Ecology and Management of Tropical Secondary Forest: Science, People and Policy

CIFOR
CENTER FOR INTERNATIONAL FORESTRY RESEARCH

CATIE
Centro Agronómico Tropical de
Investigación y Enseñanza

C818

Serie Técnica
Reuniones Tecnicas Nº4

Ecology and Management of Tropical Secondary Forest: Science, People, and Policy

**Proceedings of a conference held at CATIE, Costa Rica,
November 10-12, 1997**

Manuel R. Guariguata and Bryan Finegan, Editors

Organized by

Centro Agronómico Tropical de Investigación y Enseñanza (CATIE)
Center for International Forestry Research (CIFOR)

Promoted by

International Union of Forest Research Organizations (IUFRO)

Sponsored by

Centro Agronómico Tropical de Investigación y Enseñanza (CATIE)
Center for International Forestry Research (CIFOR)
World Wildlife Fund (WWF)
Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ)

Turrialba, Costa Rica 1998

CATIE
ST
RT-4

El CATIE es una asociación civil, sin fines de lucro, autónoma, de carácter internacional, cuya misión es mejorar el bienestar de la humanidad, aplicando la investigación científica y la enseñanza de posgrado al desarrollo, conservación y uso sostenible de los recursos naturales. El Centro está integrado por miembros regulares y miembros adherentes. Entre los miembros regulares se encuentran: Belice, Costa Rica, Colombia, Ecuador, El Salvador, Guatemala, Honduras, México, Nicaragua, Panamá, República Dominicana, Venezuela y el Instituto Interamericano de Cooperación para la Agricultura (IICA).

El Centro para la Investigación Forestal Internacional (CIFOR) fue establecido en 1993 como respuesta a los problemas globales relacionados con las consecuencias sociales, ambientales y económicas de la pérdida y degradación de los bosques. La misión del CIFOR es contribuir al bienestar de los pueblos en los países en desarrollo, particularmente en los trópicos, a travéz de una estrategia colaborativa e investigación aplicada y actividades relacionadas en sistemas forestales, y de la promoción de la transferencia de tecnologías apropiadas y la adopción de nuevos métodos de organización social para el desarrollo nacional.

BIBLIOTECA
98048
Centro Interamericano de Documentación e Información Agrícola
IICA - CIDIA

574.52642
E19 Ecology and management of tropical secondary forest: science, people, and policy. Proceedings of a conference held at CATIE, Costa Rica, November 10-12, 1997 / Manuel R. Guariguata and Bryan Finegan, eds. – Turrialba, C.R. : CATIE : IUFRO : CIFOR : WWF : GTZ, 1998.
244 p. ; 27 cm. – (Serie técnica. Reuniones técnicas / CATIE ; no. 4)

ISBN 9977-57-318-2

1. Bosque secundario – Congresos, conferencias, etc.
2. Ecología forestal – Congresos, conferencias, etc.
3. Manejo forestal – Congresos, conferencias, etc.
I. Guariguata, Manuel R., ed. II. Finegan, B., ed.
III. CATIE IV. Título V. Serie

Contents

Preface

The disturbance and destruction of the old-growth forests of the tropics continue to monopolize attention in international fora and the popular media, but a steadily growing land area is covered by secondary forest developing on sites which have been deforested and then abandoned by their erstwhile owners. The natural process of secondary forest succession offers hope that the unique combination of goods and services provided by the original old-growth forests may be at least partially recovered.

An enormous number of questions concerning secondary tropical forests and their potential role in sustainable land management and biodiversity conservation remain to be answered, however. Many of these questions are biological and ecological: What are the factors that bring about successional change in vegetation? How does biodiversity change during succession, does its similarity to the biodiversity of old-growth forests increase over time and why, or why not? How might secondary forests be manipulated to optimize their value for a given set of management objectives? Many more questions nevertheless concern people and their actions: what factors bring about land abandonment? How are secondary forests perceived and utilized by rural people? What market or policy changes may contribute to a more profitable and sustainable use of secondary forests?

We felt that the final years of the 20th century represent an opportune time to bring together researchers concerned with biological, ecological, social/organizational, financial/economic and political aspects of secondary forests and their management, to share their experiences and opinions concerning secondary tropical forests and to contribute to the development of a forward-looking, cross-disciplinary research agenda. The conference had the following objectives:

- to summarize the state of knowledge of tropical secondary forests from the standpoints of the ecological, social and political sciences

- to report the most recent results of research on secondary forests from all relevant disciplines.

