic species—*Eucalyptus deglupta*, *Gmelina arborea*, and *Cordia alliodora*. Fungus usually infects the eucalyptus, and *Cordia alliodora* is a 30-year rotation species that grows on fertile soil, but it is not suitable for degraded lands. Such governmental policies need to be reconsidered. Local people should have a role in policy-making to insure appropriate choices of land use, species, and management, for they have specific knowledge about conditions in which they live.

We advocate a strategy of gathering criteria about each local region: the economic value of the regional species; the availability of seeds or seedlings; the growth rate data of regional species; and the indications of species' effects on soil nutrients. We have found that certain native tree species have a potential to grow well on poor, degraded soils. These trees are fast-growing and contribute organic matter to the soil within three years. Their litter and small branches may be managed to obtain nutrients: the litter may be used as mulch for agriculture (for maize crops) or left on the forest floor to return

Montagnini, F. & Sancho, F. 1994. Nutrient budgets of young plantations with native trees: strategies for sustained management. pp. 213-233 In Bentley, W. & Gowen, M. (eds.). Forest resources and wood-based biomass energy as rural development assets. Winrock International and Oxford & IBH Publishing Co. New Delhi. 347 pp.

nutrients to the surface layers of degraded soils as well as prevent soil erosion. Our discussion describes these species and their combined nutrient recycling capacities.

BENEFITS OF TREE PLANTATIONS

Currently, a number of governments and private efforts in rural development throughout the tropics are promoting tree planting, including tree-crop combinations as practiced in agroforestry. Trees are regarded as a source of cash, savings, and assets for the rural poor (Chambers and Leach 1990). Since tropical plantations managed for high yields can be at least four to ten times more productive than unmanaged natural forests (Wadsworth 1983), they also can help to meet the growing global demand for timber. This type of management is expected to help decrease the pressure on natural forests (Evans 1987).

The sustained management of tree plantations becomes a biologically and socially feasible alternative on soils that are unsuitable for the continuous practicing of agriculture that uses prevailing local technologies (Gladstone and Ledig 1990). Particularly, tree plantations and tree-crop combinations represent productive alternatives for the uses of deforested lands that have poor regeneration of natural forests since they are either intensely degraded or distant from sources of propagules. Low soil fertility, soil compaction from cattle grazing, and invasion by grasses and other aggressive vegetation—all evidences of site degradation—can be serious obstacles to both forest regeneration and conventional agriculture. As the area of degradation expands, there is increasing emphasis on the planting of tree species that can grow in such poor conditions to yield potentially profitable products (timber, fuelwood and other) as well as environmental benefits (soil conservation, watershed protection) (Evans 1987).

The choice of appropriate tree species for plantation forestry or agroforestry is influenced by knowledge of a species' performance as well as by economic and environmental benefits. In local situations, the choice of a tree species is determined by the availability of its seeds or seedlings and by information on its silvicultural characteristics and management—for instance, fast growth and the possibility of intercropping during early establishment. Most reforestation or tree-planting programs and subsidies promote the use of well-known, often exotic, species. About 85% of plantation forestry in the tropics is dominated by three genera: *Pinus*, *Eucalyptus*, and *Tectona* (Evans 1987), while there may be thousands of indigenous species suitable for similar purposes. Native trees can be more appropriate than exotics because they are better adapted to local environmental conditions, seeds and propagules are locally available, and farmers are familiar with them and their uses. In addition, the use of indigenous trees in productive systems helps to preserve genetic diversity and fosters a better balance with the local flora and fauna than exotics.

Ecological Consequences of Fast-Growing Tree Plantations

The factors that influence the productivity of tropical forest plantations are poorly understood. Some studies report yield or biomass productivity in relation to climatic factors, but few refer to site characteristics such as elevation or soil type (Lugo et al. 1988). Trees can influence site characteristics through their recycling of nutrients and their interactions with the microenvironment.

The most important beneficial effects of trees on soils can include improvement of soil structure and increased availability of nutrients (Fassbender 1984, Nair 1989, Sanchez et al. 1985, Sanchez 1987). Symbiotic nitrogen fixation by trees often results in increased soil nitrogen availability (Alpizar et al. 1986, Montagnini et al. 1986, Dommergues 1987). On the other hand, young tropical tree plantations which incorporate considerable amounts of nutrients in their biomass over a relatively short period of time are rapidly aggrading ecosystems (Bruijnzeel 1991). In early stages of growth, the amount of nutrient uptake from the soil usually exceeds the amount of nutrients supplied to the soil by litterfall and wash from the canopy (Bruijnzeel 1991).

Decline of site fertility can be a serious limitation to sustained plantation forestry in tropical regions: soil fertility can be decreased through excessive removal of living biomass, particularly if nutrients in tree crowns are lost through harvesting or site preparation (Perry and Maghembe 1989). On the other hand, Wadsworth (1983) suggests that, with the possible exception of phosphorus, repeated harvests usually would not result in serious deficiencies of soil nutrients.

Lundgren (1980) proposed that the ameliorating effects of plantation forests on soils occur only during the five-to-ten-year period immediately following canopy closure (the "fallow enrichment phase"). During the maximum-production phase, actual deterioration of site quality can occur: mineral nutrients are absorbed by the trees while litter accumulates on the forest floor, but conditions are unfavorable for the decomposition of organic matter (Lundgren 1980). Sanchez et al. (1985) concluded that deleterious effects on soils occur only during plantation establishment, but they also stressed that the extraction of nutrients by harvesting and the leaching losses incurred prior to canopy closure lead to a depletion of key nutrients, particularly potassium, that should be replaced if yields are to be sustained on subsequent rotations.

Tree species vary in their rates of nutrient uptake and in their capacity for nutrient recycling. The possibility of using particular species to accumulate nutrients was suggested by Sanchez et al. (1985) from their observations that certain species have the ability (e.g., *Gmelina arborea*) to accumulate calcium and magnesium, while others favor potassium and phosphorus. Little data is available on second and third rotations, so we do not have enough clues about what the critical nutrients for maintaining site productivity are. Data on different plantation species' rates of nutrient acquisition and recycling capabilities will help to design the best management strategies that either can take advantage of the ameliorating effects of trees on site fertility or avoid site deterioration at harvest.

Assessing the Impacts of Trees on Site Nutrients: An Example from Costa Rica

Local and regional trials of tree species for reforestation often reveal outstanding performances from indigenous trees. For example, out of 13 native tree species in an experimental plantation at La Selva Biological Station of the Organization for Tropical Studies (OTS) in the Atlantic lowlands of Costa Rica, Central America, at least four—*Stryphnodendron excelsum*, *Vochysia hondurensis*, *Vochysia ferruginea*, and *Hyeronima alchorneoides*—had growth rates equal to or greater than the exotic species that were currently recommended for the region (Espinoza and Butterfield 1989). This research demonstrates the potential of many native trees for commercial purposes. Most interestingly, it shows how certain indigenous species are able to grow well on degraded sites with poor, acid soils that could not sustain conventional agriculture, and how some of the species may have positive effects on soil fertility at an early stage (Montagnini and Sancho 1990a, 1990b, Montagnini et al. 1991). Results of our studies at the same site showed that after 2.5 years, these species contributed to the restoration of soil fertility by increasing organic matter, nitrogen, and soil cation levels to values close to those considered adequate for agricultural crops (Montagnini and Sancho 1990a, 1990b).

In the following sections, we present results from our studies of nutrient budgets in the same experimental plantation as an example of how biomass measurements, coupled with information on tissue nutrients, can be used to understand the potential environmental impacts of trees on site nutrients. We compare biomass and nutrient content among the species as well as among the trees' above-ground parts, forest-floor litter, understory vegetation, and soil nutrient pools. This information can be used to design management strategies to take advantage of the trees' ameliorating effects on soils and to avoid depletion of site nutrients at harvest. These strategies should be valuable for promoting the use of systems—mixed or pure plantations, agroforestry—that include these fast-growing timber species in the area and in other tropical lowland regions with similar ecological characteristics.

THE STUDY SITE

The experimental plantation was established in December, 1985, on abandoned pasture at the OTS La Selva Biological Station (10°26'N, 86°59'W, 50 meters mean elevation, 24°C mean annual temperature, 4000 mm mean annual rainfall, with maximum in July and minimum in March) (La Selva Biological Station weather reports). Soils are Fluventic Dystropepts, derived from alluvially deposited volcanic materials; they are deep, well drained, and free of stones, with low or medium organic-matter content, moderately heavy textured, and generally acid and infertile (Sancho and Mata 1987). The area had been cleared in the 1950s, and cattle had grazed there until 1984. The dominant species in the pastures were grasses (*Olyra latifolia, Melinis minutiflora*), ferns (*Pteridium* sp.), and bushes (*Psidium guajava* and *Piper culebranum*). In the pastures, there were patches of approximately 20-year-old adjacent forest with: *Pentachlethra macroloba*, a mimosoid, nitrogen-fixing legume dominant in the primary forest at La Selva; *Piper culebranum* and species of the melastomataceae family; ferns (*Pteridium* spp.); and tree seedlings in the understory.

The site was cleaned manually before planting. The tree species were planted randomly in a block design with five replicates, each plot containing seven rows of seven trees (14 m x 14 m each), with two meters between trees. Five similar 14 m x 14 m plots were also established in an adjacent open area with grass and in a nearby patch of secondary forest. During the first year, weeds were cut manually four times. Thereafter, weeding was done mechanically until canopy closure made it no longer necessary. The grass was also similarly weeded to keep it free of trees at the same time.

The Tree Species

The criteria for species selection for this study were good growth, as determined during the first three to four years of the plantation (Espinoza Camacho and Butterfield 1989, Gonzalez et al. 1990), presence of root nodules in the leguminous species (field observations), and economic value (Gonzalez et al. 1990, Chudnoff 1984, Holdridge and Poveda 1975). *Stryphnodendron excelsum* Harms (Leguminosae, subfamily Mimosoideae) ("vainillo") is found only in Costa Rica, although representatives of this genus are native to all of tropical South America, i.e. Brazil, Costa Rica, Guiana (Allen and Allen 1981). This species grows in low elevations with very humid climates and apparently adapts to alluvial soils as well as to slopes and abandoned pastures with degraded soils (Gonzalez et al. 1990). Its timber is primarily used for general construction, and, because of its ability to take high polish, small furniture and turnery (Allen and Allen 1981). Its fruits are eaten by many species of wildlife, mostly small mammals.

Vochysia ferruginea Mart (Vochysiaceae) ("botarrama") grows in lowland forests from Nicaragua to Brazil (Whitmore and Hartshorn 1969). It is found usually on acidic, well drained, and low-fertility soils, although it can adapt to a variety of soils (Gonzalez et al. 1990). It is a self-pruning pioneer species that forms uniform, even-aged stands in abandoned fields, and its wood is used for plywood and construction.

Vochysia hondurensis Sprague (Vochysiaceae) ("mayo") is found from Mexico to Panama, at elevations up to 900 m (Whitmore and Hartshorn 1969). It usually grows in humid, low altitude areas on either alluvial or residual (less fertile) soils. Considered a substitute for mahogany, its timber is highly desirable for carpentry, plywood, and furniture.

H. alchorneoides (O) (Euphorbiaceae) ("pilon") ranges from southern Mexico to southern Brazil (Chudnoff 1984). This species grows well on hills and on abandoned grasses, but not much is known about its edaphic requirements. Its timber is used for heavy construction, furniture, cabinet work, decorative veneers, and turnery (Chudnoff 1984). Botanical characteristics of the species were described by Holdridge and Poveda (1975), Hartshorn (1983), Standley (1937-38) and Hartshorn and Hammel (unpublished). Detailed studies on seed and germination characteristics are presented by Gonzalez (1991).

METHODS

Sampling procedures and chemical methods are described in Montagnini and Sancho (1990a, 1990b), and Montagnini et al. (1991). The soils under the species, in a grassy area free of trees and in a 20-year-old secondary forest, were sampled for soil fertility, and their nitrogen availability was also measured. Tree biomass and nutrient content from stems, branches, and leaves were measured at the time of plot thinning when the plantation was four years old. The biomass and nutrient concentrations of the understory vegetation and the forest floor under the trees were also measured. Nutrient budgets were calculated by multiplying the biomass of each compartment times its nutrient concentration (nitrogen, calcium, magnesium, potassium, phosphorus).

RESULTS AND DISCUSSION

Tree Biomass

The values of whole-tree biomass reported here (table 10.1) are greater than of those reported for four-year-old *Albizia lebbek* (Parrota 1989) and of five-and-a-half-year-old *Leucaena leucocephala* (Wang et al. 1991), both growing in dense plantations for biomass production in Puerto Rico. Values shown here of the total tree above-ground net primary productivity (calculated by dividing whole-tree biomass by tree age) lie within the ranges reported elsewhere for monospecific plantations in the humid tropics. The value for *V. hondurensis* is close to that reported for *Gmelina arborea* (12.8 tons/ha/yr) in the Brazilian Amazon (Russell 1987) as well as to *Gmelina arborea* (12.7 tons/ha) and to *Albizia falcataria*, both found in the Philippines (11.3) (Kawajara et al. 1981). However, the increments shown here are lower than those reported for some of the fastest-growing trees in the humid tropics, such as *Acacia mangium* (15.5 to 18.0 tons/ha in Malaysia) and *Leucaena leucocephala* (20.0 to 30.0, and even up to 80.0 tons/ha in Hawaii and in other tropical sites, Young 1989).

Table 10.1. Means of Tree Diameter at Breast Height (dbh), Height, Aboveground Biomass and Annual Increment

			Above-ground live biomass				Mean annual increment	
	Dbh	Height	Stem	Branches	Leaves	Total	Total	Stems
	(cm)	(m)	(kg/ha)				(t ha -1 yr -1)	
S. exc.	12.0a	8.9b	35,250a	15,250a	4,325a	54,825	13.7	8.8
V. fer.	10.3a	8.1b	24,750b	14,250a	5,925a	44,925	11.2	6.2
V. hon.	10.8a	12.0a	41,750a	6,500b	7,250a	55,500	13.9	10.4
H. alc.	10.8a	9.0a	26,250b	12,250a	5,350a	43,850	12.0	6.5

Note: In this and in following tables, differences between sites for a given parameter are statistically significant when means are followed by different letters.

Annual increments of stemwood biomass for broadleafs range from 1 to 28 tons/ha/yr. Fast-growing species such as *Gmelina arborea* and *E. saligna* range from 10 to 20 and from 8 to 28 tons/ha, respectively, and relatively slower-growing species such as *Swietenia* sp. and *Tectona grandis* range from 1 to 4 and 3 to 12 tons/ha, respectively (Wadsworth 1983). Other values for fast-growing trees in tropical humid regions include various eucalyptus species grown in the Americas and in Asia (from 7.2 to 11.9 tons/ha); *Gmelina arborea* in Costa Rica (11.8 tons/ha) (Lugo et al. 1988); 1.3- to 5.3 *Leucaena leucocephala* growing in premontane and lowland humid sites (2.8 to 15.9 tons/ha); *Prosopis juliflora*, on a moist site in India (9.4 tons/ha), and *Populus deltoides*, on a subtropical site in India (6.4 tons/ha) (Lugo et al. 1990). Thus, the mean annual increments of stemwood biomass for the species in this study also fall within the ranges reported for other fast-growing tree species in the humid tropics.

Nutrient Accumulation in Above-Ground Tree Biomass

Nitrogen

Consistent with trends found in nitrogen (N) tissue concentrations (Montagnini et al. 1991), *S. excelsum* had the highest stem, branch, and total above-ground tree biomass N. Although *S. excelsum* had higher N-leaf concentrations than the other species, it had similar N-leaf biomass because its leaf biomass was relatively lower (figure 10.1). Taking leaves and branches together, approximately 200 kg/ha, or 60% of *S. excelsum*'s above-ground tree biomass

N (figure 10.1) would be left on the site at the time of harvest if only stems were removed. *V. hondurensis* had a similar proportion of N to that of *S. excelsum* in its leaves and branches portion. Again, over 50% of above-ground tree biomass N could be recycled if left at the site at the time of harvest. *V. ferruginea*, with relatively lower stem biomass, had proportionally more N in leaves (52.9%) and branches (42.1%), while *H. alchorneoides* showed a more even distribution of above-ground tree biomass N in stems (39%), branches (27%), and leaves (33.8%).

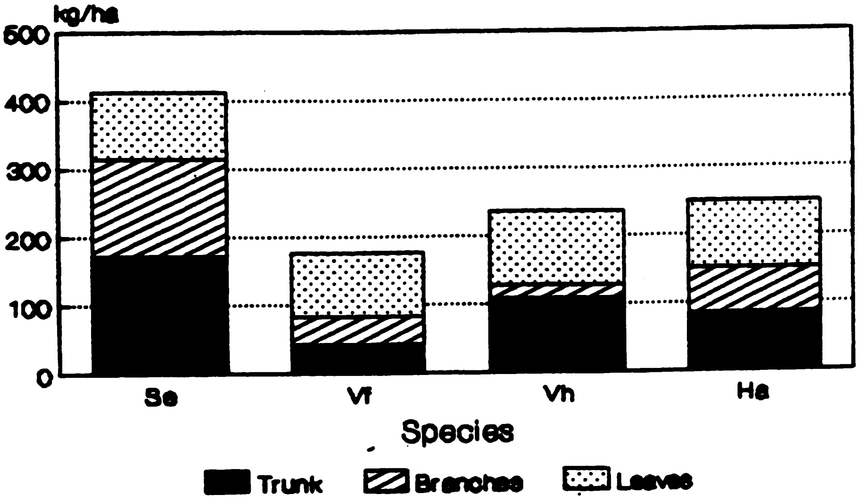


Figure 10.1. Nutrients in Tree Biomass - Nitrogen.

Calcium

V. hondurensis, with the highest stem biomass and calcium (Ca) concentration, also had the highest stemwood Ca (over 600 kg/ha, or 84% of above-ground tree biomass Ca), approximately twice as much as either *S. excelsum* or *V. ferruginea*, and several times more than *H. alchorneoides* (figure 10.2). Therefore, the harvest of *V. hondurensis* trees could substantially reduce the amount of Ca in the site. However, while the *V. hondurensis* trees are living, relatively large amounts of Ca could be recycled because, although it represented only 16% of above-ground tree biomass, the amount of Ca in leaves and branches together was over 100 kg/ha.

The proportion of Ca in stems relative to above-ground tree biomass was similar for *S. excelsum* and *V. ferruginea* (76.6% and 70.8% respectively) (figure 10.2), but the absolute amounts were less than half those of *V. hondurensis*. *H. alchorneoides* again showed a more evenly distributed quantity of Ca in stems, leaves, and branches, with above-ground tree biomass Ca slightly over half that of *S. excelsum* and *V. ferruginea*.

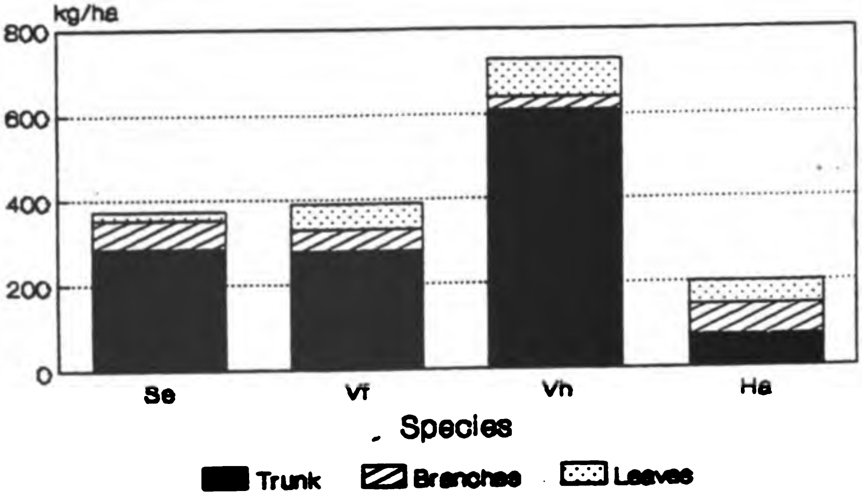


Figure 10.2. Nutrients in Tree Biomass - Calcium.

Magnesium

V. hondurensis, with its high stem biomass and high magnesium (Mg) concentration, also had the highest Mg in stemwood (55% of above-ground tree biomass, or approximately 30 kg/ha) (figure 10.3). Again, removal of *V. hondurensis* stems would affect the site's Mg budget more dramatically than for any of the other species, especially if the whole tree is harvested. The other species showed lower proportions of above-ground tree biomass Mg in their stems (30% to 46%) (figure 10.3).

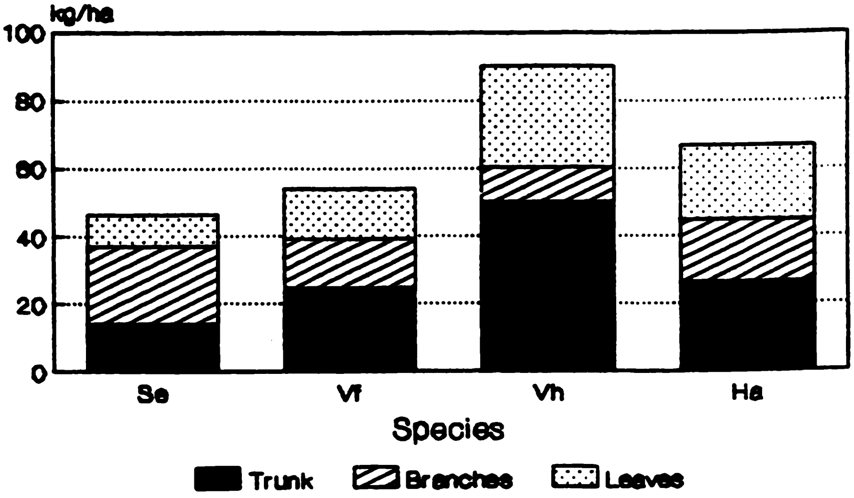


Figure 10.3. Nutrients in Tree Biomass - Magnesium.

Potassium

For potassium (K) the picture changed: the highest accumulation of K in stems was found in *H. alchorneoides* (252 kg/ha, figure 10.3), accounting for 58.7% of above-ground tree biomass K. This quantity was followed by *V. hondurensis* with 175 kg/ha, which represents 76.8% of above-ground tree biomass K. Thus, whole-tree harvest of *H. alchorneoides* and *V. hondurensis* may have the greatest effects on the K budget. *S. excelsum* and *V. ferruginea* had 33.6% and 35.4%, respectively, of K in the stem. The recycling of K from leaves and branches could be relatively more important when considering these latter two species.

Phosphorus

V. hondurensis and *H. alchorneoides* had the highest proportions of stemwood phosphorus (P) (72.4% and 62.1%, respectively) (figure 10.4). *S. excelsum* and *V. ferruginea* had relatively lower amounts of stem P, also correlating with proportions of above-ground tree biomass P (43.9% and 48.7% respectively).

Our results confirm earlier reports on the negative effects of the harvest of whole trees on site nutrient pools: for example, Bruijnzel and Wiersum (1985) studied nutrient input/output budgets for *Agathis dammara* plantations in upland Java. Their results, calculated for a thirty-year rotation, showed that total harvesting of the trees would remove the entire inputs of K and Ca, almost half of the Mg input, and twice the input of P. The authors concluded that, in order to avoid shortages of nutrients, especially P, harvesting of whole-tree biomass should not be practiced. Our results also suggest that leaving plant residues in the site could greatly decrease the negative impacts of nutrient removal at harvest, with varying consequences that would depend on the individual species.

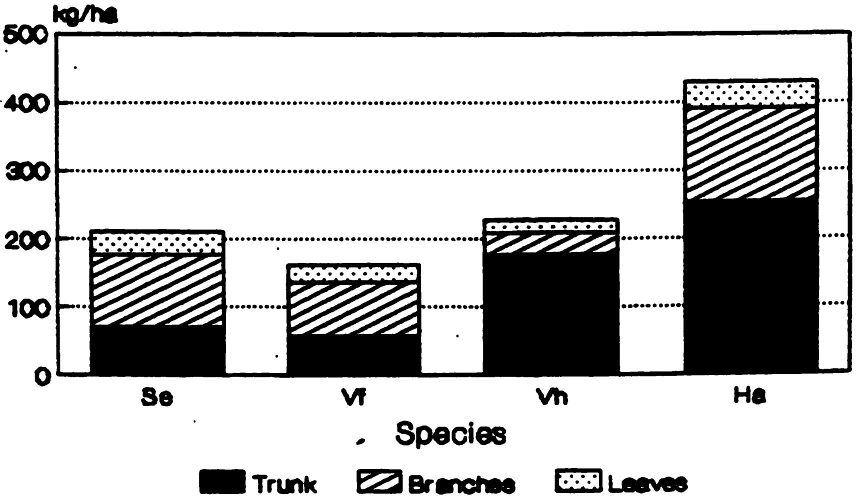


Figure 10.4. Nutrients in Tree Biomass - Potassium.

Altering the rate of nutrient removal from the site is probably one of the most important design considerations when planning sustainable plantations (Wang et al. 1991). The tree species as well as the parts of the tree removed will determine the nutrient "cost" of removal. This "cost" can be assessed in advance by nutrient and biomass sampling and estimation. By comparing the quantities of nutrients removed from a variety of species in numerous tropical sites, these authors argue that nutrient removal increases from 13% to 253%, while biomass removal increases less than 50%, when harvesting of whole-tree biomass, rather than harvesting only stems, is practiced. Additionally, they argue that shorter rotations will be more affected by this difference because the fractions of leaves and small branches of the total biomass tend to decrease with tree size. Bruijnzel and Wiersum (1985) found that stemwood P concentrations of 35-year-old *Agathis dammara* were lower than those of younger trees, whereas no such differences were found for other nutrients, and they suggest that the main effects of shorter rotations will be an increase in site disturbance.

Impacts of Trees on Soil Nutrients

Similar to the 1988 findings, higher levels of soil organic matter and N were found in the tree plantation than in grass, with values close to those of secondary forest (table 10.2), but unlike 1988, these differences were not statistically significant ($P<0.05$). P content was higher in grass than in the plantation or in the forest (table 10.2). Within the tree plantation, there were no significant differences among species in soil cation content. However, there was a trend of higher Ca under *S. excelsum* and lower Ca in *H. alchorneoides*. Higher Mg was recorded under the two *Vochysia* species, with lower values again in *H. alchorneoides* (table 10.2).

Results of similar measurements taken in May, 1990, and again in May, 1991, revealed trends like those found in 1988 and 1989. When examining data from 1988 to 1991, no increasing or decreasing trends over time were detected for any individual nutrient (Montagnini and Sancho, unpublished data). Apparently, site improvement was observed in 1988, when the trees were 2.5 years old and had developed closed canopies. Following this initial site improvement, further testing could not detect any additional positive changes in soil chemistry. In fact, as trees approach their maximum-production phase and as the "recyclable" portion (leaves and branches) of the tree decreases in relation to that of the stem, a decrease in soil nutrients can be expected (Lundgren 1980).

The impacts of plantation tree species on soil nutrient reserves will depend on the annual nutrient uptake of the trees in relation to the nutrient-supplying capacity of the soil, nutrient recycling (while the trees are living), and the parts of the tree removed, whether the whole tree or stemwood, and their biomass and nutrient content at the time of harvest. A look at these relationships for *V. hondurensis*, the fastest-growing and seemingly the most

Table 10.2. Organic Matter, Total N, P, pH, Ca, Mg, and K in Soils Under the Four Native Tree Species in Plantation, Grass and Secondary Forest, May 1989[1].

Site	Depth	OM	N	P	pH	Ca	Mg	K
	(cm)	(%)		(mg/kg)		(cmol/kg)		
S. exc.	0-15	4.50a	0.278a	2.4a	5.1a	0.68b	0.44a	0.13a
	15-30	3.29a	0.224a	2.1a	5.1ab	0.52bc	0.22bc	0.14a
	30-60	1.88a	0.196a	1.8b	5.1a	0.54a	0.16a	0.14a
V. fer.	0-15	5.06a	0.32a	3.24a	4.98a	0.63bc	0.53bc	0.16a
	15-30	3.66a	0.248a	2.48a	5.03c	0.35d	0.20c	0.10a
	30-60	2.94a	0.200a	2.50b	5.07a	0.33a	0.16a	0.15aa
V. hon.	0-15	4.30a	0.304a	2.30a	5.20a	0.47bc	0.50bc	0.10a
	15-30	3.16a	0.232a	1.82a	5.08ab	0.38cd	0.22bc	0.07a
	30-60	2.42a	0.202a	2.00b	5.13a	0.36a	0.15a	0.06a
H. alc	0-15	5.16a	0.232a	1.5a	5.1a	0.31c	0.21a	0.09a
	15-30	2.77a	0.248a	1.5a	5.1ab	0.45bcd	0.19c	0.10a
	30-60	1.21a	0.158a	1.7b	5.2a	0.46a	0.20a	0.10a
Grass	0-15	3.98a	0.296a	4.1a	5.2a	0.57bc	0.38a	0.22a
	15-30	2.94a	0.236a	3.4a	5.1ab	0.51bcd	0.27bc	0.17a
	30-60	2.46a	0.194a	8.9a	5.2a	0.47a	0.20a	0.13a
Forest	0-15	5.11a	0.288a	2.3a	5.2a	1.16a	0.49a	0.21a
	15-30	3.83a	0.244a	2.0a	5.2a	0.92a	0.45a	0.17a
	30-60	2.48a	0.206a	1.4b	5.2a	0.62a	0.27a	0.12a

[1]. Differences between sites for a given depth and parameter are statistically significant when means are followed by different letters.

nutrient-demanding species of this study, will illustrate this point. Nutrient retention by *V. hondurensis* (calculated by dividing biomass nutrient by plantation age) was an average of 58 kg of N, 181 kg of Ca, 57 kg of K, 22 kg of Mg, and 13 kg of P/ha/yr. The N, Ca, Mg, and K values are all twice as much as those reported by Wadsworth (1983) for teak plantations but the value of P is similar. Although these nutrient values are high, they should be compared with the nutrient-supplying capacity of the soil. For example, Wadsworth (1983) compared data from the rates of annual nutrient uptake of various agricultural crops on upland Ultisols and Oxisols in Puerto Rico (N = 90 - 120 kg/ha/yr, K = 50 - 90, Ca = 86 - 109, Mg = 68 - 98), with the rates of mean annual nutrient retention for fast-growing teak and pine plantations. He concluded that the capacity of the soils to supply nutrients was enough for the needs of the plantations and that plantation trees could be harvested without creating soil deficiencies, except maybe for P. Wang et al. (1991) also reported that the rate of removal of N, P, Ca, Mg and K on an annual basis for

Casuarina and *Albizia* plantations in Puerto Rico was similar to that of crop systems such as maize and sorghum.

In our analysis, we are not considering "nutrient-supplying capacity" of soils, but rather we are comparing the stocks of above-ground nutrients for each tree species with those in the soil. These quantities were calculated by multiplying the average soil nutrient concentrations for each soil layer under each species to a depth of 60 cm (table 10.2) times the weight of a hectare of the soil for the corresponding layer. Values were corrected by estimating soil bulk density for each type of vegetation (Montagnini and Sancho, unpublished data). If we assume that the nutrient content of the grassy area—where there are no trees—represents the quantity of nutrient stocks before the establishment of the plantation, and if we compare these values with nutrient concentrations found under trees, we can obtain an approximation of the effects of tree uptake on soil reserves.

Comparing soil nutrient budgets (figures 10.1-10.5) with nutrient content of tree biomass (figures 10.6-10.10), we observe that after four years, soil Ca reserves tended to decrease under all the species except for *S. excelsum*. In contrast, soil under the secondary forest appears to have almost twice as much Ca as under *V. hondurensis*, *V. ferruginea*, or *H. alchorneoides* (figure 10.7). Mg and K tended to be lower under *H. alchorneoides* (figures 10.8 and 10.9). However, the most notable overall decrease in soil nutrients occurred for P (figure 10.10), where values under all of the tree species were lower than those under grass and similar to those under the secondary forest. (We do not discuss statistically significant differences here because these measurements are already shown for soil nutrient concentrations, table 10.2). The figures for N are more difficult to compare because soil N was calculated from total N (TKN) values, which tend to be approximately 100 times larger than available N (NO_3 +NH_4), and because N fixation by *S. excelsum* is an additional input that needs to be examined separately. We are not considering other factors affecting nutrient concentration levels such as weathering or rain, the ability of the trees to absorb nutrients from below 60 cm soil depth, or recycling mechanisms (which we will examine next). However, our results tend to agree with the conclusions of Wadsworth (1983) and Bruijnzel and Wiersum (1985) that P, with its potential for depletion, is the most critical element to be considered. Our results also underscore the importance of promoting nutrient-recycling mechanisms through management practices, both in the living stand and at the time of harvest.

Biomass and Nutrient Concentration of Understory Vegetation

Nitrogen accumulation in the total understory biomass was higher under *S. excelsum* plots (14.9 kg/ha), although this amount represented only 3.6% of whole-tree biomass N (table 10.3). For *H. alchorneoides*, understory biomass N was 5.7 kg/ha, or 2.3% of above-ground tree biomass N. For the other nutrients, accumulation in understory biomass under *S. excelsum* ranged from

0.8% to 7.7%, and under *H. alchorneoides*, it ranged from 0.85% to 4.1% of above-ground tree biomass nutrients (table 10.3).

Table 10.3. Biomass and Nutrient Content of Understory Vegetation and Forest-Floor Litter[1.]

(a) Understory vegetation

	Biomass	N	Ca	Mg	K	P
	(kg/ha)			(kg/ha)		
S.exc.	874	14.9(3.6)	2.9(0.8)	3.6(7.7)	8.8(4.2)	1.1(2.0)
H. alc.	425	5.7(2.3)	3.3(1.6)	1.9(2.9)	3.3(0.8)	3.1(4.10

(b) Forest-floor litter[2]

	Biomass	N	Ca	Mg	K	P
	(kg/ha)			(kg/ha)		
S. exc.	5612	95.1(23.0)	41.6(11.1)	8.2(17.6)	6.6(3.1)	4.3(7.6)
V. fer.	17215	240.3(137.0)	187.6(47.9)	19.1(35.5)	12.1(7.5)	15.5(33.8)
V. hon.	11084	134.0(57.0)	170.0(23.4)	26.4(24.3)	9.7(4.2)	11.6(22.3)
H. alc.	4238	39.2(15.8)	55.0(27.0)	11.9(17.9)	6.8(1.6)	12.9(16.9)

[1]. Numbers between parentheses are percent in relation to whole-tree biomass nutrients.
[2]. Totals, including leaves, fragments, branches.

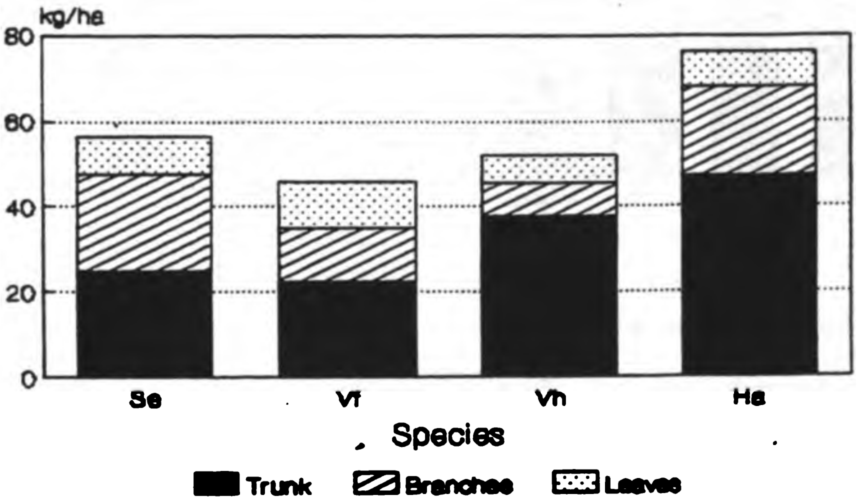


Figure 10.5. Nutrients in Tree Biomass - Phosphorus.

Since vegetation in the understory apparently accounts for a relatively small proportion of nutrients, as compared to the whole tree, manipulations of the understory should have little effect on nutrient recycling at the site. For example, weeding should have a relatively minor effect on nutrient recycling, unless the understory is removed many times a year. This hypothesis also suggests that intercropping with annual, herbaceous species that attain similar amounts of biomass as that of the understory found under *S. excelsum* or *H. alchorneoides* will not have a substantially negative effect on the balance of nutrients at the site. Since samplings of understory biomass were taken at a time when the quantity of biomass was at its peak, the amounts reported here are considered to approximate those that could be attained by crops. However, this factor deserves further research, since nutrient requirements and parts of plants and trees removed at harvest will vary according to the crops. Our results, however, tend to agree with Bruijnzeel and Wiersum (1985), who concluded that the use of controlled intercropping on tree plantations of upland Java, coupled with precautionary measures to minimize soil erosion, was an acceptable way to conserve nutrients. They argue that, in addition to their socioeconomic benefits, the use of such "taungya" practices could also prove advantageous since farmers may be willing to use fertilizers for the crops and the residual effects of these applied nutrients may increase the yield of the trees.

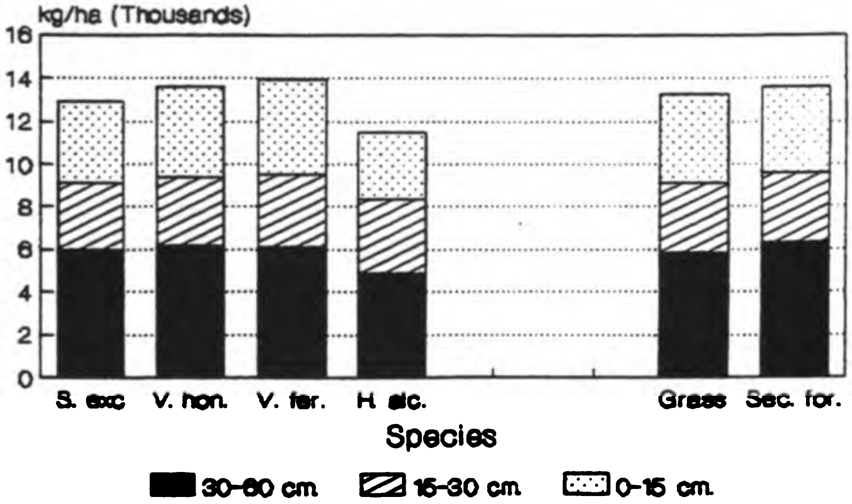


Figure 10.6 Soil Nutrient Balances - Nitrogen.

Nutrient Accumulation in Forest-floor Litter

The nutrient accumulation and forest-floor biomass were highest under *V. ferruginea*. N in forest-floor litter under *V. ferruginea* was greater than this species' above-ground tree biomass N (table 10.3). As noted above, *V. ferruginea*'s leaf-and-branch biomass accounts for a large proportion of its above-ground tree biomass. This species is self-pruning, a characteristic which enhances shedding of branches and leaves, and occasional prunings may have added even more tree litter to the forest floor. Results of our studies on the rates of litterfall and litter decomposition (Montagnini et al. 1991) suggest that litter decomposes relatively slowly under *V. ferruginea*, a factor explaining the high accumulations noted above. *V. hondurensis*, *H. alchorneoides*, and *S. excelsum* show faster rates of litter decomposition. Forest-floor litter Ca, Mg and P were also considerable under *V. ferruginea* (table 10.3), a finding especially relevant for P, since there is a potential deficiency of this element at the site, as mentioned earlier. Nutrients from forest-floor biomass were also higher under *V. hondurensis*. Again, this result was more significant for N, Ca, Mg and P. Thus, in spite of this species' fast growth rate, nutrient recycling from litter may at least partially compensate for depletion of soil nutrients. While the reverse was true for P, forest-floor litter N was more than double under *S. excelsum* than under *H. alchorneoides*, even though both species had similar forest-floor litter biomass (table 10.3).

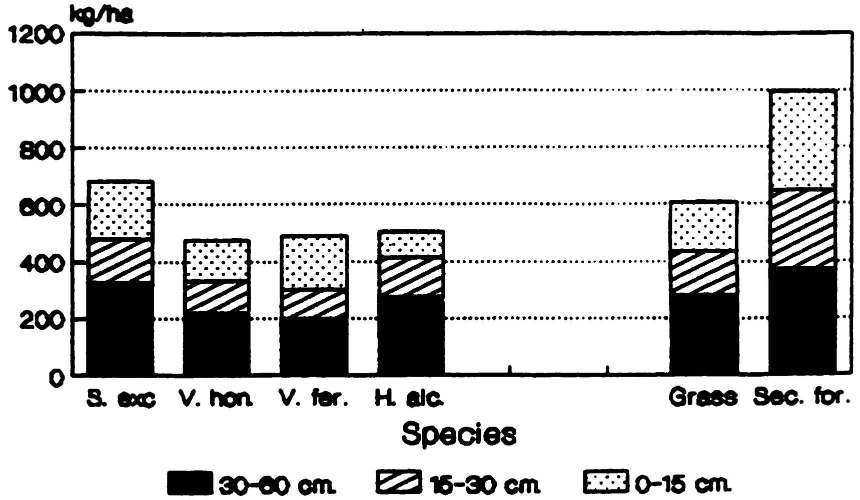


Figure 10.7. Soil Nutrient Balances - Calcium.

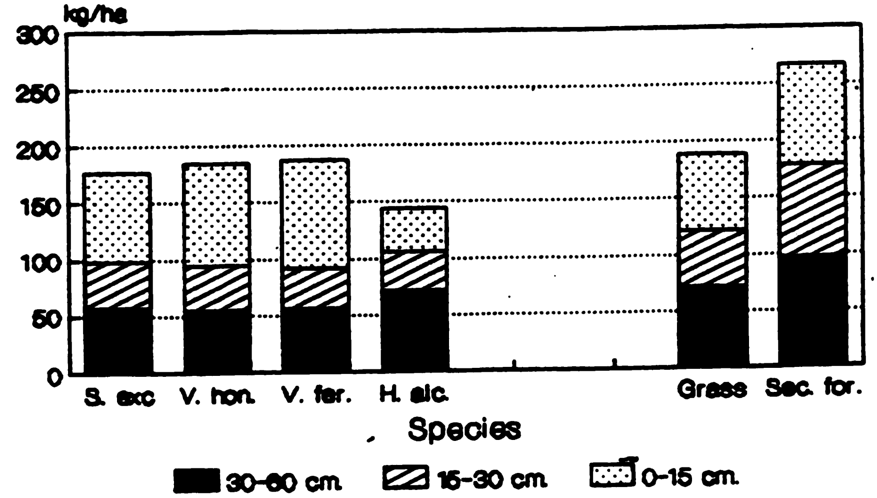


Figure 10.8. Soil Nutrient Balances - Magnesium.

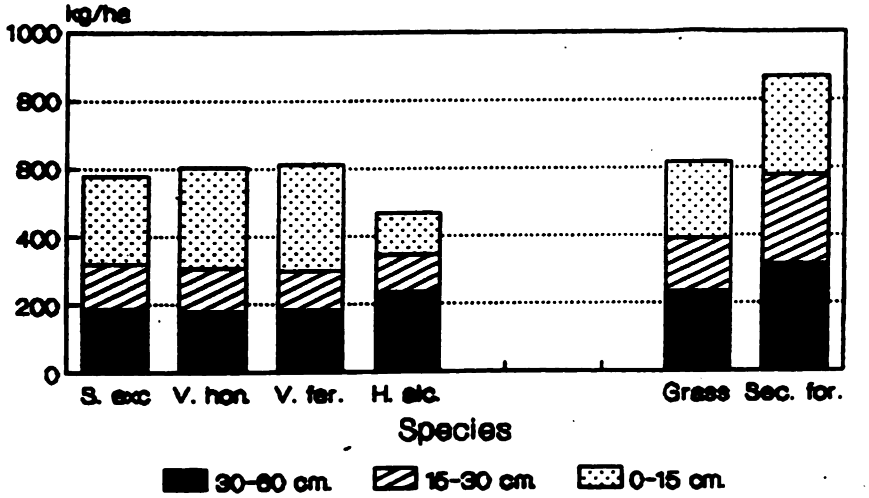


Figure 10.9. Soil Nutrient Balances - Potassium.

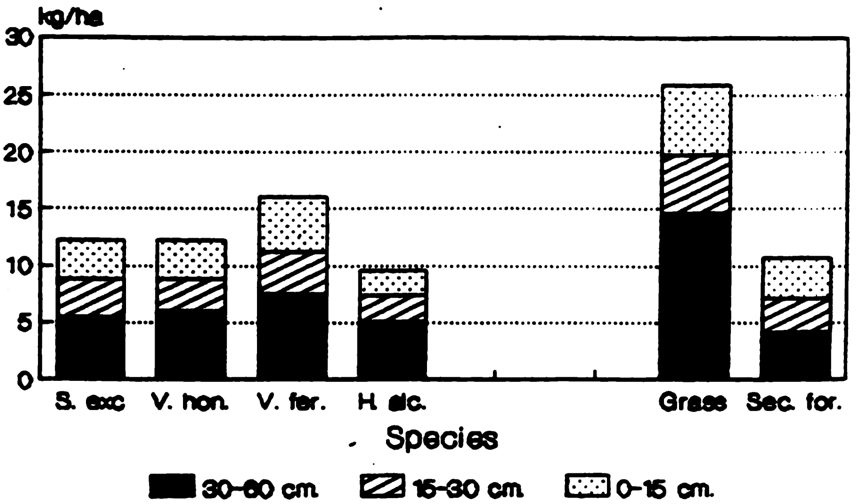


Figure 10.10. Soil Nutrient Balances - Phosphorus.

These results show that the forest floor is an important place for the accumulation and recycling of nutrients, particularly for N, Ca, Mg and P, but less for K, with marked differences among tree species. If the forest floor is affected by burning or during weeding, a substantial loss of organic matter and nutrients may occur. Wang et al. (1991) also found that with the exception of K, nutrients in forest-floor litter were equivalent to a large proportion (16-50%) of the nutrients contained in the above-ground tree biomass. They concluded that if the litter were left on the floor after harvest, it would represent a substantial reservoir of nutrients for the next rotation.

CONCLUSIONS AND RECOMMENDATIONS

1. Many indigenous tree species with good timber value can grow in open plantations on sites of low fertility and can exhibit fast growth and potential beneficial effects on soil nutrients. Moreover, their effects on soil nutrients may be observed early in the term of rotation, at canopy closure.

2. Tree species differ in their rates of nutrient accumulation in their biomass and in their tissue nutrient content. For a given species, the same trends do not hold for all nutrients: for example, a species may have the greatest effect on site Ca, but its influence on K or N may be minimal; another species may have a more significant influence on site K or P.

3. The establishment of mixed-tree plantations should be an appropriate strategy for combining the nutrient requirements of different tree species with their effects on site nutrients, so that a site may not become depleted of any particular nutrient. However, even with mixtures of trees, site deficiencies are possible for K and P in the long run.

4. Harvest of whole trees will have more negative effects on site nutrients than stem harvest only. The effects will vary according to the species and tree parts removed. Depletion of site nutrients will be greater with shorter rotations because younger trees have a larger proportion of leaf+branch tissue in relation to their stems than older trees, i.e., the potentially "recyclable" portion of the tree is greater in young trees; and harvesting shorter rotations will increase the frequency of removing nutrients from the site as well as the site disturbances associated with harvest operations (soil erosion, compaction, disturbance of the forest-floor layer, etc.).

5. Apparently, growth of understory vegetation and the corresponding accumulation of nutrients plays a relatively small role in affecting the site's nutrient budget. Therefore, agroforestry practices in the understory, such as weeding and intercropping with annual species, may not be that critical for the preservation of nutrients in the site. This situation will vary with the species planted and their management. Intercropping during early stages of tree growth, as long as the crops' nutrient requirements and their management do not provoke other deleterious effects (i.e., soil erosion, excessive nutrient removal with repeated harvests), is an alternative way to accelerate capital returns on the land and thus to stimulate local farmers to plant trees.

6. Forest-floor litter represents a major component of nutrient accumulation and recycling. Practices that affect the forest-floor litter, such as burning for weed control, harvest of litter for fuelwood or mulch, etc., can have serious deleterious effects on site nutrients.

7. The measurement of tree-tissue biomass and nutrient concentrations early in a rotation (for example, when thinning) can give a good indication of the potential impact of management practices on the conservation of site nutrients.

8. References to the rates of nutrient extraction by agricultural crops common in the region can serve as indicators of the "nutrient-supplying capacity" of soils to be compared with the rates of tree species' nutrient uptake in order to assess potential nutrient deficiencies in the site.

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Literature Cited

Allen, O. N. and E. K. Allen. 1981. *The leguminosae: a source book of characteristics, uses, and nodulation.* University of Wisconsin Press, Madison, Wisconsin.

Alpizar, L., H. W. Fassbender, J. Heuveldop, H. Folster, and G. Enriquez. 1986. Modeling agroforestry systems of cacao (*Theobroma cacao*) with laurel (*Cordia alliodora*) and poro (*Erythrina poeppigiana*) in Costa Rica. I. Inventory of organic matter and nutrients. *Agroforestry Systems* 4:175–189.

Bruijnzeel, L.A. and K. F. Wiersum. 1985. A nutrient balance sheet for *Agathis dammara* Warb: plantation forest under various management conditions. *Forest Ecology and Management* 10:195–208.

Bruijnzeel, L. A. 1991. Nutrient input-output budgets of tropical forest ecosystems: a review. *Journal of Tropical Ecology* 7:1–24.

Chambers, R. and M. Leach. 1990. Trees as savings and security for the rural poor. *Unasylva* 41:39–52.

Chudnoff, M. 1984. *Tropical timbers of the world.* USDA Forest Service, Agricultural Handbook 605, Washington, DC.

Dommergues, Y. R. 1987. The role of biological fixation in agroforestry. In: *Agroforestry: a decade of development* (Steppler, H. A. and P. K. R. Nair, eds.). Nairobi, Kenya: International Council for Research in Agroforestry. pp 245-271.

Espinoza Camacho, M. y Butterfield, R. 1989. Adaptabilidad de 13 especies nativas maderables bajo condiciones de plantacion en las tierras bajas humedas del Atlantico, Costa Rica. pp. 159-172. In: R. (ed.). Manejo y provechamiento de plantaciones forestales. con especies de uso multiple. Actas Reunion IUFRO, Guatemala, 3-7 de abril 1989. CATIE, Turrialba, Costa Rica.

Evans, J. 1987. Site and species selection - changing perspectives. *Forest Ecology and Management* 21:299–310.

Fassbender, H. W. 1984. Bases edafologicas de los sistemas de produccion agroforestales.

Serie Materiales de Ensenanza No. 21. Centro Agronomico Tropical de Investigacion y Ensenanza (CATIE), Turrialba, Costa Rica.

Gladstone, W. T., and F. T. Ledig. 1990. Reducing pressure on natural forests through high-yield forestry. *Forest Ecology and Management* 35:69–78.

Gonzalez, E. Preliminary seed trials for 36 native tree species. *Revista de Biologia Tropical* (Costa Rica). 39(1):47–51.

Gonzalez, E., R. Butterfield, J. Segleau, y M. Espinoza. 1990. Primer Encuentro Regional sobre Especies Forestales Nativas de la Zona Norte y Atlantica. Memoria. 28-29 Julio 1989. Chilamate, Costa Rica. Instituto Tecnologico de Costa Rica. Cartago, Costa Rica.

Hartshorn, G. 1983. Plants. In: *Costa Rican Natural History* (D. Janzen, ed). University of Chicago Press. pp 118-157.

Hartshorn, G. and B. Hammel. Trees of La Selva. Unpublished manuscript., La Selva Biological Station, OTS, Apdo 676, 2050 San Pedro, Costa Rica.

Holdridge, L. R. y L.J. Poveda. 1975. *Arboles de Costa Rica.* Centro Cientifico Tropical, San Jose, Costa Rica.

Lugo, A. E., S. Brown, and J. Chapman. 1988. An analytical review of production rates and stemwood biomass of tropical forest plantations. *Forest Ecology and Management* 23:179–200.

Lugo, A. E., D. Wang and F. Bormann. 1990. A comparative analysis of biomass production in five tropical tree species. *Forest Ecology and Management* 31:153–166.

Montagnini, F., B.L. Haines, L.R. Boring, and W.T. Swank. 1986. Nitrification potentials in successional black locust and mixed hardwood forest stands in the southern Appalachians, U. S. A. *Biogeochemistry* 2:197–210.

Montagnini, F. and F. Sancho. 1990a. Influencia de seis especies de arboles nativos sobre la fertilidad del suelo en una plantacion experimental en la llanura del Atlantico de Costa Rica. *Yvyrareta* (Argentina) 1(1):29–49.

Montagnini, F. and F. Sancho. 1990b. Impacts of native trees on tropical soils: a study in the Atlantic lowlands of Costa Rica. *Ambio* 19(8):386–390.

Montagnini, F., F. Sancho, K. Ramstad, and E. Stijfhoorn. 1991. Multipurpose trees for soil restoration in the humid lowlands of Costa Rica. In: *Research on multipurpose trees in Asia. Proceedings of an International Symposium, November 19-23, 1990, Los Banos, Philippines* (D. A. Taylor and K. G.MacDicken eds.). Bangkok: Winrock International Institute for Agricultural Development. pp 41-58.

Nair, P. K. R. 1989. The role of trees in soil productivity and protection. In: *Agroforestry systems in the tropics* (P.K.R. Nair, ed.). Dordrecht, The Netherlands: Kluwer Academic Publishers/International Council for Research in Agroforestry. pp 567-589.

Parrotta, J. A. 1989. The influence of management practices on the biogeochemical stability of tropical fuelwood plantations. *Tropical Ecology* 30:1–12.

Perry, D. A. and J. Maghembe. 1989. Ecosystem concepts and current trends in forest management: time for reappraisal. *Forest Ecology and Management* 26:123–140.

Russell, C. E. 1987. Plantation forestry. The Jari project, Para, Brazil. In: *Amazonian rain forests. Ecosystem disturbance and recovery* (M.G.R. Cannell and J.E. Jackson, eds.). Springer-Verlag, New York: Ecological Studies 60. pp 76-89.

Sanchez, P. A., C. A. Palm, C. B. Davey, L. T. Szott and C. E. Russell. 1985. Tree crops as soil improvers in the humid tropics? In: *Attributes of trees as crop plants.* (Cannell, M .G. R. and J. E. Jackson, eds.). Abbots Ripton, Huntingdon, England: Institute of Terrestrial Ecology, Natural Environmental Research Council. pp 327-350.

Sanchez, P. A. 1987. Soil productivity and sustainability in agroforestry. In: *Agroforestry: a decade of development* (Steppler, H. A., and P. K. R. Nair, eds.). Nairobi, Kenya: International Council for Research in Agroforestry. pp 205-223.

Sancho, F., and R. Mata. 1987. *Estudio detallado de suelos.* Estacion Biologica La Selva. Organizacion para Estudios Tropicales, San Jose, Costa Rica.

Standley, P. C. 1937-38. *Flora of Costa Rica.* Field Museum of Natural History.Chicago.

Wadsworth, F. H. 1983. Production of usable wood from tropical forests. In: *Tropical Rain Forest Ecosystems: structure and function. Ecosystems of the World 14A* (F.B. Golley, ed.). New York: Elsevier. pp 279-288.

Wang, D., F. H. Bormann, A. E. Lugo and R. D. Bowden. 1991. Comparison of nutrient-use efficiency and biomass production in five tropical tree taxa. *Forest Ecology and Management* 46:1–21.

Whitmore, J. L., and G. S. Hartshorn. 1969. *Literature review of common tropical trees.* Tropical Forestry Series, Contribution No. 8. Institute of Forest Products. College of Forest Resources, University of Washington, Seattle.

Young, A. 1989. *Agroforestry for soil conservation.* ICRAF, Science and Practice of Agroforestry. C.A.B. International and International Council for research in Agroforestry. Wallingford, UK.

Reciclaje de nutrientes en plantaciones jóvenes con árboles nativos: estrategias para un manejo sustentable

Florencia MONTAGNINI*
Fredy SANCHO**

RESUMEN

Se midió la biomasa arbórea y el contenido de nutrientes (nitrógeno, calcio, magnesio, potasio y fósforo) de ramas, tronco y follaje de cuatro especies arbóreas nativas, en una plantación experimental de cuatro años, situada en la Estación Biológica La Selva, de la Organización de Estudios Tropicales (OTS) situada en las tierras bajas atlánticas de Costa Rica, Centro América. Las cuatro especies —*Stryphnodendron excelsum* Harms, *Vochysia hondurensis* Sprague, *Vochysia ferruginea* Mart and *Hyeronima alchorneoides* (0), se compararon con respecto a su biomasa y contenido de nutrientes de la parte arbórea, así como a los compartimentos de la hojarasca del piso (mantillo) y vegetación de sotobosque. *S. excelsum* tuvo la mayor acumulación de nitrógeno en el tronco, ramas y total de biomasa arbórea. *V. hondurensis* tuvo la mayor acumulación de calcio y magnesio en la biomasa aérea, mientras que *H. alchorneoides* tuvo el mayor contenido de potasio y fósforo en el tronco. A pesar de su contenido relativamente menor de nitrógeno en el tejido, *V. ferruginea* y *H. alchorneoides* mostraron un mayor potencial para el reciclaje de nitrógeno, debido a su distribución más pareja de nitrógeno en el tronco, ramas y follaje. La acumulación de nutrientes en el sotobosque fue muy baja, en comparación con la biomasa arbórea y el mantillo.

Palabras clave: Especies nativas, Costa Rica, reciclaje de nutrientes, nitrógeno, fósforo, calcio, magnesio, potasio.

SUMMARY

Aboveground-tree biomass and nutrient content (nitrogen, phosphorus, calcium, magnesium and potassium) were measured in 4-year-old stands of four indigenus tree species: *Stryphnodendron excelsum* Harms, *Vochysia hondurensis* Sprague, *Vochysia ferruginea* Mart and *Hyeronima alchorneoides* (0), growing on infertile soils in an experimental plantation in the Atlantic humid lowlands of Costa Rica. Biomass and nutrient content among the species, and among above-ground tree biomass. *V. hondurensis* had the highest accumulation of Ca and Mg in the biomass, while *H. alchorneoides* had the highest stem K and P. In spite of their relatively lower N tissue concentrations, *V. ferruginea* and *H. alchorneoides* showed a high potential for N recycling due to its more even distribution of N in stems,

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branches and leaves. Nutrient accumulation by the understory represented a minor component in comparison with above-ground tree tissue and the forest-floor litter.

Key words: Native species, Costa Rica, nutrient recycling, nitrogen, phosphorus, calcium, magnesium, potassium.

INTRODUCCION

Nuestro estudio está enfocado a un área de tierras tropicales bajas y húmedas de Centro América, en Costa Rica, donde predominan las plantaciones de banano. La deforestación y la consecuente degradación del suelo a causa del manejo inadecuado —agricultura intensiva y pastoreo— son problemas comunes. Una precipitación de 4000 mm/año acelera la erosión de los suelos ya agotados por repetidas cosechas.

La restauración de suelos a su antigua productividad y balance ecológico se ha convertido en un interés primordial en la región. Existen agricultores dispuestos a dedicar una parte de sus tierras (10-15%) a plantaciones arbóreas, ya que las consideran como una forma de inversión. Los servicios forestales regionales alientan la plantación de especies exóticas: *Pinus caribaea, Eucalyptus deglupta, Gmelina arborea,* así como *Cordia alliodora*, una especie arbórea nativa de rotación de 30 años que crece en tierras fértiles, siendo inadecuada para tierras degradadas. La elección de especies adecuadas para sistemas de reforestación incluye los siguientes criterios: valor económico de las especies regionales; disponibilidad de semillas o plántulas; información sobre tasas de crecimiento; así como sus efectos sobre los suelos. Ciertas especies arbóreas nativas de la región bajo estudio tienen potencial para crecer bien en suelos pobres y degradados. Estas son especies de crecimiento rápido que contribuyen materia orgánica al suelo dentro de un período relativamente corto. En este trabajo describimos estas especies y su capacidad para crecer en plantaciones a cielo abierto y reciclar nutrientes en estadios tempranos de la rotación.

Beneficios de las plantaciones arbóreas

En la actualidad, un número de esfuerzos gubernamentales y privados están promoviendo la plantación de árboles para el desarrollo rural en los trópicos, incluyendo plantaciones mixtas de árboles y cultivos practicados en sistemas agroforestales. Los árboles son considerados fuente de dinero, ahorro y bienes para la población rural (Chambers y Leach 1990). Ya que las plantaciones tropicales manejadas para alto rendimiento pueden ser por lo menos de cuatro a diez veces más productivas que los bosques naturales no manejados (Wadsworth 1983), éstas también pueden ayudar a satisfacer la creciente demanda global de madera. Se espera que este tipo de manejo contribuya a disminuir la presión sobre los bosques naturales (Evans 1987).

El manejo sustentado de plantaciones arbóreas se convierte en una alternativa biológica y socialmente plausible en suelos que no son apropiados para la práctica continua de agricultura que usa las tecnologías locales predominantes (Gladstone y Ledig 1990). En especial, las plantaciones de árboles y las plantaciones mixtas de árboles y cultivos representan alternativas productivas para el uso de tierras deforestadas donde la regeneración natural es pobre debido a la degradación intensa o a la distancia de fuentes de propagación. La baja fertilidad, la compactación del suelo a causa del pastoreo y la invasión por malas hierbas —todos índices de degradación— pueden ser serios obstáculos en la reforestación y en la agricultura convencional. Cuanto más se expande el área de degradación, más se incrementa el énfasis en la plantación de especies arbóreas capaces de crecer en condiciones pobres y ofrecen productos con potencial financiero (madera, combustible y demás) así como también beneficios ambientales (conservación de suelos, protección de cuencas) (Evans, 1987).

La selección apropiada de especies arbóreas para la plantación forestal o agroforestal depende del conocimiento sobre el rendimiento de la especie y de los beneficios económicos y ambientales que ésta ofrezca. En situaciones locales, la selección de una especie arbórea es determinada por la disponibilidad de semillas o plántulas y por la información disponible acerca de sus características silviculturales y manejo —por ejemplo, crecimiento rápido y posibilidad de

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cultivo mixto durante las etapas tempranas de establecimiento. La mayoría de los programas y subvenciones de reforestación promueven el uso de especies bien conocidas y con frecuencia exóticas. Alrededor del 85% de las plantaciones forestales en los trópicos está dominada por tres géneros: *Pinus*, *Eucalyptus* y *Tectona* (Evans, 1987), mientras que existen miles de especies indígenas apropiadas para fines similares. Los árboles nativos pueden ser más apropiados que los exóticos ya que están mejor adaptados a las condiciones ambientales locales, las semillas y plántulas están localmente disponibles y los agricultores están familiarizados con ellos y con sus usos. Además, el uso de árboles nativos en sistemas productivos ayuda a la preservación de la diversidad genética y fomenta un mejor balance con la flora y fauna local.

Consecuencias ecológicas de las plantaciones arbóreas de crecimiento rápido

Los factores que influyen sobre la productividad de las plantaciones forestales tropicales son poco entendidos. Algunos estudios informan sobre rendimientos o producción de biomasa en relación a factores climatológicos, pero pocos refieren las características del sitio, tales como la elevación y el tipo de suelo (Lugo et al., 1988). Los arboles pueden influenciar las características del sitio a través del reciclaje de nutrientes y sus interacciones con el medio ambiente.

Los efectos beneficiosos más importantes de los árboles sobre los suelos pueden incluir el mejoramiento de la estructura del suelo y el incremento de nutrientes disponibles (Fassbender, 1984, Nair, 1989, Sánchez et al., 1985, Sánchez, 1987). La fijación simbiótica de nitrógeno por los árboles resulta, en muchos casos, en el incremento del nitrógeno disponible en el suelo (Alpízar et al., 1986, Montagnini et al., 1986, Dommergues, 1987). Por otro lado, las plantaciones jóvenes de árboles tropicales, las cuales incorporan cantidades considerables de nutrientes en su biomasa sobre un período de tiempo relativamente corto, son ecosistemas de crecimiento rápido (Bruijnzeel, 1991). Durante las etapas tempranas de desarrollo, la cantidad de nutrientes absorbida del suelo generalmente sobrepasa la cantidad de nutrientes suplementada al suelo por la hojarasca y por la lluvia (Bruijnzeel, 1991).

El deterioro de la fertilidad del suelo puede ser una limitación seria para la plantación forestal sustentada en regiones tropicales: la fertilidad del suelo puede ser disminuida a través de la eliminación excesiva de biomasa, especialmente si los nutrientes del dosel arbóreo son perdidos a través de la cosecha o de la preparación del sitio para el cultivo (Perry y Maghembe, 1989). Por otro lado, Wadsworth (1983) sugiere que, con la posible excepción del fósforo, las cosechas repetidas generalmente no resultarían en serias deficiencias de nutrientes en el suelo.

Lundgren (1980) propuso que los efectos beneficiosos de las plantaciones forestales ocurren sólo durante el período de cinco a diez años inmediatamente después del cierre del dosel (la fase de enriquecimiento por barbecho). Durante la fase de producción máxima, puede deteriorarse la calidad del sitio: los minerales nutritivos son absorbidos por los árboles mientras que la hojarasca se acumula en el suelo del bosque, pero las condiciones no son apropiadas para la descomposición de la materia orgánica (Lundgren, 1980). Sánchez et al. (1985) concluyeron que los efectos perjudiciales en los suelos ocurren sólo durante el establecimiento de la plantación, aunque también enfatizaron que la extracción de nutrientes a través de la cosecha y las pérdidas por lixiviación antes del cierre del dosel provocan un agotamiento de nutrientes claves, especialmente de potasio, que deberían ser repuestos si el nivel de rendimiento ha de ser mantenido en las rotaciones siguientes.

Las especies arbóreas varían en sus tasas de absorción y capacidad de reciclaje de nutrientes. La posibilidad de usar ciertas especies para la acumulación de nutrientes fue sugerida por Sánchez et al. (1985) quienes observaron que ciertas especies tienen la habilidad (por ejemplo, *Gmelina arborea*) de acumular calcio y magnesio, mientras que otras favorecen la acumulación de potasio y fósforo. Todavía son escasos los datos sobre segundas y terceras rotaciones, así que no tenemos suficientes indicios acerca de cuáles son los nutrientes críticos para el mantenimiento de la producción del sitio. La información sobre las tasas de absorción y capacidad de reciclaje de nutrientes por las diferentes especies arbóreas ayudará a diseñar las mejores estrategias de manejo que tomarán ventaja de los efectos beneficiosos de los árboles sobre la fertilidad del suelo o evitarán el deterioro del sitio en el momento de la cosecha.

Efectos de las plantaciones arbóreas sobre los nutrientes del sitio: un ejemplo de Costa Rica

Las pruebas locales y regionales de especies arbóreas para la reforestación muchas veces revelan rendimientos sobresalientes de los árboles nativos. Por ejemplo, de trece especies arbóreas nativas en una plantación experimental en la estación biológica La Selva de la Organización de Estudios Tropicales (OTS) situada en las tierras bajas atlánticas de Costa Rica, Centro América, por lo menos cuatro —*Stryphnodendron excelsum, Vochysia hondurensis, Vochysia ferruginea* y *Hyeronima alchorneoides*— presentaron tasas de crecimiento iguales o mayores que las especies exóticas recomendadas para la región (Espinoza y Butterfield, 1989). Este trabajo demuestra el potencial de muchos árboles nativos para uso comercial. Además se destaca que ciertas especies nativas crecen bien en sitios degradados de suelos pobres y ácidos que no podrían sustentar la agricultura convencional. Los resultados de nuestros estudios en el mismo sitio demostraron que después de dos años y medio estas especies contribuyeron a la restauración de la fertilidad del suelo a través del incremento de la materia orgánica, el nitrógeno y los niveles de cationes a valores aproximados a aquellos considerados apropiados para los cultivos agrícolas (Montagnini y Sancho, 1990a, 1990b).

En las siguientes secciones se compara la biomasa y contenido de nutrientes de estas especies, la hojarasca, la vegetación del sotobosque y las reservas de nutrientes del suelo. Esta información puede ser utilizada para diseñar estrategias de manejo que tomen ventaja de los efectos beneficiosos de los árboles sobre los suelos y para evitar el agotamiento de los nutrientes del sitio en el momento de la cosecha. Estas estrategias deberían ser valiosas para la promoción del uso de sistemas —mixtos o de plantaciones puras, sistemas agroforestales— que incluyan estas especies madereras de crecimiento rápido en la zona y en otras regiones tropicales con características ecológicas similares.

El sitio experimental

La plantación experimental fue establecida en diciembre de 1985, sobre un área de pastos abandonados en la Estación Biológica La Selva de la Organización para Estudios Tropicales (10 26'N, 86 59'O, 50 metros de altura media, 24 °C de temperatura media anual, 4000 mm de precipitación media anual, con precipitación máxima en julio y mínima en marzo) (Informes climatológicos de la Estación Biológica La Selva). Los suelos son Fluventic Dystropepts, derivados de material volcánico depositados aluvialmente; son profundos, bien drenados, y sin piedras, tienen un contenido de materia orgánica bajo o medio, textura moderadamente pesada, y son generalmente ácidos y poco fértiles (Sancho y Mata, 1987). El área se deforestó en la década del 50, y fue utilizada para pastoreo de ganado hasta 1984. Se realizó una limpieza manual del terreno antes de la plantación. Las especies arbóreas se plantaron al azar con cinco (5) réplicas, cada parcela (14 m × 14 m) con siete filas de siete árboles y con dos metros entre árboles. Cinco parcelas similares de 14 m × 14 m también fueron establecidas en un área adyacente con pastos y en un bosque secundario. Durante el primer año, se desmalezó manualmente cuatro veces. Después, este proceso se llevó a cabo mecánicamente hasta el cierre del dosel.

Las especies arbóreas

Las especies para este estudio eran de buen crecimiento inicial (Espinoza, Camacho y Butterfield, 1989, González et al., 1990), y valor comercial (González et al., 1990, Chudnoff, 1984, Holdridge y Poveda, 1975).

Stryphnodendron excelsum Harms (Leguminosae, subfamilia Mimosoideae) ("vainillo") se encuentra sólo en Costa Rica, aunque representantes de este género son nativos en todo América tropical (Brasil, Costa Rica, Guayana) (Allen y Allen, 1981). Esta especie crece en regiones de climas muy húmedos y aparentemente se adapta tanto a suelos aluviales como también a cerros bajos y a suelos degradados por el pastoreo (González et al., 1990). Su madera es primordialmente utilizada en construcción general y también para muebles pequeños y tornería (Allen y Allen, 1981). Su fruto sirve de alimento a muchas especies, sobre todo pequeños mamíferos.

Vochysia ferruginea Mart (Vochysiaceae) ("botarrama") crece en los bosques de tierras bajas desde Nicaragua hasta Brasil (Whitmore y Hartshorn, 1969). Se encuentran en suelos ácidos, bien drenados, y de baja fertilidad, aunque se puede adaptar a una variedad de suelos (González et al., 1990). Es una especie pionera que se autopoda y forma rodales uniformes, de edad pareja en campos abandonados su madera se usa para madera contrachapada y construcción.

Vochysia hondurensis Sprague (Vochysiaceae) ("mayo") se encuentra desde Méjico hasta Panamá, en elevaciones hasta de 900 m (Whitmore y Hartshorn, 1969). Usualmente crece en áreas húmedas y de baja altitud, en suelos aluviales o residuales (menos fértiles). Como es considerado un substituto de la caoba, su madera es muy apreciada para carpintería, madera contrachapada y mueblería.

H. alchorneoides (O) (Euphorbiaceae) ("pilón") abarca desde el sur de Méjico hasta el sur de Brasil (Chudnoff, 1984). Esta especie crece bien en cerros y en pastos abandonados, pero no se sabe mucho sobre sus requisitos edáficos. Su madera es usada en construcción pesada, mueblería, enchapados decorativos y tornería (Chudnoff, 1984). Las características botánicas de estas especies están descritas en Holdridge y Poveda (1975), Hartshorn (1983), Standley (1937-38) y Hartshorn y Hammel (no publicado). Estudios detallados sobre las semillas y las características de germinación son presentados en González (1991).

METODOS

Los procedimientos de muestreo y métodos químicos están descritos en Montagnini y Sancho (1990a, 1990b), y en Montagnini et al. (1991). Los suelos se muestrearon bajo las cuatro especies arbóreas mencionadas, en área de pastos libre de árboles y en bosque secundario de veinte años. La biomasa de los árboles y el contenido de nutrientes en tallos, ramas y hojas fueron medidos al momento del raleo de las parcelas, cuando la plantación tenía cuatro años. También se midió la biomasa y la concentración de nutrientes del sotobosque. El reciclaje de nutrientes fue calculado multiplicando la biomasa de cada compartimento por la concentración de nutrientes en el mismo (nitrógeno, calcio, magnesio, potasio, fósforo).

RESULTADOS Y DISCUSION

Biomasa arbórea

Los valores de la biomasa de árboles enteros presentados aquí (Tabla 1) son mayores que los reportados para *Albizia lebbek* de cuatro años (Parrota, 1989) y para *Leucaena leucocephala* de cinco años y medio (Wang et al., 1991), ambos creciendo en plantaciones densas para la producción de biomasa en Puerto Rico. Los valores de productividad (biomasa arbórea dividida por la edad del árbol) concuerdan con otros valores presentados en la literatura para plantaciones monoespecíficas en los trópicos húmedos. El valor para *V. hondurensis* es similar al valor reportado para *Gmelina arborea* (12,8 toneladas/ha/año) en la región amazónica del Brasil (Russell, 1987) así como también al valor para *Gmelina arborea* (12,7 toneladas/ha) y para *Albizia falcataria*, ambos en las Filipinas (11,3) (Kawajara et al., 1981, en Young, 1989). Sin embargo, los incrementos presentados aquí son menores que aquellos reportados para algunas especies de crecimiento rápido, tales como *Acacia mangium* (15,5 a 18,0 toneladas/ha en Malasia) y *Leucaena leucocephala* (20,0 a 30,0, y hasta 80,0 toneladas/ha en Hawaii y en otros sitios tropicales, Young, 1989).

Los incrementos anuales en madera para especies latifoliadas en los trópicos

Tabla 1. Promedio de diámetros a la altura del pecho (dap), altura, biomasa aérea y crecimiento anual.

Anual medio	Dap (cm)	Altura (m)	Biomasa aérea viva Fuste	 Ramas (kg/ha)	 Hojas	 Total	Crecimiento Total (t/ha/año)	 Fuste
S. exc.	12,0a	8,9b	35.250a	15.250a	4.325a	54.825	13,7	8,8
V. fer.	10,3a	8,1b	24.750b	14.250a	5.925a	44.925	11,2	6,2
V. hon.	10,8a	12,0a	41.750a	6.500b	7.250a	55.500	13,9	10,4
H. alc.	10,8a	9,0a	26.250b	12.250a	5.350a	43.850	12,0	6,5

Nota: En ésta y las siguientes tablas, las diferencias entre sitios para un parámetro dado son estadísticamente significativas cuando los promedios son seguidos por letras diferentes.

varía entre 1 y 28 toneladas/ha/año. Las especies de crecimiento rápido como *Gmelina arborea* y *E. saligna* varían entre 10 y 20 y entre 8 y 28 toneladas/ha respectivamente, y las especies de crecimiento relativamente más lento como *Swietenia* sp. y *Tectona grandis* varían entre 1 y 4 y entre 3 y 12 toneladas/ha respectivamente (Wadsworth, 1983). Otros valores para árboles de crecimiento rápido en regiones tropicales húmedas incluyen varias especies de *Eucalyptus* cultivadas en las Américas y en el Asia (entre 7,2 y 11,9 toneladas/ha); *Gmelina arborea* en Costa Rica (11,8 toneladas/ha) (Lugo et al., 1988); de 1,3 a 5,3 *Leucaena leuocephala* en sitios premontanos y en tierras bajas húmedas (entre 2,8 y 15,9 toneladas/ha); *Prosopis juliflora*, en sitios húmedos de India (9,4 toneladas/ha), y *Populus deltoides*, en sitios subtropicales de India (6,4 toneladas/ha) (Lugo et al., 1990). De modo que el promedio anual de los incrementos en madera para las especies en este estudio cae dentro de los valores reportados para otras especies arbóreas de crecimiento rápido en los trópicos húmedos.

Acumulación de nutrientes en la biomasa arbórea

Nitrógeno

Las mayores concentraciones de nitrógeno en tallos, en ramas y biomasa arbórea se encontraron en *S. excelsum*. Aproximadamente 200 kg/ha, o 60% del nitrógeno de la biomasa arbórea de *S. excelsum* (Figura 1) permanecería en el sitio al momento de la cosecha si se dejaran las ramas y hojas en el suelo. *V. hondurensis* tenía una proporción similar de nitrógeno en su porción de hojas y ramas; al igual que en *S. excelsum* más del 50% del nitrógeno de la biomasa arbórea podría ser reciclado si se dejan los restos en el sitio al momento de la cosecha. *V. ferruginea*, con una biomasa de tallos relativamente menor, proporcionalmente tenía más nitrógeno en hojas (52,9%) y en ramas (42,1%), mientras que *H. alchorneoides* tenía una distribución más pareja en la biomasa arbórea (Figura 1).

Calcio

V. hondurensis, con una mayor biomasa de tronco y una concentración elevada de calcio (Ca), también tenía la mayor cantidad de calcio en la madera (más de 600 kg/ha, equivalente a 84% del Ca de la biomasa arbórea), aproximadamente el doble de la cantidad de *S. excelsum* y de *V. ferruginea*, y varias veces más que *H. alchorneoides* (Figura 2). En consecuencia, la cosecha total de árboles de *V. hondurensis* podría reducir considerablemente la cantidad de calcio en el sitio. Sin embargo, mientras los árboles de *V. hondurensis* estén vivos, cantidades relativamente grandes de calcio podrían ser recicladas porque, aunque sólo represente el 16% de la biomasa de la parte aérea, la cantidad conjunta de calcio en las hojas y las ramas sobrepasaba 100 kg/ha.

La proporción de calcio en el tronco en relación a la biomasa total fue similar para

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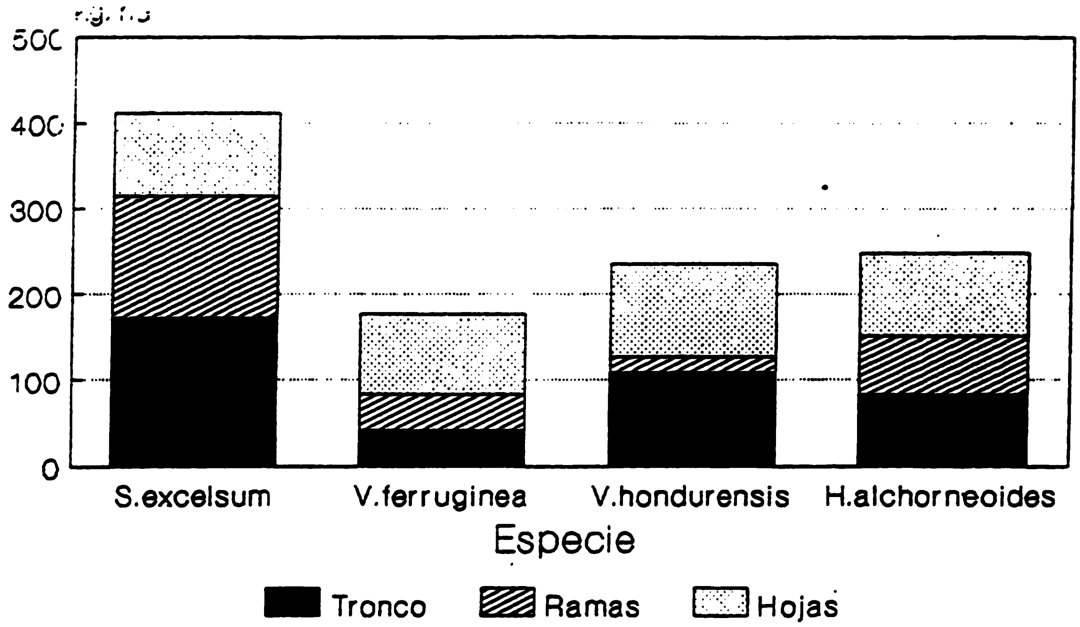

Figura 1. Nitrógeno en la biomasa arbórea.

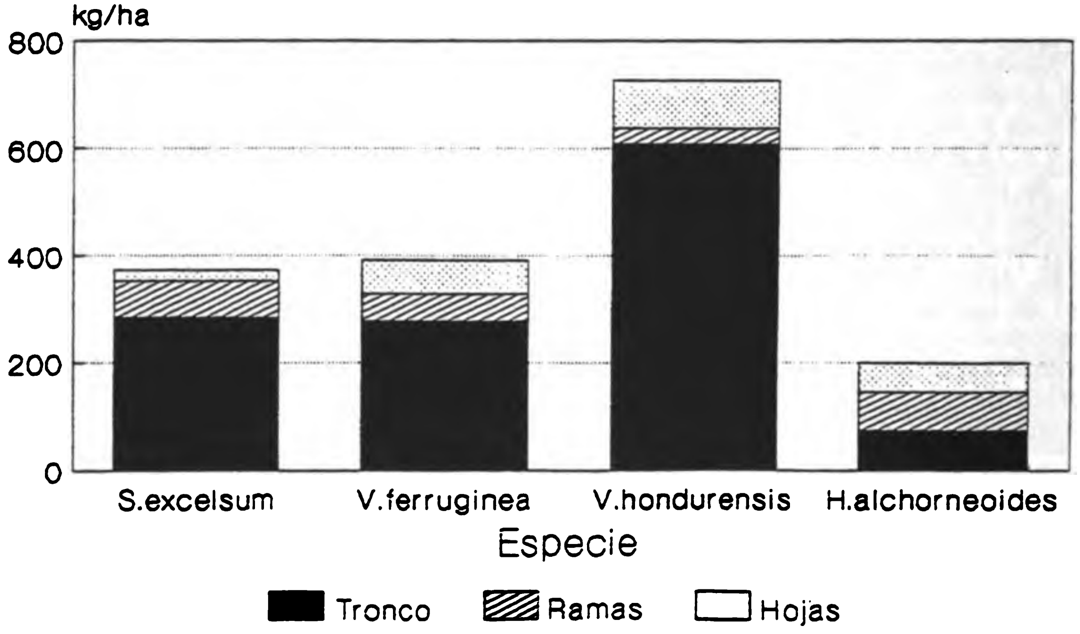

Figura 2. Calcio en la biomasa arbórea.

S. excelsum y para *V. ferruginea* (76,6% y 70,8% respectivamente) (Figura 2), pero las cantidades absolutas fueron menores que la mitad de la cantidad de *V. hondurensis*. *H. alchorneoides* otra vez tuvo una mejor distribución de calcio en los tallos, las hojas y las ramas.

Magnesio

V. hondurensis, con su alta biomasa de tronco y alta concentración de magnesio (Mg), también tuvo la mayor cantidad de Mg en la madera (55% del total del Mg contenido en la biomasa arbórea, aproximadamente 30 kg/ha) (Figura 3). En consecuencia, si se retiran los troncos de *V. hondurensis* sc afectaría el reciclaje de Mg en el sitio de una manera más dramática que cualquiera de las otras especies, especialmente si se realiza una cosecha total (Figura 3).

Potasio

El panorama cambia con el potasio (K): la mayor acumulación de K en tallos fue hallado en *H. alchorneoides* (252 kg/ha, Figura 4), representando 58,7% del K arbóreo. Esta cantidad fue seguida por *V. hondurensis* con 175 kg/ha, la cual representa 76,8% del K arbóreo. En consecuencia, la cosecha total de árboles de *H. alchorneoides* y de *V. hondurensis* podría tener los mayores efectos en el reciclaje de K. *S. excelsum* y *V. ferruginea* tenían 33,6% y 35,4% respectivamente, de K en los tallos. El reciclaje de K en las hojas y las ramas podría ser relativamente más importante cuando se considera estas últimas dos especies.

Fósforo

V. hondurensis y *H. alchorneoides* tuvieron las mayores proporciones de fósforo (P) en la madera (72,4% y 62,1% respectivamente) (Figura 5). *S. excelsum* y *V. ferruginea* tuvieron relativamente menores cantidades de P en los tallos (43,9% y 48,7% respectivamente).

Nuestros resultados confirman reportes anteriores sobre los efectos negativos de la cosecha total de árboles sobre las reservas de nutrientes del sitio: por ejemplo, Bruijnzel y Wiersum (1985) estudiaron las entradas/salidas de nutrientes en plantaciones de *Agathis dammara* en las tierras altas de Java. Sus resultados, calculados para una rotación de treinta años, indicaron que la cosecha total de los árboles eliminaría una cantidad de nutrientes equivalente a las entradas de potasio y calcio, casi la mitad de la entrada de magnesio, y el doble de la

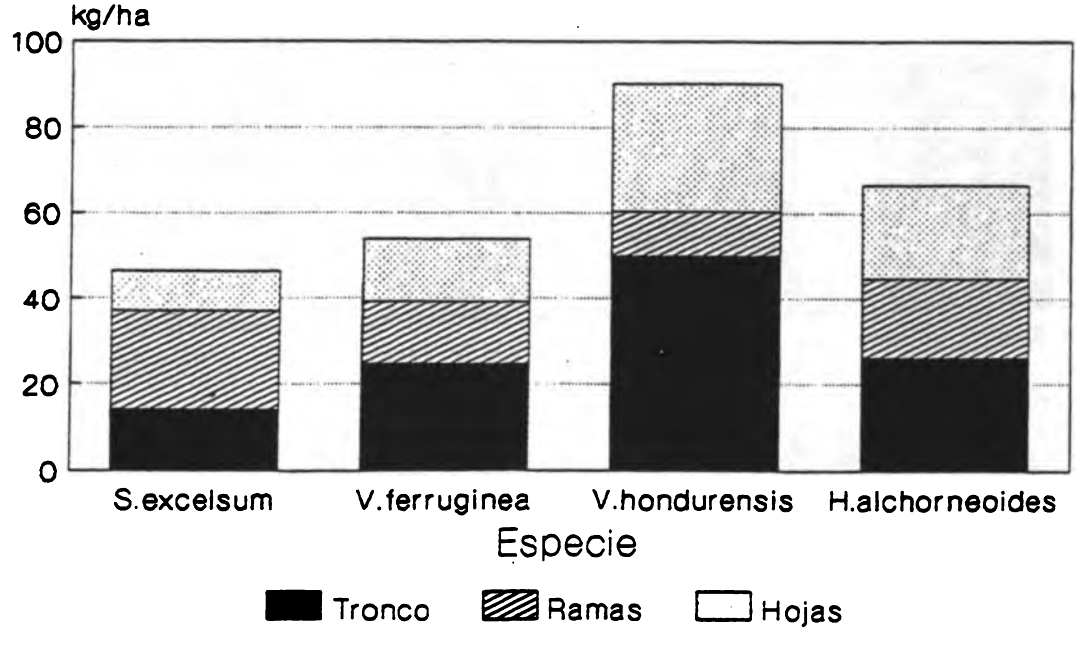

Figura 3. Magnesio en la biomasa arbórea.