This volume contains 16 papers (in the conference's official languages: english, spanish, and portuguese) related to the conceptual, ecological, silvicultural, and policy aspects of this natural resource, with a strictly neotropical focus. The first contribution by Sips and van der Linden provides an overview of the current status of secondary forests in terms of extent, origin, and management potential with its inevitable constraints. One of these constraints is presented in the following paper by Müller who examines how in Costa Rica, secondary forests lack an appropriate legal framework to cover aspects as basic as their definition, and others such as silvicultural options as is discussed in the next paper by Whitmore. This author also provides us with a pantropical view on the ecology of secondary forest succession and its component tree species, covered in more detail in the articles that follow.

The process of secondary forest succession is described by Vester in terms of how tree growth relates to the spatial display of a tree´s growing point—a term known as tree architecture—and how tree architectural patterns change in their relative importance as succession proceeds. Likewise, the contributions by Tucker et al., Oliveira, Guimaraes and Proctor, Gomide et al., and De Las Salas assess tree growth, structure, and floristics in secondary forests of different ages since site abandonment in lowland Brazil and Colombia, and most of them provide management implications. The only montane example in this volume is that of Olvera and Figueroa, who characterized oak-dominated forests in Mexico in order to develop silvicultural prescriptions. Two papers cover the subtropics. Kammesheidt evaluates the role of stump resprouts in structural and floristical recovery of successional vegetation in Paraguay, while Grau describes how exotic woody species have become an integral component of successional trajectories in NW Argentina (a relatively rare phenomenon in wet, tropical lowlands).

A thorough assessment of timber and non-timber forest products from secondary and selectively-logged forests in NE Costa Rica is offered by Chazdon and Coe. As a point of reference to Chazdon and Coe's results, Favrichon et al. provide comparative results of tree growth and forest structure in selectively-logged forests in French Guiana and Brazil. The contribution by Montagnini et al. is the only one that addresses soil fertility as a function of the type of successional vegetation, an aspect of practical importance for management purposes. Last but not least, Ortiz et al. take an innovative approach in promoting Costa Rican secondary forests as mitigators of atmospheric carbon emissions.

Although the biophysical side of secondary forest research dominated this conference, it is becoming clear that sound management of this resource will depend on interdisciplinary approaches. For example, humans both create and use secondary vegetation, so the social dimension should not be ignored. This conference was a first attempt to bring scientists from various disciplines to join efforts towards a common goal. We hope that this volume will inspire researchers to develop new ways to the management of secondary forests.

The editors

Acknowledgments

This conference would have not been possible without the help of the following people: Jaime Vindas, Lidiette Marín, Lucrecia Guillén, Diego Delgado, Martín Artavia, Edwin Pereira, and Francisco "Macho" Solano. To all of them our sincere thanks.

Presentation

Secondary forests developing on agricultural land after it is abandoned, or as the fallow period in systems of subsistence agriculture, are an increasingly important component of the forest resources of the tropics. They fix and store carbon and may contribute to the alleviation of global warming, they are refuges for biodiversity in agricultural landscapes, and they are low-cost sources of a tremendous variety of forest products. In recognition of these widely accepted attributes, a scientific meeting focusing on secondary forests was held at the Tropical Agricultural Centre for Research and Higher Education (CATIE) in November 1997. The meeting was organized by CATIE, its institutional partner the Centre for International Forestry Research (CIFOR), and the International Union of Forestry Research Organizations (IUFRO). Reflecting the policies of the organizing institutions, the meeting was multidisciplinary: scientists from the biophysical and socioeconomic camps sat together and discussed results from their own and each other's research fields. The meeting was not only multidisciplinary, however, but also satisfyingly international: thirty-six scientists representing seventeen countries, from the tropics as well as temperate countries of both northern and southern hemispheres, were present. The papers presented at the meeting were a representative and exciting cross-section of current research priorities relating to the management of tropical secondary forests. It is with the intention of permitting as many stakeholders in such forests as possible to learn and benefit from the information presented, that we present the 16 papers included in these proceedings.

Dr. Rubén Guevara
Director General
CATIE

Vast areas of forest in the tropics have been cleared for inappropriate agriculture over the past few decades. Much of this land is in frontier areas where human poverty is high, soils are not suitable for sustained arable agriculture and the optimum land use is some form of managed forest or tree crop. Many of the areas have infrastructure, often provided as part of government sponsored colonization and land development schemes and much of the land is under some form of private title. Our colleagues at CATIE have taken a lead in developing systems of management for the secondary forests that can regenerate on these abandoned agricultural lands and have demonstrated the great environmental and livelihood benefits that can be obtained through forest-based uses of these lands. CIFOR is therefore very pleased to have been able to be associated with the 1997 meeting which brought together scientists from many tropical countries and from different disciplines to review the state of knowledge of the art and science of secondary forest management. We believe that the results of the meeting will strengthen the scientific basis for secondary forest management not only in the neo-tropics but also in the abandoned agricultural lands that could be turned to more productive use in the other tropical regions. The 16 papers included in the proceedings provide an excellent strategic overview of the issues relating to the management of secondary forests and the application of the knowledge that they contain can contribute to greatly improved lives for large numbers of poor people who live at the forest margins.

Prof. Jeffrey Sayer
Director General
CIFOR

TROPICAL SECONDARY FOREST MANAGEMENT: POTENTIAL, CONSTRAINTS AND RECOMMENDATIONS

Peter A. Sips and Bert A. van der Linden

BOS Foundation, Organization for International Forestry Cooperation,
P.O. Box 23, 6700 AA Wageningen, The Netherlands

ABSTRACT

The concern about the destruction of the world's tropical forests has grown considerably in the past two decades and has resulted in national and international initiatives to reverse this trend and to develop strategies for sustainable forest management. Within this context, the potential of tropical secondary forests has long been neglected by researchers and policy makers. However, it is acknowledged that if properly managed, tropical secondary forests have the potential to produce both timber and non-timber forest products, hence contributing to remove current pressure from primary forests, and play a role in biodiversity conservation (Peet and Atkinson, 1994; Sips et al., 1996; Wilkie and Finn, 1990). Due to a steadily growing population and economic development, the demand for forest products and agricultural land is likely to accelerate (FAO, 1995). In addition, many tropical countries have considerable areas of tropical secondary forests that are increasing in area (Brown and Lugo, 1990). Tropical secondary forests originate from human activities and are often an integral part of small-scale agricultural systems. However, it appears that the substantial body of knowledge on tropical secondary forest use and management present among indigenous people and farmers has only been studied to a limited extent. In order to fully explore and utilize the potential of tropical secondary forests, their management must be primarily based on the active participation and needs of local people. Likewise, the values of these forests should be recognized and acknowledged at national and international levels.

DEFINITION, ORIGIN AND EXTENT

In the literature, tropical secondary forests are defined in several ways. Definitions mostly cover all types of forest that have been affected in some way by human disturbance, ranging from previously logged, "residual forests", to successional forests that develop after complete clearance (Brown and Lugo, 1990; Weaver, 1995). In line with Finegan and Sabogal (1988) and Lanly (1995) we define tropical secondary forests as those in a stage of reconstruction after complete removal of the original forest through natural and/or human disturbance (Corlett, 1995;

Sips et al., 1996). Logged-over or residual forests are excluded from this definition. However, given the amount of literature found in studies on tropical secondary forests and their management in Africa, Asia and Latin America this definition seems most applicable to the Latin American context and to a lesser extent to Africa and Asia. In fact, in the case of the latter two, it appears that all disturbed forests are referred to as secondary (Richards, 1996).

Until now the aerial estimates of tropical secondary forests found in the literature show large variations and are mainly tentative. This variation can partly be attributed to differences in definitions. In addition, area assessments are complicated because present remote sensing techniques do not allow a clear distinction between "old" secondary forest and primary forest. The estimates are only rough indications of the area of tropical secondary forest. FAO's Forest Resources Assessment (FAO, 1993, 1995, 1996) is illustrative of the problems concerning definition and area assessment. A land cover classification is applied by FAO in which secondary forests are included in the long and short fallow land cover class. Long fallow is described as "a mosaic of mature forest, secondary forest, various stages of natural regrowth and cultivated areas with cultivated areas covering between 5 and 30% of the total area", and short fallow as "a mosaic of young secondary forest, various stages of natural regrowth and cultivated areas with cultivated areas covering between 30 and 50% of the total area." A definition of (young) secondary forest is missing. However, based on FAO (1993, p. 51) it is most likely that the term is referring to logged-over forest. FAO (1995, 1996) estimated that the tropical secondary forest area (short fallow and long fallow) in Africa increased from 78.94 million ha in 1980 to 90.19 million ha in 1990, from 25.40 million ha to 33.06 million ha in Latin America, and from 81.50 million ha to 87.50 million ha in Asia.