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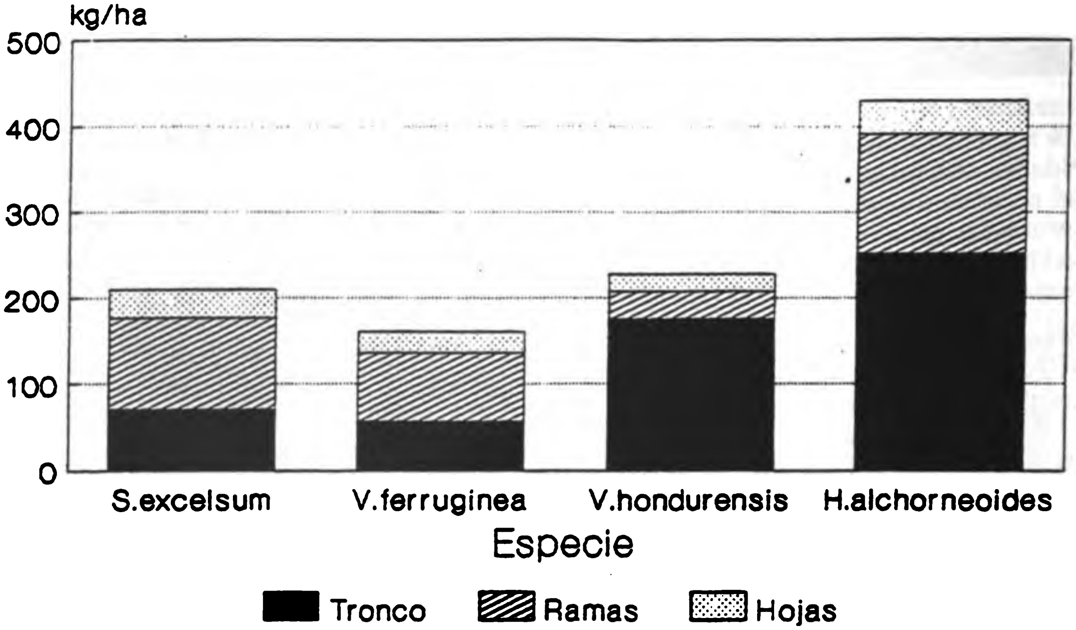

Figura 4. Potasio en la biomasa arbórea.

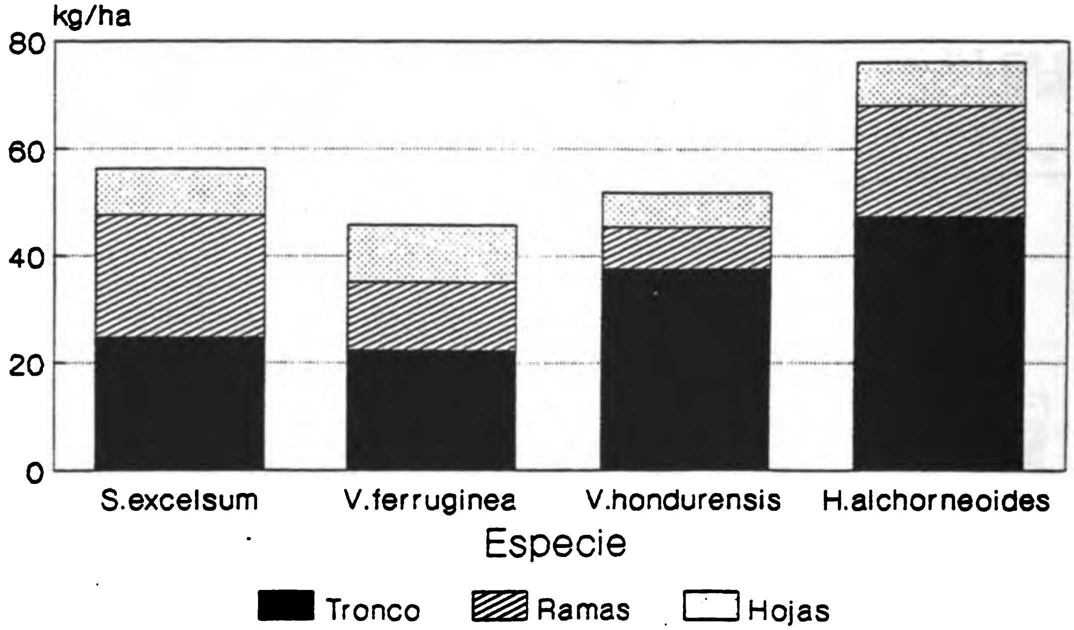

Figura 5. Fósforo en la biomasa arbórea.

Tabla 2. Materia orgánica, cantidades totales de N, P, pH, Ca, Mg y K en suelos bajo las cuatro especies arbóreas nativas en la plantación, en el área de pasto y en el bosque secundario; Mayo 1989. (1)

Sitio	Prof.	MO	N	P	pH	Ca	Mg	K
	(cm)	(%)		(mg/kg)			(cmol/kg)	
S.	0-15	4,50a	0,278a	2,4a	5,1a	0,68b	0,44a	0,13a
exc.	15-30	3,29a	0,224a	2,1a	5,1ab	0,52bc	0,22bc	0,14a
	30-60	1,88a	0,196a	1,8b	5,1a	0,54a	0,16a	0,14a
V.	0-15	5,06a	0,320a	3,24a	4,98a	0,63bc	0,53bc	0,16a
fer.	15-30	3,66a	0,248a	5,03c	5,03c	0,35d	0,20c	0,10a
	30-60	2,94a	09,200a	2,50b	5,07a	0,33a	0,16a	0,15a
V.	0-15	4,30a	0,304a	2,30a	5,20a	0,47bc	0,50bc	0,10a
hon.	15-30	3,16a	0,232a	1,82a	5,08ab	0,38cd	0,22bc	0,07a
	30-60	2,42a	0,202a	2,00b	5,13a	0,36a	0,15a	0,06a
H.	0-15	5,16a	0,232a	1,5a	5,1a	0,31c	0,21a	0,09a
alc.	15-30	2,77a	0,248a	1,5a	5,1ab	0,45bcd	0,19c	0,10a
	30-60	1,21a	0,158a	1,7b	5,2a	0,46a	0,20a	0,10a
Pasto	0-15	3,98a	0,296a	4,1a	5,2a	0,57bc	0,38a	0,22a
	15-30	2,94a	0,236a	3,4a	5,1ab	0,51bcd	0,27bc	0,17a
	30-60	2,46a	0,194a	8,9a	5,2a	0,47a	0,20a	0,13a
Bosque	0-15	5,11a	0,288a	2,3a	5,2a	1,16a	0,49a	0,21a
	15-30	3,83a	0,244a	2,0a	5,2a	0,92a	0,45a	0,17a
	30-60	2,48a	0,206a	1,4b	5,2a	0,62a	0,27a	0,12a

1. Existen diferencias estadísticamente significativas entre los sitios para una profundidad dada y los parámetros cuando los promedios son seguidos por letras diferentes.

entrada de fósforo. Los autores concluyeron que para evitar la escasez de nutrientes, especialmente de fósforo, la cosecha total de árboles no debería ser practicada. Nuestros resultados también sugieren que dejando los restos de ramas y hojas en el sitio podrían disminuir considerablemente los impactos negativos de la cosecha, con diferentes consecuencias según las especies.

Impacto de los árboles sobre los nutrientes del suelo

Los mayores niveles de materia orgánica y de N en el suelo se encontraron en la plantación arbórea, con cantidades aproximadas a los del bosque secundario (Tabla 2), aunque estas diferencias no son estadísticamente significativas ($P < 0,05$). El contenido de P fue mayor en el área de pasto que en la plantación o que en el bosque (Tabla 2). Dentro de la plantación arbórea, no hubo diferencias significativas en el contenido de cationes entre las especies. Sin embargo, sí hubo una tendencia a niveles más altos de Ca bajo *S. excelsum* y niveles menores bajo *H. alchorneoides*. Los mayores niveles de Mg fueron registrados bajo las dos especies de *Vochysia*, con contenidos menores en *H. alchorneoides* (Tabla 2). Estos resultados confirman datos de mediciones anteriores realizados en 1988 (Montagnini y Sancho, 1990a, 1990b).

Mediciones similares tomadas en mayo de 1990 y nuevamente en mayo de 1991, revelaron tendencias en la acumulación de nutrientes en el suelo similares a aquellas encontradas en 1988 y 1989. Al examinar los datos entre 1988 y 1991, no se detectaron tendencias de aumento o reducción a través del tiempo para ninguno de los nutrientes (Montagnini y Sancho, datos no publicados). Aparentemente, el aumento del nivel de nutrientes del sitio fue observado en 1988, cuando los árboles tenían dos años y medio y habían cerrado el dosel, pero después de este efecto inicial no se pudo detectar ningún otro cambio positivo.

Los impactos de la plantación de especies arbóreas sobre las reservas de nutrientes del suelo dependerán de la absorción de nutrientes por los árboles en relación a la capacidad del suelo para suplir nutrientes, del reciclaje de nutrientes (mientras los árboles estén vivos), y de las partes cosechadas del árbol, ya sea el árbol entero o la madera, y su biomasa y contenido de nutrientes al momento de la cosecha. Esto se puede ilustrar tomando como ejemplo estas relaciones para *V. hondurensis*, la especie de crecimiento más rápido y aparentemente de mayores requerimientos nutricionales en este estudio. La retención de nutrientes por *V. hondurensis* (calculado dividiendo el total de nutrientes en la biomasa por la edad de la plantación) fue un promedio de 58 kg de N, 181 kg de Ca, 57 kg de K, 22 kg de Mg y 13 kg de P/ha/año. Las cantidades de N, Ca, Mg y K son el doble de aquellas reportadas por Wadsworth (1983) para plantaciones de teca, pero el valor de P es similar. Aunque estas cantidades de nutrientes son altas, éstas deberían ser comparadas con la capacidad del suelo para suplir nutrientes. Por ejemplo, Wadsworth (1983) comparó datos de la tasa de absorción anual de nutrientes de varios cultivos agrícolas en suelos Ultisoles y Oxisoles en Puerto Rico (N = 90 - 120 kg/ha/año, K = 50 - 90, Ca = 86 - 109, Mg = 68 - 98), con las tasas de retención media anual de nutrientes de plantaciones de teca y de pino. Al examinar esos datos se concluye que la capacidad de los suelos para suplir nutrientes era suficiente para las necesidades de las plantaciones, y que los árboles podían ser cosechados sin crear deficiencias en el suelo, con la posible excepción de P. Wang et al. (1991) también repotaron que la tasa anual de absorción de N, P, Ca, Mg y K para plantaciones de *Casuarina* y *Albizia* en Puerto Rico era similar a la tasa de absorción de cultivos como el maíz y el sorgo.

En nuestro análisis, no estamos considerando la capacidad para suplir nutrientes de los suelos, pues no se dispone hasta la fecha de registros que permitan esta comparación.

Biomasa y concentración de nutrientes en la vegetación del sotobosque

La acumulación de nitrógeno en la biomasa aérea del sotobosque fue mayor bajo las parcelas de *S. excelsum* (14,9 kg/ha), aunque esta cantidad representa sólo 3,6% del N en la biomasa arbórea (Tabla 3). Para

Tabla 3. Biomasa y contenidos de nutrientes en la vegetación del sotobosque y la hojarasca del suelo del bosque (1)

(a) Vegetación del sotobosque

	Biomasa (kg/ha)	N	Ca	Mg (kg/ha)	K	P
S. exc.	874	14,9 (3,6)	2,9 (0,8)	3,6 (7,7)	8,8 (4,2)	1,1 (2,0)
H. alc.	425	5,7 (2,3)	3,3 (1,6)	1,9 (2,9)	3,3 (0,8)	3,1 (4,1)

(b) Hojarasca del suelo del bosque (2)

	Biomasa (kg/ha)	N	Ca	Mg (kg/ha)	K	P
S. exc.	5 612	95,1 (23,0)	41,6 (11,1)	8,2 (17,6)	6,6 (3,1)	4,3 (7,6)
V. fer.	17 215	240,3 (137,0)	187,6 (47,9)	19,1 (35,5)	12,1 (7,5)	15,5 (33,8)
V. hond.	11 084	134,0 (57,0)	170,0 (23,4)	26,4 (24,3)	9,7 (4,2)	11,6 (22,3)
H. alc.	4 238	39,2 (15,8)	55,0 (27,0)	11,9 (17,9)	6,8 (1,6)	12,9 (16,9)

1. Los números entre paréntesis son porcentajes en relación a la biomasa total de nutrientes del árbol.
2. Totales, incluyendo hojas, fragmentos y ramas.

H. alchorneoides, el N en la biomasa del sotobosque fue 5,7 kg/ha, o 2,3% de la biomasa arbórea. Para los otros nutrientes, la acumulación en la biomasa del sotobosque bajo *S. excelsum* varió entre 0,8% y 7,7%, y bajo *H. alchorneoides*, varió entre 0,85% y 4,1% (Tabla 3).

Ya que la vegetación del sotobosque aparentemente representa una proporción relativamente pequeña de nutrientes en relación al árbol entero, las manipulaciones del sotobosque deberían tener poco efecto sobre el reciclaje de nutrientes en el sitio. Por ejemplo, el desmalezado debería tener un efecto relativamente menor sobre el reciclaje de nutrientes, a menos que el sotobosque sea eliminado varias veces al año. Esta hipótesis también sugiere que el intercultivo de especies herbáceas anuales que alcanzan cantidades similares de biomasa a las del sotobosque bajo *S. excelsum* o *H. alchorneoides* no tendrán un efecto negativo considerable en el balance de nutrientes del sitio. Debido a que las muestras de biomasa del sotobosque fueron tomadas cuando la biomasa estaba en su apogeo, las cantidades reportadas aquí son consideradas una aproximación a las que podrían ser obtenidas en cultivos. Sin embargo, este factor merece más estudio, ya que los requerimientos de nutrientes y las partes de plantas y árboles eliminados con la cosecha variarán con los cultivos. Nuestros resultados, sin embargo, tienden a concordar con Bruijnzel y Wiersum (1985), quienes concluyeron que el uso de intercultivos en plantaciones arbóreas en Java, acompañado de medidas preventivas para reducir la erosión del suelo, era una manera aceptable de conservar nutrientes. Ellos argumentan que además de sus beneficios socioeconómicos, el uso de prácticas "taungya" podrían también resultar ventajoso ya que los agricultores podrían estar dispuestos a usar fertilizantes para los cultivos y los efectos dispuestos a usar fertilizantes para los cultivos y los efectos residuales de estos nutrientes aplicados podrían incrementar la producción de los árboles.

Acumulación de nutrientes en la hojarasca del bosque

La mayor acumulación de nutrientes y biomasa de hojarasca del suelo fue bajo *V. ferruginea*. El N en la hojarasca bajo *V. ferruginea* fue mayor que en la biomasa arbórea de la misma (Tabla 3). Como fue notado anteriormente, la biomasa de las hojas y ramas de *V. ferruginea* representa una gran porción de su biomasa arbórea. Esta especie de auto-poda, una característica que aumenta el despoje de hojas y ramas, y la poda ocasional puede haber añadido aún más hojarasca al suelo forestal. Los resultados de nuestros estudios de tasas de caída de hojarasca y de la descomposición de la misma (Montagnini et al., 1991) sugieren que la descomposición de la hojarasca es relativamente lenta bajo *V. ferruginea*, un factor que explica las altas acumulaciones mencionadas anteriormente. *V. hondurensis*, *H. alchorneoides* y *S. excelsum* exhibieron tasas de descomposición de hojarasca más aceleradas. El Ca, Mg y P de la hojarasca bajo *V. ferruginea* eran considerables (Tabla 3), un dato especialmente relevante para P, ya que existen probabilidades de deficiencias de este elemento en el sitio, tal como fue mencionado anteriormente. Los nutrientes de la biomasa del suelo forestal también fueron mayores bajo *V. hondurensis*. De nuevo, este resultado fue más significativo para N, Ca, Mg y P. Por ende, a pesar del crecimiento rápido de esta especie, el reciclaje de nutrientes proveniente de la hojarasca puede por lo menos compensar parcialmente el agotamiento de nutrientes del suelo. Mientras que lo contrario es cierto para P, el N de la hojarasca del suelo forestal fue más que el doble bajo *S. excelsum* que bajo *H. alchorneoides*, a pesar de que ambas especies tenían cantidades similares de biomasa en la hojarasca (Tabla 3).

Estos resultados sugieren que el suelo forestal es un compartimiento importante para la acumulación y el reciclaje de nutrientes, particularmente para el N, Ca, Mg y P, pero menos para el K, con marcadas diferencias entre especies arbóreas. Si el suelo forestal es afectado por quemas o las limpiezas, puede ocurrir una pérdida sustancial de materia orgánica y nutrientes. Wang et al. (1991) también encontraron que con la excepción de K, los nutrientes en la hojarasca eran equivalentes a una gran porción (16-50%) de los nutrientes contenidos en la biomasa arbórea. Ellos concluyeron que si la hojarasca fuera dejada sobre el suelo después de la cosecha, esto representaría una reserva sustancial de nutrientes para la siguiente rotación.

CONCLUSIONES Y RECOMENDACIONES

1. Algunas especies arbóreas nativas maderables de buen valor comercial pueden crecer en plantaciones abiertas, en sitios de baja fertilidad y pueden exhibir crecimiento rápido y efectos potencialmente beneficiosos sobre los nutrientes del suelo. Además, sus efectos sobre los nutrientes del suelo pueden ser observados en una etapa temprana de la rotación, al cierre del dosel.

2. Las especies arbóreas varían en sus contenidos de nutrientes en los tejidos y en sus tasas de acumulación de nutrientes en la biomasa. Para una especie dada, las mismas tendencias no son aplicables a todos los nutrientes: por ejemplo, una especie puede tener el mayor efecto sobre el Ca del sitio, pero su influencia sobre el K o el N puede ser mínima; otra especie puede tener una influencia más significativa sobre el K o el P del sitio.

3. El establecimiento de plantaciones arbóreas mixtas debería ser una estrategia apropiada para combinar los requerimientos de nutrientes de diferentes especies arbóreas con sus efectos sobre los nutrientes del suelo, de manera que no se creen deficiencias serias de ningún nutriente en particular. Sin embargo, aun con la mezcla de especies arbóreas es posible esperar deficiencias de K y P en el sitio a largo plazo.

4. La cosecha total de los árboles tendrá efectos negativos mayores sobre los nutrientes del sitio que la cosecha de los troncos. Los efectos variarán de acuerdo a la especie y a las partes cosechadas del árbol. El agotamiento de nutrientes del sitio será mayor con rotaciones cortas porque los árboles jóvenes tienen una proporción mayor de tejido de hojas y ramas en relación a sus troncos que los árboles viejos, en otras palabras, la porción potencialmente "reciclable" del árbol es mayor en árboles jóvenes; y la cosecha de rotaciones cortas aumentará la frecuencia de la eliminación de nutrientes del sitio así como también las perturbaciones al sitio asociadas con las operaciones de cosecha (erosión del suelo, compactamiento, perturbación de la hojarasca del suelo, etc.).

5. Aparentemente, el crecimiento de la vegetación del sotobosque y la correspondiente acumulación de nutrientes juega un rol relativamente pequeño en el reciclaje de nutrientes del sitio. Por eso, las prácticas que afectan al sotobosque, tales como el desmalezado y el intercultivo con especies anuales, pueden no ser críticos para la preservación de nutrientes en el sitio. Esta situación variará con las especies cultivadas y con su manejo. El intercultivo durante etapas tempranas del crecimiento arbóreo, mientras que los requerimientos de nutrientes de los cultivos y su manejo no provoquen otros efectos adversos (erosión del suelo, eliminación excesiva de nutrientes con cosechas repetidas), es una alternativa para acelerar el retorno del capital invertido y por consiguiente actúa como un estímulo para la plantación de árboles.

6. La hojarasca representa un componente mayor en la acumulación de nutrientes y en el reciclaje de los mismos. Las prácticas que afectan a la hojarasca, tales como la quema para el control de las malezas, la cosecha de la hojarasca para utilizarla como leña o "mulch" (mantillo), etc., pueden tener efectos adversos serios sobre los nutrientes del suelo.

7. La medición de la biomasa arbórea y de las concentraciones de nutrientes en etapas tempranas de la rotación (por ejemplo, durante el raleo) pueden ofrecer una buena indicación del impacto potencial de las prácticas de manejo sobre la conservación de nutrientes del sitio.

8. Las referencias a las tasas de extracción de nutrientes por cultivos agrícolas

comunes en la región pueden servir como indicadores de la capacidad para suplir nutrientes de los suelos y ser comparados con las tasas de absorción de nutrientes de las especies arbóreas, para poder estimar las deficiencias potenciales de nutrientes en el sitio.

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BIBLIOGRAFIA

ALLEN, O. N. and E. K. ALLEN. 1981. The leguminosae: A source book of characteristics, uses, and nodulation. University of Wisconsin Press, Madison , Wisconsin. 812 pp.

ALPIZAR, L., FASSBENDER, H. W.; HEUVELDOP, J.; FOLSTER, H. and ENRIQUEZ, G. 1986. Modelling agroforesty systems of cacao (*Theobroma cacao*) with laurel (*Cordia alliodora*) and poro (*Erythrina peoppigiana*) in Costa Rica. I. Inventory of organic matter and nutrients. Agroforesty Systems 4:175-189.

BRUIJNZEL, L. A. and K. F. WIERSUM. 1985. A nutrient balance sheet for *Agathis dammara* Warb. plantation forest under various management conditions. Forest Ecology and Management 10: 195-208.

BRUJIZNEL, L. A. 1991. Nutrient input-output budgets of tropical forest ecosystems: a review. Journal of Tropical Ecology 7: 1-24.

CHAMBERS, R. and M. LEACH. 1990. Trees as savings and security for the rural poor. Unasylva 41: 39-52.

CHUDNOFF, M. 1984. Tropical timbers of the world. USDA Forest Service, Agricultural Handbook 605, Washington, DC.

DOMMERGUES, Y. R. 1987. The role of biological fixation in agroforesty. pp. 245-271 *In* Steppler, H. A., and P. K. R. Nair (eds.). Agroforesty. A decade of development. International Council for Research in Agroforestry. Nairobi, Kenya.

ESPINOZA CAMACHO, M. y BUTTERFIELD, R. 1989. Adaptabilidad de 13 especies nativas maderables bajo condiciones de plantación en las tierras bajas húmedas del Atlántico, Costa Rica. pp. 159-172 *In* R. Salazar (ed.). Manejo y aprovechamiento de plantaciones forestales con especies de uso múltiple. Actas Reunión IUFRO, Guatemala, 3-7 de abril 1989. CATIE, Turrialba, Costa Rica.

EVANS, J. 1987. Site and species selection-Changing perspectives. Forest Ecology and Management 21: 299-310.

FASSBENDER, H. W. 1984. Bases edafológicas de los sistemas de producción agroforestales. Serie Materiales de Enseñanza Nº 21. Centro Agronómico Tropical de Investigación y Enseñanza (CATIE), Turrialba, Costa Rica. 191 pp.

GLADSTONE, W. T. and F. T. LEDIG. 1990. Reducing pressure on natural forests through high-yield forestry. Forest Ecology and Management 35: 69-78.

GONZALEZ, E. Preliminary seed trials for 36 native tree species. Revista de Biología Tropical (Costa Rica) 39 (1): 47-51.

GONZALEZ, E., R. BUTTERFIELD, J. SEGLEAU y M. ESPINOZA. 1990. Primer Encuentro Regional sobre Especies Forestales Nativas de la Zona Norte y Atlántica. Memoria. 28-29 julio 1989. Chilamate, Costa Rica. Instituto Tecnológico de Costa Rica. Cartago, Costa Rica. 46 pp.

HARTSHORN, G. 1983. Plants. pp. 118-157 *In* D. Janzen (ed.). Costa Rica Natural History. University of Chicago Press.

HARTSHORN, G. and B. HAMMEL. Trees of La Selva. Unpublished manuscript, La Selva Biological Station, OTS, Apdo. 676, 2050 San Pedro, Costa Rica.

HOLDRIDGE, L. R. y POVEDA, L. J. 1975. Arboles de Costa Rica. Centro Científico Tropical, San José, Costa Rica. 546 pp.

LUGO, A. E., S. BROWN and J. CHAPMAN. 1988. An analytical review of production rates and stemwood biomass of tropical forest plantations. Forest Ecology and Management 23: 179-200.

LUGO, A. E., D. WANG and F. BORMANN. 1990. A comparative analysis of biomass production in five tropical tree species. Forest Ecology and Management 31: 153-166.

LUNDGREN, B. 1980. Plantation forestry in tropical countries-physical and biological potentials and risks. Swedish University of Agricultural Sciences. International Rural Development Centre. Rural Development Series 8. Uppsala. 134 pp.

MONTAGNINI, F., HAINES, B. L., BORING, L. R. and SWANK, W. T. 1986. Nitrification potentials in successional black locust and mixed hardwood forest stands in the southern Appalachians, U.S.A. Biogeochemistry 2: 197-210.

MONTAGNINI, F. and SANCHO, F. 1990a. Influencia de seis especies de árboles nativos sobre la fertilidad del suelo en una plantación experimental en la llanura del Atlántico de Costa Rica. Yvyraretá (Argentina) 1 (1): 29-49.

MONTAGNINI, F. and SANCHO, F. 1990b. Impacts of native trees on tropical soils: a study in the Atlantic lowlands of Costa Rica. Ambio 19 (8): 386-390.

MONTAGNINI, F., F. SANCHO, K. RAMSTAD and E. STIJFHOORN. 1991. Multipurpose trees for soil restoration in the humid lowlands of Costa Rica. pp. 41-58 *In* D. A. Taylor and K. G. Mc Dicken (eds.). Research on multipurpose trees in Asia. Proceedings of an International Symposium. November 19-23, 1990, Los Banos, Philippines. Winrock International Institute for Agricultural Development. Bangcock.

Nair, P. K. R. 1989. The role of trees in soil productivity and protection. pp. 567-589 *In* Nair, P. K. R. (ed.). Agroforestry systems in the tropics. Kluwer Academic Publishers/International.

PARROTTA, J. A. 1989. The influence of management practices on the biogeochemical stability of tropical fuelwood plantations. Tropical Ecology 30: 1-12.

PERRY, D. A. and J. MAGHEMBE. 1989. Ecosystem concepts and current trends in forest management: time for reappraisal. Forest Ecology and Management 26: 123-140.

RUSSELL, C. E. 1987. Plantation forestry. The Jari project, para, Brazil. pp. 76-89 *In* Jordan, C. F. (ed.). Amazonian rain forests. Ecosystem disturbance and recovery. Ecological Studies 60. Springer-Verlag, New York.

SANCHEZ, P. A., C. A. PALM, C. B. DAVEY, L. T. SZOTT and C. E. RUSSELL. 1985. Tree crops as soil improvers in the humid tropics pp. 327-350 *In* Cannell, M. G. R. and J. E. Jackson (eds.). Atributes of trees as crop plants. Institute of Terrestrial Ecology, Natural Environmental Research Council, Abbots Ripton, Huntingdon, England.

SANCHEZ, P. A. 1987. Soil productivity and sustainability in agroforestry. pp. 205-223 *In* Steppler, H. A., and P. K. R. Nair (eds.). Agroforestry. A decade of development. International Council for Research in Agroforestry. Nairobi, Kenya.

SANCHO, F. and R. MATA. 1987. Estudio detallado de suelos. Estación Biológica La Selva. Organización para Estudios Tropicales, San José, Costa Rica. 162 pp.

STANDLEY, P. C. 1937-38. Flora of Costa Rica. Field Museum of Natural History. Chicago.

WADSWORTH, F. H. 1983. Production of usable wood from tropical forests. pp. 278-288 *In* F. B. Golley (ed.). Tropical Rain Forest Ecosystems. Structure and Function. Ecosystem of the World 14A. Elsevier. New York.

WANG, D., F. H. BORMANN, A. E. LUGO and R. D. BOWDEN. 1991. Comparison of nutrient-use efficiency and biomass production in five tropical tree taxa. Forest Ecology and Management 46: 1-21.

WHITMORE, J. L. and G. S. HARTSHORN. 1969. Literature review of common tropical trees. Tropical Forestry Series, Contribution Nº 8. Institute of Forest Products. College of Forest Resources, University of Washington, Seattle. 113 pp.

YOUNG, A. 1989. Agroforestry for soil conservation. ICRAF, Science and Practice of Agroforestry. C.A.B. International and International Council for research in Agroforestry. Wallingford, UK. 276 pp.

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Litterfall, litter decomposition and the use of mulch of four indigenous tree species in the Atlantic lowlands of Costa Rica

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Abstract. Litterfall, forest-floor litter biomass and nutrients, short-term litter decomposition and the effects of leaf mulches on initial growth of maize were studied for four indigenous tree species with agroforestry potential: *Stryphnodendron microstachyum* Poepp. et Endl. (*S. excelsum*), *Vochysia ferruginea* Mart. *Vochysia guatemalensis* Donn. Sm. (*V. hondurensis*) and *Hyeronima alchorneoides* (O), growing in a young experimental plantation in the Atlantic humid lowlands of Costa Rica. Total annual leaf litterfall was higher in *V. ferruginea* plots, followed by *S. microstachyum, V. guatemalensis* and *H. alchorneoides*; all with values comparable to those reported for other tree species grown in agroforestry combinations in humid tropical regions. Forest-floor litter accumulation was highest under *V. ferruginea* and *V. guatemalensis*. Both litterfall and forest-floor litter material had similar patterns in nutrient concentrations: N was higher in *S. microstachyum*, Ca was higher in *V. guatemalensis*, K was higher in *H. alchorneoides*; Mg was higher in *V. guatemalensis* and *H. alchorneoides*; *H. alchorneoides* and *V. guatemalensis* had the highest P. *V. ferruginea* litter decomposed more slowly, while *S. microstachyum* apparently decomposed faster than the other species. The two *Vochysia* species showed increases in N and P concentration in decomposing litter after seven weeks in the field. *H. alchorneoides* showed an increase in litter N and a decrease in litter P, and *S. microstachyum* showed a net decrease in both N and P over the same time period. The patterns found in the litter bag study were confirmed by results obtained in a tethered-leaves experiment. *S. microstachyum* and *V. ferruginea* litters lost more weight when mixed in a 1:1 proportion than either of them alone. Maize seedlings growing in plots mulched with *S. microstachyum* and *H. alchorneoides* leaves showed greatest initial growth, confirming patterns found in decomposition and nutrient release studies. The results show that these species could be used in agroforestry combinations with different advantages according to the specific objectives desired, whether these are soil protection, nutrient recycling, or enhancement of the growth of associated crops.

Introduction

The choice of tree species for plantation forestry or agroforestry is influenced by knowledge of the species' performance and their economic and environmental benefits. Most tree planting programs and subsidies promote the use of well-known, often exotic species, due to the existing knowledge on their biology, cultivation and uses. Besides, when taken to new areas, some exotics grow quickly, at least initially, probably due to the lack of natural enemies. However, several indigenous species may be more suitable than exotics [Evans, 1987] because (1) they may be better adapted to local environmental conditions; (2) seeds and other propagules are locally available; and (3) farmers are familiar with them and their uses. Additionally, the use of indigenous trees in productive systems helps preserve genetic diversity and is in better balance with the local flora and fauna.

Tree species vary in their nutrient uptake rates and recycling capacity. Litter production is a major process in the transfer of organic matter and nutrients from above-ground tree parts to the soil [Szott et al., 1991]. The addition of tree leaves and branches as mulches to soils has been shown to improve site microenvironmental conditions [Budelman, 1989] and increase the productivity of agricultural crops [Duguma et al., 1988; Gutteridge, 1990; Onim et al., 1990; Tiraa and Asghar, 1990; Yamoha and Burleigh, 1990]. The nutrient content (especially N and P) and the lignin and polyphenolic concentrations of litter strongly influence its rate of decomposition and nutrient release to the soil [Palm and Sanchez, 1990, 1991; Szott et al., 1991].

In the present article we report rates of litterfall and litter decomposition under young stands (3.5—4.5 years old) of four fast-growing, indigenous tree species in the Atlantic lowlands of Costa Rica. The four species of this study: *Stryphnodendron microstachyum* Poepp. et Endl. (*S. excelsum*), *Vochysia guatemalensis* Donn. Sm. (*V. hondurensis*), *Vochysia ferruginea* Mart and *Hyeronima alchorneoides* (O), had growth rates equal to or greater than the exotic species recommended for the region at the time [Espinoza Camacho and Butterfield, 1989]. Rates of net above-ground primary productivity of these four indigenous species were comparable to those reported for other fast-growing trees in the humid tropics, including many multiple-purpose trees commonly used in agroforestry [Montagnini and Sancho, 1993a, b]. Results of our studies on soil fertility and nutrient recycling on the same site showed that after 2.5 years, soil organic matter, nitrogen and cation levels under these species were higher than in adjacent grass, with values similar to those found in secondary forest [Montagnini and Sancho, 1990a, b]. Further studies showed that soil N availability was higher under the N-fixing *S. microstachyum* than under the other three, non-N fixing species [Montagnini et al., 1991]. Results of studies of tree biomass and nutrients [Montagnini and Sancho, 1993a, b, c] showed that *S. microstachyum* had the highest accumulation of N in tree tissue, with approximately 200 kg/ha, or 60% of above-ground biomass N in the potentially recyclable portion (leaves and branches). *V. guatemalensis* had the highest stem Ca and Mg; this species had over 120 kg/ha of Ca in the leaves + branches portion. *V. ferruginea* also had a relatively high accumulation of nutrients in above-ground biomass, with approximately 120 kg/ha of N in branches and leaves. *H. alchorneoides* had a relatively high accumulation of above-ground biomass K, with approximately 180 kg/ha in the leaves + branches portion [Montagnini and Sancho, 1993a, b, c]. Preliminary results of studies of nutrient recycling from trees to soil showed that litterfall and litter accumulation were most abundant under

V. ferruginea; *H. alchorneoides* litterfall appeared to be high but did not tend to accumulate on the floor [Montagnini et al., 1991]. These results suggested that the four species could be used to improve site quality and possibly to favor the growth of associated crops, with different advantages according to the tree species used and their management.

In this article we report rates and seasonality of litterfall, forest-floor litter accumulation, litter decomposition, and nutrient release from mulches of these four species. The influence of the trees on site microclimate (air and soil temperature), top soil compaction (bulk density) and soil moisture is also shown. The goal of this study was to provide guidelines for the use and management of these fast-growing trees in the region and in other tropical lowland, humid regions with similar soils.

Study site

The experimental plantation was established in December, 1985 on abandoned pasture at the OTS La Selva Biological Station (10°26'N, 86°59'W, 50 m m.a.s.l., 24 °C mean annual temperature, 4000 mm mean annual rainfall, with maximum in July and minimum in March) [La Selva Biological Station weather reports]. Soils are Fluventic Dystropepts derived from alluvially deposited volcanic materials; they are deep, well drained, stone-free, with low or medium organic matter content (2.5 to 4.5%), moderately heavy texture, generally very acid (pH in H_2O < 5.0), and infertile [Sancho and Mata, 1987]. Detailed soil chemistry has been published elsewhere [Montagnini and Sancho, 1990a, b]. The area had been cleared in the mid-1950s and grazed until 1981 [Pierce, 1992]. The site was cleaned manually before planting. The tree species were planted in a randomized block design with five replicates, each single-species plot containing seven rows of seven trees (14 m × 14 m each), with two meters between trees (2,500 trees ha^{-1}).

The tree species used for our comparisons of soil fertility and nutrient recycling are shown in Table 1. All the species have economic uses (timber of medium to high quality) and their seeds were collected from natural forests at La Selva and nearby in the region. Seed and germination characteristics of these species are given elsewhere [Gonzalez, 1991; Gonzalez et al., 1990].

Materials and methods

Litterfall

Litter was collected from 90 cm × 55.5 cm litterfall traps made of a wooden frame with fiberglass screen bottoms (1 mm^2 mesh size), set at 50 cm above the ground. Traps were located randomly in the plots but avoiding the edges;

Table 1. Native tree species studied for their effects on soils and nutrient cycling at La Selva Biological Station [Gonzalez et al., 1990; Holdridge and Poveda, 1975].

Scientific name	Common name	Family	Native range	Natural habitat
Stryphnodendron microstachyum Poepp. et Endl. (*S. excelsum*)	vainillo	Leguminosae (mimosoid)	Costa Rica	Low altitude, very humid climate. Alluvial as well as poor soils.
Vochysia guatemalensis Donn. Sm. (*V. hondurensis*)	mayo, chancho	Vochysiaceae	Mexico to Panama	Lowlands, up to 900 m, humid climate. Rich alluvial or poor soils.
Vochysia ferruginea Mart	botarrama	Vochysiaceae	Nicaragua to Brazil	Lowland forests. Well-drained, acidic, infertile soils.
Hyeronima alchorneoides Fr. Allemao	pilon	Euphorbiaceae	S. Mexico to S. Brazil	Hills, abandoned pastures. Alluvial as well as poor soils.

in most cases they were near the center of each plot. There was one trap per plot for the four species of the study; 20 traps total. The traps were emptied every two weeks, their contents oven-dried (70 °C), sorted (leaves and branches), and weighed. Collections began in April, 1989 and continued through February, 1991. Every three months, the material collected in one month was pooled to have enough sample for chemical analyses. The total N, Ca, Mg, K and P were measured on nitro-perchloric digests: N and P were measured using a Lachat Flow Injection Analyzer, while cations were measured using an Atomic Absorption Spectrophotometer. Analysis of variance and tests for differences among species using LSD ($p < 0.05$) were done for leaves and branches for each individual collection. Additionally, monthly means were calculated from biweekly collections to detect seasonal differences in leaf and branch litterfall. Finally, annual totals were calculated as the sum of all collections. Average nutrient concentrations were multiplied by annual litterfall (leaves and branches) to assess the annual nutrient input in litterfall from each species.

Forest-floor litter

The amount of litter accumulating on the ground under the species was measured in August and December, 1989, and in March, May and August 1990. These months were chosen to represent the local seasonality in rainfall, which was expected to influence the amounts of litter: August is the month of peak rainfall at La Selva, December is in the middle of a less rainy period, March is nearing the end of a relatively dry period, and May generally marks the beginning of the rainy season [La Selva Biological Station weather reports]. A 50 cm × 50 cm iron frame (one per plot) was used to demarcate an area within one meter of a randomly chosen tree stem; the location of sampling was generally near the center of the plots; plot edges were avoided when sampling. All material above the mineral soil within the frame was collected, oven-dried, sorted (leaves and branches), and weighed. Statistical analyses were performed on the results of each individual collection to compare the contribution of each litter component among species.

Litter decomposition

These experiments were designed to examine nutrient release by the species for their use as mulches; three short-term (maximum four months) experiments were conducted, which is frequently the length of mulch decomposition studies [Budelman, 1988]. The methods employed were: (a) a large litter bag decomposition experiment; (b) decomposition of tethered leaves; and (c) a mixed-leaf litter experiment using the conventional, smaller litter bags.

a. *Large litter bag experiment*

This experiment was done to compare litter decomposition among the four species. Litter bags were constructed out of plastic mesh (average mesh size 2 mm × 2 mm). Large litter bags (50 cm × 50 cm) presumably allowed for an environment for decomposition more similar to natural conditions in the forest floor than the more conventional, smaller bags (generally 10—15 cm to a side), which may tend to exclude soil macrofauna whose role in decomposition can be important [Budelman, 1988]. Approximately 2,500 g of whole, recently fallen leaves were collected from the ground in each species plot for *V. ferruginea*, *V. guatemalensis*, and *H. alchorneoides*. Leaves from *S. microstachyum*, leaflets and rachis of which are difficult to collect from the ground, were collected fresh. Due to the large volume of material, air drying was unpractical; therefore, all leaves were dried at 70 °C prior to filling litter bags. Each bag was filled with 100 g of dried leaves, weighed to 0.1 g. Two subplots were designated randomly in each of the four species plots, which were replicated five times. An area slightly larger than the litter bags was cleared of leaf litter; two bags were placed in each plot (40 bags total); and then they were covered with most of the displaced litter. The soil under the bags was exposed but not entirely bare of decomposing leaves. Litter bags were weighed and sampled on June 6 (time of initiation of the experiment), and on June 18, June 28, and July 10 and July 25; i.e., approximately every two weeks for a total of one and a half months. At each collection time, the bags were taken to the lab for weighing and subsampling. Subsampling consisted of removing 30—60 g of the field weight of the leaves, which were then dried at 70 °C to determine a field weight:dry weight ratio. These subsamples of litter from each collection were processed and analyzed for N and P as described above for other tissue. After subsampling, the bags were returned to the field. Weight loss due to decomposition was calculated by comparing the expected weight loss (loss due to sample removed) with the actual weight loss. The actual weight loss was determined by the wet:dry ratio of the subsample taken from the bag. Statistical analyses (analysis of variance and LSD for differences among means) were done to compare weight loss as a percent of the initial weight, as well as nutrient concentrations, among species for each collection.

b. *Tethered leaves experiment*

The results from this method were compared with those from the large litter bags. However, the method allowed for comparison of *V. ferruginea*, *V. guatemalensis* and *H. alchorneoides* litters only; *S. microstachyum* could not be included due to the small size of its leaflets. The tethered leaves were set loose in the litter layer instead of being enclosed in bags. Thus they were more in contact with the natural environment and provided a more realistic measure of short-term decomposition rates [La Caro and Rudd, 1985]. Recently fallen leaves collected from the litter layer below each species were dried in circulating, ambient air for about a week. All the leaves were whole, with entire margins. The leaves were tied with dental floss around their petioles to make several strings of leaves, with numbers of leaves per string depending on leaf size. The leaf strings were weighed to 0.001 g and then labeled prior to placing in the field. Subsamples were oven-dried to determine an ambient:oven dry weight ratio for calculations. Random areas of approximately 0.25 m^2 were located near the center of five plots per species, and they were cleaned of all litter. The leaf strings were placed inside these areas and anchored down with sticks, one string per mini-plot. The leaves were removed from the field two weeks later when the leaves of *H. alchorneoides* began to lose their structure and shape; leaving them longer would have made it difficult to recover them. The leaves were oven-dried at 70 °C for two days and then weighed. No chemical analyses were conducted due to the small amount of tissue recovered.

c. *Mixed-leaf litter experiment*

This experiment was done to examine the influence of mixing an N-rich litter (*S. microstachyum*) with a less N-rich, presumably more decomposition-resistant litter (*V. ferruginea*). The hypothesis was that the addition of the leguminous leaves would increase the rate of weight loss of the *V. ferruginea* litter. Fiberglass bags (1 mm^2 mesh), approximately 15 cm × 15 cm, were filled with either 5 g of *S. microstachyum* or *V. ferruginea* leaves alone, or a mixture of 2.5 g of each species. The leaves had been left to dry at ambient air temperature prior to filling the bags. Subsamples of leaves were oven-dried to determine the ambient:dry weight ratio for calculations. The bags were stapled shut and fastened together with light wire in groups of three (one of each treatment), and placed in the field on 1 August 1991. Half of the bags were randomly placed in *S. microstachyum* plots and half in *V. ferruginea* plots; each species plot, hence each treatment, was replicated five times. Thus there were a total of 60 bags (3 treatments × 5 replicates × 4 collections). The bags were collected after two weeks (15 August), one month (1 September), two months (1 October) and four months (1 December), from each plot. The bags were oven-dried and their contents weighed to 0.001 g to determine weight loss over time. As in the other two decomposition studies, statistical analysis was performed to compare weight loss as a proportion of initial weight among treatments, for each collection.

Mulch experiment

A field bio-assay was conducted to examine the influence of nutrient release from mulches of the four tree species on plant growth. Maize was used as a test species, due to its generally good growth response to added nutrients; however, this was a short-term experiment, and it was not intended to measure crop yields. Maize seedlings were grown for 40 days in small plots mulched with the litter of each of the four species. A small amount of pasture (7 m × 7 m) was cleared to soil level. In this clearing, 25 plots measuring 50 cm × 50 cm each and spaced 30 cm apart were laid out in a square, five plots on each side. Grass was cleared within 1—2 m of the plots, shade and sun patterns were consistent over the plots, and a chicken-wire fence was erected around the entire experiment area. For each treatment, including the control with no mulch, there were five replicates; all were set at random.

For mulch, 100 g of air-dried leaves of each species were broken into smaller pieces by hand, and then they were incorporated into the top 10—15 cm of soil in an appropriate plot with a trowel. After a week, each plot was planted with 25 maize seeds. The maize was a local, non-hybrid variety that had been cleaned and culled beforehand. After cleaning it exhibited a 96% germination rate in the laboratory. The seed was planted at 3-cm depth, 8—12 cm apart, using a planting dibble. Ten days after planting (approximately one week after germination), 100 g ground leaves were again laid on the soil in the maize plots. With this second application, the total addition of mulch was at a rate of 8 tons ha^{-1}; this rate was chosen based on preliminary results of litterfall measurements under the four species, to use an amount which could be possibly collected from under the tree plots. This amount also corresponds to measured production rates of pruned material from leguminous shade trees in coffee plantations [Beer, 1988]. An initial germination rate of at least 92% occurred in all but two plots. Every time the mulch was added to the treated plots, the soil in the controls was turned over, for similar cultivation effects.

Maize seedlings were measured at 10-day intervals, beginning 10 days after sowing. The height of each seedling was recorded to the highest point when the plant was held vertically against a meter stick. Forty days after planting, the maize seedlings were carefully dug up. Shoots and roots from the top 10—15 cm of soil were washed, separated (shoots from roots), oven-dried and weighed. Subsamples of shoots and roots were processed and analyzed for N and P as described above for nutrient determinations in plant materials.

Influence of tree canopies on the microenvironment

Soil temperatures at 2.5-cm depth were monitored using Weksler™ soil thermometers. The air temperature was measured with standard hardware thermometers held from sticks at 50-cm height from the ground. The soil bulk density was measured at 0—5 cm depth using a 4.8 cm diameter × 5-cm long corer equipped with an extensible hammer and a sleeve. Soil moisture was measured gravimetrically on the samples obtained for bulk density. Two replicate samples were taken from each plot. The results from the two replicate samples from each plot were averaged to obtain one value per plot. All these measurements were done in the five replicate plots of the four species, and in five of each adjacent 20-year-old secondary forest and grass sites for comparison. Analysis of variance and tests for means were conducted as described above.

Results

Litterfall

The total annual leaf litterfall was highest under *V. ferruginea*, followed by *V. guatemalensis*, *S. microstachyum* and *H. alchorneoides*, while branch litterfall was higher under *S. microstachyum* and *V. ferruginea* (Fig. 1, Table 2); these results are consistent with our earlier findings [Montagnini et al., 1991]. For leaf litterfall, annual totals from March, 1990 to February, 1991 were 4—19% lower than for the previous 12-month period, with the largest decrease in *V. ferruginea*; for branches, there were increases as well as decreases in the annual totals (although no statistics were run to compare these totals) [Montagnini and Sancho, unpublished data]. In 1989—90, *V. ferruginea* and *V. guatemalensis* exhibited peaks in leaf fall in May—June and October—December (beginning and end of rainy season, respectively) (Fig. 2). *S. microstachyum* showed a single peak in November and *H. alchorneoides* had the most even distribution, with no obvious peaks. In 1990—91, all species showed peaks in May—June; the two *Vochysia* peaked again in October—November and in January, while *S. microstachyum* and *H. alchorneoides* litterfall did not vary (Fig. 2). Seasonality in branch litterfall was similar to that of leaf fall: peaks occurred in May—June, and in October—January (Fig. 2). The differences among species noted above for peaks of leaf or branch litterfall were statistically significant ($p < 0.05$).

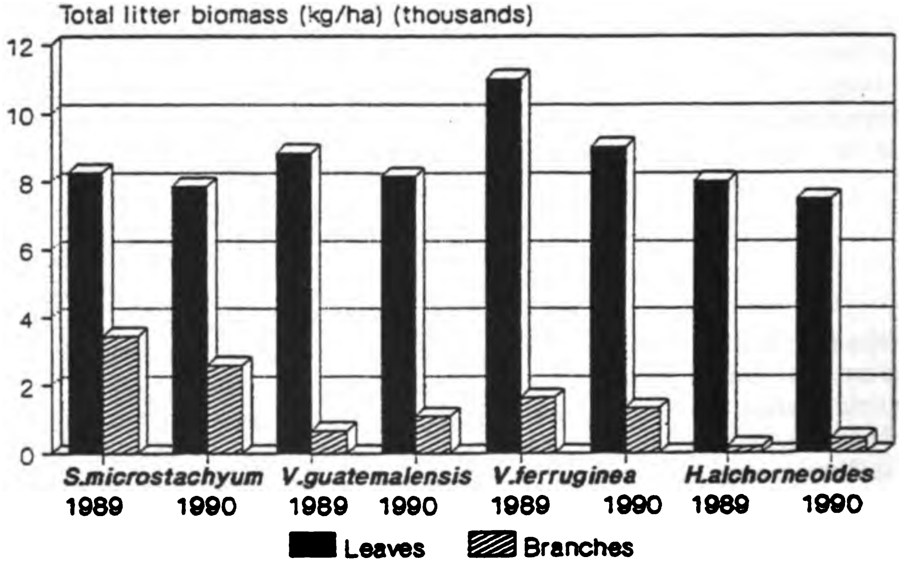

Fig. 1. Total annual litterfall (1989—1990); leaf and branch totals by species.

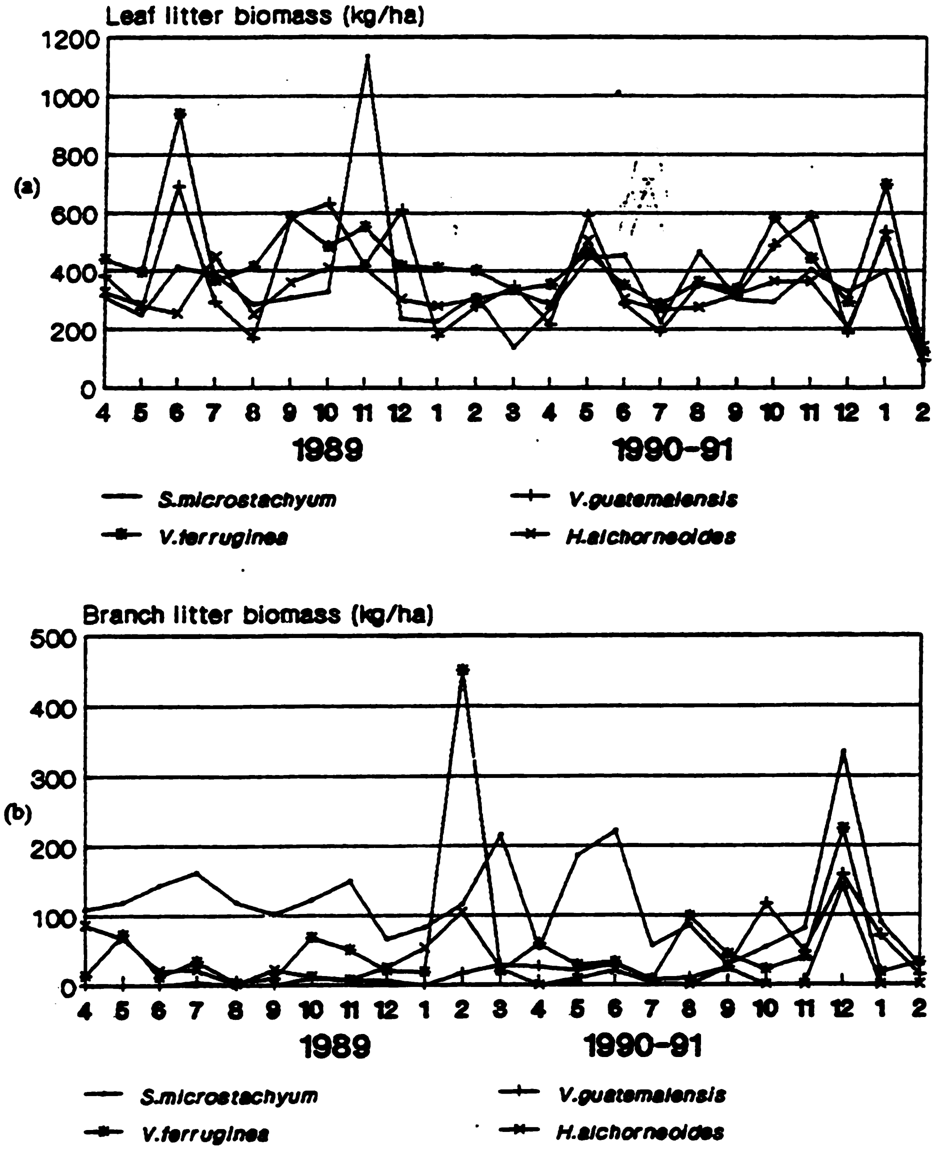

Fig. 2. Litterfall, monthly averages from April, 1989 to February, 1991. (a) Leaves; (b) Branches.

Leaf litter N concentration was 20—40% lower in October 1989 than on the other sampling dates; there were no other clear trends for Ca, Mg, K or P; differences in nutrient concentrations among species were consistent throughout the 1989—1991 sampling record [Montagnini and Sancho, unpublished data]. Results for October, 1989 were chosen for comparison because the data were more complete than for other dates, due to the high amount of litter collected for all species in that month (Fig. 2). *S. microstachyum* had the highest N concentration in leaf litter (Table 3). *H. alchorneoides* and *V. guatemalensis* had the highest Ca and Mg, *H. alchorneoides* had the highest K, and *H. alchorneoides* and *S. microstachyum* had

Table 2. Total annual litterfall biomass and nutrient content, April 1989—March 1990.

	Biomass	N	Ca	Mg	K	P
	(kg/ha)					
Leaves						
S. microstachyum	8273	106.7	142.3	24.0	13.2	15.7
V. guatemalensis	8854	65.5	201.9	36.3	12.4	9.7
V. ferruginea	11017	78.2	217.0	24.2	16.5	11.0
H. alchorneoides	8019	70.6	191.7	43.3	29.7	14.4
Branches						
S. microstachyum	3435	22.3	46.7	5.5	8.9	3.4
V. guatemalensis	664	3.3	14.5	2.0	1.4	1.8
V. ferruginea	1616	5.2	29.1	7.4	2.1	2.6
H. alchorneoides	185	1.1	2.7	0.4	0.2	0.2
Total (leaves + branches)						
S. microstachyum	11708	129.0	189.0	29.5	22.2	19.2
V. guatemalensis	12633	68.8	216.3	38.3	13.8	11.5
V. ferruginea	9518	83.4	246.1	31.7	18.6	13.6
H. alchorneoides	8204	71.7	194.4	43.7	29.9	14.6

Table 3. Litter nutrient concentrations (October 1989).[1]

	N (%)	Ca (%)	Mg (%)	K (%)	P (%)
Leaves					
S. microstachyum	1.27a	1.72d	0.29c	0.16b	0.19ab
V. guatemalensis	0.74bc	2.28ab	0.41b	0.14b	0.11b
V. ferruginea	0.71c	1.97c	0.22c	0.15b	0.10b
H. alchorneoides	0.88bc	2.39a	0.54a	0.37ab	0.18ab
Branches					
S. microstachyum	0.65a	1.36b	0.16bc	0.26b	0.10b
V. guatemalensis	0.50ab	2.18a	0.30ab	0.21b	0.27a
V. ferruginea	0.32b	1.80ab	0.46a	0.13b	0.16b
H. alchorneoides	0.59ab	1.47ab	0.21ab	1.13a	0.11b

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[1] For each nutrient and tissue category (branches or litter), differences among species are statistically significant when means are followed by different letters ($p < 0.05$).

the highest P in leaf litter; these differences were statistically significant ($p < 0.05$). Nutrient concentrations of branch litter were lower than those of leaf litter (Table 3). There were no statistically significant differences in N, Ca or Mg concentrations in branch litter. *H. alchorneoides* had the highest K, and *V. guatemalensis* had the highest P; these differences were statistically significant ($p < 0.05$) (Table 3). Total annual nutrient contribution in litter is shown for April 1989—March 1990 only, because the record was more complete than that of 1990—91 (Table 2): *S. microstachyum*, with the highest N concentration and high litterfall also had the highest amount of N in annual litterfall; this species also had the highest amount of P in annual litterfall (Table 2). *V. ferruginea* and *V. guatemalensis* had approximately 25% higher contributions of Ca in annual litterfall than *S. microstachyum*, with similar values among them. *H. alchorneoides* had the highest amounts of Mg and K in litterfall.

Forest-floor litter

Forest-floor leaf litter accumulation was highest under *V. ferruginea* at all times except for August, 1990 when it was similar to *V. guatemalensis* (Fig. 3). The higher amount of leaves found in *V. guatemalensis* in that month was attributed to a natural cause (e.g., a full branch fell into the litterfall trap); there was no reason to reject the data. There was an apparent increase in the accumulation of leaf litter on the forest floor with time of sampling under all species, but this trend was more marked for *V. ferruginea* and *V. guatemalensis* (Fig. 3). Apparently there was a build up of litter on the forest floor under these two species, which tends to suggest both rapid tree growth with fast crown development, and relatively slow decomposition; both *Vochysia* species are self-pruning. For branch litter, again *V. ferruginea* and *V. guatemalensis* showed the highest values of accumulation on the forest floor (Fig. 3), except in March 1990, when *S. microstachyum* had the highest branch litter accumulation.

Nutrient concentrations in forest-floor material revealed a pattern similar to that of litterfall: N was higher in *S. microstachyum*; Ca was higher in *V. guatemalensis*; K was higher in *H. alchorneoides*; Mg was higher in *V. guatemalensis* and *H. alchorneoides*; *H. alchorneoides* and *V. guatemalensis* had the highest P [Montagnini and Sancho, 1993b].

Litter decomposition

a. *Litter bags*

Although the difference among decomposition rates (percent of initial weight remaining) was not significant (Table 4), the differences in weight loss among species stayed fairly consistent throughout the experiment. The variance within the treatments was larger than expected; this was attributed to the unanticipated accumulation of mud in the litter bags and problems with

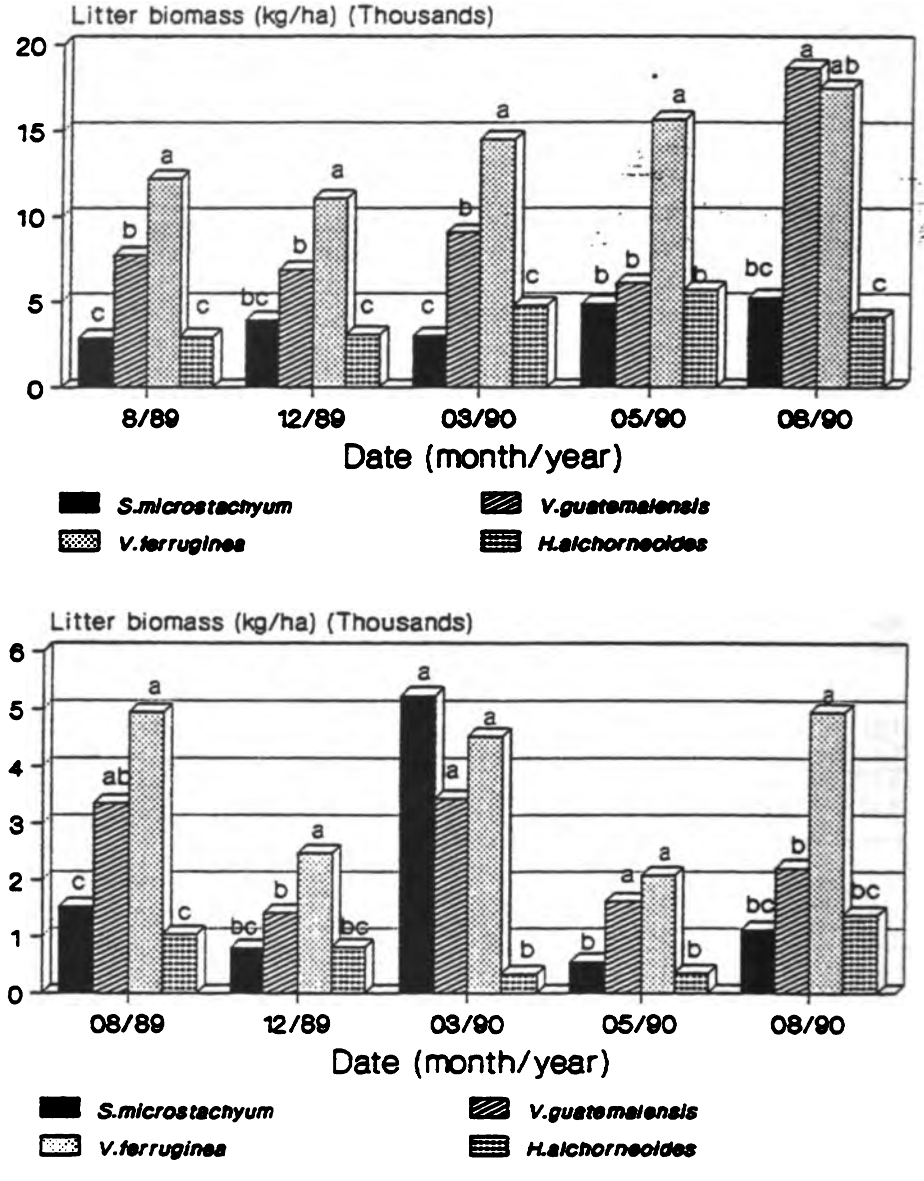

Fig. 3. Forest-floor litter, five collection dates in 1989—1990. a) Leaves; b) Branches. (For each individual collection date, different letters on the bars indicate statistically significant differences among species ($p < 0.05$)).

removing it completely from leaf fragments. Other authors have reported similar difficulties with handling small leaflets, such as those of *Leucaena leucocephala*, also encountering problems of contamination of the mulch with soil particles [Budelman, 1988]. Overall, however, the data suggest that

V. ferruginea leaves decompose more slowly, while *S. microstachyum* leaves would seem to decompose faster than the leaves of the other species.

The initial N concentrations in the leaf litter used for decomposition studies were higher, and the P values were lower (Table 4) than those reported in Table 3 for data from litter traps; this could be attributed to time of sampling and to differences in the age of the material, the litter for the decomposition study being slightly fresher than the litter collected in litter traps; however, comparing the N and P values for the four species (Tables 3 and 4) the differences among species were consistent in all cases. All changes between initial and final N and P concentrations in litter were statistically significant ($p < 0.05$), except for *H. alchorneoides*' N (Table 4). With the exception of *S. microstachyum* litter, N concentrations increased for all species. The two *Vochysia* species showed increases in litter P concentration, while the *H. alchorneoides* and *S. microstachyum* litters both showed net reduction in P concentrations when compared with initial levels. Apparently,

Table 4. Leaf litter decomposition, litter bag experiment, June—July 1990.[1]

a) Percent of initial weight remaining (since 6/6/90).

	Date of collection			
Species	6/18	6/28	7/10	7/25
S. microstachyum	96.9a	78.9a	77.1a	74.9a
V. guatemalensis	92.3a	81.8a	76.1a	77.6a
V. ferruginea	96.2a	87.6a	81.7a	83.6a
H. alchorneoides	86.6a	81.0a	78.9a	77.8a
Sig. level	< 0.2669	< 0.5874	< 0.8157	< 0.5206

b) Initial and final (after 7 weeks) N and P concentrations in litter.[2]

Species		N (%)	P (%)
S. microstachyum	init.	2.84a	0.15a
	final	2.21b	0.11b
V. guatemalensis	init.	1.26b	0.06b
	final	1.45a	0.09a
V. ferruginea	init.	1.10b	0.04b
	final	1.33a	0.05a
H. alchorneoides	init.	1.26b	0.09a
	final	1.39a	0.05b

[1] For each individual collection, differences among species are statistically significant when means are followed by different letters.

[2] Differences among initial and final nutrient concentrations for a given species are statistically significant when means are followed by different letters ($p < 0.05$).

the two *Vochysia* litters applied as mulch would tend to immobilize N and P, and *H. alchorneoides* would tend to immobilize N, at least initially; thus these nutrients would not be as readily available for crop use.

b. *Tethered leaves*
H. alchorneoides and *V. guatemalensis* litter showed the highest rate of weight loss (*S. microstachyum* was not included in the experiment), while *V. ferruginea* showed the lowest rate of loss in initial weight after two weeks (Table 5). These results confirm patterns suggested by the litter-bag experiment, as well as by the relative accumulation of forest-floor litter under these species.

Table 5. Weight change of tethered leaves with respect to initial weight.[1]

Species	Initial weight remaining (%)
V. guatemalensis	82.1b
V. ferruginea	93.7a
H. alchorneoides	79.8b
Sig. level	< 0.001

[1] Differences among species are statistically significant when means are followed by different letters.

c. *Mixed-leaf litter*
Non-mixed *S. microstachyum* and *V. ferruginea* litters retained 63.9% and 84.0% of their initial weight, respectively, after 4.5 months (Table 6), confirming trends found in the litter-bag experiment. Both species' litter lost more weight when mixed than alone, although differences between *V. ferruginea* alone and mixed were not statistically significant. Differences between *S. microstachyum* litter alone and mixed were statistically significant in the first three sampling dates but not in the last date (Table 6), suggesting that the effects of mixing the litters may last less than four months.

Mulch experiment

Differences in maize seedling heights between treatments were statistically significant ($p < 0.005$) and consistent throughout the experiment (Table 7). Within the treatments there was little variance. Initially, maize growing in plots with *H. alchorneoides* and *S. microstachyum* showed greatest growth, while seedlings in the unmulched control plots showed significantly inferior growth. After 20 days, maize growth in the *H. alchorneoides* plots began to slow relative to the *S. microstachyum*, but plants in those plots remained larger and stronger than the maize seedlings in either of the *Vochysia*

Table 6. Decomposition rate of *S. microstachyum* and *V. ferruginea* leaves in 1:1 mixture and alone.[1]

Treatment	Initial (1 Aug.) weight left (%)			
	15 Aug	1 Sept	1 Oct	1 Dec
Sm Alone	87.2b	80.9b	76.0b	63.9a
Sm in Mixture	79.4a	77.4a	65.6a	62.9a
Vf Alone	98.4c	96.2c	90.4c	84.0b
Vf in Mixture	97.9c	95.3c	88.9c	79.2b
Sig. Levels	< 0.0001	< 0.0001	< 0.0001	< 0.0001

[1] For each individual collection, differences among treatments are statistically significant when means are followed by different letters.

Table 7. Growth of maize seedlings in plots with mulch of four tree species.

a) Seedling growth (cm).[1]

Treatment	Date			
	6/28	7/7	7/17	7/28
S. microstachyum	17.9a	36.8a	48.9a	53.7a
V. guatemalensis	15.1b	25.2b	30.8b	39.5b
V. ferruginea	15.2b	24.2b	29.6b	35.7b
H. alchorneoides	17.9a	30.9a	38.1a	44.6a
Control	12.7c	19.8c	23.8c	25.2c
Sig. level	< 0.0002	< 0.0001	< 0.0006	< 0.0021

b) Shoot and root biomass (mean dry weight (g) per plot at the end of the experiment).[2]

Treatment	Shoots	Roots
S. microstachyum	16.5a	5.1a
V. guatemalensis	5.7b	2.7b
V. ferruginea	5.1b	2.3b
H. alchorneoides	8.2b	3.3b
Control	2.8c	1.6c
Sig. level	< 0.0465	< 0.0004

[1] For each individual date, differences among treatments are statistically significant when means are followed by different letters.

[2] For each individual parameter, differences among treatments are statistically significant when means are followed by different letters.

treatments. The control plots were slow-growing throughout the experiments and the seedlings in these plots were noticeably weaker and yellower than the plants in the other plots. Differences in dry shoot weights were statistically significant ($p < 0.05$) as well. The primary difference was between the shoots of the maize grown in *S. microstachyum* mulch and all the others (Table 7). Shoot weight of the maize grown in *S. microstachyum* plots was 2 to 8 times greater than that grown in other plots. Roots of maize grown in *S. microstachyum* mulch also had the greatest biomass.

There were no statistical differences in N concentrations in maize shoots (Table 8). Maize roots had higher N concentrations in the *S. microstachyum* mulch treatment and in control plots, than in either of the other three species (Table 8). The differences in maize P concentrations were statistically significant for both shoots and roots: the highest maize shoot P was found in the *V. ferruginea* and the lowest in the *S. microstachyum* mulch treatments; while the highest root P was in the controls. A more clear picture of the circulation of N and P from mulches to maize tissue is seen when examining the relationship between N and P uptake by maize (calculated by multiplying maize tissue nutrient content × tissue biomass at harvest), and the N and P application rates with the mulches (mulch nutrient concentrations × application rate), both extrapolated to kg/ha (Table 9). For N, maize uptake in the *S. microstachyum* treatment was over three times that in both *Vochysia*,

Table 8. Maize seedling tissue nitrogen and phosphorus concentrations, mulch experiment.[1]

Treatment	Shoots	Roots
Nitrogen		
S. microstachyum	1.99a	1.59a
V. guatemalensis	1.85a	1.17b
V. ferruginea	2.00a	1.19b
H. alchorneoides	1.69a	1.05c
Control	1.82a	1.55a
Sig. Levels	< 0.1828	<0.0001
Phosphorus		
S. microstachyum	0.21c	0.15b
V. guatemalensis	0.25b	0.14c
V. ferruginea	0.29a	0.15b
H. alchorneoides	0.26ab	0.13c
Control	0.25b	0.19a
Sig. Levels	< 0.0421	< 0.0001

[1] For each individual nutrient and tissue category (shoots or roots), differences among treatments are statistically significant when means are followed by different letters.

Table 9. Total N and P in maize biomass and applied as mulch (kg/ha).

Treatment	N in maize	N applied as mulch
S. microstachyum mulch	16.43	22.6
V. guatemalensis mulch	5.48	10.08
V. ferruginea mulch	5.18	8.88
H. alchorneoides mulch	7.49	10.08
Control (no mulch)	3.03	0.0
Treatment	P in maize	P applied as mulch
S. microstachyum mulch	1.72	1.20
V. guatemalensis mulch	0.72	0.48
V. ferruginea mulch	0.72	0.32
H. alchorneoides mulch	1.04	0.72
Control (no mulch)	0.40	0.0

more than double that in *H. alchorneoides*, and over five times that in the controls (Table 9).

Influence of tree canopies on the microenvironment

The average air temperature tended to be at least 2 °C lower under the tree canopies than in open grass (Table 10), with no significant differences among species. The lowest average soil temperature was found under *V. ferruginea*, with a value similar to that in secondary forest and 4 °C lower than in grass; soil temperature under the other canopies was also lower (by 1.7—3 °C) than in grass. Soil moisture was higher under the two *Vochysia*, with values close to those in secondary forest, and lower under *S. microstachyum* and *H. alchorneoides*, similar to grass. The soil bulk density was lower under the tree species, except for *S. microstachyum*; the lower values were found under the two *Vochysia*, where they were intermediate between grass and secondary forest.

Discussion

Litterfall and litter decomposition

The rates of leaf litterfall of the four species of this study are comparable to others reported for pure stands in tropical humid regions: for example, our values are similar to those reported for *Acioa barteri* (9.8 ton ha^{-1} yr^{-1}) and for teak (9.0 ton ha^{-1} yr^{-1}) in Nigeria [Okeke and Omaliko, 1991]. Our values are also comparable with those reported for species grown for shade

Table 10. Influence of tree canopies on microenvironmental parameters: air and soil temperatures and soil moisture; soil bulk density (0—5 cm depth) also shown.[1]

Site	Air temp. (°C)	Soil temp. (°C)	Moisture (%)	Bulk density (g/cm³)
S. microstachyum	29.8b	27.6b	42.9bc	0.80a
V. guatemalensis	29.0b	27.3b	45.3a	0.75b
V. ferruginea	29.0b	26.4c	45.2a	0.75b
H. alchorneoides	29.1b	28.6b	41.9c	0.78ab
Grass	32.3a	30.3a	41.1c	0.81a
Secondary forest	ND	26.7c	44.6ab	0.70c

[1] For each individual parameter, differences among sites are statistically significant when means are followed by different letters ($p < 0.05$).
ND: no data available.

in agroforestry systems of humid and sub-humid climates, which range between 2 and 4 ton ha^{-1} yr^{-1} [Young, 1989] for stands generally with lower density than in the present study. For example, *S. microstachyum* at 2,500 trees ha^{-1}, with approximately 8 ton ha^{-1} yr^{-1} litterfall compares well with reports for natural litterfall from *Cordia alliodora* (2.9—3.3); *Inga jinicuil* (6.9) and *I. leptoloba* (5.3), all used for shade of crops in humid tropical regions of Latin America, although these trees were at much lower densities (185—278 trees ha^{-1}) [Beer, 1988]. The species of this study could be used with advantage in agroforestry combinations when the goal is high organic matter production to protect soils and enhance nutrient recycling; however for use as shade trees, tree densities should be much lower than the plots of this study, and therefore nutrient recycling would also be greatly reduced.

For *S. microstachyum* and *H. alchorneoides*, total annual leaf litterfall, at approximately 8 ton ha^{-1} yr^{-1} was about twice the amount of the litter on the forest floor in August, 1989, December, 1989 and March, 1990, although accumulation in the forest floor increased thereafter. For *V. ferruginea* accumulation of litter on the forest floor was larger than the total annual input. For *V. guatemalensis* the amounts of litter on the forest floor increased through the sampling period to values larger than the total annual input. This gives an approximate indication of decomposition; i.e., presumably about half the annual litter input decomposes during the same year for *S. microstachyum* and *H. alchorneoides*; in contrast litter may take over one year to decompose under both *Vochysia* species, and more so for *V. ferruginea*. The results of the decomposition studies point to similar trends. These may be influenced not only by differences in nutrient quality but also in microenvironmental conditions under the tree canopies: the below canopy environment of the *V. ferruginea* plots was both cooler (Table 10) and darker than the other plots. From a silvicultural point of view, these results suggest that at 2 m × 2 m tree spacing, after 3.5 years it would be necessary to thin the plots to allow more light and higher temperatures in the litter layer, to increase decomposition and favor tree growth.

Apparently, N and P immobilization occurred in the early stages of decomposition of the two *Vochysia* species, while N immobilization occurred in *H. alchorneoides* (Table 4). Although in many cases the litter N content is a good predictor of initial decomposition rates, apparently the amount of fiber, lignin and polyphenolic compounds play a significant role in the control of release of N and P from decomposing litter in tropical ecosystems [La Caro and Rudd, 1985; Palm and Sanchez, 1990, 1991; Rout and Gupta, 1987]. High aluminum concentrations of the two *Vochysia*'s leaf tissue [Rundell, unpublished data; Montagnini and Sancho, unpublished data] could also be involved in the observed differences; this subject deserves further attention.

The use of the species leaves for mulches

The results of the mulch experiment suggest that tree leaf mulches played a significant role in maize seedling growth. This may be in part attributed to improvements of the microsite conditions by the physical presence of the mulches: e.g., better aeration, increased water retention and lower temperatures. These effects may be significant in a compacted soil pasture as that of the experiment. However, nutrient release from the mulches was also influencing seedling growth, since the results also showed that some species had more important effects on initial maize growth. In particular, maize seedlings grown with the *Stryphnodendron* mulch were taller and visibly healthier looking than the other seedlings. The addition of mulch of leguminous leaves has been shown to have a positive influence on maize growth [Hussian et al., 1990; Kaufusi and Asghar, 1990; Tiraa and Asghar, 1990]. The lackluster growth of the seedlings grown in both *Vochysia* treatments may be due to a variety of factors; for example, Al^{+} ions released from the litter in the upper strata of soil may affect maize seedling growth. Alternatively, N immobilization in the two *Vochysia* treatments (Table 4) may result in temporary soil N deficiencies. These processes should be studied in detail if these species are to be used in tree-crop combinations where the crop species are not Al-tolerant.

With respect to N and P extraction by maize, results confirm trends suggested by the decomposition experiment, with larger N release from N-rich *S. microstachyum* leaves (Table 9) and potential N immobilization by *V. ferruginea* leaves. For P, maize grown in the *S. microstachyum* mulch treatment had extracted approximately 4 times more than in the controls. P extraction was more than double in the *H. alchorneoides* mulch treatment than in the control; while maize grown in the two *Vochysia* plots extracted less than either *S. microstachyum* or *H. alchorneoides* (Table 9). For both N and P, increased amounts added in mulches resulted in greater amounts extracted by the maize. For N, in each treatment, the amount extracted by maize was less than the rate applied; for P, the maize extracted more than applied in any treatment. Apparently, the seedlings took up additional P from the soil: if P in maize in the control (which represents what can be taken up from soil with no mulches) is subtracted from the P in maize of the mulch treatments, it is clear that the extra P provided by the mulches makes up the difference.

The desirability of a species' litter for mulch depends on the specific objective of mulching; in some cases a fast mulch decomposition rate may be needed to favor the growth of associated crops on poor soils, while in others a more persistent litter may be desired. For example, the high litter accumulation recorded under *V. ferruginea* makes it well suited for protecting the soil against erosion; the high organic matter accumulation in soil under *V. ferruginea* [Montagnini and Sancho, 1990a, b] may be related to this species' high rates of litterfall, as well as slower decomposition. In contrast, *S. microstachyum* with high N litter content and relatively faster decomposition rate may favor N recycling. *H. alchornoides* litter, although less abundant than the other three species, because of its relatively faster decomposition would tend to promote fast nutrient recycling, especially for Ca, Mg, K and P; while *V. guatemalensis* litter may be especially important for Ca recycling (Table 2). These differences should be taken into account in order to design systems so that each species' nutrient requirements and contributions can be adequately complemented. The results of the mixed *S. microstachyum/V. ferruginea* litter experiment suggest that at least initially, mixing the litters increases decomposition rates. Possibly the *V. ferruginea* leaves contributed a different microflora which was able to decompose faster the N-rich leaflets of *S. microstachyum*; or the *V. ferruginea* litter, with larger leaves, maintains a more favorable microenvironment for decompostiion than the smaller *S. microstachyum* leaflets. This is important if *V. ferruginea* is chosen to help protect soil against erosion, but at the same time a relatively faster decomposition rate is desired; this could be attained by mixing the litter with *S. microstachyum* litter; similar results could be obtained in a *S. microstachyum/V. ferruginea*-mixed stand.

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References

Beer J (1988) Litter production and nutrient cycling in coffee (*Coffea arabica*) or cacao (*Theobroma cacao*) plantations with shade trees. Agroforestry Systems 7: 103—114

Budelman A (1988) The decomposition of the leaf mulches of *Leucaena leucocephala*, *Gliricidia sepium* and *Flemingia macrophylla* under humid tropical conditions. Agroforestry Systems 7: 33—45

Budelman A (1989) The performance of selected leaf mulches in temperature reduction and moisture conservation in the upper soil stratum. Agroforestry Systems 8: 53—66

Duguma B, Kang BT and Okali DUU (1988) Effect of pruning intensities of three leguminous species grown in alley cropping with maize and cowpea on an alfisol. Agroforestry Systems 6: 19—35

Espinoza Camacho M and Butterfield R (1989) Adaptabilidad de 13 especies nativas maderables bajo condiciones de plantacion en las tierras bajas humedas del Atlantico, Costa Rica. In: Salazar R, ed, Manejo y Aprovechamiento de Plantaciones Forestales con Especies de Uso Multiple, Actas Reunion IUFRO, Guatemala, 3—7 de abril 1989, pp 159—192. CATIE, Turrialba, Costa Rica

Evans J (1987) Site and species selection — changing perspectives. Forest Ecology and Management 21: 299—310

Gonzalez E (1991) Recoleccion y germinacion de semillas de 26 especies arboreas del bosque humedo tropical. Revista de Biologia Tropical (Costa Rica) 39(1): 47—51

Gonzalez E, Butterfield R, Segleau J and Espinoza M (1990) Primer Encuentro Regional sobre Especies Forestales Nativas de la Zona Norte y Atlantica, Memoria, Chilamate, Costa Rica, 28—29 Julio 1989. Instituto Tecnologico de Costa Rica, Cartago, Costa Rica, 46 pp

Gutteridge RC (1990) The use of the leaf of nitrogen fixing trees as a source of nitrogen for maize. Nitrogen Fixing Tree Research Reports 8: 27—28

Holdridge LR and Poveda LJ (1975) Arboles de Costa Rica. Centro Cientifico Tropical, San Jose, Costa Rica. 546 pp

Hussain A, Ranjha AM, Sharar MS and Ghaffar A (1990) Release of nitrogen during decomposition of legume tree leaves. Nitrogen Fixing Tree Research Reports 8: 51—53

Kaufusi P and Asghar M (1990) Effects of incorporating plant materials on corn growth. Nitrogen Fixing Tree Research Reports 8: 81—82

La Caro F and Rudd RL (1985) Leaf litter disappearance rates in Puerto Rican montane rain forest. Biotropica 19(4): 269—276

Montagnini F and Sancho F (1990a) Influencia de seis especies de arboles nativos sobre la fertilidad del suelo en una plantacion experimental en la llanura del Atlantico de Costa Rica. Yvyrareta (Argentina) 1(1): 29—49

Montagnini F and Sancho F (1990b) Impacts of native trees on tropical soils: a study in the Atlantic lowlands of Costa Rica. Ambio 19(8): 386—390

Montagnini F, Sancho F, Ramstad K and Stijfhoorn E (1991) Multipurpose trees for soil restoration in the humid lowlands of Costa Rica. In: Taylor DA and McDicken KG, eds, Research on Multipurpose Trees in Asia. Proceedings of an International Symposium, November 19—23, 1990, Los Banos, Philippines, pp 41—58. Winrock International Institute for Agricultural Development, Bangkok

Montagnini F and Sancho F (1993a) Nutrient budgets of young plantations with native trees: strategies for sustained management. Paper presented at the workshop: Forests and Wood-Based Biomass Energy as Rural Development Assets. Winrock/Yale University, Old Saybrook, CT, USA, February 23—27, 1992. In press

Montagnini F and Sancho F (1993b) Aboveground biomass and nutrients in young plantations of indigenous trees on infertile soils in Costa Rica: implications for site nutrient conservation. Journal of Sustainable Forestry. In press

Montagnini F and Sancho F (1993c) Reciclaje de nutrientes en plantaciones jovenes con arboles nativos: estrategias para un manejo sustentable. Yvyrareta (Argentina). In press

Okeke AI and Omaliko CPE (1991) Nutrient accretion to the soil via litterfall and throughfall in *Acioa barteri* stands at Ozala, Nigeria. Agroforestry Systems 16: 223—229

Onim JFM, Mathuva M, Otieno K and Fitzhugh HA (1990) Soil fertility changes and response of maize and beans to green manures of leucaena, sesbania and pigeonpea. Agroforestry Systems 12: 197—215

Palm CA and Sanchez PA (1990) Decomposition and nutrient release patterns of the leaves of three tropical legumes. Biotropica 22(4): 330—338

Palm CA and Sanchez PA (1991) Nitrogen release from the leaves of some tropical legumes as affected by their lignin and polyphenolic contents. Soil Biology and Biochemistry 23(1): 83—88

Pierce SM (1992) La Selva Biological Station history: colonization/land use/deforestation of Sarapiqui, Costa Rica. MS Thesis, Department of Forest Science, Colorado State University, Fort Collins, Colorado, USA, 321 pp

Rout SK and Gupta SR (1987) Effect of chemical composition of leaf litter decomposition on forest soil. Proceedings of the Indian Academy of Science (Plant Science) 97(5): 399—404

Sancho F and Mata R (1987) Estudio detallado de suelos. Estacion Biologica La Selva, Organizacion para Estudios Tropicales, San Jose, Costa Rica, 162 pp

Szott LT, Fernandes ECM and Sanchez PA (1991) Soil-plant interactions in agroforestry systems. Forest Ecology and Management 45: 127—152

Tiraa AN and Asghar M (1990) Corn growth as affected by nitrogen fixing tree and grass plant materials supplemented by P and K fertilizers. Nitrogen Fixing Tree Research Reports 8: 83—84

Yamoha CF and Burleigh JR (1990) Alley cropping *Sesbania sesban* (L) Merill with food crops in the highland region of Rwanda. Agroforestry Systems 10: 169—181

Young A (1989) Agroforestry for Soil Conservation. ICRAF, Science and Practice of Agroforestry. C.A.B. International and International Council for Research in Agroforestry, Wallingford, UK, 276 pp

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Net nitrogen mineralization in soils under six indigenous tree species, an abandoned pasture and a secondary forest in the Atlantic lowlands of Costa Rica

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Abstract

Nitrogen mineralization, nitrification potentials, pH, total N, C, extractable P and cations were measured in soils under 4-year-old, mono-specific stands of six fast-growing, native tree species, an abandoned pasture, and a 20-year-old secondary forest, as part of a study on the use of indigenous tree species for rehabilitation of soil fertility on degraded pastures at the La Selva Biological Station in the Atlantic humid lowlands of Costa Rica. Soil net nitrification potential rates were higher under two N-fixing, leguminous species, *Stryphnodendron microstachyum* Poepp. et Endl. (1.1–1.9 mg kg^{-1} day^{-1}) and *Dalbergia tucurensis* Donn. Smith (0.7–1.5 mg $kg^{-1}day^{-1}$), than under the non-N-fixing trees in the plantation, *Vochysia guatemalesis* Don. Sm., *Vochysia ferruginea* Mart, *Dipteryx panamensis* (Pittier) Record and Mell and *Hyeronima alchorneoides* Fr. Allemao (0.2–0.8 mg kg^{-1} day^{-1}). Values under the N-fixing trees were comparable to those found in secondary forest. There were no statistically significant differences in soil total N or in other nurtients between the species. Results of pH measurements done before and after incubation did not show any clear evidence of a pH drop attributable to nitrification.

Introduction

The incorporation of N-fixing trees in production systems is frequently followed by higher yields of associated crops or trees (Alpizar et al., 1986; Dommergues, 1987; Szott et al., 1991). Symbiotic N fixation by trees often results in increased soil N mineralization and nitrification, with consequent higher availability of mineral forms of N (ammonium, NH_4^+, and nitrate, NO_3^-) in the soil and solution (Binkley et al., 1982; Montagnini et al., 1986; 1991a; Van Miegroet and Cole, 1984). Increased soil nitrification may also result in lower soil pH (Binkley and Sollins, 1990; Van Miegroet and, Cole 1984). The acidifying effects of nitrification may be of concern because low pH can affect soil cation exchange capacity and nutrient availability (Uehara and Gillman, 1981).

As in many other regions of the lowland humid tropics, soils in the Sarapiqui district of the Costa Rican Atlantic humid lowlands have low fertility because of low pH (<5.5), high Al saturation (10–50%), low cation exchange capacity (<4 μmol kg^{-1} and low extractable P (<10 mg kg^{-1}) (Berstch, 1986). Nitrogen is not usually included among the soil fertility parameters evaluated in regional land-use capability assessments (Berstch, 1986); however, N fertilizers are heavily used in agriculture in the Atlantic lowlands, indicating that low N availability may be and additional factor in the region's generally low fertility (Montagnini, 1994).

We have been evaluating the potential of indigenous tree species for soil fertility rehabilitation on abandoned pastures at the La Selva Biological Station in the Sarapiqui district of the Atlantic humid lowlands of Costa Rica since 1987. The study focused on two N-fixing leguminous trees: *Stryphnodendron microstachyum* Poepp. et Endl. (ex *S. excelsum* Harms) and *Dalbergia tucurensis* Donn. Smith, and four non-

N-fixing trees: *Vochysia guatemalensis* Donn. Sm. (ex *V. hondurensis* Sprague), *Vochysia ferruginea* Mart, *Dipteryx panamensis* (Pittier) Record and Mell and *Hyeronima alchorneoides* Fr. Allemao, all growing in a young plantation on abandoned pasture soils. Results of previous studies showed that after 2.5 years, soils in the tree plantation had higher organic matter and higher total N, exchangeable K and Mg than adjacent areas of abandoned pasture (Montagnini and Sancho, 1990). Among the species in the plantation, the highest soil total N was found under *V. ferruginea*, a non-N fixing tree (Montagnini and Sancho 1990). However, preliminary results showed that soil NO_3^- concentrations and net nitrification potential rates were highest under the two N-fixing species in the plantation than under the other species (Montagnini and Sancho, 1990). Apparently, soil total N measurements were not enough to assess the influence of the trees on soil N availability. The goal of the present study was to compare N mineralization and nitrification potentials, as a measure of N availability (Keeney, 1982) in soils under 4-year-old, mono-specific stands of the six fast-growing, native tree species named above, an adjacent abandoned pasture, and a 20-year-old secondary forest. The potential effects of nitrification on soil pH were also examined.

Study site

The experimental plantation where the present study was conducted was established in December 1985 on abandoned pasture at the La Selva Biological Station of the Organization for Tropical Studies (10°26'N, 86°59'W, 50 meters mean elevation, 24°C mean annual temperature, 4000 mm mean annual rainfall, with maximum in July and minimum in March) (La Selva Biological Station weather reports). Soils are Fluventic Dystropepts derived from alluvially deposited volcanic materials: they are deep, well drained, stone-free, of low or medium organic matter content, of moderately heavy texture, and generally acidic and infertile (Sancho and Mata, 1987). The area had been cleared in the mid-1950s and grazed until 1981. The dominant species in the pastures were grasses (*Cynodon* spp., *Paspalum fasciculatum*, *Brachiaria* spp., *Melinis minutiflora*, and *Panicum maximum*), herbs (*Desmodium* spp., *Mimosa pudica*, among others), ferns (*Nephrolepis viscerata*, *Hylepis repens*) and bushes (*Psidium guajava* and *Piper culebranum*). In the pastures there were patches of approximately 20-year-old forest with *Pentaclethra macroloba* (a mimosoid, N-fixing legume dominant in the primary forest at La Selva), *Piper culebranum*, species of the Melastomataceae family, ferns and tree seedlings in the understory. The tree plantation had a randomized block design with five replicates, each single-species plot containing seven rows of seven trees (14 m × 14 m each), with two meters between trees. There were also five 14 m × 14 m plots in an adjacent abandoned pasture, and in a nearby patch of secondary forest.

General characteristics of the tree species of this study are shown in Table 1. All the species are of medium (e.g., *S. microstachyum*, *V. ferruginea*) to high (e.g., *Hyeronima alchorneoides*, *V. guatemalensis*) timber value (Gonzalez et al., 1990; Holdridge and Poveda, 1975).

Materials and methods

Superficial roots (0–15 cm depth) of the three leguminous species of this study (*S. microstachyum*, *D. tucurensis* and *Dipteryx panamensis*) were excavated and examined for the presence of root nodules. At least five trees per plot, located along diagonal transects, were examined to give 25 trees for each species.

Net nitrogen mineralization and nitrification potentials

These measurements were taken in March (end of the dry season), May and August (beginning and middle of the rainy season, respectively) of 1990, i.e. when the plantation trees were 4–4.5-years old. Nitrogen mineralization and nitrification potentials were measured in aerobic laboratory incubations (Keeney, 1982). Buried polyethylene bags for in-situ measurements (Montagnini and Buschbacher, 1989; Westermann and Crothers, 1980) were damaged by insects after two or three days in the field, although we had used bags of different thickness (Gordon et al., 1987), and thus were not used. Soils were sampled at 0-15 cm with a 2.5-cm diameter soil corer near the center of each plot. Soils were also sampled at random locations in the five abandoned pasture and five secondary forest plots. In the forest plots, samples were taken within a circle of one meter radius from a tree trunk. Two samples were composited into one sample per plot, 40 composite samples total. NO_3^- and NH_4^+ were extracted with 2*N* KCl, using a proportion of 1:4 soil:extracting solution, and measured using a Lachat Flow Injection Analyser. One subset of samples was extracted immediately after sampling; another subset was incu-

Table 1. Native tree species studied for their effects on soils and nutrient cycling at La Selva Biological Station (Gonzalez et al. 1990, Holdridge and Poveda 1975)

Scientific name	Common name	Family	Native range	Natural habitat
Stryphnodendron microstachyum Poepp. et Endl.	Vainillo	Leguminosae (mimosoid)	Costa Rica	Low altitude, very humid climate. Alluvial as well as poor soils
Dalbergia tucurensis Donn. Sm.	Granadillo	Leguminosae (papilionoid)	Belize, Honduras, Costa Rica	Low to mid-elevation, humid and very humid climate (no information on soils)
Vochysia guatemalensis Donn. Sm.	Mayo	Vochysiaceae	Mexico to Panama	Lowlands, up to 900m, humid climate. Rich alluvial or poor soils.
Vochysia ferruginea Mart	Botarrama	Vochysiaceae	Nicaragua to Brazil	Lowland forests. Well-drained, acidic, infertile soils
Dipteryx panamensis (Pittier) Record & Mell	Almendro	Leguminosae (papilionoid)	Nicaragua to Colombia	Low elevations, very moist climate. Flat terrain, alluvial soils. Not reported to nodulate
Hyeronima alchorneoides Fr. Allemao	Pilon	Euphorbiaceae	S. Mexico to S. Brazil	Hills, abandoned pastures. Alluvial as well as poor soils

bated in plastic cups in the laboratory (Keeney, 1982) at room temperature in the dark for seven days. Cups were opened daily to maintain aerobic conditions. Soil percent moisture was measured gravimetrically before incubation. Soils were at approximately field capacity at the time of sampling; moisture levels remained constant during the short incubation time used. The difference between final (after incubation) and initial NO_3^- concentrations or NO_3^- + NH_4^+ concentrations gave the net nitrification or net N mineralization potential rates, respectively (Keeney 1982).

Soil pH was measured on separate sub-samples before and after incubation, in deionized water and in 1*N* KCl using a 1:2.5 mixture of soil:water or KCl solution. Analysis of variance and test of means (LSD, $p <$ 0.05) were done to compare soil parameters between pasture, forest and the six species in plantation for each sampling date. For the pH, ANOVAS were done on H^+-ion concentrations and the calculated means were then converted back to pH values.

Soil fertility

For general chemical characteristics of the soils, samples were taken with a 'Dutch type' auger at 0–15, 15–30 and 30–60 cm depth. Composite samples were taken in each of the five replicate plots for each species, and in the secondary forest and pasture plots. Soils were sampled in May (end of dry season) of 1989, 1990 and 1991. Chemical analyses were performed at the Soils Laboratory of the College of Agriculture, University of Costa Rica, following standard methods currently used by soil testing laboratories in the country. The pH was measured in a 1:2.5 mixture of soil:deionized water. Ca and Mg were extracted with a 1*N* KCl solution, while P, K and micronutrients were extracted with a modified Olsen solution (Diaz

Romeu and Hunter, 1978). Cations were measured using an Atomic Absorption Spectrophotometer. P was measured colorimetrically after reaction with acid $(NH_4)_2MoO_4$ and $SnCl_2$, using a Spectrophotometer. Organic matter was measured with the Walkley-Black technique (Allison, 1975) and total N was measured using a semi-Micro-Kjeldahl technique (Bremner and Mulvaney, 1982). Analysis of variance and LSD tests were run to compare the means for each parameter and soil depth (n=5) among sites.

Results

Root nodules were evident on all trees examined for *S. microstachyum* and *D. tucurensis*; these were apparently active N-fixing nodules as suggested by their reddish coloration in laboratory observations (J Gordon, pers. comm.). No nodules were found in any of the *D. panamensis* trees examined; this species has not been reported to nodulate (Allen and Allen, 1981; Halliday, 1984).

Soil N mineralization and nitrification

Results of measurements taken in 1990 (Table 2) confirmed the preliminary results reported for May 1989 (Montagnini and Sancho, 1990): although there were differences among the 1990 sampling dates, there was a trend of higher soil mineral N and higher net nitrification potential rates under the two leguminous, N-fixing species (*S. microstachyum* and *D. tucurensis*), as well as under secondary forest and sometimes under pasture. In March (Table 2a), soil NO_3^- concentrations. Net nitrification potentials were significantly higher under pasture than under either forest or plantation species *D. tucurensis* and *S. microstachyum*. There were no significant differences in net N mineralization potential rates. For *D. panamensis, H. alchorneoides*, pasture and forest, net N mineralization was less than net nitrification because final NH_4^+ values were smaller than the initial ones; this suggests that a portion of the NH_4^+ had been nitrified, and another portion had been taken up (immobilized) by other microorganisms in the soil. Although March is a relatively dry month at La Selva, soil moisture was high because it had rained during the three days preceeding sampling. Gravimetric soil moisture was highest in the forest and lowest under *D. panamensis*. In May (Table 2b), NO_3^- and NH_4^+ concentrations were higher under the forest. The highest net nitrification was under *S. microstachyum*. With the exception of *H. alchorneoides*, all N mineralization values were negative, suggesting again immobilization of NH_4^+ by soil microorganisms. Soil moisture was higher than in March, and it was again higher in forest. In August (Table 2c), NO_3^- was significantly higher under *S. microstachyum* and forest, while NH_4^+ was highest under *H. alchorneoides*. Both net nitrification and N mineralization potentials were highest under *S. microstachyum*. In all cases except *H. alchorneoides* and pasture, N mineralization was higher than nitrification, possibly indicating a plentiful supply of NH_4^+ to soil nitrifiers. Gravimetric soil moisture was less than in May, and it was again higher in the forest.

Soil pH before and after incubation

In March (Table 2a), initial and final (after incubation) water pH were highest in *V. ferruginea, V. guatemalensis* and *D. panamensis* soils. The pH was less after incubation than before in *S. microstachyum, D. tucurensis* and forest soils; the greatest decrease in soil water pH was in the forest soil. In May (Table 2b), initial water pH was higher in *V. ferruginea, V. guatemalensis* and *D. panamensis*, pasture and forest soils; there were no significant differences in final soil water pH. There was a slight trend of a decrease in final water pH in pasture and forest soils. In August (Table 2c), there were no significant differences in initial soil water pH. Soil water pH tended to be lower after incubation in all soils except *H. alchorneoides* and forest; the greatest decrease in soil water pH were in pasture and in *D. tucurensis* incubated soils. Soil KCl pH showed similar trends as water pH, but with overall lower values.

Soil fertility

Analysis of samples collected in 1989 showed similar trends of differences in organic matter and N among sites as in 1988 (Montagnini and Sancho, 1990), but unlike 1988, these differences were not statistically significant ($p < 0.05$) (Table 3). Soils under secondary forest had higher exchangeable Ca than either pasture or plantation plots in the 0–15 - and 15–30 cm depths. Within the tree plantation, there were no significant differences among species in soil nutrient concentrations. Results of soil measurements done in 1990 and 1991 showed trends similar to those found in 1988 and 1989. When examining data from 1988 to 1991, no increasing or decreasing trends with time were apparent for any individual nutrient (Montagnini and Sancho, 1994b).

Table 2. Soil NO_3^- and NH_4^+ concentrations, net nitrification and N mineralization potentials, gravimetric moisture and soil water pH for the six tree species of this study, an abandoned pasture and a secondary forest: sampling done in March, May and August, 1990[a]

Site	Soil parameter						
	NO_3^- (mg kg^{-1})	NH_4^+ (mg kg^{-1})	Net Nitrification Potential (mg NO_3^- kg.day^{-1})	Net N Mineralization Potential (mg NO_3^- + NH_4^+ kg.day^{-1})	%H_2O	Initial pH-H_2O	Final pH-H_2O
a. March 1990							
S. microstachyum	2.36b	4.30a	1.44ab	1.76a	38.9bc	4.65ab	4.53b
D. tucurensis	3.63b	2.15a	1.55a	3.81a	39.0b	4.61ab	4.51b
V. ferruginea	0.64b	2.18a	0.40c	0.59a	39.2ab	4.80a	4.78a
V. guatemalensis	0.28b	1.10a	0.35c	0.98a	39.2ab	4.91a	4.88a
D. tucurensis	0.47b	2.10a	0.50c	0.33a	39.9ab	4.82a	4.83a
H. alchorneoides	1.06b	4.16a	0.64bc	0.33a	36.0c	4.51b	4.55b
Pasture	15.2a	2.19a	0.61bc	0.55a	38.6bc	4.50b	4.46b
Forest	3.40b	2.90a	1.02ab	0.69a	42.1a	4.71ab	4.55b
b. May 1990							
S. microstachyum	3.80ab	15.8ab	1.08a	–0.74ab	39.8b	4.65ab	4.10a
D. tucurensis	2.63b	15.3ab	0.74abc	–1.17abc	39.8b	4.68ab	4.72a
V. ferruginea	1.09b	13.5bc	0.37bcd	–1.29abc	40.8ab	4.77a	4.78a
V. guatemalensis	0.75b	13.6bc	0.22d	–1.44bc	39.8b	4.91a	4.90a
D. panamensis	1.03b	12.9bc	0.41bcd	–1.18abc	40.3b	4.84a	4.87a
H. alchorneoides	2.96ab	6.3c	0.45bcd	0.16a	42.3ab	4.52b	4.63a
Pasture	4.15ab	14.9bc	0.25cd	–1.56bc	42.6ab	4.78a	4.73a
Forest	6.36a	24.7a	0.78ab	–2.49c	46.1a	4.90a	4.80a
c. August 1990							
S. microstachyum	3.45a	3.86bc	1.98a	3.77a	37.4bc	4.46a	4.30bc
D. tucurensis	1.81ab	0.45bc	1.03bc	1.42ab	37.3bc	4.57a	4.35abc
V. ferruginea	0.15b	0.58bc	0.43c	0.83c	38.6b	4.52a	4.36abc
V. guatemalensis	0.02b	0.36c	0.44c	0.82c	37.8bc	4.49a	4.40abc
D. tucurensis	0.17b	2.84bc	0.70c	1.31ab	36.7bc	4.50a	4.47abc
H. alchorneoides	0.51b	10.5a	0.80c	-0.20c	36.2c	4.54a	4.54ab
Pasture	0.87ab	5.04b	1.05bc	0.83c	36.3c	4.72a	4.29c
Forest	3.61a	5.11b	1.72ab	1.97ab	41.3a	4.38a	4.60a

[a] Differences between sites for a given parameter and date are statistically significant when means are followed by different letters(p<0.05).

Discussion

Soil N mineralization and nitrification potentials

The presence of the N-fixing *Pentaclethra macroloba* may account for the high soil mineral N and net nitrification found in the secondary forest; abundant nodulation was found in superficial roots of adult individuals and seedlings of this species. *Pentaclethra macroloba* is considered a promising N-fixing tree of economic value (Nichols and Rodriguez, 1990). High rates of N mineralization and nitrification in the pasture may be explained by the presence of leguminous herbs (*Mimosa pudica, Desmodium ovalifolium*) which were also observed to be nodulated.

Although no statistical analysis was performed to discern differences among sampling times, values of total soil mineral N concentrations (NO_3^- + NH_4^+) were

Table 3. Organic matter (OM), total N, extractable P, pH, exchangeable Ca, Mg, and K in soils under six native tree species in plantation, an abandoned pasture and a secondary forest: sampling done in May, 1989

Site	Depth	OM	N	P	pH	Ca	Mg	K
	(cm)	(%)	(mg kg^{-1})			(cmol kg^{-1})		
S. microstachyum	0–15	4.50a	0.278a	2.40a	5.1a	0.68b	0.44ab	0.13a
	15–30	3.29a	0.224a	2.10a	5.1ab	0.52bc	0.22bc	0.14a
	30–60	1.88a	0.196a	1.80b	5.1a	0.54a	0.16a	0.14a
D. tucurensis	0–15	4.77a	0.278a	3.08a	4.9a	0.55bc	0.32bc	0.13a
	15–30	3.45a	0.224a	2.30a	5.0c	0.50bcd	0.18c	0.13a
	30–60	2.46a	0.202a	1.74b	5.1a	0.44a	0.14a	0.09a
V. ferruginea	0–15	5.06a	0.320a	3.24a	4.9a	0.63bc	0.53a	0.16a
	15–30	3.66a	0.248a	2.48a	5.0c	0.35d	0.20c	0.10a
	30–60	2.94a	0.200a	2.50b	5.1a	0.33a	0.16a	0.15a
V. guatemalensis	0–15	4.30a	0.304a	2.30a	5.2a	0.47bc	0.50ab	0.10a
	15–30	3.16a	0.232a	1.82a	5.1ab	0.38cd	0.22bc	0.07a
	30–60	2.42a	0.202a	2.00b	5.1a	0.36a	0.15a	0.06a
D. panamensis	0–15	4.28a	0.290a	3.38a	5.3a	0.63bc	0.59a	0.14a
	15–30	2.62a	0.214a	2.02a	5.3a	0.54b	0.30b	0.11a
	30–60	2.45a	0.206a	1.38b	5.3a	0.66a	0.27a	0.10a
H. alchorneoides	0–15	5.16a	0.232a	1.50a	5.1a	0.31c	0.21bc	0.09a
	15–30	2.77a	0.248a	1.50a	5.1ab	0.45bcd	0.19c	0.10a
	30–60	1.21a	0.158a	1.70b	5.2a	0.46a	0.20a	0.10a
Pasture	0–15	3.98a	0.296a	4.10a	5.2a	0.57bc	0.38ab	0.22a
	15-30	2.94a	0.236a	3.40a	5.1ab	0.51bcd	0.27bc	0.17a
	30–60	2.46a	0.194a	8.90a	5.2a	0.47a	0.20a	0.13a
Forest	0–15	5.11a	0.288a	2.30a	5.2a	1.16a	0.49ab	0.21a
	15–30	3.83a	0.244a	2.00a	5.2a	0.92a	0.45a	0.17a
	30–60	2.48a	0.206a	1.40b	5.2a	0.62a	0.27a	0.12a

[a] Differences between sites for a given depth and parameter are statistically significant when means are followed by differenmt: letters ($p < 0.05$).

generally higher in May (Table 2), while net nitrification potentials tended to be higher in August. The lower soil mineral N pools found in March may indicate slower decomposition rates during a relatively drier month. The smaller soil mineral N pool found in August may be due to higher rainfall leading to greater NO_3^- leaching. Alternatively, lower NO_3^- + NH_4^+ pools may be the result of more rapid uptake by plants and microorganisms after the rains began, or by losses to denitrification. Root and leaf litter decomposition may be also higher in August than in May, resulting in faster N mineralization and nitrification.

Nitrification is generally controlled by the availability of ammonium in most humid tropical ecosystems (Montagnini and Buschbacher, 1989; Robertson, 1984; Vitousek, 1984; Vitousek and Denslow, 1985). As all the NH_4^+ was consumed during the incubation of soils from all sites in this study, it appears that NH_4^+ availability controls nitrification in these soils as well. Thus, an increase in soil ammonium as an indirect result of N fixation is expected to enhance nitrification. Although nitrification rates were higher under the N-fixing species, overall the rates were relatively low. For example, values reported here for secondary forest were lower than those reported for a successional forest on volcanic soils near Turrialba, Costa Rica (Matson et al., 1987). Soils at the Turrialba site were Typic Dystrandepts with large amounts of organic carbon and nitrogen (Matson et al., 1987), therefore although Matson et al. did not report soil chemistry, we suspect that the soils at our site are less fertile, with lower pH, lower exchangeable P and cations and lower available N. With respect to general soil chemical characteristics, the results of the present study suggest that after the initial site improvement found in 1988, approximately one year after canopy closure (Montagnini and Sancho, 1990), no further positive or negative changes in soil chemistry were detected. Continued soil measurements at the La Selva site will be needed to confirm the trends reported for 1988–1991.

Our values of soil net mineralization and nitrification potentials were also generally lower than those reported for successional and mature forest at La Selva (Robertson, 1984); again the site of Robertson's study was on alluvial soils, more fertile than ours. However, the rates reported in this study were higher than those found in an Amazon forest and successional sites on poorer, more acidic soils near San Carlos de Rio Negro, Venezuela (Montagnini and Buschbacher, 1989).

Changes in soil pH during incubation

Results of pH measurements taken before and after incubation do not show any clear evidence of a pH drop attributable to nitrification. Probably the incubation time was too short to show any clearer trends. Alternatively, other factors which determine soil acidification, such as base saturation, the quantity of weak acids, and acid strength (Binkley and Sollins, 1990), may have greater influence on the pH of these soils than H^+-ion production from nitrification.

Implications for the use of S. microstachyum *and* D. tucurensis *in mixed-production systems*

Of the species studied, *S. microstachyum* and *D. tucurensis* increased soil N availability, as shown by the higher N mineralization and nitrification potential rates measured in soils under these species (Table 2). Results of other studies showed that *S. microstachyum* had fast growth (over 3.0 cm diameter at breast height per year), high N concentration in leaf (2.25%) and branch (0.93%) tissue, high rates of litter fall, and relatively fast leaf litter decomposition rates (Montagnini et al., 1993). *D. tucurensis* had slower growth rate (Gonzalez et al., 1990) and lower rates of litter fall than *S. microstachyum*, but it also had high N concentrations in leaf and branch tissue (Montagnini et al., 1991b). Additionally, results of other research also showed that total above-ground biomass N accumulation by *S. microstachyum* was 176 kg ha^{-1} larger than *V. guatemalensis*, a non-N fixing tree species with similar growth in the same plantation (Montagnini and Sancho, 1994a,b). Furthermore, maize seedlings grown in soils mulched with *S. microstachyum* leaves showed better growth and extracted more N from the soil than those mulched with non-N-fixing tree species, or than the unmulched controls (Montagnini et al., 1991b, 1993). Because of its better growth and its nutrient recycling characteristics, *S. microstachyum* showed greater potential than *D. tucurensis* for its incorporation into mixed-production systems. Apparently *S. microstachyum's* faster litter decomposition rates and higher litter N concentration (Montagnini et al., 1993) resulted in the observed higher mineralization and nitrification rates in the soil. Farmers in the La Selva region are already planting this species with good results (Maroto Villalobos, 1990) in terms of initial tree growth and yields of associated crops, mainly cassava (*Manihot esculenta* Crantz). However, experiences in the region are still too recent for generalizations on the success of these systems. We are currently using *S. microstachyum* as part of mixed-tree plantation experiments at La Selva (Montagnini, 1992). We expect that mixed-species plantations, if designed with a consideration on the nutrient demands and potential impacts of each species on soils, will grow better and will have more long-term beneficial impacts on site nutrient conservation.

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References

Allen O N and Allen E K 1981 The Leguminosae: A Source Book of Characteristics, Uses, and Nodulation. University of Wisconsin Press, Madison, Wisconsin. 812 p.

Allison L E 1975 Organic carbon. *In* Methods of Soil Analysis, Part 2. Ed. C A Black. pp 1367–1378. Amer. Soc. Agron., Inc., Madison, Winsonsin.

Alpizar L, Fassbender H W, Heuveldop J, Folster H and Enriquez G 1986 Modelling agroforestry systems of cacao *(Theobroma cacao)* with laurel *(Cordia alliodora)* and poro*(Erythrina poeppigiana)* in Costa Rica. I. Inventory of organic matter and nutrients. Agrofor. Sys. 4, 175–189.

Bertsch F H 1986 Manual para Interpretar la Fertilidad de los Suelos en Costa Rica. Universidad de Costa Rica, Escuela de Fitotecnia. San Jose, Costa Rica. 76 p.

Binkley D, Kimmins J P and Feller M C 1982 Water chemistry profiles in an early-and a mid-successional forest in coastal British Columbia. Can. J. For. Res. 12, 240–248.

Binkley D and Sollins P 1990 Factors determining differences in soil pH in adjacent conifer and alder-conifer stands. Soil Sci. Soc. Am. J. 54, 1427–1433.

Bremner J M and Mulvaney S S 1982 Nitrogen-total. *In* Methods of Soil Analysis, Part 2, 2nd. ed. Eds. A L Page, R H Miller and R R Keeney. pp 595–624. Am. Soc. Agron., Inc., Madison, Wisconsin.

Diaz-Romeu R and Hunter A 1978 Metodo para el Muestero de Suelos, Analisis Quimico de Suelos y Tejido Vegetal e Investigacion en Invernaderos. CATIE, Turrialba, Costa Rica. pp 9–11 and 15–27.

Dommergues Y R 1987 The role of biological fixation in agroforestry. *In* Agroforestry. A decade of development. Eds. H A Steppler and P K R Nair. pp 245–271. International Council for Research in Agroforestry. Nairobi, Kenya.

Gonzalez E, Butterfield R, Segleau J and Espinoza M 1990 Primer Encuentro Regional sobre Especies Forestales Nativas de la Zona Norte y Atlantica. Memoria. Julio 1989. Chilamate, Costa Rica. Instituto Tecnologico de Costa Rica. Cartago, Costa Rica. 76 p.

Gordon A M, Tallas M and Van Cleeve K 1987 Soil incubations in polyethylene bags: effects of bag thickness and temperature on nitrogen transformations and CO_2 permeability. Can. J. Soil Sci. 68, 65–75.

Halliday J 1984 Register of nodulation reports for leguminous trees and other arboreal genera with nitrogen fixing members. Nitr. Fix. Tree Res. Reports 2, 38–45.

Holdridge L R and Poveda L J 1975 Arboles de Costa Rica. Centro Cientifico Tropical, San Jose, Costa Rica. 546 p.

Keeney D R 1982 Nitrogen-availability indexes. *In* Methods of Soil Analysis, Part 2, 2nd ed. Eds. A L Page, R H Miller and R R Keeney. pp 711–730 Am. Soc. Agron. Inc., Madison, Wisconsin.

Maroto Villalobos O 1990 Aportes para un Sistema de Inventario Forestal Continuo dentro de la Fase II del Proyecto de Ensayos Forestales de la Organizacion para Estudios Tropicales, Sarapiqui, Heredia, Costa Rica. Informe de practica de especialidad. Departamento de Ingenieria Forestal, Instituto Tecnologico de Costa Rica. Cartago, Costa Rica. 42 p.

Matson P A, Vitousek P M, Ewel J J and Robertson G P 1987 Nitrogen transformations following tropical forest felling and burning of a volcanic soil. Ecol. 68, 491–502.

Montagnini F, Haines B L, Boring L R and Swank W T 1986 Nitrification potentials in sucessional black locust and mixed hardwood forest stands in the southern Appalachians, USA. Biogeochemistry 2, 197–210.

Montagnini F and Buschbacher R 1989 Nitrification rates in two undisturbed tropical rain forests and three slash-and-burn sites of the Venezuelan Amazon. Biotrop. 21, 9–14.

Montagnini F and Sancho F 1990 Impacts of native trees on tropical soils: a study in the Atlantic lowlands of Costa Rica. Ambio 19, 386–390.

Montagnini F, Haines B and Swank W T 1991a Soil-solution chemistry in black locust, pine/mixed-hardwoods and oak/hickory forest stands in the southern Appalachians, U S A. For. Ecol. Manage. 40, 199–208.

Montagnini F, Sancho F, Ramstad K and Stijfhoorn E 1991b Multipurpose trees for soil restoration in the humid lowlands of Costa Rica. *In* Research on Multipurpose Trees in Asia. Eds. D A Taylor, and K G Mc Dicken. pp 41–58. Winrock International Institute for Agricultural Development. Bangkok.

Montagnini F 1992 Mixed-tree plantations with native trees: land use systems for economic returns and soil restoration. Experiments in Costa Rica and Argentina. Agrofor. Today. July-September, 1992, pp 4–6.

Montagnini F 1994 Agricultural systems in the La Selva region. *In* La Selva: Ecology and Natural History of a Neotropical Rainforest. Eds. L A McDade, K Bawa, H A Hespenheide and G S Hartshorn. pp 307–316. University of Chicago Press.

Montagnini F and Sancho F 1994a Nutrient budgets of young plantations with native trees: strategies for sustained management. *In* Forests and Wood-Based Biomass Energy as Rural Development Assets. Eds. W Bentley and M Gowen. Winrock International Institute for Agricultural Development. Morrilton, Arkansas, U S A. (*In press*).

Montagnini F and Sancho F 1994b Above-ground-biomass and nutrients in young plantations of four indigenous tree species: implications for site nutrient conservation. J. Sustain. For. (*In press*).

Montagnini F, Ramstad K and Sancho F 1993 Litterfall, litter decomposition and the use of mulch of four indigenous tree species in the Atlantic lowlands of Costa Rica. Agrofor. Sys. 23, 39–61.

Nichols D and Rodriguez E 1990 Costa Rican nitrogen fixing trees with possibilities for greater use. Nitr. Fix. Tree Res. Reports 8, 30–31.

Robertson G P 1984 Nitrification and nitrogen mineralization in a lowland rainforest succession in Costa Rica, Central America. Oecol. 61, 99–104.

Sancho F. and Mata R 1987 Estudio Detallado de Suelos. Estacion Biologica La Selva. Organizacion para Estudios Tropicales. San Jose, Costa Rica. 162 p.

Szott L T, Fernandes E C M and Sanchez P A 1991 Soil-plant interactions in agroforestry systems. For. Ecol. Manage. 45, 127–152.

Uehara G and Gillman G 1981 The Mineralogy, Chemistry and Physics of Tropical Soils with Variable Charge Clays. Westview Press, Boulder, Colorado. 170 p.

Van Miegroet H and Cole D W 1984 The impact of nitrification on soil acidification and cation leaching in a red alder ecosystem. J. Environ. Qual. 13, 586–590.

Vitousek P M 1984 Litterfall, nutrient cycling, and nutrient limitation in tropical forests. Ecol. 65, 285–298.

Vitousek P M and Denslow J S 1985 Nitrogen and phosphorus availability in treefall gaps of a lowland tropical rainforest. J. Ecol. 74, 1167–1178.

Westermann D T and Crothers S E 1980 Measuring soil nitrogen mineralization under field conditions. Agron. J. 72, 1009–1012.

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RELACIÓN ENTRE ÁREA BASAL ARBÓREA Y PROPIEDADES QUÍMICAS DEL SUELO EN UN BOSQUE TROPICAL SECUNDARIO DE 10 AÑOS DE EDAD

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RESUMEN

El área basal arbórea y las propiedades químicas del suelo fueron medidas en tres sitios de bosque tropical secundario de 10 años de edad en las tierras bajas húmedas de la zona Atlántica de Costa Rica. El total del área basal arbórea varió entre 4.34 m^2/ha en un sitio con extensa cubierta de pasto y con *Alchornea costaricensis* como el árbol más abundante, y 24.7 m^2/ha en áreas más densamente pobladas de árboles, dominadas por *Pentaclethra macroloba*. Otras especies consideradas como árboles emergentes de los bosques de la región, tales como *Stryphnodendron microstachyum* y *Hyeronima alchorneoides*, también estuvieron presentes en los sitios con mayor área basal. El Ca intercambiable del suelo, el pH, y el P y el Cu extraible fueron mayores en el sitio con menor área basal, mientras que la materia orgánica del suelo y el N total fueron mayores en los sitios con más árboles. Cuando submuestras del suelo bajo pasto y bajo árboles fueron comparadas, el N total del suelo resultó mayor en lugares poblados con árboles, y el P extraible mayor en áreas cubiertas por pasto, sin diferencias estadísticamente significativas en otros parámetros. Hubieron correlaciones positivas y estadísticamente significativas entre el área basal total y la materia orgánica del suelo, el N total, y la acidez intercambiable, con coeficientes de correlación entre 0.33 y 0.52, mientras que hubo una correlación significativa pero negativa entre área basal y P y K. Estos resultados son útiles para la comprensión del desarrollo futuro del bosque o para tomar decisiones sobre el manejo de tales áreas.

Palabras clave: bosque secundario, trópicos húmedos, materia orgánica del suelo, Costa Rica, Pentaclethra macroloba, Stryphnodendron microstachyum.

ABSTRACT

Tree basal area and soil chemical properties were measured in three sites of 10-year-old tropical secondary forest in the Atlantic humid lowlands of Costa Rica. Total tree basal area ranged from 4.34 m2/ha in a site with extensive grass cover and with Alchornea costaricensis as the most abundant tree, to 24.7 m2/ha in more dense areas dominated by Pentaclethra macroloba. Other species which are considered emergent trees of the forests of the region such as Stryphnodendron microstachyum and Hyeronima alchorneoides were also present in the sites of highest basal area. Soil exchangeable Ca, pH, extractable P and Cu were higher in the site with lower basal area, while soil organic matter and total N were higher in the sites with more trees. When subsamples from under grass and under trees were compared, soil total N was higher under patches of trees, and soil extractable P was higher in areas covered with grass, with no statistically significant differences among the other parameters. There were positive and statistically significant correlations between total tree basal area, and soil organic matter, total N, and acidity, with correlation coefficients ranging from 0.33 to 0.52, while there was a significant but negative correlation between basal area and P and K. These findings are useful as a tool in assessing future forest development or management of such areas.

Key words: secondary forest, humid tropics, soil organic matter, Costa Rica, Pentaclethra macroloba, Stryphnodendron microstachyum

INTRODUCCIÓN

Simultáneamente con la actual deforestación y conversión mundial de los bosques tropicales, aproximadamente 5 millones de hectáres de bosques secundarios son generados cada año (Lugo 1988). Aproximadamente el 60% del área de bosques secundarios en América Latina se origina de la conversión de bosques vírgenes, mientras que en

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Asia y Africa, un 72-76% proviene de la tala de bosques (Brown & Lugo 1990). La estructura, diversidad y funciones de los bosques secundarios son variables, dependiendo de la fertilidad del sitio, el uso previo de la tierra y la distancia a las fuentes de semillas (Nepstad et al. 1990; Finegan 1992). Los bosques secundarios pueden representar refugios para la fauna y flora nativa, y constituyen una manera de restaurar la productividad de tierras abandonadas (Wadsworth 1987). Se necesita más información sobre las relaciones entre los usos previos de la tierra y la diversidad y productividad de bosques secundarios, y su potencial de manejo en sitios degradados (Finegan 1992; del Amo & Ramos 1993).

Generalmente es aceptado que la productividad de bosques es limitada por la disponibilidad de nutrientes del suelo, aunque hasta ahora se ha encontrado poca correlación entre la composición química del suelo y la estatura del bosque natural (Proctor 1992). Sin embargo, la mayoría de los estudios relacionando la biomasa forestal y los nutrientes del suelo, se refieren a bosques tropicales maduros y no a la vegetación joven secundaria con tasas de crecimiento relativamente mayores. Cuando un bosque secundario reemplaza a un cultivo o pasto, la rápida tasa de producción de biomasa vegetal y las menores temperaturas del suelo bajo el dosel del bosque aumentan las contribuciones de materia orgánica al suelo. El tiempo necesario para la restauración de la materia orgánica del suelo después del abandono de la agricultura o el pastoreo depende de la velocidad con la que se establezca el barbecho del bosque secundario. Esta velocidad, a su vez, depende de la precipitación, las condiciones físicas y químicas del suelo, la topografía y la erosión. Típicamente, la mayoría de las áreas tropicales húmedas requieren períodos de barbecho de 5 a 15 años para que los suelos recuperen niveles de materia orgánica similares a los del bosque original (Van Wambeke 1992). Debido a que la recuperación de la materia orgánica del suelo depende del desarrollo de la vegetación en el sitio abandonado, la evaluación de la cobertura arbórea, tal como la medición del área basal, podría dar una indicación de las condiciones de los nutrientes del suelo en el área en un período dado en el desarrollo de la sucesión.

Desde 1990 hemos conducido estudios sobre alternativas para la rehabilitación de bosques y suelos en la Estación Biológica La Selva de la Organización para Estudios Tropicales (OET) en la zona Atlántica de tierras bajas húmedas en Costa Rica. Como parte de un estudio sobre el uso de árboles nativos para la rehabilitación de bosques y suelos en pastos abandonados, en 1991-92 un sitio de aproximadamente 10 ha fue escogido para plantaciones experimentales futuras en el Anexo La Guaria de La Selva (Montagnini 1992; Montagnini et al. 1993). Antes de limpiar el área para las plantaciones, la vegetación existente fue inventoriada para evaluar las condiciones del bosque secundario, y el suelo fue muestreado como parte de la caracterización del sitio. En este manuscrito reportamos la relación entre el área basal arbórea y los macronutrientes del suelo para la nueva vegetación secundaria, 10 años después del abandono del pastoreo intensivo, y sin ninguna otra intervención humana. Los resultados deberían ser útiles en la caracterización de bosques secundarios en situaciones ecológicas similares, para ayudar en la evaluación del desarrollo futuro del bosque o en el manejo de tales áreas.

Sitio Experimental

El sitio experimental está localizado en la porción norte del Anexo La Guaria, Estación Biológica La Selva de la OET (10°26'N, 86°59'O, altitud media 50 metros, temperatura media anual 24°C, precipitación anual 4000 mm, con máxima en julio y mínima en marzo) (Reportes climatológicos de la Estación Biológica La Selva). El Anexo La Guaria, de 120 ha, fue comprado por OET en 1981 para servir de zona de amortiguamiento para la reserva forestal y para conducir estudios experimentales sobre suelos y plantaciones arbóreas. El área donde se realizó este estudio fue talado a principios de los años 50 para la extracción de maderas comerciales (*Cedrela, Cordia, Hyeronima, Hymenolobium, Lecythis, Zanthoxylum*, fueron los géneros principales escogidos para la extracción). Después de la extracción de madera, el área fue despejada y se cultivó arroz por dos o tres años, pero esta actividad altamente mecanizada fue abandonada por razones financieras. Los campos de arroz fueron levemente quemados y sembrados con pasto: *Cynodom nlenfuensis* (Pasto estrella, una especie nativa), y las exóticas *Pennisetum maximum* (pasto de Guinea), *Pennisetum purpureum, Brachiaria* spp. y *Melinis minutiflora* (calinguero, San Juan) fueron los pastos principales usados para el ganado de carne y de leche. La cría de ganado duró aproximadamente 20 años, hasta que la hacienda fue vendida a la OET (Pierce 1992). Este patrón de uso de la tierra era típico en la región en ese entonces: el corte selectivo dirigido a las maderas más valiosas, seguido por la tala rasa para un período breve (2-3 años) de agricultura intensiva, cría de ganado, y abandono del pastoreo a causa de una producción deficiente y bajos precios de la carne (Montagnini 1994).

Al momento de realizarse el presente estudio, el sitio experimental tenía áreas de pasto así como áreas con helechos y pasto, y porciones de bosque secundario. No se llevó a cabo ningún tipo de manejo u otra intervención en el sitio después del abandono del pastoreo. El área experimental se encuentra en un terreno plano y uniforme. Los suelos son Fluventic Dystropepts derivados de aluviones volcánicos; son profundos, bien drenados, libres de piedras, con contenido de materia orgánica baja o media (2.5-4.5%), textura moderadamente pesada, y generalmente ácidos (pH in H_2O <5.0) e infértiles (Sancho & Mata 1987).

MÉTODOS

a- Inventario de la vegetación

Un inventario de la vegetación fue llevado a cabo en los tres sitios escogidos para plantaciones experimentales futuras. Cada sitio de plantación era 96 m x 256 m (24,576m^2) subdivido en cuatro bloques, y con seis parcelas de 32 m x 32 m cada una. Para el muestreo de la vegetación y el suelo, cada una de las 24 parcelas marcadas para cada plantación fue usada como una unidad de muestra. Todos los árboles y arbustos en cada parcela fueron identificados y contados, y el diámetro a la altura del pecho (dap) fue medido en todos los troncos mayores de 2 cm dap. Aunque se tienen los datos para cada parcela y bloque, por brevedad sólo se presentan el número total de individuos y el área basal por especie en m^2/ha en cada uno de los tres sitios experimentales.

b- Fertilidad del suelo

Las muestras compuestas fueron tomadas en cada una de las seis parcelas en cada bloque de cada sitio. Las muestras fueron tomadas con un barreno tipo holandés a 0-15, 15-30 y 30-60 cm de profundidad. Los suelos fueron muestreados durante la estación lluviosa de 1991. Los promedios de los resultados de las seis parcelas en cada bloque fueron calculados para obtener promedios por bloque para cada factor de suelo analizado. Seguidamente, los datos de los cuatro bloques de cada sitio fueron usados para comparar los tres sitios en un análisis de la variancia, usando Intervalos de Confianza para pruebas de promedios ($p<0.05$).

El Sitio 1 tenía una gran proporción cubierta con varias especies de pastos y helechos, así como también partes de bosque secundario, mayormente con *Pentaclethra macroloba*. Los datos correspondientes a las áreas de pasto y bosque del Sitio 1 fueron tratados independendientemente en un análisis de variancia para una comparación de los parámetros de la fertilidad del suelo entre los dos tipos de vegetación.

El análisis químico fue realizado en el Laboratorio de Suelos de la Facultad de Agronomía, Universidad de Costa Rica, siguiendo métodos estándar actualmente utilizados por laboratorios de suelos en el país. El pH fue medido en una mezcla 1:2.5 de suelo:agua deionizada. El Ca y Mg fueron extraídos con una solución 1N KCl, mientras que el P, K y los micronutrientes fueron extraídos con un solución Olsen modificada (Díaz-Romeu & Hunter 1978). Los cationes fueron medidos usando un Espectrofotómetro de Absorción Atómica. El P fue medido colorimétricamente después de reacción con ácido $(NH_4)_2MoO_4$ y $SnCl_2$, usando un espectrofotómetro. La materia orgánica fue medida por la técnica de Walkley-Black (Allison 1975) y el N total fue medido usando una técnica semi-Micro-Kjeldahl (Bremner & Mulvaney 1982). El análisis de la variancia y las pruebas de Intervalos de Confianza fueron llevados a cabo para comparar los promedios de cada parámetro y la profundidad de suelo (n=4) entre sitios.

Un análisis de regresión simple fue usado para correlacionar el área basal total con cada parámetro del suelo, usando los datos de suelos de las parcelas individuales y el área basal de todas las parcelas de los tres sitios. Los parámetros de suelo utilizados en este análisis incluyeron materia orgánica, el N total, P, Ca, Mg, y K extraibles, la acidez intercambiable y el pH. Los micronutrientes Cu, Fe, Mn y Zn fueron excluídos porque no se esperaba que mostraran correlaciones significativas con la cubierta vegetativa. Para las correlaciones, los valores de pH fueron transformados a concentraciones de iones de H^+. Ambas regresiones, linear y exponencial, fueron calculadas. El análisis fue hecho usando los datos originales y las transformaciones logarítmicas. Los datos de la profundidad de suelo de 0-15 cm fueron usadas porque las diferencias más signi-ficativas en los parámetros de suelo entre sitios fueron encontradas a esa profundidad del suelo.

RESULTADOS

a- Vegetación original

El Sitio 1 tenía menos árboles que los Sitios 2 y 3 (Tablas 1, 2, 3). El total del área basal fue 4.34, 16.4 y 24.7 m^2/ha, y el número de individuos arbóreos totalizó 22, 149 y 139/ha en los Sitios 1, 2 y 3, respectivamente. Los pastos eran una mezcla de especies nativas, que generalmente crecen en bosques despejados, y algunas especies introducidas, las cuales habían sido sembradas para mejorar la calidad del pasto nativo (Pierce 1992). Entre las especies nativas estaban *Cynodon* spp. (pasto estrella) y *Paspalum fasciculatum* (gamalote); el gamalote no es preferido por el ganado. Entre los pastos exóticos, estaban *Brachiaria* spp., *Melinis minutiflora* (calinguero, San Juan), y *Panicum maximum* (pasto Guinea). También en manchones y mezclados con los pastos, habían dos especies de helechos: *Nephrolepis viscerata* (Polypodiaceae) (helecho serrucho o Boston), e *Hylepis repens*. Aunque menos abundante, las mismas mezclas de hierbas y helechos estuvieron presentes en las áreas despejadas de los Sitios 2 y 3.

En el Sitio 1, *Alchornea costaricensis* (fosforillo) fue el árbol más abundante con 52.8% del total del área basal y 37.0% de los individuos (Tabla 1). La mayoría de los individuos eran de estatura baja (<15 m), con doseles redondos y copas abiertas. *Pentaclethra macroloba* siguió con 32.9% del total del área basal y 31.7% del número de individuos.

En contraste, en los Sitios 2 y 3 *P. macroloba* fue más prevalente, con la mayor proporción del área basal y número de individuos, y *A. costaricensis* mucho menos abundante, con <2% del total del área basal (Tablas 2 y 3). En el Sitio 2, entre los más abundantes estaba también *Ficus* spp. (Tabla 2). Sin embargo, otras especies consideradas como emergentes o árboles de dosel del bosque natural (i.e. *Hyeronima alchorneoides*) también estuvieron presentes con valores >2% del total del área basal (Tabla 2). Otras especies maderables fueron menos abundantes, cada una con <2% del total del área basal: *Cedrela odorata*, *Dipteryx panamensis* y *Zanthoxyllum panamensis* (Tabla 2). La presencia de especies como *Bactris gasipaes* (pejibaye), *Psidium guajava* (guava) y *Elaeis guianensis* (palma de aceite) (Tabla 2) evidenció la ocupación humana relativamente reciente en el área. En particular, *Gliricidia sepium*, aunque en proporciones bajas (3.3% del área basal y 4.9% del total del número de individuos medidos), es frecuentemente usado en cercas vivas en la región.

El Sitio 3 tuvo la mayor área basal, pero menor número de individuos que el Sitio 2 (Tabla 3). La composición de especies era similar a la del Sitio 2, con otras especies emergentes en los bosques de la región, tales como *Stryphnodendron microstachyum* y *Dipteryx panamensis*. Sólo cuatro árboles de tamaño comercial fueron extraídos en el momento de la limpieza del sitio para el establecimiento de las plantaciones experimentales: un *Cordia alliodora* del Sitio 1, un *Cedrela odorata* del Sitio 2, y un *Cedrela odorata* y un *Carapa guianensis* del Sitio 3.

b- Fertilidad del suelo

El Ca intercambiable del suelo y el pH fueron más altos en el Sitio 1 que en los Sitios 2 y 3 en las profundidades examinadas, mientras que la materia orgánica fue mayor en los Sitios 2 y 3 ($p<0.05\%$). El P y Cu extraible fueron mayores en el Sitio 1 que en los Sitios 2 y 3 a 0-15 y 15-30 cm de profundidad (Tabla 4). No hubo diferencias estadísticamente significativas en el Mg, K, acidez, Fe y Mn intercambiable. El Zn fue mayor en el Sitio 3 a 30-60 cm de profundidad solamente. Aunque las diferencias no fueron estadísticamente significativas ($p<0.05$), el N total tendió a ser mayor en los Sitios 2 y 3 que en el Sitio 1.

En el Sitio 1, el N total en el suelo fue mayor en áreas bajo árboles, y el P extraible del suelo fue mayor en las áreas cubiertas con pasto y/o helechos a 0-15 cm de profundidad (Tabla 5). No hubieron diferencias estadísticamente significativas en cationes, pH, materia orgánica, Cu, Fe, Mn y Zn entre los suelos bajo pasto y/o helechos y árboles a ninguna de las profundidades estudiadas.

El análisis de regresión de parámetros para el total del área basal arbóreo y la fertilidad del suelo para los tres sitios demostró que había correlaciones positivas y estadísticamente significativas entre el total del área basal arbóreo y la materia orgánica del suelo, el N total, y la acidez, con coeficientes de correlación entre 0.33 y 0.52 (Tabla 6). Estos resultados fueron obtenidos calculando regresiones lineares, usando valores no-transformados de los parámetros utilizados: los coeficientes de correlación disminuyeron cuando las regresiones exponenciales o las transformaciones logarítmicas de los datos fueron usados para el análisis. Hubo una relación negativa, pero estadísticamente significativa entre el área basal y el P y K extraible. No hubieron correlaciones estadísticamente significativas entre el área basal y el Ca, Mg o las concentraciones de iones de H^+ del suelo (Tabla 6).

DISCUSIÓN

Desarrollo futuro del bosque en sitios de crecimiento secundario

Esta discusión está basada en los resultados del muestreo de árboles maduros, ya que no se tomó información sobre las clases de tamaño menores (plantones y árboles jóvenes) que determinan el potencial de regeneración futura de un sitio. Los Sitios 2 y 3, con mayor área basal, mayor número de árboles, y mayor materia orgánica y N en el suelo, aparentemente ofrecían más alternativas que el Sitio 1 con respecto al desarrollo futuro de los árboles, ya sea natural o manejado. La especie más abundante, *Pentaclethra macroloba*, es dominante en el bosque natural de La Selva, y es comúnmente encontrada tanto en bosques primarios como en secundarios en la región Atlántica de Costa Rica (Hartshorn 1983; Peralta et al. 1987; Finegan & Sabogal 1988). Esta especie también fue la más abundante en un bosque talado en regeneración de 5 años cerca de La Selva (González & Chaves 1993). La mayoría de los árboles de *P. macroloba* en los Sitios 2 y 3 eran muy delgados, encontrándose en alta densidad alrededor de árboles adultos padres que no habían sido talados durante el corte selectivo del bosque. El número mayor de árboles encontrado en los Sitios 2 y 3 en comparación con el Sitio 1 es probablemente el resultado de la proximidad de una quebrada relativamente profunda. De acuerdo con mapas aéreos de 1981, justo cuando la OET compró La Guaria (archivos de La Selva), el Sitio 1 estaba cubierto con pasto y árboles esparcidos, mientras que el Sitio 2 tenía una cerca de árboles, muchos de los cuales podrían haber sobrevivido o servido como fuentes de semillas después del abandono del pastoreo. En general, los Sitios 2 y 3 tenían una alta abundancia de arbustos y árboles de corta vida e intolerantes a la sombra (especies pioneras, como por ejemplo, *Apeiba* spp., *Cecropia* spp., *Hampea* spp., *Miconia* spp.), lo cual es característico en las etapas tempranas de la sucesión vegetal de bosques neotropicales (Budowski 1965; Denslow 1980; Swaine & Whitmore 1988). La intervención silvicultural para facilitar a los individuos preferidos en esta fase de la sucesión no es recomendable, porque los tratamientos podrían revertir el proceso de sucesión al incrementar el nivel de luz que favorece al crecimiento del pasto (Finegan 1992). En esta temprana etapa, las alternativas para ayudar el proceso de regeneración podría incluir técnicas de regeneración artificial, es decir, enriquecimiento con plantones arbóreos de especies nativas, ya sea en líneas o en áreas de claros del bosque secundario (Weaver 1987; Ramos & del Amo 1992).

En contraste, el Sitio 1 con su distancia relativamente mayor a fuentes de semillas, su cubierta de pasto y helechos extensa, el bajo número de especies arbóreas y la menor área basal demostró menos potencial para el desarrollo rápido del bosque secundario.En este tipo de situación, para ayudar a los procesos de rehabilitación de bosques y suelos, una alternativa potencial involucra la reforestación con especies arbóreas nativas, de crecimiento rápido, adaptadas a la alta luminosidad y a suelos relativamente infértiles. Los árboles de crecimiento rápido con alta capacidad para el reciclaje de nutrientes pueden mejorar la fertilidad del suelo en muchas regiones húmedas tropicales (Sánchez et al. 1985; Lugo 1988; Montagnini & Sancho 1990a, b). Aparte del rol potencial en la restauración de la productividad del sitio, las plantaciones arbóreas pueden acelerar el proceso de regeneración en ciertos sitios: por ejemplo, los árboles pueden servir como hábitat para aves y estimular la regeneración natural de las especies locales (Parrotta 1992).

Correlación entre las propiedades químicas del suelo y el área basal arbórea

El rango de valores de los parámetros del suelo para los tres sitios de este estudio fue comparable a los encontrados en otro sitio en el Anexo La Guaria de La Selva con un patrón del uso de la tierra similar (Montagnini & Sancho 1990a, b), excepto que el pH tendía a ser más bajo en este estudio (4.1-5.2) que en el otro sitio (5.3-5.5) a profundidades del suelo de 0-15 cm. Además, las diferencias en los parámetros del suelo entre las áreas de pasto y árboles del Sitio 1 (Tabla 5) fueron comparables a los hallados en las áreas de pasto abandonado y bosque en regeneración del otro sitio en La Guaria (Montagnini & Sancho 1990a, b). En otra comparación de suelos bajo bosques y pastos en el mismo sitio (Asbjornsen & Montagnini 1994), el pH fue menor bajo árboles que bajo pasto o helecho, pero no hubo diferencias significativas entre tipos de vegetación en los otros parámetros estudiados.

El Sitio 1, con la menor área basal (Tablas 1, 2 y 3) también tenía menos materia orgánica que los Sitios 2 y 3 (Tabla 4). En los Sitios 2 y 3, la dominancia por *Pentaclethra macroloba*, un árbol leguminoso fijador de nitrógeno (Nichols & Rodríguez 1990), puede que contribuya, aunque sea parcialmente, a una mayor materia orgánica y a la tendencia a mayor N encontrado en estos sitios. El Sitio 1 tenía más P que los Sitios 2 y 3. Esta tendencia es similar a la encontrada por Montagnini & Sancho (1990a,b): menos P bajo árboles que bajo pastos. La alta demanda por P por árboles leguminosos (*Pentaclethra macroloba*) para la fijación de nitrógeno podría explicar el bajo nivel de P extraible del suelo.

Los resultados del análisis de regresión demostraron correlaciones estadísticamente significativas entre el área basal arbórea y la materia orgánica del suelo, el N total, la acidez intercambiable y el P extraible. Aunque los coeficientes de correlación fueron relativamente bajos (0.3-0.5), dado que las cantidades de nutrientes en el suelo en un sitio particular son el resultado de muchos factores interactivos (tales como el clima, el material parental, la topografía, la vegetación), es llamativo que hasta un 30-50% de un efecto en particular pueda ser atribuído a un factor individual, la vegetación (área basal). Se reconoce que las correlaciones no demuestran relaciones de causa y efecto; es decir que una mayor área basal puede ser encontrada en suelos más ricos porque la mayor fertilidad del suelo probablemente favoreció el crecimiento arbóreo, o, de manera contraria, que las condiciones mejoradas del suelo pueden ser encontradas en áreas de mayor cubierta arbórea a causa de los efectos beneficiosos de los árboles sobre los suelos. El patrón de distribución espacial de árboles encontrado aquí aparenta estar muy relacionado con la proximidad de otros árboles que fueron dejados en pie al momento del corte del sitio y que aparentemente sirvieron como fuentes de semillas, como explicamos anteriormente. Probablemente una imagen más clara de los efectos de los árboles en regeneración sobre los factores del suelo puede ser obtenida en una situación donde un corte o limpieza completa (tala rasa) es seguido por la regeneración natural arbórea. En tales situaciones, las medidas de área basal arbóreo podrían ser una herramienta útil para la evaluación de las alternativas de desarrollo del bosque.

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BIBLIOGRAFIA

* Allison, L.E. 1975. Organic carbon. In: Black, C.A. (ed.) *Methods of Soil Analysis, Part 2*, pp. 1367-1378. Amer. Soc. Agron., Inc., Madison, Wisconsin.

* Amo, R. S. del & Ramos, P.J. 1993. Use and management of secondary vegetation in a humid-tropical area. *Agrofor. Sys.* 21: 27-42.

Asbjornsen, H. & Montagnini, F. 1994. Vesicular-arbuscular mycorrhizal inoculum potential affects the growth of Stryphnodendron excelsum seedlings in a Costa Rican humid tropical lowland. *Mycorrhyza*. In press.

* Bremner, J.M. & Mulvaney, C.S. 1982. Nitrogen-total. In: Page, A.L., Miller, R.H. & Keeney, R.R. (eds.) *Methods of Soil Analysis, Part 2, 2nd. ed.*, pp. 595-624. Amer. Soc. Agron., Inc., Madison, Wisconsin.

* Brown, S. & Lugo, A.E. 1990. Tropical secondary forests. *J. Trop. Ecol.* 6:1-32.

* Budowski, G. 1965. Distribution of tropical American trees in the light of successional processes. *Turrialba* 15: 40-42.

* Denslow, J. S. 1980. Gap partitioning among tropical forest trees. *Biotrop.* 12 (Suppl): 47-55.

* Díaz-Romeu, R. & Hunter, A. 1978. *Método para el muestro de suelos, análisis químico de suelos y tejido vegetal e investigación en invernaderos*, pp. 9-11 and 15-27. CATIE, Turrialba, Costa Rica.

* Finegan, B. 1992. The management potential of neotropical secondary lowland rain forest. *For. Ecol. Manage.* 47: 295-321.

* Finegan, B. & Sabogal, C. 1988. El desarrollo de sistemas de producción sostenible en bosques tropicales húmedos de bajura: un estudio de caso en Costa Rica. *El Chasqui* (Costa Rica) 17:3-24.

* González, E. & Chaves, E. 1993. Estructura y composición de un bosque húmedo tropical explotado en la región norte de Costa Rica. *Yvyraretá* (Argentina) 5:

* Hartshorn, G. S. 1983. Plants. In: D. Janzen (ed.) *Costa Rican Natural History*. pp. 158-183. Univ. of Chicago Press. Chicago.

* Lugo, A.E. 1988. The future of the forest. Ecosystem rehabilitation in the tropics. *Environ.* 30(7):17-20 and 41-45.

* Montagnini, F. & Sancho, F. 1990a. Influencia de seis especies de árboles nativos sobre la fertilidad del suelo en una plantación experimental en la llanura del Atlántico de Costa Rica. *Yvyraretá* (Argentina) 1(1):29-49.

* Montagnini, F. & Sancho, F. 1990b. Impacts of native trees on tropical soils: a study in the Atlantic lowlands of Costa Rica. *Ambio* 19(8): 386-390.

* Montagnini, F. 1992. Mixed-tree plantations with native trees: land-use systems for economic returns and soil restoration. Experiments in Costa Rica and Argentina. *Agrofor. Today* 4(3):4-6.

* Montagnini, F. 1994. Agricultural systems in the La Selva Region. In: McDade, L.A., Bawa, K., Hespenheide, H.A. & Hartshorn, G.S. (eds.) *La Selva: Ecology and Natural History of a Neotropical Rainforest*, pp. 307-316. University of Chicago Press, Chicago.

* Montagnini, F., Sancho, F., González, E. & Moulaert, A. 1993. El uso de especies maderables nativas en plantaciones mixtas para la reforestación de terrenos degradados: resultados preliminares de experiencias en la llanura del Atlántico de Costa Rica. *VII Jornadas Técnicas: Ecosistemas Forestales Nativos: Uso, Manejo y Conservación.* 10-12 Nov. 1993. pp. 190-210. Univ. Nac. Misiones, Fac. Cs. Forestales. Eldorado, Misiones, Argentina.

* Nepstad, D., Uhl, C. & Serrao, E.A. 1990. Surmounting barriers to forest regeneration in abandoned, highly degraded pastures: A case study from Paragominas, Pará, Brazil. In: Anderson,

A.B. (ed.) *Alternatives to deforestation: steps towards sustainable utilization of the Amazon rain forest*, pp. 215-229. Columbia Univ. Press. New York.

* Nichols, D. & Rodríguez, E. 1990. Costa Rican nitrogen fixing trees with possibilities for greater use. *Nitr. Fix. Tree Res. Rep.* 8:30-31.

* Parrotta, J. A. 1992. The role of plantation forests in rehabilitating degraded tropical ecosystems. *Agric., Ecos. and Environ.* 41:115-133.

* Peralta, R., Hartshorn, G.S., Lieberman, D. & Lieberman, M. 1987. Reseña de estudios a largo plazo sobre composición florística y dinámica del bosque tropical en La Selva, Costa Rica. In: Clark, D.A., Dirzo, R. & Fetcher, N. (eds.) *Ecología y ecofisiología de plantas en los bosques mesoamericanos*. Rev. Biol. Trop. 35 (Suppl. 1): 23-40.

* Pierce, S.M. 1992. *La Selva Biological Station history: Colonization/land use/ deforestation of Sarapiquí, Costa Rica.* M.S. Thesis. Colorado State Univ., Ft. Collins, 321 pp.

* Proctor, J. 1992. Soils and mineral nutrients: what do we know, and what do we need to know, for wise rain forest management? In: Miller, F.R. & Adam K.L. (eds.) *Wise management of tropical forests*, pp. 27-35. Oxford Forestly Institute, Univ. of Oxford, Oxford.

* Ramos, J.M. & del Amo, S. 1992. Enrichment planting in a tropical secondary forest in Veracruz, Mexico. *For. Ecol. and Manage.* 54: 289-304.

* Sánchez, P.A., Palm, C.A., Davey, C.B., Szott, L.T. & Russell, E.C. 1985. Tree crops as soil improvers in the humid tropics? In: Cannell, M.G.R. & Jackson, J.E. (eds.) *Attributes of trees as crop plants*, pp. 327-350. Inst. of Terr. Ecol., Nat. Environ. Res. Council, Abbots Ripton, Huntingdon, England.

* Sancho, F. & Mata, R. 1987. *Estudio detallado de suelos. Estación Biológica La Selva.* Organización para Estudios Tropicales, San José, Costa Rica. 162 pp.

* Swaine, M.D. & Whitmore, T.C. 1988. On the definition of ecological species groups in tropical rain forests. *Vegetatio* 75: 81-86.

* Wadsworth, F.H. 1987. A time for secondary forestry in tropical America. In: Figueroa, J.C., Wadsworth, F.H. & Branham, S. (eds.) *Management of the forests of tropical America: Prospects and technologies*, pp. 189-197. Inst. of Trop. For., USDA Forest Service, San Juan, Puerto Rico.

* Van Wambeke, A. 1992. Vegetation, soil organic matter, and crops. In: Van Wambeke, A. (ed.). *Soils of the tropics. Properties and appraisal.* pp. 69-95. McGraw-Hill. New York.

* Weaver, P. L. 1987. Enrichment planting in tropical America. In: Figueroa, J.C., Wadsworth, F.H. & Branham, S. (eds.) *Management of the forests of tropical America: Prospects and technologies*, pp. 259-278. Inst. of Trop. For., USDA Forest Service, San Juan, Puerto Rico.e

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Tabla 1. Inventario de vegetación en un bosque secundario de 10 años en La Selva, Costa Rica: Sitio 1, Mayo 1991.

Especies arbóreas	Area Basal		Número de individuos	
	m²/ha	Relativa(%)	Totales/ha	Relativa(%)
≥2% del área basal total:				
Alchornea costaricensis	2.28	52.84	8.14	36.90
Cecropia obtusifolia	0.21	4.75	0.41	1.85
Nectandra membranacea	0.16	3.65	0.82	3.69
Pentaclethra macroloba	1.43	32.99	7.00	31.71
≤2% del área basal total:				
Apeiba membranacea	0.01	0.29	0.41	1.85
Cordia bicolor	0.05	1.16	0.41	1.85
Dipteryx panamensis	0.01	0.29	0.41	1.85
Gliricidia sepium	0.04	0.81	0.82	3.69
Hampea appendiculata	0.01	0.17	0.41	1.85
Psidium guajava	0.04	0.98	2.04	9.24
Pterocarpus spp.	0.04	0.81	0.41	1.85
Vitex cooperi	0.06	1.33	0.82	3.69
Totales	4.34	100.00	22.1	100.00

Tabla 2. Inventario de vegetación en un bosque secundario de 10 años en la La Selva, Costa Rica: Sitio 2, Julio 1991.

Especies arbóreas	Area Basal		Número de individuos	
	m²/ha	Relativa(%)	Totales/ha	Relativa(%)
>2% del área basal total:				
Cordia alliodora	0.65	3.94	12.21	8.19
Ficus spp.	0.96	5.83	4.07	2.73
Guarea spp.	0.33	2.00	0.41	0.28
Gliricidia sepium	0.55	3.34	7.32	4.91
Hyeronima alchorneoides	0.46	2.79	0.41	0.28
Nectandra membranacea	0.50	3.03	7.33	4.92
Pentaclethra macroloba	9.43	58.29	65.10	43.70
<2% del área basal total:				
Alchornea costaricensis	0.11	0.67	2.85	1.91
Andira inermis	0.05	0.30	0.82	0.55
Apeiba membranacea	0.42	2.55	2.44	1.64
Bactris gasipaes	0.05	0.34	2.04	1.37
Brosimum alicastrum	0.02	0.09	0.82	0.56
Casearea arborea	0.05	0.30	0.82	0.55
Cassia fruticosa	0.03	0.18	1.22	0.82
Cecropia obtusifolia	0.07	0.42	3.26	2.19
Cedrela odorata	0.36	2.19	2.85	1.91
Clusia spp.	0.13	0.79	1.22	0.82
Cordia bicolor	0.02	0.12	0.41	0.28
Dendropanax arboreus	0.15	0.91	0.41	0.28
Dipteryx panamensis	0.23	1.39	0.82	0.55
Genipa americana	0.03	0.18	0.41	0.28
Hampea appendiculata	0.02	0.12	0.41	0.28
Inga spp	0.01	0.06	0.41	0.28
Laetia procera	0.09	0.55	0.41	0.28
Luehea semannii	0.16	0.97	1.63	1.09
Miconia affinis	0.14	0.85	5.70	3.82
Neea psychotroides	0.02	0.12	0.41	0.28
Piper spp.	0.01	0.06	0.41	0.28
Pithecellobium macrademium	0.03	0.18	0.41	0.28
Protium glabrum	0.01	0.06	0.41	0.28
Psidium guajava	0.08	0.49	3.66	2.46
Pterocarpus spp.	0.17	1.03	2.44	1.64
Rollinia microsepala	0.16	0.97	1.22	0.82
Simarouba amara	0.19	1.15	2.44	1.64
Socratea durissima	0.01	0.06	0.41	0.28
Tabebuia guayacan	0.09	0.59	0.41	0.28
Trema spp.	0.02	0.12	0.82	0.55
Especie desconocida 1	0.16	0.97	0.82	0.55
Especie desconocida 2	0.01	0.06	0.41	0.28
Virola sebifera	0.02	0.12	0.25	0.28
Vismia panamensis	0.31	1.90	6.92	4.64
Vitex cooperi	0.09	0.55	1.22	0.82
Zanthoxylum panamensis	0.07	0.42	0.82	0.55
Totales	16.45	100.00	149.03	100.00

Tabla 3. Inventario de vegetación en un bosque secundario de 10 años en La Selva, Costa Rica: Sitio 3, Julio 1991.

Especies arbóreas	Area Basal m²/ha	Area Basal Relativa (%)	Número de individuos Totales/ha	Número de individuos Relativa(%)
<u>>2% del área basal total:</u>				
Andira inermis	0.54	2.17	3.26	2.25
Casearea arborea	1.90	7.69	4.07	2.82
Ficus spp.	0.90	3.62	2.44	1.69
Miconia affinis	0.66	2.65	9.77	6.76
Nectandra membranacea	0.98	3.95	8.14	5.64
Pentaclethra macroloba	12.93	52.29	48.42	33.53
Pithecellobium macrademium	0.65	2.63	0.82	0.56
Stryphnodendron microstachyum	0.88	3.56	0.41	0.28
<u><2% del área basal total:</u>				
Alchornea costaricensis	0.48	1.95	2.79	1.93
Apeiba membranacea	0.32	1.27	5.29	3.66
Bactris gasipaes	0.30	1.22	0.41	0.28
Cassia fruticosa	0.01	0.03	0.41	0.28
Cecropia obtusifolia	0.09	0.36	2.04	1.41
Cedrela odorata	0.18	0.74	0.41	0.28
Clusia spp.	0.10	0.41	2.44	1.69
Cordia alliodora	0.42	1.69	7.33	5.07
Cupania spp.	0.33	1.33	2.44	1.69
Dendropanax arboreus	0.33	1.31	0.41	0.28
Dipteryx panamensis	0.01	0.05	1.63	1.13
Elaeis guianensis	0.08	0.32	0.41	0.28
Genipa americana	0.01	0.05	0.41	0.28
Gliricidia sepium	0.02	0.06	0.41	0.28
Guatteria invicta (diospirioides)	0.08	0.31	0.41	0.28
Guarea spp.	0.13	0.51	0.41	0.28
Hampea appendiculata	0.02	0.06	0.41	0.28
Hyeronima alchorneoides	0.49	1.97	0.41	0.28
Hura crepitans	0.02	0.08	0.82	0.56
Hymenollobium mesoamericana	0.10	0.40	0.41	0.28
Inga spp.	0.27	1.07	0.82	0.56
Laetia procera	0.09	0.34	1.63	0.13
Lonchocarpus spp.	0.19	0.77	0.82	0.56
Luehea semanii	0.16	0.63	8.14	5.64
Neea psychotroides	0.04	0.14	1.22	0.84
Pachira aquatica	0.04	0.17	0.41	0.28
Protium glabrum	0.01	0.05	0.41	0.28
Psidium guajava	0.31	1.26	6.51	4.51
Pterocarpus spp.	0.15	0.62	3.26	2.26
Rollinia microsepala	0.05	0.18	2.04	1.41
Simarouba amara	0.21	0.84	3.26	2.26
Spondias radlkoferi	0.06	0.22	1.22	0.85
Especie desconocida 1 (Ficus)	0.07	0.29	0.82	0.56
Especie desconocida 2 (Solanaceae)	0.01	0.04	0.41	0.28
Especie desc. 3 (arborescent fern)	0.01	0.01	0.41	0.28
Virola sebifera	0.01	0.05	0.41	0.28
Vismia panamensis	0.07	0.26	4.48	3.10
Vitex cooperi	0.03	0.10	0.82	0.56
Totales	24.73	100.00	138.82	100.00

Tabla 4. Características químicas de los suelos en los Sitios 1, 2 y 3: Ca, Mg, K, acidez intercambiable, pH, materia orgánica (MO), N total, P extraible y micronutrientes.

Sitio	Prof. (cm)	Ca	Mg (cmol+.l-1)	K	Acidez	pH	MO	N (%)	P	Cu (mg.kg-1)	Fe	Mn	Zn
1	0-15	1.29a	0.36a	0.16a	1.14b	4.9a	5.21b	0.23b	8.9a	39.0a	1749a	47.8a	3.80a
	15-30	1.12a	0.30a	0.13a	1.14a	5.0a	3.36b	0.16a	7.6a	38.7a	1260a	41.3a	2.76a
	30-60	1.12a	0.17a	0.09a	1.01a	5.0a	2.69b	0.12a	6.0a	32.5a	585a	35.0a	2.70b
2	0-15	0.81b	0.47a	0.18a	1.40ab	4.5b	5.66ab	0.26ab	5.9b	33.5b	1382a	89.9a	3.70a
	15-30	0.66b	0.27a	0.13a	1.27a	4.6b	3.20b	0.17a	5.8b	31.6b	936a	67.9a	2.24a
	30-60	0.59b	0.21a	0.11a	1.12a	4.7b	2.15b	0.10a	4.8a	33.6a	461a	55.7a	2.55b
3	0-15	1.03ab	0.47a	0.15a	1.19a	4.4b	6.30a	0.28a	3.3c	32.5b	1504a	88.2a	2.92a
	15-30	0.87ab	0.27a	0.11a	1.70a	4.4b	4.35a	0.17a	2.7b	30.7b	1004a	65a	2.24a
	30-60	0.89ab	0.23a	0.09a	1.44a	4.5b	3.58a	0.13a	2.1b	30.1a	597a	55a	5.08a

Las diferencias entre promedios son estadísticamente significativas cuando son seguidas por letras diferentes (P<0.05).

Tabla 5 Características químicas de los suelos bajo áreas arboladas y de pasto en el Sitio 1: Ca, Mg, K, acidez intercambiable, capacidad de intercambio catiónico. efectiva (CICE), pH, materia orgánica (MO), N total, P extraible y micronutrientes en los suelos muestreados en Mayo 1991.

Tipo de Veget.	Prof. (cm)	Ca	Mg (cmol+.l-1)	K	Acidez	CICE	pH	MO (%)	N	P	Cu (mg . kg-¹)	Fe	Mn	Zn
Arboles														
	0-15	1.35a	0.35a	0.14a	1.22a	3.06a	4.8a	5.58a	0.278a	5.87b	38.0a	1688.7a	55.5a	3.20a
	15-30	1.12a	0.27a	0.10a	1.02a	2.52a	4.9a	3.81a	0.183a	4.10a	39.0a	1120.0a	43.2	2.10a
	30-60	1.05a	0.12a	0.07a	0.85a	2.10a	5.0a	2.51a	0.158a	2.55b	36.5a	529.7a	41.7a	2.10a
Pasto														
	0-15	1.20a	0.35a	0.16a	1.00a	2.71a	4.9a	4.50a	0.218b	10.27a	38.7a	1773.0a	49.0a	3.95a
	15-30	1.12a	0.27a	0.14a	1.05a	2.59a	5.0a	3.18a	0.163a	8.00a	37.2a	1275.7a	46.7a	2.85a
	30-60	1.15a	0.17a	0.10a	0.92a	2.37a	5.4a	2.21a	0.098a	6.67a	31.0a	579.2a	38.2a	2.77a

Las diferencias entre promedios son estadísticamente significativas cuando son seguidas por letras diferentes (P<0.05).

Tabla 6. Análisis de correlación entre área basal arbórea y propiedades del suelo superficial, n=56.

Propiedad del suelo	Coeficiente de correlación	R^2	P<
Materia orgánica	0.52	0.27	0.00004
N	0.32	0.10	0.015
P	-0.33	0.11	0.013
Ca	-0.18	0.03	0.179
Mg	-0.033	0.001	0.809
K	-0.32	0.10	0.017
Acidez	0.45	0.20	0.0005
Iones H+	-0.002	0.0	0.986

INFLUENCIA DE SEIS ESPECIES DE ARBOLES NATIVOS SOBRE LA FERTILIDAD DEL SUELO EN UNA PLANTACION EXPERIMENTAL EN LA LLANURA DEL ATLANTICO DE COSTA RICA

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RESUMEN

La influencia de los árboles sobre las propiedades de los suelos debería ser un factor determinante en la selección de especies para plantaciones forestales o para combinaciones con cultivos, pero la información sobre este aspecto es escasa, particularmente en lo que respecta a especies nativas. Se está llevando a cabo un proyecto para comparar la fertilidad de los suelos bajo seis especies de árboles nativos en una plantación experimental de tres años de edad, en una sección sin árboles (con pastos) y en un bosque de sucesión secundaria de aproximadamente 20 años, ubicados en la Estación Biológica La Selva, en la región de la llanura atlántica de Costa Rica. Se mide el contenido de calcio, magnesio, potasio, el pH, la acidez intercambiable, materia orgánica, el nitrógeno total, fósforo y elementos menores extraíbles (cobre, hierro, manganeso y zinc). Las especies arbóreas en estudio, todas ellas de valor económico potencial, son las siguientes: *Stryphnodendron excelsum* Harms., *Dalbergia tucurensis* Donn. Smith (ambas especies fijadoras de N.), *Dipteryx panamensis* (Pittier) Record & Mell, *Vochysia hondurensis* Sprague, *Vochysia ferruginea* Mart y *Tabebuia rosea* (Vertol.) DC.

A los 2.5 años de edad de la plantación se encontraron en ésta niveles mayores de materia orgánica y nitrógeno, que en los pastos, con valores cercanos al del bosque secundario adyacente. Se observaron tendencias similares en el contenido de Ca, Mg, saturación de bases, Cu, Mn y Fe. Entre las especies de la plantación, se encontró mayor contenido de materia orgánica y N bajo V. ferruginea, y se observaron tendencias a un mayor contenido de Ca, Mg, P y elementos menores bajo esta misma especie.

SUMMARY

The influence of trees on soil characteristics should be a decisive factor. For selecting tree species apt for plantation and or combination of some with crops. Information, however, is scarce, especially about native species.

A field project is under way to compare soil fertility under six species of native trees in a three year old experimental plantation, in a grassy treeless lot and in a twenty year old secondery succesion forest, both situatad in the La Selva Biológical Station on the Eastarn coastal plain of Costa Rica.

This process includes such measurenents as calcium, magnesium, potassium, P.H. contents, exchangeable acidity, organic matter, total nitrogen, phosphorus and lesser extractable elements (copper, iron, zinc)

The three species under study are all potencial economically valuable. They are: Stryphnodendron excelsum Harms, Dalbergia tucurensis Donn. Smith (both species N. fixing) Dipteryx panamencis (Pittier) Record & Mell, Vochysia hondurensis Sprague, Vochysia ferrugínea Mart y Tabebuia rosea (Vartol) D.C.

In the 2.5 year old plantation higher organic matter and nitrogen levels than in grassland were found. These levels neared those of neerly secondary wooded plantation.

Similar trends were observed in Ca, Mg, coutents and in saturated bases: Cu, Mg, Fe.

Among the species planted, a higher organic matter and nitrogen contents was found in V. ferruginia tress as a higher Ca, Mg, P. contents and lesser elements within the same specie.

INTRODUCCION

Ante el avance continuo de la deforestación y de prácticas de manejo de suelos poco adecuadas en regiones tropicales y subtropicales, se hace cada vez más perentorio difundir sistemas de uso de la tierra que tiendan a recuperar o mantener la capacidad productiva de los suelos a más largo plazo. Tanto en los planes de reforestación como en los de promoción de sistemas agroforestales, es necesario dar recomendaciones sobre especies arbóreas a utilizar, que sean beneficiosas

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desde el punto de vista económico, es decir, que provean productos útiles a los agricultores, o tengan buen valor comercial, y que, al mismo tiempo, produzcan impactos favorables sobre los suelos.

Los efectos beneficiosos de los árboles sobre las características físicas y químicas de los suelos pueden incluír: 1) mejoramiento de la estructura del suelo; 2) protección contra la erosión; 3) aumento de la conservación de nutrientes del suelo; y 4) aumento en la disponibilidad de nutrientes (Fassbender 1984, Nair 1984). Los impactos de las especies de árboles sobre los suelos varían dependiendo de : 1) los requerimientos individuales de nutrientes y agua de las especies; 2) características del sistema radicular; 3) capacidad de fijación de N; 4) calidad y cantidad de hojarasca producida por el árbol. También pueden ocurrir efectos perjudiciales, tales como disminución del pH y del contenido y disponibilidad de nutrientes del suelo; este es un tema de controversia (Cozzo 1976, de las Salas y Fassbender 1984, Fernández 1987, Lundgren 1978, Montagnini 1988, Sánchez *et al.* 1985).

Los efectos de las especies arbóreas sobre los suelos son muy variables. Por ejemplo, se ha observado que los suelos bajo *Gmelina arbórea*, especie ampliamente difundida en los trópicos húmedos, presentaban mayor contenido de Ca y P, y mayor p H que los suelos bajo bosque o bajo pino, en tres localidades diferentes (Sanchez *et al.* 1985, Chijicke 1980, Ojeniyi y Agbede 1980); en dos de los sitios, los suelos bajo *Gmelina* también tenían mayor contenido de Mg y K. Efectos semejantes sobre los cationes y el pH del suelo en regiones tropicales han sido observados en *Terminalia ivorensis* (Bolfoni et. al. sin publicar), *Cordia trichotoma* y *Caesalpina equinata* (Silva 1983). El impacto potencial de estas especies sobre el aumento del pH y del contenido de cationes y P del suelo podría ser importante en áreas del tropico donde el pH bajo, la baja disponibilidad de P y la toxicidad del aluminio tienen influencia negativa sobre el crecimiento de las plantas. En contraste, también han sido documentados los efectos de *Pinus* spp. sobre la disminución del pH y del contenido de nutrientes del suelo (Bolfoni *et al.*, sin publicar, de Barros y Brandi 1975); asimismo , existen evidencias de los efectos perjudiciales de la palma africana (*Elaesis guineensis*) (Ollagnier *et al.* 1978. Kowal y Tinker 1959). Existen numerosos informes sobre el efecto beneficioso de especies de árboles fijadores de nitrógeno en regiones tropicales, con respecto a la conservación de este elemento, y sobre otros nutrientes del suelo (por ejemplo, Alpízar et al. 1986, Cadima Zeballos y Alvim 1967, Carlson y Dawson 1985, Roskowski 1982, Santana y Cabala-Rosand 1982).

La información sobre la influencia de los árboles sobre las propiedades de los suelos se concentra en unas pocas especies de amplio uso. Muy pocas veces se tienen en cuenta estos factores como determinantes en la elección de especies arbóreas para plantaciones o para combinaciones con cultivos (OTS/CATIE 1986).

En la región atlántica de Costa Rica (América Central) la Dirección General Forestal (DGF) lleva a cabo ensayos para la prueba de especies de árboles para plantaciones a campo abierto. Entre las especies recomendedas actualmente para la región (*Gmelina arborea*, *Pinus caribaea*, *Eucalyptus deglupta* y *Cordia alliodora*), solamente una (*C. alliodora*) es nativa. En 1985 la DGF estableció un ensayo para la prueba de 13 especies nativas, en la Estación Biológica La Selva de la Organización para Estudios Tropicales (OET) Entre las 13 especies, al menos cuatro: *Stryphnodendron excelsum*, *Vochysia hondurensis*, *V. ferruginea* y *Hieronyma oblonga*, mostraron a los tres años crecimiento equivalente o superior al de las especies recomendadas para la región (Espinoza y Butterfield 1989). Esto muestra el gran potencial de muches especies nativas para su aprovechamiento con fines económicos.

En 1986 se inició un proyecto independiente para el estudio de la influencia de seis especies de este mismo ensayo, sobre la fertilidad de los suelos y mecanismos de reciclaje de nutrientes. Entre las seis especies escogidas para este estudio, dos de ellas (*Dalbergia tucurensis* y *Stryphnodendron excelsum*) se eligieron por ser leguminosas, para examinar su efecto sobre la disponibilidad de nitrógeno, y sobre otros elementos, en comparación con especies no fijadoras. Entre las otras especies, *Vochysia hondurensis* y *V. ferruginea* han sido mencionadas como acumuladoras de aluminio (más de 10,000 ppm en el tejido foliar, P.W. Rundel, datos sin publicar) Esta característica ha sido encontrada en otras especies de la misma familia, asociéndose con un mejor crecimiento en comparación con otras especies, en suelos ácidos y con problemas de toxicidad de aluminio en los trópicos (Goodland 1971) Sobre las dos restantes, *Tabebuia rosea* y *Dipteryx panamensis*, no existían datos preliminares que dieran indicios sobre su posible efecto sobre los suelos, pero fueron incluídas en el estudio por su valor económico y su amplia distribución en América tropical. En este trabajo presentamos los resultados de las mediciones de fertilidad del suelo, poniendo énfasis en el efecto de la plantación en conjunto sobre la conservación de nutrientes, en el potencial de cada especie desde el punto de vista de su efecto mejorador sobre los suelos, y en los posibles mecanismos involucrados en estos efectos.

Descripción del sitio experimental.

La plantación forestal de 13 especies nativas fue establecida en diciembre de 1985 en el anexo "La Guaria" (cercano a la población de este mismo nombre), perteneciente a la Estación Biológica La Selva de la OET (10º 26' lat. N, 86º 59' long. O, elevación promedio 50 m sobre el nivel del mar). El clima es típicamente tropical, con 24º C de temperatura media anual y 3,800 mm de precipitación anual, con máximas en junio-agosto, y octubre-diciembre (300-400 mm), y mínimas de enero a mayo (150-200 mm) (datos de la Estación Meteorológica de La Selva, promedios de 1957 a 1988) La vegetación natural es de bosque lluvioso tropical de bajura (Hartshorn 1983). El bosque primario en el área experimental había sido cortado en la décad de

1950. El área fue pastoreada con ganado de carne hasta 1984 y luego fue abandonada. En las áreas con pastos se encuentran gramíneas: Olyra latifolia, Melinis minutiflora, helechos (Pteridium spp.), y algunos arbustos (Psidium guajava, Piper culebranum). En partes que no fueron pastoreadas se desarrolló un bosque secundario, actualmente de aproximadamente 20 años. En este bosque las especies dominantes son Pentaclethra macroloba, especie leguminosa mimosoidea, fijadora de nitrógeno, dominante en el monte primario de La Selva; también se encuentran abundantes piperáceas (Piper culebranum y otras) y melastomatáceas, con helechos (Pteridium spp.) y plántulas de las especies arbóreas en el sotobosque.

La plantación experimental se estableció sobre terreno plano, aproximadamente 60 m sobre el nivel del mar. El sitio fue limpiado con machete y se cortaron algunos arbustos pequeños de guayaba. Las ramas pequeñas se dejaron en el sitio, mientras que las más grandes se apartaron. Se quemó parcialmente los restos de ramas que se habían dejado y se plantó con plántulas de bolsa. Durante el primer año se desmalezó a mano cuatro veces, a partir del segundo año , se demalezó con una cultivadora mecánica, también con una frecuencia aproximada de cuatro veces por año. A mediados de 1987, antes de comenzar el presente trabajo, se cortaron los arbustos pequeños de una franja adyacente a la plantación, para tener un terreno libre de árboles para comparación. En esta área de pastos sin árboles, se desmalezó cada vez que se desmalezaba la plantación, para mantener al área sin árboles, y con un tratamiento similar a la plantación en lo referente a las limpiezas. A partir de mediados de 1988 no fue necesario desmalezar las parcelas donde ya se había cerrado el dosel (las dos especies de Vochysia y Hieronyma oblonga).

Los suelos han sido clasificados como Fluventic Dystropepts, originados sobre aluviones volcánicos (Sancho y Mata 1987). Son suelos profundos, bien drenados, sin pedregosidad o rocosidad, de colores pardo oscuro en la superficie a pardo amarillento oscuro en el subsuelo. Los contenidos de materia orgánica son de medios a bajos, con textura moderadamente pesada a pesada; en general la unidad se puede considerar de suelos ácidos y poco fértiles. En la Tabla 1 se resumen las características químicas de un perfil típico de este tipo de suelos (Sancho y Mata 1987).

Métodos

a– Delimitación del área experimental

Las 13 especies se encontraban dispuestas en bloques completos al azar, con cinco repeticiones, en parcelas de 14 m x 14 m, con 49 árboles cada una, a 2 m de distancia entre árboles. Para el presente trabajo se utilizaron las cinco repeticiones de las seis especies mencionadas anteriormente. En el área adyacente con pastos, sin árboles, se delimitaron cinco parcelas de 14 m x 14 m, ubicadas a lo largo de una franja bordeando el lado este de la plantación. En el bosque secundario, que bordea el lado sur, se delimitaron también cinco parcelas de 14 m x 14 m; El área experimental incluyendo la plantación, los pastos y el bosque secundario, era de 19,159 m2, con caminos de 7 m de ancho entre la plantación y las áreas de pastos y de bosque.

b– Elección de las especies arbóreas.

Los criterios para la eleción de especies para este estudio fueron: 1) crecimiento: se eligieron las que presentaban mejor crecimiento a comienzos de 1988, cuando la plantación tenía dos años; 2) valor económico: todas las especies del ensayo tienen madera valiosa, comercializable; 3) capacidad fijadora de nitrógeno: se examinaron las raíces de todos los árboles en una diagonal en las cinco repeticiones de cada especie leguminosa del ensayo, en junio de 1987 y en marzo de 1988. Se encontraron nódulos en las raíces de todos los árboles examinados de S. excelsum y de D. tucurensis; no se encontraron nódulos en D. panamensis ni tampoco esta especie ha sido incluída en listas de especies tropicales fijadoras de N (Halliday 1984); 4) otros posibles efectos sobre los suelos: posible efecto mejorador del suelo bajo las especies acumuladoras de aluminio (V. ferruginea y V. hondurensis)

Aunque no existen experiencias silviculturales con ninguna de estas especies, se han realizado descripciones botánicas y estudios de su biología o fenología; por ejemplo, los estudios forestales de Holdridge et al. 1971; Bethel, 1976, Hartshorn, 1972, 1978; Lieberman et al., 1985; de biología y fenología de Bawa et al., 1985; efectos de los suelos sobre el crecimiento de especies arbóreas, de Huston 1980, 1982; y efectos del régimen de luz y microclima sobre el crecimiento (Budowski, 1961; Denslow 1980; Fetcher et al., 1983; Chazdon y Fetcher, 1984).

Stryphnodendron excelsum ("vainillo"; leguminosa, mimosoidea) y Dalbergia tucurensis ("granadillo"; leguminosa, papilionoidea) tienen madera de valor comercial (Holdridge y Poveda 1975); ambas especies dan sombra moderada, lo cual podría ser una característica adecuada para su asociación con cultivos en sistemas agroforestales, o en plantaciones mixtas. Dipteryx panamensis ("almendro"; leguminosa, papilionoidea) se encuentra ampliamente distribuída en América tropical, y su madera dura es muy apreciada (Holdridge y Poveda 1975) Vochysia ferruginea ("botarrama"; vochysiácea) y Vochysia hondurensis ("mayo"; vochisiácea) son ambas muy apreciadas por su madera; ambas proveen sombra bastante densa; V. ferruginea es una especie pionera en la sucesión secundaria (Berner y Finegan 1988), se auto-poda y produce abundante ramificación baja y hojarasca. Tabebuia rosea ("roble sabana"; bignoniácea) es muy apreciada por su madera y como ornamental, y también se encuentra ampliamente distribuída en América tropical (Holdridge y Poveda 1975).

c– Estudio de las características químicas de los suelos.