VALUES OF TROPICAL SECONDARY FORESTS

Tropical secondary forests have several values for both human use and nature conservation. Studies have indicated the importance of successional processes as a basis for different forms of sustainable land use by (indigenous) rural people and the management potential of tropical secondary forests for the production of food and forest products. In ancient Mayan culture for example agro-silvicultural management of tropical secondary forest resources played a central role in the food supply (Gómez-Pompa, 1991; Gómez-Pompa and Bainbridge, 1995). Nowadays many (indigenous) small-scale farmers still use secondary succession as a basis for different forms of land use management. This concerns particularly agroforestry systems and enriched forest fallows (Anderson, 1990; Del Amo and Ramos, 1993; Penot, 1995; Posey, 1991). Tropical secondary forests may also be valuable for local timber production (Browder et al., 1996; Klock, 1995, King et al., 1997; Sips, 1993). Several studies have indicated the commercial value of many secondary forest tree species. In addition, other tree species and several palm species produce fruits, oil and medicines (Browder et al., 1996; Finegan, 1992; King et al., 1997; Lamprecht, 1989; Pals and Delnoye, 1995; Sips, 1993; Weaver, 1986).

Tropical secondary forests may also play an important role in counter-acting the greenhouse-effect. Lugo and Brown (1992) report above-ground carbon accumulations between 2-3.5 x 10^6 g C/ha/year for young (less than 20 years old), tropical secondary forests, compared to 1.4-4.8 x 10^6 g C/ha/year for plantations. Furthermore, forest plantations on degraded sites and established near tropical secondary or primary forests can facilitate and accelerate succession. Besides the production of wood, such plantations can contribute to erosion control, improvement of soil quality and ecosystem and biodiversity rehabilitation (González and Fisher, 1994; King et al. 1997). Crucial to the success of this approach are the selection of species and planting densities, and the proximity to seed sources and availability of dispersal agents (Lugo, 1988; Parrotta, 1993). In this respect more attention should be paid to the establishment of uneven-aged, mixed native and exotic species plantations. Secondary forests may also play an important role in the conservation and restoration of biodiversity. They can serve as useful buffer zones around reserves as well as a refugium for fauna, and as corridors between forest areas.

POTENTIAL OF TROPICAL SECONDARY FOREST MANAGEMENT

Most tropical secondary forest areas are part of private farms and are located near settlements. Sustainable management of these forests must therefore be based on their active participation. Given their diverse needs (for food, firewood and construction material) multi-purpose management of tropical secondary forests by and for local people is the most obvious alternative (Del Amo and Ramos, 1993; Forestry and Biodiversity Support Group, 1993; Finegan, 1992; Peltier and Pity, 1993; Sips, 1995). Tropical secondary forest management may contribute to generate additional income and improving living conditions, and may open ways for the establishment of more sustainable land use practices.

The management potential of tropical secondary forests is influenced to a high degree by population pressure. Within the socio-economic conditions of the small-scale farmers, characterized by the lack of funds and insecure land (use) rights, forest fallows are mainly a mechanism to restore soil productivity and hence seen as potential agricultural land. In most cases conversion to agricultural land takes place after 6-8 years. If local population pressure is growing it is very likely that the forest fallow period is shortened and the cultivation period extended. Consequently, the soil fertility can no longer be restored and the site will become unproductive and eventually may deteriorate.

Studies on small farmers' land use have indicated that management practices involving the transformation of forest fallows into agroforests or enriched fallows, is promising. However, the possibilities of management intensification seem to be directly correlated with the possibility to generate extra income (Allen, 1985; Gouyon et al, 1993; Penot, 1995). If population pressure is relatively low the need for food production will be less. Forest fallows may develop into young and old secondary forests and long-term management (10-20 years) focusing on the production of forest products becomes possible. Management may involve the conversion to an enriched fallow, the establishment of an agroforest or the production of fuelwood. This may create a diversified array of forest products, including fruits, medicinal plants and construction materials. If the forest is rich in valuable species, medium-to long-term management aimed at the production of quality timber may be considered.