Los suelos se muestrearon bajo las seis especies de la plantación, las parcelas de pastos y el bosque secundario, en abril (época menos húmeda, promedio de alrededor de 200 mm en el mes) y en agosto (época más lluviosa, promedio de alrededor de 400 mm) de 1988 (datos pluviométricos de la Estación La Selva). Se utilizaron barrenos de tipo holándes, de 8 cm de diámetro. Se muestró a 0-15, 15-30 y 30-60 cm de profundidad.

Las muestras se procesaron en el Laboratorio de Suelos de la Facultad de Agronomía de la Universidad de Costa Rica, siguiendo los métodos corrientes para determinación de fertilidad de suelos empleados en el país. Se midieron los siguientes parámetros: Ca, Mg, K, capacidad de intercambio catiónico, pH en agua, acidez extraíble, materia orgánica, nitrógeno total, fósforo extraíble y elementos menores (Cu, Fe, Mn, Zn).

El pH se determinó en una relación suelo : agua de 1:2.5, utilizando un potenciómetro Corning 7. Para las muestras de abril, el Ca, Mg., K y la capacidad de intercambio catiónico (CIC) se determinaron por medio de extracción con una solución 1 N de acetato de amonio a pH 7. Además, en abril el Ca y el Mg se extrajeron también con una solución de KCl 1N. En este caso, la capacidad de intercambio catiónico efectiva (CICE) se calculó como la suma de bases más la acidez extraída con la solución de KCl 1N. Para las muestras de agosto, el Ca y el Mg. se extrajeron con KCl solamente.

El P, K y elementos menores se extrajeron con solución de Olsen modificada, la cual consiste en una mezcla de $NaHCO_3$ 0.5 N, EDTA di-sódico 0.01 N y Superfloc 127 (Díaz Romeu y Hunter 1978). Los cationes se midieron utilizando un Espectrofotómetro de Absorción Atómica Perkin Elmer 2380. El P se midió colorimétricamente, luego de reacción con $(NH_4)_2MoO_4$ ácido y $SnCl_2$ como reductor, utilizando un Espectrofotómetro Perkin Elmer-Coleman 295.

La materia orgánica se midió utilizando la técnica de Walkley-Black (Allison 1975). El nitrógeno total se midió por un método semi-micro Kjeldahl (Bremer y Mulvaney 1982).

Resultados

Los resultados de las mediciones de la composición química de los suelos realizados en abril se presentan en las Tablas 2 a 4 y Figs. 1 a 5. Los valores de Ca y Mg obtenidos mediante extracción con acetato de amonio fueron mayores a los obtenidos en la extracción con KCl (Tablas 2 y 3). Esta diferencia era más acentuada para el Ca que para el Mg: por ejemplo, en el horizonte superficial (0-15 cm de profundidad), para S. excelsum el Ca era casi 1.5 veces mayor en acetato de amonio que en KCl, mientras que para esta misma especie, el Mg extraído con acetato de amonio era 1.2 veces mayor que el extraído con KCl (Tablas 2 y 3). Además, bajo esta misma especie para el Ca esta diferencia se acentuaba con la profundidad: el Ca a 15-30 y 30-60 cm era el doble en acetato de amonio que en KCl, mientras que para el Mg la diferencia se mantenía en niveles semejantes para las tres profundidades. Tendencias similares a aquéllas ejemplificadas con S. excelsum se manifestaban para los otros sitios.

El análisis de la varianza no reveló diferencias significativas entre los sitios para Ca, tanto para los resultados de la extracción en acetato de amonio como para los de KCl. Sin embargo, en las extracciones con acetato de amonio, a 0-15 cm de profundidad se notó una tendencia a una mayor concentración de Ca en el suelo bajo V. ferruginea (1.02 cmol/1, en bosque secundario (0.96 cmol/1) y en D. panamensis (0.93 cmol/1), en comparación con otras especies como por ejemplo S. excelsum (0.67 cmol/1), o bajo el pasto (0.47 cmol/1). La misma tendencia se observó en las extracciones en KCl para este mismo horizonte superficial del suelo; bajo V. ferruginea la concentración de Ca era 0.73 cmol/1, bajo bosque 0.68 y bajo D. panamensis 0.52, mientras que bajo S. excelsum era 0.45 cmol/1 y bajo pasto 0.32 cmol/1. Estas tendencias a diferencias entre sitios eran menos marcadas con la profundidad (Tablas 2 y 3).

Con respecto al Mg., en las extracciones con acetato de amonio existían diferencias significativas entre los sitios, para las tres profundidades en el horizonte superficial, la concentración de Mg era mayor bajo todas las especies del ensayo (entre 0.48 y 0.84 cmol/1) y bajo el bosque (0.72 cmol/1). que bajo el pasto (0.32 cmol/1) (probabilidad menor del 5 o/o). En el subsuelo, la concentración de Mg era mayor en el bosque que en el pasto y que en las seis especies del ensayo (probabilidad menor del 10 o/o) (Tabla 3).En las extracciones con KCl, las diferencias eran menos pronunciadas, pero se observó una mayor concentración de Mg en el horizonte superficial en el bosque, que en las especies del ensayo, y en éstas a su vez se observó una mayor concentración de Mg que bajo pasto, para una probabilidad menor del 10 o/o en ambos casos. No había diferencias significativas entre sitios en la concentración de Mg en el subsuelo (Tabla 2).

Con respecto al K, no se observaron diferencias significativas entre sitios, aunque se observó una tendencia de mayor contenido de K bajo D. panamensis, S. excelsum, D. tucurensis y V. ferruginea (Tabla 2). Los tres cationes considerados disminuían con la profundidad (Tabla 2).

El pH en el horizonte superficial era mayor bajo T. rosea y D. panamensis (pH 5.5, probabilidad menor de 5 o/o) , que bajo bosque y pasto (pH 5.3), con valores intermedios bajo las otras especies (Tabla 2 y Fig. 1) A 15-30 cm el pH era menor bajo bosque que bajo las especies o bajo pasto (pH 5.4) ; no había diferencias significativas entre los sitios a mayor profundidad. Se observó una tendencia a un aumento de pH con la profundidad, aunque este aumento era de 0.1-0.2 unidades solamente, es decir de igual magnitud que las diferencias de pH entre los sitios (Tabla 2 y Fig. 1).

La acidez extraíble fue menor en el horizonte superficial bajo T. rosea (1.28 cmol/1) y D. panamensis (1.18) que bajo V. hondurensis (1.86) (probabilidad menor que 5 o/o); con valores intermedios en los otros sitios (Tabla 2 y Fig. 2) No hubo diferencias significativas entre sitios a mayores profundidades; la acidez extraíble disminuyó con la profundidad, excepto en S. excelsum, D. tucurensis y bosque secundario (Fig. 2).

No se observaron diferencias significativas entre los sitios enla suma de bases extraídas con KC1, a ninguna profundidad (Tabla 2), aunque se observó una tendencia de menor cantidad de bases bajo V. hondurensis (0.73 cmol/1) y bajo pasto (0.77) en el horizonte superficial, en comparación con los otros sitios (Tabla 2 y Fig. 3), con valores entre 1.06 y 1.64 cmol/1.

La capacidad de intercambio catiónico (CIC) medida en acetato de amonio fue mayor (entre 7 y 10 veces) en todos los casos, que la capacidad de intercambio catiónico efectiva (CICE) (Tablas 2 y 3). No hubo diferencias significativas en los valores de CIC o de CICE, para ninguna de las tres profundidades consideradas (Tablas 2 y 3). La saturación de bases en el horizonte superficial fue menor bajo V. hondurensis (28.2 o/o probabilidad menor que 5 o/o) que en los otros sitios; bajo pasto, también fue menor (34.8 o/o, probabilidad menor de 10 o/o) (valores calculados según extracción con KC1); la saturación de bases tendió a disminuír con la profundidad (Tabla 2 y Fig. 4) La saturación de acidez fue mayor bajo V. hondurensis (71.8 o/o probabilidad menor de 5 o/o) y bajo pasto (65.2 o/o. probabilidad menor de 5 o/o) , en los 0-15 y en los 15-30 cm de profundidad, con valores intermedios en los otros sitios (Tabla 2). No hubo diferencias significativas entre sitios a 30-60 cm de profundidad. La saturación de acidez tendió a aumentar con la profundidad.

La materia orgánica en el horizonte superficial fue mayor en el bosque (7.58 o/o, probabilidad menor del 1 o/o) que en los otros sitios (Tabla 4). A su vez, la materia orgánica en el horizonte superficial fue mayor bajo las seis especies del ensayo (5.31 a 6.60 o/o) que bajo pasto (4.83 o/o) (probabilidad menor de 5 o/o) Aunque no hubo diferencias significativas entre las seis especies, se notó una tendencia a mayor contenido de materia orgánica en el suelo superficial bajo V. ferruginea (6.60 o/o). A 15-30 cm, la materia orgánica fue mayor en el bosque que en los otros sitios (probabilidad menor de 10 o/o) No hubo diferencias significativas entre sitios a 30-60 cm. La materia orgánica disminuyó con la profundidad.

El nitrógeno total a 0-15 cm fue mayor bajo bosque (0.328 o/o) que bajo pasto (0.224 o/o), con valores intermedios en las especies del ensayo (0.260 a 0.318 o/o) (probabilidades menores de 5 o/o) (Tabla 4) El mayor valor de nitrógeno total (0.318 o/o) se encontró bajo V. ferruginea, aunque la diferencia no fue significativa (probabilidad menor del 10 o/o). A 15-30 cm, el nitrógeno total fue mayor en el bosque (probabilidad menor del 5 o/o), no habiendo diferencias significativas entre los otros sitios. A 30-60 cm el nitrógeno total fue mayor en el bosque que en el pasto (probabilidad menor de 5 o/o) , sin diferencias entre los otros sitios. El nitrógeno total disminuyó con la profundidad. No hubo diferencias significativas entre sitios en la relación C/N a ninguna de las tres profundidades (Tabla 4).

El fósforo extraíble fue menor a 0-15 cm de profundidad bajo el bosque (3.64 mg/kg, probabilidad menor de 5 o/o) que en los otros sitios (4.90 a 7.10 mg/kg, con el menor valor en el pasto y el mayor en V. ferruginea, aunque las diferencias no fueron estadísticamente significativas) (Tabla 4 y Fig. 5.) No existieron diferencias significativas en P extraíble entre sitios a 15-30 o 30-60 cm, aunque los valores tendieron a ser mayores en V. ferruginea y menores en pasto y en bosque. El P también disminuyó con la profundidad (Fig. 5).

En cuanto a los elementos menores, no hubo diferencias significativas entre sitios a ninguna profundidad para Cu, Zn o Mn. Sin embargo, a 0-15 cm se observó mayor cantidad de Cu bajo V. ferruginea, D. tucurensis y D. panamensis, que bajo pasto y bajo bosque, con valores intermedios en los otros sitios (Tabla 4). El Zn tendió a ser mayor bajo V. ferruginea, V. hondurensis y bosque, mientras que el Mn tendió a ser menor en T. rosea y en pastos que en los otros sitios. El Zn tendió a aumentar o mantener sus valores con la profundidad, mientras que el Cu y el Mn disminuyeron a mayor profundidad. El Fe fue significativamente mayor en el suelo bajo bosque, para las tres profundidades consideradas, que en los otros sitios (probabilidad menor de 1 o/o) y tendió a disminuír con la profundidad.

Los resultados de las mediciones realizadas en agosto se presentan en Tablas 5 y 6 y Figs. 6 y 7. No se observaron diferencias significativas en Ca, Mg o K, para ninguna de las tres profundidades consideradas (Tabla 5). Sin embargo, se observó una tendencia a mayor contenido de Ca en el horizonte superficial en V. ferruginea, T. rosea y bosque, mayor Mg bajo V. ferruginea, V. hondurensis, T. rosea y bosque, y mayor K bajo V. ferruginea, T. rosea y bosque.

No hubo diferencias significativas en el pH entre los sitios, excepto a 15-30 cm, donde el pH fue menor en el bosque (5.1) que en los otros sitios (5.2-5.3– (probabilidad menor del 10 o/o) A 0-15 cm el pH variaba de 4.9 (bosque y pasto) a 5.2 (T. rosea) (Tabla 8) Se observó al igual que en abril, una tendencia a un aumento del pH a mayor profundidad. La acidez extraíble fue menor en T. rosea y D. panamensis que en los otros sitios, para las tres profundidades (probabilidad menor de 5 o/o).

La capacidad de intercambio catiónico efectiva (CICE),. fue mayor en el bosque, para las tres profundidades, que en los demás sitios (probabilidad menor del 5 o/o). No hubo diferencias significativas en el porcentaje de saturación de bases entre los sitios para 0-15 y 15-30 cm; solamente a 30-60 cm la saturación de bases fue mayor en T. rosea que en los demás sitios (probabilidad menor de 15 o/o) De igual manera, no se observaron diferencias significativas en la saturación de acidez entre los sitios a 0-15 y 15-30, pero se encontraron diferencias significativas a 30-60 cm, con los menores valores bajo T. rosea y D panamensis (probabilidad menor del 15 o/o) (Tabla 5). La saturación de acidez aumentó con la profundidad.

La materia orgánica fue significativamente mayor en el bosque (probabilidad menor de 5 o/o) y en *V. ferruginea* (probabilidad menor de 15 o/o) a 0-15 y a 15-30 cm (Tabla 6 y Fig. 6) Los menores valores correspondieron al pasto. A 30-60 cm, la materia orgánica fue mayor bajo bosque que bajo las especies del ensayo y que bajo el pasto, en ese orden (Tabla 6 y Fig 6). El nitrógeno siguió una tendencia similar al de la materia orgánica, con mayores valores en *V. ferruginea* y bosque (Tabla 6 y Fig. 7) No hubo diferencias significativas en la relación C/N entre los sitios (Tabla 6) No se observaron diferencias significativas en el contenido de P, aunque se observó una tendencia a mayor P bajo *V. ferruginea* y menor contenido bajo bosque.

El Cu fue mayor bajo bosque a 0-15 cm (probabilidad menor del 10 o/o) El Zn fue mayor bajo bosque a las tres profundidades. No hubo diferencias significativas en el contenido de Mn, excepto a 30-60 cm, donde el contenido fue menor en el pasto. Existió una tendencia a mayor contenido de hierro bajo bosque, que era significativa a 15-30 y 30-60 (Tabla 6).

Comparando los valores de abril con los de agosto, se manifestó una menor concentración de Ca, Mg y K (menor suma de bases) en agosto, una mayor acidez extraíble (Fig. 8) , menor pH, y mayor saturación de acidez. En algunos casos también se notaron menores valores de materia orgánica y nitrógeno total, aunque no ocurrió esto en las parcelas que tenían mayores contenidos, como en *V. ferruginea* y bosque. El P, Mn y Fe fueron menores en agosto, mientras que el Zn fue mayor en agosto que en abril, y el Cu fue mayor o menor según los sitios.

Discusión

Características químicas de los suelos en el área experimental.

Al comparar los datos de las características químicas de los suelos de la consociación La Guaria (Sancho y Mata 1987, Tabla 1) con los resultados de la presente investigación, se observa que en el horizonte superficial del bosque se encontró un contenido similar de Ca y Mg (extracciones en acetato de amonio en ambos casos), mayor contenido de materia orgánica, menor contenido de K y de P, un mayor pH, y contenidos similares de elementos menores. Los niveles generales son lo suficientemente parecidos como para considerar que los suelos en el ensayo podrían ser parte de la consociación mencionada, con diferencias debidas a la vegetación que se encontrara en el sitio muestreado por Sancho y Mata (1987).

En concordancia con lo expresado por Sancho y Mata (1987) en referencia a los suelos de la consociación La Guaria, en general se puede observar que el contenido de Ca y Mg en la plantación experimental, en el pasto y en el bosque fue relativamente bajo, tanto en abril como en agosto, con valores menores de los considerados críticos para los cultivos agrícolas, según niveles utilizados por el Ministerio de Agricultura de Costa Rica (Tabla 7 , Berstch 1986). Estos niveles críticos fueron determinados para los mismos extractantes utilizados en el presente estudio, y son utilizados para la mayoría de los cultivos en el país.

El contenido de potasio en el horizonte superficial de este ensayo fue menor o mayor que el nivel crítico, según el sitio considerado, en el muestreo de abril; mientras que los datos de agosto muestran en todos los casos valores menores que los críticos. El menor contenido de bases en agosto en todos los sitios (Fig. 8) se atribuye al mayor lavado durante la época de mayores precipitaciones: el total de lluvia para el mes de agosto de 1988 fue de 457 mm, mientras que en abril fue 43.6 mm (datos de la estación meteorológica de La Selva) Los contenidos de Cu, Mn y Fe fueron superiores al nivel crítico, y existió una aparente deficiencia de Zn; esto para todos los sitios en ambos muestreos. Los valores de pH fueron bajos en los dos muestreos, pero mostraron una tendencia a bajar en el muestreo de agosto, con un aumento en la acidez extraíble en todos los sitios en conjunto (Fig. 8), coincidiendo esto también con la época más lluviosa en la cual existe un mayor lavado de bases.

Los valores de materia orgánica y N en general parecen relativamente altos en este ensayo. Esto podría deberse a la presencia anterior de un bosque maduro en el sitio, y a la dominancia de especies fijadoras de N como *Pentacrethra macroloba*, en el bosque de bajura de la región, que ocupaba el sitio antes de su corta en los años 1950. Excepto por estos dos últimos parámetros, los suelos del área muestreada eran muy poco fértiles. Como la materia orgánica es responsable en gran parte de la capacidad de retención de nutrientes del suelo, las prácticas de manejo que tienden a disminuir el tenor de materia orgánica, tales como quemas repetidas, sobrepastoreo, falta de cobertura vegetal, tenderán a disminuir aún más su fertilidad, hasta hacer muy difícil su recuperación para niveles productivos. La disminución de la materia orgánica con la profundidad que se observó en todos los sitios del ensayo puede ser la causa del aumento relativo del pH en el subsuelo; puesto que la materia orgánica es una fuente de acidez. El aumento de pH con la profundidad no podría atribuirse a un aumento en el contenido de bases, pues todas estas disminuyeron en el subsuelo.

Influencias de la plantación experimental, pasto y bosque sobre la fertilidad.

Siendo el contenido de materia orgánica un factor clave en la recuperación y mantenimiento de la fertilidad, se puede considerar que en menos de tres años la presencia de la plantación experimental en conjunto había aumentado la fertilidad del sitio, pues si se compara el promedio de materia orgánica en el horizonte superior del suelo en el pasto en abril (4.83 o/o) con los valores en la plantación, que variaron entre 5.31 y 6.6 o/o se nota un incremento sustancial en este parámetro, con un valor cercano al del bosque (7.58 o/o) Se observó una tendencia similar en el subsuelo en ambos muestreos; asimismo, en agosto los resultados fueron similares (Fig. 6). El nitrógeno total reveló una situación parecida, con valores de 0.260-0.318 o/o en la plantación, mayores que en el pasto (0.224) y cercanos a los del bosque (0.328) (datos de abril; con resultados similares en agosto; Fig. 7). Un incremento entre 0.5 y casi 2.0 unidades porcentuales en lo que respecta a materia orgánica en el suelo superficial es sustantivo, por su contribución a la retención de nutrientes. El coeficiente de correlación entre el contenido de materia orgánica y la suma de bases, considerando los datos de las tres profundidades muestreadas, fue de 0.40 en abril y de 0.60 en agosto, mostrando la estrecha relación entre ambos parámetros importantes para la fertilidad.

Asimismo, tomados en conjunto, los valores de Ca y Mg en el suelo de la plantación fueron mayores que en el pasto, con los valores cercanos a los que se encontraron en el bosque (Fig. 3); la saturación de bases fue similar o mayor en la plantación que en el bosque, y también mayor que en el pasto (Fig. 4), mientras que se dió la situación inversa con referencia a la saturación de acidez. Con el potasio la situación fue diferente, con valores bajos en general y sin una clara tendencia con respecto a diferencias entre sitios. Una tendencia también diferente se encontró para el P extraíble, cuyos valores fueron en general bastante bajos (menores que el nivel crítico) y aún más en el bosque (Fig. 5) La tendencia con respecto a los elementos menores fue similar a la encontrada con los cationes básicos, con valores en la plantación mayores que en el pasto y menores que en el bosque. Sin embargo serían necesarias mediciones a más largo plazo para confirmar estas tendencias, y para dilucidar los mecanismos involucrados. Además, debe recalcarse que el área de pastos en este ensayo no representa un pasto abandonado típico de la región, pues como se aclaró antes, esta área ha sido mantenida bajo pasto con el fin de tener un sitio de comparación, con todos los tratamientos que se le daban a ésta, incluídos los desmalezados. El área de pastos representa entonces una porción de terreno sobre los mismos suelos, donde se dan condiciones idénticas excepto la presencia de especies arbóreas, y debe tomarse como tal en la interpretación de estos resultados. Asimismo el bosque representa un terreno sobre los mismos suelos, con árboles que han estado en el sitio por un período más prolongado, de aproximadamente 20 años, y podría considerarse representativo de otros bosques secundarios de la región.

Comparando las seis especies dentro de la plantación, en las extracciones en acetato de amonio se notaron tendencias más claras que en las realizadas con KC1; si bien el KC1 sería mas apropiado por realizarse la extracción en condiciones de pH más parecidas a las de campo, por otro lado con valores tan bajos se oscurecen algunas diferencias potenciales, por lo cual es posible que otro tipo de solución extractora sea una alternativa más adecuada.

Aún en las extracciones con KC1, en el horizonte superficial se revelaron tendencias a una mayor concentración de Ca y Mg, con una mayor suma de bases bajo *V. ferruginea* (Fig. 3) . La acumulación se debe posiblemente a la movilización de cationes de capas profundas al árbol y su deposición en la capa superficial a partir de la hojarasca. También bajo esta especie se observó mayor contenido de materia orgánica y nitrógeno total (Figs. 6 y 7), lo cual sugiere la importancia de la materia orgánica en la retención de nutrientes en estos suelos. Se observa una gran acumulación de hojarasca de hojas y ramas bajo esta especie, mucho mayor que en las otras especies del ensayo. Como *V. ferruginea* es una de las especies de mejor crecimiento del ensayo, su influencia positiva sobre la fertilidad del suelo aumenta su importancia como especie para la reforestación y para la recuperación de áreas degradadas. En la segunda fase del presente proyecto, se está muestreando la caída de hojarasca y su contenido de nutrientes bajo las seis especies de árboles. También se muestrea el piso de hojarasca, para examinar la distribución de sus diferentes partes (material reciente, material en estado de descomposición) y su contenido de nutrientes. Asimismo, se han muestreado las raíces en los mismos espesores de suelo que han sido considerados para los análisis químicos. Estas investigaciones contribuirán a explicar los mecanismos involucrados en estas diferencias y tendencias.

Otras diferencias entre especies incluyen el mayor pH y la menor acidez intercambiable bajo *T. rosea* y *D. panamensis* y la tendencia inversa (menor pH y mayor acidez) bajo *V. hondurensis* (Figs. 1 y 2). Entre las especies en estudio, tanto *D. panamensis* como *T. rosea* son las de menor crecimiento hasta la fecha, en contraste con *V. hondurensis*, que es una de las de mayor crecimiento. Posiblemente debido al menor crecimiento de las dos primeras, exite una menor absorción de bases, en comparación con *V. hondurensis*, que por su rápido crecimiento tendría una mayor demanda. No sería muy probable que estas diferencias se debieran al reciclaje de bases en *T. rosea* y *D. panamensis*, pues en estas parcelas el dosel no había cerrado completamente en el momento de los muestreos, y es poco probable que los mecanismos de reciclaje se hubieran establecido. Al igual que en el caso anterior, las mediciones que se están realizando en la segunda fase del proyecto contribuirán a explicar estos mecanismos. Posiblemente estas pequeñas diferencias en el pH y acidez entre especies, al igual que otros parámetros, cambien a más largo plazo.

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Referencias

Allison, L. E. 1975. Organic carbon. Pp. 1367-1378 In Black, C.A. (ed.). Methods of soil analysis. Part 2. American Society of Agronomy, Inc. Madison, Wisconsin.

Alpízar, L., H. W. Fassbender, J. Heuveldop, H. Folster and G. Enríquez. 1986. Modelling agroforestry systems of cacao (Theobroma cacao) with laurel (*Cordia alliodora*) and poró (*Erythrina poeppigiana*) in Costa Rica. I. Inventory of organic matter and nutrients. Agroforestry Systems 4:175-189.

de Barros, N.F. y R. M. Brandi. 1975. Influencia de tres especies florestais sobre a fertilidade de solo de pastagem en Vicosa, M. G. Brasil Florestal 6:24. Rio de Janeiro.

Bawa, K. S., S. H. Bullock, D. R. Perry, R. E. Coville and M. H. Grayum. 1985. Reproductive biology of tropical lowland rainforest trees. II Pollination systems. American J. Bot. 72: 346-356.

Berner, P. O., and B. Finegan. 1988. Natural management of montane tropical forest and anthropogenically disturbed lowland tropical forest: from ecological research towards a silvicultural system. 25 Aniversario de la Organización para Estudios Tropicales. Exhibición de afiches sobre estudios tropicales en Costa Rica. Museo Nacional - Junio 5-12, 1988.

Bethel, J. S. 1976. Forest in Central America and Panamá: wich kind, how large and where? Revista Biología Tropical 24 (Supl): 143-175.

Bertsch, F. H. 1986. Manual para interpretar la fertilidad de los suelos en Costa Rica. Universidad de Costa Rica. Escuela de Fitotécnia. 76 pp.

Bolfoni, D., M. L. Jimenez, J. F. Moreira and E. Fonseca. Biomasa e nutrientes de duas especies florestais em Viscosa. Universidad Federal de Vicosa. Brazil. Manuscrito sin publicar.

Bremmer, J. M. and. C. S. Mulvaney. 1982. Nitrogen-total. Pp 595-624 - In A. L. page, R. H. Miller and R. R. Keeney (eds.) Methods of Soil Analysis. Part. 2. 2nd. ed. American Society of Agronomy. Madison Wisconsin.

Budowski, G. 1961. Studies in forest succesión in Costa Rica and Panáma. Ph. D. dissertation. Yale University, New Haven

Cadima Zeballos, A., and P. de T. Alvin. 1967. Influencia del árbol de sombra *Erythrina glauca* sobre algunos factores edafológicos relacionados con la producción del cacaotero. Turrialba 17: 330-336.

Carlson, P. J. and. J. O. Dawson. 1985. Soil nitrogen changes, early groth, and response to soil internal drainage of a plantation of *Alnus jorullensis* in the Colombian highlands. Turrialba 35(2): 141-150.

Chazdon. R. L. and. N. Fetcher. 1984. Photosynthetic ligh environments in lowland tropical rainforest in Costa Rica. J. Ecology 72: 553-564.

Chijike, E. O. 1980. Impacts on soils of fast-growing species in lowlands humid tropics. FAO.For.Pap.., No. 21.

Cozzo, D 1976. Tecnología de la forestación en Argentina y América Latina. Ed. Hemisferic Sur. Buenos Aires. 610 pp.

Denslow, J. S. 1980. Gap partitioning among tropical rain forest trees. Biotropica (supl.): 45-55.

Diaz-Romeu, R. y A. Hunter. 1978. Método para el muestreo de suelos, análisis químico de suelos y tejido vegetal e investigación en invernaderos. Turrialba, Costa Rica, CATIE, pp. 9-11 and 15-27

Espinoza Camacho, M. y R. Butterfield. 1989. Adaptabilidad de 13 especies nativas maderables bajo condiciones de plantación en las tierras bajas húmedas del Atlántico, Costa Rica. Reunión de IUFRO, IV Grupo, S1-07-09, Silvicultura de Plantaciones en América Latina. Guatemala, 3-7 de abril 1989

Fassbender, H. W. 1984. Bases edafológicas de los sistemas de producción agroforestales. Centro Agronómico Tropical de Investigación y Enseñanza (CATIE). Turrialba. Costa Rica. Serie Materiales de Enseñanza No. 21 191 pp.

Fernández, R. A. 1987. Influencia del sistema de desmonte-reforestación con Pinus spp. sobre algunas características químicas de los suelos. Ciencia del Suelo 5(2) : 123-129.

Fetcher, N., B. R. Strain and S. F. Oberbauer. 1983. Effects of light regime on the growth, leaf morphology and water relations of seedlings of two species of tropical trees. Oecología 58: 314-319.

Goodland, R. 1971. Oligotrofismo e aluminio no cerrado. _In._ Ferri, M. G. (ed.) III Simposio sobre o Cerrado. Univ. Sao Paulo, e Blucia, Sao Paulo, 239 pp.

Halliday, J. 1984. Register of nodulation reports for leguminous trees and other arboreal genera with nitrogen fixing members. Nitrogen Fixing Tree Research Reports 2: 38-45.

Hartshorn, G. S. 1972. The ecological life history and population dynamics of _Pentaclethra macroloba_, a tropical wet forest dominant and _Stryphnodendron excelsum_, an occasional associate. Ph. D. dissertation. University of Washington. Seattle.

Hartshorn, G. S. 1978. Tree falls and tropical dynamics. Pp. 617-638. In. P. B. Tomlinson and M. H. Zimmermann eds). Tropical trees as living systems. Cambridge University Press. Cambridge

Hartshorn, G. 1983. Plants Pp. 118-157 In. D. H. Janzen (ed.) Costa Rican Natural History. The University of Chicago Press. Chicago and London.

Holdridge, L. R. W. C. Grenke, W. H. Hatheway, T. Liang and J. A. Tosi. 1971. Forest environments in tropical life zones: a pilot study. Pergamon Press, New York.

Holdridge, L. R., y L. J. Poveda. 1975. Arboles de Costa Rica. Centro Científico Tropical. San José, Costa Rica. 546 pp.

Huston, M. A. 1980. Soil nutrients and tree species richness in Costa Rican forests. J. Biogeography 7: 147-157.

Huston, M. A. 1982. The effect of soil nutrients anf light on the growth and interactions during tropical forest succession: experiments in Costa Rica. Ph. D. dissertation. University of Michigan. Ann Arbor.

Kowal, J. M. L. and P. B. H. Tinker. 1989 . Soil changes under a plantation established from high secondary forest. J. W. Afr. Inst. Oil Palm Res. 2:376-389.

Lieberman, M., D. Lieberman, G. S. Hartshorn and R. Peralta. 1985. Small-scale altitudinal variation in lowland tropical forest vegetation. J. Ecology 73: 505-516.

Lundgren, B. 1978. Soil conditions and nutrient cycling under natural and plantation forest in Tanzanian highlands (Reports in forest ecology and forest soils No 31). Uppsala: Swedish University of Agricultural Sciencies.

Montagnini, F. 1988. Agroforestry in the humid tropics: the role of aplied ecology. In the application of ecology to enhancing economic development in the humid tropics. Proceedings of a workshop. Columbus, Ohio, August 1987. Sponsored by the World Bank. In press.

Nair, P. K. R. 1984. Soil productivity aspects of agroforestry Intamatiotal Council for Research in Agroforestry. Nairobi. 85 pp.

Ojeniyi, S. O. and. O. O. Agbede. 1980. Effect of interplantig *Gmelina arborea* with food-crops on soil condition. Turrialba 30 (3): 268-271.

Ollagnier, M. A. Laurezeral, J. Olivin and R. Ochs. 1978. Evolution des sols sous palmerail apres defrichement de la foret. Oleagineux 3: 527-547.

Organización para Estudios Tropicales. Centro Agronómico Tropical de Investigación y Enseñanza. (OTS/CATIE) 1986. Sistemas Agroforestales. Principios y Aplicaciones en los Trópicos OTS. San Jose. Costa Rica. 818 pp.

Roskowski, J. P. 1982. Nitrogen fixation in a Mexican coffee plantation. Plant & Soil 67: 283-291.

de las Salas, G. y H. Fassbender. 1984. Factores edáficos en los sistemas de producción agroforestales. Pp. 30-36 In J. Heuveldop y J. Lagemann (eds.). Agroforestería. Actas del seminario realizado en el CATIE. 23 de febrero - 3 de marzo 1981 - Serie Técnica. Boletín Técnico No. 14. Centro Agronómico Tropical de Investigación y Enseñanza. Departamento de Recursos Naturales Renovables. Turrialba. Costa Rica.

Sánchez. P. A. , C. A. Palm, C. B. Dabey, L. T. Szott and C. E. Russel. 1985. Tree crops as soil improvers in the humid tropics? Pp. 327-350 - In M. G. R. Cannel and J. E. Jackson 9tds). Atributes of trees as crop plants. Institute of Terrestrial Ecology. Natural Environmental Research Council. Abbots Ripton, Huntingdon, England.

Sancho, F., and R. Mata. 1987. Estudio detallado de suelos. Estación Biológica La Selva. Organización para Estudios Tropicales. Ser. José Costa Rica. 162 pp.

Santana, M. B. M. and P. Cabala Rosand. 1982 - Dynamics of nitrogen in a shaded caco plantation. Plant & Soil 67: 271-281.

Silva, L. F. 1983. Infuencia de cultivos e sistemas de manejo nas modificacoes edáficas dos oxisols de tabuleiro (Harplorthox) do sul de Bahia. Belem (Brazil): CEPLAC, Departamento Especial de Amazonia.

Tabla 1. Composición química de un perfil típico de la Consociación La Guaria (tomado de Sancho y Mata 1987).

HORIZONTE	A	AB	Bw1	Bw2	IIA
Profundidad (cm)	0-15	15-38	38-79	79-106	106+
H_2O	4.6	5.0	5.0	4.9	5.0
pH KCl	4.2	4.7	4.4	4.7	4.8
NaF	9.4	9.7	9.8	9.6	9.7
MAT.ORG. (%)	2.80	2.14	T	T	0.34
Cmol/l					
Ca	0.80	0.73	0.73	0.75	0.75
Mg	0.46	0.33	0.29	0.25	0.25
K	0.77	0,66	0.87	0.41	0.41
Acidez	1.4	0.9	0.8	0.5	0.5
CIC	13.5	15.9	14.0	14.4	13.8
SAT. BASES (%)	15.0	10.8	13.5	9.8	10.2
SAT.ACIDEZ (%)	10.3	5.6	5.7	3.5	3.6
mg/kg					
P	12.6	3.2	13.1	12.2	10.7
Cu	20.0	9.5	7.4	10.5	9.2
Zn	1.7	0.6	1.9	1.7	3.9
Mn	68.0	28.9	27.5	29.0	43.0
Fe	663	98	186	166	163
ARENA (%)	51	53	52	50	60
LIMO (%)	8	11	2	11	17
ARCILLA (%)	41	36	46	39	23
NOMBRE TEXTURAL	Aa	Aa	Aa	Aa	FAa

Tabla 2. Contenido de Ca, Mg y K, pH, acidez, suma de bases, capacidad de intercambio catiónico efectivo, saturación de acidez y de bases, en suelos bajo las seis especies del ensayo, pasto y bosque; abril 1988 (Ca y Mg extraídos con KCl, K extraído con acetato de NH_4)[1].

SITIO	PROFUNDIDAD (cm)	Ca (cmol/kg)	Mg (cmol/kg)	K (cmol/kg)	pH	Acidez (cmol/kg)	Suma de bases (cmol/kg)	CICE (cmol/kg)	% SATURACION BASES	% SATURACION ACIDEZ
Str. exc.	0-15	0.45a	0.63ab	0.27a	5.4ab	1.66ab	1.34a	3.00a	45.5a	54.5bc
	15-30	0.33a	0.35a	0.19a	5.4a	1.54a	0.87a	2.41a	37.2a	62.7b
	30-60	0.26a	0.22a	0.17a	5.6a	1.88a	0.65a	2.53a	34.2a	65.7a
Dal. tuc.	0-15	0.44a	0.41ab	0.22a	5.4ab	1.46ab	1.07a	2.53a	41.6a	58.4bc
	15-30	0.32a	0.24a	0.15a	5.4a	1.54a	0.71a	2.25a	31.6a	68.4bc
	30-60	0.24a	0.15a	0.11a	5.6a	1.42a	0.49a	1.91a	26.8a	73.2a
Voch. ferr.	0-15	0.73a	0.61ab	0.22a	5.4ab	1.20ab	1.56a	2.76a	52.8a	47.2bc
	15-30	0.66a	0.39a	0.21a	5.6a	1.12a	1.26a	2.38a	47.3a	52.7bc
	30-60	0.42a	0.28a	0.17a	5.6a	1.06a	0.86a	1.92a	42.5a	57.5a
Voch. hond.	0-15	0.25a	0.37ab	0.11a	5.3b	1.86a	0.73a	2.59a	28.2bc	71.8a
	15-30	0.19a	0.18a	0.09a	5.4a	1.58a	0.46a	2.04a	22.5bc	77.5a
	30-60	0.17a	0.32a	0.08a	5.5a	1.32a	0.57a	1.89a	27.5a	72.5a
Tab. rosea	0-15	0.42a	0.50ab	0.15a	5.5a	1.28b	1.06a	2.35a	44.1a	55.9b
	15-30	0.28a	0.26a	0.12a	5.6a	1.12a	0.66a	1.78a	35.5a	64.5b
	30-60	0.28a	0.24a	0.13a	5.7a	0.98a	0.65a	1.63a	38.8a	61.2a
Dip. pan.	0-15	0.52a	0.74ab	0.38a	5.5a	1.18b	1.64a	2.82a	53.4a	46.5bc
	15-30	0.36a	0.45a	0.29a	5.5a	1.06a	1.09a	2.19a	46.2a	53.8bc
	30-60	0.28a	0.28a	0.19a	5.6a	1.08a	0.75a	1.83a	38.9a	60.1a
PASTO	0-15	0.32a	0.27b	0.19a	5.3b	1.40ab	0.77a	2.17a	34.8ab	65.2ab
	15-30	0.31a	0.28a	0.17a	5.4a	1.32a	0.76a	2.08a	35.7ab	64.2ab
	30-60	0.23a	0.15a	0.10a	5.5a	1.26a	0.48a	1.74a	27.1a	72.9a
BOSQ. SECUN.	0-15	0.68a	0.55b	0.17a	5.3b	1.54ab	1.39a	2.93a	46.9a	53.1bc
	15-30	0.60a	0.42a	0.13a	5.4a	1.60a	1.15a	2.75a	42.2a	57.7bc
	30-60	0.42a	0.28a	0.18a	5.5a	1.34a	0.87a	2.21a	39.5a	60.5a

[1] En ésta y en las tablas siguientes, los valores de cada parámetro, para una misma profundidad y para los diferentes sitios, presentan diferencias estadísticamente significativas cuando están seguidos de letras diferentes.

Tabla 3. Ca, Mg y capacidad de intercambio catiónico (CIC) determinados por extracción en acetato de amonio, en abril de 1988.

SITIO	PROFUNDIDAD (cm)	Ca	Mg	CIC
		(cmol / kg)		
Stryphnodendron excelsum	0-15	0.67a	0.80a	21.5a
	15-30	0.67a	0.51b	19.9a
	30-60	0.54a	0.28b	18.2a
Dalbergia tucurensis	0-15	0.68a	0.48ab	21.4a
	15-30	0.68a	0.39b	19.3a
	30-60	0.63a	0.26a	18.2a
Vochysia ferruginea	0-15	1.02a	0.69a	22.3a
	15-30	0.98a	0.47b	19.5a
	30-60	0.74a	0.39b	18.5a
Vochysia hondurensis	0-15	0.65a	0.56a	22.1a
	15-30	0.54a	0.32b	19.1a
	30-60	0.57a	0.26b	18.2a
Tabebuia rosea	0-15	0.69a	0.58a	25.9a
	15-30	0.57a	0.37b	19.0a
	30-60	0.52a	0.40b	17.9a
Dipteryx panamensis	0-15	0.93a	0.84a	21.5a
	15-30	0.76a	0.59b	19.8a
	30-60	0.66a	0.41b	18.7a
PASTOS	0-15	0.47a	0.32b	20.6a
	15-30	0.50a	0.30b	18.7a
	30-60	0.54a	0.22b	24.6a
BOSQUE SECUNDARIO	0-15	0.96a	0.72a	23.3a
	15-30	0.89a	0.58a	21.5a
	30-60	0.62a	0.36a	19.0a

Tabla 4. Materia orgánica, N total, C/N, P y elementos menores en los suelos muestreados en abril 1988.

SITIO	PROFUNDIDAD	M.O.	N	C/N	P	Cu	Zn	Mn	Fe
	(cm)	(%)	(%)			(mg/kg)			
Str. exc.	0-15	6.04ab	0.288b	12.2a	5.58a	18.6a	1.90a	85.8a	344b
	15-30	4.52b	0.234b	11.2a	5.70a	16.6a	1.64a	97.2a	258b
	30-60	2.54a	0.142a	10.4a	5.54a	9.2a	2.08a	67.8a	126b
Bal. tuc.	0-15	5.47ab	0.292ab	10.9a	5.48a	20.0a	1.92a	104a	315b
	15-30	4.06b	0.214b	11.1a	4.60a	38.0a	1.50a	88.4a	218b
	30-60	2.70a	0.132a	11.9a	4.24a	15.4a	1.72a	77.6a	182b
Voch. ferr.	0-15	6.60ab	0.318b	12.1a	7.18a	22.2a	2.76a	105a	331b
	15-30	4.60b	0.218b	11.9a	5.30a	20.4a	3.14a	96.4a	219b
	30-60	3.34a	0.156a	12.6a	4.66a	20.6a	2.42a	91.0a	152b
Voch. hond.	0-15	5.46ab	0.288ab	11.0a	5.16a	18.2a	2.36a	115a	323b
	15-30	3.87b	0.204b	11.0a	4.60a	17.6 a	1.90a	93.2a	218b
	30-60	2.70a	0.142a	11.0a	4.46a	13.2a	1.78a	79.4a	177b
Tab. rosea	0-15	5.63ab	0.288ab	11.4a	5.10a	19.8a	1.60a	89.0a	277b
	15-30	3.92b	0.194b	11.6a	4.64a	18.2a	1.44a	81.2a	165b
	30-60	3.00a	0.164a	10.7a	4.66a	18.0a	1.56a	78.2a	138b
Dip. pan.	0-15	5.31ab	0.260ab	11.8a	5.34a	20.0a	1.80a	114a	333b
	15-30	4.42b	0.200b	12.4a	5.14a	18.0a	1.60a	96.0a	200b
	30-60	2.96a	0.146a	11.6a	5.58a	20.8a	2.18a	89.4a	158b
PASTOS	0-15	4.83bc	0.224b	12.8a	4.90a	15.0a	1.40a	96.8a	297b
	15-30	4.03b	0.176b	14.0a	4.44a	14.2a	1.46a	110a	226b
	30-60	2.73a	0.138b	11.8a	4.24a	15.0a	2.04a	82.4a	138b
BOSQ. SECUN.	0-15	7.58a	0.328a	13.6a	3.64b	16.2a	2.26a	113a	664a
	15-30	6.40a	0.278a	13.4a	3.34b	15.2a	2.24a	101a	461a
	30-60	3.29a	0.170a	11.2a	3.60a	11.2a	2.32a	91.8a	300a

Tabla 5. Contenido de Ca, Mg y K, pH, acidez, suma de bases, capacidad de intercambio catiónico efectiva (CICE), y saturación de bases y acidez, en suelos muestreados en agosto 1988.

SITIO	PROFUNDIDAD (cm)	Ca	Mg	K	pH	Acidez	Suma de bases	CICE	SATURACION (%) BASES	ACIDEZ
		(cmol/kg)				(cmol/kg)				
Str. exc.	0-15	0.28a	0.38a	0.11a	5.0a	1.70a	0.77a	2.48b	30.5a	69.5a
	15-30	0.20a	0.22a	0.10a	5.2a	1.64a	0.51a	2.16b	23.5a	76.5a
	30-60	0.20a	0.11a	0.07a	5.4a	1.46a	0.37a	1.84b	20.5b	79.5a
Bal. tuc.	0-15	0.27a	0.29a	0.14a	5.0a	1.70a	0.71a	2.40b	29.1a	70.9a
	15-30	0.21a	0.19a	0.13a	5.1a	1.58a	0.52a	2.08b	25.1a	74.9a
	30-60	0.17a	0.11a	0.09a	5.3a	1.52a	0.37a	1.90b	19.6ab	80.4a
Vach. ferr.	0-15	0.55a	0.43a	0.16a	5.0a	1.72a	1.13a	2.86b	35.2a	64.8a
	15-30	0.22a	0.17a	0.11a	5.3a	1.52a	0.50a	2.02b	24.6a	75.4a
	30-60	0.19a	0.11a	0.10a	5.4a	1.38a	0.40a	1.80b	22.2b	77.8a
Vach. hond.	0-15	0.27a	0.43a	0.12a	5.1a	1.70a	0.82a	2.52b	31.5a	68.5a
	15-30	0.14a	0.13a	0.08a	5.2a	1.70a	0.34a	2.06b	17.4a	82.6a
	30-60	0.13a	0.10a	0.07a	5.3a	1.56a	0.30a	1.84b	16.1b	83.9a
Tab. rosea	0-15	0.39a	0.50a	0.18a	5.2a	1.46b	1.08a	2.54b	41.4a	58.6a
	15-30	0.22a	0.22a	0.12a	5.3a	1.46b	0.55a	2.02b	27.1a	72.9a
	30-60	0.18a	0.14a	0.09a	5.5a	1.24b	0.41a	1.66b	25.8a	74.2b
Dip. pan.	0-15	0.21a	0.25a	0.15a	5.1a	1.64b	0.61a	2.24b	27.6a	72.4a
	15-30	0.21a	0.22a	0.12a	5.2a	1.56b	0.56a	2.12b	25.2a	74.8a
	30-60	0.17a	0.15a	0.10a	5.4a	1.54b	0.41a	1.94b	21.5b	78.5b
PASTO	0-15	0.22a	0.28a	0.15a	4.9a	2.06a	0.65a	2.70b	23.5a	76.5a
	15-30	0.17a	0.15a	0.11a	5.2a	2.10a	0.42a	2.54b	16.2a	83.8a
	30-60	0.17a	0.14a	0.09a	5.3a	1.88a	0.40a	2.28b	17.4b	82.6b
BOSQ. SECUN.	0-15	0.60a	0.51a	0.19a	4.9a	2.34a	1.30a	3.62a	31.0a	69.0a
	15-30	0.28a	0.25a	0.11a	5.1a	2.34a	0.64a	2.96a	20.9a	79.1a
	30-60	0.20a	0.14a	0.08a	5.2a	2.60a	0.42a	3.02a	13.6b	86.4a

Tabla 6. Materia orgánica, N total, C/N, P y elementos menores, muestras recolectadas en agosto 1988.

SITIO	PROFUNDIDAD (cm)	MO	N	C/N	P	Cu	Zn	Mn	Fe
		(%)*			(mg/kg)				
Str. exc.	0-15	5.38ab	0.286b	10.9a	4.10a	17.4b	2.22b	57.4a	235a
	15-30	3.86ab	0.222b	10.2a	4.16a	17.6a	1.74b	42.2a	199b
	30-60	2.20ab	0.130b	10.0a	3.98a	18.1a	1.52b	32.6a	132b
Bal. tuc.	0-15	5.44ab	0.266b	11.9a	4.96a	18.6b	2.64b	54.8a	241a
	15-30	3.72ab	0.210b	10.2a	3.76a	21.5a	1.92b	52.2a	238b
	30-60	2.14ab	0.120b	9.0a	3.14a	21.7a	2.14b	43.2a	145b
Vach. terr.	0-15	6.42a	0.326a	11.4a	5.18a	23.4b	3.24b	61.4a	336a
	15-30	4.08a	0.216a	10.9a	4.42a	22.6a	2.22b	55.2a	245b
	30-60	2.22ab	0.122b	10.6a	3.24a	20.7a	1.96b	63.2a	166b
Vach. hand.	0-15	5.34ab	0.28ab	11.0a	4.72a	22.9b	2.78b	78.0a	294a
	15-30	3.12ab	0.186ab	9.8a	4.02a	26.6a	2.30b	52.6a	224b
	30-60	1.74ab	0.112b	9.0a	5.44a	30.8a	2.74b	39.6a	146b
Tab. rosea	0-15	5.34ab	0.280a	11.0a	4.74a	20.8b	2.48b	78.0a	272a
	15-30	3.26ab	0.176a	11.2a	3.36a	19.2a	1.74b	64.2a	180b
	30-60	1.80ab	0.112b	9.3a	2.26a	19.8a	2.78b	41.4a	101b
Dip. pan.	0-15	4.82ab	0.260b	10.7a	4.00a	22.6b	2.34b	55.4a	267a
	15-30	3.20ab	0.184b	10.1a	3.50a	21.4a	2.04b	53.6a	184b
	30-60	1.82ab	0.112b	9.3a	3.20a	24.2a	2.42b	42.0a	109b
PASTO	0-15	4.20b	0.258b	9.4b	4.56a	19.2b	2.56b	48.8a	273a
	15-30	2.90b	0.186b	8.9a	3.60a	23.8a	2.54b	35.0a	215b
	30-60	1.70b	0.128b	7.7b	2.84a	27.5a	3.34b	27.8b	86.8b
BOSQ. SEC.	0-15	6.30a	0.380a	9.6b	4.04a	25.4a	4.32a	61.6a	309a
	15-30	4.32a	0.282a	9.4a	2.94a	26.4a	4.28a	57.8a	356a
	30-60	2.90a	0.164a	10.6b	3.54a	27.5a	5.10a	40.4a	220a

Tabla 7. Niveles de parámetros del suelo utilizados para interpretar análisis de fertilidad, basados en procedimientos utilizados por el Ministerio de Agricultura de Costa Rica (Bertsch 1986).

Parámetro	Nivel		
	Bajo	Optimo	Alto
pH	5.0	5.5-6.5	7.0
cmol/l:			
Al		0.3	1.5
Ca	4.0	4-20	20
Mg	1.0	1-10	10
K	0.2	0.2-1.5	1.5
mg/l:			
P	10	10-40	40
Mn	5.0	5-50	50
Zn	3.0	3-15	15
Cu	1.0	1-20	20
Fe	10	10-50	50

Fig 1.

Efecto del tipo de cobertura sobre la reacción del suelo.

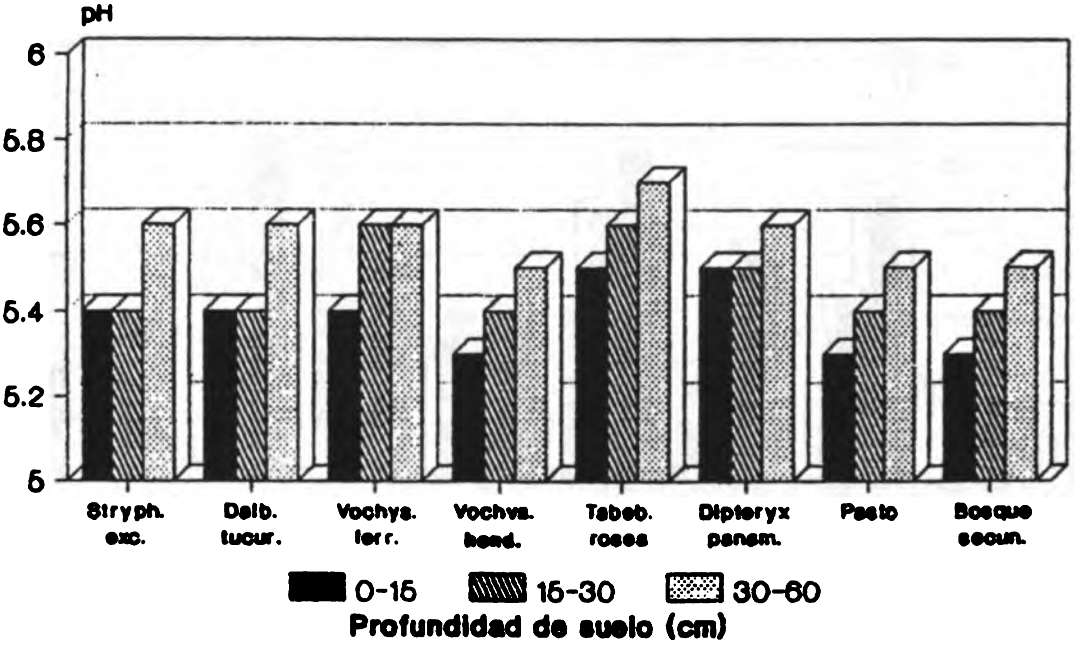


Fig 2.

Efecto del tipo de cobertura sobre la acidez extraíble.

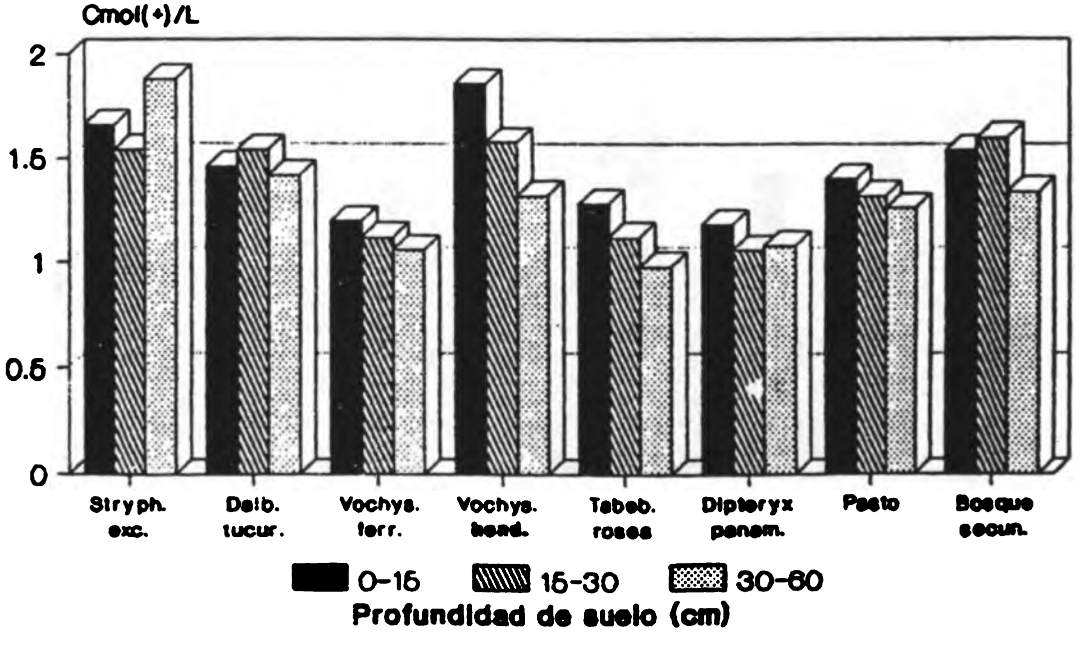


Fig 3.

Efecto del tipo de cobertura sobre la suma de bases.

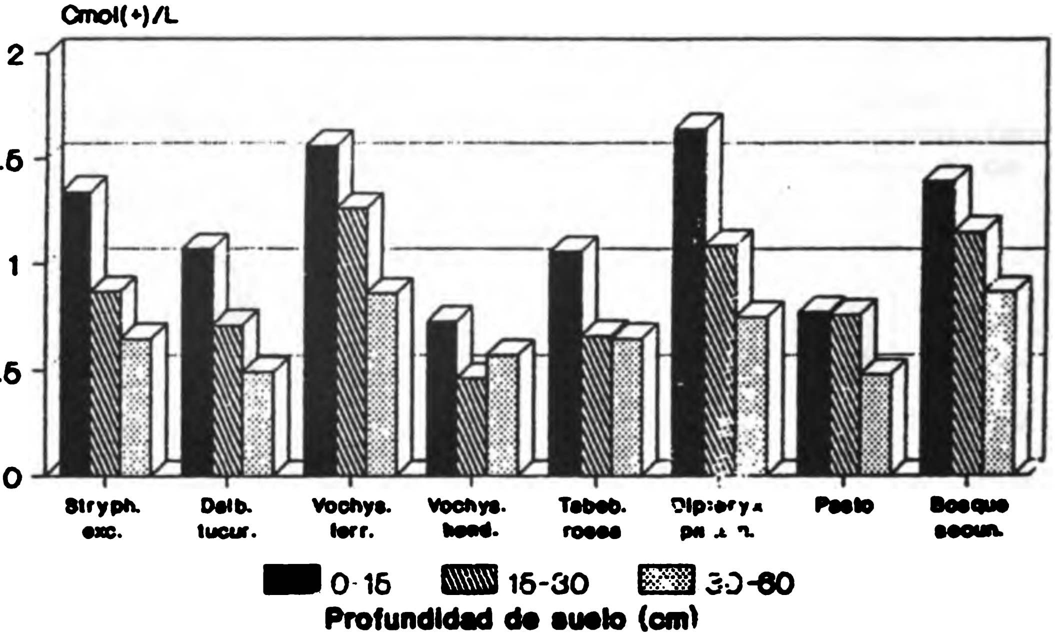


Fig 4.

Efecto del tipo de cobertura sobre la saturación de bases.

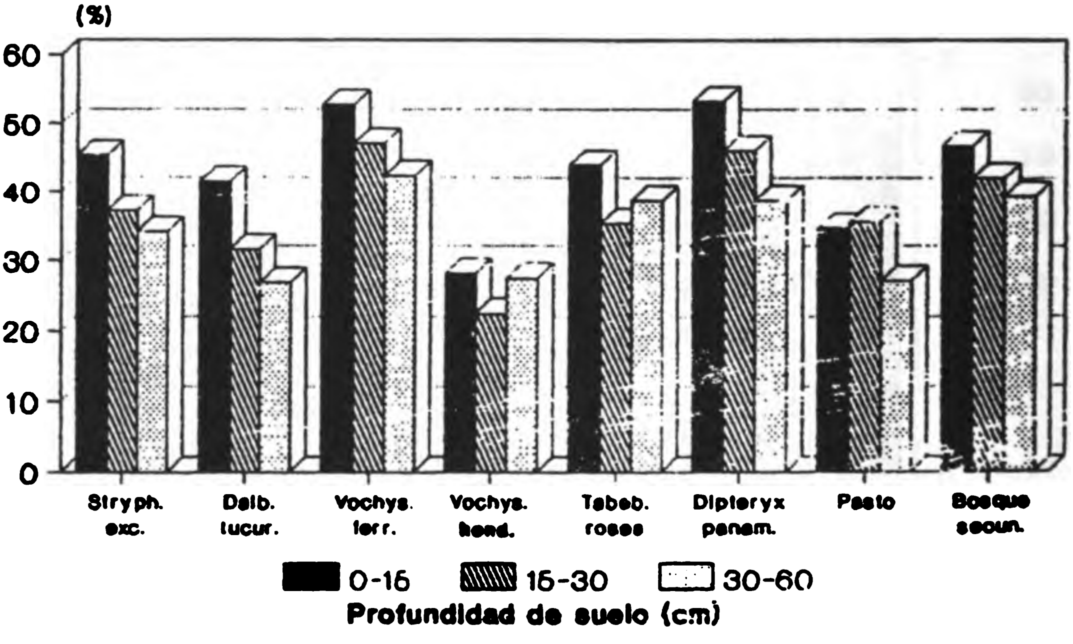


Fig 5.

Efecto del tipo de cobertura sobre el contenido de fósforo en el suelo.

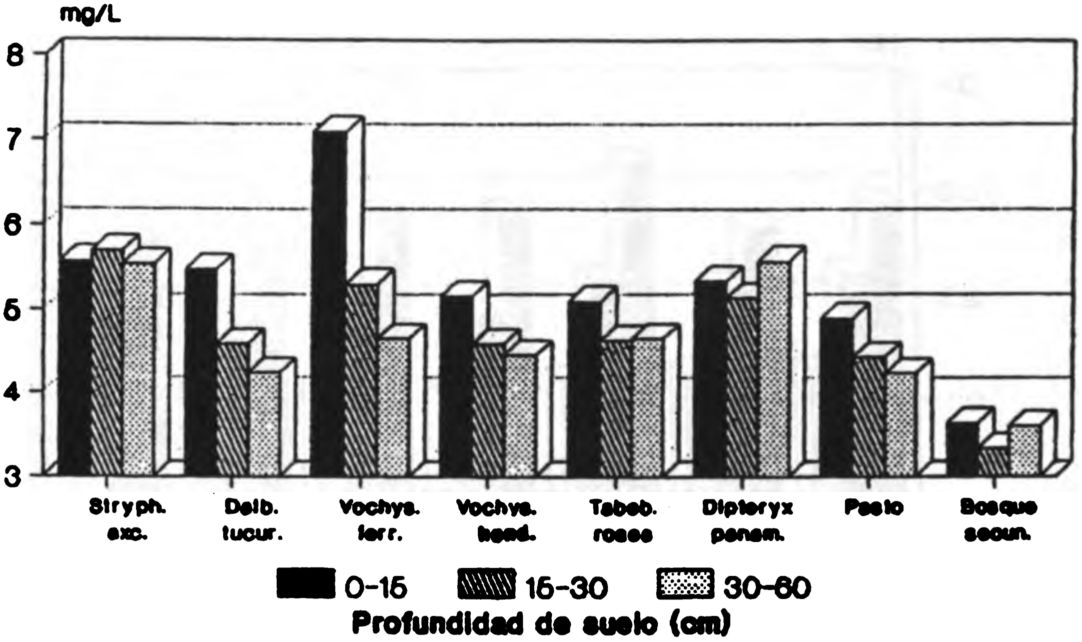


Fig 6.

Efecto del tipo de cobertura sobre el contenido de materia orgánica.

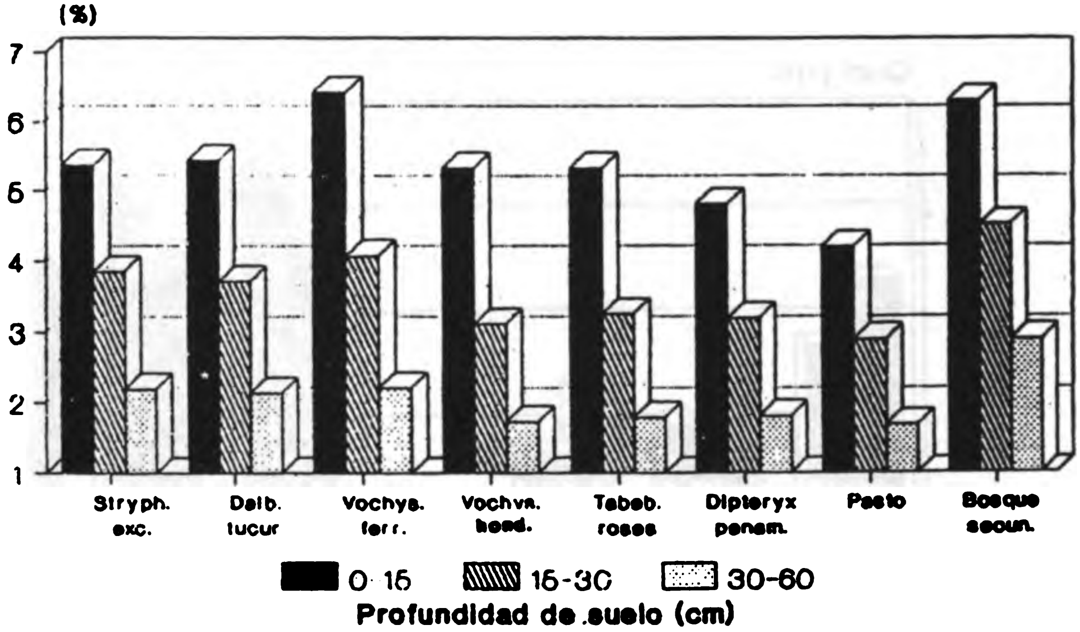


Fig 7.

Efecto del tipo de cobertura sobre el contenido de nitrogeno.

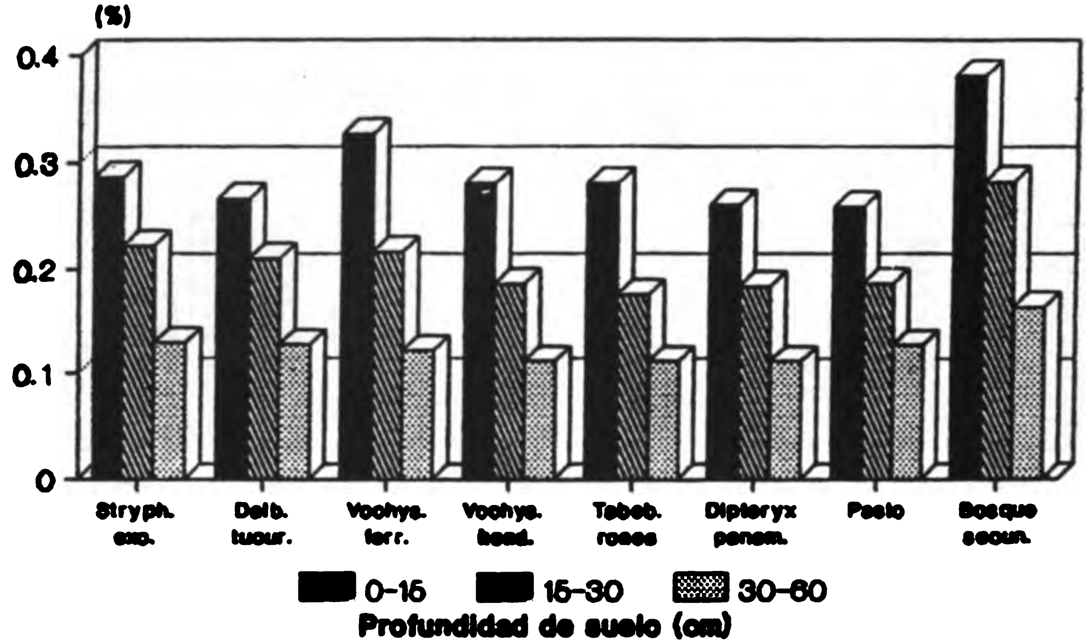
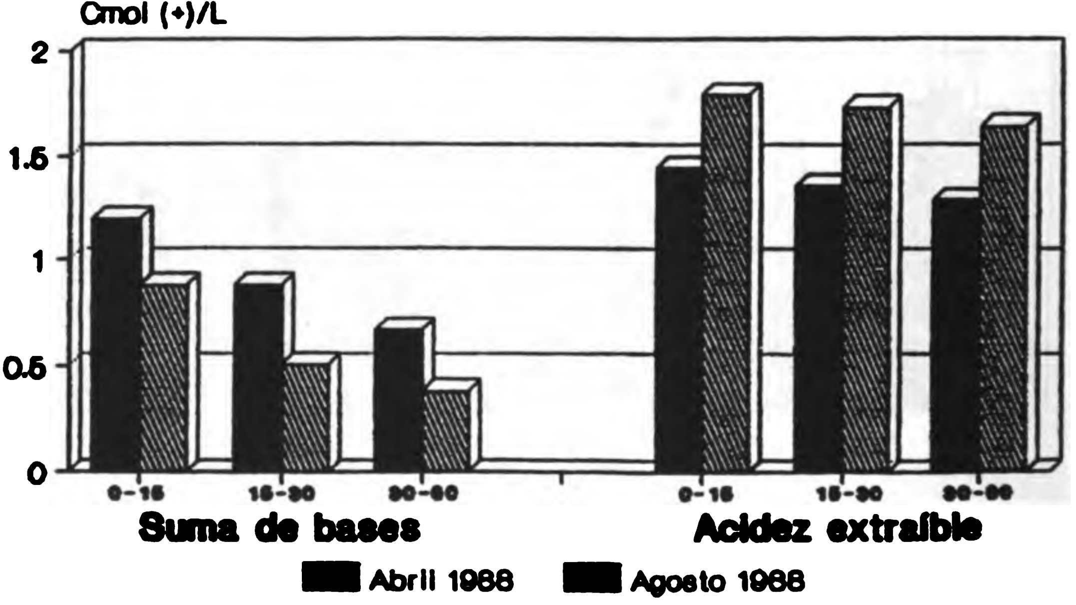


Fig 8.

Variación en la suma de bases y acidez extraíble en dos muestreos.



Florencia Montagnini

Impacts of Native Trees on Tropical Soils: A Study in the Atlantic Lowlands of Costa Rica

The influence of trees on soil properties should be a determining factor in the choice of species for tree-crop combinations or for tree plantations in the humid tropics. However, information of this kind is scarce, particularly for native species. Soil fertility parameters were compared under six tree species in a 2.5-year-old experimental plantation, under grass, and in a 20-year-old secondary forest. The site is located at the La Selva Biological Station of the Organization for Tropical Studies, in the Atlantic humid lowlands of Costa Rica, Central America. Soil extractable Ca, Mg, K, P, Fe, Mn, Cu and Zn, the pH, exchangeable acidity, organic matter and total N were measured under *Stryphnodendron excelsum, Dalbergia tucurensis, Dipteryx panamensis, Vochysia hondurensis, Vochysia ferruginea* and *Tabebuia rosea*. All species are native and of economic value for the timber industry. Higher soil N and levels of organic matter were found in the tree plantation than under grass, with values close to those in the secondary forest. Within the tree plantation, the highest values for soil organic matter, total N, Ca, and P were found under *V. ferruginea*. There was an apparent trend of higher soil nitrate content under *S. excelsum* and *D. tucurensis*, both leguminous nitrogen-fixing species. The results will be used to make recommendations on species for plantations or for agrogorestry, emphasizing the potential positive effects on soil properties for recovery of degraded pastures in the region.

INTRODUCTION

There is an increasing need in the lowland humid tropics for promoting land-use systems which can contribute to supplying the demands for timber, fuelwood, and other tree products without continuing the well-documented patterns of deforestation and land-resource degradation (1). Agroforestry systems and tree plantations can contribute to these goals when properly implemented (2). More information is needed on the performance of native tree species grown in plantations or in agroforestry systems; additionally, information on the impacts of trees on soil fertility should be a determining factor on species choice for these systems (2).

The most important beneficial effects of trees on soils can include improvement of soil structure and increases in nutrient availability (3–5). For example, higher pH, Ca, Mg, and N have been reported under plantations of *Gmelina arborea* than under pine or pastures in Brazil and in Nigeria (5). Two to threefold increases in Ca, Mg and K have been found in plantations of *Cordia trichotoma* and *Caesalpina equinata*, compared to levels in native forest, in southern Bahia (Brazil) (6). Symbiotic N fixation by trees can result in increased soil N availability (7–10).

In the Atlantic lowlands of Costa Rica, Central America, the Costa Rican Forest Service, Dirección General Forestal (DGF) is conducting experiments on the growth performance of tree species for plantation. Among the species presently recommended by DGF to farmers (*Gmelina arborea, Pinus caribaea, Eucalyptus deglupta*, and *Cordia alliodora*), only one (*C. alliodora*) is native. In 1985, DGF established a plantation of 13 native tree species at the La Selva Biological Station of the Organization for Tropical Studies (OTS). Measurements after three years showed that, among these species, at least four: *Stryphnodendron excelsum, Vochysia hondurensis, Vochysia ferruginea*, and *Hieronyma oblonga*, exhibited growth rates similar to or above those reported for the species which are recommended for the region after three years (11). This suggests the potential of many native trees for commercial purposes.

In 1988, we initiated an independent study on the impacts of six species on soil fertility and mechanisms of nutrient recycling (12). Two of the species, *Dalbergia tucurensis* Donn. Smith ("granadillo") and *Stryphnodendron excelsum* Harms. ("vainillo") were leguminous, nitrogen-fixing trees. The presence of root nodules was verified before choosing the species for comparison (no inoculation was done). Among the other four, *Vochysia ferruginea* Mart ("botarrama") and *V. hondurensis* Sprague ("mayo") (Vochysiaceae) have been reported to be aluminum accumulators (over 10 000 mg · kg^{-1} in foliar tissue) (13). This characteristic has been associated with better growth compared to other species for which acid soils cause aluminum toxicity problems (14). *Tabebuia rosea* (Vertol.) DC ("roble sabana", Bignoniaceae) and *Dipteryx panamensis* (Pittier) Record and Mell, ("almendro") (Leguminosae, but not an N fixer) were chosen because of their wide distribution in the Latin American tropics (15).

Here we report results of a comparison of soil fertility under the species of the plantation (when it was 2.5 years old), under grass, and in an adjacent 20-year-old secondary forest, emphasizing the effects of the species on soil nutrient conservation, and the possible mechanisms involved in the observed responses. The results will aid understanding of the environmental impacts of native tree species of economic value for forestry and agroforestry. Results may also be applicable to other humid tropical areas where soils are similar.

STUDY SITE

The plantation was established in December 1985 on an abandoned pasture at the OTS La Selva Biological Station (10°26'N, 86°59'W, 50 meters mean elevation, 24°C mean annual temperature, 4000 mm mean annual rainfall, with maximum in July and minimum in March). The soils are Fluventic Dystropepts, derived from alluvially deposited volcanic materials; they are deep, well drained, stone-free, with low or medium organic-matter content, moderately heavy texture, and generally acid and unfertile (16). The area had been cut in the 1950s and grazed until 1984. The dominant species in the pastures were grasses (*Olyra latifolia, Melinis minitiflora*), ferns (*Pteridium* sp.), and brushes (*Psidium guajava* and *Piper culebranum*). The dominant species in the 20-year-old adjacent forest were *Pentachlethra macroloba*, a mimosoid, N-fixing leguminous tree dominant in the primary forest at La Selva; *Piper culebranum*, and species of the Melastomataceae family; with ferns (*Pteridium* spp.) and tree seedlings in the understory. The site was cleaned manually before planting. The trees were planted in a randomized block design with five replicates. Each plot (14 m · 14 m) had seven trees each, with two meters distance between trees. Five 14 m · 14 m plots were also established in an adjacent open area with grass and in an adjacent secondary forest. During the first year of plantation establishment, weeds were cut manually four times. Thereafter, weeding was done mechanically until canopy closure made it no longer necessary. The grass areas were weeded simultaneously to keep them free of trees and were treated in a comparable manner.

under the six native tree species in plantation, grass and secondary forest; April 1988[1].

Site	Depth (cm)	Ca	Mg	K	pH	Acidity	Sum of bases	CEC	Saturation (%) bases	Saturation (%) acidity
		(cmol · kg⁻¹)				(cmol · kg⁻¹)				
S. excelsum	0–15	0.45a	0.63ab	0.27a	5.4ab	1.66ab	1.34a	3.00a	45.5a	54.5bc
	15–30	0.33a	0.35a	0.19a	5.4a	1.54a	0.87a	2.41a	37.2a	62.7b
	30–60	0.26a	0.22a	0.17a	5.6a	1.88a	0.65a	2.53a	34.2a	65.7a
D. tucurensis	0–15	0.44a	0.41ab	0.22a	5.4ab	1.46ab	1.07a	2.53a	41.6a	58.4bc
	15–30	0.32a	0.24a	0.15a	5.4a	1.54a	0.71a	2.25a	31.6a	68.4bc
	30–60	0.24a	0.15a	0.11a	5.6a	1.42a	0.49a	1.91a	26.8a	73.2a
V. ferruginea	0–15	0.73a	0.61ab	0.22a	5.4ab	1.20ab	1.56a	2.76a	52.8a	47.2bc
	15–30	0.66a	0.39a	0.21a	5.6a	1.12a	1.26a	2.38a	47.3a	52.7bc
	30–60	0.42a	0.28a	0.17a	5.6a	1.06a	0.88a	1.92a	42.5a	57.5a
V. hondurensis	0–15	0.25a	0.37ab	0.11a	5.3b	1.86a	0.73a	2.59a	28.2bc	71.6a
	15–30	0.19a	0.18a	0.09a	5.4a	1.58a	0.46a	2.04a	22.5bc	77.5a
	30–60	0.17a	0.32a	0.09a	5.5a	1.32a	0.57a	1.89a	27.5a	72.5a
T. rosea	0–15	0.42a	0.50ab	0.15a	5.5a	1.28b	1.06a	2.35a	44.1a	55.9b
	15–30	0.28a	0.28a	0.12a	5.8a	1.12a	0.66a	1.78a	35.5a	64.5b
	30–60	0.28a	0.24a	0.13a	5.7a	0.98a	0.65a	1.63a	38.8a	61.2a
D. panamensis	0–15	0.52a	0.74ab	0.38a	5.5a	1.18b	1.64a	2.82a	53.4a	46.5bc
	15–30	0.36a	0.45a	0.29a	5.5a	1.06a	1.09a	2.19a	46.2a	53.8bc
	30–60	0.28a	0.28a	0.19a	5.8a	1.08a	0.75a	1.83a	38.8a	60.1a
Grass	0–15	0.32a	0.27b	0.19a	5.3b	1.40ab	0.77a	2.17a	34.8ab	65.2ab
	15–30	0.31a	0.28a	0.17a	5.4a	1.32a	0.75a	2.08a	35.7ab	64.2ab
	30–60	0.23a	0.15a	0.10a	5.5a	1.28a	0.48a	1.74a	27.1a	72.9a
Secon. forest	0–15	0.68a	0.55b	0.17a	5.3b	1.54ab	1.39a	2.93a	46.9a	53.1bc
	15–30	0.60a	0.42a	0.13a	5.4a	1.60a	1.15a	2.75a	42.2a	57.7bc
	30–60	0.42a	0.28a	0.18a	5.5a	1.34a	0.87a	2.21a	39.5a	60.5a

[1] In the present and following tables differences between sites for a given depth and parameter are statistically significant when means are followed by different letters.

Figure 1. Effects of native tree species in plantation, grass and secondary forest on soil organic matter content.

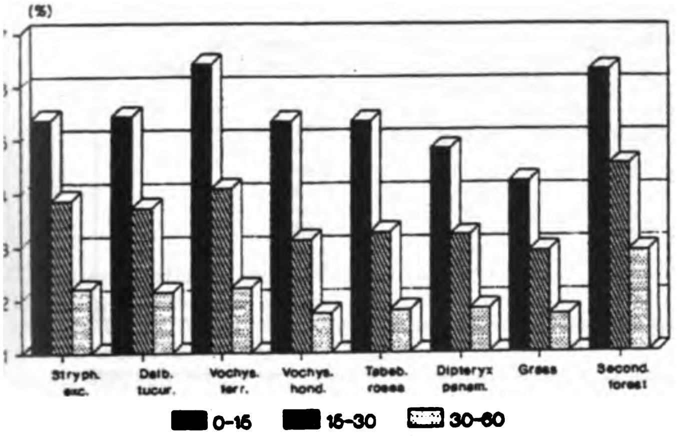
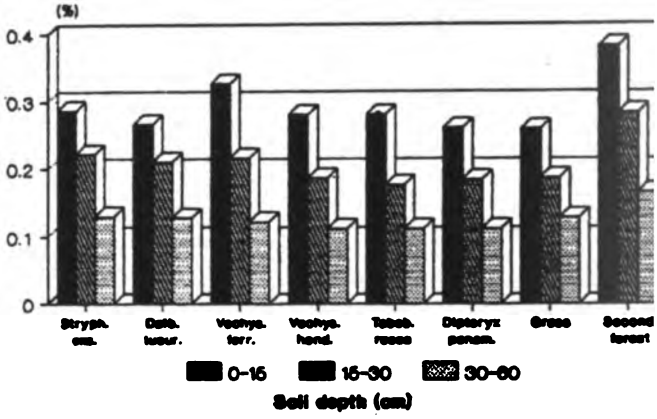


Figure 2. Effects of native tree species in plantation, grass and secondary forest on soil total nitrogen content.



MATERIALS AND METHODS

For the general chemical characteristics of soils, sampling was done with a "Dutch type" ("Edelman") auger, at 0–15, 15–30, and 30–60 cm depth, in April (dry season) and in August (rainy season) of 1988. Chemical analyses were done at the Soils Laboratory of the College at Agriculture, University of Costa Rica, following standard methods currently used by soil testing laboratories in the country (17). The pH was measured in a 1:2.5 mixture of soil: deionized water using a Corning 7 pH meter. Ca and Mg were extracted with a 1 N KCl solution, while P, K and micronutrients were extracted with a modified Olsen solution (17). Cations were measured using a Perkin Elmer 2380 Atomic Absorption Spectrophotometer. Effective cation-exchange capacity was calculated as the sum of Ca, Mg and K, plus the exchange acidity as measured by titration of 1 N KCl soil extracts with 0.01 N NaOH. P was measured colorimetrically after reaction with acid $(NH_4)_2MoO_4$ and $SnCl_2$, using a Perkin Elmer-Coleman 295 Spectrophotometer. Organic matter was measured with the Walkley-Black technique (18) and total N was measured using a semi-micro-Kjeldahl technique (19). For N mineralization and nitrification studies soils were sampled at 0–15 cm with a 2.5 cm diameter soil corer using the same plots as for soil general chemistry, starting in May 1989. NO_3-N and NH_4-N were extracted on field moist soils with 2 N KCl, and measured using a Lachat Flow Injection Analyzer (10500 N Port Wash Rd, Mequon, WI, USA). One subset of samples was extracted immediately after sampling while another subset was inc bated in plastic cups in the laboratory (2 for seven days.

The difference between final (after inc bation) and initial NO_3-N+NH_4-N cc centrations gave the net nitrification or r N mineralization potential rates, which a a measurement of soil N availability (2(

RESULTS AND DISCUSSION

Soil organic matter and total N conte were the highest in the secondary fore followed by the tree plantation, while t grass had the lowest values (Table 1, Fig and 2). Apparently, in just 2.5 years the had been an increase in soil organic mat from a mean of 4.83% in grass to 5.3 6.60% in the plantation, in the upper cm of the soil. The highest mean value the plantation, found under *Vochysia ferruginea*, was close to the mean in the secondary forest (7.58%). A similar trend was found at 15–30 and at 30–60 cm (Fig. 1). Total N in the tree plantation was 0.26–0.32% (Table 1, Fig. 2), again values higher than in grass (0.22%), with the highest content under *V. ferruginea*, close to the mean found in the forest (0.33%).

Soil NO_3-N concentrations at 0–15 cm depth (Table 2) were higher in grass, possibly due to the presence of leguminous herbs which were invading the area. Within the plantation, NO_3-N was higher under *S. excelsum*, with values similar to those under forest, and there was a trend of higher concentration under *D. tucurensis*. There were no statistically significant differences in NH_4-N or in total N mineralization potential rates (Table 2). The highest net nitrification was under *S. excelsum* followed by grass, forest and *D. tucurensis*, in that order. Apparently, there was a trend of higher NO_3-N production under N fixing species in the plantation, although possibly rates of N fixation in the young plantation were still too low to result in significant changes in soil N availability and total N content.

P concentrations were higher in the plantation than in grass, but they were lower in the forest (Table 1). This is probably due to immobilization of P in plant biomass and in soil organic matter in the forest. Cu concentrations exhibited a similar trend (higher in the tree plantation, lower in grass and forest) (Table 1). The pattern for Zn, Mn and Fe was similar to that of Ca and Mg (Tables 1 and 3).

Soil Ca and Mg content were higher in the plantation than in grass, with values close to those in the forest (Table 3). Within the tree plantation, there were no significant differences among species in soil cation content (Table 3). However, there was a tendency for higher Ca under *D. panamensis* and *V. ferruginea*, higher Mg under *S. excelsum* and *D. tucurensis*, *D. panamensis* and *V. ferruginea*. Based on the cation levels determined by the Ministry of Agriculture of Costa Rica for soil fertility assessments (21) these higher values were close to those acceptable for agricultural crops; under the species mentioned above, soil Mg and K were at or above the critical levels for agriculture, representing an improvement over the grass in only 2.5 years. The base saturation was equal or higher in the plantation (6.1–9.9%) than in the forest, and higher than in the grass, while the reverse was true for pH and the acidity saturation (Table 3).

Results of the measurements done in August 1988 showed similar trends of differences among sites (12), but the soil base content was lower. This was accompanied by higher soil exchangeable acidity (Fig. 3), possibly resulting from leaching of bases during the time of peak precipitation (457 mm in August, in comparison with only 43.6 mm in April 1988, data from La Selva weather station).

A close relation was found between organic matter content and the sum of bases (Fig. 4), showing that organic matter was responsible for much of the cation retention capacity. Hence, poor management practices, such as repeated burning, lack of good soil cover, overgrazing and compaction, which all tend to decrease organic matter content (22), could lower significantly the fertility of these soils, even possibly reaching a point of very difficult recovery. In contrast, practices such as tree planting with species that tend to increase organic-matter content, such as the species in this project, would tend to increase and maintain soil fertility. For example, as shown in Figure 4, a 1–2% increase in soil organic matter in the range of 4–6% would result in a more than double increase in base content, reaching values in the range recommended for agriculture (21).

The results shown above suggest a potential ameliorating effect of these native tree species on soil fertility, especially with respect to organic matter and base content. Results of similar measurements done in 1989 showed trends similar to those found in 1988 (23). It is important to empasize that these effects were apparently occurring at an early stage, during the first years of plantation establishment.

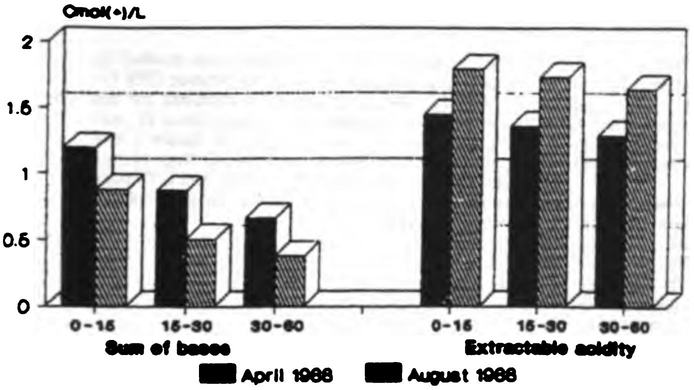
Table 2. Soil nitrate and ammonium concentrations at the time of sampling, net nitrification and net N-mineralization potential rates (0–15 cm depth, May 1989).

Site	NO_3-N ($mg \cdot kg^{-1}$)	NH_4-N ($mg \cdot kg^{-1}$)	Nitrification (mg NO_3-N $kg^{-1} \cdot d^{-1}$)	N mineralization (mg NO_3-N + NH_4-N $kg^{-1} \cdot d^{-1}$)
S. excelsum	2.52^{bc}	7.30^{a}	4.75^{a}	5.01^{a}
D. tucurensis	1.99^{c}	6.83^{a}	2.96^{bc}	2.96^{a}
V. ferruginea	0.81^{c}	7.06^{a}	0.88^{d}	0.49^{a}
V. hondurensis	0.76^{c}	4.38^{a}	1.24^{d}	0.60^{a}
T. rosea	0.34^{d}	6.34^{a}	1.46^{cd}	1.96^{a}
D. panamensis	0.53^{d}	5.84^{a}	1.26^{d}	0.53^{a}
Grass	5.62^{a}	7.77^{a}	3.80^{ab}	4.00^{a}
Forest	2.82^{b}	6.73^{a}	3.49^{ab}	2.79^{a}

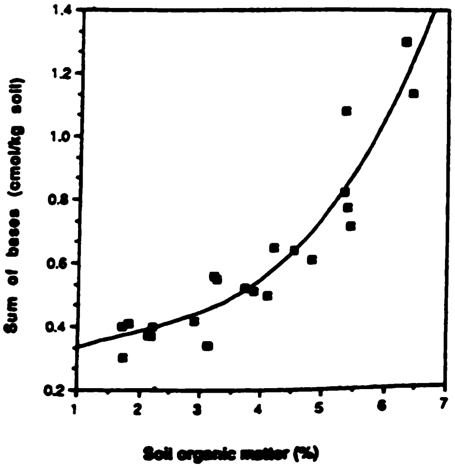
Table 3. Organic matter, total N, C/N, P and micronutrients in soils sampled in April 1988.