Experiments involving management of old, secondary forests using natural regeneration and enrichment planting indicate that the prospects of tropical secondary forest management for sustainable production of quality timber are good (Adjers et al., 1995; Finegan and Sabogal, 1988; Finegan, 1992; Hutchinson, 1995; Korpelainen et al., 1995; Wadsworth, 1995). If commercial production of quality timber is considered, polycyclic management on a 40-60 years basis of old-secondary forests based on natural regeneration appears to be a promising option. The experiments with enrichment planting indicate that this form of management should be restricted to younger forests that are poor in valuable species and well below 20 m. However, the high costs involved and the severe reduction of the initial secondary forest stand needed for the establishment and growth of the planted tree species put the sustainability of this form of timber production in question (Sips, 1993).

CONSTRAINTS

In order to fully explore and utilize the potential role of tropical secondary forest management several constraints have to be attended to. First of all, the issue of definition has to be dealt with. A clear distinction should be made between tropical secondary forests and logged-over forests in order to facilitate distinctive policies, research, statistics, projects, and allocation of funds. Secondly, the apparent substantial body of knowledge on tropical secondary forest use and management present among indigenous people and farmers has not yet been adequately studied and documented. Only if funds are made available and research is coordinated can the full potential of tropical secondary forest management be determined. Likewise, more insight has to be gained into ecological, socio-economic and silvicultural factors determining present and potential future use and management of tropical secondary forests. Thirdly, on the political level, various issues have to be attended in order to create better policy, institutional and financial conditions for research, and development of tropical secondary forest management and its operationalization (Forestry and Biodiversity Support Group, 1993). In this respect, policy and institutional reforms at national and local level have to be made, including security of land rights and incentives for local farmers and local forest industries (Almeida and Campari, 1995; Bakker, 1993).

RECOMMENDATIONS

On national and international level policy makers, donor agencies, banks and research institutions have to be informed and convinced of the potential of tropical secondary forest management. Tropical secondary forest management should be incorporated in local, national and international policies, strategies and projects dealing with land use planning and land tenure. Funds have to be made available for research, pilot projects on sustainable tropical secondary forest management, and the dissemination of information. A network on tropical secondary forest should be established as a forum for the exchange of information on knowledge, experiences, and research, and the promotion at national and international political and financial levels.

To conclude, we suggest that more research should focus on

-The socio-political causes of tropical secondary forests (e.g., through land tenure, unbalanced land right relations, land speculation, and fiscal policies).

-Focusing on the substantial body of knowledge on tropical secondary forest use and management among indigenous people and farmers.

-The role and promotion of tropical secondary forests in development of more sustainable land use practices (e.g., agroforestry, enriched fallows) and the conservation of forest ecosystems (e.g., through improvement of the socio-economic value of tropical secondary forests, land tenure, education, the development of incentives for local people and forest products industries).

-The development of people's participation mechanisms and incentive/penalty systems to stimulate tropical secondary forest management in sustainable land use.

-The ecological and silvicultural aspects of tropical secondary forest management.

If the potential of tropical secondary forest management is acknowledged and if the necessary actions are taken to stimulate their management, tropical secondary forests may become of global importance for both man and nature.

REFERENCES

Adjers, G., Hadengganan, S., Kuusipalo, J. Nutyanto, K. and L. Vesa, 1995. Enrichment planting of dipterocarps in logged-over secondary forests: effect of width, direction and maintenance method of planting line on selected *Shorea* species. Forest Ecology and Management 73: 259-270.

Almeida, A.L.O. de and J.S. Campari, 1995. Sustainable settlement in the Brazilian Amazon. World Bank, Washington, D.C.

Allen, B.J., 1985. Dynamics of fallow successions and introduction of robusta coffee in shifting cultivation areas 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. In: Anderson, A.B. (ed.). Alternatives to deforestation. Steps towards sustainable use of the Amazon rain forest. Columbia University Press, New York. p. 65-85.

Bakker, L.M., 1993. Colonization and land use in the humid tropics of Latin America. Ministry of Foreign Affairs, Directorate General of International Cooperation, The Hague/National Reference Centre for Nature Management of the Ministry of Agriculture, Nature Management and Fisheries/ BOS Foundation, Organization for International Forestry Cooperation. The Netherlands. Werkdocument IKC-N/LNV no. 34, 39 pp.