Site	Depth (cm)	OM (%)	N (%)	C/N	P	Cu	Zn	Mn	Fe
					($mg \cdot kg^{-1}$)				
S. excelsum	0–15	6.04ab	0.288b	12.2a	5.58a	18.6a	1.90a	85.8a	344b
	15–30	4.52b	0.234b	11.2a	5.70a	18.6a	1.64a	97.2a	258b
	30–60	2.54a	0.142a	10.4a	5.54a	9.2a	2.08a	67.6a	128b
D. tucurensis	0–15	5.47ab	0.292ab	10.9a	5.48a	20.0a	1.92a	104a	315b
	15–30	4.06b	0.214b	11.1a	4.60a	38.0a	1.50a	88.4a	218b
	30–60	2.70a	0.132a	11.9a	4.24a	15.4a	1.72a	77.6a	182b
V. ferruginea	0–15	6.60ab	0.318b	12.1a	7.10a	22.2a	2.76a	105a	331b
	15–30	4.60b	0.218b	11.9a	5.30a	20.4a	3.14a	96.4a	219b
	30–60	3.34a	0.156a	12.6a	4.66a	20.8a	2.42a	91.0a	152b
V..hondurensis	0–15	5.46ab	0.288ab	11.0a	5.16a	18.2a	2.36a	115a	323b
	15–30	3.87b	0.204b	11.0a	4.60a	17.6a	1.90a	93.2a	218b
	30–60	2.70a	0.142a	11.0a	4.46a	13.2a	1.78a	79.4a	177b
T. rosea	0–15	5.63ab	0.288ab	11.4a	5.10a	19.8a	1.80a	89.0a	277b
	15–30	3.92b	0.194b	11.6a	4.64a	18.2a	1.44a	81.2a	165b
	30–60	3.00a	0.164a	10.7a	4.66a	18.0a	1.56a	78.2a	138b
D. panamensis	0–15	5.31ab	0.260ab	11.8a	5.34a	20.0a	1.80a	114a	333b
	15–30	4.42b	0.208b	12.4a	5.14a	18.0a	1.60a	96.0a	200b
	30–60	2.96a	0.146a	11.6a	5.58a	20.8a	2.18a	89.4a	158b
Grass	0–15	4.83bc	0.224b	12.8a	4.90a	15.8a	1.40a	96.8a	297b
	15–30	4.03b	0.176b	14.0a	4.44a	14.2a	1.48a	110a	226b
	30–60	2.73a	0.138b	11.8a	4.24a	15.0a	2.04a	82.4a	138b
Secon. forest	0–15	7.58a	0.328a	13.6a	3.64b	16.2a	2.26a	113a	664a
	15–30	6.40a	0.278a	13.4a	3.34b	15.2a	2.24a	101a	461a
	30–60	3.29a	0.170a	11.2a	3.60a	11.2a	2.32a	91.8a	300a

sampling (April and August 1988).



and base content, soils sampled in August 1988.



***Vochysia hondurensis* Sprague ("mayo") (Vochysiaceae), after 3.5 years. Photo: F. Montagnini.**

Forest floor under *Vochysia ferruginea* Mart.; note abundance of litter and lack of understory growth. Photo: F. Montagnini.

These early effects are certainly a great advantage when there is pressure to produce timber or fuelwood in the short term and to improve soil fertility in degraded areas. This relatively early positive impact on soil fertility will greatly facilitate the demonstration of the potential benefits of plantations or tree-crop combinations using these species.

To help in making this kind of recommendation to farmers, it is necessary to understand the potential mechanisms responsible for such responses. For example. preliminary results of measurements of rates of litter fall suggest that higher organic-matter content in soils under *V. ferruginea* could be related to high amounts of leaf litter fall under this species. *V. ferruginea* is a pioneer species in abandoned fields. forming uniform. even-aged stands (23); it is self-pruning and its wood is used for plywood and construction. Apparently. this species has numerous advantages as a fast-growing tree with additional positive effects on soil nutrients.

We expect that the results of our studies will be disseminated to farmers of the region through the action of the local institutions: for example. through collaboration with DGF. which maintains its interest in the project and is already promoting the plantation of native trees among local farmers. We are continuing long-term measurements of soil fertility to assess the true impacts of the tree species on soil amelioration. To gain a better understanding of processes responsible for differences among species we are presently measuring root density, whole tree biomass and tissue chemistry, leaf litter fall and litter decomposition, and soil N availability. Understanding these mechanisms may help us to anticipate the results of using these species in other areas with similar soils.

References and Notes

1. Montagnini. F. 1990. Ecology applied to agroforestry in the humid tropics. In: *Race to Save the Tropics. Ecology and Economics for a Sustainable Future*. Goodland. R.A. (ed.). Isiand Press. Washington. DC. p. 49–58.
2. Organization para Estudios Tropicales. Centro Agronómico Tropical de Investigación y Enseñanza. (OTS/CATIE). 1986. *Sistemas Agroforestales. Principios y Aplicaciones en los Trópicos*. OTS. San José. Costa Rica. 818 p. (In Spanish).
3. Fassbender. H.W. 1984. *Bases Edafológicas de los Sistemas de Producción Agroforestales*. Serie Materials de Enseñanza No. 21 Centro Agronómico Tropical de Investigación y Enseñanza (CATIE). Turrialba. Costa Rica. 191 p. (In Spanish).
4. Nair. P.K.R. 1984. *Soil Productivity Aspects of Agroforestry*. International Council for Research in Agroforestry. Nairobi. 85 p.
5. Sánchez. P.A.. Palm. C.A.. Davey. C.B.. Szott. L.T. and Russell. C.E. 1985. Tree crops as soil improvers in the humid tropics? In: *Attributes of Trees as Crop Plants*. Cannell. M.G.R. and Jackson. J. E. (eds). Institute of Terrestrial Ecology. Natural Environmental Research Council. Abbots Ripton. Huntingdon. England. p. 327–350.
6. Silva. L.F. 1983. *Influencia de Cultivos e Sistemas de Manejo nas Modificacoes Edáficas dos Oxisols de Tabuleiro (Haplorthox) do Sul da Bahia*. CEPLAC. Departemento Especial da Amazonia. Belem (Brazil) (In Portuguese)
7. Alpízar. L., Fassbender, H.W., Heuveldop. J., Folster. H. and Enríquez, G. 1986. Modelling agroforestry systems of cacao (*Theobroma cacao*) with laurel (*Cordia alliodora*) and poró (*Erythrina poeppigiana*) in Costa Rica. I. Inventory of organic matter and nutrients. *Agrof. Sys. 4*, 175–189.
8. Cadima Zeballos. A. and Alvim, P de T. 1967. Influencia del árbol de sombra *Erythrina glauca* sobre algunos factores edafológicos relacionados con la producción del cacaotero. *Turrialba 17*, 330–336. (In Spanish).
9. Montagnini. F., Haines, B.L., Boring, L. R. and Swank. W.T. 1986. Nitrification potentials in successional black locust and mixed hardwood forest stands in the southern Appalachians. USA. *Biogeochemistry 2*, 197–210.
10. Roskowski. J.P. 1982. Nitrogen fixation in a Mexican coffee plantation. *Plant & Soil 67*, 283–291.
11. Espinoza Camacho, M. and Butterfield, R. 1989. Adaptabilidad de 13 especies nativas maderables bajo condiciones de plantación en las tierras bajas húmedas del Atlántico, Costa Rica. In: *Manejo y Aprovechamiento de Plantaciones Forestales con Especies de Uso Múltiple. Actas Reunión IUFRO. Guatemala 3–7 Abril 1989*. Salazar. R. (ed.). Catie. Turrialba. Costa Rica, p. 159–172. (In Spanish).
12. Montagnini. F. and Sancho. F. Influencia de seis especies de árboles nativos sobre la fertilidad del suelo en una plantación experimental en la llanura del Atlántico de Costa Rica. *Ciencia Forestal* (Uni-

versidad Nacional de Misiones. Facultad de Ciencias Forestales. Eldorado. Misiones. Argentina). (In Spanish) (In print).
13. Rundel. P.W. Laboratory of Biomedical and Environmental Sciences. University of California. Los Angeles. CA 90024. USA. unpublished data.
14. Goodland. R. 1971. Oligotrofismo e aluminio no cerrado. In: *III Simposio Sobre o Cerrado*. Ferrá. M.G. (ed.). Univ. São Paulo. a Blucla. São Paulo. 239 p. (In Portuguese).
15. Holdridge. L.R.. and Poveda. L.J. 1975. *Arboles de Costa Rica*. Centro Científico Tropical. San José. Costa Rica. 546 p. (In Spanish).
16. Sancho. F. and Mata. R. 1987. *Estudio detallado de Suelos Estación Biológica La Selva*. Organización para Estudios Tropicales. San José. Costa Rica. 162 p. (In Spanish).
17. Diaz-Romeu. R. and Hunter. A. 1978. *Método para el Muestro de Suelos. Análisis Químico de Suelos y Tejido Vegetal e Investigación en Invernaderos*. CATIE. Turrialba. Costa Rica. p. 9–11 and 15–27. (In Spanish).
18. Allison. L.E. 1975. Organic carbon. In: *Methods of Soil Analysis. Part 2*. Black, C.A. (ed.). American Society of Agronomy. Inc., Madison. Wisconsin. p. 1367–1378.
19. Bremmer. J.M. and Mulvaney, C.S. 1982. Nitrogen-total. In: *Methods of Soil Analysis. Part 2. 2nd ed.* Page, A.L., Miller. R.H. and Keeney. R.R. (eds). American Society of Agronomy, Inc., Madison. Wisconsin, p. 595–624.
20. Keeney, D.R. 1982. Nitrogen-availability indexes. In: *Methods of Soil Analysis. Part 2. 2nd ed.* Page, A.L., Miller. R.H. and Keeney, R.R. (eds). American Society of Agronomy. Inc., Madison Wisconsin, p. 711–730.
21. Bertsch, F.H. 1986. *Manual para Interpretar la Fertilidad de los Suelos en Costa Rica*. Universidad de Costa Rica. Escuela de Fitotecnia, 76 p. (In Spanish).
22. Sánchez, P.A. 1976. *Properties and Management of Soils in the Tropics*. Wiley, New York, 618 p.
23. Montagnini. F. and Sancho. F. Yale University. School of Forestry and Environmental Studies. 370 Prospect St., New Haven. CT 06511. USA. and Centro de Investigaciones Agronómicas. Universidad de Costa Rica. Ciudad Universitaria. San José. Costa Rica. Central America, unpublished data.
24. Berner. P.O. and Finegan. B. 1988. *Natural Management of Montane Tropical Forests and Anthropogenically Disturbed Lowland Tropical Forests: From Ecological Research Towards a Silvicultural System*. 25 Aniversario de la Organización para Estudios Tropicales. Exhibición de afiches sobre estudios tropicales en Costa Rica. Museo Nacional. Junio 5–12. 1988.
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Article

Thomas R. Preston

Future Strategies for Livestock Production in Tropical Third World Countries

Present day systems of livestock production in both industrialized and Third World countries are subjected to political, economic and environmental pressures that infer the need to introduce new production technologies which are more sustainable. Foreign exchange shortages present an opportunity for developing new production systems using local resources which are less dependent on fossil-fuel derived inputs. Environmental pressures will force a decreasing role for fossil fuel and an increasing reliance on renewable biomass. Concern for animal welfare and natural food quality is leading to deintensification of production systems and incentives for organic agriculture. Tropical regions are in a strong position to take advantage of these changes, being richly endowed with natural resources in the form of solar energy, soil and water, and biological diversity. Correctly harnessed, these resources can form the basis of production systems which will confer a real competitive advantage to livestock production in these regions. An example of this latter approach is presented, designed specifically for tropical zones, the widespread adoption of which will help to close the production-utilization gap for carbon dioxide with a more than tenfold reduction in emission of methane per unit meat production, compared with traditional tropical systems based exclusively on cattle ranching. Such technologies are sustainable and especially appropriate for use on small-scale family farms in tropical regions. They create innovative research possibilities for use of noncon-

THE CHANGING LIVESTOCK SCENE

The last five years have witnessed a marked change in the economic and political pressures to which livestock production is subjected in both industrialized and Third World countries. In most industrialized countires political support for farming has been weakened by food surpluses, the high degree of government subsidization in the agricultural sector and tariff barriers to food imports from developing contries. The resultant high prices have reduced demand for most agricultural products. Farming systems throughout the world are threatened by (i) the increasing prices of fossil fuels (and the agrochemicals derived from them) due to decreasing reserves and political instability in the principal supplying countries; and (ii) the concern over the increasing atmospheric and terrestrial contamination, much of which can be traced to agricultural activities. There is increasing advocacy for free markets in agricultural products. greater discrimination by consumers and

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Montagnini, F. 1990. Ecology applied to agroforestry in the humid tropics. **pp. 49-58** In Goodland, R. A. (ed). *Race to Save the Tropics. Ecology and Economics for a Sustainable Future*. Island Press. Washington, D.C.

Chapter 2

ECOLOGY APPLIED TO AGROFORESTRY IN THE HUMID TROPICS

FLORENCIA MONTAGNINI

In the lowland humid tropics, more and more often, we see the need to develop alternative land-use systems that contribute to supply timber, fuel wood, and other tree products without continuing the well-documented patterns of extensive agriculture, deforestation, and land resources degradation. Alternative land-use systems should be productive while at the same time help preserve natural resources. Agroforestry systems can contribute to these goals when properly implemented.

Agroforestry systems, which combine trees with crops or pastures, are one of the alternatives for sustainable land use in the tropics. The incorporation of trees in the production system can shade animals and crops; improve the nutrient status of the soil, especially when nitrogen-fixing species are used; control soil erosion; provide tree products such as timber, fuelwood, fruits, and forage; make better use of the land through the association of species; and diversify the system, thus decreasing economic risks of crop failure and dependence on markets.

Proper choice of tree species for agroforestry systems can decrease the need for fertilizers and pesticides. For example, nitrogen-fixing species can help maintain soil fertility. In agroforestry systems, the appropriate association of trees with crops can reduce the need for herbicides, and insecticides. Costa Ricans, for example, grow coffee under open sun in extensive, high-input plantations owned by large companies. Small farmers cannot afford to buy the agrochemicals required. But they can grow coffee in association with nitrogen-fixing trees and other species valuable for lumber, fruit, and other tree products. The coffee plantations are productive for many more years and provide benefits beyond their cash-crop function. At the same time the risk of crop failure and market dependence decreases when the crop is diversified.

CHOICE OF TREE SPECIES

In agroforestry systems soil-improving tree species help increase productivity of low-resource agriculture. The improved supply of forest and agricultural products decreases the pressure over natural forests and virgin lands. Using fewer agrochemicals diminishes soil and water pollution. Better protection of headwaters decreases soil erosion and helps maintain water supply for agricultural, industrial, and domestic use.

Since the 1950s more people have become interested in experimenting with agroforestry practices. Some of these practices have existed for centuries, but are not well understood from a scientific point of view. In the neotropics several agroforestry systems are integrated into current practices and others are being developed. But, in most cases, studies that can help us understand mechanisms that influence their performance are missing.

In the Latin American tropics, studies are being conducted to test the performance of trees for reforestation or for agroforestry (Cozzo, 1976; CATIE, 1986; and others). Exotic species such as ***Leucaena leucocephala, Acacia mangium, Gmelina arborea, Eucalyptus*** spp., and ***Pinus*** spp. are widely used in agroforestry, although these represent only a small fraction of the trees that might prove useful in the tropics (NAS, 1983). Researchers concentrate on a small number of exotic species because of the experience generated in years of trials, genetic improvement, and silvicultural experiments.

However, the incorporation of native tree species offers several advantages. Native trees are well adapted to the local environment and are thus less likely to be affected by pests, diseases, and adverse weather conditions. Because they are adapted to local soils and vegetation, the design of mixed systems (as in agroforestry) is more feasible. Native species are in better balance with the natural ecosystem and allow better preservation of habitats for wildlife. Hence they help preserve biological diversity. The spread of the use of native species in profitable systems will increase the appreciation for these resources and help preserve the native flora of potential economic value.

In Costa Rica, tree trials for forestry and agroforestry have included exotic and a few native, generally fast-growing species. These trials are being conducted by institutions such as the Forest Service (Dirección General Forestal, DGF), Centro Agronómico Tropical de Investigación y Enseñanza (CATIE) (see, for example, Alpízar et al., 1986, CATIE, 1986; Glover and Beer, 1986), and private enterprises. In most of the regions where these projects are being conducted, we need strategies to help restore soil fertility, to decrease soil erosion and compaction, and to protect headwaters. However, very few projects devote resources to studies of potential effects of these tree species on soil properties (Montagnini, in press).

Research projects are needed to help fill this gap. In some cases there are not even enough data on general soil properties in the established systems. Thus, very often we cannot interpret differences in performance between systems. As a general consequence, it is often risky to extrapolate the results to other areas. Failure or success remains related to local conditions, and years and resources spent in the trials are not as profitable as they could be.

The Organization for Tropical Studies (OTS) and the Costa Rican Forest Service (Dirección General Forestal, DGF) have been studying the performance of 14 native tree species since 1985 at the OTS La Selva Biological Station (at Puerto Viejo de Sarapiquí, in the Atlantic Lowlands of Costa Rica) with funding from the Canadian Embassy (Table 1). The original objectives of the project were to provide local farmers with information on the potential of native trees for plantation forestry and agroforestry by establishing demonstration plots for use in a community-based environmental education program. Currently, funding is being requested from the U.S. Agency for International Development (AID) for an independent project to use the native tree-species plots to measure effects of these species on soil properties. The results of this project will provide more information on the native trees and increase the value of the demonstration plots.

TABLE 1

SPECIES USED IN THE OTS-DGF NATIVE TREES TRIALS

Tree Species	Family	Common Name
Hieronyma oblonga	Euphorbiaceae	Pilón
Calophyllum brasiliensis	Guttiferae	Cedro María
Cordia alliodora	Boraginaceae	Laurel
**Dipteryx panamensis*	Papilionaceae	Almendro
Lonchocarphus velutinus	Papilionaceae	Chaperno
Vitex cooperi	Verbenaceae	Cacho de venado
Dalbergia tucurensis	Papilionaceae	Granadillo
Pterocarpus officianalis	Papilionaceae	Sangrillo
**Schizolobium parahyloum*	Caesalpiniaceae	Gallinazo
**Stryphnodendron excelsum*	Mimosaceae	Vainillo
**Tabebuia rosea*	Bignoniaceae	Roble de sabana
Terminalia spp.	Combretaceae	Surá
**Vochysia ferruginea*	Vochysiaceae	Botarrama
**Vochysia hondurensis*	Vochysiaceae	Chancho

* Species of better growth after one year.

In January 1987, OTS began a major project funded by the MacArthur Foundation to study the performance of exotic and native trees at La Selva, Costa Rica. It emphasizes growth performance of a large number of species; separate blocks were established for future use in studying the effects of 10 to 12 species on soil properties. Independent investigators can use the plots to study soil parameters and specific processes in far more detail than is planned in the MacArthur-funded project. Soil studies emphasize native tree species with the specific goal of putting existing regional resources into use for tree plantation and agroforestry.

A major contribution of OTS and CATIE to this area of applied ecology has been the production of the first agroforestry textbook in Spanish (OTS and CATIE, 1986), with funding from AID's Forestry Support Program. The book compiles information on the functioning of agroforestry systems, along with several case studies, bibliographies, inventories, and sources of information, covering most technical aspects. Besides its wide use as a university textbook and by extensionists, it represents a first step in gathering essential information useful as a starting point for a research program.

Soil-improving tree species are the key to the success of agroforestry systems. The performance of promising tree species and their effects on soil properties should be investigated in detail. This basic knowledge is needed before recommending the concept to farmers.

EFFECTS OF TREES ON SOIL PROPERTIES

The most important beneficial effects of trees on soil properties include improvement of soil structure and increase of soil nutrient availability. Deleterious effects such as decreases in soil acidity (pH) and soil nutrient content can also occur. Note, however, that this is a highly controversial issue (Cozzo, 1976; de las Salas and Fassbender, 1984; Lundgren, 1978; c.f. Sánchez et al., 1985) and that most of the reports of soil differences for different tree species do not indicate the processes involved (Lundgren, 1978).

Sánchez et al. (1985) concluded that the overall effect of mature fast-growing trees on nutrient availability is positive, but major differences exist among species. We also need to compare well-characterized soils, and to experiment with various tree/crop combinations compared with annual crops, pastures, or fallows to demonstrate to what degree trees improve or maintain soil properties in the humid tropics.

Tree species can influence soil pH, cations (calcium, magnesium, potassium), organic matter, and total nitrogen and phosphorus content and availability. For example, in a plantation of *Gmelina arborea* on an Ultisol soil in Brazil the soil pH was 5.2, while under *Pinus* (pine) the soil pH was 3.9—about the same as under native rain forest. The soil under *Gmelina* also had more exchangeable calcium (860 kilograms per hectare) than under pine (100) or native forest (40). Exchangeable manganese, exchangeable potassium, and total nitrogen under *Gmelina* were similar to rain forest, while the soil under pine had much lower potassium, magnesium, and total nitrogen content. Thirteen-year-old *Gmelina* plantations on Alfisol soil in Nigeria showed similar effects: an increase in soil pH from 4 to 5.5, a decrease in aluminum saturation from 58 percent to 6 percent, a two to three times increase in exchangeable calcium, and an increase in exchangeable manganese. Ten-year-old plantations of *Cordia trichotoma* and *Caesalpina equinata* showed a two to three times increase in exchangeable calcium, magnesium, and potassium, in comparison with the native forest; in contrast, no changes in soil properties were observed under *Dalbergia nigra*. These examples show how the effects of trees on soils differ among species.

Three species of eucalyptus exert the deleterious effect of extracting three to eight times more calcium and potassium from the soil than other forestry species, depending on silvicultural management. On the other hand, organic matter content was four times higher, and calcium, magnesium, and potassium content two times higher than in an adjacent pasture. Eucalyptus can absorb nutrients from deep layers of the soil with its 2- to 4-meter-deep root system, and contribute to increased soil nutrient content through litter-fall.

Controversial effects have also been reported for pine. Soils under an eight-year-old pine forest in Brazil had lower pH (4.2) and higher organic matter (5.3 percent) than an adjacent pasture of *Melinis minutiflora* 4.4 pH and 4.3 percent organic matter content. Soils under pine also had less calcium and much less potassium but higher magnesium content; there were no differences in phosphorus.

Apparently significant improvement of soil physical conditions—mainly increased porosity and decreased bulk density—occur only after tree canopy closure. Positive effects on soil physical properties are relevant in degraded lands where cattle have compacted soils, a common case in abandoned pastures in the humid tropics.

Obviously an understanding of the mechanisms whereby a tree species affects soil structure and nutrient availability is important to assess a species' true effects and to predict the outcome of its use. We must then use this understanding when designing agroforestry systems. In particular, knowledge of the effects of certain trees on soil properties can be used to achieve any management goals and to associate complementary tree/tree or tree/crop species.

THE ROLE OF APPLIED ECOLOGY: CASE STUDIES

Applied ecological projects can play a significant role by providing information needed for the design of successful systems. Studies of nutrient-cycling processes can be useful in the design and management of agroforestry systems, as the following examples illustrate.

Litter-fall (along with root decomposition) is frequently a main pathway of nutrient transfer (or recycling) from trees to soils. A thick layer of litter on the floor can also help maintain soil humidity and protect against soil erosion. These are also significant benefits from trees used for shade in agroforestry systems. For example, the net harvest output of nitrogen in a cacao plantation in Venezuela equaled the input of nitrogen to the soil in shade-tree leaf litter.

In Costa Rica, when organic matter and nutrients in the components of a system of cacao under shade trees were inventoried, leaf litter under the nitrogen-fixing leguminous tree ***Erythrina poeppigiana*** (commonly used in agroforestry systems in Costa Rica) was found to have more nitrogen than under ***Cordia alliodora***, but less potassium, calcium, magnesium, and phosphorus. In another project in Costa Rica, the amount of nutrients recycled via litter-fall by associated trees (***Cordia alliodora*** and ***Erythrina poeppigiana***) was found to reach the recommended levels of fertilizer for coffee production.

Nitrogen-fixing trees are a prominent component of several agroforestry systems worldwide, because they can improve the performance of the associated crops or pastures. For example, nitrogen fixation by the leguminous tree ***Inga jinicuil*** was 53 percent of the average amount of fertilizer nitrogen applied annually on coffee plantations in Veracruz, Mexico. In Turrialba, Costa Rica, ***Erythrina poeppigiana***, a widely used tree in agroforestry systems, was found to have a high potential for nitrogen fixation.

The influence of nitrogen-fixing tree species on soil nutrients other than nitrogen has also been reported, although the tendency has been to focus studies on effects on soil nitrogen and organic matter content. Soil properties in areas close and distant from ***Erythrina glauca*** trees in an old association with cacao in Brazil were compared: in three of five cases the pH was .2 to .3 units lower—closer to ***Erythrina*** than away from ***Erythrina***. Phosphorus content was 50 percent lower under ***Erythrina***, while calcium, magnesium, and potassium were twice as high under ***Erythrina*** than away from ***Erythrina***. Soil bulk density was 1.55 under ***Erythrina*** and 1.61 away from this tree. It is interesting to notice the potential impacts of this nitrogen-fixing tree on phosphorus and soil pH.

Researchers in Costa Rica compared soils of cacao plantations associated with ***Cordia alliodora*** and with ***Erythrina poeppigiana*** trees. Soils under cacao plus ***Erythrina*** had 6 percent less phosphorus, 15 percent more organic matter, 22 percent more calcium, 15 percent more magnesium, and 19 percent more potassium than under ***Cordia***. The effects of nitrogen-fixing species on soil nitrogen and cations can be positive, but questions arise as to their effects on soil pH and phosphorus content. We need comparisons of soil cations, phosphorus, nitrogen, organic matter, and pH between soils under nitrogen-fixing and other tree species to assess more realistically the role of nitrogen fixing and other tree species on these soil parameters.

Other projects stress the need of applied ecology to contribute to the design of agroforestry systems. In a hypothetical model of nitrogen, phosphorus, and potassium for a cacao/coconut association in Brazil, leaching of potassium was approximately 50 percent less than in a coconut monoculture. The appropriate choice of species for an association can thus contribute to nutrient conservation.

In southeast Bahia, Brazil, failure to expand promising agroforestry practices to a desirable extent was ascribed to the lack of scientific knowledge on the subject. As part of a crop diversification program in the traditional cacao-growing area, farmers combined clove trees with coffee or coconuts, cloves with passion fruit, papaya and coffee, cloves and vanilla, cardamom and coffee, and rubber trees, cacao, and other groups. This was successful, but the practitioners of these systems would not easily divulge the information on the management and production particulars in their farms. We need much more research and development if we are to realize the full potential of these systems.

PROMOTION OF APPLIED ECOLOGICAL PROJECTS

Applied ecological projects of the kind listed above may not always appeal to scientists who are interested in asking very specific questions and doing more sophisticated hypothesis testing. Since so much basic information is missing, many of these applied studies must start with preliminary inventories and comparisons. However, so many mechanisms of these systems need elucidation that it is hard to believe that scientists would not be stimulated to examine them. The implementation of applied ecology projects can be encouraged by science administrators who promote the funding of projects that would not be considered under their regular programs; by university professors and researchers from other academic institutions who encourage graduate students and fellow scientists to do theses and projects in the tropics; and by the scientific community as a whole, which can bridge the gap between basic and applied ecology and thus contribute to stimulating the kind of projects that are needed for this purpose.

Agroforestry systems—the combination of trees with crops or pastures—can be a productive and environmentally sound alternative land-use in the humid tropics. The choice of appropriate tree species is key to the success of these systems. Tree species differ widely in their effects on soils and in their nutrient requirements. The effects of tree species (including nitrogen-fixing trees) on soil properties remains controversial. We very much need projects that examine the performance of native tree species in agroforestry combinations, the effects of different tree species on soil properties, and tree/crop combinations that contribute to efficient nutrient usage and soil nutrient conservation. Applied ecology projects can contribute basic information on the systems to support the recommendations given to farmers.

References Cited and Sources of Further Information

Alpízar, L., H.W. Fassbender, J. Heuveldop, H. Folster and G. Enríquez, 1986. Modelling agroforestry systems of cacao (*Theobroma cacao*) with laurel (*Cordia alliodora*) and poro (*Erythrina poeppigiana*) in Costa Rica. I. Inventory of organic matter and nutrients. Agroforestry Syst. 4:175–189.

Alvim, R., and P.K.R. Nair, 1986. Combination of cacao with other plantation crops: an agroforestry system in Southeast Bahia, Brazil. Agroforestry Syst. 4:3–15.

Aranguren, J., G. Escalante, and R. Herrera, 1982. Nitrogen cycle of tropical perennial crops under shade trees. II. Cacao. Plant and Soil 67:259–269.

Cadima Zeballos, A., and P. de T. Alvin, 1967. Influencia del árbol de sombra *Erythrina glauca* sobre algunos factores edafológicos relacionados con la producción del cacaotero. Turrialba 17:330–336.

Centro Agronómico Tropical de Investigación y Enseñanza (CATIE), 1986. Silvicultura de species promisorias para producción de leña en América Central. Departamento de Recursos Naturales Renovables. Turrialba, Costa Rica, 219 pp.

Cozzo, D., 1976. Tecnología de la forestación en Argentina y América Latina. Buenos Aires: Ed. Hemisferio Sur, 610 pp.

de Barros, N.F., and R.M. Brandi, 1975. Influencia de trés espécies forestaes sobre a fertilidade de solo de pastagem en Viscosa, M. G. Brasil florestal (Rio de Janeiro) 6:24.

de las Salas, G., and H. Fassbender, 1984. Factores edáficos en los sistemas de producción agroforestales. *In* Heuveldop, J. and Lagemann, J. (eds.), Agroforestería. Actas del seminario realizado en el CATIE, 23 febrero—3 de marzo 1981. Serie técnica—Boletín Técnico No. 14. Centro Agronómico Tropical de Investigación y Enseñanza. Turrialba, Costa Rica: Departamento de Recursos Naturales Renovables, pp. 30–36.

Fassbender, H.W., 1984. Bases edafológicas de los sistemas de producción agroforestales, Serie Materiales de Enseñanza No. 21. Turrialba, Costa Rica: Centro Agronómico Tropical de Investigación y Enseñanza (CATIE).

Glover, N., and J. Beer, 1986. Nutrient cycling in two traditional Central American agroforestry systems. Agroforestry Syst. 4:77–87.

International Council for Research in Agroforestry (ICRAF), 1983. Resources for agroforestry diagnosis and design, Working Paper No. 7. Nairobi: ICRAF, 383 pp.

Khanna, P.K., and P.K.R. Nair, 1980. Evaluation of fertilizer practices for coconuts under pure and mixed cropping systems in the west coast of India based on a systems analysis approach. *In:* K.T. Joseph, (ed.), Proc. Conf. Classification and Management of Tropical Soils, 1977. Kuala Lumpur: Malaysian Soc. Soil Sci., pp. 457–466.

Linblad, P., and R. Russo, 1986. C_2H_2-reduction by *Erythrina poeppigiana* in a Costa Rican coffee plantation. Agroforestry Syst. 4:33–37.

Lundgren, B., 1978. Soil conditions and nutrient cycling under natural and plantation forests in Tanzanian highlands, Reports in Forest Ecology and Forest Soils No. 31. Uppsala: Swedish University of Agricultural Sciences.

Montagnini, F., in press. Ciclaje de nutrientes en sistemas agroforestales. Primer Congreso Forestal Nacional, 1986. San José, Costa Rica.

Nair, P.K.R., 1984. Soil productivity aspects of agroforestry. Nairobi: International Council for Research in Agroforestry, 85 pp.

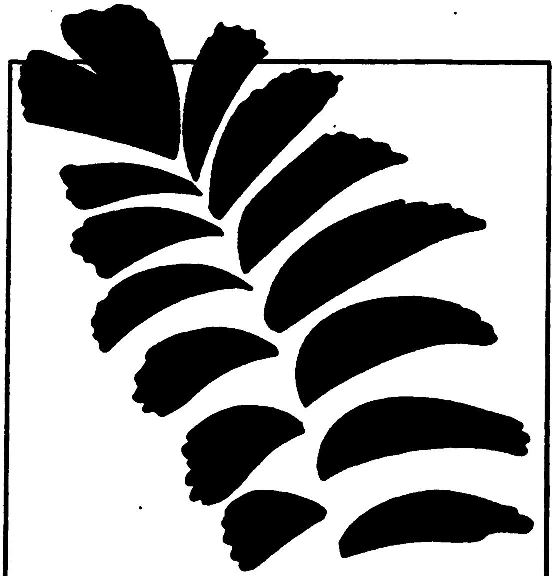
National Academy of Sciences (NAS), 1983. Calliandra: a versatile small tree for the humid tropics. Washington, DC: NAS, 52 pp.

Organización para Estudios Tropicales (OTS) and Centro Agronómico Tropical de Investigación y Enseñanza (CATIE), 1986. Sistemas Agroforestales. Principios y Aplicaciones en los Trópicos. San José, Costa Rica: OTS/CATIE, 818 pp.

Roskoski, J.P., 1982. Nitrogen fixation in a Mexican coffee plantation. Plant and Soil 67:283–291.

Sánchez, P.A., C.A. Palson, C.B. Dabey, L.T. Szott, and C.E. Russell, 1985. Tree crops as soil improvers in the humid tropics? *In:* M.G.R. Cannell and J.E. Jackson (eds.), Attributes of trees as crop plants. Huntingdon, England: Abbots Ripton, pp. 327–350.

Silva, L.F., 1983. Influencia de cultivos e sistemas de manejo nas modificacoes edáficas dos oxisols de tabuleiro (Haplorthox) do sul da Bahía. Belem (Brazil): CEPLAC, Departamento Especial da Amazonia.



LA SELVA

Ecology and Natural History of a Neotropical Rain Forest

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24

Agricultural Systems in the La Selva Region

Florencia Montagnini

iety of land uses representative of the Costa Rican Atlan- wlands can be observed in the vicinity of the La Selva gical Station, including pastures, tree plantations, home ns, and extensive monocultures in addition to primary econdary forests. This diversity is amenable to compara- udies of the function of agroecosystems, including eval- ı of their productivity and sustainability under local con- s.

Costa Rica the agricultural sector accounts for approxi- y 17.9% of the gross national product, for 28% of total yment, and for 72.3% of export income (Banco Central sta Rica [BCCR], Costa Rican Central Bank, 1988). The pal agricultural exports are coffee, bananas, beef, sugar, nd ornamentals (BCCR 1988). Costa Rica has the eco- l conditions and technical capability to produce all of its ood but has not done so because of crop preferences farmers prefer to grow coffee and other traditional ; low yields (e.g., cacao is often imported to satisfy local d); high costs (e.g., weed control in rice); cheaper im- (e.g., wheat, apples, grapes); and lack of incentives.

Costa Rica most regional development programs are ting agricultural diversification to decrease farmers' de- nce on external markets, cushion against fluctuating ields, and increase exports. For example, when interna- coffee prices are low (as in 1990), farmers who have a diverse production system (e.g., coffee with citrus) are etter position than those who grow coffee in monocul- Additionally, those who have planted trees may be able timber at good prices during years of low crop yields. diverse agricultural production would make the country independent of fluctuating international prices of ex- roducts.

e Atlantic lowlands of Costa Rica include the Atlantic orthern regions, which are administrative divisions used Government Office for Planning (SEPSA 1982). The ic Region is a 9,756 km^2 area covering the eastern por- f the Atlantic lowlands, including the whole province of ı and part of Heredia (DGEC 1987). In Heredia the At- Region includes the Horquetas District up to the Sara- River (fig. 23.1, chap. 23). All of La Selva except La ı Annex is in this region. The Northern Region includes rapiquí, Puerto Viejo and La Virgen districts near La and extends northwest to include the counties of San ;, Guatuso, and Los Chiles, and the San Isidro de Peñas as and Río Cuarto districts (SEPSA 1982). In this chap- efer to the Atlantic lowlands as a whole and emphasize the Atlantic Region near La Selva (the watershed of the Sarapiquí River and the Horquetas District in Heredia Province).

The Atlantic Region is 19.1% of the total surface of Costa Rica, but the area in farms (owned by farmers or agricultural enterprises) comprises only 9% of the country's total, which is the lowest among the country's regions. Of the total area in farms 48% is not under active cultivation and remains under forest cover; only 49.4% is in agricultural use, again the lowest value for the entire country (Flores Silva 1987). The region has until recently been so strongly dedicated to banana and cacao cultivation that other crops have received little attention. In the 1990s the region produces more than 70% of the country's total production of bananas along with 62.5% of coconuts and 20.5% of plantains but only 4% of basic grains and 5% of beef cattle. The region generates a large proportion of foreign income because bananas are grown mostly for export (Flores Silva 1987). The level of economic development in the region, however, does not reflect its significance for the country's export income. Agricultural diversification could contribute to the development of a stronger regional economy, offering options beyond employment generated by the banana companies.

In the Atlantic Region agricultural diversification has already begun to respond to the opening of new markets and to improved transportation. The paving of the road between San José and Puerto Viejo de Sarapiquí, which was completed in early 1986, significantly stimulated agriculture, forestry, and other economic activities in the region. Diversification has involved expansion of macadamia, citrus, fish culture, dwarf coconut, and other crops (Flores Silva 1987). Many of these species were chosen based on market value and presumed adaptability to the climatic conditions of the lowlands but without much previous in situ evaluation or experimentation with management practices. Most of these activities are too recent for evaluation of their economic success or ecological impact. If the region is to play a more significant role in the whole country's development, much more needs to be done to develop and implement economically productive and ecologically sustainable agricultural and forestry systems.

A number of local and international institutions such as Ministerio de Agricultura ([MAG], Ministry of Agriculture), Dirección General Forestal ([DGF] Forest Service), Junta de Administración Portuaria y de Desarrollo Económico de la Vertiente Atlántica ([JAPDEVA] Council for Harbour Administration and Economic Development of the Atlantic Lowlands), Instituto de Desarrollo Agrario ([IDA] Institute for

Agrarian Development), University of Costa Rica (UCR), Centro Agronómico Tropical de Investigación y Enseñanza ([CATIE] Tropical Agriculture Research and Training Center), Escuela Agropecuaria para la Región Tropical Húmeda ([EARTH] College of Agriculture for Humid Tropical Regions) are operating in the Atlantic lowlands. Although their objectives differ, the overall goal is to develop alternative, ecologically sound land use systems. La Selva has begun to take part in this effort, but it can have a much more significant role both in evaluating current practices and in making scientifically based recommendations for better land-use practices.

In this chapter I survey traditional and more innovative land-use systems in the La Selva region, and emphasize opportunities for improvements, summarize Organization for Tropical Studies (OTS) involvement in research on the ecological basis of sustainable and productive land-use systems, and present recommendations for future agroecological research in the region.

ECOLOGICAL CONDITIONS OF THE ATLANTIC REGION

La Selva Biological Station is in the Atlantic Region of Costa Rica at its western border with the Northern Region. Except for the northern portion of the Talamanca mountain range, a small portion of the Cordillera Central, and small, extinct volcanoes, the region lies below 100 m elevation. The average slope is 6° (11%) in the upper parts, and 1°–2° (1%–3%) in the lower areas. Because of the flat terrain, swamps and areas with poor drainage are common. The general geology consists principally of recent alluvial deposits and lahars (Madrigal and Rojas 1980). The indigenous vegetation in the region was tropical rain forest.

The Atlantic lowlands are crossed by the only rivers in Costa Rica that are navigable for any distance from the coast: the San Juan and its tributaries, the San Carlos, and the Sarapiquí. Because of the influence of the trade winds and strong convection forces, the region receives abundant precipitation, with annual means from 2,000 to 9,000 mm. In many years there is no pronounced dry season, and farmers generally need to adapt to an excess rather than to a scarcity of water. Heavy rainfall and heat made the area inhospitable to European settlers, and significant settlement occurred only in the twentieth century.

In a general soil fertility survey of Costa Rica the Sarapiquí District was diagnosed as having problems of low fertility because of low pH (<5.5), high aluminum saturation (10%–50%), low cation exchange capacity (<5 meq/100g), low calcium (<4 meq/100 g), low magnesium (<1 meq/100 g), and low extractable phosphorous (<10 μg/g) (Bertsch 1986). Levels of micronutrients and potassium were considered adequate for most agricultural crops. Nitrogen is not generally included as part of routine soil tests because levels of soil total nitrogen are not a good indicator of nitrogen availability, and nitrogen demand by crops is usually measured with fertilizer experiments. Nitrogen fertilizers are heavily used in agriculture in the Atlantic lowlands, indicating that low nitrogen may be an additional factor in the region's generally low fertility (E. Bornemisza pers. comm.). Soils of the Sarapiquí area, thus, have low fertility and potential problems with acidity and high aluminum saturation. Fifty percent of the Río Frío re has been placed in class 3 land-use capability (Tosi 19 which corresponds to conditions of moderate to low soil fe ity, strong acidity, and moderate to poor drainage. These c acteristics restrict the possibilities for crop species (U 1984). Research on soils at La Selva is summarized in cha four. La Selva's soils share many features with other soil the Costa Rican Atlantic lowlands as well as with other gions of the lowland humid tropics; thus, soils research a Selva has broad regional as well as local significance.

TRADITIONAL LAND USE IN THE ATLANTIC LOWLANDS

The present land-use pattern in the Atlantic Region is comp and is not simply related to the ecological conditions that fa each activity. Land-use patterns can be better understood examining the history of agricultural colonization in the gion as well as the socioeconomic and ecological factors fluencing agricultural production. In this section I examine traditional land uses in pre-Hispanic times and the chang resulting from colonization by Hispano-American settlers the late-1800s to 1900s.

Pre-Columbian Period

Archaeological investigations carried out in the Atlantic lo lands reveal a cultural complex similar to that in northe South America with dietary habits and ceramics most li those of people inhabiting the coastal Caribbean plains of C lombia (Hall 1984). It is likely that a single humid tropic forest culture extended from the Amazon and Orinoco riv basins along the Caribbean coast to Honduras (Snarsk 1975, 1976).

Agricultural practices in the Atlantic lowlands in pr Columbian times apparently had a very strong South Amer can influence: most of the crops grown in the Atlantic lo lands were native to tropical forest zones in the northern p of South America (Hall 1984). These include tuber crop such as cassava (*Manihot esculenta*) and tiquisque (*Xanth soma violaceum*). Cultivation of pejibaye (peach palm, *Bactr gasipaes*) spread from the Orinoco valley. Cacao (*Theobrom cacao*) was also apparently introduced from South Americ and its pods were used in religious ceremonies in the Amazo and Orinoco river basins (Stone 1977). It was generally be lieved that corn was introduced to the region from Mexico a Guatemala. Corn with South American characteristics, date A.D. 100–300, however, has been discovered in excavations the Atlantic lowlands (Snarskis 1975), suggesting that the v riety grown here was of South American origin. Storage corn must have been a problem because of the very humi climate of the region. In contrast, root tubers such as cassa produce year-round and store well in the ground, from whic they can be harvested as needed.

During pre-Columbian times land-use patterns allowed f the regeneration of most forests. The relatively low populatio density permitted long periods of forest regeneration follow ing slash and burn agriculture (Hall 1984). It is only durin the twentieth century that settlers of European descent acce erated the deforestation process.

gricultural Colonization

ettlement of the Atlantic lowlands resulted from three princi-al phenomena: spontaneous migrations from other regions of he country; the establishment of banana plantations by U.S. ompanies; and government colonization policies such as the stablishment of prison colonies in the 1950s to 1960s and e more recent settlement projects of IDA. These different ources of colonization have determined land-use and tenure ystems, agricultural practices, and the market economies of e region. These historical patterns also influence the kinds f changes that are feasible as well as the mechanisms appro-riate for implementing change.

he Early Settlements: Subsistence Agriculture. After ree centuries of European settlements largely restricted to e Central Valley, colonists began moving out in all directions out one hundred years ago. These early settlers were few d faced isolation from the Central Valley because of rugged ountains and a nearly total lack of roads and marketing po-ntial for their products (Sandner·1961).

During this period forest cutting by individual pioneers or nall groups of settlers with machetes and axes removed the rgest trees, leaving stumps and understory seedlings to dry r burning. Commercial wood exploitation was very limited cause of inadequate transportation and the absence of saw-ills, markets, and technologies suited for tropical forest spe-es. Small amounts of wood were used by settlers for con-ruction and for firewood; a few stems were sold to local dustries for furniture and construction. Commercially unde-rable species were burned or left to decompose (Tosi 1971, 74). Sandner (1959) estimated that 60%–80% of the area forested between 1860 and 1960 was initially used for shift-g agriculture. Settlers could buy public lands at low prices d obtain property title once the land was under cultivation. practice, however, many farmers settled without claiming operty titles (Hall 1984).

The small subsistence farms operated very much like in-genous agriculture. After two to three years of cultivation, lds were abandoned and new areas were cleared. On subsis-nce farms, traditional home gardens were planted to meet usehold needs. These gardens grew basic foodstuffs: rice, m, plantains, beans, "robusta" coffee (adapted to low eleva-ns), sugar cane, and various fruits and vegetables. These all farms also had chickens, pigs, and, frequently, a few ws. Some of the products were occasionally marketed to tain cash for other needs. With relatively low population essure, shifting agriculture was a viable alternative for the rly colonizers. In many areas of the Atlantic lowlands, how-er, ecological conditions were not suitable for agriculture; lonists found that yields were too low for sustained cultiva-n, and settlers often sold their land to speculators and oved to other areas (Lambert 1969).

e Beginnings of Extensive Cattle Ranching. Large hold-gs in the area were acquired in most cases through buy-outs small settlers as described. On large properties extensive ef cattle ranching was the most feasible land use before the velopment of modern transportation (Sandner 1961) be-use live steers could be transported to markets without sig-ficant deterioration. Efforts to establish plantations in inaccessible regions such as the Sarapiquí valley often failed because of lack of railroads or paved roads for transportation of relatively fragile agricultural products to potential markets (León 1943).

The initiation of beef exports to United States markets in 1957 provided a major new economic incentive to the cattle industry in Costa Rica. Ranchers began to direct their efforts toward the colonization zones, and in one decade (1963–1973) the area in pasture in Costa Rica increased 62% (Parsons 1983). The center for ranching in Costa Rica traditionally has been Guanacaste Province because of its long dry season. With strong economic incentives after 1957 landscapes in Valle del General and Coto Brus, Turrúbares, Puriscal, Parrita, San Carlos, Sarapiquí, and Arenal became increasingly dominated by cattle pastures. The more humid areas of the Atlantic lowlands were spared from cattle encroachment, and only in the mid-1960s were cattle ranches established in this area.

In the late 1950s many farmers in the Atlantic lowlands planted rice on the flat areas of their farms. This "rice fever" lasted until the mid-1960s, when most farmers stopped growing rice because of the difficulty in controlling weeds after two to three years of cultivation. During the "rice fever" areas not suited for rice were dedicated to beef cattle. With higher beef prices in the mid-1960s ranching expanded to occupy the old rice fields.

Although these conditions promoted the establishment of ranches in the Atlantic lowlands, the region is not well-suited ecologically for extensive cattle raising, and management practices were inadequate. There were very few permanent workers on cattle ranches, and displaced farmers made up most of the labor force. Natural grasses were very unproductive, and exotic pasture species with higher yields were introduced only about fifteen years ago. As a result, productivity of cattle ranching was very low and extensive areas were degraded by inappropriate management practices and overgrazing (Parsons 1983).

Plantation Agriculture: The Beginnings of High-input Commercial Production. In the late nineteenth and early twentieth centuries, a number of plantations with similar characteristics were established in the Costa Rican Atlantic Region as well as in several other areas of the lowland humid Latin American tropics. Extensive virgin lands were then still available for agriculture, and governments exerted little control over the activities of multinational companies (Casey 1979). In the Atlantic lowlands of Costa Rica, banana plantations were started by the United Fruit Company (United Brands) in the Limón area in the late 1870s. Limón was the principal region for banana cultivation until the mid-1930s. Banana production declined after 1913 because of low prices, high incidence of fungal diseases (Sigatoka and Panama diseases caused by *Micosphaerella musicola* and *Fusarium oxysporum*, respectively), soil degradation, and labor unrest. By 1942 banana exports from Limón had ceased, and the region underwent severe economic depression. Alternative crops were planted (cacao, rubber, subsistence food crops) in the 1940s and early 1950s.

In the early 1950s considerable migration from other regions of Costa Rica to the Atlantic lowlands took place with settlers occupying new land as well as areas abandoned by

United Fruit. As the railroad system was expanded to Río Frío and Estrella, Standard Fruit Company, a subsidiary of Dole Fresh Fruit Company, installed banana plantations in 1956 in the areas near Limón previously occupied by United Fruit as well as in the Río Frío zone just east of La Selva. In the 1990s Standard Fruit expanded its operations to areas northeast of La Selva along the Río Sucio. United Fruit has moved its operations to the Pacific Coast where it grows mostly African oil palm although recently it has come back to the Atlantic Region to reinitiate banana production. In the mid-1960s the Costa Rican government gave incentives for banana production ("crédito bananero") to stimulate the establishment of plantations by local companies. By 1979 Costa Rican companies produced approximately 60% of bananas in the Atlantic Region although they still market their produce through Standard Fruit.

The banana companies established their plantations on the most fertile, well-drained riparian soils. In the early days of banana plantations (late 1800s) with intensive land use and inappropriate soil management these good soils deteriorated after seven to ten years of monoculture and had to be fallowed for about ten years before they could be put back into banana cultivation (Casey 1979). Immigrants from Jamaica and Costa Rican migrants from other regions of Costa Rica worked in the plantations. Independent banana producers also grew bananas on farms ranging from less than 10 ha to more than 20,000 ha and sold their produce to United Fruit (Casey 1979). Local farmers also had home gardens with subsistence crops, apart from bananas. Jamaican immigrants introduced Afro-Caribbean subsistence production systems, including polycultures with bread fruit, citrus, plantains, cassava, yams, and sweet potatoes for food and cacao and coconuts as cash crops. While the banana industry flourished, however, subsistence agriculture did not meet local demand for foodstuffs; most of the products for consumption by banana workers and local farmers were either imported or brought from other regions of the country (Jones and Morrison 1952). This was beneficial for the banana companies, who sold those products in their own stores.

In contrast to areas colonized by individual or group settlers, plantations were established from the start as highly specialized commercial agriculture. Standard Fruit Company grows "grand Cavendish" and "dwarf Cavendish" varieties of bananas, which are exported to the United States and Europe through Limón. Bananas are an ecologically demanding species; they require high temperature, high humidity, and abundant soil nutrients. They are a typical large-scale plantation crop because of high risk of crop failures from natural catastrophes and the high costs of site preparation, drainage, and labor administration. Banana cultivation requires intense use of agrochemicals: fertilizers are applied monthly (N, K, Mg, and micronutrients), and nematocides are applied four times per year. Fungicides and insecticides are also applied frequently. Fungicide applications are aerial; fertilizer and nematocide applications are manual. Some areas around Río Frío were abandoned by Standard Fruit because the high incidence of fungal diseases and nematode damage required such intensive application of agrochemicals that banana cultivation was no longer profitable.

In contrast to bananas, cacao has played a minor role in the development of commercial plantations in Costa Rica. In t Atlantic lowlands cacao was a major export crop in the 194 and early 1950s (between the banana boom periods) as in t nineteenth century. With the reestablishment of the banana i dustry, however, cacao took a secondary position. In fact, c cao does best in areas with an extended dry season and t Atlantic lowlands are not ideal for the crop because of hi annual rainfall and lack of a well-defined dry season. T strong rains and high humidity favor the spread of fungal di eases (e.g. *Monilia roreri*), delay or impede ripening of fruit and complicate their collection and processing. The norther plains (especially Upala) áre ecologically more appropriate.

In the Atlantic Region of Costa Rica cacao is mostly grow on farms managed by individuals or families with far less ad vanced technology than is used in bananas. In the 1990s in th Atlantic lowlands most cacao is grown on land abandone from banana plantations or in remnants of forest. Cacao has a highly fluctuating price on the international market, and interest in its cultivation follows these price cycles. Because of high risks of crop failure and fluctuating prices, the Costa Rican Ministry of Agriculture recommends that farmers who grow cacao should diversify their production with coconuts, tuber crops (cassava, tiquisque), and spices (black pepper, ginger).

Plantation agriculture had and still has a strong socioeconomic impact in Costa Rica. As foreign companies converted land, installed drainage and transportation systems, and built ports and living facilities, they contributed to development of large areas. Until recently, however, most revenue from these enterprises left the country, yielding little benefit to the Costa Rican economy (Casey 1979). The establishment of plantations resulted in a rapid transformation of the forested landscape into fruit monocultures, but these also declined very rapidly when the banana industry was hit by fungal diseases and economic depressions. Hundreds of hectares of secondary forest developed in the areas abandoned by United Fruit in the early 1900s.

Despite past and present problems, bananas are still seen as a key crop for regional economic development owing to relatively favorable conditions in the Atlantic lowlands and the employment opportunities offered. In the 1990s the banana companies contribute much more to the local and national economy than in the past. They hire a higher proportion of local technical and administrative personnel, and the government imposes a tax on exported bananas and on company revenues (Gaceta Oficial, Government Public Document, 1978).

In the late-1950s to 1980s the construction of good roads eliminated the principal barrier to development of commercial agriculture in the Atlantic lowlands. An ongoing secondary colonization process began on land already partially deforested and populated (see chap. 23).

LAND USE IN THE ATLANTIC REGION AND FUTURE PROSPECTS

Land-use patterns in the Atlantic lowlands of Costa Rica changed over the 1980s in response to increased population, the improvement of roads, and a general trend in the country to diversify agricultural production. These changes, however have often outstripped technical expertise and the capacity of agricultural extension agents. For example, technical problems in cacao management have restricted its expansion while enthusiasm for the cultivation of a promising ornamental, *Dracaena* spp., oversaturated the market. Thus, the transition from subsistence agriculture and extensive cattle raising to more intensive land-use systems is not complete: large areas (up to 70% of the area in farms in many districts) are still ranches. In spite of low productivity per hectare a cultural predilection for ranching sustains the practice. In many cases land is deforested and fenced, and cattle are installed just to claim he land. Additionally, lack of adequate markets and infrastructure has limited the production of food crops for local onsumption (González Vega et al. 1970). In spite of better ommunications and more and better roads, the market structure is still not adequate to foster the production of many crops or local consumption or for export.

Land-use patterns in the Atlantic lowlands are changing ontinuously in response to changes in markets, agricultural echnology, and economic policies. Between 1963 and 1982 e area in farms tripled, and the area in pastures increased everalfold while the forested area decreased sharply (table 4.1). Among agricultural crops, perennial crops predominate, mostly reflecting the large areas in bananas (table 24.1). present the principal agricultural practices in the Atlantic Reion, their main constraints, and potential for improvement ext.

griculture

the general statistics for the most commonly grown crops the Atlantic Region presented in table 24.2 the area in cacao ay be an overestimate because many plantations have been andoned owing to fungal diseases (*Monilia*). The most freent annual crops comprise a mix of subsistence and comercial crops (table 24.2). The data in table 24.2 are for the tire Atlantic Region, including farms of all sizes. Most rms in the region are small (table 24.3): 68% of farms are aller than 20 ha and 19% are smaller than 4 ha. Farms less n 20 ha, however, cover only 16% of the total area. Medium 0–200 ha) and large farms (>200 ha) dominate. These areas e primarily devoted to bananas.

A different picture of crop preferences emerges if small rms are examined separately. In a survey of recently established IDA settlements (farms <20 ha) in the Río Frío region near La Selva (UCR 1984) 63% of the land owned by these farmers was under cultivation; the rest was unused principally because of inadequate economic resources (table 24.4). Of the land under cultivation 39% was planted to annual crops and 23% to perennials, and 38% was used for cattle. Small farmers grew a mix of annual and perennial subsistence crops, and more than half of these farmers combined cattle with crops. Cattle were raised for market and local consumption. Although most crops were grown in monoculture, some examples of crop combinations were cacao and cassava, corn and beans, plantains and corn, plantains and beans, and plantains with cassava and cacao.

ble 24.1 Land use in the Atlantic Region, 1963–1982

	Total Hectares Covered		
nd-use Category	1963	1973	1982
nual crops	—	ca. 76.000	19.000
rennial crops	39.100	44.400	78.300
sture	35.000	71.800	232.900
ea in farms	205.200	140.800	—
nagricultural land (mostly forest)	767.500	728.200	352.500

Sources: Dirección General de Estadísticas y Censos ([DGEC] Naal Office of Statistics and Census) 1974 and 1975: Unidad Regional Asistencia Técnica ([IDA/RUTA] Reginal Unit for Technical Assisce) 1984 in Van Sluys et al. 1989.

Table 24.2 Principal crops in the Atlantic Region, 1973

Crops	Total Area (ha)	Farms (No.)
Perennial		
Bananas	20.698	802
Cacao	17.224	1.935
Plantains	1.551	664
Coconuts	940	781
Coffee	485	343
Annual		
Corn	5.245	1.532
Rice	753	474
Cassava	566	553
Beans	171	189
Sugarcane	146	122

Source: DGEC 1974, in Van Sluys et al. (1989).

Table 24.3 Farm size distribution in the Atlantic Region, 1984

	Distribution				
Farm Size (ha)	Number	Percentage of Total	Area (ha)	Percentage of Total	Mean Size (ha)
<4	1.754	19	3.400	1	2
4–20	4.445	49	43.000	15	10
21–200	2.577	29	125.100	44	49
>200	252	3	286.200	40	455
Total	9.028	100	286.200	100	32

Source: Preliminary results of 1984 Agricultural Census in Van Sluys et al. 1989.

Perennial Crops. *Bananas* are largely produced and exclusively marketed by foreign companies; the Costa Rican companies sell their produce through Standard Fruit. The Costa Rican Association for Banana Production (ASBANA) supports local producers with technical research and extension. As noted, bananas are not a good crop for small farmers owing to high production costs. Commercial banana plantations, however, are expanding in the region.

Plantains are grown by small farmers for home consumption, whereas the produce of midsized farms is sold to local markets, principally San José; small amounts are exported. In general, both inputs and productivity of plantains are lower than bananas. In the early-1980s plantains began to be af-

Table 24.4 Frequency of crops in the Río Frío region

Crop	Cultivated Area[a] (% of total)	Farmers[b] (% of total)
Corn	20	68
Plantains	18	38
Cacao	14	30
Beans	8	64
Cassava	7	57
Aroids	7	45
Pineapple	7	30
Rice	6	30
Bananas	5	11
Pejibaye	4	11
Coffee	2	11
Fruit crops	2	8

Source: Univerity of Costa Rica 1984.

[a] Percentage of total area cultivated by small farmers.

[b] Percentage of farmers who grow them.

fected by the Sigatoka disease, and cultivation was drastically reduced (Van Sluys et al. 1989).

Cacao was the principal crop on small and midsized farms, especially in the southern part of the Atlantic Region, until 1978 when the *Monilia roreri* fungus became a serious problem. *Monilia* attacks only the pods; it can be controlled by planting resistant hybrids, eliminating the infected fruits, and reducing shade (intense shade creates a humid microclimate that favors the spread of the fungus). These measures are costly, however, and many plantations were instead abandoned. In the 1980s, there was renewed interest in cacao cultivation and new government incentives (MIDEPLAN 1984).

Coconuts are grown for oil and fresh fruit. In the Río Frío area coconuts are grown for local consumption. Most coconut plantations are along the Caribbean coast north and south of Limón. Plantations of dwarf coconuts can be found elsewhere, but these are generally small and show low productivity (Rojas 1978).

Coffee is cultivated primarily near Volcán Turrialba and along the Siquirrès-Turrialba road. Most areas of the Atlantic Region are too low in elevation for optimal productivity of coffee. In lower areas conditions are better suited for other crops such as macadamia.

Macadamia and pejibaye are new to the Atlantic Region, and both are promising. At present, they are attractive only to large-scale farmers who have access to export markets. There is, however, a small national market for pejibaye fruit and heart of palm.

Annual Crops. *Corn* is a subsistence crop grown by small farmers throughout the Atlantic Region. On midsized farms, especially near Guácimo and Cariari, it is an important crop. The produce is sold to Consejo Nacional de Producción, ([CNP] National Production Council) at subsidized prices. Corn is not very profitable, apparently because of the high costs of chemical weeding, insect control, tillage, harvesting, and transportation.

Rice is grown as a commercial crop on midsized farms, especially in the areas around Batáan-Matina (NNW of Limón). Its production is highly mechanized and costly as result.

Cassava is grown by small farmers for subsistence a on midsized farms for the export market, especially to t United States.

Most Promising Crops for Agricultural Expansio Among the more innovative crops the cultivation of aroid with edible tubers, including white tiquisque (*Xanthosom sagitifolium*), red tiquisque (*X. violaceum*), and malanga (*Co ocasia esculenta*) is very promising for export (especially t the United States where demand for them is increasing amon the growing Hispano-American population). These crops ar well adapted to the region, but they are highly susceptible t viral diseases. Because crops are propagated vegetatively, viral diseases are easily spread when new plantings are established. Investigators at the University of Costa Rica (UCR) are working to produce virus-resistant strains.

Ornamentals, principally foliage, ferns, itabo (*Yucca elephantipes*), and others are grown mainly for export to the United States; their cultivation is expanding after the opening of additional export markets (Japan, Europe). Ornamentals require intensive management and are, thus, an important source of employment.

At the UCR experimental farm in Río Frío, the adzuko bean (*Vigna angularis*) is under study; it has edible seeds and good yields, can be grown year-round and is disease tolerant. The lack of acceptance by consumers accustomed to black beans may limit its expansion.

Peach palm (pejibaye, *Bactris gasipaes*) cultivation for heart of palm was begun by Industrias de Desarrollo Agropecuario ([INDACO] Institute of Agricultural Development) for local industry and for export. This company at present absorbs most of the local crop. The species is well suited to the Atlantic Region and maybe an interesting alternative for cash income as the market expands.

Among fruit trees, citrus appears most promising. Cultivation of oranges for export to the United States is expanding, and a juice-processing plant (for oranges, pineapple, and other fruits) will soon be operating in the Sarapiquí area, built by Tico-Fruiti, a private company with Florida producers as partners.

The cultivation of bamboo (*Bambusa guadua*) for home construction and furniture is being promoted in the Atlantic Region through a project recently begun with financing from the Dutch government and the United Nations Development Program and technical assistance from IDA, DGF, and MAG.

Other crops that have been introduced or improved by UCR are fruit trees such as mamón chino (*Litchi chinensis*), carambola (*Averrhoa carambola*), water apple (*Eugenia malaccensis*), messina lemon (*Citrus aurantifolia*), and grapefruit (*Citrus grandis*). These should be well suited to the region, and they merit exploration. Examples of other innovative crops include chilis (*Capsicum* spp.), passion fruit (*Passiflora* spp.), papaya (*Carica papaya*), cardamom (*Elletaria cardamomo*), achiote (*Bixa orellana*), and medicinal plants mainly for the Costa Rican market for herb teas.

Ecological Constraints on Agricultural Production. Agricultural production in the Atlantic Region has a low yield/

ost ratio owing to problems with weed control, pests and dis- ases, soil drainage and fertility, and labor administration. The cological problems are aggravated by the high costs of gricultural inputs, lack of credit, and high interest rates Van Sluys et al. 1989).

Although the climate is relatively uniform, occasional dry eriods or excessive rains may impede growth or ripening of ops. In some years, as in 1985, hurricanes may considerably mage bananas (Van Sluys et al. 1989). Drainage problems cur in large areas, limiting crop choices, increasing costs, d interfering with management practices.

Weeds are a major problem for annual crops; as men- oned, high costs of weed control in rice ended the "rice ver" in the Sarapiquí valley in the mid-1960s. Weed control labor intensive and involves the use of toxic and expensive rbicides that may contaminate soil. Pests and diseases cause nsiderable losses (e.g., rotting of corn and cacao) and may crease production costs (e.g., *Monilia* control in cacao). oblems may be serious enough to discourage the cultivation certain crops as was the case with Panama disease in ba- nas and *Monilia* in cacao. A few management recommenda- ns exist to solve pest and disease problems, including selec- n of more favorable areas (drier areas for plantains), nipulating the microclimate (reducing shade in cacao plan- ions), and timing production (planting corn so that it ripens ring a relatively dry period).

Management problems are related to soil characteristics g., bad drainage, steep slopes) and climate (e.g., excessive ins). Problems of low soil fertility will probably increase th increasing pressure on the land and lack of appropriate actices to maintain soil fertility (Van Sluys et al. 1989).

frastructure and Institutional Constraints. Constraints lude financing, access to agricultural inputs, availability d transfer of agricultural technology, and physical access to rkets (Van Sluys et al. 1989). Many small farmers have lit- access to credit. Land titles are needed to obtain credit, and erest rates are high. The establishment of perennial crops, particular, requires high initial investments and many years interest payments before any benefits accrue. Labor costs generally high because the large banana companies in the jon pay relatively good salaries. Many farmers need to rk outside the farm to supplement their incomes (Van Sluys l. 1989).

Both farmers and government employees in charge of ag- ultural extension point to a lack of technical information on ricultural crops. Most of the available information comes m outside the region, which means that local experience th many crops is very limited. The foreign banana compa- s have developed their own technology, but they are not lling to share it with local producers. Even when local tech- logy exists, its transfer is often inadequate. For example, as ntioned, the technology to control *Monilia* disease in cacao nsists of planting resistant hybrids, pruning trees, reducing de, and eliminating infected pods. Many farmers have ard about these techniques, a few know how to apply them, t the majority are not using these recommendations. Appar- tly, both research and extension are not effectively reaching mers (Van Sluys et al. 1989).

Access to good markets is another constraint to agricultural production. For some products, such as corn and rice, CNP guarantees the purchasing price, but it is not certain how long this policy can be sustained by the government. For other products (e.g., plantains) there is a free market. The market for export crops, such as bananas, roots and tubers, ornamentals, and macadamia, is controlled by foreign companies, which generally have foreign headquarters. Small farmers, then, have access to these markets only through foreign companies, if at all.

Farmers need to improve this situation and have the potential to do so, but few farmers have access to capital, inputs, technology, and markets. The potential of alternative crops such as ornamentals, cardamom, macadamia, and pejibaye will not be realized as long as these constraints remain.

Livestock

Of the large increases in pasture areas in the Atlantic Region since the 1970s (table 24.1) only a small portion is used for intensive milk production. Most is used for extensive beef production with productivity values per hectare lower than many crops. The principal farming systems that include cattle are

Farms with dual purpose cattle (meat and milk) producing milk for consumption on the farm. Most such farms are small and also grow annual subsistence crops (corn, beans), as well as some perennial crops (cacao, plantains). Some may also have pigs and poultry. Sometimes part of the family's income is from sources outside the farm. Generally, productivity is very low; lack of cash and credit are the principal constraints to improvement.

Farms with dual purpose cattle producing milk for market. Dairy products are marketed locally and can generate a regular income that can be invested in improved pastures and stock and mineral supplements for cows. The most common races of cattle are Brahman, Indo-Brasil, Holstein-Frisian, and Jersey.

Specialized dairy farms. Generally, these are larger farms (up to 100 ha), with modern dairies and substantial investment in pastures, feed supplements, and veterinary care for cows. Products are generally sold commercially through large dairy companies (Borden, Dos Pinos).

Beef cattle ranches. These ranches either raise calves for sale to other ranches at about 150 kg, or eight months, or buy calves at this age and raise them to 500 kg (2–2.5 more years). Both operations occasionally take place on the same farm. Ranching at this scale requires improved pastures on fertile, well-drained soils. Such ranches often occupy recently cleared land in areas where land is still cheap.

Farms with pigs. A few specialized farms raise pigs, using banana residues and waste from dairy farms as feed.

Among the IDA farmers of Río Frío raising dairy cows for milk and cheese production generally occupies more than one-third of the area in farms, both at the subsistence level (fewer than four cows) and at the commercial level. Dairy farming has increased because many farmers in the IDA settlements came from the San Carlos valley (Northern Region in the Atlantic lowlands) and are familiar with this activity.

Dairy farming is seen as a promising activity in spite of its requirements: technological knowledge, high investments, and reliable markets (UCR 1984). CATIE and IDA promoted dairy farming in the region through credits, technical advice, and marketing facilities offered by the CATIE Dairy Farming Program in the 1970s to early 1980s; CATIE has ceased these activities.

Despite institutional efforts to promote technological improvements in dairy farming innovations are still not widespread among farmers. Mostly native grasses are used in pastures although they support only low production. Introduced grasses, such as *Cynodon nlemfuensis*, *Brachiaria decumbens*, and *Pennisetum purpureum*, are considered by UCR researchers to be most promising in yield and nutritional value for dairy cattle in the region.

In contrast to dairy cattle farming beef production is an extensive and almost exclusively commercial activity. Most beef cattle in the region are range fed, but even the more productive exotic pasture grass species are low in protein and fiber (Parsons 1983). Because of this dependence on pastures, most ranches are large and the mean stocking rate is only one animal per hectare. As a result, ranching generates few employment opportunities and promotes migration to cities. The ecological impacts of expansion of beef cattle ranching have been incalculable, including serious problems of soil deterioration (Parsons 1976). Excessive grazing may result in soil compaction, which exacerbates drainage problems and leads to soil erosion on steep slopes. With poor management productivity is low and after a few years new areas are cleared and put into pasture. Forest regeneration on abandoned pastures is often slow because of soil deterioration and distance from seed sources in large cleared areas.

Livestock Management Problems. The principal technical problems of dairy and beef cattle raising are high production costs that are not compensated by high prices, dependence on grasses of low productivity and quality, little integration with agriculture (e.g., crop residues and manure are underused as feed and fertilizer, respectively), and high incidence of cattle diseases, which are often related to the hot, humid climate and muddy pastures (Van Sluys et al. 1989).

Institutional Problems with Cattle Production. The problems encountered in livestock production mirror those encountered in agriculture (Van Sluys et al. 1989). Extension and veterinary services are few and, therefore, ranchers find little useful advice. Ranchers have little control of market institutions, which have been poorly organized (e.g., until recently, beef cattle were sold in Alajuela, and small farmers generally had to sell to middlemen). Large producers depend on the international market and confront fluctuating prices for their products. Whether selling to middlemen or directly to dairy companies, farmers must organize transportation themselves. There is little opportunity to expand the national market for dairy products because most such products are too expensive for the majority of the population to buy.

Dairy and beef cattle ranches can be most feasibly improved by intensifying management rather than by expanding onto marginal lands. Key strategies are improving pastures by planting more productive fodder species, using rotational grazing practices to avoid overgrazing and decrease risks soil compaction and nutrient depletion, and adopting agrosi vopastoral systems that include fodder trees in pastures and living fences. CATIE's livestock project is experimenting wit these techniques near Guápiles and at the Los Diamantes Ex periment Station. These more intensive practices can now seen on a few farms in the vicinity of La Selva. If these prac tices are financially feasible (i.e., if increased productivi pays for the additional costs of intensive management), the may represent viable alternatives for management of ranche in the region.

FUTURE DIRECTIONS IN AGROECOSYSTEM RESEARCH IN THE ATLANTIC REGION

Apparently, there is still no clear consensus as to the mos profitable agricultural activities in the Atlantic Region. Agriculture is developing quickly and in different directions depending on the initiatives of individual land owners, investors in commercial agriculture and forestry, and the national and foreign institutions dedicated to research, education, and development. Many production systems are economically and ecologically sound (e.g., cultivation of pejibaye, use of living fences in farms, intensive dairy farming). Other systems have problems but are still practiced because they are traditional in the region (e.g., cacao and rice production, extensive cattle raising). In many cases the availability of capital is the principal factor influencing the choice of a system (e.g., bananas, macadamia, and large-scale production of ornamentals require considerable capital investment). Farmers are experimenting with production systems according to their own interests (e.g., with techniques for growing macadamia). National and international institutions (MAG, UCR, CATIE) are investigating and promoting production systems for specific sectors (generally, the small farmers of the region).

Any organized effort to promote sound agricultural development should start by dividing the region into subregions of relatively homogeneous ecological and socioeconomic conditions (e.g., Horquetas, Río Frío, Guápiles, the Caribbean coast south or north of Limón). Within these subregions the sectors to which efforts are directed need to be clearly defined (small-, medium-, or large-scale farmers). Land-use capability must be assessed for each subregion, considering slope, soils, and other production factors to determine appropriate land uses (intensive agriculture, cattle, forestry, or agroforestry). Finally, research and extension should begin by examining existing ecologically and economically sound practices and should concentrate on improving them and on designing and promoting new systems if needed.

Agricultural diversification should supply farmers' needs for subsistence crops and cash by promoting cultivation of home gardens and of cash crops for local markets and for export. Agricultural research should focus on crops that are (or are expected to be) most profitable or those that contribute strongly to subsistence nutrition. In a small country such as Costa Rica it is possible to saturate markets quickly, with negative results for otherwise very promising crops such as passion fruit and chilis. Research should be concentrated on crops that are accepted by farmers, such as pejibaye and corn; those that are ecologically appropriate (macadamia, cardamom, pejıye); those with excellent market potential even though they ıy have some technical problems (rice, plantains); and the ditional subsistence crops (cassava, beans, bread fruit, uisque, fruit trees, among many).

Agricultural diversification at both farmer and regional els can also be attained by using agroforestry practices, ide- y, combining subsistence crops with more marketable or ex- rt species. Agroforestry systems may successfully combine ıber trees with cacao, rubber, coconuts, and ornamentals. ıny annual crops, however, are shade intolerant and, thus, not suited for agroforestry. Trees and crops may be profit- y combined in the early stages of tree plantations (first to ond year, depending on the species and planting distance) en trees do not provide much shade. Agroforestry practices ıld decrease the need for weeding, and trees may have itive effects on soil properties (Montagnini 1990a). Many as in the region should be better suited for trees than for ventional or mechanized agriculture because of steep pes, low fertility, and problems with soil compaction. On ividual farms land that is not suited for agriculture can be d to grow trees in association with crops. Besides, many oforestry practices require less labor than intensive agri- ure and allow for more flexibility in management and tim- of harvest (Kapp 1989). The following agroforestry tems already are present in the Atlantic Region (Kapp 9):

- Cacao, coffee, and other perennial crops with native trees for shade, many of which are valuable timber species (for a complete list see Kapp 1989)
- Pastures with native trees (same as those with perennial crops)
- Annual crops with native trees
- Crops or pastures in alternating rotation with tree fallows
- Living fences (*Gliricidia sepium*, *Diphysa robinioides*, *Bursera simaruba*, and others)
- Mixed home gardens with food crops and many fruit and timber trees

ortunities to improve these systems include

- The promotion of better spatial designs (e.g., planting in lines rather than haphazardly to facilitate management practices)
- Selection of tree species more appropriate for combinations with crops (eucalypts and pines, very much used in the region, are not well suited for combinations with crops; *Gmelina*, also common in the region, and many native trees are better)
- Choice of shade-tolerant crop or pasture species (cassava and other root crops are more shade-tolerant than corn or rice, among forage species legumes are more shade tolerant than grasses)
- Developing detailed management schemes (e.g., timing pruning and thinning to provide more light and increase inputs in the form of residues from pruning to the soil when crops can most use these resources).

To design improved systems that will be accepted by farm- the socioeconomic and institutional constraints described ıe previous sections must also be considered.

OTS INVOLVEMENT IN EDUCATION AND RESEARCH ON SUSTAINABLE LAND-USE SYSTEMS IN THE ATLANTIC LOWLANDS

The involvement of OTS in agricultural research is a very recent phenomenon that began with small projects by participants in OTS agricultural ecology courses inaugurated in 1985. OTS offered its first agroecology course in Spanish in 1988, an outstanding promotion of agroecology education in Latin America. Research by course participants consists of projects completed in a few days although some students return for longer-term research. Topics examined are varied: herbivory, soil chemistry and microbiology, mycorrhizae, nitrogen fixation, crop ecophysiology, general surveys of socioeconomic aspects of land-use patterns, crop preferences, and land-use alternatives. Course projects also orient theses and other long-term projects. Most importantly, agroecologically oriented courses can influence the philosophy of those already involved in agricultural or forestry research, education, or practice toward greater concern for environmental issues and a more integrative, holistic approach to agriculture and forestry.

Increased interacuon between OTS and Costa Rican institutions involved in agricultural and forestry research, training, and extension is desirable. Students in course projects can take advantage of data and recommendations resulting from local agricultural and forestry projects, and, in turn, provide data and innovative ideas toward solving specific problems. OTS research fellowships for students are making a good contribution by funding projects by Latin American scientists at La Selva. OTS might additionally strengthen ties between foreign researchers and local scientists by helping to identify local faculty to serve as advisers to foreign students working on applied problems at La Selva. Through its connections with its Costa Rican member institutions OTS can also facilitate collaborative research involving local and foreign scientists. Especially when one works on applied research, local expertise is valuable to ensure that the project is well-grounded in social, political, and institutional realities.

Other educational efforts can be implemented through OTS's Environmental Education Program. Initially focused on ecology and conservation, this program has recently expanded into agroecology and forestry through interaction with forestry projects at La Selva.

RECOMMENDATIONS FOR AGROECOLOGICAL RESEARCH AT LA SELVA

As noted, La Selva has soils that are representative of the Atlantic Region of Costa Rica as well as of many lowland areas in tropical America. Thus, research on soil fertility, soil/plant interactions, soil chemistry, and microbiology have potential for wide applicability. Research on management of traditional and more innovative agroecosystems could be applicable to other areas in Latin America as evidenced by the similarity of traditional cropping systems across broad areas of the lowland wet tropics.

Agroecological research at La Selva should focus on the most promising land-use systems for the economic benefit of farmers and the country, including subsistence crops. Existing forestry plots at La Selva can be used by OTS researchers and students in collaboration with the principal investigators of the projects to study management techniques, impact of trees on soils, and agroforestry uses of the species planted.

Buffer zones for protected areas offer interesting opportunities for agroecological research at La Selva, both on station property (La Guaria Annex, El Peje, La Flaminea) and elsewhere in the Atlantic lowlands (e.g., via participation in the recently funded Forest Resources for a Stable Environment Project [FORESTA]. This type of research fits well with OTS goals and is also becoming an important aspect of tropical ecological research as new areas are protected and surrounding lands need to be managed in ways that foster protection of the core. Agroforestry, management of secondary forests, and development of ecologically sound land-use systems are a frequent component of management plans for buffer zones in areas of tropical rain forest.

Whenever possible, research should be conducted in collaboration with local institutions (MAG, DGF, UCR, CATIE). Much research is currently undertaken by local institutions to design innovative land-use systems. For example, F. Bertsch and V. Vega (UCR) are conducting soil fertility research at the UCR experimental farm in Río Frío as part of a network of studies in the lowland humid tropics coordinated by North Carolina State University (Bertsch and Vega 1990). The experiment, which is in its early stages, consists of continuous cropping of a rice (*Oryza sativa*)-cowpea (*Vigna unguiculata*)-mucuna (*Styzolobium* spp., a legume fallow) sequence. Researchers from Wageningen Agricultural University (Holland) have been working at CATIE since 1986 in collaboration with MAG's "Atlantic Zone Programme" (Atlantic Zone Programme 1987). The objectives are to contribute to sustainable development in the Atlantic zone of Central America and Panama through research and training activities. Research focuses on production systems and on regional land-use planning. Other projects at CATIE could be of interest to La Selva researchers (Nitrogen-fixing Tree Project, agroforestry, wildlands management, and others). OTS researchers and course participants could take advantage of such experiments and projects to visit, exchange ideas, and, potentially, to initia collaborative research.

Likewise, researchers involved in agroecological work La Selva should be aware of the efforts of local institutions the same discipline and encouraged to interact actively wi their colleagues by sharing results and by collaborating c mutual projects whenever appropriate. This sort of interactic could be encouraged by organizing joint activities, such : workshops, seminars, and field trips. La Selva already facil tates local research by providing cheaper station fees for Cos Ricans. The opportunities at La Selva could be better publ cized in local universities and other institutions by more fr quent communication and by organizing seminars by La Selv researchers on subjects of common interest. Loc researchers could supply background data and help to defin priorities and goals. This type of interaction will magnif the contribution by OTS students and researchers at local an national levels.

Biologists in many projects at La Selva already interac with local researchers and employ local technicians and students, and more direct involvement of local scientists and collaborators is a highly desired next step. For example, data from local institutions that are concerned with development and with socioeconomic aspects of agriculture and forestry should be useful for defining goals and subjects of study for La Selva researchers. OTS can play a more significant role in its host country by building upon its educational and research programs and, especially, by capitalizing upon its pivotal position to improve linkages between U.S. and Latin American scientists and the general public.

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Reciclaje de nutrientes en plantaciones jóvenes con árboles nativos: estrategias para un manejo sustentable

Florencia MONTAGNINI*
Fredy SANCHO**

RESUMEN

Se midió la biomasa arbórea y el contenido de nutrientes (nitrógeno, calcio, magnesio, potasio y fósforo) de ramas, tronco y follaje de cuatro especies arbóreas nativas, en una plantación experimental de cuatro años, situada en la Estación Biológica La Selva, de la Organización de Estudios Tropicales (OTS) situada en las tierras bajas atlánticas de Costa Rica, Centro América. Las cuatro especies —*Stryphnodendron excelsum* Harms, *Vochysia hondurensis* Sprague, *Vochysia ferruginea* Mart and *Hyeronima alchorneoides* (0), se compararon con respecto a su biomasa y contenido de nutrientes de la parte arbórea, así como a los compartimentos de la hojarasca del piso (mantillo) y vegetación de sotobosque. *S. excelsum* tuvo la mayor acumulación de nitrógeno en el tronco, ramas y total de biomasa arbórea. *V. hondurensis* tuvo la mayor acumulación de calcio y magnesio en la biomasa aérea, mientras que *H. alchorneoides* tuvo el mayor contenido de potasio y fósforo en el tronco. A pesar de su contenido relativamente menor de nitrógeno en el tejido, *V. ferruginea y H. alchorneoides* mostraron un mayor potencial para el reciclaje de nitrógeno, debido a su distribución más pareja de nitrógeno en el tronco, ramas y follaje. La acumulación de nutrientes en el sotobosque fue muy baja, en comparación con la biomasa arbórea y el mantillo.

Palabras clave: Especies nativas, Costa Rica, reciclaje de nutrientes, nitrógeno, fósforo, calcio, magnesio, potasio.

SUMMARY

Aboveground-tree biomass and nutrient content (nitrogen, phosphorus, calcium, magnesium and potassium) were measured in 4-year-old stands of four indigenus tree species: *Stryphnodendron excelsum* Harms, *Vochysia hondurensis* Sprague, *Vochysia ferruginea* Mart and *Hyeronima alchorneoides* (0), growing on infertile soils in an experimental plantation in the Atlantic humid lowlands of Costa Rica. Biomass and nutrient content among the species, and among above-ground tree biomass. *V. hondurensis* had the highest accumulation of Ca and Mg in the biomass, while *H. alchorneoides* had the highest stem K and P. In spite of their relatively lower N tissue concentrations, *V. ferruginea* and *H. alchorneoides* showed a high potential for N recycling due to its more even distribution of N in stems,

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branches and leaves. Nutrient accumulation by the understory represented a minor component in comparison with above-ground tree tissue and the forest-floor litter.

Key words: Native species, Costa Rica, nutrient recycling, nitrogen, phosphorus, calcium, magnesium, potassium.

INTRODUCCION

Nuestro estudio está enfocado a un área de tierras tropicales bajas y húmedas de Centro América, en Costa Rica, donde predominan las plantaciones de banano. La deforestación y la consecuente degradación del suelo a causa del manejo inadecuado —agricultura intensiva y pastoreo— son problemas comunes. Una precipitación de 4000 mm/año acelera la erosión de los suelos ya agotados por repetidas cosechas.

La restauración de suelos a su antigua productividad y balance ecológico se ha convertido en un interés primordial en la región. Existen agricultores dispuestos a dedicar una parte de sus tierras (10-15%) a plantaciones arbóreas, ya que las consideran como una forma de inversión. Los servicios forestales regionales alientan la plantación de especies exóticas: *Pinus caribaea, Eucalyptus deglupta, Gmelina arborea*, así como *Cordia alliodora*, una especie arbórea nativa de rotación de 30 años que crece en tierras fértiles, siendo inadecuada para tierras degradadas. La elección de especies adecuadas para sistemas de reforestación incluye los siguientes criterios: valor económico de las especies regionales; disponibilidad de semillas o plántulas; información sobre tasas de crecimiento; así como sus efectos sobre los suelos. Ciertas especies arbóreas nativas de la región bajo estudio tienen potencial para crecer bien en suelos pobres y degradados. Estas son especies de crecimiento rápido que contribuyen materia orgánica al suelo dentro de un período relativamente corto. En este trabajo describimos estas especies y su capacidad para crecer en plantaciones a cielo abierto y reciclar nutrientes en estadios tempranos de la rotación.

Beneficios de las plantaciones arbóreas

En la actualidad, un número de esfuerzos gubernamentales y privados están promoviendo la plantación de árboles para el desarrollo rural en los trópicos, incluyendo plantaciones mixtas de árboles y cultivos practicados en sistemas agroforestales. Los árboles son considerados fuente de dinero, ahorro y bienes para la población rural (Chambers y Leach 1990). Ya que las plantaciones tropicales manejadas para alto rendimiento pueden ser por lo menos de cuatro a diez veces más productivas que los bosques naturales no manejados (Wadsworth 1983), éstas también pueden ayudar a satisfacer la creciente demanda global de madera. Se espera que este tipo de manejo contribuya a disminuir la presión sobre los bosques naturales (Evans 1987).

El manejo sustentado de plantaciones arbóreas se convierte en una alternativa biológica y socialmente plausible en suelos que no son apropiados para la práctica continua de agricultura que usa las tecnologías locales predominantes (Gladstone y Ledig 1990). En especial, las plantaciones de árboles y las plantaciones mixtas de árboles y cultivos representan alternativas productivas para el uso de tierras deforestadas donde la regeneración natural es pobre debido a la degradación intensa o a la distancia de fuentes de propagación. La baja fertilidad, la compactación del suelo a causa del pastoreo y la invasión por malas hierbas —todos índices de degradación— pueden ser serios obstáculos en la reforestación y en la agricultura convencional. Cuanto más se expande el área de degradación, más se incrementa el énfasis en la plantación de especies arbóreas capaces de crecer en condiciones pobres y ofrecen productos con potencial financiero (madera, combustible y demás) así como también beneficios ambientales (conservación de suelos, protección de cuencas) (Evans, 1987).

La selección apropiada de especies arbóreas para la plantación forestal o agroforestal depende del conocimiento sobre el rendimiento de la especie y de los beneficios económicos y ambientales que ésta ofrezca. En situaciones locales, la selección de una especie arbórea es determinada por la disponibilidad de semillas o plántulas y por la información disponible acerca de sus características silviculturales y manejo —por ejemplo, crecimiento rápido y posibilidad de

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cultivo mixto durante las etapas tempranas de establecimiento. La mayoría de los programas y subvenciones de reforestación promueven el uso de especies bien conocidas y con frecuencia exóticas. Alrededor del 85% de las plantaciones forestales en los trópicos está dominada por tres géneros: *Pinus, Eucalyptus* y *Tectona* (Evans, 1987), mientras que existen miles de especies indígenas apropiadas para fines similares. Los árboles nativos pueden ser más apropiados que los exóticos ya que están mejor adaptados a las condiciones ambientales locales, las semillas y plántulas están localmente disponibles y los agricultores están familiarizados con ellos y con sus usos. Además, el uso de árboles nativos en sistemas productivos ayuda a la preservación de la diversidad genética y fomenta un mejor balance con la flora y fauna local.

Consecuencias ecológicas de las plantaciones arbóreas de crecimiento rápido

Los factores que influyen sobre la productividad de las plantaciones forestales tropicales son poco entendidos. Algunos estudios informan sobre rendimientos o producción de biomasa en relación a factores climatológicos, pero pocos refieren las características del sitio, tales como la elevación y el tipo de suelo (Lugo et al., 1988). Los arboles pueden influenciar las características del sitio a través del reciclaje de nutrientes y sus interacciones con el medio ambiente.

Los efectos beneficiosos más importantes de los árboles sobre los suelos pueden incluir el mejoramiento de la estructura del suelo y el incremento de nutrientes disponibles (Fassbender, 1984, Nair, 1989, Sánchez et al., 1985, Sánchez, 1987). La fijación simbiótica de nitrógeno por los árboles resulta, en muchos casos, en el incremento del nitrógeno disponible en el suelo (Alpízar et al., 1986, Montagnini et al., 1986, Dommergues, 1987). Por otro lado, las plantaciones jóvenes de árboles tropicales, las cuales incorporan cantidades considerables de nutrientes en su biomasa sobre un período de tiempo relativamente corto, son ecosistemas de crecimiento rápido (Bruijnzeel, 1991). Durante las etapas tempranas de desarrollo, la cantidad de nutrientes absorbida del suelo generalmente sobrepasa la cantidad de nutrientes suplementada al suelo por la hojarasca y por la lluvia (Bruijnzeel, 1991).

El deterioro de la fertilidad del suelo puede ser una limitación seria para la plantación forestal sustentada en regiones tropicales: la fertilidad del suelo puede ser disminuida a través de la eliminación excesiva de biomasa, especialmente si los nutrientes del dosel arbóreo son perdidos a través de la cosecha o de la preparación del sitio para el cultivo (Perry y Maghembe, 1989). Por otro lado, Wadsworth (1983) sugiere que, con la posible excepción del fósforo, las cosechas repetidas generalmente no resultarían en serias deficiencias de nutrientes en el suelo.

Lundgren (1980) propuso que los efectos beneficiosos de las plantaciones forestales ocurren sólo durante el período de cinco a diez años inmediatamente después del cierre del dosel (la fase de enriquecimiento por barbecho). Durante la fase de producción máxima, puede deteriorarse la calidad del sitio: los minerales nutritivos son absorbidos por los árboles mientras que la hojarasca se acumula en el suelo del bosque, pero las condiciones no son apropiadas para la descomposición de la materia orgánica (Lundgren, 1980). Sánchez et al. (1985) concluyeron que los efectos perjudiciales en los suelos ocurren sólo durante el establecimiento de la plantación, aunque también enfatizaron que la extracción de nutrientes a través de la cosecha y las pérdidas por lixiviación antes del cierre del dosel provocan un agotamiento de nutrientes claves, especialmente de potasio, que deberían ser repuestos si el nivel de rendimiento ha de ser mantenido en las rotaciones siguientes.

Las especies arbóreas varían en sus tasas de absorción y capacidad de reciclaje de nutrientes. La posibilidad de usar ciertas especies para la acumulación de nutrientes fue sugerida por Sánchez et al. (1985) quienes observaron que ciertas especies tienen la habilidad (por ejemplo, *Gmelina arborea*) de acumular calcio y magnesio, mientras que otras favorecen la acumulación de potasio y fósforo. Todavía son escasos los datos sobre segundas y terceras rotaciones, así que no tenemos suficientes indicios acerca de cuáles son los nutrientes críticos para el mantenimiento de la producción del sitio. La información sobre las tasas de absorción y capacidad de reciclaje de nutrientes por las diferentes especies arbóreas ayudará a diseñar las mejores estrategias de manejo que tomarán ventaja de los efectos beneficiosos de los árboles sobre la fertilidad del suelo o evitarán el deterioro del sitio en el momento de la cosecha.

Efectos de las plantaciones arbóreas sobre los nutrientes del sitio: un ejemplo de Costa Rica

Las pruebas locales y regionales de especies arbóreas para la reforestación muchas veces revelan rendimientos sobresalientes de los árboles nativos. Por ejemplo, de trece especies arbóreas nativas en una plantación experimental en la estación biológica La Selva de la Organización de Estudios Tropicales (OTS) situada en las tierras bajas atlánticas de Costa Rica, Centro América, por lo menos cuatro —*Stryphnodendron excelsum, Vochysia hondurensis, Vochysia ferruginea* y *Hyeronima alchorneoides*— presentaron tasas de crecimiento iguales o mayores que las especies exóticas recomendadas para la región (Espinoza y Butterfield, 1989). Este trabajo demuestra el potencial de muchos árboles nativos para uso comercial. Además se destaca que ciertas especies nativas crecen bien en sitios degradados de suelos pobres y ácidos que no podrían sustentar la agricultura convencional. Los resultados de nuestros estudios en el mismo sitio demostraron que después de dos años y medio estas especies contribuyeron a la restauración de la fertilidad del suelo a través del incremento de la materia orgánica, el nitrógeno y los niveles de cationes a valores aproximados a aquellos considerados apropiados para los cultivos agrícolas (Montagnini y Sancho, 1990a, 1990b).

En las siguientes secciones se compara la biomasa y contenido de nutrientes de estas especies, la hojarasca, la vegetación del sotobosque y las reservas de nutrientes del suelo. Esta información puede ser utilizada para diseñar estrategias de manejo que tomen ventaja de los efectos beneficiosos de los árboles sobre los suelos y para evitar el agotamiento de los nutrientes del sitio en el momento de la cosecha. Estas estrategias deberían ser valiosas para la promoción del uso de sistemas —mixtos o de plantaciones puras, sistemas agroforestales— que incluyan estas especies madereras de crecimiento rápido en la zona y en otras regiones tropicales con características ecológicas similares.

El sitio experimental

La plantación experimental fue establecida en diciembre de 1985, sobre un área de pastos abandonados en la Estación Biológica La Selva de la Organización para Estudios Tropicales (10 26'N, 86 59'O, 50 metros de altura media, 24 °C de temperatura media anual, 4000 mm de precipitación media anual, con precipitación máxima en julio y mínima en marzo) (Informes climatológicos de la Estación Biológica La Selva). Los suelos son Fluventic Dystropepts, derivados de material volcánico depositados aluvialmente; son profundos, bien drenados, y sin piedras, tienen un contenido de materia orgánica bajo o medio, textura moderadamente pesada, y son generalmente ácidos y poco fértiles (Sancho y Mata, 1987). El área se deforestó en la década del 50, y fue utilizada para pastoreo de ganado hasta 1984. Se realizó una limpieza manual del terreno antes de la plantación. Las especies arbóreas se plantaron al azar con cinco (5) réplicas, cada parcela (14 m × 14 m) con siete filas de siete árboles y con dos metros entre árboles. Cinco parcelas similares de 14 m × 14 m también fueron establecidas en un área adyacente con pastos y en un bosque secundario. Durante el primer año, se desmalezó manualmente cuatro veces. Después, este proceso se llevó a cabo mecánicamente hasta el cierre del dosel.

Las especies arbóreas

Las especies para este estudio eran de buen crecimiento inicial (Espinoza, Camacho y Butterfield, 1989, González et al., 1990), y valor comercial (González et al., 1990, Chudnoff, 1984, Holdridge y Poveda, 1975).

Stryphnodendron excelsum Harms (Leguminosae, subfamilia Mimosoideae)

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("vainillo") se encuentra sólo en Costa Rica, aunque representantes de este género son nativos en todo América tropical (Brasil, Costa Rica, Guayana) (Allen y Allen, 1981). Esta especie crece en regiones de climas muy húmedos y aparentemente se adapta tanto a suelos aluviales como también a cerros bajos y a suelos degradados por el pastoreo (González et al., 1990). Su madera es primordialmente utilizada en construcción general y también para muebles pequeños y tornería (Allen y Allen, 1981). Su fruto sirve de alimento a muchas especies, sobre todo pequeños mamíferos.

Vochysia ferruginea Mart (Vochysiaceae) ("botarrama") crece en los bosques de tierras bajas desde Nicaragua hasta Brasil (Whitmore y Hartshorn, 1969). Se encuentran en suelos ácidos, bien drenados, y de baja fertilidad, aunque se puede adaptar a una variedad de suelos (González et al., 1990). Es una especie pionera que se autopoda y forma rodales uniformes, de edad pareja en campos abandonados su madera se usa para madera contrachapada y construcción.

Vochysia hondurensis Sprague (Vochysiaceae) ("mayo") se encuentra desde Méjico hasta Panamá, en elevaciones hasta de 900 m (Whitmore y Hartshorn, 1969). Usualmente crece en áreas húmedas y de baja altitud, en suelos aluviales o residuales (menos fértiles). Como es considerado un substituto de la caoba, su madera es muy apreciada para carpintería, madera contrachapada y mueblería.

H. alchorneoides (O) (Euphorbiaceae) ("pilón") abarca desde el sur de Méjico hasta el sur de Brasil (Chudnoff, 1984). Esta especie crece bien en cerros y en pastos abandonados, pero no se sabe mucho sobre sus requisitos edáficos. Su madera es usada en construcción pesada, mueblería, enchapados decorativos y tornería (Chudnoff, 1984). Las características botánicas de estas especies están descritas en Holdridge y Poveda (1975), Hartshorn (1983), Standley (1937-38) y Hartshorn y Hammel (no publicado). Estudios detallados sobre las semillas y las características de germinación son presentados en González (1991).

METODOS

Los procedimientos de muestreo y métodos químicos están descritos en Montagnini y Sancho (1990a, 1990b), y en Montagnini et al. (1991). Los suelos se muestrearon bajo las cuatro especies arbóreas mencionadas, en área de pastos libre de árboles y en bosque secundario de veinte años. La biomasa de los árboles y el contenido de nutrientes en tallos, ramas y hojas fueron medidos al momento del raleo de las parcelas, cuando la plantación tenía cuatro años. También se midió la biomasa y la concentración de nutrientes del sotobosque. El reciclaje de nutrientes fue calculado multiplicando la biomasa de cada compartimento por la concentración de nutrientes en el mismo (nitrógeno, calcio, magnesio, potasio, fósforo).

RESULTADOS Y DISCUSION

Biomasa arbórea

Los valores de la biomasa de árboles enteros presentados aquí (Tabla 1) son mayores que los reportados para *Albizia lebbek* de cuatro años (Parrota, 1989) y para *Leucaena leucocephala* de cinco años y medio (Wang et al., 1991), ambos creciendo en plantaciones densas para la producción de biomasa en Puerto Rico. Los valores de productividad (biomasa arbórea dividida por la edad del árbol) concuerdan con otros valores presentados en la literatura para plantaciones monoespecíficas en los trópicos húmedos. El valor para *V. hondurensis* es similar al valor reportado para *Gmelina arborea* (12,8 toneladas/ha/año) en la región amazónica del Brasil (Russell, 1987) así como también al valor para *Gmelina arborea* (12,7 toneladas/ha) y para *Albizia falcataria*, ambos en las Filipinas (11,3) (Kawajara et al., 1981, en Young, 1989). Sin embargo, los incrementos presentados aquí son menores que aquellos reportados para algunas especies de crecimiento rápido, tales como *Acacia mangium* (15,5 a 18,0 toneladas/ha en Malasia) y *Leucaena leucocephala* (20,0 a 30,0, y hasta 80,0 toneladas/ha en Hawaii y en otros sitios tropicales, Young, 1989).

Los incrementos anuales en madera para especies latifoliadas en los trópicos

Tabla 1. Promedio de diámetros a la altura del pecho (dap), altura, biomasa aérea y crecimiento anual.

Anual medio	Dap (cm)	Altura (m)	Biomasa aérea viva Fuste	Ramas (kg/ha)	Hojas	Total	Crecimiento Total (t/ha/año)	Fuste
S. exc.	12,0a	8,9b	35.250a	15.250a	4.325a	54.825	13,7	8,8
V. fer.	10,3a	8,1b	24.750b	14.250a	5.925a	44.925	11,2	6,2
V. hon.	10,8a	12,0a	41.750a	6.500b	7.250a	55.500	13,9	10,4
H. alc.	10,8a	9,0a	26.250b	12.250a	5.350a	43.850	12,0	6,5

Nota: En ésta y las siguientes tablas, las diferencias entre sitios para un parámetro dado son estadísticamente significativas cuando los promedios son seguidos por letras diferentes.

varía entre 1 y 28 toneladas/ha/año. Las especies de crecimiento rápido como *Gmelina arborea* y *E. saligna* varían entre 10 y 20 y entre 8 y 28 toneladas/ha respectivamente, y las especies de crecimiento relativamente más lento como *Swietenia* sp. y *Tectona grandis* varían entre 1 y 4 y entre 3 y 12 toneladas/ha respectivamente (Wadsworth, 1983). Otros valores para árboles de crecimiento rápido en regiones tropicales húmedas incluyen varias especies de *Eucalyptus* cultivadas en las Américas y en el Asia (entre 7,2 y 11,9 toneladas/ha); *Gmelina arborea* en Costa Rica (11,8 toneladas/ha) (Lugo et al., 1988); de 1,3 a 5,3 *Leucaena leuocephala* en sitios premontanos y en tierras bajas húmedas (entre 2,8 y 15,9 toneladas/ha); *Prosopis juliflora*, en sitios húmedos de India (9,4 toneladas/ha), y *Populus deltoides*, en sitios subtropicales de India (6,4 toneladas/ha) (Lugo et al., 1990). De modo que el promedio anual de los incrementos en madera para las especies en este estudio cae dentro de los valores reportados para otras especies arbóreas de crecimiento rápido en los trópicos húmedos.

Acumulación de nutrientes en la biomasa arbórea

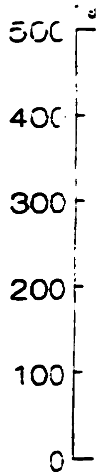
Nitrógeno

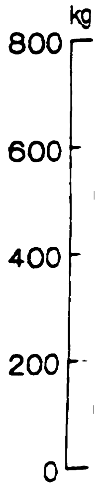
Las mayores concentraciones de nitrógeno en tallos, en ramas y biomasa arbórea se encontraron en *S. excelsum*. Aproximadamente 200 kg/ha, o 60% del nitrógeno de la biomasa arbórea de *S. excelsum* (Figura 1) permanecería en el sitio al momento de la cosecha si se dejaran las ramas y hojas en el suelo. *V. hondurensis* tenía una proporción similar de nitrógeno en su porción de hojas y ramas; al igual que en *S. excelsum* más del 50% del nitrógeno de la biomasa arbórea podría ser reciclado si se dejan los restos en el sitio al momento de la cosecha. *V. ferruginea*, con una biomasa de tallos relativamente menor, proporcionalmente tenía más nitrógeno en hojas (52,9%) y en ramas (42,1%), mientras que *H. alchorneoides* tenía una distribución más pareja en la biomasa arbórea (Figura 1).

Calcio

V. hondurensis, con una mayor biomasa de tronco y una concentración elevada de calcio (Ca), también tenía la mayor cantidad de calcio en la madera (más de 600 kg/ha, equivalente a 84% del Ca de la biomasa arbórea), aproximadamente el doble de la cantidad de *S. excelsum* y de *V. ferruginea*, y varias veces más que *H. alchorneoides* (Figura 2). En consecuencia, la cosecha total de árboles de *V. hondurensis* podría reducir considerablemente la cantidad de calcio en el sitio. Sin embargo, mientras los árboles de *V. hondurensis* estén vivos, cantidades relativamente grandes de calcio podrían ser recicladas porque, aunque sólo represente el 16% de la biomasa de la parte aérea, la cantidad conjunta de calcio en las hojas y las ramas sobrepasaba 100 kg/ha.

La proporción de calcio en el tronco en relación a la biomasa total fue similar para





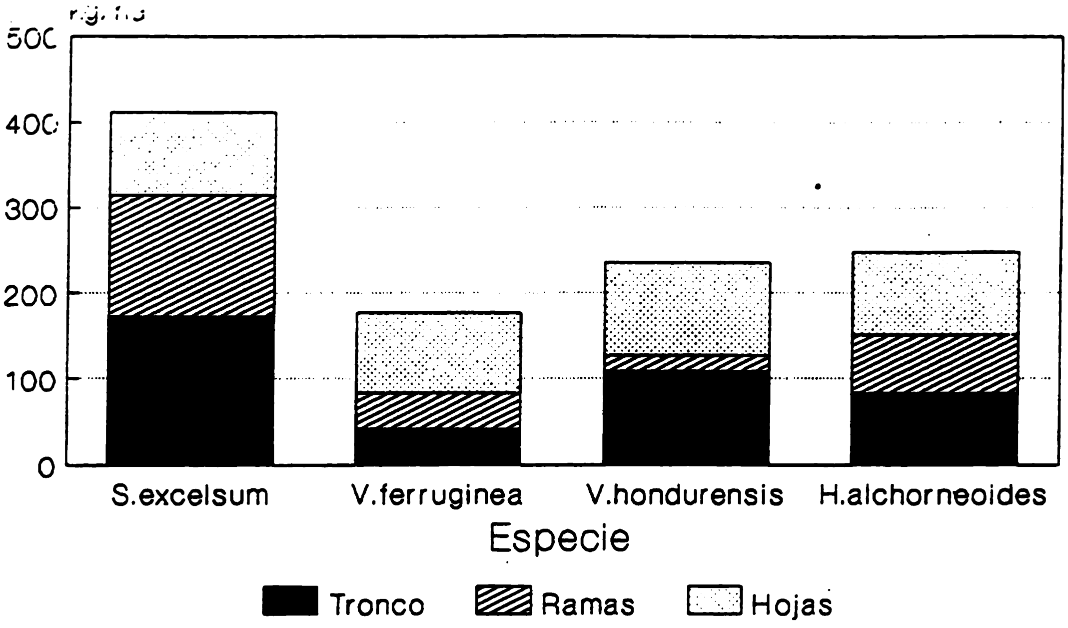


Figura 1. Nitrógeno en la biomasa arbórea.

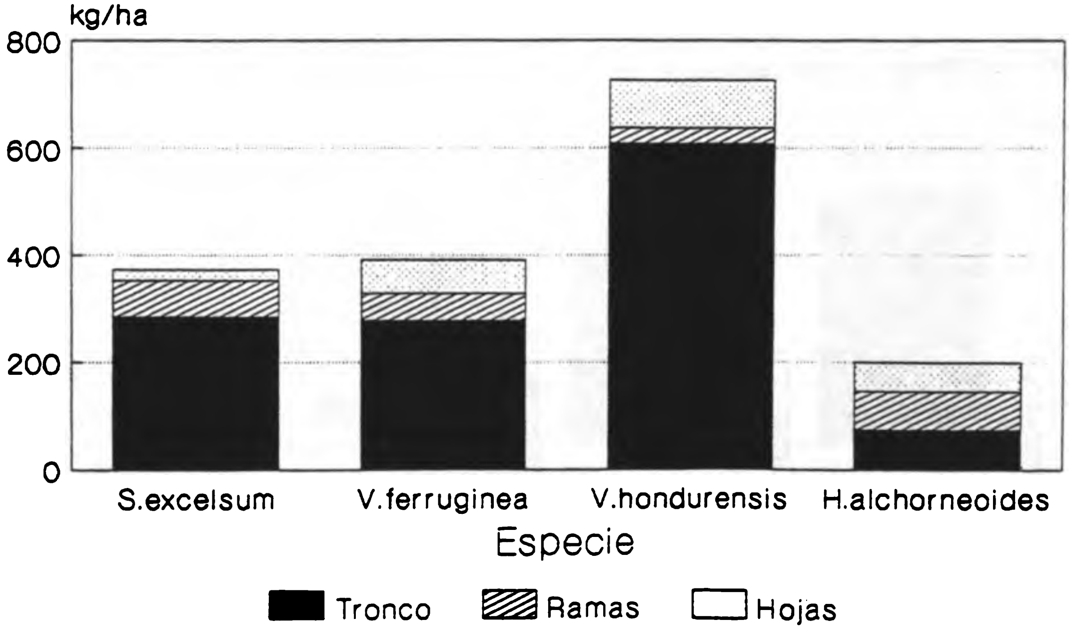


Figura 2. Calcio en la biomasa arbórea.

S. excelsum y para *V. ferruginea* (76,6% y 70,8% respectivamente) (Figura 2), pero las cantidades absolutas fueron menores que la mitad de la cantidad de *V. hondurensis*. *H. alchorneoides* otra vez tuvo una mejor distribución de calcio en los tallos, las hojas y las ramas.

Magnesio

V. hondurensis, con su alta biomasa de tronco y alta concentración de magnesio (Mg), también tuvo la mayor cantidad de Mg en la madera (55% del total del Mg contenido en la biomasa arbórea, aproximadamente 30 kg/ha) (Figura 3). En consecuencia, si se retiran los troncos de *V. hondurensis* se afectaría el reciclaje de Mg en el sitio de una manera más dramática que cualquiera de las otras especies, especialmente si se realiza una cosecha total (Figura 3).

Potasio

El panorama cambia con el potasio (K): la mayor acumulación de K en tallos fue hallado en *H. alchorneoides* (252 kg/ha, Figura 4), representando 58,7% del K arbóreo. Esta cantidad fue seguida por *V. hondurensis* con 175 kg/ha, la cual representa 76,8% del K arbóreo. En consecuencia, la cosecha total de árboles de *H. alchorneoides* y de *V. hondurensis* podría tener los mayores efectos en el reciclaje de K. *S. excelsum* y *V. ferruginea* tenían 33,6% y 35,4% respectivamente, de K en los tallos. El reciclaje de K en las hojas y las ramas podría ser relativamente más importante cuando se considera estas últimas dos especies.

Fósforo

V. hondurensis y *H. alchorneoides* tuvieron las mayores proporciones de fósforo (P) en la madera (72,4% y 62,1% respectivamente) (Figura 5). *S. excelsum* y *V. ferruginea* tuvieron relativamente menores cantidades de P en los tallos (43,9% y 48,7% respectivamente).

Nuestros resultados confirman reportes anteriores sobre los efectos negativos de la cosecha total de árboles sobre las reservas de nutrientes del sitio: por ejemplo, Bruijnzel y Wiersum (1985) estudiaron las entradas/salidas de nutrientes en plantaciones de *Agathis dammara* en las tierras altas de Java. Sus resultados, calculados para una rotación de treinta años, indicaron que la cosecha total de los árboles eliminaría una cantidad de nutrientes equivalente a las entradas de potasio y calcio, casi la mitad de la entrada de magnesio, y el doble de la

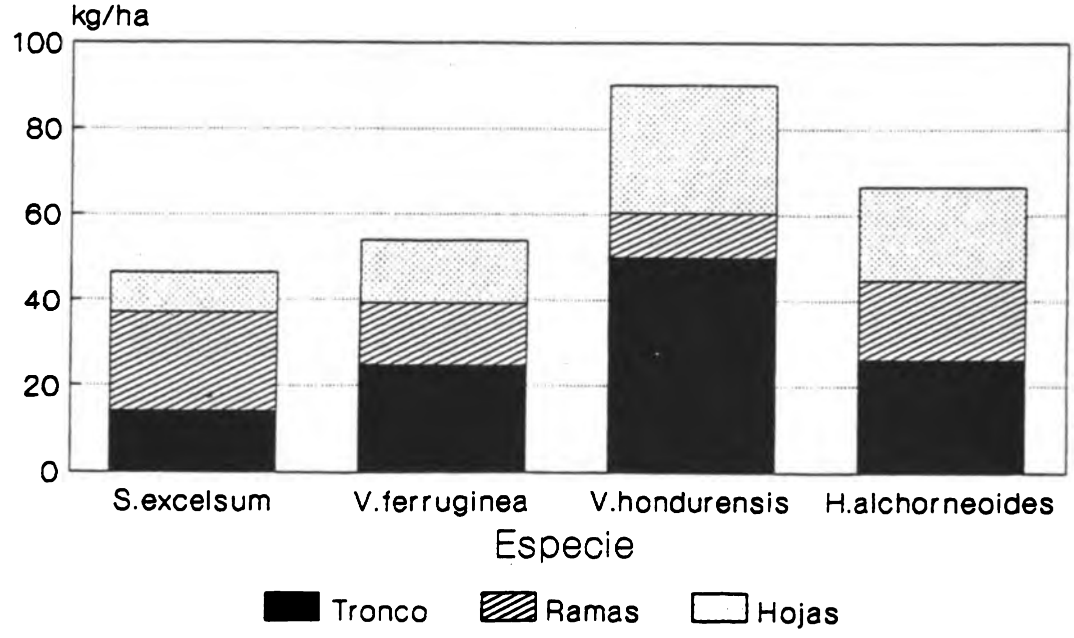


Figura 3. Magnesio en la biomasa arbórea.

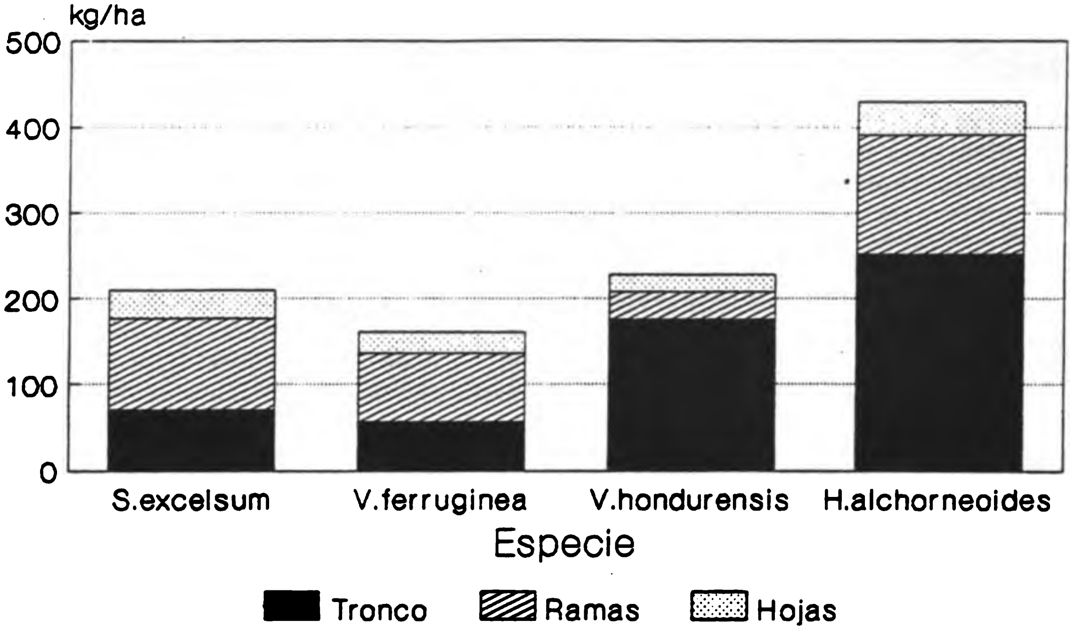


Figura 4. Potasio en la biomasa arbórea.

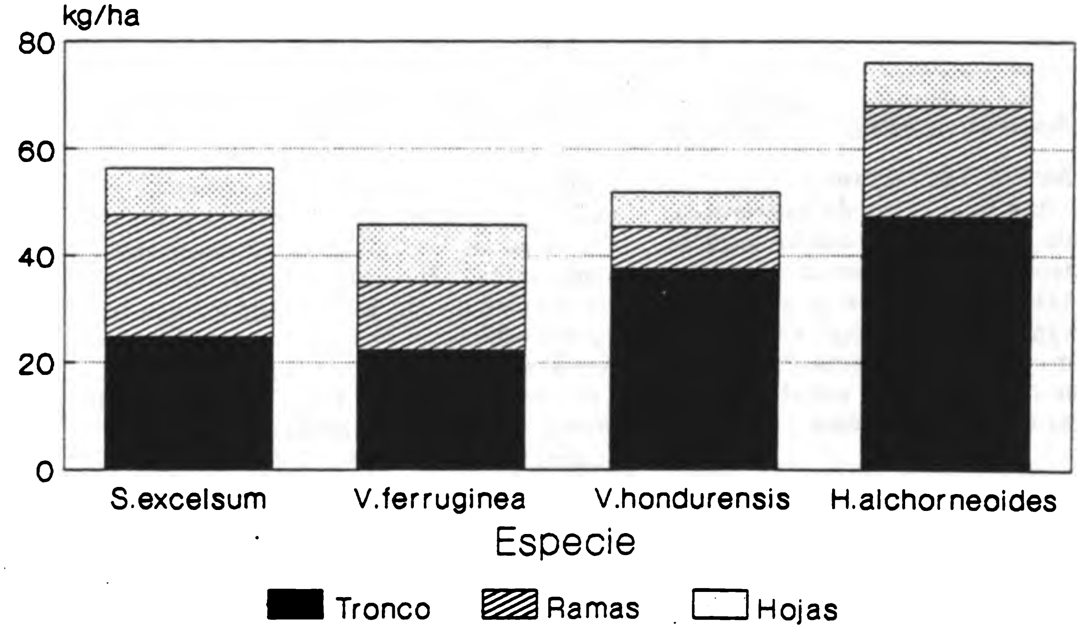


Figura 5. Fósforo en la biomasa arbórea.

Tabla 2. Materia orgánica, cantidades totales de N, P, pH, Ca, Mg y K en suelos bajo las cuatro especies arbóreas nativas en la plantación, en el área de pasto y en el bosque secundario; Mayo 1989. (1)

Sitio	Prof.	MO	N	P	pH	Ca	Mg	K
	(cm)	(%)		(mg/kg)			(cmol/kg)	
S. exc.	0-15	4,50a	0,278a	2,4a	5,1a	0,68b	0,44a	0,13a
	15-30	3,29a	0,224a	2,1a	5,1ab	0,52bc	0,22bc	0,14a
	30-60	1,88a	0,196a	1,8b	5,1a	0,54a	0,16a	0,14a
V. fer.	0-15	5,06a	0,320a	3,24a	4,98a	0,63bc	0,53bc	0,16a
	15-30	3,66a	0,248a	5,03c	5,03c	0,35d	0,20c	0,10a
	30-60	2,94a	09,200a	2,50b	5,07a	0,33a	0,16a	0,15a
V. hon.	0-15	4,30a	0,304a	2,30a	5,20a	0,47bc	0,50bc	0,10a
	15-30	3,16a	0,232a	1,82a	5,08ab	0,38cd	0,22bc	0,07a
	30-60	2,42a	0,202a	2,00b	5,13a	0,36a	0,15a	0,06a
H. alc.	0-15	5,16a	0,232a	1,5a	5,1a	0,31c	0,21a	0,09a
	15-30	2,77a	0,248a	1,5a	5,1ab	0,45bcd	0,19c	0,10a
	30-60	1,21a	0,158a	1,7b	5,2a	0,46a	0,20a	0,10a
Pasto	0-15	3,98a	0,296a	4,1a	5,2a	0,57bc	0,38a	0,22a
	15-30	2,94a	0,236a	3,4a	5,1ab	0,51bcd	0,27bc	0,17a
	30-60	2,46a	0,194a	8,9a	5,2a	0,47a	0,20a	0,13a
Bosque	0-15	5,11a	0,288a	2,3a	5,2a	1,16a	0,49a	0,21a
	15-30	3,83a	0,244a	2,0a	5,2a	0,92a	0,45a	0,17a
	30-60	2,48a	0,206a	1,4b	5,2a	0,62a	0,27a	0,12a

1. Existen diferencias estadísticamente significativas entre los sitios para una profundidad dada y los parámetros cuando los promedios son seguidos por letras diferentes.

entrada de fósforo. Los autores concluyeron que para evitar la escasez de nutrientes, especialmente de fósforo, la cosecha total de árboles no debería ser practicada. Nuestros resultados también sugieren que dejando los restos de ramas y hojas en el sitio podrían disminuir considerablemente los impactos negativos de la cosecha, con diferentes consecuencias según las especies.

Impacto de los árboles sobre los nutrientes del suelo

Los mayores niveles de materia orgánica y de N en el suelo se encontraron en la plantación arbórea, con cantidades aproximadas a los del bosque secundario (Tabla 2), aunque estas diferencias no son estadísticamente significativas (P < 0,05). El contenido de P fue mayor en el área de pasto que en la plantación o que en el bosque (Tabla 2). Dentro de la plantación arbórea, no hubo diferencias significativas en el contenido de cationes entre las especies. Sin embargo, sí hubo una tendencia a niveles más altos de Ca bajo *S. excelsum* y niveles menores bajo *H. alchorneoides*. Los mayores niveles de Mg fueron registrados bajo las dos especies de *Vochysia*, con contenidos menores en *H. alchorneoides* (Tabla 2). Estos resultados confirman datos de mediciones anteriores realizados en 1988 (Montagnini y Sancho, 1990a, 1990b).

Mediciones similares tomadas en mayo de 1990 y nuevamente en mayo de 1991, revelaron tendencias en la acumulación de nutrientes en el suelo similares a aquellas encontradas en 1988 y 1989. Al examinar los datos entre 1988 y 1991, no se detectaron tendencias de aumento o reducción a través del tiempo para ninguno de los nutrientes (Montagnini y Sancho, datos no publicados). Aparentemente, el aumento del nivel de nutrientes del sitio fue observado en 1988, cuando los árboles tenían dos

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Tabla 3.

(a) Vegeta

S. exc.
H. alc.

(b) Hojara

S. exc.
V. fer.
V. hond.
H. alc.

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años y medio y habían cerrado el dosel, pero después de este efecto inicial no se pudo detectar ningún otro cambio positivo.

Los impactos de la plantación de especies arbóreas sobre las reservas de nutrientes del suelo dependerán de la absorción de nutrientes por los árboles en relación a la capacidad del suelo para suplir nutrientes, del reciclaje de nutrientes (mientras los árboles estén vivos), y de las partes cosechadas del árbol, ya sea el árbol entero o la madera, y su biomasa y contenido de nutrientes al momento de la cosecha. Esto se puede ilustrar tomando como ejemplo estas relaciones para *V. hondurensis*, la especie de crecimiento más rápido y aparentemente de mayores requerimientos nutricionales en este estudio. La retención de nutrientes por *V. hondurensis* (calculado dividiendo el total de nutrientes en la biomasa por la edad de la plantación) fue un promedio de 58 kg de N, 181 kg de Ca, 57 kg de K, 22 kg de Mg y 13 kg de P/ha/año. Las cantidades de N, Ca, Mg y K son el doble de aquellas reportadas por Wadsworth (1983) para plantaciones de teca, pero el valor de P es similar. Aunque estas cantidades de nutrientes son altas, éstas deberían ser comparadas con la capacidad del suelo para suplir nutrientes. Por ejemplo, Wadsworth (1983) comparó datos de la tasa de absorción anual de nutrientes de varios cultivos agrícolas en suelos Ultisoles y Oxisoles en Puerto Rico (N = 90 - 120 kg/ha/año, K = 50 - 90, Ca = 86 - 109, Mg = 68 - 98), con las tasas de retención media anual de nutrientes de plantaciones de teca y de pino. Al examinar esos datos se concluye que la capacidad de los suelos para suplir nutrientes era suficiente para las necesidades de las plantaciones, y que los árboles podían ser cosechados sin crear deficiencias en el suelo, con la posible excepción de P. Wang et al. (1991) también repotaron que la tasa anual de absorción de N, P, Ca, Mg y K para plantaciones de *Casuarina* y *Albizia* en Puerto Rico era similar a la tasa de absorción de cultivos como el maíz y el sorgo.

En nuestro análisis, no estamos considerando la capacidad para suplir nutrientes de los suelos, pues no se dispone hasta la fecha de registros que permitan esta comparación.

Biomasa y concentración de nutrientes en la vegetación del sotobosque

La acumulación de nitrógeno en la biomasa aérea del sotobosque fue mayor bajo las parcelas de *S. excelsum* (14,9 kg/ha), aunque esta cantidad representa sólo 3,6% del N en la biomasa arbórea (Tabla 3). Para

Tabla 3. Biomasa y contenidos de nutrientes en la vegetación del sotobosque y la hojarasca del suelo del bosque (1)

(a) Vegetación del sotobosque

	Biomasa	N	Ca	Mg	K	P
	(kg/ha)			(kg/ha)		
S. exc.	874	14,9 (3,6)	2,9 (0,8)	3,6 (7,7)	8,8 (4,2)	1,1 (2,0)
H. alc.	425	5,7 (2,3)	3,3 (1,6)	1,9 (2,9)	3,3 (0,8)	3,1 (4,1)

(b) Hojarasca del suelo del bosque (2)

	Biomasa	N	Ca	Mg	K	P
	(kg/ha)			(kg/ha)		
S. exc.	5 612	95,1 (23,0)	41,6 (11,1)	8,2 (17,6)	6,6 (3,1)	4,3 (7,6)
V. fer.	17 215	240,3 (137,0)	187,6 (47,9)	19,1 (35,5)	12,1 (7,5)	15,5 (33,8)
V. hond.	11 084	134,0 (57,0)	170,0 (23,4)	26,4 (24,3)	9,7 (4,2)	11,6 (22,3)
H. alc.	4 238	39,2 (15,8)	55,0 (27,0)	11,9 (17,9)	6,8 (1,6)	12,9 (16,9)

1. Los números entre paréntesis son porcentajes en relación a la biomasa total de nutrientes del árbol.
2. Totales, incluyendo hojas, fragmentos y ramas.

H. alchorneoides, el N en la biomasa del sotobosque fue 5,7 kg/ha, o 2,3% de la biomasa arbórea. Para los otros nutrientes, la acumulación en la biomasa del sotobosque bajo *S. excelsum* varió entre 0,8% y 7,7%, y bajo *H. alchorneoides*, varió entre 0,85% y 4,1% (Tabla 3).

Ya que la vegetación del sotobosque aparentemente representa una proporción relativamente pequeña de nutrientes en relación al árbol entero, las manipulaciones del sotobosque deberían tener poco efecto sobre el reciclaje de nutrientes en el sitio. Por ejemplo, el desmalezado debería tener un efecto relativamente menor sobre el reciclaje de nutrientes, a menos que el sotobosque sea eliminado varias veces al año. Esta hipótesis también sugiere que el intercultivo de especies herbáceas anuales que alcanzan cantidades similares de biomasa a las del sotobosque bajo *S. excelsum* o *H. alchorneoides* no tendrán un efecto negativo considerable en el balance de nutrientes del sitio. Debido a que las muestras de biomasa del sotobosque fueron tomadas cuando la biomasa estaba en su apogeo, las cantidades reportadas aquí son consideradas una aproximación a las que podrían ser obtenidas en cultivos. Sin embargo, este factor merece más estudio, ya que los requerimientos de nutrientes y las partes de plantas y árboles eliminados con la cosecha variarán con los cultivos. Nuestros resultados, sin embargo, tienden a concordar con Bruijnzel y Wiersum (1985), quienes concluyeron que el uso de intercultivos en plantaciones arbóreas en Java, acompañado de medidas preventivas para reducir la erosión del suelo, era una manera aceptable de conservar nutrientes. Ellos argumentan que además de sus beneficios socioeconómicos, el uso de prácticas "taungya" podrían también resultar ventajoso ya que los agricultores podrían estar dispuestos a usar fertilizantes para los cultivos y los efectos dispuestos a usar fertilizantes para los cultivos y los efectos residuales de estos nutrientes aplicados podrían incrementar la producción de los árboles.

Acumulación de nutrientes en la hojarasca del bosque

La mayor acumulación de nutrientes y biomasa de hojarasca del suelo fue bajo *V. ferruginea*. El N en la hojarasca bajo *V. ferruginea* fue mayor que en la biomasa arbórea de la misma (Tabla 3). Como fue notado anteriormente, la biomasa de las hojas y ramas de *V. ferruginea* representa una gran porción de su biomasa arbórea. Esta especie de auto-poda, una característica que aumenta el despoje de hojas y ramas, y la poda ocasional puede haber añadido aún más hojarasca al suelo forestal. Los resultados de nuestros estudios de tasas de caída de hojarasca y de la descomposición de la misma (Montagnini et al., 1991) sugieren que la descomposición de la hojarasca es relativamente lenta bajo *V. ferruginea*, un factor que explica las altas acumulaciones mencionadas anteriormente. *V. hondurensis, H. alchorneoides* y *S. excelsum* exhibieron tasas de descomposición de hojarasca más aceleradas. El Ca, Mg y P de la hojarasca bajo *V. ferruginea* eran considerables (Tabla 3), un dato especialmente relevante para P, ya que existen probabilidades de deficiencias de este elemento en el sitio, tal como fue mencionado anteriormente. Los nutrientes de la biomasa del suelo forestal también fueron mayores bajo *V. hondurensis*. De nuevo, este resultado fue más significativo para N, Ca, Mg y P. Por ende, a pesar del crecimiento rápido de esta especie, el reciclaje de nutrientes proveniente de la hojarasca puede por lo menos compensar parcialmente el agotamiento de nutrientes del suelo. Mientras que lo contrario es cierto para P, el N de la hojarasca del suelo forestal fue más que el doble bajo *S. excelsum* que bajo *H. alchorneoides*, a pesar de que ambas especies tenían cantidades similares de biomasa en la hojarasca (Tabla 3).

Estos resultados sugieren que el suelo forestal es un compartimiento importante para la acumulación y el reciclaje de nutrientes, particularmente para el N, Ca, Mg y P, pero menos para el K, con marcadas diferencias entre especies arbóreas. Si el suelo forestal es afectado por quemas o las limpiezas, puede ocurrir una pérdida sustancial de materia orgánica y nutrientes. Wang et al. (1991) también encontraron que con la excepción de K, los nutrientes en la hojarasca eran equivalentes a una

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gran porción (16-50%) de los nutrientes contenidos en la biomasa arbórea. Ellos concluyeron que si la hojarasca fuera dejada sobre el suelo después de la cosecha, esto representaría una reserva sustancial de nutrientes para la siguiente rotación.

CONCLUSIONES Y RECOMENDACIONES

1. Algunas especies arbóreas nativas maderables de buen valor comercial pueden crecer en plantaciones abiertas, en sitios de baja fertilidad y pueden exhibir crecimiento rápido y efectos potencialmente beneficiosos sobre los nutrientes del suelo. Además, sus efectos sobre los nutrientes del suelo pueden ser observados en una etapa temprana de la rotación, al cierre del dosel.

2. Las especies arbóreas varían en sus contenidos de nutrientes en los tejidos y en sus tasas de acumulación de nutrientes en la biomasa. Para una especie dada, las mismas tendencias no son aplicables a todos los nutrientes: por ejemplo, una especie puede tener el mayor efecto sobre el Ca del sitio, pero su influencia sobre el K o el N puede ser mínima; otra especie puede tener una influencia más significativa sobre el K o el P del sitio.

3. El establecimiento de plantaciones arbóreas mixtas debería ser una estrategia apropiada para combinar los requerimientos de nutrientes de diferentes especies arbóreas con sus efectos sobre los nutrientes del suelo, de manera que no se creen deficiencias serias de ningún nutriente en particular. Sin embargo, aun con la mezcla de especies arbóreas es posible esperar deficiencias de K y P en el sitio a largo plazo.

4. La cosecha total de los árboles tendrá efectos negativos mayores sobre los nutrientes del sitio que la cosecha de los troncos. Los efectos variarán de acuerdo a la especie y a las partes cosechadas del árbol. El agotamiento de nutrientes del sitio será mayor con rotaciones cortas porque los árboles jóvenes tienen una proporción mayor de tejido de hojas y ramas en relación a sus troncos que los árboles viejos, en otras palabras, la porción potencialmente "reciclable" del árbol es mayor en árboles jóvenes; y la cosecha de rotaciones cortas aumentará la frecuencia de la eliminación de nutrientes del sitio así como también las perturbaciones al sitio asociadas con las operaciones de cosecha (erosión del suelo, compactamiento, perturbación de la hojarasca del suelo, etc.).

5. Aparentemente, el crecimiento de la vegetación del sotobosque y la correspondiente acumulación de nutrientes juega un rol relativamente pequeño en el reciclaje de nutrientes del sitio. Por eso, las prácticas que afectan al sotobosque, tales como el desmalezado y el intercultivo con especies anuales, pueden no ser críticos para la preservación de nutrientes en el sitio. Esta situación variará con las especies cultivadas y con su manejo. El intercultivo durante etapas tempranas del crecimiento arbóreo, mientras que los requerimientos de nutrientes de los cultivos y su manejo no provoquen otros efectos adversos (erosión del suelo, eliminación excesiva de nutrientes con cosechas repetidas), es una alternativa para acelerar el retorno del capital invertido y por consiguiente actúa como un estímulo para la plantación de árboles.

6. La hojarasca representa un componente mayor en la acumulación de nutrientes y en el reciclaje de los mismos. Las prácticas que afectan a la hojarasca, tales como la quema para el control de las malezas, la cosecha de la hojarasca para utilizarla como leña o "mulch" (mantillo), etc., pueden tener efectos adversos serios sobre los nutrientes del suelo.

7. La medición de la biomasa arbórea y de las concentraciones de nutrientes en etapas tempranas de la rotación (por ejemplo, durante el raleo) pueden ofrecer una buena indicación del impacto potencial de las prácticas de manejo sobre la conservación de nutrientes del sitio.

8. Las referencias a las tasas de extracción de nutrientes por cultivos agrícolas

comunes en la región pueden servir como indicadores de la capacidad para suplir nutrientes de los suelos y ser comparados con las tasas de absorción de nutrientes de las especies arbóreas, para poder estimar las deficiencias potenciales de nutrientes en el sitio.

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BIBLIOGRAFIA

ALLEN, O. N. and E. K. ALLEN. 1981. The leguminosae: A source book of characteristics, uses, and nodulation. University of Wisconsin Press, Madison , Wisconsin. 812 pp.

ALPIZAR, L., FASSBENDER, H. W.; HEUVELDOP, J.; FOLSTER, H. and ENRIQUEZ, G. 1986. Modelling agroforesty systems of cacao (*Theobroma cacao*) with laurel (*Cordia alliodora*) and poro (*Erythrina peoppigiana*) in Costa Rica. I. Inventory of organic matter and nutrients. Agroforesty Systems 4:175-189.

BRUIJNZEL, L. A. and K. F. WIERSUM. 1985. A nutrient balance sheet for *Agathis dammara* Warb. plantation forest under various management conditions. Forest Ecology and Management 10: 195-208.

BRUJIZNEL, L. A. 1991. Nutrient input-output budgets of tropical forest ecosystems: a review. Journal of Tropical Ecology 7: 1-24.

CHAMBERS, R. and M. LEACH. 1990. Trees as savings and security for the rural poor. Unasylva 41: 39-52.

CHUDNOFF, M. 1984. Tropical timbers of the world. USDA Forest Service, Agricultural Handbook 605, Washington, DC.

DOMMERGUES, Y. R. 1987. The role of biological fixation in agroforesty. pp. 245-271 *In* Steppler, H. A., and P. K. R. Nair (eds.). Agroforesty. A decade of development. International Council for Research in Agroforestry. Nairobi, Kenya.

ESPINOZA CAMACHO, M. y BUTTERFIELD, R. 1989. Adaptabilidad de 13 especies nativas maderables bajo condiciones de plantación en las tierras bajas húmedas del Atlántico, Costa Rica. pp. 159-172 *In* R. Salazar (ed.). Manejo y aprovechamiento de plantaciones forestales con especies de uso múltiple. Actas Reunión IUFRO, Guatemala, 3-7 de abril 1989. CATIE, Turrialba, Costa Rica.

EVANS, J. 1987. Site and species selection-Changing perspectives. Forest Ecology and Management 21: 299-310.

FASSBENDER, H. W. 1984. Bases edafológicas de los sistemas de producción agroforestales. Serie Materiales de Enseñanza Nº 21. Centro Agronómico Tropical de Investigación y Enseñanza (CATIE), Turrialba, Costa Rica. 191 pp.

GLADSTONE, W. T. and F. T. LEDIG. 1990. Reducing pressure on natural forests through high-yield forestry. Forest Ecology and Management 35: 69-78.

GONZALEZ, E. Preliminary seed trials for 36 native tree species. Revista de Biología Tropical (Costa Rica) 39 (1): 47-51.

GONZALEZ, E., R. BUTTERFIELD, J. SEGLEAU y M. ESPINOZA. 1990. Primer Encuentro Regional sobre Especies Forestales Nativas de la Zona Norte y Atlántica. Memoria. 28-29 julio 1989. Chilamate, Costa Rica. Instituto Tecnológico de Costa Rica. Cartago, Costa Rica. 46 pp.

HARTSHORN, G. 1983. Plants. pp. 118-157 *In* D. Janzen (ed.). Costa Rica Natural History. University of Chicago Press.

HARTSHORN, G. and B. HAMMEL. Trees of La Selva. Unpublished manuscript, La Selva Biological Station, OTS, Apdo. 676, 2050 San Pedro, Costa Rica.

HOLDRIDGE, L. R. y POVEDA, L. J. 1975. Arboles de Costa Rica. Centro Científico Tropical, San José, Costa Rica. 546 pp.

LUGO, A. E., S. BROWN and J. CHAPMAN. 1988. An analytical review of production rates and stemwood biomass of tropical forest plantations. Forest Ecology and Management 23: 179-200.

LUGO, A. E., D. WANG and F. BORMANN. 1990. A comparative analysis of biomass production in five tropical tree species. Forest Ecology and Management 31: 153-166.

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restry.

LUNDGREN, B. 1980. Plantation forestry in tropical countries-physical and biological potentials and risks. Swedish University of Agricultural Sciences. International Rural Development Centre. Rural Development Series 8. Uppsala. 134 pp.

MONTAGNINI, F., HAINES, B. L., BORING, L. R. and SWANK, W. T. 1986. Nitrification potentials in successional black locust and mixed hardwood forest stands in the southern Appalachians, U.S.A. Biogeochemistry 2: 197-210.

MONTAGNINI, F. and SANCHO, F. 1990a. Influencia de seis especies de árboles nativos sobre la fertilidad del suelo en una plantación experimental en la llanura del Atlántico de Costa Rica. Yvyraretá (Argentina) 1 (1): 29-49.

MONTAGNINI, F. and SANCHO, F. 1990b. Impacts of native trees on tropical soils: a study in the Atlantic lowlands of Costa Rica. Ambio 19 (8): 386-390.

MONTAGNINI, F., F. SANCHO, K. RAMSTAD and E. STIJFHOORN. 1991. Multipurpose trees for soil restoration in the humid lowlands of Costa Rica. pp. 41-58 *In* D. A. Taylor and K. G. Mc Dicken (eds.). Research on multipurpose trees in Asia. Proceedings of an International Symposium. November 19-23, 1990, Los Banos, Philippines. Winrock International Institute for Agricultural Development. Bangcock.

Nair, P. K. R. 1989. The role of trees in soil productivity and protection. pp. 567-589 *In* Nair, P. K. R. (ed.). Agroforestry systems in the tropics. Kluwer Academic Publishers/International.

PARROTTA, J. A. 1989. The influence of management practices on the biogeochemical stability of tropical fuelwood plantations. Tropical Ecology 30: 1-12.

PERRY, D. A. and J. MAGHEMBE. 1989. Ecosystem concepts and current trends in forest management: time for reappraisal. Forest Ecology and Management 26: 123-140.

RUSSELL, C. E. 1987. Plantation forestry. The Jari project, para, Brazil. pp. 76-89 *In* Jordan, C. F. (ed.). Amazonian rain forests. Ecosystem disturbance and recovery. Ecological Studies 60. Springer-Verlag, New York.

SANCHEZ, P. A., C. A. PALM, C. B. DAVEY, L. T. SZOTT and C. E. RUSSELL. 1985. Tree crops as soil improvers in the humid tropics pp. 327-350 *In* Cannell, M. G. R. and J. E. Jackson (eds.). Atributes of trees as crop plants. Institute of Terrestrial Ecology, Natural Environmental Research Council, Abbots Ripton, Huntingdon, England.

SANCHEZ, P. A. 1987. Soil productivity and sustainability in agroforestry. pp. 205-223 *In* Steppler, H. A., and P. K. R. Nair (eds.). Agroforestry. A decade of development. International Council for Research in Agroforestry. Nairobi, Kenya.

SANCHO, F. and R. MATA. 1987. Estudio detallado de suelos. Estación Biológica La Selva. Organización para Estudios Tropicales, San José, Costa Rica. 162 pp.

STANDLEY, P. C. 1937-38. Flora of Costa Rica. Field Museum of Natural History. Chicago.

WADSWORTH, F. H. 1983. Production of usable wood from tropical forests. pp. 278-288 *In* F. B. Golley (ed.). Tropical Rain Forest Ecosystems. Structure and Function. Ecosystem of the World 14A. Elsevier. New York.

WANG, D., F. H. BORMANN, A. E. LUGO and R. D. BOWDEN. 1991. Comparison of nutrient-use efficiency and biomass production in five tropical tree taxa. Forest Ecology and Management 46: 1-21.

WHITMORE, J. L. and G. S. HARTSHORN. 1969. Literature review of common tropical trees. Tropical Forestry Series, Contribution Nº 8. Institute of Forest Products. College of Forest Resources, University of Washington, Seattle. 113 pp.

YOUNG, A. 1989. Agroforestry for soil conservation. ICRAF, Science and Practice of Agroforestry. C.A.B. International and International Council for research in Agroforestry. Wallingford, UK. 276 pp.

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Factors Controlling Nitrification in Soils of Early Successional and Oak/Hickory Forests in the Southern Appalachians

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ABSTRACT

Montagnini, F., Haines, B. and Swank, W., 1989. Factors controlling nitrification in soils of early successional and oak/hickory forests in the southern Appalachians. *For. Ecol. Manage.*, 26: 77-94.

Factors regulating nitrification were examined in three forests of contrasting nitrifying activity in the southern Appalachians of North Carolina, U.S.A. NH_4-N availability was the main factor regulating nitrification in pine/mixed-hardwood and black locust (*Robinia pseudo-acacia* L.)-dominated early successional forests. Litter leachate solutions from black locust had high concentrations of N and other nutrients, but their influence upon nitrification as estimated in laboratory-amended soil incubations was relatively small.

In a mature oak/hickory forest, nitrification was not stimulated by NH_4-N amendments, nor by amendments of black-locust litter leachate solutions. Amendments with $CaCO_3$ and $CaCl_2$ stimulated ammonification but did not stimulate nitrification in the soils of this forest. Laboratory incubations of soils amended with oak/hickory live leaves, litter, and forest-floor extracts suggested a possible inhibitory action on nitrification from oak leaves. Low nitrification was also found in glucose-amended laboratory incubations of black-locust soils, suggesting that an increase of the C : N ratio of the soil following amendment with extracts could be responsible for low nitrification rates.

INTRODUCTION

Nitrogen availability often limits plant productivity in terrestrial ecosystems (Chapin, 1980). Factors controlling N mineralization and nitrification have been studied because these processes determine the availability of N for

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plant and microbial uptake. Nitrification results in the formation of nitrate ions, which can be leached, taken up by plants or reduced and lost in gaseous forms. Recent reviews on nitrification include those of Painter (1970), Focht and Verstraete (1977), and Schmidt (1982). The main factors that affect nitrification in soil are temperature, moisture, pH, and the substrates NH_4-N, O_2 and CO_2 (Stevenson, 1986). Evidence that nitrification is inhibited by decomposition products of organic residues in soils, or by metabolites excreted by plants or microorganisms, is still not conclusive (Schmidt, 1982).

Studies on nitrification started at the Coweeta Hydrologic Laboratory (North Carolina, U.S.A.) in the mid-1970s. Results of previous studies showed higher nitrifier populations in successional than in more mature forests (Todd et al., 1975; R. Rowe, unpublished Coweeta Lab. files, 1978). Nitrification rates were higher in an early successional watershed (WS6) dominated by black locust (*Robinia pseudo-acacia* L.), a nitrogen-fixing tree, than in a reference watershed (WS14) with more mature hardwoods (Montagnini, 1985; Montagnini et al., 1986). Within the early successional watershed, areas dominated by black locust had higher nitrification rates than areas with pine/mixed hardwoods. Ammonification rates were the main factor controlling nitrification in early successional stands, and there was no evidence of inhibition of nitrification in the hardwoods soils (Montagnini et al., 1986). The aim of the present study was to further examine factors controlling nitrification in these forests of contrasting nitrifying activity and treatment history. The following factors were examined: (1) general soil physical and chemical characteristics; (2) availability of ammonium; (3) availability of other soil mineral nutrients; (4) calcium content and soil pH; (5) populations of nitrifying bacteria; and (6) allelochemical inhibition of nitrification.

STUDY SITE

The 2185-ha Coweeta Hydrologic Laboratory (35°N, 83°W) is part of the Blue Ridge province of the southern Appalachian mountains of North Carolina, U.S.A. Precipitation is rather evenly distributed throughout the year, with an annual mean of 1800 mm at lower elevations and 2500 mm on the upper slopes; the mean annual temperature is 13°C (Swank, 1986). The forests of the reference watersheds have remained relatively undisturbed since 1924 (Johnson and Swank, 1973) and the vegetation consists of mature mixed hardwoods. Seventy percent of the basal area at low elevations consists of oak (*Quercus prinus*, *Q. coccinea*, *Q. rubra* and others), hickory (*Carya glabra* and other species) and red maple (*Acer rubrum* L.) (Day and Monk, 1974).

The reference WS14 and the successional WS6 are adjacent and northwest-facing. The mixed-hardwood forest of WS6 was cut in 1958 and sawlogs were removed. The watershed was limed, fertilized, seeded to fescue grass in 1959, and refertilized in 1965. In 1966 and 1967 the grass was killed by herbicide applications and the watershed was left for revegetation to occur (Johnson and Swank, 1973). In 1969 it was dominated by herbaceous species, in 1970 there were abundant woody shrubs, and by 1980 it was dominated by black locust, blackberries (*Rubus* spp.), and other woody species. The soils of both watersheds are Evard-Cowee gravelly loams (Typic Hapludults) on the slopes and Saunookee gravelly loams (Humic Hapludults) at lower elevations and coves (Swank, personal observations, 1987).

METHODS

Soil sampling

Soil was sampled at nine points along three transects running from the stream to the ridge in a pine/mixed hardwood and in a dense black-locust stand in the successional watershed (WS6) and in an oak/hickory forest stand in the adjacent reference watershed (WS14). Since the three stands were on the same soil series, major differences in soil characteristics among them may primarily reflect differences in treatment and vegetation type.

Samples of the 0–5 and 5–15-cm soil depths were collected with a 2.5-cm-diameter soil-corer. These are the zones of highest nitrifier activity (Montagnini, 1985), and correspond to the upper and lower portions of the A horizon. At each sampling point a composite of at least five samples was collected from each depth. Sampling was carried out in May, July, October (just before leaf-fall), and November (after leaf-fall) in 1983, and monthly from April to October in 1984.

Soil physical and chemical characteristics

Soil texture was measured with the hydrometer method (Day, 1983). Soil bulk density was estimated from soil cores 4.8 cm diameter and 5 cm long. Soil pH was measured in a 1:1 mixture of soil:deionized water (McLean, 1982) using a glass electrode. Total Kjeldahl nitrogen (TKN) and organic matter were determined on air-dried sub-samples of the <2-mm fraction. Kjeldahl-N was measured by acid digestion on a heater block, followed by colorimetric determination of NH_4-N in a Technicon Auto-Analyzer (Anonymous, 1977). Organic matter was measured by the Walkley-Black technique (Allison, 1975). Moisture content was determined by drying sub-samples at 70°C for 48 h.

Soil incubations

Nitrification rates were measured in aerobic laboratory incubations (Keeney, 1982). Samples were refrigerated at 4°C until analysis and were processed within 72 h after collection. The <4-mm fraction of field-moist soils was incubated in glass vials, and aerated every 3–4 days. Incubations were run in a dark cabinet, at 22 ± 2 °C, for 4 weeks. In 1983, time-course incubations were run using replicate sub-sets. Seven to nine sub-sets were extracted with 2*N* KCl before incubation. The extracts were analyzed colorimetrically with a Technicon Auto-Analyzer (Anonymous, 1970) to obtain the initial concentrations of NH_4-N and NO_3-N. At the end of the incubation time, other sub-sets were also extracted and analyzed as described above. Final-minus-initial values of NH_4-N + NO_3-N gave net N-mineralization rates, and final-minus-initial concentrations of NO_3-N gave a measurement of net nitrification rate. Final-minus-initial NH_4-N concentrations indicated NH_4-N consumption or production (ammonification). Net ammonification rates can be negative when all the NH_4-N present in the soil before incubation is consumed. Net nitrification rates can be lower than net N-mineralization rates when all the initial NH_4-N is consumed and part of the NH_4-N is immobilized by heterotrophic microorganisms. Net nitrification rates can be negative when NO_3-N is immobilized or denitrified, giving a lower value at the end of the incubation.

Forest-floor incubations

The forest floor (O_1 layer) in black locust, pine/mixed hardwoods and oak/hickory was collected in October 1984 with a 15-cm diameter plastic ring. The samples were pooled by stand, put in plastic bags and refrigerated until analysis. Following the procedures described for soils, 2 g of fresh material was incubated, and pH, TKN and percent moisture were determined.

Buried-bag incubations

For testing the effect of site temperature on nitrification, buried-bag incubations (Westermann and Crothers, 1980) were done in April and June of 1984. Soils of the 0–5-cm depth from the same points as already described were put in polyethylene bags and buried at the depth of sampling. Sub-sets were taken to the laboratory to measure the initial mineral N concentrations. Bags were collected after 4 weeks and soils were extracted. Incubations were also run in the laboratory for comparison.

Amended soil incubations

Soils of the nine sampling points of each stand were pooled, and sieved through 2-mm sieves. Soils were allowed to dry for 1/2 day until they reached 17–20% (*w*/*w*) moisture. Amendments were done by adding solutions at rates which would restore water content of 30–33%. Deionized water amendments served as controls. Soils were homogenized with a spatula after additions of solutions or deionized water.

(1) Ammonium additions

Ammonium was added to soils collected in April 1984. NH_4-Cl was added at a rate of 100 mg NH_4-N/kg of moist soil. This was calculated as the maximum amount of NH_4-N which could be nitrified in the soils of higher nitrifier activity (the black-locust soils), in a 4-week period (Montagnini et al., 1986).

(2) Calcium additions

Calcium amendments were performed in September 1984. Calcium was added at a rate of 20 g/kg of moist soil as either a 13.33% solution of $CaCO_3$ or a 12% solution of $CaCl_2$. $CaCO_3$ was added to increase the pH of the soil by 1–2 units, while $CaCl_2$ was added to decrease the pH by 1–2 units, to investigate the effects of the interaction between Ca availability and H^+-ion concentration on nitrification. Amendments were done to soils from all three sites and to a 1:1 mixture of oak/hickory: black-locust soils. Black-locust soils were used as an inoculum of high nitrifying activity to the oak/hickory soils.

(3) Forest-floor leachate additions

Amendments to soil incubations with forest-floor leachates were done in October 1984. It was expected that immediately after the initiation of leaf-fall, the forest-floor leachates would have the greatest effect on nitrification, with temperatures still high and a high rate of leaching of nutrients from the fresh leaf-litter. Black-locust forest-floor leachates were added to pine/mixed hardwoods and oak/hickory soils to examine the influence of a nutrient-rich solution on nitrification. Oak/hickory forest-floor leachates were added to all three soils to test a possible inhibitory action. Forest-floor leachates were collected in plastic containers which were set on top of the mineral soil. The bottom of the containers had fiberglass screens to hold the forest floor. Several holes were punched in the bottom to allow leachates to pass through and be collected in a plastic holder. The collectors were set at the sampling points of each forest stand, and collections were made as soon as possible following rains. Leachates were analyzed for pH, NH_4-N, NO_3-N and total N. Cations were analyzed by Atomic Absorption Spectrophotometry, and PO_4-P was analyzed by the colorimetric method of Strickland and Parsons (1972) using a spectrophotometer.

(4) Amendments with extracts of live leaves, leaf-litter, forest floor, and with glucose

Extracts of live leaves, leaf-litter and forest floor from oak/hickory were added to black-locust and to oak/hickory soils in October 1984, to test for the possible influence of substances inhibitory to nitrification. Leaves of oak, rhododendron and sassafrass were collected from tree seedlings in the oak/hickory site. Samples of fresh-fallen litter and the forest floor were collected from inside a 15-cm-diameter plastic ring, which was set at the top of the mineral soil. At least 10 pooled samples were taken at each sampling point. All materials were refrigerated for transportation to the laboratory, and kept at 4°C until processing. Leaves were pooled by species, and 6 g were diced and macerated in 30 ml of deionized water with a mortar and pestle. This viscous material was centrifuged at 3000 rpm for 5 min and the supernatant used. Litter samples were pooled and 20-g portions were blended with 200 ml deionized water. Forest-floor samples were processed similarly to the litter. All amendments were at a rate of 0.75 ml/g dry soil.

Low nitrification rates may result from competition for NH_4-N by heterotrophic microorganisms, whose activity may be stimulated by the addition of a carbon source with the extracts. To evaluate this effect, C was added in the form of glucose, at a rate of 1.0 g/100 g moist soil. This rate was calculated to correspond to the C addition in annual litter-fall, and it was also calculated to increase the soil C:N ratio to 40:1.

Statistical analysis

A correlation analysis between nitrification rates and soil parameters was done with the Correlation Procedure of the Statistical Analysis System (Helwig and Council, 1979). Analysis of variance on the results of nitrification potentials was done using the General Linear Models (GLM) Procedure and Duncan's Multiple Range Test of SAS (Helwig and Council, 1979).

RESULTS

Soil physical and chemical characteristics

Soil texture and bulk density were similar in the three forest stands (Montagnini, 1985). Soil NO_3-N concentrations (Table 1) were higher in black-locust than in pine/mixed hardwoods, and they were very low or undetectable in oak/hickory. There were no significant differences in NH_4-N concentrations, TKN or C:N among the three sites (Table 1). Although differences were not statistically significant, soil C concentrations were lower in pine/mixed hardwoods than in oak/hickory or black locust. Soil pH (Table 1) was similar in pine/mixed hardwoods and black locust, and was significantly lower in oak/hickory. Moisture percentage did not differ among the three sites. At all sites, NO_3-N, NH_4-N, TKN and C concentrations were lower at 5–15-cm than at 0–5-cm soil depth (Table 1). There were no differences in pH or soil moisture between the two depths. Patterns of differences between the three forests were similar to the 0–5-cm depth.

TABLE 1

Soil general characteristics in the forest floor (O_1) and at 0–5 and 5–15-cm soil depth, for the 1984 sampling season

	Depth (cm)	Pine/mixed hardwoods	Black locust	Oak/hickory
NO_3-N	O_1	7.2^b	49.5^a	1.5^c
(mg/kg)	0–5	1.14^b	11.7^a	0.03^c
	5–15	0.14^b	3.3^a	0.0^c
NH_4-N	O_1	79.1^a	44.8^b	74.4^a
(mg/kg)	0–5	3.07^a	4.86^a	2.0^a
	5–15	1.79^a	1.68^a	3.7^a
TKN	O_1	1.28^a	1.18^b	1.49^c
(%)	0–5	0.28^a	0.334^a	0.319^a
	5–15	0.145^a	0.151^a	0.171^a
C	0–5	3.86^a	4.33^a	4.56^a
(%)	5–15	2.43^a	2.23^a	2.63^a
C/N	0–5	14.1^a	13.6^a	14.8^a
	5–15	17.8^a	15.2^a	10.8^a
pH	O_1	5.84^{ab}	6.26^{ab}	5.57^a
	0–5	5.79^a	5.60^a	4.88^b
	5–15	5.53^a	5.65^a	4.89^b
Moisture	O_1	29.9^c	31.6^b	68.1^a
(%)	0–5	27.3^a	29.7^a	33.1^a
	5–15	27.4^a	28.5^a	30.2^a

Means with non-matching superscript letters indicate significant differences among forest types for a given depth and analysis ($n = 54$, $P < 0.05$). (The forest floor was only sampled in October 1984.)

Nitrogen mineralization and nitrification rates by forest type

As the record was more complete in 1984, only those results are presented; results of 1983 were similar. In the 0–5-cm layer, net N-mineralization and nitrification rates were substantially higher in black locust and pine/mixed hardwoods than in oak/hickory (Table 2). Net nitrification rates followed closely total net N-mineralization rates for black locust and pine/mixed hardwoods. In contrast, in the oak/hickory site net nitrification rates were almost negligible. All the NH_4-N was consumed in pine/mixed hardwoods and black locust, but NH_4-N accumulated in oak/hickory. At 5–15 cm, N mineralization and nitrification were lower than at 0–5 cm (Table 2).

TABLE 2

Net N mineralization, nitrification and NH_4-N production in the forest floor (O_1) and at 0–5 and 5–15 cm soil depth, for the 1984 sampling season

Depth (cm)	Pine/mixed hardwoods	Black locust	Oak-hickory
N mineralization (mg NH_4-N+NO_3-N kg^{-1} 30 days)			
O_1	117.5^a	221.9^{bc}	719.9^c
0–15	26.3^a	33.0^a	12.2^b
0–15	5.4^b	26.9^a	8.8^b
Nitrification (mg NO_3-N kg^{-1} 30 days)			
O_1	7.9^a	59.1^a	1.7^b
0–5	27.0^a	36.0^a	2.0^b
5–15	6.5^b	25.8^a	1.6^c
NH_4-N production (mg kg^{-1} 30 days)			
O_1	109.5^a	9.6^b	718.2^c
0–5	-1.2^b	-3.6^b	10.3^a
5–15	-1.0^b	0.75^b	7.1^a

Means with non-matching superscript letters indicate significant differences among forest types for a given depth and analysis ($n=54$, $P<0.05$).

Net N-mineralization was higher in the oak/hickory forest floor than in pine/mixed hardwoods or black locust. Nitrification rates and nitrate concentrations were higher in black locust than in pine/mixed hardwoods and oak/hickory forest floor (Tables 1 and 2). NH_4-N concentrations were higher in pine/mixed hardwoods and in oak/hickory than in black-locust forest floor. The TKN concentration was higher in oak/hickory than in pine/mixed hardwoods or black-locust forest floor. The pH was lower and the percent moisture was higher in the oak/hickory than in the pine/mixed hardwoods and black-locust forest floor.

Correlation of nitrification rates with soil parameters

The highest correlations of nitrification rates were: net N-mineralization rates ($r^2=0.85$, $P<0.0001$); total mineral N ($r^2=0.38$, $P<0.001$); and initial NO_3-N concentrations ($r^2=0.37$, $P<0.0001$; Montagnini, 1985). There were also significant, but low, positive correlations between nitrification and initial soil NH_4-N concentration ($r^2=0.09$, $P<0.001$), TKN content ($r^2=0.07$, $P<0.0001$) and negative correlations with NH_4-N production ($r^2=-0.18$, $P<0.0001$) and with soil H^+ ion concentration ($r^2=-0.13$, $P<0.0001$). Correlation analysis was also done with data from black locust and pine/mixed hardwoods only, to obtain indication of factors controlling nitrification in the two successional forests. When the oak/hickory forest site was deleted from the correlation analysis, the correlation coefficient of nitrification and H^+ ion concentration decreased from $r^2 = -0.13$ ($P < 0.0001$) to -0.03 ($P < 0.008$). The correlation coefficient between nitrification and net N-mineralization increased from $r^2 = 0.85$ to $r^2 = 0.97$. Correlation coefficients between nitrification and TKN and C:N ratio also increased from $r^2 = 0.13$ to 0.28 and from $r^2 = -0.07$ to -0.12, respectively. Correlations between nitrification and percent soil moisture and carbon concentration became significant with $r^2 = 0.15$ and 0.14, respectively. Values of other parameters remained similar to those obtained when the oak/hickory site was included in the analysis (Montagnini, 1985).

Comparison between field and laboratory incubations

The comparison of nitrification rates as measured in the laboratory and in the field for April is shown in Table 3. Similar results were obtained in June (Montagnini, 1985). Net N-mineralization and nitrification rates in pine/mixed hardwoods were about 2× higher in the laboratory than in the field. Net N-mineralization and nitrification rates of black-locust soils were 1.7× higher in laboratory than in field incubations. Net N mineralization was 5× higher, and nitrification 10× higher in oak/hickory laboratory incubations than in the field. NH_4-N was consumed during incubation of pine/mixed hardwoods and black-locust soils, whereas NH_4-N accumulated in oak/hickory, with ac-

TABLE 3

Comparison of net N mineralization, nitrification and NH_4-N production rates in soils from pine/mixed hardwoods, black locust and oak/hickory forest stands incubated in the laboratory and in the field, for April, 1984

Pine/mixed hardwoods		Black locust		Oak/hickory	
Lab.	Field	Lab.	Field	Lab.	Field
N mineralization (mg NH_4+NO_3-N kg^{-1} 30 days)					
28.8^a	14.9^a	33.4^a	19.2^a	22.0^a	4.1^a
Nitrification (mg NO_3-N kg^{-1} 30 days)					
28.7^a	14.4^{ab}	32.8^a	19.1^a	8.3^b	0.9^b
NH_4-N production (mg NH_4-N kg^{-1} 30 days)					
0.12^a	0.58^b	0.6^a	0.1^b	13.7^a	3.2^a

Means with non-matching superscript letters indicate significant differences among forest types for a given analysis (but not between laboratory vs. field; $n = 9$, $P < 0.05$).

cumulation about 4 × higher in the laboratory. Differences in rates among sites were the same for both incubation methods: net N mineralization was higher in black locust than in pine/mixed hardwoods or oak/hickory (although differences were not statistically significant in either field or laboratory) and nitrification was higher in black locust and pine/mixed hardwoods than in oak/hickory (difference was statistically significant in both field and laboratory).

Amended soil incubations

(1) Ammonium additions

All the added NH_4-N was nitrified in black locust and pine/mixed-hardwood soils (Table 4). Nitrification rates exceeded total net N-mineralization rates in both soils. The addition of NH_4-N did not increase nitrate production in oak/hickory. No NH_4-N was found at the end of the incubation in oak/hickory, suggesting that it had been immobilized by heterotrophic soil microorganisms.

TABLE 4

Net N mineralization, nitrification and NH_4-N production rates, initial NO_3-N and NH_4-N concentrations in control (unamended) and NH_4-N-amended pine/mixed hardwoods, black locust and oak/hickory soils

Pine/mixed hardwoods		Black locust		Oak/hickory	
Control	Amended	Control	Amended	Control	Amended
N mineralization (mg NH_4-N+NO_3-N kg^{-1} 30 days)					
27.4^a	-1.6^b	49.5^a	-0.78^b	18.1^a	-107.8^b
Nitrification (mg NO_3-N kg^{-1} 30 days)					
31.3^b	126.4^a	52.1^b	152.6^a	1.2^a	0.47^a
NH_4-N production (mg NH_4-N kg^{-1} 30 days)					
-3.9^a	-128.0^b	-2.6^a	-153.3^b	16.9^a	-108.3^b
Initial NO_3-N concentration (mg/kg)					
2.2^a	2.11^a	13.5^a	12.8^a	0.0^a	0.24^a
Initial NH_4-N concentration (mg/kg)					
4.7^b	33.6^a	3.9^b	153.4^a	7.3^b	144.4^a

Means with non-matching superscript letters indicate statistically significant differences between control and amended for a given soil ($n = 9$, $P < 0.05$).

TABLE 5

pH, N mineralization, nitrification, NH_4-N consumption rates, NO_3-N and NH_4-N concentrations for control and Ca-amended soils

Pine/mixed hardwoods			Black locust			Oak/hickory			Black locust/Oak-hickory 1:1 mixture		
Control	$+CaCO_3$	$+CaCl_2$	Control	$+CaCO_3$	$+CaCl_2$	Control	$+CaCO_3$	$+CaCl_2$	Control	$+CaCO_3$	$+CaCl_2$
pH											
6.16^a	6.88^a	5.04^b	5.48^b	6.63^a	4.44^c	5.21^b	6.48^a	4.05^c	5.33^b	6.67^a	4.23^c
N mineralization (mg NH_4-N+NO_3-N kg^{-1} 30 days)											
21.7^b	18.7^b	66.3^a	48.9^b	51.5^b	100.5^a	21.4^b	26.3^b	138.8^a	46.1^b	39.6^b	119.6^a
Nitrification (mg NO_3-N kg^{-1} 30 days)											
21.3^a	23.9^a	0.50^b	56.5^b	63.1^a	3.7^c	0.93^b	1.4^a	0.78^b	46.4^a	44.6^a	2.3^b
NH_4-N production (mg NH_4-N kg^{-1} 30 days)											
0.40^b	−5.2^b	66.3^a	−7.6^b	−11.6^b	96.8^a	20.5^b	26.3^b	138.8^a	−0.25^b	−4.9^b	117.2^a

Means with non-matching superscript letters indicate significant differences between treatments for a given soil ($n=7$, $P<0.05$).

(2) Calcium additions

The addition of $CaCO_3$ increased soil pH by 0.72–1.34 units, and the addition of $CaCl_2$ decreased soil pH by 1.04–1.16 units (Table 5). $CaCO_3$ amendment increased nitrification in black locust, but resulted in only a small increase in oak/hickory, and did not increase nitrification in oak/hickory:black-locust soils mixture (Table 5). The rate of nitrification in the oak/hickory:black-locust unamended mixture was much higher than in the oak/hickory $CaCO_3$ amended and unamended soils, with values close (82%) to those of the unamended black-locust soils (Table 5).

$CaCl_2$ amendment resulted in very low nitrification rates in all cases (Table 5). NH_4-N accumulated in all the $CaCl_2$-amended incubations: the highest values of NH_4-N accumulation were found in oak/hickory followed by the oak/hickory:black-locust mixture, black locust, and pine/mixed hardwoods.

(3) Forest-floor leachate additions

The pH of the black-locust forest-floor leachate was higher (7.17) than that of oak/hickory (5.96). Cation concentrations in black-locust leachates were: Ca, 50.9; K, 88.8; and Mg, 17.7 mg/l, 2–3× higher than in oak/hickory. PO_4-P was 3.2, NO_3-N was [illegible] 5 and NH_4-N was 8.8 mg/l, with respective values 14.0, 23.0 and 31.0× higher than in oak/hickory (Montagnini, 1985).

(a) Black-locust forest-floor leachate amendments. Amendments did not result in pH changes in either pine/mixed hardwoods or oak/hickory soils (data not presented). Net nitrification was higher in pine/mixed-hardwoods amended (37.2 mg NO_3-N kg^{-1} 30-days) than in unamended (33.2 mg kg^{-1} 30-days) soils, but differences were not statistically significant. Net nitrification rates were slightly lower in the amended (1.2 mg kg^{-1} 30-days) than in the unamended (2.1 mg kg^{-1} 30-days) oak/hickory soils, and the difference was statistically significant.

(b) Oak/hickory forest-floor leachate amendments. In pine/mixed hardwoods, there were no significant differences in pH between the amended and the unamended soils (data not presented). Net nitrification was 9.4% lower in the amended soils, although differences were not statistically significant. Net N mineralization rates were 10.9% lower in the unamended soils, but differences were not statistically significant ($P < 0.05$). All the NH_4-N was consumed during the incubation of amended and unamended pine/mixed-hardwood soils.

In black locust, the pH was significantly lower in the amended than in the unamended soils, but the difference was only 0.04 units. In contrast to the response of pine/mixed-hardwoods soils, nitrification rates were significantly higher in black-locust amended (59.6 mg kg^{-1} 30-days) than in the unamended (51.3 mg kg^{-1} 30-days) soils. As in the pine/mixed-hardwood soils, all the NH_4-N was consumed during the incubations of amended and unamended black-locust soils.

In oak/hickory, there were no differences in pH between amended and unamended soils. Net N mineralization and nitrification rates were slightly lower in the amended than in the unamended soils, but differences were not statistically significant.

(4) *Amendment with leaf, litter and forest-floor extracts and glucose*

In oak/hickory, nitrification was undetectable following amendments of leaf, litter, and forest-floor extracts, and in the unamended soils (Table 6). NO_3-N production was higher and NH_4-N accumulated in the glucose-amended soils. There were no differences in pH (data not presented) between amended and unamended soils.

In black locust, the nitrification rate was negative following amendment with oak-leaf extracts, indicating either denitrification or immobilization of NO_3-N (Table 6). In soils amended with sassafrass and rhododendron-leaf extracts, and in soils amended with litter and forest-floor extracts, nitrification rates were lower than or similar to the unamended soils. The NH_4-N was consumed during the incubation of black-locust soils amended with extracts and in the controls. Nitrification rates were negative and NH_4-N accumulated in the glucose-amended black-locust soil. There were no differences in pH between amended and control soils (data not presented).

TABLE 6

Nitrate and ammonium production for oak/hickory and black-locust soils amended with extracts of *Quercus*, *Sassaf*[illegible]d *Rhododen*[illegible]n leaves, litter, forest floor and glucose

Oak	Sassafras	Rhododendron	Litter	Forest floor	Glucose	Control
Oak/hickory						
NO_3-N production (mg kg^{-1} 30 days)						
n.d.	n.d.	n.d.	n.d.	n.d.	0.67^a	n.d.
NH_4 production (mg kg^{-1} 30 days)						
-1.0^b	0.04^b	-4.4^b	-0.5^b	9.2^a	1.2^a	14.5^a
Black locust						
NO_3-N production (mg kg^{-1} 30 days)						
-15.1^b	10.2^a	25.4^a	12.6^a	25.1^a	-0.8^a	27.1^a
NH_4-N production (mg kg^{-1} 30 days)						
-2.1^a	-2.8^a	-6.32^{ab}	-5.6^b	-8.1^b	1.2^a	-9.5^b

Means with non-matching superscript letters indicate significant differences between treatments for a given site ($n=7$, $P<0.05$, n.d. = not detectable).

DISCUSSION

Factors controlling nitrification rates: influence of general soil chemical and physical characteristics

The influence of soil physical characteristics on differences in nitrification between sites is likely to be minimal. Results of buried-bag incubations, in which soil structure is preserved, indicated the same differences between sites as in the laboratory incubations. The soil manipulations (sieving, mixing) in the laboratory may create more-aerated conditions as compared with the field. The interaction of constant temperature and soil manipulation increased nitrification in laboratory incubations as compared to buried bags, with similar effects on all soils. Site temperature did not appear to influence differences in nitrification between sites, because the same magnitudes of differences were found in the field as in the laboratory (Table 3).

Results of the laboratory and field incubations, the correlation analysis, and the NH_4-N amendments suggest that nitrification is controlled by ammonification rates in pine/mixed hardwoods and black locust but not in oak/hickory. Apparently, pine/mixed-hardwoods and black-locust soils have a high capacity to nitrify above the average levels shown in Table 2, with no other factors preventing oxidation of the added NH_4-N. The nitrification rates in pine/mixed hardwoods and black-locust NH_4-N-amended soils (Table 4) are equivalent to the highest rates reported for temperate forests (Robertson, 1982a).

In the black-locust-dominated areas, with higher nitrification, the availability of NH_4-N must be higher, possibly as a result of increased N inputs from N fixation. The leaching of mineral and organic N, cations and P from black-locust forest-floor may stimulate nitrification in the mineral soil. Black-locust forest-floor leachate amendments non-significantly increased nitrification in pine/mixed-hardwoods soils, although the effect was small. The amount of NH_4-N added with the leachate cannot account for the observed increase in nitrification. More likely, the increase resulted from the addition of mineral and organic N and other nutrients with the leachate. Concentrations of Ca, Mg, K and P were higher in the black-locust litter leachates, than in pine/mixed-hardwoods and oak/hickory. PO_4-P has been demonstrated to influence nitrification (Purchase, 1974; Hue and Adams, 1984). Inputs of dissolved organic N from forest-floor leaching may also stimulate ammonification and nitrification. If black-locust litter leachates contain dissolved organic N in a labile form, they may increase NH_4-N availability for nitrification.

Influence of soil Ca content and pH on N mineralization and nitrification

The increase of pH and Ca content through $CaCO_3$ amendment did not enhance nitrification in the oak/hickory soils (Table 5). Hence, low pH or low

Ca content do not appear to cause low nitrification in oak/hickory. Soil pH does not appear to influence differences in nitrification between black locust and pine/mixed hardwoods; pH differences between these two sites were small, and the amendment with $CaCO_3$ resulted in only a 10% increase in nitrification in both sites. Amendments with $CaCl_2$ resulted in decreased nitrification in all soils. Net ammonification was higher in the soils amended with $CaCl_2$, than in those amended with $CaCO_3$. Suppression of NH_4-N oxidation could only partially explain NH_4-N accumulation: 30% in pine/mixed-hardwoods, 55% in black locust and 15% in oak/hickory. Therefore, in spite of lowered pH, the addition of $CaCl_2$ increased net ammonification in all soils, with greatest effects in oak/hickory. The increase in the production of NH_4-N was apparently the result of lower immobilization of NH_4-N and higher ammonification rates.

Effects of decreased soil pH on soil N transformations vary with soil type, length of the experiments and soil chemistry (Strayer et al., 1981; Novick et al., 1984). Diminished soil nitrification at low pH appears to be due to inhibitory effects of free nitrous acid on *Nitrobacter* spp. (Prosser and Cox, 1982). Effects of salt amendments on ammonification and nitrification vary depending on the amounts and salts and soil type (McClung and Frankenberger, 1985). These authors reported that, in three different soils, nitrification was inhibited more by $CaCl_2$ than by NaCl and Na_2SO_4, whereas ammonification was either not affected or was stimulated, with greatest effects following addition of $CaCl_2$ and NaCl, in that order. Similar effects of chloride salts on nitrification have been reported by Laura (1974), Westerman and Tucker (1974), and Heilman (1975). Mechanisms of decreased nitrification following salt amendments to soils consist of both osmotic and indirect ion effects (Runge, 1983).

Factors controlling nitrification in the older-growth oak/hickory forest

Nitrification occurred occasionally and at low rates in oak/hickory. The lack of response to NH_4-N and $CaCO_3$ amendments and accumulation of NH_4-N suggested allelochemical inhibition of nitrification was occurring in oak/hickory. However, in black-locust: oak/hickory 1:1 mixture, nitrification rates were greater than expected from the mixture, suggesting tht part of the NH_4-N of oak/hickory had been nitrified. These results agree with those of an earlier experiment (Montagnini, 1985).

Christensen and MacAller (1985) reported that nitrification did not increase following NH_4-N additions, or addition of nutrients other than N to four hardwood soils in the piedmont of North Carolina, and suggested that factors other than nutrient availability may limit N transformations in those soils. Vitousek et al. (1982) observed lags in nitrification in eight of 17 forest sites in the U.S.A., and attributed this response to low nitrifier bacterial populations due to competition by roots, mycorrhyzae and heterotrophs, or to inhibition of nitrification by plant secondary compounds. Populations of nitrifiers in the oak/hickory forest of WS18, adjacent to WS14, were very low (Todd et al., 1975); R. Rowe (unpublished data, Coweeta Lab. files, 1978) also reported low nitrifier populations at the oak/hickory forest of WS2, another reference watershed at Coweeta. Vitousek (cited in Montagnini, 1985) measured nitrification in oak/hickory soil and in mixtures with soils of high nitrifying activity, and identified low bacterial populations as one of the factors controlling nitrification in the oak/hickory forest of WS2.

The oak/hickory forest-floor leachate amendment depressed nitrification in pine/mixed hardwoods and oak/hickory, suggesting an inhibitory effect. However, these amendments stimulated nitrification in black locust; possibly, in black locust with high nitrification, the inhibitory action was not enough to depress nitrifier activity.

Amendments with extracts of leaves, litter, and forest floor did not stimulate nitrification in oak/hickory, but NH_4-N was consumed during the incubation, suggesting that the extracts might have provided a C source which stimulated heterotrophic growth and immobilization of NH_4-N.

This evidence suggests that allelochemical inhibition does not have an influence on nitrification in oak/hickory. Rates of nitrate production were not affected by amendments of ground-litter and whole-leaf extracts to incubated soils in a North Carolina piedmont secondary sere (Montes and Christensen, 1979). Robertson (1982b) investigated the presence of labile inhibitors of nitrification in a secondary sere in the New Jersey piedmont by applying soil, litter and whole-leaf washings and extracts to incubated soils. Allelochemical inhibition of nitrification did not appear to regulate nitrification in these secondary successional sites.