Browder, J.O., Matricardi, E. and W. Abdala, 1996. Is sustainable tropical timber production viable? A comparative analysis of mahogany silviculture among small farmers in the Brazilian Amazon. Ecological Economics. No. 16. p. 147-159. Elsevier Science Publishers. The Netherlands.

Brown, S. and A.E. Lugo, 1990. Tropical secondary forests. Journal of Tropical Ecology 6: 1-32.

Corlett, R.T., 1995. Tropical secondary forests. Progress in Physical Geography, 19: 159-172.

Del Amo, R.S. and P.J. Ramos, 1993. Use and management of secondary vegetation in a humid-tropical area. Agroforestry Systems 21: 27-42.

FAO, 1993. Forest resources assessment 1990. Tropical countries. FAO Forestry Paper No.122. Rome. 59 pp.

FAO, 1995. Forest resources assessment 1990. Global synthesis. FAO Forestry Paper No.124. Rome. 44 pp.

FAO, 1996. Forest resources assessment 1990. Survey of tropical forest cover and study of change processes. FAO Forestry Paper No. 130. Rome. 152 pp.

Finegan, B. and C. Sabogal, 1988. El desarrollo de sistemas de produccion sostenible en bosques tropical humedos de Bajura: un estudio de caso en Costa Rica. El Chasqui 17: 3-24.

Finegan, B., 1992. The management potential of neotropical secondary lowland rain forest. Forest Ecology and Management 47: 295-321.

Fisher, R.F., 1996. Amelioration of degraded rain forest soils by plantations of native trees. Lecture held on 21st of May, 1996 at the Institute for Forest and Nature Research (IBN), Wageningen, The Netherlands.

Forestry and Biodiversity Support Group, 1993. Report of the Workshop "secondary forests "held on November 19, 1993. National Reference Centre for Nature Management, Ministry of Agriculture, Nature Management and Fisheries, Wageningen, The Netherlands.

Gómez-Pompa, A., 1991. Learning from traditional ecological knowledge: insights from Mayan silviculture. In: Gómez-Pompa, A., Whitmore, T.C. and M. Hadley (eds.). Rain Forest Regeneration and Management. Man and Biosphere Series. Vol. 6. p. 335-342. UNESCO. Paris.

Gómez-Pompa, A. and D.A. Bainbridge, 1995. Tropical forestry as if people mattered. In: Lugo, A.E. and C. Lowe (eds.). Tropical forests: management and ecology. Ecological Studies, Vol. 112. Springer Verlag. New York. p. 408-422.

González, J.E. and R.F. Fisher, 1994. Growth of native species planted on abandoned pasture land in Costa Rica. Forest Ecology and Management 70: 159-167.

Gouyon, A., Foresta, H. de and P. Levang, 1993. Does 'jungle rubber' deserve its name? An analysis of rubber agroforestry systems in southeast Sumatra. Agroforestry Systems 22: 181-206.

Hutchinson, I.D., 1995. Techniques for silviculture and management in natural tropical forests, logged and secondary. In: Parrotta, J.A. and M. Kanashiro. Management and rehabilitation of degraded lands and secondary forests in Amazonia. Proceedings of an international symposium/workshop, Santarém, Pará, Brazil. p. 117-128.

King, J., Moutsinga, J-B. and G. Doufoulon, 1997. Conversion of anthropogenic savanna to production forest through fire-protection of the forest-savanna edge in Gabon, Central Africa. Forest Ecology and Management 94: 233-247.

Klock, J., 1995. Indigenous woodlot management and ethnobotany in Ifugao, Philippines. International Tree Crops Journal 8: 95-106.

Korpelainen, H., Kuusipalo, J., Nuryanto, K. and A. Otsamo, 1995. Profitability of rehabilitation of overlogged dipterocarp forest: a case study from South Kalimantan, Indonesia. Forest Ecology and Management 79: 207-215.

Lamprecht, H., 1989. Silviculture in the tropics. Tropical forest ecosystems and their tree species - possibilities and methods for their long-term utilization. GTZ, Eshborn, Germany. 296 pp.

Lanly, J.P., 1995. The status of tropical forests. In: Lugo, A.E. and C. Lowe (eds.). Tropical forests: management and ecology. Ecological Studies, Vol. 112. Springer Verlag. New York. p. 18-32.

Lugo, A.E., 1988. Ecosystem rehabilitation in the tropics. Environment 30: 17.