Competition for NH_4-N by heterotrophic microorganisms may influence low nitrification in oak/hickory forest soils at Coweeta. This is supported by the results of glucose amendments, which resulted in very low nitrification rates in black-locust soils. Competition for NH_4-N may be enhanced through inputs of organic matter of high C:N ratio to the soils, such as oak leaves and litter. Competition for NH_4-N heterotrophic soil microbes decreases numbers of nitrifiers, as they are weaker competitors (Jones and Richards, 1977), but competition for other nutrients such as Ca and P may later result in even lower nitrifier populations in the mature forests.

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REFERENCES

Allison, L.E., 1975. Organic carbon. In: C.A. Black (Editor), Methods of Soil Analysis. Am. Soc. Agron., Madison, Wisc., pp. 1367–1378.

Anonymous, 1970. Operation Manual for the Technicon Auto-Analyzer II System. Technicon Industrial Systems, Tarrytown, NY, Tech. Publ. TA1-0170-01.

Anonymous, 1977. Technicon Industrial Method No. 369-75A/B, digestion and sample preparation for the analysis of total nitrogen using the Technicon BD-20 block digestor. Technicon Industrial Systems, Tarrytown, NY.

Chapin, F.S. III, 1980. The mineral nutrition of wild plants. Annu. Rev. Ecol. Syst., 11: 233–260.

Christensen, N.L. and MacAller, T., 1985. Soil mineral nitrogen transformations during succession in the Piedmont of North Carolina. Soil Biol. Biochem., 17: 675–681.

Day, P.R., 1983. Particle fractionation and particle size analysis. In: C.A. Black (Editor), Methods of Soil Analysis. Am. Soc. Agron., Madison, Wisc., pp. 545–567.

Day, F.P. Jr. and Monk, C.D., 1974. Vegetation patterns on a southern Appalachian Watershed. Ecology, 55: 1064–1074.

Focht, D.D. and Verstraete, W., 1977. Biochemical ecology of nitrification and denitrification. Adv. Microb. Ecol., 1: 135–214.

Heilman, P., 1975. Effects of added salts on nitrogen release and nitrate levels in forest soils of the Washington Coastal Area. Soil Sci. Soc. Am. Proc., 39: 778–782.

Helwig, J.T. and Council, K.A., 1979. SAS User's Guide. SAS Institute Inc., Cary, NC, 494 pp.

Hue, N.V. and Adams, F., 1984. Effect of phosphorus level on nitrification rates in three low-phosphorus Ultisols. Soil Sci., 137: 324–330.

Johnson, P.L. and Swank, W.T., 1973. Studies of cation budgets in the Appalachians on four experimental watersheds with contrasting vegetation. Ecology, 54: 70–80.

Jones, J.M. and Richards, B.N., 1977. Effects of reforestation on turnover of ^{15}N labelled nitrate and ammonium in relation to changes in soil microflora. Soil Biol. Biochem., 9: 383–392.

Keeney, D.R., 1982. Nitrogen-availability indexes. In: D.L. Page, R.H. Miller and D.R. Keeney (Editors), Methods of Soil Analysis. Part 2. Chemical and Microbiological Properties (2nd edition). Am. Soc. Agron., Madison, Wisc., pp. 711–730.

Laura, R.D., 1974. Effects of neutral salts on carbon and nitrogen mineralization of organic matter in soil. Plant Soil, 44: 587–596.

McClung, G. and Frankenberger, W.T., Jr., 1985. Soil nitrogen transformations as affected by salinity. Soil Sci., 139: 405–411.

McLean, E.O., 1982. Soil pH and lime requirement. In: A.L. Page, R.H. Miller and D.R. Keeney (Editors), Methods of Soil Analysis, Part 2. Chemical and Microbiological Properties (2nd edition). Am. Soc. Agron., Madison, Wisc., pp. 199–224.

Montagnini, F., 1985. Nitrogen turnover and leaching from successional and mature ecosystems in the southern Appalachians. Ph.D. Dissertation, Univ. of Georgia, Athens, GA, 251 pp.

Montagnini, F., Haines, B., Boring, L. and Swank, W., 1986. Nitrification potentials in successional black locust and in mixed hardwood forest stands in the southhern Appalachians, U.S.A. Biogeochemistry, 2: 197–210.

Montes, R.A. and Christensen, N.L., 1979. Nitrification and succession in the piedmont of North Carolina. For. Sci., 25: 287–297.

Novick, N.J., Klein, T.M. and Alexander, M., 1984. Effect of simulated acid precipitation on nitrogen mineralization and nitrification in forest soils. Water Air Soil Pollut., 23: 317-330.

Painter, H., 1970. A review of the literature of inorganic nitrogen metabolism in microorganisms. Water Res., 4: 493-450.

Prosser, J.I. and Cox, D.J., 1982. Nitrification. In: R.G. Burns and J.H. Slater (Editors), Experimental Microbial Ecology. Blackwell, Oxford, pp. 178-193.

Purchase, B.S., 1974. The influence of phosphate deficiency on nitrification. Plant Soil, 41: 527-539.

Robertson, G.P., 1982a. Nitrification in forested ecosystems. Philos. Trans. R. Soc. Lond., B, 296: 445-457.

Robertson, G.P., 1982b. Factors regulating nitrification in primary and secondary succession. Ecology, 63: 1561-1573.

Runge, M., 1983. Physiology and ecology of nitrogen nutrition. In: O.L. Lange, P.S. Nobel, C.B. Osmond and H. Ziegler (Editors), Physiological Plant Ecology III. Responses to the Chemical and Biological Environment. Springer, New York, pp. 163-200.

Schmidt, E.L., 1982. Nitrification in soil. In: F.J. Stevenson (Editor), Nitrogen in Agricultural Soils. Am. Soc. Agron., Madison, Wisc., pp. 253-288.

Stevenson, F.J., 1986. Cycles of Soils Carbon, Nitrogen, Phosphorus, Sulphur, Macronutrients. Wiley, New York, 380 pp.

Strayer, R.S., Chyi-Jiin Lin and Alexander, M., 1981. Effect of simulated acid rain on nitrification and nitrogen mineralization in forest soils. J. Environ. Qual., 10: 547-551.

Strickland, J.D. and Parsons, T.R., 1972. A Manual of Seawater Analysis (2nd. edition). Fisheries Research Board of Canada, Ottawa, Bull. 167, pp. 49-52.

Swank, W.T., 1986. Biological control of solute losses from forest ecosystems. In: S.T. Trudgill (Editor), Solute Processes. Wiley, New York, pp. 87-139.

Todd, R.L., Swank, W.T., Douglass, J.G., Kerr, P.C., Brockway, D.L. and Monk, C.D., 1975. The relationship between nitrate concentration in the southern Appalachian mountain streams and terrestrial nitrifiers. Agro-Ecosystems, 2: 127-132.

Vitousek, P., Gosz, J.R., Grier, C.C., Melillo, J.M. and Reiners, W.A., 1982. A comparative analysis of potential nitrification and nitrate mobility in forest ecosystems. Ecol. Monogr., 52: 155-177.

Westermann, D.T. and Crothers, S.E., 1980. Measuring soil nitrogen mineralization under field conditions. Agron. J., 72: 1009-1012.

Westerman, R.L. and Tucker, T., 1974. Effect of salts and salts plus nitrogen-15-labeled ammonium chloride on mineralization of soil nitrogen, nitrification and immobilization. Soil Sci. Soc. Am. Proc., 38: 602-605.

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Soil-solution chemistry in black locust, pine/mixed-hardwoods and oak/hickory forest stands in the southern Appalachians, U.S.A.

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ABSTRACT

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Soil-solution chemistry was measured over a 15-month period in three forest stands of contrasting nitrogen mineralization and nitrification rates in the southern Appalachians of North Carolina, U.S.A., using porous-cup lysimeters. In a black-locust-dominated stand, soil solution NO_3-N was 3.73 and 5.04 mg l^{-1} at 30- and 60-cm depth respectively, and dissolved organic N (DON) was 0.718 and 0.582 mg l^{-1} respectively. Values at 30 and 60 cm for a pine/mixed-hardwood stand were 0.032 and 0.058 mg l^{-1} NO_3-N, and 0.201 and 0.168 mg l^{-1} DON (values are means over the whole duration of the study). At both depths, soil solution conductivity, pH, Ca, Mg, K and PO_4-P were higher in black locust than in pine/mixed-hardwoods, and there were no differences in soil solution Na. In an oak/hickory stand, soil solution NO_3-N at 30-cm depth was 0.008 mg l^{-1}, and DON was 0.357 mg l^{-1}. At 30-cm depth, soil-solution conductivity, Ca, Mg and PO_4-P were higher in black locust than in oak-hickory, with no differences in pH, K and Na; DON, pH and K were higher in oak/hickory than in pine/mixed-hardwoods. In the oak/hickory and pine/mixed-hardwoods forest stands, with relatively lower soil N turnover rates, DON was a major portion of soil solution N.

INTRODUCTION

Increased soil-nitrate leaching is a frequent response to disturbance in terrestrial ecosystems. Several investigators have studied factors determining the magnitude of soil-nitrate leaching following disturbance in temperate ecosystems (e.g., Likens et al., 1969; Vitousek et al., 1979, 1981, 1982; Vitousek and Matson, 1984). Nitrate leaching is accompanied by cation leaching

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(Likens et al., 1969; Vitousek, 1984). In terrestrial ecosystems, generally less than 10% of the soil organic N pool is mineralized annually (Keeney, 1982) and thus susceptible to leaching. Leaching of organic N can also be quantitatively important (Swank and Waide, 1980; Sollins and McCorison, 1981; Sollins et al., 1981).

The influence of N_2-fixing trees on elevated soil solution N concentration, and on other aspects of soil-solution chemistry, has been reported by Binkley et al. (1982) and by Van Miegroet and Cole (1984, 1985), in temperate ecosystems of North America. In this paper, we report soil-solution chemistry in two forest stands located in an early successional watershed, and in another stand in a mixed-hardwood forest watershed, at the Coweeta Hydrologic Laboratory, in the southern Appalachians of North Carolina (U.S.A.). Within the early successional watershed, areas dominated by black locust (*Robinia pseudo-acacia* L.), a leguminous, N_2-fixing tree, were compared with areas of pine/mixed-hardwoods to assess the influence of black locust on soil-solution chemistry.

Areas with black locust had high N inputs from symbiotic N_2 fixation, which has been documented for this tree in another watershed at Coweeta (Boring and Swank, 1984), and high N content in annual litterfall (White, 1986; White et al., 1988). Results of earlier studies showed that nitrification rates were higher in black-locust soil (36.0 mg kg^{-1} 30 $days^{-1}$) than in pine-mixed hardwoods soil (27 mg mg^{-1} 30 $days^{-1}$); nitrification was much lower in the oak/hickory forest stand of the adjacent watershed (2.04 mg kg^{-1} 30 $days^{-1}$; values averaged for one sampling season (Montagnini, 1985; Montagnini et al., 1986, 1989)). The objective of the present study was to compare soil-solution chemistry (mineral and organic N, pH, conductivity, Ca, Mg, K, Na and PO_4-P) between these sites with different vegetation and contrasting soil nitrifying activity.

STUDY SITE

The study was conducted at the 2185-ha Coweeta Hydrologic Laboratory (35°N lat., 83°W long.), in the Blue Ridge Province of the southern Appalachian Mountains of North Carolina, U.S.A. Annual precipitation varies from 1800 mm at lower elevations to 2500 mm on the upper slopes. Precipitation is rather evenly distributed throughout the year, and the mean annual temperature is 13°C (Swank, 1986). Annual NO_3-N inputs in bulk precipitation average 2.9 kg/ha (means over a 10-year period, 1973–1982, at watershed 18, adjacent and with same aspect as the watersheds in this study; Swank and Waide, 1988).

The successional watershed was an 8.86-ha north-facing catchment that had been left to natural revegetation since 1968. When this study was conducted, vegetation consisted of dense black-locust stands on 73% of the watershed, and pine/mixed-hardwoods and mesic mixed-hardwoods, with low densities of black locust, on the remaining 12 and 15% of the area, respectively.

The mixed forest on the adjacent 61.1-ha north-facing watershed was dominated by oak (*Quercus* spp.) and hickory (*Carya* spp.), with mountain laurel (*Kalmia latifolia* L.) and rose-bay rhododendron (*Rhododendron maximum* L.) as the most important understory species (Day and Monk, 1974). This forest had been undisturbed since 1924 (Swank and Douglass, 1977).

The three forest stands were on Ultisols (Orthic Acrisols in the F.A.O. system), of the Saluda series, Evard-Cowee gravelly loams (members of the family of Typic Hapludults) on the slopes, and Sawnookee gravelly loams (members of the family of Humic Hapludults; U.S. Soil Taxonomy) on the lower elevations (Swank, unpublished data, 1985). Textural analysis of A_1 horizons at four elevations from stream banks to ridges showed similar sandy loams (Montagnini, 1985). Detailed data on soil chemical characteristics and soil N mineralization and nitrification rates are presented in Montagnini et al. (1986, 1989, 1990).

METHODS

The soil solution was sampled at the same sites where soil N mineralization, nitrification and inorganic- and organic-N pools were measured, as part of studies on factors controlling nitrification and soil N accumulation (Montagnini et al., 1986, 1989). The soil solution was sampled with porous-cup lysimeters (Hansen and Harris, 1975) at three elevations from stream banks to ridge tops, at nine sampling points in both a black-locust and a pine/mixed-hardwood stand in the successional watershed. Depth of samplers in black locust and pine/mixed-hardwoods was 30 cm (below the main rooting zone) and 60 cm (bottom of the mineral soil). In the oak/hickory forest, three collectors were installed at three sampling points at 30-cm depth. A tension of −20 kPa, approximating that of soil water at field capacity, was created with a hand vacuum pump. Collectors were installed in May 1983 and sampled 2-weekly from September 1983 until December 1984. Samples were expelled into acid-washed polypropylene bottles by positive pressure from a hand pump.

Phenyl mercuric acetate (PMA) at a rate of 0.5 ml/l was added to all solution samples as a preservative. PMA was prepared by dissolving 0.1 g of phenyl mercuric acetate in 15 ml of dioxane and completing volume to 100 ml with deionized water. Samples were kept at 4°C until analysis. NH_4-N and NO_3-N were analyzed with a Technicon Auto-Analyzer (Anonymous, 1970). Total Kjeldahl Nitrogen (TKN) was analyzed by acid digestion in a heater block followed by colorimetric determination of NH_4-N in the digests with a Technicon Auto-Analyzer (Anonymous 1977a,b). Soil-solution samples were not filtered before Kjeldahl digestion, as they had passed through the 1.2-μm pore size of the ceramic cups. Dissolved organic nitrogen (DON) was calculated as the difference between TKN and NH_4-N.

The conductivity was measured with a Hach conductivity meter (City State of MFG, Loveland, Colorado, U.S.A.) calibrated with a 1000 mg/l solution of sodium chloride (NaCl). The pH was measured with a glass electrode and an Orion 701-A Ion Analyzer (Orion Research, Cambridge, Massachusetts, U.S.A.). Cations (Ca, Mg, K, Na) and PO_4-P were analyzed in a sub-set of samples (two collections in October 1984). Cations were measured with a Perkin Elmer 5000 Atomic Absorption Spectrophotometer (Perkin Elmer, Norwalk, Connecticut, U.S.A.) and PO_4-P was measured by the Strickland and Parsons (1972) colorimetric test, using a Spectronic 700 spectrophotometer (Bausch and Lomb, Rochester, New York, U.S.A.). Certified standards (Water Pollution Quality Control, Nutrient Samples, Environmental Monitoring and Support Laboratory, Cincinnati, Ohio, U.S.A.) of low (< 1

TABLE 1

Soil-solution chemistry for pine/mixed-hardwoods ($n = 150$), black locust ($n = 150$) and oak/hickory ($n = 100$) forest sites (means and standard errors)[1]

	Depth (cm)	Pine/mixed-hardwoods	Black locust	Oak/hickory
NO_3-N (mg/l)				
	30	0.032 (0.01)^{b}	3.73 (0.25)^{a}	0.008(0.007)^{b}
	60	0.058 (0.02)^{b}	5.04 (0.33)^{a}	-
DON (mg/l)				
	30	0.201 (0.03)^{c}	0.718 (0.05)^{a}	0.357 (0.04)^{b}
	60	0.168 (0.03)^{b}	0.582 (0.07)^{a}	-
pH	30	6.14 (0.01)^{b}	6.28 (0.03)^{a}	6.27 (0.05)^{a}
	60	6.04 (0.03)^{b}	6.18 (0.03)^{a}	-
conductivity (μS/cm)				
	30	14.3 (1.2)^{b}	52.4 (3.9)^{a}	15.08 (1.4)^{b}
	60	11.4 (0.45)^{b}	54.37 (4.4)^{a}	-
Ca	30	1.2 (0.2)^{b}	7.4 (0.8)^{a}	1.1 (0.3)^{b}
(mg/l)	60	0.76 (0.1^{b}	7.0 (1.5)^{a}	-
Mg	30	0.87 (0.2)^{b}	4.4 (0.4)^{a}	1.1 (0.3)^{b}
(mg/l)	60	0.52 (0.04)^{b}	6.0 (1.8)^{a}	-
K	30	0.27 (0.05)^{b}	3.59 (0.97)^{a}	1.48 (1.1)^{a}
(mg/l)	60	0.74 (0.29)^{a}	1.62 (0.19)^{a}	-
Na	30	0.49 (0.05)^{a}	0.48 (0.03)^{a}	0.51 (0.03)^{a}
(mg/l)	60	0.40 (0.03)^{a}	0.62 (0.04)^{a}	-
PO_4-P (mg/l)				
	30	0.013 (0.002)^{b}	0.046 (0.02)^{a}	0.008 (0.004)^{b}
	60	0.007 (0.003)^{a}	0.015 (0.003)^{a}	-

[1] Values are means for the whole duration of the study. Means with non-matching superscript letters indicate significant differences ($P < 0.001$) between sites (not between depths). Cations and PO_4-P were measured on a subset of samples from two collections in October 1984.

mg/l) and high (> 10 mg/l) NH_4-N and NO_3-N and low (< 1 mg/l) and TKN and PO_4-P were run with each set of determinations. Statistical analyses were done with the means and GLM procedures of SAS (Helwig and Council, 1979).

RESULTS

NH_4-N was undetectable in the soil solution in all samples from the three forest stands; therefore, the dissolved organic nitrogen (DON) equaled the TKN values. NO_3-N, DON, pH, conductivity, Ca, Mg, K and PO_4-P were higher in black-locust soil solution than in pine/mixed-hardwoods, at both 30- and 60-cm depth, and there were no differences in Na (Table 1). NO_3-N concentrations were higher at 60 cm than at 30 cm for black locust (statistics not shown).

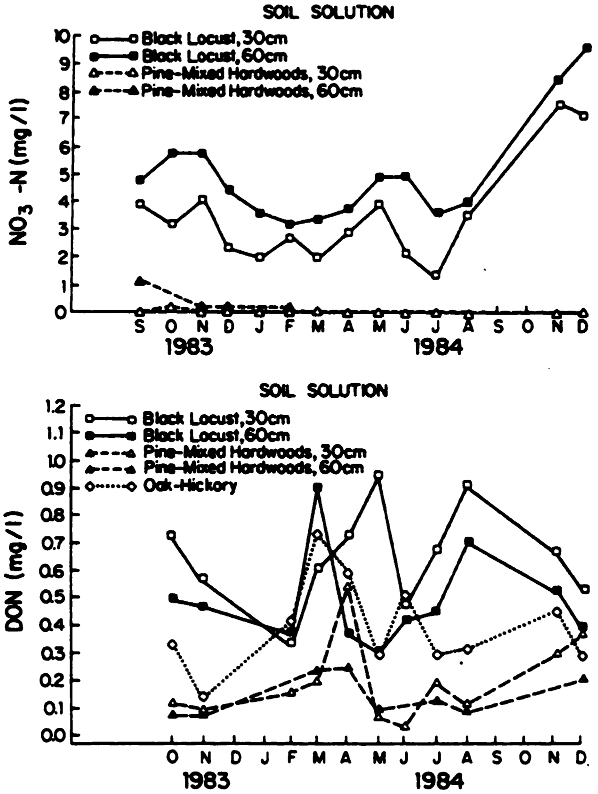

Fig. 1 Soil-solution nitrate and dissolved organic nitrogen (DON) for black locust, pine/mixed-hardwoods and oak/hickory (monthly means from September 1983 to December 1984). NO_3-N values for oak/hickory were too low to show in the figure.

At 30 cm, NO_3-N, DON, Ca, Mg, PO_4-P and conductivity were higher in black locust than in oak/hickory, with no differences in pH, K and Na, while DON, pH and K were higher in oak/hickory than in pine/mixed-hardwoods (Table 1).

In black locust, soil-solution NO_3-N concentrations at both 30- and 60-cm depths peaked in October and November 1983, then declined through the winter months with an additional peak in May (Fig. 1). High concentrations (> 7 mg/l) were again observed in November and December 1984. Low NO_3-N concentrations in pine/mixed-hardwoods and oak/hickory prevented detection of seasonal changes in concentrations. No clear or consistent seasonal trends of DON soil solution concentrations were apparent in either of the three stands (Fig. 1).

DISCUSSION

Influence of black locust on soil-solution nitrate concentrations

Greater NO_3-N concentrations in black-locust soil solution suggest that this area of the successional watershed was a potentially important source of NO_3-N to the saturated zones of the catchment. As greater concentrations were found at 60- than at 30-cm depth in black locust, apparently anion exchange capacity was low and little NO_3-N was retained at exchange sites at that depth; high nitrate concentrations at 60 cm may also result from nitrification taking place between 30- and 60-cm soil depth. Concentrations of NO_3-N in the soil solution at 60-cm depth were 87 times higher in black locust than in pine/mixed-hardwoods. Since black locust constituted about 70% of the basal area of the successional watershed, areas dominated by this tree were the main source of NO_3-N to groundwater.

At 30-cm depth, soil solution NO_3-N concentration was greater in black locust than in either pine/mixed-hardwoods or oak/hickory. Increased NO_3-N soil-solution concentrations under N_2-fixing trees have been reported elsewhere. For example, Binkley et al. (1982) found that soil-solution NO_3-N concentrations were 6.2 times higher in a younger ecosystem dominated by red alder (*Alnus rubra* Bong.) and Douglas fir (*Pseudotsuga menziessi* (Mirb.) Franco), than in an older ecosystem dominated by western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), Douglas fir, and western cedar (*Thuja plicata* Donn.), in coastal British Columbia, Canada. Greater NO_3-N concentrations in the soil solution under the younger ecosystem were probably a result of N fixation by red alder. Van Miegroet and Cole (1984) also found that NO_3-N concentrations in the soil solution were greater in a red-alder ecosystem than in an adjacent Douglas-fir ecosystem located in the Cascade Mountains, Washington, U.S.A.; concentrations under red alder periodically exceeded 10 mg/l, which is close to the concentrations reported here for black locust at Coweeta.

The seasonal pattern of NO_3-N concentration in soil solution is the result of the interaction of nitrification, plant and microbial uptake, denitrification and leaching. Concentrations at 30- and 60-cm depth were least during the winter months, possibly due to limited nitrifying activity, and they were also less in July, which is the time when plant uptake rates are greater. Peaks in NO_3-N concentrations in the soil solution in October and November suggest that NO_3-N production was still occurring in autumn while uptake by vegetation decreased. The NO_3-N peak in May suggests that nitrification in the soil started early in spring, while uptake by vegetation was low, resulting in a high NO_3-N content in the soil solution. A periodic variation of nutrient levels in the root zone is the general case, with a minimum in early autumn and a maximum in the spring (Wiklander, 1974).

Soil solution cation, H^+ and PO_4-P concentrations

In addition to greater NO_3-N, black-locust soil solution had higher conductivity, pH, Ca, Mg and PO_4-P than pine/mixed-hardwoods at both 30- and 60-cm depth. Consistent with the findings at Coweeta, Binkley et al. (1982) reported that conductivity, and NO_3-N, Ca, Mg and K concentrations, were higher in the soil solution in the ecosystem dominated by an N_2-fixing tree (alder). However, unlike the results at Coweeta, the pH of the mineral soil leachate was lower in the alder-dominated ecosystem. Van Miegroet and Cole (1984, 1985) also reported that subsurface solutions were more acid under red alder than under Douglas fir; the acidification of the solution coincided with intensive nitrification under red alder. They estimated that the actual amount of H^+ in the soil solution was less than calculated from nitrification, indicating partial buffering of the soil solution against acidification. The oxidation of NH_4-N to NO_3-N leads to the release of H^+ that can acidify the soil, the soil solution, or both. The extent to which acidification proceeds depends on the rate of H^+ release relative to neutralization. Processes that can counteract the acidifying effects of nitrification include the uptake of NO_3-N, high decomposition rates, adsorption of H^+ at soil-exchange sites (Binkley, 1986) and denitrification. The sensitivity to pH changes in soils depends on cation exchange capacity and Ca saturation (Reuss and Johnson, 1986). Possibly, the acidifying effects of elevated nitrification in the black-locust soil were neutralized due to its high base saturation of 47.3%, and high Ca, 73.5 mg/100 g (data from 0–15 cm depth; cation exchange capacity was calculated as sum of bases plus exchangeable hydrogen; cations were extracted with double acid solution of $0.025N$ H_2SO_4 and $0.05N$ HCl; Montagnini et al., 1986).

With generally greater concentrations in the soil solution, areas with black locust had greater potential for leaching of Ca, Mg, K, Na and PO_4-P from the soil column, than areas with pine/mixed-hardwoods. Binkley et al. (1982) and Van Miegroet and Cole (1984) also reported that cation leaching was greater in the ecosystems dominated by red alder. Increased cation leaching in the areas dominated by the N_2-fixing trees was related to the presence of large amounts of NO_3-N in the soil solution. Vitousek (1984) reported a large increase of cation losses following disturbance of a mixed forest in southern Indiana. This increase was related to an increase of NO_3-N production and loss, and the results tended to support a model that suggests that anion and cation leaching through soils is controlled by the supply and mobility of ions (Johnson and Cole, 1980).

Soil-solution dissolved organic-N concentrations

Dissolved organic-N concentrations at 30-cm depth were about three times greater in black locust than in pine/mixed-hardwoods, and two times higher than in oak/hickory (Table 1). However, in black locust, dissolved organic-N concentrations at 30- and 60-cm depth were 5–8 times less than those of NO_3-N (Table 1), and NO_3-N was the major form of N leaching from these stands. Binkley et al. (1982) measured DON on a few test samples in the soil solution in a red-alder stand, and found that organic N accounted for 25–65% of the total (mineral + organic) N.

Soil N mineralization and nitrification rates, and soil NO_3-N, NH_4-N and TKN concentrations in black locust, pine/mixed-hardwoods and oak/hickory were reported by Montagnini (1985), and Montagnini et al. (1986, 1989, 1990). Nitrogen turnover rates, calculated as the proportion of N mineralized/total soil N, for a six-month growing-season (May–October) were calculated as 3.48, 1.83 and 0.23% of total soil N for black locust, pine/mixed-hardwoods and oak/hickory, respectively (Montagnini, 1985). In pine/mixed-hardwoods and oak/hickory, DON concentrations in the soil solution at 30-cm depth were relatively greater than those of NO_3-N: six times higher in pine/mixed-hardwoods, and 44 times higher in oak/hickory. Therefore, in these two forest stands where N turnover was relatively smaller, leaching losses of N in dissolved organic forms had greater importance than those in mineral forms. In another oak/hickory forest at Coweeta, Qualls (1988) found that the average annual DON output from the forest floor was 31% of the input in solid litterfall, and that over 95% of total dissolved organic matter was removed as the water percolated through the soil profile, leaving the ecosystem in groundwater. Our results suggest that, in soils with low nitrification rates, DON leaching may have a relative larger contribution to total soil N leaching.

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REFERENCES

Anonymous, 1970. Operations Manual for the Technicon AutoAnalyzer II System. Technicon Industrial Systems, Tarrytown, NY, Tech. Publ. TA 1-0170-01.

Anonymous, 1977a. Digestion and sample preparation for the analysis of total Kjeldhal nitrogen and/or total phosphorus in water samples using the Technicon BD-40 block digestor. Industrial Method 376-75W/B, Technicon Industrial Systems, Tarrytown, New York.

Anonymous, 1977b. Individual/simultaneous determination of nitrogen and/or phosphorus in BD acid digests. Industrial Method 329-74W/B, Technicon Industrial Systems, Tarrytown, New York.

Binkley, D., 1986. Forest Nutrition Management. Wiley, New York, pp. 50–73.

Binkley, D., Kimmins, J.P. and Feller, M.C., 1982. Water chemistry profiles in an early - and a mid-successional forest in coastal British Columbia. Can. J. For. Res., 12: 240–248.

Boring, L.R. and Swank, W.T., 1984. Symbiotic nitrogen fixation by black locust (*Robinia pseudo-acacia* L.). For. Sci., 3: 528–537.

Day, F.P. and Monk, C.D., 1974. Vegetation patterns on a southern Appalachian watershed. Ecology, 55: 1064–1074.

Hansen, E.A. and Harris, A.R., 1975. Validity of soil-water samples collected with porous ceramic cups. Soil Sci. Soc. Am. Proc., 39: 528–536.

Helwig, J.T. and Council, K.A., 1979. SAS User's Guide. SAS Institute Inc., Cary, North Carolina, pp. 237–263.

Johnson, D.W. and Cole, D.W., 1980. Anion mobility: relevance to nutrient transport from forest ecosystems. Environ. Int. 3: 79–90.

Keeney, D.R., 1982. Nitrogen – Availability indices. In: L.A. Page, R.H. Miller, and D.R. Keeney (Editors), Methods of Soil Analysis. Part 2, Chemical and Biological Properties (2nd. edition) Agronomy Society of America, Madison, Wisconsin, pp. 711–734.

Likens, G.E., Bormann, G.H. and Johnson, N.M., 1969. Nitrification: importance to nutrient losses from a cutover forested ecosystem. Science, 163: 1205–1206.

Montagnini, F., 1985. Nitrogen turnover and leaching from successional and mature ecosystems in the southern Appalachians. Ph.D. dissertation, University of Georgia, Athens, GA, 251 pp.

Montagnini, F., Haines, B.L., Boring, L.R. and Swank, W.T., 1986. Nitrification potentials in early successional black locust and mixed hardwood forest stands in the southern Appalchians. Biogeochemistry, 2: 197–212.

Montagnini, F., Haines, B.L. and Swank, W.T., 1989. Factors controlling nitrification in soils of black locust and mixed hardwood forest stands in the southern Appalachians. For. Ecol. Manage., 26: 77–94.

Montagnini, F., Haines, B.L., Swank, W.T. and Waide, J.B., 1990. Nitrification in undisturbed mixed hardwoods and manipulated forests in the southern Appalachian mountains of North Carolina, U.S.A. Can. J. For. Res., 19: 1226–1234.

Qualls, R.G., 1988. The biogeochemical properties of dissolved organic matter in a deciduous forest ecosystem: their influence on the retention of nitrogen and phosphorus. Ph.D. dissertation, University of Georgia, Athens, GA.

Reuss, J.O. and Johnson, D.W., 1986. Acid Deposition and the Acidification of Soils and Waters. Springer, New York, pp. 73–80.

Sollins, P. and McCorison, F.M., 1981. Nitrogen and carbon solution chemistry of an old growth coniferous forest watershed before and after cutting. Water Resour. Res. 17: 1409–1418.

Sollins, P., Cromack, K. Jr., McCorison, F.M., Waring, R.H. and Harr, D., 1981. Changes in nitrogen cycling at an old-growth Douglass-fir site after disturbance. J. Environ. Qual., 10: 37–42.

Strickland, J.D. and Parsons, T.R., 1972. A Manual of Seawater Analysis. Fisheries Research Board of Canada, Ottawa.

Swank, W.T., 1986. Biological control of solute losses from forest ecosystems. In: J.T. Trudgill (Editor), Solute Processes. Wiley, New York, pp. 87–139.

Swank, W.T. and Douglass, J.E., 1977. Nutrient budgets for undisturbed and manipulated hardwood forest ecosystems in the mountains of North Carolina. In: D.L. Correll (Editor). Watershed Research in Eastern North America: A Workshop to Compare Results. Smithsonian Institution, Edgewater, MD, pp. 344–363.

Swank, W.T. and Waide, J.B., 1980. Interpretation of nutrient cycling research in a managment context: evaluating the potential effects of alternative management strategies on site productivity. In: R.W. Waring (Editor), Forests: Fresh Perspectives from Ecosystem Analysis. Oregon State University Press, Corvallis, pp. 137–158.

Swank, W.T. and Waide, J.B., 1988. Characterization of baseline precipitation and stream chemistry and nutrient budgets for control watersheds. In: W.T. Swank and D.A. Crossley Jr. (Editors), Forest Hydrology and Ecology at Coweeta. Springer, New York, pp. 57–79.

Van Miegroet, H. and Cole, D.W., 1984. The impact of nitrification on soil acidification and cation leaching in a red alder ecosystem. J. Environ. Qual., 13: 586–590.

Van Miegroet, H. and Cole, D.W., 1985. Acidification sources in red alder and Douglas-fir soils – Importance of nitrification. Soil Sci. Soc. Am. J., 49: 1274–1279.

Vitousek, P.M., 1984. Anion fluxes in three Indiana forests. Oecologia, 61: 105–108.

Vitousek, P.M. and Matson, P.A., 1984. Mechanisms of nitrogen retention in forest ecosystems: a field experiment. Science, 225: 51–52.

Vitousek, P.M., Gosz, J.R., Grier, C.C., Melillo, J.M., Reiners, W.A. and Todd, R.L., 1979. Nitrate losses from disturbed ecosystems. Science, 204: 469–474.

Vitousek, P.M., Reiners, W.A., Melillo, J.M., Grier, C.C. and Gosz, J.R., 1981. Nitrogen cycling and loss following forest perturbation: the components of response. In: G.W. Barrett and R. Rosemberg (Editors), Stress Effects on Natural Ecosystems. Wiley, New York, pp. 115–127.

Vitousek, P.M., Gosz, J.R., Grier, C.C., Melillo, J.M. and Reiners, W.A., 1982. A comparative analysis of potential nitrification and nitrate mobility in forest ecosystems. Ecol. Monogr., 52: 155–177.

White, D.L., 1986. Litter production, decomposition, and nitrogen dynamics in black locust and pine-mixed hardwood stands of the southern Appalachians. M. Sc. thesis, University of Georgia, Athens.

White, D.L., Haines, B.L. and Boring, L.R., 1988. Litter decompostion in southern Appalachian black locust and pine-hardwood stands: litter quality and nitrogen dynamics. Can. J. For. Res., 18: 54–63.

Wiklander, L., 1974. Leaching of plant nutrients in soils. I. General principles. Acta Agric. Scand., 24: 349–356.

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Nitrification potentials in early successional black locust and in mixed hardwood forest stands in the southern Appalachians, USA

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Abstract. Soil nitrogen mineralisation and nitrification potentials, and soil solution chemistry were measured in black locust (*Robinia pseudo-acacia* L.), in pine-mixed hardwood stands on an early successional watershed (WS6), and in an older growth oak-hickory forest located on an adjacent, mixed hardwood watershed (WS14) at Coweeta Hydrologic laboratory, in the southern Appalachian mountains, U.S.A. Nitrification potentials were higher in black locust and pine-mixed hardwood early successional stands than in the oak-hickory forest of the older growth watershed. Ammonification rates were the main factor controlling nitrification in the early successional stands. There was no evidence of inhibition of nitrification in soils from the older growth oak-hickory forest site.

Within the early successional watershed, black locust sites had net mineralisation and nitrification rates at least twice as high as those in the pine mixed-hardwood stands. Concentrations of exchangeable nitrate in the soil of black locust stands were higher than in pine-mixed hardwoods at 0–15 cm in March and they were also higher at 0–15, 16–30 and 31–45 cm depth in the black locust dominated sites in July. Soil solution nitrate concentrations were higher under black locust than under pine-mixed hardwoods. Areas dominated by the nitrogen fixing black locust had greater nitrogen mineralisation and nitrification rates, resulting in higher potential for leaching losses of nitrate from the soil column in the early successional watershed.

Introduction

Nitrification, the oxidation of ammonium to nitrate, often increases following disturbance in terrestrial ecosystems (Vitousek and Melillo 1979). Thus, increased nitrate loss via stream water is an indicator of certain types of ecosystem stress. Increased stream export of nitrate during periods of intense defoliation in two mixed hardwood watersheds (WS27 and WS36) in the Coweeta Basin (Swank et al. 1981) suggested accelerated rates of nutrient turnover in litter and soil horizons in the defoliated forests. During the mid-1970s, the mean annual nitrate concentration in the stream water draining watershed 6 (WS 6), an early successional ecosystem dominated by the nitrogen fixing black locust (*Robinia pseudo-acacia* L.), was at least three times higher than concentrations in streams draining other disturbed forested ecosystems at the Coweeta Hydrologic Laboratory, North Carolina, in the southern Appalachians, U.S.A. (Swank and Douglass 1977). Nitrate concentrations in the stream draining watershed 6 showed an abrupt increase in 1979 concurrent with infestations of the stem boring beetle (*Megacyllene robiniae* Forster) and defoliating beetles (Chrysomelideae) in the *R. pseudoacacia* stands (Swank personal data).

In an attempt to explain how insect-induced stress led to increased nitrate loss from the early successional WS6, we studied processes involved in this ecosystem-level response. In this paper we report on controls of nitrification in the ecosystem dominated by black locust. The objective was to assess the relationship between black locust, nitrification potentials and nitrate concentrations in the soil and soil solution in this early successional watershed. The following hypotheses were tested: 1) nitrification potentials are controlled by ammonification rates in the early successional watershed, 2) black locust dominated areas have high rates of net nitrogen mineralisation and nitrification, 3) nitrate concentrations in the soil and soil solution are greater in black locust than in pine-mixed hardwood stands of the early successional watershed, and 4) nitrification potential rates are lower in an oak-hickory forest stand located on an adjacent watershed exhibiting lower stream nitrate concentrations than in either black locust or pine-mixed hardwood stands of the early successional watershed.

The oak-hickory forest was chosen for comparison, because it was expected to have low levels of nitrifying activity, and therefore, by contrast, could aid in understanding factors regulating nitrification rates and nitrate concentrations in the early successional forested ecosystem.

Study site

The early successional watershed (WS6) dominated by black locust and the older growth, mixed hardwood watershed (WS14) are part of the 2185 ha Coweeta Hydrologic Laboratory in western North Carolina (35 °N lat, 83 °W long). The basin is located in the Blue Ridge Province of the Southern Appalachian Mountains. The mean annual temperature is 13 °C, the mean annual precipitation is 181 cm, and the mean elevation is 1000 m (Swank and Douglas 1977).

Watershed 6 is an 8.86 ha, north-facing catchment that was clearcut, logged, converted to fescue grass, limed and fertilised in 1958. Two more fertiliser and lime applications were made in 1960 and 1965 (Johnson and Swank 1973). Starting in May 1966 and for two years thereafter, the grass cover was killed by herbicide application (Douglass et al. 1969) and the watershed was left for natural revegetation. In 1969 the watershed was dominated by a dense cover of a variety of herbaceous species; in 1970, woody shrubs became established; and in 1980 the watershed was dominated by black locust, blackberries (*Rubus spp.*), and numerous vines (*Vitis spp.*, *Clematis spp.*, and *Smilax spp.*). Presently, dense black locust stands occupy 44% of the watershed on the northwest-facing area and 29% of the watershed on the northeast aspect. A remaining 12 and 15% are occupied by northwest-facing pine-mixed hardwood and northeast-facing mesic mixed hardwood stands, respectively, which have low densities of black locust. In 1982, 21% of the black locust trees were standing dead, and 18% had greater than 50% crown dieback, primarily resulting from damage by the locust stem borer (*Megacyllene robiniae* Forster).

The dominant soil series at low elevations and in coves is the Brevard-Saunookee, a member of the fine-loamy, mixed mesic family of Humic Hapludults (Swank personal data). On the slopes and ridges soils belong to the Evard-Cowee series, a member of the loamy, mixed, mesic, shallow family of Typic Hapludults. Textural analysis showed similar sandy loam A_1 horizons on both northeast and northwest facing sites at four elevations from stream banks to ridges. The depth of surface horizons increased from the ridges to the stream.

The mixed hardwood watershed 14 is a 61.1 ha catchment supporting an uneven-aged forest dominated by *Quercus spp.* and *Carya spp.* The most important understory species are mountain laurel (*Kalmia latifolia* L.) and rose-bay rhododendron (*Rhododendron maximum* L.)(Day and Monk 1974). American chestnut (*Castanea dentata* (Marsh.) Borkh.) was originally a major constituent of the forest but was reduced to a minor component by the chestnut blight in the middle 1930's (Johnson and Swank 1973). Logging in the area ceased in 1923 and the forest has had no human disturbance at least since 1924 (Swank and Douglass 1977). The same soil series as those on the early successional watershed are dominant: Evard-Cowee stony loams on the slopes and Brevard-Saunookee stony loams on the lower elevations (Swank personal data).

Methods

In order to assess the impact of black locust on nitrification, WS6 was categorised by vegetation and aspect for soil sampling. Colour infrared imagery and quadrat analysis were used to locate three stands: a northeast and a northwest aspect stand dominated by black locust, and a northwest aspect pine-mixed hardwood stand. Three parallel transects, each from low to high elevation on the slopes were established in each stand so as to divide it into three sections of approximately equal size. The distance between transects ranged from 15 to 20 meters being closer together at the bottoms and farther apart at the tops of the slopes. Three 5 m x 5 m plots were located along each transect, at three elevations from stream banks to ridge tops on the slopes. Thus, there were a total of nine plots per stand, with three plots per elevation. Nine plots were also located in an oak-hickory forest stand located on the adjacent watershed (WS14) at comparable physiographic locations. Sampling was performed in March and July 1982.

Soils were sampled at 0–15, 16–30 and 31–45 cm depths using of a 2.5 cm diameter soil corer. Five cores were combined for a plot sample and were refrigerated at 4 °C for 24 to 72 hours until the time of analysis. Field moist soils were passed through a 4-mm sieve. Four-gram subsamples were extracted with 20 mls of 2 N KCl and shaken mechanically for one hour. NO_3-N and NH_4-N were measured on the filtrates with a Technicon Auto-Analyzer (Technicon 1970). Other subsamples were oven dried at 70 °C for gravimetric determination of moisture content.

Soil solution was sampled at 30 and 60 cm depth with porous cup lysimeters (Hansen and Harris 1975). Solution samples were collected biweekly and analysed for NO_3-N and NH_4-N with a Technicon Auto-Analyzer (Technicon 1970).

Nitrogen mineralisation and nitrification potentials were measured by thirty-day aerobic incubations in the laboratory (Keeney 1982). Temperature and moisture conditions were kept uniform through the incubation period; thus, differences in ammonium and nitrate production between samples were due to activity of bacteria and quality and amount of substrate initially present in the soil. From each of the nine composite soil samples collected from each stand, field moist soil sub-samples of 0–15 and 16–30 cm depth were incubated at 22 °C in an environmental chamber for one month. At the end of the incubation period the samples were extracted and analysed for NH_4-N and NO_3-N. Final minus initial nitrate concentrations provided a measure of net nitrate production over the incubation period. Final minus initial concentrations of total mineral N (nitrate + ammonium) gave an estimate of laboratory net N mineralisation rates. There were no differences in moisture content of the soils between stands, therefore no adjustment for uniform water content was needed for the incubations.

To test for the presence of substances inhibitory to nitrification in the soils of the older growth mixed hardwood forest, incubations were run on mixtures of soil from black locust and oak-hickory stands. Three grams of field moist soil collected from each of the nine plots in the older growth mixed hardwood forest stand were mixed with three grams of soil collected from nine plots under black locust. Nine 6 gram incubations of oak-hickory and black locust soil were also run for comparison. All samples were incubated for two weeks and were processed as described above. Soils for this experiment were collected in May 1983.

For determination of general soil characteristics, air dried subsamples were processed for total Kjeldahl nitrogen (TKN) by acid digestion on a heater block, and by colorimetric determination of NH_4-N (Technicon 1977). Percent organic carbon was measured by the Walkley-Black wet oxidation technique (Allison 1975). Double acid extraction (0.025 N H_2SO_4 and 0.05 N HCl) was performed on the soils (Nelson et al. 1953), and extracts were analysed for cations and P with a Jarrell-Ash plasma emission spectrograph (Jones 1977). Exchangeable hydrogen was determined following the procedure of Adams and Evans (1962), in which soil pH is measured in a buffered solution of p-nitrophenol, borate, potassium chloride and potassium hydroxide. Cation exchange capacity was calculated as the sum of Na, Ca, Mg, K and exchangeable H^+ concentrations in milli-equivalents per 100 grams of soil. The pH was measured on air dry samples using a 1:1 (weight to weight) soil:deionised water mixture and a glass electrode. Statistical analysis was performed using SAS (Helwig and Council 1979). Analysis of variance was performed with the use of the GLM procedure of SAS.

Results

Nitrate concentrations and nitrification potentials were slightly higher in all the lower elevation plots than in the remaining plots in the early successional WS6, but differences between elevations as determined by analysis of variance ($P < 0.05$), were not statistically significant. Therefore results were averaged over the three elevations, making a total of nine plots for each stand. Also, there were no differences in results from the black locust plots located on different slope aspects; therefore data were averaged together making a total of eighteen plots for black locust. In the oak-hickory forest stand, results were also averaged over the three elevations.

Soil and soil solution nitrate and ammonium concentrations

Nitrate concentrations in soils from the black locust sites at the three depths were significantly higher than under pine-mixed hardwoods in July (Table 1). In March, a time of lower temperatures and less biological activity, concentrations were significantly higher only at 0–15 cm. These results identify black locust stands as sites with highest nitrate concentrations throughout the soil profile and indicate that these sites are the primary areas of WS6 where nitrate leaching losses may take place.

Soil nitrate concentrations in the oak-hickory forest stand in WS14 were several times lower than in either pine-mixed hardwoods or black locust stands (Table 1).

Soil ammonium concentrations were lower in the oak-hickory forest than in either pine-mixed hardwoods or black locust stands. There were no significant differences in soil ammonium concentrations between black locust and pine-mixed hardwoods at any depth, for either March or July (Table 1).

Soil solution NO_3-N concentrations were higher in both black locust and pine-mixed hardwoods than in the older oak-hickory stand (Table 2). At both 30 and 60 cm depth, soil solution nitrate concentrations were higher in black locust than in pine-mixed hardwood stands of the successional watershed. Soil solution NH_4-N concentrations were undetectable in the three stands (Table 2).

Table 1. Soil NO_3-N and NH_4-N concentrations, laboratory-determined set N mineralisation and nitrification rates for black locust ($n = 18$) pine-mixed hardwood ($n = 9$) and oak-hickory forest stands ($n = 9$)(means and standard errors). Common superscript letters in a line for a given date indicate no significant differences between sites ($P < 0.05$) as determined by analysis of variance and Duncan's Multiple Range Test

	Black locust		Pine-mixed hardwoods		Oak hickory	
	March	July	March	July	March	July
NO_3-N (mg/kg)						
0–15 cm	4.45(0.26)^{a}	3.25(0.42)^{a}	1.98(0.62)^{b}	0.50(0.22)^{b}	0.26(0.02)^{c}	0.02(0.02)^{b}
16–30 cm	1.56(0.15)^{a}	0.86(0.16)^{a}	1.02(0.36)^{a}	0.02(0.02)^{b}	0.38(0.04)^{b}	0.0 (0.0)^{b}
31–45 cm)	1.40(0.11)^{a}	0.50(0.08)^{a}	0.97(0.23)^{a}	0.11(0.03)^{b}	0.34(0.04)^{b}	0.14(0.04)^{b}
NH_4-N (mg/kg)						
0–15 cm	3.92(0.46)^{a}	2.62(0.20)^{a}	4.26(0.56)^{a}	3.16(0.82)^{a}	1.34(0.19)^{c}	0.25(0.08)^{c}
16–30 cm	3.31(.0.20)^{a}	2.18(0.15)^{a}	3.46(0.40)^{a}	2.36(0.38)^{a}	2.16(0.16)^{c}	0.95(0.32)^{c}
31–45 cm	2.78(0.31)^{a}	2.03(0.17)^{a}	2.90(0.42)^{a}	1.61(0.29)^{a}	2.30(0.14)^{c}	0.93(0.02)^{c}
Net N mineralisation rate (mg kg^{-1} 30 $days^{-1}$)						
0–15 cm	34.94(4.29)^{a}	30.94(1.37)^{a}	12.02(3.53)^{b}	12.00(3.32)^{b}	4.41(1.36)^{c}	2.14(0.45)^{c}
16–30 cm	12.21(2.90)^{a}	7.39(0.73)^{a}	3.58(1.56)^{b}	3.44(1.07)^{b}	2.87(0.63)^{b}	0.27(0.28)^{c}
Net nitrification rate (mg kg^{-1} 30 $days^{-1}$)						
0–15 cm	34.53 (4.34)^{a}	34.26(1.36)^{a}	9.45(3.59)^{b}	15.74(4.11)^{b}	0.32(0.06)^{c}	0.79(0.47)^{c}
16–30 cm	12.02(2.81)^{a}	10.24(0.90)^{a}	2.89(1.14)^{b}	4.58(1.25)^{b}	0.11(0.05)^{c}	0.29(0.12)^{c}

Table 2. Soil solution NO_3-N concentrations (mg/l) at 30 and 60 cm depth (means and standard errors) in black locust, pine-mixed hardwoods and oak-hickory forest stands. Results averaged through six collections from October 1983 to January 1984. There were nine collectors at each depth in black locust and pine-mixed hardwood stands, and three collectors at 30 cm depth in the oak-hickory forest stand

Depth (cm)	Black locust	Pine-mixed hardwoods	Oak-hickory forest
30	3.23 (0.34)	0.07 (0.02)	0.02 (0.01)
60	5.35 (0.57)	0.11 (0.076)	–

Nitrogen mineralisation and nitrification rates

Net N mineralisation rates were more than twice as high under black locust than under pine-mixed hardwoods in both March and July (Table 1). This fact points to black locust stands as sites of rapid N turnover.

Nitrification potential rates at 0–15 cm depth under black locust were at least twice as high as those under pine-mixed hardwoods in both March and July. Most of the nitrifier activity in both stands was in the top 15 cm of the soil, the rates being about three times higher in the 0 to 15 cm layer than in the 16 to 30 cm soil layer. Net nitrification potential rates were only slightly higher during the summer.

In both pine-mixed hardwood and black locust stands of the early successional watershed, net N mineralisation rates were close to nitrification rates. Nitrification rates were less than mineralisation rates only in March in pine-mixed hardwoods. As most of the ammonium was consumed during the incubation time, the availability of ammonium appears to be the main factor controlling nitrification in both pine-mixed hardwood and black locust stands.

In the older growth oak-hickory forest, net nitrification rates were only 7% and 37% of net N mineralisation rates in March and July, respectively (Table 1). Apparently, low nitrification rates were not a result of the presence of inhibitory substances: results from the black locust/oak-hickory soil mixture incubations showed no evidence of an inhibitory effect from the oak-hickory forest soils. Nitrification rates in black locust averaged 19.98 ± 2.53 mg NO_3-N kg^{-1} 14 $days^{-1}$ ($\bar{x} \pm$ S.E.), in the older growth forest it was undetectable, and in a mixture of the two soils it averaged an intermediate value of 7.80 ± 1.21. If no inhibition occurred, the expected nitrification rate for the mixture would have been half the value of the black locust soils, i.e. 9.9. The nitrification rate of the mixture was only slightly lower than expected.

General soil characteristics

Within the early successional watershed, no significant differences were found in soil total N, organic C or C:N ratios between black locust and pine-mixed hardwood stands (Table 3). Total N concentrations were higher in the oak-hickory forest stand than in black locust or pine-mixed hardwood stands in March (Table 3).

Table 3. Soil chemical characteristics for black locust ($n = 18$) pine-mixed hardwood ($n = 9$) and oak-hickory ($n = 9$) forest stands (means and standard errors). Common superscript letters in a row for a given date indicate no significant differences between sites ($P < 0.05$) as determined by analysis of variance and Duncan's multiple range test

	Black locust		Pine-mixed hardwoods		Oak-hickory	
	March	July	March	July	March	July
Total N (%)						
0–15 cm	0.122(0.005)^{b}	0.142(0.005)^{a}	0.144(0.013)^{b}	0.118(0.007)^{a}	0.179(0.006)^{a}	0.158(0.007)^{a}
16–30 cm	0.058(0.004)^{b}	0.062(0.005)^{a}	0.084(0.013)^{b}	0.056(0.005)^{a}	0.098(0.009)^{a}	0.088(0.007)^{a}
31–45 cm	0.040(0.004)^{b}	0.038(0.004)^{a}	0.054(0.010)^{b}	0.029(0.005)^{a}	0.061(0.004)^{a}	0.042(0.006)^{a}
Organic C (%)						
0–15 cm	2.38(0.10)^{b}	2.63(0.15)^{b}	2.82(0.18)^{a}	2.38(0.11)^{b}	3.54(0.31)^{a}	3.74(0.22)^{a}
16–30 cm	1.15(0.07)^{b}	1.26(0.08)^{b}	1.48(0.29)^{a}	0.96(0.09)^{b}	1.90(0.20)^{a}	1.94(0.23)^{a}
C/N						
0–15 cm	19.72(0.70)^{a}	18.34(0.58)^{a}	20.08(1.09)^{a}	20.55(1.20)^{a}	19.94(1.58)^{a}	22.23(0.79)^{a}
16–30 cm	20.28(0.77)^{a}	21.18(1.18)^{a}	20.07(4.69)^{a}	17.11(0.40)^{a}	19.24(0.59)^{a}	21.52(1.43)^{a}
Ca (mg/100 g)						
0–15 cm	73.51(6.90)^{a}	77.26(5.89)^{a}	60.78(4.94)^{a}	47.39(2.87)^{b}	20.68(9.45)^{b}	17.88(4.42)^{c}
16–30 cm	30.69(3.66)^{a}	32.20(4.08)^{a}	27.81(4.49)^{a}	20.62(2.39)^{a}	11.32(4.75)^{b}	7.72(3.10)^{b}
K (mg/100 g)						
0–15 cm	11.39(0.96)^{a}	9.44(0.87)^{a}	9.94(1.45)^{a}	7.74(0.95)^{a}	6.09(0.26)^{b}	6.09(0.25)^{a}
16–30 cm	6.85(0.79)^{a}	6.27(0.75)^{a}	5.78(1.02)^{a}	4.84(0.76)^{a}	4.08(0.36)^{b}	4.59(0.40)^{a}
Mg (mg/100 g)						
0–15 cm	14.90(1.38)^{a}	15.09(1.25)^{a}	11.83(0.84)^{a}	11.57(0.89)^{b}	5.35(1.16)^{b}	5.37(0.80)^{c}
16–30 cm	8.62(0.71)^{a}	8.17(0.80)^{a}	7.10(0.60)^{a}	7.05(0.80)^{a}	3.90(0.79)^{b}	4.10(0.65)^{b}
P (mg/100 g)						
0–15 cm	1.07(0.13)^{a}	0.980(0.102)^{a}	0.709(0.058)^{a}	0.607(0.045)^{a}	0.659(0.025)^{b}	0.723(0.030)^{b}
16–30 cm	0.57(0.12)^{a}	0.391(0.029)^{a}	0.426(0.057)^{a}	0.317(0.020)^{a}	0.393(0.029)^{b}	0.525(0.035)^{a}

Table 3 (*continued*)

	Black locust		Pine mixed hardwoods		Oak-hickory	
	March	July	March	July	March	July
Exchangeable H (mg/100 g)						
0–15 cm	5.50(0.13)^b	6.29(0.10)^b	5.94(0.27)^b	6.43(0.25)^b	9.16(0.004)^a	8.20(0.30)^a
16–30 cm	5.24(0.19)^b	6.26(0.16)^b	5.98(0.35)^b	6.37(0.29)^b	7.75(0.36)^b	7.56(0.28)^a
pH						
0–15 cm	–	5.83^a	–	5.71^a	–	4.73^b
Cation exchange capacity (milliequivalents/100 g)						
0–15 cm	10.72(0.43)^a	11.67(0.37)^a	10.24(0.46)^a	9.98(0.26)^b	10.81(0.53)^a	9.71(0.25)^b
16–30 cm	7.67(0.35)^a	8.73(0.30)^a	8.12(0.57)^a	8.13(0.37)^a	8.76(0.41)^a	8.43(0.34)^a
Base saturation (%)						
0–15 cm	47.35(2.31)^a	45.18(1.90)^a	41.73(1.89)^a	35.29(1.94)^b	14.05(3.72)^b	15.42(2.70)^b
16–30 cm	20.79(1.88)^a	27.40(2.09)^a	26.01(1.59)^a	21.58(1.89)^a	11.07(2.77)^b	10.01(1.83)^b

Soil concentrations of calcium and magnesium were higher in both stands of the early successional watershed than in the oak-hickory forest stand in March and July. Potassium and phosphorus were significantly higher in the early successional watershed in March (Table 3). The percent base saturation was higher in the soils of the early successional watershed (Table 3).

Cation exchange capacity, percent base saturation, calcium, magnesium and phosphorus were higher for the 0—15 cm depth in black locust than in pine-mixed hardwood stands in July (Table 3). The pH of the soils at 0—15 cm depth was 5.8 in black locust, 5.7 in pine-mixed hardwoods, and 4.7 in the oak-hickory forest stand (Table 3).

Discussion

Factors controlling nitrification in the black locust, pine-mixed hardwoods and oak-hickory forests

Many investigators have examined the controls of nitrification in temperate terrestrial ecosystems (Rice and Pancholy 1973, Jones and Richards 1977, Lodhi 1977, 1982, Matson and Vitousek 1981, Montes and Christensen 1979, Robertson and Vitousek 1981, Robertson 1982, Vitousek et al. 1982). Robertson and Vitousek (1981) found that rates of nitrification appeared to be controlled by rates of mineralisation in primary and secondary successional seres. Nitrification seemed to be controlled by availability of ammonium in the majority of the primary successional sites and in all sites in the secondary successional sere (Robertson 1982). Montes and Christensen (1979) did not find conclusive evidence of higher nitrification in early successional stages, and additions of ammonium and lime to soil incubations stimulated nitrification in most cases. These authors suggested that their results could have been influenced by differences between soils such as texture and chemical composition from the different vegetation types. Rice and Pancholy (1973), and Lodhi (1977, 1982), showed evidence of the existence of inhibitory substances to nitrification in later successional sites, supporting the hypothesis of progressive inhibition of nitrification through the course of ecological succession. Vitousek et al. (1982) investigated the controls of potential N mineralisation, nitrate production and nitrate mobilisation in a wide range of forest ecosystems. They found a direct relationship between the amount of N in annual litterfall and the proportion of forest floor N mineralised in laboratory incubations. No direct relationship was found between nitrification and soil characteristics such as pH and base saturation. They found a positive correlation between the mean concentration of soil mineral N (mostly ammonium) and the rate of nitrate production upon incubation in the laboratory.

In the early successional WS6 ecosystem, the rate of ammonification appeared to be the main factor controlling nitrification in both black locust and in non-black locust areas. The primary reason for high nitrification rates in the entire watershed may be related to its treatment history. The soils of this watershed, with higher nutrient content and higher pH, possibly as a result of liming and fertilising history, may be more favourable for the growth of nitrifiers than the soils of the older growth mixed hardwood forest stand.

Within the early successional watershed, net nitrification rates were higher in black locust than in pine-mixed hardwood stands. Lower pH, cation and P content of the pine-mixed hardwood soils could result in lower nitrification in this forest. However when soil laboratory incubations were amended with $CaCO_3$ to increase Ca content and pH (Montagnini 1985) nitrification increased only 10% in both pine-mixed hardwoods and black locust soils. In another experiment (Montagnini 1985), all the added NH_4-N was nitrified in both black locust and pine-mixed hardwood amended soil incubations, suggesting that NH_4-N availability rather than any other soil chemical characteristic is controlling nitrification in these two forests.

In black locust stands, higher N inputs, as a result of N fixation, may be the main factor resulting in high N mineralisation and nitrification rates. Substantial quantities of N fixation were documented for black locust in a regenerating clearcut (WS7) at Coweeta (Table 4) (Boring and Swank 1984a), and inputs to the soil may be high as a result of N fixation. Black locust, with high N tissue content, (Boring and Swank 1984b) may contribute more N in litterfall (Bartuska and Lang 1981, Hirschfeld et al. 1984), throughfall and root and nodule turnover than do trees in the pine-mixed hardwood stands. Moreover, we suggest that insect-induced stress associated with high stand mortality may accelerate these processes and increase ammonium availability for nitrification.

Table 4. Nitrification potentials for sites with and without black locust on a regenerating clearcut (WS7) for 2–6 years old successional vegetation and in an older growth oak-hickory forest of an adjacent control watershed (WS2) in the Coweeta basin. Values were averaged from November 1979 through June 1983 (means and standard errors)

	Regenerating clearcut		Older growth forest
	With black locust ($n = 44$)	Without black locust ($n = 54$)	($n = 34$)
Net nitrification potentials (mg nitrate kg soil^{-1} 33 days^{-1})	26.99 (4.42)	6.30 (2.09)	4.56 (1.42)
Ca (mg/100 g)	67.97 (10.16)	47.47 (15.52)	3.77 (0.55)
P (mg/100 g)	1.054 (0.082)	0.847 (0.067)	0.617 (0.030)
pH	5.61	4.96	5.32

Soil total N concentrations were not significantly different between pine-mixed hardwood and black locust stands in the early successional watershed. Ike and Stone (1958) found N accumulation in the 0–45 cm soil layer beneath 16–20-year-old black locust stands in Tompkins County, New York, with statistically significant increases occurring only in the 0–15 cm soil depth. Jencks et al. (1982) reported that N concentrations at 0–5, 5–10 and 10–15 cm depth were higher in mine soils seeded with black locust than in adjacent native soils in West Virginia; the rate of increase was slower in the lower depths. In the present study, differences in N accretion in the soil may not have been detected at 0–15 or 16–31 cm depth, due to: 1) fast soil N turnover, 2) leaching of organic N from the soil column, or 3) slow accretion taking place only at shallower depths of soil, with potential differences not detectable at 0–15 cm.

Nitrification rates were very low in the older growth oak-hickory forest of WS14. In the experiment to test for the presence of inhibitory substances to nitrification in the soils of this forest, rates were found to be intermediate between those expected from a 100% black locust soil and those expected for an oak-hickory forest soil. If inhibitory substances were present, lower nitrification rates would have been expected. Allelochemic inhibition does not appear to influence low nitrification rates in the soils of this forest.

From the results of this study it is not clear if pH influences low nitrification in the mixed hardwood forest soils of WS14. When $CaCO_3$ was added to laboratory incubations of the oak-hickory forest soils of WS14 on two different occasions (Montagnini 1985) there was no increase in nitrification in comparison with control, unamended soils. Additionally, no significant increase in nitrification was detected following $CaCO_3$ amendment of oak-hickory forest soils which had been mixed with soils of high nitrifying activity, suggesting that the interaction of low Ca, low pH and low populations of nitrifiers was not the cause of low nitrification in the soils of this forest (Montagnini 1985).

Nitrate losses from the black locust dominated watershed

On WS6 black locust dominated areas have high rates of net N mineralisation and nitrification, increasing the potential for leaching losses of nitrate from the soil column. Nitrate concentrations in soil solution sampled with porous-cup lysimeters at 30 and 60 cm depths were also higher under black locust than in pine-mixed hardwoods (Table 2). Boring and Swank (1984b) also reported that the soil under 4, 17 and 38 year old black locust stands at Coweeta had elevated nitrate concentrations.

These results support the hypothesis of Vitousek et al. (1981, 1982) that the amount of N circulated (mineralised from soil and taken up by plants) annually prior to perturbation is probably the main factor controlling leaching losses of nitrate from terrestrial ecosystems. In black locust forest stands, with high N inputs and fast soil N turnover, soil mineral N may be available much in excess of plant uptake and bacterial immobilisation. In the absence of sufficient plant utilisation or high denitrification, significant amounts of nitrate could be leached from the soil column and into the stream water. In the black locust dominated ecosystem a disturbance such as tree death may be of sufficient magnitude to disrupt even more the balance between N mineralisation and plant uptake. This imbalance would result in even higher availability of nitrate to be leached from the system.

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References

Adams F and Evans CE (1962) A rapid method for measuring lime requirements of red-yellow podzolic soils. Soil Science Society of America Proceedings 26:355–7.

Allison LE (1975) Organic carbon. Pages 1367–1378 in Black CA (ed.). Methods of Soil Analysis. American Society of Agronomy, Inc., Madison, Wisconsin.

Bartuska AM and Lang GE (1981) Detrital processes controlling the accumulation of forest litter on black locust revegetated surface mines in central West Virginia. Pages 359–365 in Symposium on Surface Mining Hydrology, Sedimentology and Reclamation. University of Kentucky, Lexington, Kentucky.

Boring LR and Swank WT (1984a) Symbiotic nitrogen fixation by black locust (*Robinia pseudo-acacia* L.). Forest Science 3:528–37.

Boring LR and Swank WT (1984b) The role of black locust (*Robinia pseudo-acacia*) in forest succession. Journal of Ecology 72:749–66.

Day FP Jr. and Monk CD (1974) Vegetation patterns on a southern Appalachian watershed. Ecology 55:1064–74.

Douglass JE, Cochrane DR and Hill DW (1969) Low herbicide concentration found in streamflow after a grass cover is killed. United States Department of Agriculture Forest Service, Research Note SE-108.

Hansen EA and Harris AR (1975) Validity of soil-water samples collected with porous ceramic cups. Soil Science Society of America Proceedings 39 (3):528–36.

Helwig JT and Council KA (1979) SAS user's guide. SAS Institute Inc., Cary, North Carolina.

Hirschfeld JR, Finn JT and Patterson WA III (1984) Effects of *Robinia pseudo-acacia* on leaf litter decomposition and nitrogen mineralization in a northern hardwood stand. Canadian Journal of Forest Research 14:201–205.

Ike AF Jr and Stone EL (1958) Soil nitrogen accumulation under black locust. Soil Science Society of America Proceedings 27:346–349.

Jencks EM, Tyron EH and Contri M (1982) Accumulation of nitrogen in minesoils seeded to black locust. Soil Science Society of America Journal 46:1290–1293.

Johnson PL and Swank WT (1973) Studies of cation budgets in the Appalachians on four experimental watersheds with contrasting vegetation. Ecology 54:70–80.

Jones JB Jr (1977) Elemental analysis of soil extracts and plant tissue ash by plasma emission spectroscopy. Communications in Soil Science and Plant Analysis 8:349–65.

Jones JM and Richards BN (1977) Effects of reforestation on turnover of ^{15}N-labelled nitrate and ammonium in relation to changes in soil microflora. Soil Biology and Biochemistry 9:383–92.

Keeney DR (1982) Nitrogen-availability indexes. Pages 711–730 in Page, DL, Miller RH and Keeney DR. Methods of soil analysis. Part 2. Chemical and Microbiological Properties. 2nd edition. Agronomy Society of America, Inc., Madison, Wisconsin.

Lodhi MAK (1977) The influence and comparison of individual forest trees on soil properties and possible inhibition of nitrification due to intact vegetation. American Journal of Botany 64(3):260–64.

Lodhi MAK (1982) Additional evidence of inhibition of nitrifiers and possible cycling of inhibitors produced by selected plants in a climax community. Bulletin of the Torrey Botanical Club 109(2):199–204.

Matson PA and Vitousek PM (1981) Nitrogen mineralization and nitrification potentials following clearcutting in the Hoosier National Forest, Indiana. Forest Science 27 (4):781–91.

Montagnini F (1985) Nitrogen turnover and leaching from successional and mature ecosystems in the southern Appalachians. Ph.D. Dissertation. University of Georgia, 251 pp.

Montes RA and Christensen NL (1979) Nitrification and succession in the piedmont of North Carolina. Forest Science 25(2):287–97.

Nelson WL, Mehlich A and Winters E(1953) The development, evaluation, and use of soil tests for phosphorus availability. Pages 153–188 in Pierre WH and Norman AG (eds). Soil and fertilizer phosphorus in crop nutrition. Academic Press, Inc. New York.

Rice EL and Pancholy SK (1973) Inhibition of nitrification by climax ecosystems. II. Additional evidence and possible role of tannins. American Journal of Botany 60 (7):691–702.

Robertson GP (1982) Factors regulating nitrification in primary and secondary succession. Ecology 63(5):1561–73.

Robertson GP and Vitousek PM (1981) Nitrification potentials in primary and secondary succession. Ecology 62(2):376–86.

Swank WT and Douglass JE (1977) Nutrient budgets for undisturbed and manipulated hardwood forest ecosystems in the mountains of North Carolina. Pages 344–63 in Correll DL (ed). Watershed Research in Eastern North America: A Workshop to Compare Results. Smithsonian Institution, Edgewater, Md.

Swank WT, Waide JB, Crossley DA Jr and Todd RL (1981) Insect defoliation enhances nitrate export from forest ecosystems. Oecologia 51:297–99.

Technicon Industrial Systems (1970) Operations Manual for the Technicon Auto Analyzer II System. Technical Publication TA1-0170-01.

Technicon Autoanalyzer II (1977) Industrial method No. 369-75A/B, Digestion and sample preparation for the analysis of total Kjeldahl nitrogen using the Technicon BD-20 block digestor. Technicon industrial systems. Tarrytown, N.Y.

Vitousek PM and Melillo JM (1979) Nitrate losses from disturbed forests: patterns and mechanisms. Forest Science 25(4):605–19.

Vitousek PM, Gosz JR, Grier CC, Melillo JM and Reiners WA (1982) A comparative analysis of potential nitrification and nitrate mobility in forest ecosystems. Ecological Monographs 52(2):155–77.

Vitousek PM, Reiners WA, Melillo JM, Grier CC and Gosz JR (1981) Nitrogen cycling and loss following forest perturbation: the components of response. Pages 115–127 in Barrett GW and Rosenburg R (eds). Stress effects on natural ecosystems. John Wiley and Sons, New York.

Nitrification Rates in Two Undisturbed Tropical Rain Forests and Three Slash-and-Burn Sites of the Venezuelan Amazon[1]

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ABSTRACT

Nitrification was measured during the rainy season in two undisturbed tropical rain forests and three slash-and-burn sites in the Amazon region of southwestern Venezuela. Nitrification was higher in the soils of the slash-and-burn sites than in the undisturbed forests. Rates of nitrate production were 14.9 mg/kg/30 days in a forest on an Oxisol, 3.5 mg/kg/30 days in a forest on Ultisol, 23.2 mg/kg/30 days in a 1.5-yr-old slash-and-burn agricultural site on an Oxisol, 12.9 mg/kg/30 days in a 0.5-yr-old slash-and-burn agricultural site on Ultisol, and 12.1 mg/kg/30 days in a 3.0-yr-old pasture on Ultisol. In the undisturbed forests, rates of nitrate production in the root mat averaged 93.5 mg/kg/30 days on Oxisols and 11.2 mg/kg/30 days on Ultisols. Nitrification rates closely followed total nitrogen mineralization rates. Ammonium availability appears to regulate nitrification in both the undisturbed forests and in the slash-and-burn sites. Rates of nitrification in the undisturbed forests in this Amazon site on poor soils were lower than in other tropical forests on more nutrient rich soils.

RESUMEN

Se midió la tasa de nitrificación durante la estación lluviosa en dos bosques tropicales no perturbados y en tres parcelas de agricultura de corte y quema, en la región amazónica del suroeste de Venezuela. La nitrificación era mayor en los suelos de las parcelas de agricultura de corte y quema que en los bosques no perturbados. La tasa de producción de nitrato era 14.9 mg/kg/30 días en un bosque sobre Oxisoles, 3.5 mg/kg/30 días en un bosque sobre Ultisoles, 23.2 mg/kg/30 días en una parcela de agricultura de corte y quema de un año y medio sobre Oxisoles, 12.9 mg/kg/30 días en una parcela de agricultura de corte y quema de medio año sobre Ultisoles, y 12.1 mg/kg/30 días en una parcela de pasturas de tres años sobre Ultisoles. En los bosques no perturbados, la tasa de producción de nitrato en la estera de raíces era 93.5 mg/kg/30 días sobre Oxisoles y 11.2 mg/kg/30 días sobre Ultisoles. En todos los casos la tasa de nitrificación era semejante a la tasa de mineralización. La disponibilidad de amonio aparentemente regula la nitrificación en los bosques no perturbados y en las parcelas de agricultura de corte y quema. Las tasas de nitrificación en estos dos bosques amazónicos no perturbados sobre suelos pobres eran más bajas que en otros bosques tropicales sobre suelos más fértiles.

MINERAL FORMS OF N (NH_4-N AND NO_3-N) ARE AVAILABLE for uptake by plants and microorganisms. Nitrate has a negative charge, and is more likely to be lost through leaching from soils with low anion exchange capacities. Nitrate can also be reduced and lost in gaseous forms through denitrification. Thus, ammonification (the transformation of organic N to NH_4-N) and nitrification (the oxidation of NH_4-N to NO_3-N) play a key role in the N cycle by making N available for plants and microbes, and by making N susceptible to leaching and denitrification losses.

In tropical ecosystems, P availability may more commonly limit primary productivity in late successional forests (Vitousek 1984). However, nitrification and nitrate leaching may increase following clearcutting and burning of tropical rain forests; hence, losses of N and soil cations may more persistently affect productivity in many cleared and early successional systems (Robertson 1982).

Nitrogen mineralization has been measured in only a few tropical forest soils (Vitousek & Sanford 1986): these authors report that high rates of N mineralization and nitrification have been found in tropical fertile soils, and on lowland oxisols and ultisols, while low rates have been found in a spodosol and in montane tropical soils.

In tropical ecosystems, N-conserving mechanisms may be better developed in nutrient poor than in nutrient rich environments (Jordan *et al.* 1979, 1982; Jordan & Herrera 1981). For example, Jordan *et al.* (1979) found very low numbers of soil nitrifying bacteria in an undisturbed rain forest on Oxisol of low nutrient content at San Carlos de Río Negro, in southwestern Venezuela. They attributed the low number of nitrifying bacteria to low pH and high concentration of tannins in the root mat. They also hypothesized that this was a mechanism of N conservation in the undisturbed rain forest; and that these mechanisms may be lost following cutting, burning and agricultural use (Jordan *et al.* 1979, 1983).

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In the present study we compared N mineralization and nitrate production rates in two old-growth rain forests and three slash-and-burn sites at San Carlos de Río Negro, Venezuela. The objectives were: 1) to compare the rates of N mineralization and nitrate production in the nutrient poor Amazon sites with those reported from more nutrient rich tropical environments such as the rain forest of La Selva, Costa Rica (Robertson 1984) (we expected lower rates of N mineralization and nitrification in the nutrient poor environment); 2) to measure N mineralization and nitrate production rates in the dense root mat that covers the soil of the San Carlos rain forest; and 3) to compare rates of N mineralization and nitrate production between two old-growth, undisturbed rain forests and three nearby slash-and-burn sites. We expected rates of nitrate production to be lower in the old-growth sites than in the disturbed systems.

STUDY SITE

The study area is about 4 km east of the small settlement of San Carlos de Río Negro (1°56'N, 67°03'W, 119 m elevation) in the Amazon region of southwestern Venezuela. The climate is typically equatorial with 26°C annual mean temperature and 3500 mm annual rainfall (Heuveldop 1980). Five study sites were chosen, including mature forest and disturbed (slash-and-burn) sites on similar soils. The sites were: 1) an undisturbed mixed forest on an Oxisol, 2) an undisturbed forest on an Ultisol, 3) a 1.5-yr-old slash-and-burn agricultural site on an Oxisol, 4) a 0.5-yr-old slash-and-burn agricultural site on Ultisol, and 5) a 3.0-yr-old pasture on Ultisol. The age of the sites refers to time after cutting and burning the mature forests.

The Oxisols support a predominantly evergreen equatorial-tropical lowland forest 25–40 m height (Uhl & Murphy 1981). *Monopteryx* sp. (Leguminaceae) comprised 56 percent of basal area and 63 percent of aboveground biomass in the undisturbed site on Ultisols (Buschbacher 1984); no information was available on N fixing capability of this tree. Slash-and-burn agriculture is common practice in the San Carlos region (Uhl *et al.* 1983) and *Manihot esculenta* Crantz (cassava) is the main crop. The pasture site was developed after cutting and burning a portion of the mature forest on Ultisol and it was dominated by *Brachiaria decumbens* Stapf., an introduced grass that is commonly planted in Amazon pastures. Chemical and physical characteristics of the forest and pasture sites on Ultisols are described in Buschbacher (1984) while those of the forest on Oxisols are described in Jordan (1982).

METHODS

Nitrogen mineralization and nitrification potentials were measured with buried polyethylene bags (Westermann & Crothers 1980). Sampling was done in June 1983, in the middle of the rainy season. Ten sampling points were designated 10 meters apart along transects on each of the five study sites. Soil samples were composites of 10 corings taken within one meter of each other at each sampling point. Depth of sampling was 0–10 cm which includes only the mineral soil just above the aluminum and iron oxide concretion layer on the sites on Oxisols. In the two undisturbed forests, a dense root mat covers the soil (Stark & Spratt 1977). In these two sites the bottom of the root mat, which includes finely divided humus material and fine (less than 2 mm) roots just above the mineral soil, was sampled separately. Five root mat samples were manually collected and composited at each sampling point. All samples were buried in polyethylene bags at the depth of sampling and left in place for one month.

Extraction of samples for determination of initial and final NH_4-N and NO_3-N concentrations was done in a local laboratory. Subsamples of root mat and soils were passed through a 4 mm sieve and extracted with 2 N KCl. Samples were manually shaken 4–10 times for 4–12 hr and the extracts were filtered. Phenyl mercuric acetate (PMA) at a rate of 0.5 ml per liter was added to the solution of KCl as a preservative. The PMA solution was prepared by dissolving 0.1 g of phenyl mercuric acetate in 15 ml of dioxane and completing volume to one liter. All solutions were prepared with fresh rain water which was filtered through a Crystalab Deeminizer Water demineralizer (Crystalab, 612 Capitol Ave., Hartford, Connecticut 06106, U.S.A.). All samples were extracted within 24 hr of collection except those from the Ultisol forest soil and root mat which were extracted 42 hr after collection. Replicate extractions and blanks were run in order to assure quality control. Additionally, 50 g subsamples were oven dried at 78°C to constant weight for determination of moisture content.

Extracts and samples from each site were transported to the U.S. for analysis at the Institute of Ecology, University of Georgia. NH_4-N and NO_3-N were analyzed colorimetrically with a Technicon Auto-Analyzer (Technicon 1970). Final (after one month) minus initial concentrations of NH_4-N + NO_3-N gave a measure of total net N mineralization. Final minus initial concentrations of NO_3-N gave an estimate of net NO_3-N production. Total net N mineralization rates are sometimes lower than net nitrification rates, when all the NH_4-N is consumed during the incubation time.

The pH was measured in a 1:1 mixture of soil : deionized water (McLean 1982) using a glass electrode and an Orion 701A digital ion analyzer (Orion Research Incorporated, 380 Putman Ave., Cambridge, Massachusetts 02139, U.S.A.). Organic matter was measured by the Walkley Black technique (Allison 1975). Total Kjeldahl nitrogen (TKN) was measured by acid digestion of samples on a heater block followed by colorimetric determi-

TABLE 1. *Net N mineralization and nitrification rates, NO_3-N and NH_4-N concentrations, TKN, C, C/N and pH (means and standard errors) for undisturbed tropical rain forests on Oxisol and Ultisol at San Carlos de Río Negro (0–10 cm soil depth). Common superscript letters in a row indicate no significant differences between sites ($P < 0.005$).*

	Amazon forest on Oxisol	Amazon forest on Ultisol
N mineralization rate (mg NH_4-N + NO_3-N kg^{-1} 30 d^{-1})	13.96 (3.99)^a	1.81 (1.87)^b
Nitrification rate (mg NO_3-N kg^{-1} 30 d^{-1})	14.91 (3.90)^a	3.54 (1.57)^b
NO_3-N (mg/kg)	2.88 (0.16)^a	1.22 (0.41)^b
NH_4-N (mg/kg)	1.18 (0.48)^b	3.13 (0.40)^a
TKN (%)	0.147 (0.007)^a	0.117 (0.0005)^b
C (%)	2.01 (0.20)^a	1.61 (0.54)^a
C/N	13.69 (1.35)^a	13.76 (2.70)^a
pH	3.25^a	3.49^a

nation of ammonium in a Technicon Auto-Analyzer (Technicon 1977). Root mat samples were also analyzed for TKN content. Statistical analyses were done using SAS GLM procedure and Duncan's Multiple Range test (Helwig & Council 1979).

RESULTS

Net N mineralization and nitrification rates were higher in the forest on Oxisols than in the forest on Ultisols (Table 1). NO_3-N concentrations were significantly higher and NH_4-N concentrations were significantly lower in the undisturbed forest on Oxisol as compared with the undisturbed forest on Ultisol (Table 1). Soil TKN and carbon appeared higher in the Oxisol than in the Ultisol forest site, although differences were not statistically significant. There were no significant differences in soil carbon to nitrogen ratio (C/N) or pH between the two forest sites (Table 1). All the NH_4-N was consumed during the incubation of both types of forest soils.

For both forest types, the rates of N mineralization and nitrification (on a per weight basis) were almost ten times higher in the root mat as compared to the soil (Table 2). Rates of net N mineralization and nitrification were higher in the root mat of the Oxisol forest than in the Ultisol forest, the same pattern that was observed for the soil. NO_3-N concentrations were higher in the root mat of the Oxisol than in that of the Ultisol forest, while NH_4-N concentrations were higher in the root mat of the Ultisol forest. Again, this pattern is analogous to that observed for the soil. There was no significant difference in TKN between the root mat layer of Oxisol and Ultisol forest sites (Table 2).

TABLE 2. *Net N mineralization and nitrification rates, NO_3-N and NH_4-N concentrations, TKN and pH (means and standard errors) for the root mat layer of two undisturbed tropical rain forests at San Carlos de Río Negro. Common superscript letters in a row indicate no significant differences between sites ($P < 0.005$).*

	Root mat layer of Oxisol forest	Root mat layer of Ultisol forest
N mineralization rate (mg NH_4-N + NO_3-N kg^{-1} 30 d^{-1})	182.7 (26.4)^a	25.31 (13.9)^b
Nitrification rate (mg NO_3-N kg^{-1} 30 d^{-1})	93.47 (9.16)^a	11.25 (7.47)^b
NO_3-N (mg/kg)	8.98 (1.72)^a	5.86 (1.67)^b
NH_4-N (mg/kg)	28.77 (4.94)^b	80.75 (14.37)^a
TKN (%)	1.10 (0.09)^a	1.00 (0.02)^a
pH	2.94^a	3.72^a

Nitrogen mineralization and nitrification rates were higher in the two slash-and-burn sites on Ultisols than in the undisturbed forest site on Ultisols (Table 3). All the NH_4-N was consumed during the incubation time of the soils of the slash-and-burn sites. Nitrate-N concentrations were higher in the 0.5-yr-old slash-and-burn than in the undisturbed Ultisol forest site. There was no difference in NO_3-N concentrations between the 3.0-yr-old pasture on Ultisol and the undisturbed forest on Ultisol (Table 3). There was no difference in soil NH_4-N concentrations between the three Ultisol sites. Soil TKN concentrations were higher in the two Ultisol slash-and-burn sites than in the undisturbed Ultisol forest site. There were no differences in soil carbon, C/N or pH between the three Ultisol sites.

When the forest on Oxisol is compared with the 1.5-yr-old slash-and-burn site on Oxisol, net N mineralization and nitrification rates appeared higher in the agricultural than in the undisturbed forest site, but the differences were not statistically significant (Table 4). All the NH_4-N was consumed during the incubation time. Soil NO_3-N concentrations were significantly higher in the slash-and-burn agricultural site than in the undisturbed forest (Table 4). There was no significant difference in soil NH_4-N concentrations between the two Oxisol sites. Soil TKN concentrations also appeared higher in the slash-and-burn agricultural site than in the undisturbed forest, but differences were not significant. There were no differences in soil carbon, C/N or pH between the two Oxisol sites (Table 4).

DISCUSSION

As all the NH_4-N was consumed during the incubation time, the availability of NH_4-N would appear to regulate nitrification in these forest and slash-and-burn sites. Ni-

TABLE 3. *Net N mineralization and nitrification rates, NO_3-N and NH_4-N concentrations, TKN, C, C/N and pH (means and standard errors) for an undisturbed forest and two slash-and-burn sites on Ultisols (0–10 cm soil depth). Common superscript letters in a row indicate no significant differences between sites ($P < 0.005$).*

	Undisturbed rain forest on Ultisol	0.5-yr-old slash-and-burn agricultural site on Ultisol	3.0-yr-old slash-and-burn pasture on Ultisol
N mineralization rate (mg NH_4-N + NO_3-N kg^{-1} 30 d^{-1})	1.81 $(1.87)^c$	13.05 $(1.33)^a$	8.20 $(1.34)^b$
Nitrification rate (mg NO_3-N kg^{-1} 30 d^{-1})	3.54 $(1.57)^b$	12.91 $(1.85)^a$	12.07 $(1.15)^a$
NO_3-N (mg/kg)	1.22 $(1.41)^b$	3.72 $(0.33)^a$	0.67 $(0.42)^b$
NH_4-N (mg/kg)	3.13 $(0.40)^a$	2.46 $(0.70)^a$	3.83 $(0.66)^a$
TKN (%)	0.117 $(0.0005)^b$	0.153 $(0.003)^a$	0.150 $(0.007)^a$
C (%)	1.61 $(0.31)^a$	2.19 $(0.22)^a$	1.64 $(0.23)^a$
C/N	13.76 $(2.69)^a$	14.39 $(1.78)^a$	11.15 $(2.56)^a$
pH	3.49^a	3.38^a	3.59^a

trogen mineralization and nitrification rates were higher in the Oxisol than in the Ultisol undisturbed forest site. Soil properties such as TKN, carbon, C/N, or pH do not fully explain this pattern. Other soil chemical and physical characteristics of these two forest sites are summarized in Table 5. Calcium, potassium, and cation exchange capacity are higher in the Oxisol than in the Ultisol forest site. Results suggest that soil fertility parameters influence N mineralization and nitrification in these sites. This work was done during the rainy season, when the highest microbial activity was expected. Seasonal or year to year variation in activity cannot be assessed from this one-time measurement.

Soil chemical and physical characteristics, and N mineralization and nitrification rates of the two undisturbed Amazon forest sites were compared with those of a 60-yr-old lowland tropical rain forest of La Selva, Costa Rica (Robertson 1984) (Table 5). This comparison is limited by the fact that Robertson (1984) did laboratory incubations of soil samples while in the present study incubations were done in the field. However Robertson incubated the samples at ambient temperature in polyethylene containers; therefore conditions for nitrification were comparable to those in the buried bags. Nitrogen mineralization and nitrification rates in the two undisturbed Amazon forests of San Carlos de Río Negro were much lower than in the old-growth forest of La Selva. The soil of the Costa Rican forest was more fertile than at San Carlos: Ca con-

TABLE 4. *Net N mineralization and nitrification rates, NO_3-N and NH_4-N concentrations, TKN, C, C/N and pH (means and standard errors) for an undisturbed forest and a slash-and-burn agricultural site on Oxisol (0–10 cm soil depth). Common superscript letters in a row indicate no significant differences between sites ($P < 0.005$).*

	Undisturbed rain forest on Oxisol	Slash-and-burn agricultural site on Oxisol
N mineralization rate (mg NH_4-N + NO_3-N kg^{-1} 30 d^{-1})	13.96 $(4.00)^a$	21.88 $(3.25)^a$
Nitrification rate (mg NO_3-N kg^{-1} 30 d^{-1})	14.91 $(3.90)^a$	23.20 $(3.17)^a$
NO_3-N (mg/kg)	2.88 $(0.17)^a$	1.40 $(0.26)^b$
NH_4-N (mg/kg)	1.18 $(0.48)^a$	2.51 $(0.50)^a$
TKN (%)	0.147 $(0.007)^a$	0.158 $(0.007)^a$
C (%)	2.01 $(0.20)^a$	1.57 $(0.50)^a$
C/N	13.69 $(1.36)^a$	9.45 $(2.83)^a$
pH	3.25^a	3.48^a

TABLE 5. *Comparison of N mineralization and nitrification rates and soil properties of undisturbed Amazon forests at San Carlos de Río Negro, southwestern Venezuela, and a 60-yr-old lowland tropical rain forest at La Selva, Costa Rica. Cation data for Oxisols are taken from Uhl and Jordan (1984). Cation data for Ultisols are taken from Buschbacher (1984). All Costa Rican forest data are taken from Robertson (1984) (daily rates from Robertson 1984 were multiplied by 30 to obtain monthly rates).*

	Amazon forest on Oxisol	Amazon forest on Ultisol	Costa Rican forest
N mineralization (mg kg^{-1} 30 d^{-1})	13.96	1.80	102.8
Nitrification (mg kg^{-1} 30 d^{-1})	14.91	3.50	102.8
C/N	13.69	13.76	8.60
Ca (meq/kg)	0.26	0.06	6.00
K (meq/kg)	0.32	0.14	1.80
Cation exchange capacity (meq/100 g)	4.11	1.26	25.00
pH	3.25	3.49	5.30
Clay (%)	4.30	4.00	8.60
Bulk density	1.17	1.03	0.58

centration was 20–100 times higher, K concentration was 7–12 times higher, the pH was one unit higher, the C/N ratio was lower, and cation exchange capacity and clay content were higher. This again suggests that in these tropical rain forests fertility parameters have a large influence on N mineralization rates. From our results it appears that low nitrification rates in the undisturbed Amazon forest sites are not likely caused by allelopathic effects by vegetation (Jordan *et al.* 1979), but they may be influenced by low pH, as it was also suggested by Jordan *et al.* (1979). Robertson (1984) found that NH_4-N availability regulated nitrification in the Costa Rican sites. Within the constraints set by soil fertility, the availability of NH_4-N appears to be the main factor regulating nitrification in both nutrient rich and nutrient poor tropical rain forests.

Nitrogen mineralization and nitrification rates were measured in early secondary successional and recently cleared sites, on relatively fertile soils in Turrialba, also in the Atlantic lowlands in Costa Rica (Matson *et al.* 1987). Background levels of N mineralization rates were on the same range as those reported by Robertson (1984) for the La Selva sites. In an experiment with addition of $^{15}NH_4$-N to soils most of the inorganic N recovered was in the form of nitrate, suggesting that NH_4-N availability controls nitrification in these fertile tropical soils.

The root mat density of Oxisol (Stark & Spratt 1977) and Ultisol forest (Buschbacher 1984) is 3193 and 4770 g/m^2, respectively. Rates of nitrification were multiplied times respective mass of root mat and soil layers to estimate rates on an areal basis. Nitrification was 5.8 times higher in the mineral soil than in the root mat of the Oxisol forest, and 4.0 times higher in the mineral soil than in the root mat of the Ultisol forest. Thus, when calculated on an areal basis, the contribution of a very dense and thick root mat layer to total NO_3-N and NH_4-N stocks is less than that of the mineral soil. However if NH_4-N and NO_3-N are rapidly taken up by roots in that superficial zone, losses of N through leaching from the soil column would be lessened. Herrera *et al.* (1978), Stark & Jordan (1978), Jordan & Escalante (1980), Uhl *et al.* (1983) have hypothesized that high rates of nutrient loss are prevented by the thick mat of roots on or near the soil surface which is able to take up nutrients before they are leached into the subsoil.

Soil N mineralization and nitrification were higher in the three slash-and-burn than in the two undisturbed forest sites. Matson *et al.* (1987) also found high N mineralization and nitrification in the burned tropical fertile sites at Turrialba. Soil total N was also higher in the slash-and-burn than in the undisturbed forest sites at San Carlos. As N mineralization and nitrification appear to be influenced by soil fertility in these forests, the increase in soil cations and total N content that follows cutting and burning (Uhl *et al.* 1983, Buschbacher 1984) may increase N mineralization and nitrification rates. Thus cutting and burning may increase net N mineralization, nitrification, and N availability for crops, but may also increase the potential for N losses. If uptake of nutrients by regrowing vegetation, crop or pasture is not sufficient, N losses may result through NO_3-N leaching and denitrification.

At the low pH levels of the San Carlos soils there is probably greater anion than cation retention and nitrate could be held in the exchange sites, a process that can be important on variable-charge clays in the tropics (Uehara & Gillman 1981). Matson *et al.* (1987) reported that 12 percent of the ^{15}N labeled nitrogen added to a cleared plot on which vegetation had been prevented in Turrialba, Costa Rica, was retained as exchangeably-bound NO_3-N deep in the soils, and suggested that this can be an important mechanism maintaining the fertility of cleared tropical sites. However, increased NO_3-N and cation leaching in slash-and-burn agricultural and pasture sites as compared with undisturbed forests has been reported for the San Carlos de Río Negro sites. The rate of NO_3-N leaching in a slash-and-burn agricultural site on Oxisol was about 3.6 times higher than in the undisturbed forest, and K leaching was 20 times greater than in the control, undisturbed forest (Uhl *et al.* 1983). The rates of NO_3-N, Ca, Mg, and K leaching were also higher in a slash-and-burn pasture than in an undisturbed forest on Ultisol at San Carlos (Buschbacher 1984). In nutrient poor ecosystems this may lead to rapid depletion of soil nutrients of agricultural and pasture sites.

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LITERATURE CITED

ALLISON, L. E. 1975. Organic carbon. *In* C. A. Black (Ed.). Methods of soil analysis, 2nd Ed., pp. 1367–1378. American Society of Agronomy, Inc., Madison, Wisconsin.

BUSCHBACHER, R. 1984. Changes in productivity and nutrient cycling following conversion of Amazon rain forest to pasture. Ph.D. Dissertation, Univ. of Georgia, Athens. 193 pp.

Helwig, J. T., and K. A. Council. 1979. SAS User's Guide. SAS Institute Inc., Cary, North Carolina.

Herrera, R., C. F. Jordan, H. Klinge, and E. Medina. 1978. Amazon ecosystems: their structure and functioning with particular emphasis on nutrients. Interciencia 3: 223–231.

Heuveldop, J. 1980. Bioklima von San Carlos de Río Negro, Venezuela. Amazoniana 7: 7–17.

Jordan, C. F., R. L. Todd, and G. Escalante. 1979. Nitrogen conservation in a tropical rainforest. Oecologia 39: 123–129.

———, and G. Escalante. 1980. Root productivity in an Amazonian rain forest. Ecology 61: 14–18.

———, and R. Herrera. 1981. Tropical rain forests: are nutrients really critical? Amer. Nat. 117: 167–180.

———. 1982. The nutrient balance of an Amazonian rain forest. Ecology 63: 647–654.

———, W. Caskey, G. Escalante, R. Herrera, F. Montagnini, R. L. Todd, and C. Uhl. 1982. The nitrogen cycle in a "Terra Firme" Rainforest on Oxisol in the Amazon Territory of Venezuela. Plant and Soil 67: 325–332.

———, ———, ———, ———, ———, ———, and ———. 1983. Nitrogen dynamics during conversion of primary Amazonian rain forest to slash and burn agriculture. Oikos 40: 131–139.

Matson, P. A., P. M. Vitousek, J. J. Ewel, M. J. Mazzarino, and G. P. Robertson. 1987. Nitrogen transformations following tropical forest felling and burning on a volcanic soil. Ecology 68: 491–502.

Mc Lean, E. O. 1982. Soil pH and lime requirement. *In* A. L. Page, R. H. Miller, and D. R. Keeney (Eds.). Methods of soil analysis, 2nd Ed., pp. 199–224. American Society of Agronomy, Inc., Madison, Wisconsin.

Robertson, G. P. 1982. Nitrification in forested ecosystems. Phil. Trans. Roy. Soc. Lond. B 296: 445–457.

———. 1984. Nitrification and nitrogen mineralization in a lowland rainforest succession in Costa Rica, Central America. Oecologia 61: 99–104.

Stark, N., and C. F. Jordan. 1978. Nutrient retention in the root mat of an Amazonian rain forest. Ecology 59: 434–437.

———, and M. Spratt. 1977. Root biomass and nutrient storage in rain forest oxisols near San Carlos de Río Negro. Trop. Ecol. 18: 1–9.

Technicon Industrial Systems. 1970. Operation manual for the Technicon Auto-Analyzer II System. Technical Publication TAI-0170-01.

Technicon Autoanalyzer. 1977. Industrial Method No. 369-75A-B, Digestion and sample preparation for the analysis of total Kjeldahl Nitrogen using the Technicon BD-20 Block Digestor. Technicon Industrial Systems, Tarrytown, New York.

Uehara, G., and G. Gillman. 1981. The mineralogy, chemistry, and physics of tropical soils with variable charge clays. Westview Press, Boulder, Colorado.

Uhl, C., and P. Murphy. 1981. Composition, structure, and regeneration of a Tierra Firme forest in the Amazon Basin of Venezuela. Trop. Ecol. 22: 219–237.

———, C. F. Jordan, and F. Montagnini. 1983. Traditional and innovative approaches to agriculture on Amazon Basin tierra firme sites. *In* R. Lowrance, R. L. Todd, L. E. Asmussen, & R. A. Leonard (Eds.). Nutrient cycling in agricultural ecosystems, pp. 73–95. Univ. of Georgia College of Agric. Exp. Sta. Spec. Pub. 23.

———, and ———. 1984. Succession and nutrient dynamics following forest cutting and burning in Amazonia. Ecology 65: 1476–1490.

Vitousek, P. M. 1984. Litterfall, nutrient cycling, and nutrient limitation in tropical forests. Ecology 61: 285–298.

———, and R. L. Sanford, Jr. 1986. Nutrient cycling in moist tropical forests. Annu. Rev. Ecol. Syst. 17: 137–167.

Westermann, D. T., and S. E. Crothers. 1980. Measuring soil nitrogen mineralization under field conditions. Agron. J. 72: 1009–1012.

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THE ROLE OF INSECTS IN THE PRODUCTIVITY DECLINE OF CASSAVA (*MANIHOT ESCULENTA* CRANTZ) ON A SLASH AND BURN SITE IN THE AMAZON TERRITORY OF VENEZUELA

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ABSTRACT

Montagnini, F. and Jordan, C.F., 1983. The role of insects in the productivity decline of cassava (*Manihot esculenta* Crantz) on a slash and burn site in the Amazon Territory of Venezuela. *Agric. Ecosystems Environ.*, 9: 293—301.

The consumption of bitter cassava by root boring, leaf chewing and leaf sucking insects was measured on a slash and burn agricultural site in the Amazon Territory of Venezuela. Chewing and boring insects consumed less than 3% of the tissue, possibly because of the presence of cyanogenic glucosides in the cassava plants. In contrast to the boring and chewing insects, leaf sucking insects were more effective herbivores. They may be able to consume the phloem sap without activating the hydrocyanic acid. However, even sucking insects consumed only about 14% of the phosphorus uptake of the plants. We conclude that insect herbivory did not play a major role in the decline of productivity on the slash and burn agricultural site.

INTRODUCTION

It has been established that the decline in crop production in the Amazon Basin is often due to low levels of available nutrients in the soil (Sanchez, 1976). However, insect damage can also be an important factor in the decline of productivity in slash and burn agriculture in the tropics (Watters, 1971). As part of a study of the structure and function of an Amazon rain forest ecosystem in the Amazon Territory of Venezuela (Herrera et al., 1978; Jordan, 1982a), studies have been carried out on the factors contributing to the decline in productivity of the principal regional crop, cassava (*Manhot esculenta* Crantz). Here, we report on a study of the role of insects in the decline of cassava productivity.

METHODS

The experimental site

The research was conducted on a 2000 m^2 plot, 4 km east of San Carlos de Rio Negro (1° 56′ N, 67° 03′ W) in the Amazon Territory of Venezuela. The plot is on a well-drained Oxisol (Jordan, 1982b), and it supported primary forest before conversion to traditional slash and burn agriculture in January 1977.

Population density of leaf insects

Insects were sampled using a rim and bag capture technique similar to that described by Crossley et al. (1976). It consisted of a rim 50 cm in diameter with a large plastic trash bag attached. The bag could be closed almost instantaneously over the plant by quickly pulling a drawstring. The sample was discarded if any insect was observed to escape from the bag. The insects were killed by adding ethyl acetate to the bag. The total leaf area of every sample was estimated and the corresponding areas of terrain sampled were calculated according to eqn. 1:

$$\text{ground area sampled (m}^2\text{)} = \frac{\text{TLA (cm}^2\text{)}}{\text{LAI} \times 10\,000} \qquad (1)$$

where TLA is the total leaf area corresponding to the total number of leaves in the sample; LAI is the leaf area index of the cassava crop at the time of sampling (from Uhl, 1980); and 10 000 is the conversion factor from cm^2 to m^2.

Nine samples per week were taken for an 18-month period. Because individual samples were very small, all samples of insects were pooled monthly in composites in one of five categories. The insects were identified to families and sorted according to feeding habits and trophic levels (Table I). Each monthly value for a given category represents a pool resulting from three samples taken three times a week for 1 month, resulting in 36 individual samples. Statistical analysis of differences between densities of sucking and chewing insects was performed by using the monthly composites as replicates for means in *t*-tests. Thus the means represent average densities over the sampling period and not at any particular time.

Leaf chewing damage

Chewing insect consumption of cassava leaves was estimated as the percentage of the total leaf area removed by this group. The oldest (i.e., lowest) leaf was removed from 150 plants selected randomly along transects across the site at two different times. Areas of leaves were measured and then remeasured after missing areas had been filled in with foil overlays in order to calculate the percentage area missing from leaves. The leaf area/leaf weight ratio of cassava leaves (Uhl, 1980) was then used to obtain the leaf biomass removed by insects. Data on total cassava net production (Uhl, 1980) and phosphorus concentration of cassava leaves (Jordan, in preparation) were used to estimate consumption as percentage of total phosphorus uptake by

TABLE I

Categories of insects found at the cassava site in San Carlos de Rio Negro

		Order	Family	Number of morphotypes
I.	Leaf chewing insects	Coleoptera	Chrysomelidae	21
			Carabidae	1
			Others	10
		Lepidoptera	Various families	7
		Orthoptera	Acrididae	11
			Tettigonidae	2
		Hymenoptera	Formicidae	7
			Others	7
		Diptera	Cecidomyidae	1
II.	Leaf sucking insects	Hemiptera	Pentatomidae	2
			Coreidae	2
			Largidae	1
		Homoptera	Cicadellidae	9
			Membracidae	1
			Aleyrodidae	4
III.	Stem borers	Coleoptera	Buprestidae	2
IV.	Ants	Hymenoptera	Formicidae	1
V.	Predators	Coleoptera	Coccinellidae	1
		Hemiptera	Reduviidae	1
			Lygaeidae	1

the crop. In an attempt to estimate changes in leaf hole area during growth of plants, we punched small holes in a series of young leaves. However, almost all of the punched leaves died.

Root borer insect damage

At the time that the tubers were harvested, each tuber was examined externally for signs of insect damage or insect penetration. Damaged tubers had holes and tunnels, and presumably these allowed entrance of pathogens as sometimes rotten areas surrounded the tunnels. Damaged tubers were examined further and classified according to whether damaged tissue was less than 25% of the tuber, between 25 and 50%, or more than 50%.

Leaf sucking insect consumption

To estimate sucking insect ingestion rate, two field experiments with ^{32}P were carried out. In the first, 10 cassava plants were labelled with an aqueous solution of radioactive orthophosphoric acid with stable phosphorus carrier. Depending upon the size of the plant, 250—500 μCi of ^{32}P in 25—100 μl of solution were injected into the lower portion of the stem of each plant. The soil under the area chosen for the experiment was covered with a plastic cloth to facilitate the collection of insects at the end of the experiment. Twenty-four hours after injection, a 2 × 2 × 2 m cage with walls of fine cloth was suspended over the plants and then dropped into place. This effectively captured all the insects on the plants. While the cage prevented the emigration of insects originally on the enclosed plants, it also prevented immigration of others, and the total ^{32}P consumed by the insects should have been approximately the same as would have occurred, had the cage not been there. After 4 days insects were spray killed, and both plants and insects were collected, digested, and counted for radioactivity using standard liquid scintillation techniques (Horrocks, 1962).

A second experiment was performed in order to estimate elimination of ^{32}P by the sucking insects. Eight small cassava plants were injected with 25 μl (80 μCi) of a ^{32}P solution. Twenty-four hours later the plants were covered with small fine-cloth cages (40 × 40 × 40 cm). Several sucking insects were placed in the cages to feed on the labelled plants. In this way the insects received an initial radioisotope concentration. The following day the labelled plants were removed and replaced by unlabelled ones. The untagged food was renewed daily. The decrease in concentration following the change to unlabelled leaves gave the isotope elimination rate. Insects were collected every 24 h beginning 1 day after they were caged. Collections from each plant for each day were pooled to obtain countable samples. Samples of the labelled plants and the insects were processed to measure their radioactivity by scintillation counting. The biological half-life of ^{32}P in the insects was estimated and the elimination rate was calculated from eqn. 2 (Williams and Reichle, 1968):

$$K = \frac{0.693}{Tb} \qquad (2)$$

where K is the elimination rate; Tb the biological half-life; and 0.693 the natural logarithm of 2.

Using the results of both experiments we applied the equation

$$r = \frac{K \times Qe}{a} \qquad (3)$$

where r is the radioisotope ingestion rate; a the assimilation of the radionuclide; K the elimination coefficient and Qe the activity density of the radioisotope in the insect body at equilibrium. Since the turnover time of phosphorus in the insects was about 1 day (Montagnini, 1980), assumption of equilibrium was reasonable. The assimilation was assumed to be 90% of ingested ^{32}P (Hubbel et al., 1965; Reichle et al., 1970). The ingestion rate of food was then calculated by dividing the result obtained from eqn. 3 by the radioisotope concentration in the food.

The concentration of stable phosphorus of cassava leaves (Jordan, in preparation) was used to estimate ingestion rate in terms of this nutrient. Data on mean population densities of this group of insects were used to obtain total P consumption. Information on total production of the cassava crop (Uhl, 1980) was used to estimate this consumption as a percentage of total phosphorus uptake by cassava.

RESULTS

Insect population density

The mean sucking insect density during the first 7 months of the sampling period (Fig. 1) was 20.6 mg dry weight m^{-2}, much higher than that of chewing insects (8.2 mg m^{-2}). A *t*-test showed that this difference was significant ($P<0.01$). Sucking insect density decreased sharply after the eighth month, due to the perturbation of the crop as a result of the harvest of one section of the site and the beginning of the rainy season. Heavy rains affected small insects by washing them off the leaves. Following this decline, populations of sucking and chewing insects were not significantly different. Population densities of the other four groups of insects were extremely low; stem borers were less than 2 mg dry weight m^{-2}, no leaf-cutting ants were found, and predators ranged from 0.4 to 5.8 mg dry weight m^{-2}.

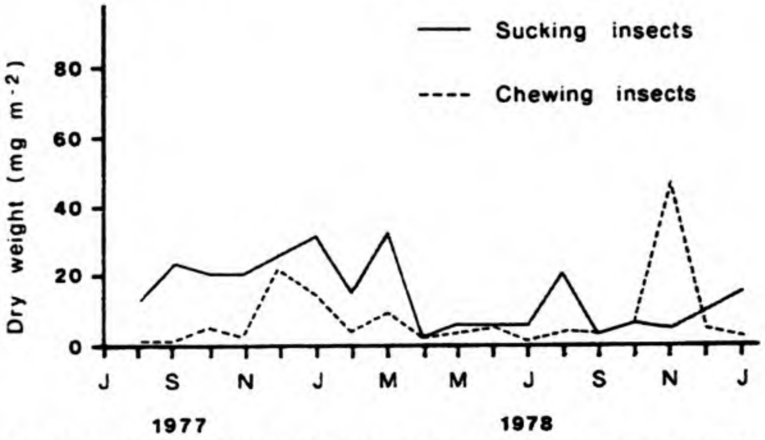

Fig. 1. Sucking and chewing insect densities (mg dry weight m^{-2}) for the 18-month sampling period.

Root boring and leaf chewing insect consumption

The percentage of tubers damaged by insects ranged from 3.9 for the first crop to 6.1 for the last crop (Montagnini, 1980). However, of the number infested, 95% had less than 25% of the tuber damaged. This means there was less than 2% of the total crop lost to root boring insects.

Chewing insects consumed only about 2% of the total leaf production. Uhl (1980), in an independent study of the productivity of cassava in the same plantation, estimated losses to be less than 3%. Phosphorus removal by leaf chewing insects was 0.97% of the total uptake by the crop.

Sucking insect consumption

Sucking insects of the order Homoptera constituted about 39% of the total insect biomass at the site, but they accounted for 96% of the total radioactivity of the insects contained in the cage. Their activity density (pCi mg^{-1} dry weight) averaged 4072 pCi mg^{-1} dry weight, 36 times higher than that of other groups of insects also confined in the cage, suggesting both a higher uptake and also a higher concentration of ^{32}P in their food source, the leaf phloem sap. These insects are relatively small, with a mean dry weight of 0.027 mg per individual. The relatively small biomass, short life span, and the relatively high uptake causes a relatively rapid turnover of phosphorus in these insects.

The ratio of activity density of insects to activity density of leaves on which insects had fed was used to determine the rate of ^{32}P elimination by insects. The initial value of the ratio was considered to be 100% retention. On Day 2, the ratio was 27.1% of the initial value. A biological half-life (Tb_1) of 13.6 h was calculated for this first phase. On Day 5 the ratio was 11.1% of the initial value. This slower elimination of the remaining ^{32}P in the insects yielded a Tb_2 value of 3.95 days. Collections for Days 3 and 4 were too small to count adequately. An elimination rate (K) of 0.630 per day was calculated as a weighted average between Tb_1 and Tb_2 according to the portions of radioactivity eliminated in each phase. Equation 3 was applied and an ingestion rate of 2849 pCi mg^{-1} dry weight of insects per day was obtained. To calculate the percentage of phosphorus in plants lost to sucking insects, it is necessary to know the radioactivity and the phosphorus concentration in the leaf phloem sap. After 4 days an average of 133.6 pCi g^{-1} dry weight was found in the cassava leaves. The radioactivity of the leaf phloem sap was estimated to range between 334 and 668 pCi mg^{-1} and the phosphorus concentration in the sap was estimated to be 2.02 $\mu g\ mg^{-1}$ dry weight (Montagnini, 1980). The ingestion rate ranged between 4 and 8 mg of food per mg of insects per day. This figure is within the values of ingestion rates that are mentioned for sucking insects in laboratory experiments (Duffus and Gold, 1967; Pollard, 1973).

The percentage of phosphorus taken up by cassava which was removed by these insects was calculated as follows (eqn. 4):

$$\% = \frac{I \times D \times P}{\text{Plant P}} \times C \qquad (4)$$

where I is the ingestion rate of ^{32}P by insects; D the insect population density; P the P concentration in sap; Plant P the annual P uptake by cassava; and C the correction factor for % and for weight and time units.

$$\% = \frac{(4\text{–}8)(20.6)(2.02)(10^{-3})(365)(10^{2})}{(828.8\text{–}889.6)} = 7.33\text{–}13.66 \quad (5)$$

where 4—8 mg sap per mg dry wt of insect per day is the ingestion rate; 20.6 mg dry wt of insects m^{-2} is the mean population density of the insects for the first 7 months of sampling; 2.02 μg P per mg dry wt of sap is the P concentration in the sap; 10^{-3} is the conversion from μg to mg; 365 is the conversion from days to years; 828.8—889.6 mg P m^{-2} is the range of total P uptake per year by cassava; and 10^2 is the conversion for percentage.

DISCUSSION

Influence of insects on productivity of the cassava crop

The population levels of chewing and sucking insects were relatively low. This suggests that insect consumption of net plant production would also be low. Other studies have shown that in sites where the density of herbivorous insects was 60—300 mg of dry weight m^{-2}, consumption was less than 2% of net primary production (Table II). Hence, low population levels of the main herbivorous species seem to indicate that their role in the decline of plant production might be minimal. This appeared to be the case for root boring and leaf chewing insects. Root boring insect consumption was less than 2% of the total tuber crop, and leaf chewing insects also consumed only 2% of total leaf production. The low consumption of cassava by chewing and boring insects may be due to the presence of cyanogenic glucosides in the 'bitter' variety of cassava grown in the San Carlos region. These glucosides are converted into hydrocyanic acid under the influence of the enzyme linamarase, which is also present in the plant (Levin, 1976; Onwueme, 1978). This may be an effective defense mechanism against chewing and

TABLE II

Population densities of chewing and sucking insects and consumption of net primary production at four different sites

Site	Insect consumption (% of NPP)[1]	Insect density (mg dry weight m^{-2})		Source
		Sucking insects	Chewing insects	
Old field	<0.5	n.d.[2]	60	Wiegert (1965)
Lespedeza stand	0.4—1.4	22	25	Menhinick (1967)
Natural grassland	9.6	22	1070	Van Hook (1971)
Natural grassland	<2	n.d.	300	Bailey and Mukerji (1977)

[1] NPP = net primary production.

[2] n.d. = no data were presented.

boring insects. The indigenous people prefer to plant the 'bitter' variety of cassava, because it can be left in the ground for months with very little damage. This is an important advantage, because cassava roots begin to deteriorate rapidly a day or two after they are harvested (Onwueme, 1978). In order to render the tuber suitable for consumption, the local people soak, grate, press and then heat it. Linamarase is deactivated above 75°C.

In contrast to the chewing insects at the San Carlos site, sucking insects of the order Homoptera were relatively effective herbivores. They consumed 7.33—13.66% of the total phosphorus uptake by the cassava plants. Even after insect populations declined (Fig. 1) sucking insect consumption of P was calculated to range between 3.09 and 6.18% of the total P uptake by the crop. However, the phosphorus taken from plants by sucking insects is probably quickly returned to the soil in the form of excretions, faeces and insect bodies. Even if none of the phosphorus was returned, our maximum estimate is of a 14% loss per year. However, productivity in the cassava crop declined 50% (Jordan, in preparation). This indicates that insect consumption was not the major factor in the decline of cassava crop production in the San Carlos region.

Adaptations of sucking insects

Price (1975) suggests that sucking insects may achieve a spatial avoidance of plant chemical defenses, as their fine mouth parts enable them to feed between pockets or ducts of toxin in the host plant. Alternatively, sucking insects may be ingesting the cyanogenic compounds in the leaf phloem sap, but do not break the cells and release the enzyme which hydrolizes the glucosides into hydrocyanic acid, hence the toxin does not affect them.

This evasion of chemical defenses by the sucking insects in cassava plantations may be recent and could cause problems in these crops. Some species of Homoptera are mentioned as cassava pests which produce moderate damage (Bellotti and van Schoonhoven, 1978). However, recently, Albuquerque (1976) reported that a sucking insect of the genus *Phenacoccus* (Homoptera:Pseudococcidae) is appearing in Brazilian plantations of cassava, and did serious damage to 150 varieties of this crop. From the description of the insect, it seems possible to us that a sucking insect of the same genus is also present in the plantation reported here.

CONCLUSION

Insect consumption plays a minor role in the decline of productivity and the abandonment of cassava crops, possibly because of the presence of natural defenses in the varieties of cassava that are grown in the San Carlos region. However, there is the danger that sucking insects may be able to overcome this defense mechanism and become increasingly important as the crop is more intensely cultivated.

REFERENCES

Albuquerque, M.D., 1976. Mealy bug attack on cassava in Amazonia. In: J. Cock, R. MacIntyre and M. Graham (Editors). Proceedings of the 4th Symposium of the International Society for Tropical Root Crops, Ottawa, pp. 207.

Bailey, C.G. and Mukerji, M.K., 1977. Energy dynamics of *Melanoplus bivitattus* and *Melanoplus femurrubrum* (Ortoptera:Acrididae) in a grassland ecosystem. Can. Entomol., 109(4): 605—614.

Bellotti, A. and van Schoonhoven, A., 1978. Mite and insect pests of cassava. Annu. Rev. Entomol., 23: 39—67.

Crossley, D.A., Jr., Callahan, J.T., Gist, C.S., Maudsley, J.R. and Waide, J.B., 1976. Compartmentalization of arthropod communities in forest canopies at Coweeta. J. Ga Entomol. Soc., 11: 44—49.

Duffus, J.E. and Gold, A.H., 1967. Relationship of tracer-measured aphid feeding to acquisition of Beet Western Yellow Virus and to feeding inhibitors in plant extracts. Phytopathology, 57: 1237—1241.

Herrera, R., Jordan, C.F., Klinge, H. and Medina, E., 1978. Amazon ecosystems: Their structure and functioning with particular emphasis on nutrients. Interciencia, 3: 223—232.

Horrocks, D., 1962. Liquid scintillation counting of inorganic radioactive nuclides. Packard Instrument Co. Tech. Bull. No. 2., Downers Grove, Illinois.

Hubbel, S.P., Sikora, A. and Paris, D.H., 1965. Radiotracer, gravimetric, and calorimetric studies of ingestion and assimilation rates of an isopod. Health Phys., 11: 1485—1501.

Jordan, C.F., 1982a. Amazon rain forests. Am. Sci., 70: 394—401.

Jordan, C.F., 1982b. The nutrient balance of an Amazonian rain forest. Ecology, 63: 647—654.

Jordan, C.F. An Amazonian Ecosystem. Univ. of Chicago Press (in preparation).

Levin, D.A., 1976. The chemical defenses of plants to pathogens and herbivores. Annu. Rev. Ecol. Syst., 7: 121—159.

Menhinick, E.F., 1967. Structure, stability, and energy flow in plants and arthropods in a *Sericea lespedeza* stand. Ecol. Monogr., 37: 255—272.

Montagnini, F., 1980. Influencia de los insectos sobre el ciclo de nutrientes y productividad primaria en los ecosistemas de conucos de San Carlos de Río Negro, Territorio Federal Amazonas. Trabajo de grado para Magister Scientiarum en Biología, mención Ecología. Instituto Venezolano de Investigaciones Científicas, Caracas, Venezuela.

Onwueme, J.C., 1978. The Tropical Tuber Crops. Wiley, Chichester, 234 pp.

Pollard, D.G., 1973. Plant penetration by feeding aphids (Hemiptera:Aphidoidea): a review. Bull. Entomol. Res., 62: 631—741.

Price, P.W., 1975. Insect Ecology. Wiley, New York, 514 pp.

Reichle, D.E., Dunaway, P.B. and Nelson, D.J., 1970. Turnover and concentration of radionuclides in food chains. Nucl. Saf., 11(1): 43—55.

Sanchez, P.A., 1976. Properties and Management of Soils in the Tropics. Wiley, New York, 618 pp.

Uhl, C., 1980. Studies of forest, agricultural, and successional environments in the upper Rio Negro region of the Amazon Basin. Ph.D. dissertation. Dept. of Botany and Plant Pathology. Michigan State University, East Lansing, Michigan.

Van Hook, R.I., 1971. Energy and nutrient dynamics of spider and orthopteran populations in a grassland ecosystem. Ecol. Monogr., 47(1): 1—25.

Watters, R.F., 1971. Shifting Cultivation in Latin America. FAO Forestry Development Paper No. 17. FAO Rome, 305 pp.

Wiegert, R.G., 1965. Energy dynamics of the grasshopper populations in old field and alfalfa field ecosystems. Oikos, 16: 161—176.

Williams, E.C., Jr. and Reichle, D.E., 1968. Radioactive tracers in the study of energy turnover by a grazing insect (*Chrysochus auratus* Fab.) (Coleoptera:Chrysomelidae). Oikos, 19: 10—18.

OIKOS 40: 131–139. Copenhagen 1983

Nitrogen dynamics during conversion of primary Amazonian rain forest to slash and burn agriculture

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The standing stocks and fluxes of nitrogen were measured for four years in an experimental slash and burn agricultural site and control forest in the Amazon Basin of Venezuela. During the study, there was a decrease of about 15% in nitrogen in the system as a whole due to leaching, harvesting, and denitrification. However, nitrogen levels in the soil did not change, due to replenishment by nitrogen entering the soil from decomposing slash. Since nitrogen levels in the soil remained high, scarcity of nitrogen is probably not responsible for the observed decline in crop yields, and lack of nitrogen is not expected to affect secondary succession in the abandoned agricultural plot.

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Урожай на корню и потоки азота измерили в течение 4-х лет на экспериментальном вырубленном и выжженном участке агроценоза и в контрольном лесу Амазонского Бассейна в Венесуэле. В ходе исследования наблюдалось снижение количества азота до 15% в системе в целом, в результате выщелачивания, сбора урожая и денитрификации. Однако, уровни содержания азота в почве не изменились в результате пополнения азота, поступающего в почву из разлагающегося материала на вырубке. По-скольку уровни содержания азота в почве остаются высокими, дефицит азота видимо не является причиной снижения урожая, и отсутствие азота не должно влиять на вторичную сукцессию залежного участка агроценоза.

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1. Introduction

Increasing rates of tropical deforestation (NAS 1980) have caused alarm about possible consequences of continued exploitation of the tropical rain forests (Gelber and Lord 1980). One of the most frequent warnings is that destruction of the forest could cause rapid loss of nutrients with consequent decreased productive capacity of the ecosystems, and impaired ability of the ecosystem to recover following abandonment. The dangers of nutrient depletion are particularly strong for rain forests of central Amazonia, because of the low capacity of the mineral soil to retain nutrients (Camargo and Falesi 1975, Sanchez 1976, Van Wambeke 1978).

As part of an ecosystem study of the structure and function of a tropical rain forest in the Amazon Territory of Venezuela (Medina et al. 1977, Herrera et al. 1978), we have been studying the nutrient dynamics of the undisturbed forests and the changes in the dynamics when the forests are cut and burned for cultivation. One of the principal questions addressed by the project is whether slash and burn agriculture causes significant nutrient loss from Amazonian ecosystems. In this study we report on the nitrogen budget of a primary forest on an Oxisol and the changes in the budget when the forest is converted to slash and burn agriculture typical of the region.

2. The study site

The study area is near the confluence of the Casiquiare River and the Rio Negro in the Amazon Territory of Venezuela (1°56'N, 67°03'W, 119 m a.s.l.). The climate is typically equatorial with a 26°C annual mean temperature, and average annual rainfall is about 3500 mm. No month receives less than an average of 100 mm of rain, but there is considerable monthly and yearly variability in rainfall. River level follows a modal pattern with the peak in July-August being about 6 m higher than the low in January-February (Brunig et al. 1977). The topography consists of gently rolling hills which rise up to 25 m above the surrounding terrain. The hills are composed of plinthitic material (laterite) which contains abundant ferric concretions. Forming an irregular cover over the clay is a sand horizon which may have formed in place or which may be sediment washed in from the sandstone remnants of the Guiana Shield which arises to the north and east. With the exception of the variable sand cover, the soil is similar to the xanthic ferralsol soil type which is mapped as the dominant soil in the central Amazon Basin (FAO–UNESCO 1971). Ferralsols are equivalent to Oxisols in the U.S. soil taxonomy system and to Latasols in the Brazilian system (Sanchez 1976). The soils are locally referred to as "tierra firme." In the depressions between the tierra firme hills there are acid Spodsols with well developed B horizons which support vegetation similar to that of the Brazilian Amazon caatinga or campina and the heath forests of Borneo (Herrera 1979).

The study reported here was carried out on a tierra firme site 4 km east of the village of San Carlos de Rio Negro, Venezuela. The tierra firme sites support a weakly seasonal, predominantly evergreen, very complex equatorial-tropical lowland forest 25–40 m in height.

3. Methods

Studies of forest standing stocks of nitrogen, nitrogen fluxes, and plant productivity began on the study site in 1974. After collecting one year of baseline data, we cut and burned a 0.25 ha subplot for farming in late 1976. The subplot will be referred to as the "conuco," the local name for slash and burn agriculture sites. Measurements continued in both the conuco and the adjacent control forest for a three-year period.

3.1. Standing stocks

The total standing stock of nitrogen in the forest was measured before cutting by determining the biomass (Stark and Spratt 1977, Jordan and Uhl 1978) and the nutrient content of this biomass. Nitrogen concentrations were determined for samples of leaves, stems, bark, and roots from 42 trees and for the mat of organic humus on top of the soil for 40 samples. These samples were ground and digested in a mixture of $HClO_4$ and H_2SO_4 in the presence of vanadium pentoxide. Total nitrogen was determined by a micro-Kjeldahl method adapted from Bremner (1977).

Forty soil samples were taken in the root zone of the undisturbed forest before cutting to determine nitrogen concentration in the soil. Total nitrogen was determined after digestion at 400°C in the above acid mixture. Soil mass was determined from 18 soil pits (Stark and Spratt 1977).

Forty samples of soil and forty of superficial humus were taken immediately after the burn, and then at six-month to one-year intervals until conuco abandonment. Samples were analyzed as above. At the time of the conuco abandonment, all trunks remaining in the conuco were measured, and 20 were sampled for specific gravity and for chemical analysis. Nitrogen analysis was carried out as above.

Six pits 50 cm on a side were dug for estimates of final standing crop of roots (i.e., roots from the pre-existing forest). Values for trunk and root standing crops in the interval between cutting and abandonment were estimated by interpolation.

3.2. Nitrogen dynamics

After forest cutting and burning the conuco was planted to yuca, pineapple, plantain, and cashew. Nitrogen in

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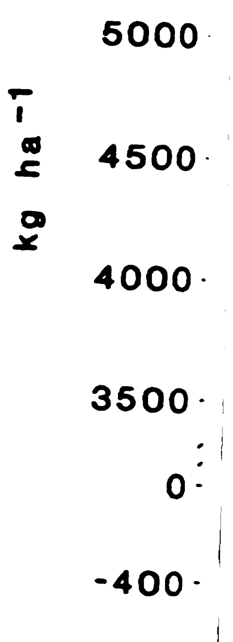

Fig. 1. Changes in th
(below the abscissa).

both total and edible annual production of all crop species and total annual weed production was measured from the time of the first planting until the conuco was abandoned in December 1979 (Uhl and Murphy 1981).

Measurements of ammonium and nitrate nitrogen in precipitation began in 1975. Methods of collection and analysis have been given by Jordan (1978) and Jordan et al. (1980). Nitrogen in subsurface runoff was determined by multiplying ammonium and nitrate nitrogen concentrations in collections from lysimeters (soil water collectors) located below the root zone times total runoff determined from the water balance (Jordan and Heuveldop 1981).

Nitrogen fixation was determined by the acetylene reduction technique (Hardy et al. 1968). In the control site, samples were taken from leaves of 18 species (half of the leaves with and half without epiphyllic lichens), bark of four species with and without lichens, three root-mat samples, three nodulated root samples, and three soil samples in March 1977, July 1977, and February 1978.

Nitrogen fixation in the conuco was measured in both the dry and wet season. Leaf and stem samples of six yuca plants, six soil samples, and six litter samples were taken at each survey period. Rates were multiplied times respective leaf areas and soil weights to obtain total fixation rates ha^{-1}.

Denitrification was estimated from measurements of denitrifying activity in soil slurries during Phase I of denitrification (Smith et al. 1978). Triplicate samples of the humus layer and mineral soil were taken in the primary forest and the conuco during the dry and the wet season. Total denitrification rates were determined by multiplying measured rates times mass of respective compartments.

4. Results and discussion

Entire system

Total standing crop of nitrogen in the experimental site changed from 5583 kg ha^{-1} before the burn to 4492 kg ha^{-1} at the time of abandonment. Twenty percent of the original standing crop of nitrogen was removed or lost from the system. Fig. 1 graphically illustrates the dynamic changes in the nitrogen balance throughout the experiment.

Cutting and burning had relatively little impact on the standing stocks of nitrogen, compared to subsequent decomposition (Fig. 1). The burn consumed all the

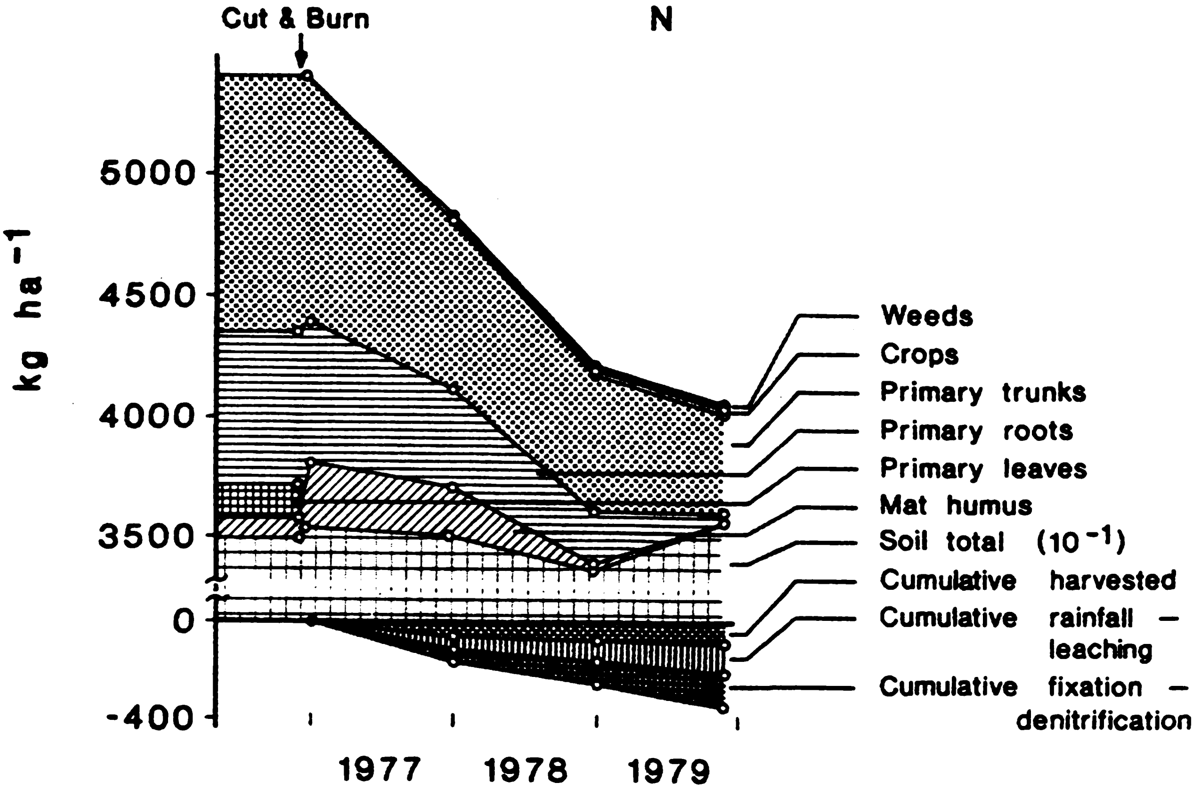

Fig. 1. Changes in the standing stocks of nitrogen due to slash and burn agriculture (above the abscissa) and cumulative losses (below the abscissa).

dried leaves of the primary forest left as slash following cutting, and presumably all the nitrogen in the leaves was volatilized. Leaves contained about 3% of the nitrogen in the undisturbed forest (Tab. 3). The burn did not appear to affect the trunk biomass. Bark of trees was barely scorched. Incompletely burned organic matter from twigs and branches which fell to the ground during the fire caused the marked increase in nitrogen in the mat of humus on the soil surface. Decrease in the standing stock of nitrogen in the wood and roots occurred as a result of decomposition during the three-year period. Uptake of nitrogen by crop and secondary successional species was only a very small proportion of the total nitrogen in the system (Fig. 1).

Total cumulative nutrient losses from the system are shown below the horizontal axis in Fig. 1. Approximately one-third of the total net loss was due to harvest, about 25% of which was in edible form, one-third of the net loss was due to an excess of leaching of nitrates and ammonium over entry in precipitation, and one-third to an excess of denitrification over nitrogen fixation.

In contrast, the average net change in the control site due to an excess of nitrogen fixation over denitrification and precipitation over leaching was less than plus one percent of the total standing stock of nitrogen.

Despite losses of nitrogen from decomposing trunks, and loss from the system as a whole, the amount of nitrogen in the soil did not decrease during the three-year cultivation period (Fig. 1). Apparently, the downward movement of nitrogen from the decomposing primary trunks and roots, either in mineralized form or in small particulate organic matter, replaced nitrogen which had been lost from the soil. Part of the storage could have been in the form of nitrates which may be readily adsorped in tropical soils (Vitousek and Melillo 1979).

Because nitrogen levels in the soil at the time of abandonment were relatively high (Fig. 1), it does not seem likely that the recovery of the area through secondary succession will be limited by a lack of nitrogen. It also seems unlikely that lack of nitrogen in the soil is responsible for the decline in yuca yield which Uhl and Murphy (1981) found to be 32% between the first and second crops.

It is interesting to compare the estimated losses in our experimental site with the difference between original and final standing crop. Original standing crop of nitrogen was 5583 kg ha^{-1} and final standing crop was 4492 kg ha^{-1}. Losses through harvest, denitrification, and leaching totaled 392 kg ha^{-1}. If all the nitrogen in leaves of the primary forest was volatilized, this is an additional loss of 143 kg ha^{-1}. This leaves an additional 556 kg ha^{-1} to be accounted for. While this could have come from volatilization of nitrogen in fine twigs during the burn, it also could be a result of lack of precision in characterizing some of the large but variable nitrogen pools such as the soil.

Tab. 1. Rates of nitrogen fixation in the conuco and primary forest at San Carlos and at other sites.

Site	Nitrogen fixation Kg ha^{-1} yr^{-1}	Authority
Tropical		
Amazon rain forest – total	~16.	This study
leaf epiphylls	<1. (0.48)[a]	
bark-lichens	<1. (0.53)[a]	
humus-soil surface	8. (1.35)[a]	
mineral soil	7. (0.44)[a]	
Amazon slash and burn agriculture – total	~0.3	This study
mineral soil	<0.3 (1.2)[a]	
plants	<0.1 (1.3)[a]	
Colombian rain forest	1.5–8	Forman 1975
Nigeria – savanna soil	3–80	Stewart et al. 1978
Ghana – savanna soil	6	Nye and Greenland 1960
Ghana – forest soil	17	Nye and Greenland 1960
Temperate		
Hardwoods, North Carolina	12.04	Todd et al. 1978
Phyllosphere, Douglas fir, England	7–23	Jones 1970
Douglas fir, Oregon	6.2	Sollins et al. 1980
Hardwoods, New Hampshire	14.2	Likens et al. 1977
Conifers, Sweden	0.3–3.2	Granhall and Lindberg 1978
Scotland, soils	1–2	Stewart et al. 1978

a. Value in parentheses is average coefficient of variation determined from means and standard deviations of N fixation rates for each series of determinations.

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5. Comparisons with other studies

There are many uncertainties in measurements of nitrogen budgets, especially in the dynamics of fixation and denitrification (Clark and Rosswall 1981). It is not even certain how to put error terms around such fluxes as nitrogen fixation on an ecosystem level. Each set of fixation measurements has its own standard deviation, but fixation rate must be multiplied times biomass estimate, which has its own error term, and this must be multiplied times a seasonal time factor which can change from year to year. Van Veen et al. (1981) discussed some of these problems and concluded that models of the nitrogen budget have limited usage as predictive devices, and that their main strength is their role in identifying critical fluxes and storages in ecosystems.

Nevertheless, comparisons of nitrogen models can yield useful regional and world-wide perspectives, and important in such comparisons are error terms around average values. The coefficient of variation, that is, the standard deviation divided by the mean, is a useful statistic here, because coefficients of variation from several subgroups can be averaged to give a single mean coefficient of variation. For example, all the nitrogen concentrations from the leaves of one species can be averaged, and the standard deviation and the coefficient of variation obtained. The process is repeated for each species. Then the coefficients of variation for all the species are averaged. A similar procedure is carried out for fluxes for different seasons of the year. This procedure still does not give us error terms for the entire nitrogen budget, since the estimates of biomass have their own error term, but since estimates of nitrogen concentrations are of primary interest here, these are the values for which the error term will be given.

Tab. 2. Rates of denitrification in the conuco and primary forest at San Carlos and at other sites.

Site	Kg ha^{-1} yr^{-1}	Authority
Amazon rain forest ……	4 (0.23)[a]	This study
Amazon slash and burn agriculture ………	50 (0.18)[a]	This study
Hardwoods, North Carolina ……….	18.2	Todd et al. 1975
Agriculture, North Carolina ……….	10–20	Thomas and Gilliam 1978
Paddy fields, Japan ……	46–67	Yatazawa 1978

a. Value in parentheses is average coefficient of variation determined from means and standard deviations of denitrification rates for each series of determinations.

5.1. Fixation

Rates of nitrogen fixation in the control forest are comparable to rates found in other tropical and temperate forests, and higher than rates at high latitudes (Tab. 1), and are within the range of 19 values presented by Van Cleve and Alexander (1981). Rates of fixation by leaf epiphylls must be taken with caution in light of findings by Bentley and Carpenter (1980) who found that the amount of moisture on the leaf surface at the time of sampling greatly affects the observed fixation rates. Under dry conditions, fixation rates are low, while after wetting, rates increased dramatically. We sampled the San Carlos forest during wet and dry seasons, and ex-

Tab. 3. Standing stocks of nitrogen in undisturbed forests.

	Forest Tierra Firme[a]	Seasonal forest Banco I Ivory Coast[b]	Hardwood forest Coweeta North Carolina[c]	Hardwood forest Hubbard Brook New Hampshire[d]	Douglas fir Andrews Forest Oregon[e]
Kg ha^{-1}					
Leaves …………………………….	143 (0.26)[f]	}1150	} 995	} 351	144
Stems and branches and bark ……….	941 (0.52)[f]				394
Roots ……………………………..	586 (0.30)[f]	–	–	181	197
Litter and superficial humus ………..	406 (0.23)[f]	–	140	1100	798
Soil ………………………………	3507 (0.53)[f]	6500	6917	3626	3397
Total standing crop …………………	5583	7650	8052	5258	4930

a. This study.
b. Bernhard–Reversat 1975.
c. Todd et al. 1978, Swank and Douglass 1975, Henderson et al. 1978.
d. Bormann et al. 1977.
e. Sollins et al. 1980.
f. Value in parentheses is the coefficient of variation of concentrations of nitrogen averaged for all species for respective compartments.
} Symbol means that values for two rows were combined in original report.

Tab. 4. Precipitation input and leaching losses of nitrate and ammonium in various ecosystems.

	Kg ha⁻¹ yr⁻¹ N						
	Rain input			Leaching output			
	NO_3	NH_4	Σ	NO_3	NH_4	Σ	
Disturbed systems							
Amazonian slash and burn agriculture	0.19 (1.51)[a]	11.26 (1.19)[a]	11.45	20.76 (0.58)[a]	22.58 (0.86)[a]	43.34	This study
Clear-cut – Michigan	2.1	4.1	6.2	0.1–0.2	0.1	0.2	Richardson and Lund 1975
Hardwoods, West Virginia – clear-cut				1.90	1.70	3.60	Aubertin and Patric 1974
Hardwood forests, North Carolina – experimental	3.4	2.6	6.0	2.4	0.06	2.5	Swank and Douglass 1975
Northern Hardwoods – clear-cut	4.5	2.0	6.5	58.1	1.2	59.3	Bormann et al. 1968
Various experimental forests, U.S.				0.26–97			Vitousek et al. 1979
Agricultural systems, U.S. (fertilized)						0.1–73	Thomas and Gilliam 1978
Tropical undisturbed systems							
Amazon Rain Forest	0.19 (1.51)[a]	11.26 (1.19)[a]	11.45	5.66 (0.89)[a]	8.36 (0.87)[a]	14.02	This study
Tropical seasonal, Ivory Coast			21.2			21–32	Bernhard-Reversat 1975
Moist tropical, Ghana	2.46	11.52	13.98				Nye 1961
Gambia			14–47				Thornton 1965
Nigeria	1.3	53	56.3				Jones 1960
Non-tropical undisturbed systems							
Aspen, Michigan	2.1	4.1	6.2	0.1–0.3	0.1–0.2	0.2	Richardson and Lund 1975
Douglas fir			1.1			0.6	Cole et al. 1967
Hardwoods, West Virginia – control				0.64	1.07	1.71	Aubertin and Patric 1974
Northern hardwoods – control	4.5	2.0	6.5	1.5	0.25	1.7	Bormann et al. 1968
Douglas fir, Oregon			2.0			1.9	Sollins et al. 1980
Various control forests, U.S.				0.08–3.9			Vitousek et al. 1979
Various grasslands, western U.S.			1.5–7.5	0	0		Woodmansee 1978
Hardwood forests, North Carolina – control	3.6	2.7	6.3	0.1	0.06	0.16	Swank and Douglass 1975
Forests, California			1–2			0.1–0.6	Coats et al. 1976
Forests, New Mexico	2.7	1.7	4.4	0.1	0.1	0.2	Gosz 1980
Various Europe			2.1–6.9				Gore 1968
Artic tundra	0.03	0.2	0.23				Barsdate and Alexander 1975

a. Value in parentheses is the coefficient of variation of concentrations of ions in fluxes.

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Nitrogen fixation in the conuco was very low compared to the control forest (Tab. 1). There is much more surface area on which algae and bacteria live in the undisturbed forest than in the conuco site, and this probably accounts for the aboveground differences in fixation rates. The generally drier conditions at the soil surface in the conuco probably are the cause of the relatively low rates there compared to the control forest. Conuco values also are lower than rates in many other cultivated crops (Hauck 1981).

5.2. Denitrification

Because of the difficulty of carrying out denitrification studies, and because of the problems associated with extrapolating from samples to a yearly estimate, there are few studies with which to compare our results. Annual rates of denitrification in a hardwood forest in the U.S. was higher than the rate in the primary forest at San Carlos (Tab. 2). One possible reason for the low rate at San Carlos might be that the high concentration of tannins in the leaves which gives rise to the black water of the region could partially inhibit denitrification.

In the slash and burn site, rates of denitrification are comparable to other agricultural sites on a yearly basis (Tab. 2).

5.3. Standing stocks

Standing stock of nitrogen in the undisturbed forest at San Carlos is similar to that in other undisturbed forests (Tab. 3). Van Cleve and Alexander (1981) summarized 28 studies of standing stocks along a latitudinal gradient and found values ranging from 3000 to 15000 kg ha^{-1}.

5.4. Precipitation and leaching

Nitrogen input via precipitation in the tropics appears to be primarily in the form of ammonium (Tab. 4). Rates of ammonium input in the tropics, including those of this study, are higher than inputs in temperate zones (Tab. 4). Burning of forests can be an important atmospheric input of nitrogen in the tropics (Crutzen et al. 1979), and rains following the end of a tropical dry season can flush large amounts of nitrogen compounds out of the atmosphere (Lewis 1981). Soil dust transported from Africa to South America is deposited periodically in French Guiana, only three degrees north of San Carlos (Prospero et al. 1981). Since dust in rain water of the tropics carries a large amount of nitrogen (Visser 1964), this dust could be one source of the nitrogen found in the rain water in San Carlos.

Rates of nitrogen loss via leaching from disturbed ecosystems may not be high if the disturbance is simply cutting or logging (Tab. 4). In a Michigan clear-cut, a West Virginia clear-cut, and a North Carolina clear-cut, annual losses per hectare were 0.2 kg, 3.6 kg, and 3.0 kg (Tab. 4). However, if the cutting is followed by burning, herbicide treatment, or other disturbance, losses can be much higher (Tab. 4). The results from the slash and burn treatment fall midway in the range of values for highly disturbed terrestrial systems reported by Vitousek et al. (1979).

For undisturbed systems, our results are comparable to the one other tropical value we encountered, but higher than for temperate ecosystems (Tab. 4).

6. Conclusion

Nitrogen disappeared from a slash and burn agricultural ecosystem at at rate of 7% of the original stock per year. Amount of nitrogen in the soil did not decrease during a normal three-year slash and burn rotation, because losses from the soil are compensated for by input from decomposing slash. Lack of nitrogen should not hamper the ability of the system to return to primary forest. However, if the exploitation were carried on for a decade or more, nitrogen losses through denitrification, leaching, and harvesting could seriously deplete the nitrogen reserves of the system.

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References

Aubertin, G. M. and Patric, J. H. 1974. Water quality after clear-cutting a small watershed in West Virginia. – J. Environ. Qual. 3: 243–249.

Barsdate, R. J. and Alexander, V. 1975. The nitrogen balance of arctic tundra: pathways, rates, and environmental implications. – J. Environ. Qual. 4: 111–117.

Bentley, B. and Carpenter, E. J. 1980. Effects of dessication and rehydration on nitrogen fixation by epiphylls in a tropical rainforest. – Microb. Ecol. 6: 109–113.

Bernhard-Reversat, F. 1975. Recherches sur L'ecosysteme de la foret subequatoriale de basse Cote-D'Ivoire. VI. Les cycles des macrolements. – Terre Vie 29: 229–254.

Bormann, F. H., Likens, G. E., Fisher, D. W. and Pierce, R. S. 1968. Nutrient loss accelerated by clear-cutting of a forest ecosystem. – Science 159: 882–884.

– , Likens, G. E. and Melillo, J. M. 1977. Nitrogen budget for an aggrading northern hardwood forest ecosystem. – Science 196: 981–983.

Bremner, J. M. 1977. Role of organic matter in volatilization of sulfur and nitrogen from soils. – In: Soil organic matter studies. IAEC, Vienna, pp. 229–240.

Brunig, E. E., Herrera, R., Heuveldop, J., Jordan, C., Klinge, H. and Medina, E. 1977. The international Amazon project. – In: Brunig, E. F. (ed.), Transactions of the International MAB–IUFRO Workshop on Tropical Rain Forest

Ecosystems Research. Chair of World Forestry. Univ. of Hamburg, Hamburg-Reinbek, pp. 104–120.

Camargo, M. N. and Falesi, I. C. 1975. Soils of the Central Plateau and Transamazonic Highway of Brazil. – In: Bornemiza, E., and Alvarado, A. (eds.), Soil Management of Tropical America. Soil Science Dept, North Carolina State Univ., Raleigh, N.C., pp. 25–45.

Clark, F. E., and Rosswall, T. (eds.), 1981. Terrestrial nitrogen cycles, processes, ecosystem strategies, and management impacts. – Ecol. Bull. (Stockholm) 33: 714 pp.

Coats, R. N., Leonard, R. and Goldman, C. R. 1976. Nitrogen uptake and release in a forested watershed, Lake Tahoe Basin, California. – Ecology 57: 995–1004.

Cole, D. W., Gessel, S. P. and Dice, S. F. 1967. Distribution and cycling of nitrogen, phosphorus, potassium, and calcium in a second-growth Douglas-Fir ecosystem. – In: Symposium on Primary Productivity and Mineral Cycling in Natural Ecosystems. College of Life Sciences and Agriculture, Univ. of Maine, pp. 198–232.

Crutzen, P. J., Heidt, L. E., Kransnec, J. P., Pollock, W. H. and Seiler, W. 1979. – Biomass burning as a source of atmospheric gases CO, H_2 N_2O, NO, CH_3Cl, and COS. – Nature, Lond. 282: 253–256.

FAO–UNESCO. 1971. Soil map of the world. Vol. IV. South America. – FAO, Paris.

Forman, R. T. T. 1975. Canopy lichens with blue-green algae: a nitrogen source in a Colombian rain forest. – Ecology 56: 1176–1184.

Gelber, A. and Lord, M. 1980. Vanishing forests. – Newsweek, Nov. 24, 1980, pp. 117–122.

Gore, A. J. P. 1968. The supply of six elements by rain to an upland peat area. – J. Ecol. 56: 483–495.

Gosz, J. R. 1980. Nutrient budget studies for forests along an elevational gradient in New Mexico. – Ecology 61: 515–521.

Granhall, U. and Lindberg, T. 1988. Nitrogen fixation in some coniferous forest ecosystems. – Ecol. Bull. (Stockholm) 26: 178–192.

Hardy, R. W. F., Holsten, R. D., Jackson, E. K. and Burns, R. C. 1968. The acetylene-ethylene assay for N_2 fixation: Laboratory and field evaluation. – Plant Physiol. 43: 1185–1207.

Hauck, R. D. 1981. Nitrogen fertilizer effects on nitrogen cycle processes. – In: Clark, F. E. and Roswall, T. (eds.), Terrestrial nitrogen cycles. Processes, ecosystem strategies, and management impacts. Ecol. Bull. (Stockholm) 33: 551–562.

Henderson, G. S., Swank, W. T., Waide, J. B. and Grier, C. C. 1978. Nutrient budgets of Appalachian and Cascade region watersheds: a comparison. – For. Sci. 24: 385–397.

Herrera, R. 1979. Nutrient distribution and cycling in an Amazon caatinga forest on Spodosols in southern Venezuela. – Ph.D. Dissertation, Dept of Soil Science, Univ. of Reading.

– , Jordan, C. F., Klinge, H. and Medina, E. 1978. Amazon ecosystems: their structure and functioning with particular emphasis on nutrients. – Interciencia 3: 223–232.

Jones, E. 1960. Contribution of rainwater to the nutrient economy of soil in northern Nigeria. – Nature, Lond. 188–432.

Jones, K. 1970. Nitrogen fixation in the phyllosphere of the Douglas fir *Pseudotsuga douglasii*. – Ann. Bot. 34: 239–244.

Jordan, C. F. 1978. Stem flow and nutrient transfer in a tropical rain forest. – Oikos 31: 257–263.

– , Golley, F., Hall, J. D. and Hall, J. 1980. Nutrient scavenging of rainfall by the canopy of an Amazonian rain forest. – Biotropica 12: 61–66.

– and Heuveldop, J. 1981. The water budget of an Amazonian rain forest. – Acta Amazonica 11: 87–92.

– and Uhl, C. 1978. Biomass of a "tierra firme" forest of the Amazon Basin. – Oecol. Plant. 13: 387–400.

Lewis, W. M. 1981. Precipitation chemistry and nutrient loading by precipitation in a tropical watershed. – Water Resources Research 17: 169–181.

Likens, G. E., Bormann, F. H., Pierce, R. S., Eaton, J. S. and Johnson, N. M. 1977. Biogeochemistry of a forested ecosystem. – Springer, New York.

Medina, E., Herrera, R., Jordan, C. and Klinge, H. 1977. The Amazon project of the Venezuelan Institute for Scientific Research. – Nature and Resources (UNESCO) 13 (3): 4–6.

NAS. 1980. Conversion of tropical moist forest. – National Academy of Sciences, Washington, D.C.

Nye, P. H. 1961. Organic matter and nutrient cycles under moist tropical forest. – Plant Soil 13: 333–346.

– and Greenland, D. J. 1960. The soil under shifting cultivation. Tech. Comm. No. 51. – Commonwealth Bureau of Soils, Farnham Royal, Bucks, England.

Prospero, J. M., Glaccum, R. A. and Nees, R. T. 1981. Atmospheric transport of soil dust from Africa to South America. – Nature, Lond. 289: 570–572.

Richardson, C. J. and Lund, J. A. 1975. Effects of clear-cutting on nutrient losses in aspen forests on three soil types in Michigan. – In: Howell, F. G., Gentry, J. B. and Smith, M. H. (eds.), Mineral cycling in southeastern ecosystems. ERDA, Washington, D.C.

Sanchez, P. A. 1976. Properties and management of soils in the tropics. – Wiley, New York.

Smith, M. S., Firestone, M. K. and Tiedje, J. M. 1978. The acetylene inhibition method for short-term measurement of soil denitrification and its evaluation using nitrogen-13. – Soil Sci. Soc. Am. J. 42: 611–615.

Sollins, P., Grier, C. C., McCorison, F. M., Cromack, K. and Fogel, R. 1980. The internal element cycles of an old-growth Douglas-fir ecosystem in western Oregon. – Ecol. Monogr. 50: 261–285.

Stark, N. and Spratt, M. 1977. Root biomass and nutrient storage in rain forest oxisols near San Carlos de Rio Negro. – Trop. Ecol. 18: 1–9.

Stewart, W. D. P., Sampaio, M. J., Isichei, A. O. and Sylvester-Bradley, R. 1978. Nitrogen fixation by soil algae of temperate and tropical soils. – In: Döbereiner, J., Burris, R. H. and Hollaender, A., (eds.), Limitations and potentials for biological nitrogen fixation in the tropics. Plenum, N.Y., pp. 41–63.

Swank, W. T. and Douglass, J. E. 1975. Nutrient flux in undisturbed and manipulated forest ecosystems in the Southern Appalachian mountains. – Publ. no 117 de l'Association Internationale des Sciences Hydrologiques Symposia de Tokyo (Dec. 1975).

Thomas, G. W. and Tilliam, J. W. 1978. Agro-ecosystems in the U.S.A. – In: Frissel, M. J. (ed.), Cycling of nutrients in agricultural ecosystems. Elsevier, Amsterdam, pp. 182–243.

Thornton, I. 1965. Nutrient content of rainwater in Gambia. – Nature, Lond. 188: 432.

Todd, R. L., Meyer, R. D. and J. B. Waide. 1978. Nitrogen fixation in a deciduous forest in the southeastern United States. – In: U. Granhall (ed.), Environmental role of nitrogen-fixing blue-green algae and a symbotic bacteria. Ecol. Bull. (Stockholm) 26: 172–177.

– , Waide, J. B. and Cornaby, B. W. 1975. Significance of biological nitrogen fixation and denitrification in a deciduous forest ecosystem. – In: Howell, F. G., Gentry, J. B. and Smith, M. H. (eds.), Mineral cycling in southeastern ecosystems. ERDA, Washington, D.C., pp. 729–735.

Uhl, C. and Murphy, P. 1981. A comparison of productivities and energy values between slash and burn agriculture and secondary succession in the upper Rio Negro region of Venezuela. – Agro-ecosystems 7: 63–83.

Van Cleve, K. and Alexander, V. 1981. Nitrogen cycling in tundra and boreal ecosystems. – In: Clark, F. E. and Rosswall, T. (eds.), Terrestrial nitrogen cycles. Processes,

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ecosystem strategies, and management impacts. Ecol. Bull. (Stockholm) 33: 375–404.

Van Veen, J. A., McGill, W. B., Hunt, H. W., Frissel, M. J., and Cole, C. V. 1981. Simulation models of the terrestrial nitrogen cycle. – In: Clark, F. E. and Roswall, T. (eds.), Terrestrial nitrogen cycles. Processes, ecosystem strategies, and management impacts. Ecol. Bull. (Stockholm) 33: 25–48.

Van Wambeke, A. 1978. Properties and potentials of soils in the Amazon Basin. – Interciencia 3: 233–241.

Visser, S. A. 1964. Origin of nitrates in tropical rainwater. – Nature, Lond. 201: 35–36.

Vitousek, P. M. and Melillo, J. M. 1979. Nitrate losses from disturbed forests: patterns and mechanisms. – Forest Sci. 25: 605–619.

– , Gosz, J. R., Grier, C. C., Melillo, J. M., Reiners, W. A. and Todd, R. L. 1979. Nitrite losses from disturbed ecosystems. Science 204: 469–474.

Woodmansee, R. G. 1978. Additions and losses of nitrogen in grassland ecoystems. – BioScience 28: 448–453.

Yatazawa, M. 1978. Agro-ecosystems in Japan. – In: Frissel, M. J. (ed.), Cycling of mineral nutrients in agricultural ecosystems. Elsevier, Amsterdam, pp. 167–179.

HEAVY METAL CONCENTRATIONS IN SOME NON-VASCULAR PLANTS IN AN AMAZONIAN RAINFOREST

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Abstract. The presence of acid rain in the remote Amazon rainforest of southwestern Venezuela suggests the possibility of long-range transport of industrial pollutants to that region. Heavy metal concentrations were analyzed in samples of bryophytes and epiphyllous organisms growing on leaves and on bark in this forest. Concentrations of Cd, Pb, Ni, and Cr were higher in leaves with epiphylls than in leaves without epiphylls. All heavy metal concentrations in bryophytes from the Amazon basin site were lower than in bryophytes from temperature zones. The results indicate that long-range transport of air pollutants from industrial centers to the remote Amazon basin is occurring at only extremely low rates. Heavy metal concentrations in bryophytes and epiphylls at this site may still be considered close to present day background levels.

1. Introduction

Long-range transport of air pollutants to remote areas has been recently documented (Zoller *et al.*, 1974). Atmospheric gas concentrations have increased from 1975 to 1980 (Rasmussen *et al.*, 1981). In addition, organic pollutants in rain and air samples in remote marine areas have been measured by Atlas and Giam (1981), indicating long-range transport from continental sources. Long-range atmospheric transport of soil dust from Asia to the Tropical North Pacific has been suggested by Duce *et al.* (1980).

The presence of acid rain at San Carlos de Rio Negro in the remote Amazon rain forest of Southwestern Venezuela may result from long-range transport of industrial pollutants. Haines *et al.* (1983) reported rain pH values of 4.7 averaged over 70 storms through a 1 yr period at San Carlos de Rio Negro. San Carlos de Rio Negro is located about 900 km from industrial areas in Venezuela and 3000 km from industrial areas in Brazil. However, due to the wind pattern in the Amazon Basin, pollutants released in industrial areas of Venezuela, Guyana and Brazil may be carried to this location.

Lichens and mosses are sensitive bioindicators of heavy metal contamination of natural environments (Little and Martin, 1974) and can concentrate heavy metals to a higher degree than vascular plants (Grodzinska, 1978). In the present study, heavy metal

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concentrations in samples of epiphylls, and bryophytes growing on tree trunks at San Carlos de Rio Negro were analyzed. If concentrations were found to be higher in leaves with epiphylls than in leaves without, this would be an indication of accumulation of ions from the atmosphere, suggesting that long distance transport of pollutants may be occurring to this remote forest. In addition, by comparing heavy metal concentrations in bryophytes from San Carlos with those that have been reported for other areas of the world which are undergoing different degrees of industrial pollution, the relative magnitude with which long distance transport of pollutants is presently occurring could be estimated.

2. Methods

Sampling was done in an undisturbed area of a lowland tropical rain forest about 5 km east of the small settlement of San Carlos de Rio Negro, Venezuela. Annual rainfall averages 3500 mm yr^{-1} (Medina *et al.*, 1977), 50% of which is internally recycled (Salati *et al.*, 1978). Bryophytes were taken from ten living tree trunks and ten dead tree trunks. Bryophytes on each trunk were composited in approximately 200 g wet weight samples. Replicate 0.5 g dry weight subsamples were processed for analysis. Canopy leaves did not have epiphyllic growth, therefore leaves with and without epiphylls were taken from tree saplings. Two to three leaves were taken from 100 tree saplings of various species along a 200 m transect. Leaves from ten saplings were pooled giving a total of ten samples with epiphylls and ten without epiphylls. A list of the epiphylls and bryophytes collected and analyzed is given in Table I.

TABLE I

Epiphylls and bryophytes collected at San Carlos de Rio Negro, Territorio Federal Amazonas, Venezuela

Growth substrate	Life form	Species
Leaves of vascular plants	liverwort	*Ceratolejuena sp.* Schiffn.
	blue green algae	unidentified
	moss	?
Live trunks	liverwort	*Bazzania sp.* S.F. Gray
	liverwort	*Micropterygium leiophyllum* Spruce
	moss	*Octoblepharum albidum* Hedw.
Dead trunks	moss	*Leucobryum glaucum* (Hedw.) Angstr. Ex. Fr.
	moss	*Sematophyllum sp.* Mitt
	liverwort	*Micropterygium leiophyllum* Spruce

Samples were ashed in a muffle furnace at 450 °C for 4 hr in ceramic crucibles, and 20 ml of 10% HNO_3 were added to each sample. No metal containers or instruments were used while processing the samples. Two replicates of each sample were run. Two blanks and three orchard leaf standard samples were processed for every set of 20 samples.

Orchard leaf standards of 0.125, 0.25, and 0.75 g were run to confirm that recovery efficiency did not change with changes in heavy metal concentrations.

Elements were analyzed on a Jarrell-Ash Plasma Emission Spectrograph. Accuracy, precision, and sensitivity of the inductively coupled plasma emission instrument were evaluated by Blood *et al.* (1981). Concentrations were corrected using blanks and internal standards. The percent recovery of each element was calculated for the orchard leaf standard samples based on the National Bureau of Standards certified values.

3. Results and Discussion

Heavy metal concentrations in bryophytes and in leaves of saplings with and without epiphylls are shown in Table II. Mean concentrations of Cd, Pb, Ni, Fe, Mn, and Cr were significantly higher in the leaves with epiphylls than in the leaves without epiphylls. No significant differences occurred between bryophyte samples from live and dead trunks except for Mn, where the mean concentration was higher in mosses from dead trunks.

TABLE II

Heavy metal concentrations (ppm dry weight) in bryophytes and leaves of tree saplings collected in Amazon rainforest in sourthern Venezuela. Numbers in parentheses are $S\bar{x}$ ($N = 10$). Means within a particular metal with non-matching letters are significantly different ($P < 0.05$).

	Fe	Mn	Cu	Zn	Co	Cr	Ni	Pb	Cd
Bryophytes on live trunks	103.0^{a} (22)	12.6^{d} (1.6)	3.7^{a} (0.2)	7.3^{a} (2.3)	0.5^{a} (0.1)	0.2^{a} (0.1)	0.01^{a} (<0.1)	1.6^{a} (0.5)	0.1^{b} (<0.1)
Bryophytes on dead trunks	164.0^{a} (36)	20.8^{c} (1.6)	3.6^{a} (0.2)	16.5^{a} (4.3)	0.8^{a} (0.2)	0.3^{a} (0.1)	0.2^{a} (<0.1)	3.7^{a} (0.8)	0.1^{b} (<0.1)
Leaves with epiphylls	47.5^{b} (3.3)	91.7^{a} (17.9)	2.7^{a} (0.5)	9.3^{a} (2.9)	0.4^{a} (<0.1)	0.4^{a} (0.1)	0.3^{a} (<0.1)	3.3^{a} (0.7)	0.3^{a} (<0.1)
Leaves without epiphylls	29.0^{c} (2.0)	34.4^{b} (6.2)	3.8^{a} (0.3)	11.1^{a} (1.9)	0.1^{a} (0.3)	<0.1 (<0.1)	0.1^{a} (<0.1)	0.9^{b} (0.5)	<0.1 (<0.1)

For both the bryophytes on trunks and the epiphyllous and non-epiphyllous leaves, mean concentrations of the heavy metals Cd, Pb, Ni, and Cr were all very low, the highest being 3.74 ppm Pb in bryophytes on dead trunks. This suggests that long-range transport of air pollutants to this forest is occurring at only extremely low rates. The fact that heavy metal concentrations were significantly higher in epiphyllous than in non-epiphyllous leaves could be explained as resulting from low levels of pollutant transport and accumulation of metals by epiphylls. Alternatively, this difference may also be due to an age factor, since the epiphyllous leaves were always older than the non-epiphyllous leaves.

Concentrations of Pb and Ni in the bryophytes growing on dead and live trunks at San Carlos were much lower than those from temperate forests which are distant from point sources of air pollution (Table III). Lead concentrations at San Carlos lie within the same range as those reported by Lawrey and Hale (1979) for a lichen in Barro Colorado Island, Panama, and they are lower than those reported by Onianwa and Egunyomi (1983) for mosses from rural areas of Nigeria. The dominant bryophyte species at San Carlos de Rio Negro, the moss *Leucobryum glaucum* Hedw., also occurs in temperate forests. The lower concentrations in this particular species at San Carlos as compared to populations in temperate areas further substantiate the suggestion that long range deposition of industrial pollutants at this site is occurring at only very low rates. We are aware that the comparisons in Table III are limited by factors such as variation in growth rate, substrate, locality, and precipitation amounts which may affect concentrations of heavy metals within a species, and that even within the same locality different species may have different concentrations of heavy metals (Folkeson 1979; Pilegaard *et al.*, 1979; Rasmussen *et al.*, 1980). However, the magnitude of the differences of Pb and Ni between rural, non-industrial temperate areas and San Carlos de Rio Negro suggests that present concentrations of heavy metals in bryophytes at San Carlos should be considered close to present day background levels.

TABLE III

Heavy metal concentrations (ppm dry weight) in bryophytes from a remote tropical rainforest and both industrial and non-industrial temperate regions. Cited values are ranges of ppm reported by authors.

Location	Species	Cu	Zn	Cr	Ni	Pb	Cd
Denmark, mosses collected after 214 days exposure to air pollution (Pilegaard, 1979)	*Hypogimnia physodes* (L.) Nyl. and *Dicranoweisia cirrata* (Hedw.) Lindb.	11.6–172.0	139.0–2208.0	4.7–47.0	0.9–27.0	83.1–18.0	0.7–7.1
Industrial N.E. U.S. (Groet, 1976)	*Leucobryum glaucum* (Hedw.) Angstr. ex. Fr.	5.8–19.7	30.0–88.0	1.4–11.4	5.1–18.3	27.0–258.0	0.4–1.3
Denmark, mosses before exposure to air pollution (Pilegaard, 1979)	*Hypogimnia physodes* (L.) Nyl. and *Dicranoweisia cirrata* (Hedw.) Lindb.	8.3–10.3	84.0–100.0	3.9–4.3	1.0–3.0	75.0–96.0	0.4–0.7
Non industrial areas of U.S. (Groet, 1976)	*Leucobryum glaucum* (Hedw.) Angstr. ex. Fr.	14.0	83.0	11.7	11.9	157.0	1.0
San Carlos de Rio Negro, Amazonas, Venezuela (this study)	Mainly *Leucobryum glaucum* (Hedw.) Angstr. ex. Fr.	1.3–8.2	5.4–74.5	0.1–1.0	0.1–0.5	1.3–7.7	<0.1–0.3

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References

Atlas, E. and Giam, C. S.: 1981, *Sci.* **211**, 163.
Blood, E. R., Tate, C., and Nicora, M.: 1981, Unpub. Manuscript.
Duce, R. A., Unni, C. K., Ray, B. J., Prospero, J. M., and Merrill, J. T.: 1980, *Sci.* **209**, 1522.
Folkeson, L.: 1979, *Water, Air, and Soil Pollut.* **11**, 253.
Grodzinska, K.: 1978, *Water, Air, and Soil Pollut.* **9**, 83.
Groet, S. S.: 1976, *Oikos* **27**, 445.
Haines, B. L., Jordan, C. F., Clark, H. L., and Clark, K.: 1983, *Tellus* **35B**, 77.
Lawrey, J. D. and Hale, M. E.: 1979, *Sci.* **204**, 423.
Little, P. and Martin, M. H.: 1974, *Environ. Poll.* **6**, 1.
Medina, E., Herrera, R., Jordan, C. F., and Klinge, H.: 1977, *Nat. and Res.* **13**, 4.
Onianwa, P. C. and Egunyomi, A.: 1983, *Environ. Poll.* **5**, 71.
Pilegaard, K.: 1979, *Water, Air, and Soil Pollut.* **11**, 77.
Pilegaard, K., Rasmussen, L., and Gydesen, H.: 1979, *J. Appl. Ecol.* **16**, 843.
Rasmussen, L., Pilegaard, K., and Gydesen, H.: 1980, *Bot. Tidsskr.* **75**, 93.
Rasmussen, R. A., Khalil, M. A. K., and Dalluge, R. W.: 1981, *Sci.* **211**, 285.
Salati, E., Marques, J., and Molion, L. C. B.: 1978, *Interciencia* 3, 200.
Zoller, W. H., Gladney, E. S., and Duce, R. A.: 1974, *Sci.* **183**, 198.

HEAVY METAL CONCENTRATIONS IN SOME NON-VASCULAR PLANTS IN AN AMAZONIAN RAINFOREST

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bstract. The presence of acid rain in the remote Amazon rainforest of southwestern Venezuela suggests he possibility of long-range transport of industrial pollutants to that region. Heavy metal concentrations vere analyzed in samples of bryophytes and epiphyllous organisms growing on leaves and on bark in this orest. Concentrations of Cd, Pb, Ni, and Cr were higher in leaves with epiphylls than in leaves without piphylls. All heavy metal concentrations in bryophytes from the Amazon basin site were lower than in ryophytes from temperature zones. The results indicate that long-range transport of air pollutants from ndustrial centers to the remote Amazon basin is occurring at only extremely low rates. Heavy metal oncentrations in bryophytes and epiphylls at this site may still be considered close to present day ackground levels.

1. Introduction

Long-range transport of air pollutants to remote areas has been recently documented (Zoller *et al.*, 1974). Atmospheric gas concentrations have increased from 1975 to 1980 (Rasmussen *et al.*, 1981). In addition, organic pollutants in rain and air samples in remote marine areas have been measured by Atlas and Giam (1981), indicating long-range transport from continental sources. Long-range atmospheric transport of soil dust from Asia to the Tropical North Pacific has been suggested by Duce *et al.* (1980).

The presence of acid rain at San Carlos de Rio Negro in the remote Amazon rain forest of Southwestern Venezuela may result from long-range transport of industrial pollutants. Haines *et al.* (1983) reported rain pH values of 4.7 averaged over 70 storms through a 1 yr period at San Carlos de Rio Negro. San Carlos de Rio Negro is located about 900 km from industrial areas in Venezuela and 3000 km from industrial areas in Brazil. However, due to the wind pattern in the Amazon Basin, pollutants released in industrial areas of Venezuela, Guyana and Brazil may be carried to this location.

Lichens and mosses are sensitive bioindicators of heavy metal contamination of natural environments (Little and Martin, 1974) and can concentrate heavy metals to a higher degree than vascular plants (Grodzinska, 1978). In the present study, heavy metal

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concentrations in samples of epiphylls, and bryophytes growing on tree trunks at San Carlos de Rio Negro were analyzed. If concentrations were found to be higher in leaves with epiphylls than in leaves without, this would be an indication of accumulation of ions from the atmosphere, suggesting that long distance transport of pollutants may be occurring to this remote forest. In addition, by comparing heavy metal concentrations in bryophytes from San Carlos with those that have been reported for other areas of the world which are undergoing different degrees of industrial pollution, the relative magnitude with which long distance transport of pollutants is presently occurring could be estimated.

2. Methods

Sampling was done in an undisturbed area of a lowland tropical rain forest about 5 km east of the small settlement of San Carlos de Rio Negro, Venezuela. Annual rainfall averages 3500 mm yr^{-1} (Medina *et al.*, 1977), 50% of which is internally recycled (Salati *et al.*, 1978). Bryophytes were taken from ten living tree trunks and ten dead tree trunks. Bryophytes on each trunk were composited in approximately 200 g wet weight samples. Replicate 0.5 g dry weight subsamples were processed for analysis. Canopy leaves did not have epiphyllic growth, therefore leaves with and without epiphylls were taken from tree saplings. Two to three leaves were taken from 100 tree saplings of various species along a 200 m transect. Leaves from ten saplings were pooled giving a total of ten samples with epiphylls and ten without epiphylls. A list of the epiphylls and bryophytes collected and analyzed is given in Table I.

TABLE I

Epiphylls and bryophytes collected at San Carlos de Rio Negro, Territorio Federal Amazonas, Venezuela

Growth substrate	Life form	Species
Leaves of vascular plants	liverwort	*Ceratolejuena sp.* Schiffn.
	blue green algae	unidentified
	moss	?
Live trunks	liverwort	*Bazzania sp.* S.F. Gray
	liverwort	*Micropterygium leiophyllum* Spruce
	moss	*Octoblepharum albidum* Hedw.
Dead trunks	moss	*Leucobryum glaucum* (Hedw.) Angstr. Ex. Fr.
	moss	*Sematophyllum sp.* Mitt
	liverwort	*Micropterygium leiophyllum* Spruce

Samples were ashed in a muffle furnace at 450 °C for 4 hr in ceramic crucibles, and 20 ml of 10% HNO_3 were added to each sample. No metal containers or instruments were used while processing the samples. Two replicates of each sample were run. Two blanks and three orchard leaf standard samples were processed for every set of 20 samples.

Orchard leaf standards of 0.125, 0.25, and 0.75 g were run to confirm that recovery fficiency did not change with changes in heavy metal concentrations.

Elements were analyzed on a Jarrell-Ash Plasma Emission Spectrograph. Accuracy, recision, and sensitivity of the inductively coupled plasma emission instrument were valuated by Blood *et al.* (1981). Concentrations were corrected using blanks and nternal standards. The percent recovery of each element was calculated for the orchard eaf standard samples based on the National Bureau of Standards certified values.

3. Results and Discussion

eavy metal concentrations in bryophytes and in leaves of saplings with and without piphylls are shown in Table II. Mean concentrations of Cd, Pb, Ni, Fe, Mn, and Cr ere significantly higher in the leaves with epiphylls than in the leaves without epiphylls. o significant differences occurred between bryophyte samples from live and dead unks except for Mn, where the mean concentration was higher in mosses from dead unks.

TABLE II

eavy metal concentrations (ppm dry weight) in bryophytes and leaves of tree saplings collected in Amazon inforest in sourthern Venezuela. Numbers in parentheses are $S\bar{x}$ ($N = 10$). Means within a particular metal with non-matching letters are significantly different ($P < 0.05$).

	Fe	Mn	Cu	Zn	Co	Cr	Ni	Pb	Cd
ryophytes on live trunks	103.0^{a} (22)	12.6^{d} (1.6)	3.7^{a} (0.2)	7.3^{a} (2.3)	0.5^{a} (0.1)	0.2^{a} (0.1)	0.01^{a} (<0.1)	1.6^{a} (0.5)	0.1^{b} (<0.1)
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eaves without epiphylls	29.0^{c} (2.0)	34.4^{b} (6.2)	3.8^{a} (0.3)	11.1^{a} (1.9)	0.1^{a} (0.3)	<0.1 (<0.1)	0.1^{a} (<0.1)	0.9^{b} (0.5)	<0.1 (<0.1)

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TABLE III

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San Carlos de Rio Negro, Amazonas, Venezuela (this study)	Mainly *Leucobryum glaucum* (Hedw.) Angstr. ex. Fr.	1.3–8.2	5.4–74.5	0.1–1.0	0.1–0.5	1.3–7.7	<0.1–0.3

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References

Atlas, E. and Giam, C. S.: 1981, *Sci.* **211**, 163.
Blood, E. R., Tate, C., and Nicora, M.: 1981, Unpub. Manuscript.
Duce, R. A., Unni, C. K., Ray, B. J., Prospero, J. M., and Merrill, J. T.: 1980, *Sci.* **209**, 1522.
Folkeson, L.: 1979, *Water, Air, and Soil Pollut.* **11**, 253.
Grodzinska, K.: 1978, *Water, Air, and Soil Pollut.* **9**, 83.
Groet, S. S.: 1976, *Oikos* **27**, 445.
Haines, B. L., Jordan, C. F., Clark, H. L., and Clark, K.: 1983, *Tellus* **35B**, 77.
Lawrey, J. D. and Hale, M. E.: 1979, *Sci.* **204**, 423.
Little, P. and Martin, M. H.: 1974, *Environ. Poll.* **6**, 1.
Medina, E., Herrera, R., Jordan, C. F., and Klinge, H.: 1977, *Nat. and Res.* **13**, 4.
Onianwa, P. C. and Egunyomi, A.: 1983, *Environ. Poll.* **5**, 71.
Pilegaard, K.: 1979, *Water, Air, and Soil Pollut.* **11**, 77.
Pilegaard, K., Rasmussen, L., and Gydesen, H.: 1979, *J. Appl. Ecol.* **16**, 843.
Rasmussen, L., Pilegaard, K., and Gydesen, H.: 1980, *Bot. Tidsskr.* **75**, 93.
Rasmussen, R. A., Khalil, M. A. K., and Dalluge, R. W.: 1981, *Sci.* **211**, 285.
Salati, E., Marques, J., and Molion, L. C. B.: 1978, *Interciencia* **3**, 200.
Zoller, W. H., Gladney, E. S., and Duce, R. A.: 1974, *Sci.* **183**, 198.