Lugo, A.E. and S. Brown, 1992. Tropical forests as sinks of atmospheric carbon. Forest Ecology and Management 54. 239-255.

Pals, R. and R. Delnoye, 1995. Teak planting by farmers in Lao PDR. BOS NEWSLETTER, 14 (3): 30-41.

Parrotta, J.A. 1993. Secondary forest regeneration on degraded tropical lands. The role of plantations as "foster ecosystems". In: Leith, H. And M. Lohmann (eds.). Restoration of tropical forest ecosystems. p. 63-73. Kluwer Academic Publishers. The Netherlands.

Peet, N.B. and P.W. Atkinson, 1994. The biodiversity and conservation of the birds of Sao Tome and Principe. Biodiversity and Conservation 3: 851-867.

Peltier, R. and B. Pitty, 1993. From slash-and-burn to sustainable agroforestry system through improved fallow. Bois et Forest des Tropiques 235: 49-57.

Penot, E., 1995. Taking the 'jungle' out of the rubber: improving rubber in Indonesian agroforestry systems. Agroforestry Today 7:11-13.

Posey, D., 1991. Kayapo indians: experts in synergy. ILEIA Newsletter. 1991. p. 3-5.

Richards, P.W., 1996. The tropical rainforest. 2nd Edition. Cambridge University Press, Cambridge, UK. 575 pp.

Sips, P.A., 1993. Management of tropical secondary rain forests in Latin America. Today's challenge, tomorrow's accomplished fact!? National Reference Centre for Nature Management of the Ministry of Agriculture, Nature Management and Fisheries/BOS Foundation, Organization for International Forestry Cooperation. The Netherlands. Werkdocument IKC-N/LNV no. 27, 71 pp.

Sips, P.A., 1995. Polycyclic multi-purpose management of tropical secondary rainforests. In: Parrotta, J.A. and M. Kanashiro. Management and rehabilitation of degraded lands and secondary forests in Amazonia. Proceedings of an international symposium/workshop, Santarém, Pará, Brazil. p. 180-187.

Sips, P.A., Linden, B.A. and K. van Dijk, 1996. The potential of tropical secondary rainforest management in Latin America. Paper presented at the Symposium on Accelerating Native Forest Regeneration on Degraded Lands. IUFRO-World Bank-USDA Forest Service. Washington, DC, USA.

Wadsworth, F.H., 1995. A forest research institution in the West Indies: the first 50 years. In: Lugo, A.E. and C. Lowe (eds.). Tropical forests: management and ecology. Ecological Studies, Vol. 112. Springer Verlag. New York. p. 33-58.

Weaver, P.L., 1986. La evaluacion de los recursos forestales secundarios y su potencial para el manejo de la masa forestal. El primer seminario internacional sobre manejo de bosques tropical húmedo en la región de Centro América (SEMBOTH) ESNACIFOR.Siguatepeque, Honduras. 15 pp.

Weaver, P. L. 1995. Secondary forest management. In: Parrota, J. A. and M. Kanashiro. Management and rehabilitation of degraded lands and secondary forests in Amazonia. Proceedings of an international symposium. Santarém. Pará, Brazil. p. 117-128.

Wilkie, D.S. and J.T. Finn, 1990. Slash-burn cultivation and mammal abundance in the Ituri forest, Zaire. Biotropica 22: 90-99.

LAND USE POLICY AND SECONDARY FOREST MANAGEMENT IN THE NORTHERN ZONE OF COSTA RICA

Eva Müller
GTZ - COSEFORMA, Costa Rica

ABSTRACT

In Costa Rica, tropical primary forests outside of National Parks and other protected areas are privately owned and, in the past 50 years, have been greatly diminished by deforestation. However, recent abandonment of agricultural and pasture land has led to the establishment of more than 400,000 ha of secondary forests. Land use policy has played a major role in deforestation as well as in secondary forest development. Agricultural policy related to cattle production and meat exports was the most important factor, especially in the Northern Region of Costa Rica. During the 1960's and the 1970's cattle production for export to the United States was regarded as a model for regional development and was strongly subsidized by the Costa Rican Government. As a result, large areas of tropical primary forest were cleared. When meat prices and US meat imports from Costa Rica dropped in the 1980's, pastures were abandoned which permitted the development of secondary forests. Land colonization policy in the past directly favored the destruction of forests. To obtain land titles, farmers had to demonstrate that they had "worked' the land, i.e. removed the original forest cover. Although this policy is no longer being applied, landowners still prefer to eliminate natural regeneration of forest vegetation in order to avoid invasion by squatters. Agricultural policies related to banana exports also have had a negative influence on forest cover. Removal of secondary forests in favor of banana cultivation was common and only stopped when the European Community introduced import quota for bananas from Latin America. Forest policy has long ignored the existence and potential of secondary forests. Due to the alarming rate of deforestation in the 1980's, the government provided financial incentives for reforestation, while secondary forests were not considered. In many cases, young secondary forests were removed to establish forest plantations. In 1996, a new Forest Law was established providing a legal base for subsidies to promote secondary forest development. However, other aspects of the Law constitute a disincentive for landowners who consider secondary forests as a potential land use option. In view of this situation, secondary forests clearly require a different legal framework which allows owners more flexibility in the management and utilization of this forest resource.

INTRODUCTION

More than 25% of the national territory of Costa Rica have been set aside as conservation areas by way of an extensive system of national parks and other protected areas. Forests outside of protected areas, however, are generally privately owned and, in the past 50 years, have been greatly diminished by land clearing for agriculture and pasture establishment. Today, there are only about 200,000 hectares of primary forest left in Costa Rica. On the other hand, according to data published in 1991, more than 400,000 hectares of secondary forest have established themselves through natural regeneration on abandoned agricultural and pasture land (Centro

Científico Tropical, 1991). This means, that secondary forests currently constitute the most abundant forest resource in the country.

Research carried out by CATIE (Centro Agronómico Tropical de Investigación y Enseñanza) and the COSEFORMA project (Proyecto Cooperación en los Sectores Forestal y Maderero) has shown that secondary forests in Costa Rica have a positive influence on soil characteristics, contain a large proportion of commercial species, are fast growing and can be managed for wood production as well as production of other goods and services (e.g.: Finegan, 1992; Fedlmeier, 1996) . The existence of secondary forests, however, is not the result of a conscious choice by landowners in recognition of their economic and ecological potential. The development and management of secondary forests is to a large extent a result of land use policy of the past and present.

This paper analyzes the ways in which policy related to agriculture, livestock management and forestry has influenced the development and management of secondary forests in Costa Rica, especially in the Northern Region, and how forest policy needs to be modified to provide a stimulus for land owners to establish new secondary forest areas and manage existing ones.

INFLUENCE OF LAND USE POLICY ON SECONDARY FORESTS

Land colonization policy

During the first half of the century, land colonization policy, especially the granting of land titles strongly favored deforestation. In order to obtain land titles, by law, farmers had to demonstrate that the had "improved" the land, which generally implied the clearing of forests for establishing crops or pasture. Although this law no longer exists, maintaining the land "clean", i.e. removing forest succession on abandoned pastures or crop land, is still very common because it is considered as a mechanism for protection from squatters and thus assures land title. In addition, there is a cultural notion that the appearance of the first stages of secondary succession on farm land is evidence of abandonment and bad farm management. Secondary forests usually develop when farmers do not have the resources and labor available to maintain the land clear of invading vegetation.

Livestock policy

Livestock policy played a major role in deforestation as well as secondary forest establishment. Table 1 summarizes the main economic and policy aspects which led to large scale deforestation during the sixties and seventies, when cattle ranching was considered as a model for rural development and was strongly subsidized not only by the Costa Rican Government, but also by international development agencies.

Table 1. Development of the Livestock Sector between 1954 and 1979 and its impact on forests (based on Ortíz Valverde, 1996)

Policy aspects	Impact on forests
Favorable credit policy for the livestock sector • Low interest rates	• Destruction of 874,000 ha of forests, of which 57% were converted into pastures
• Increasing demand for beef in the USA led to increased meat exports	
• USA as main importer of Costa Rican beef (95%) • Stable and attractive meat prices in export markets	• Pasture land increased from 600,000 ha in 1954 to 1.7 million ha in 1974

When meat consumption patterns changed in the United States during the eighties, meat imports from Costa Rica dropped and resulted in a strong decline of the Livestock Sector (Table 2). The number of cattle was reduced and pastures were abandoned. In many cases, farmers had no alternative options for using the pastures and lacked the resources to maintain the land clear of invading vegetation. Without the influence of human activity, fire and grazing, secondary forest vegetation established itself due to the relative abundance of nearby seed sources (remnants of virgin and logged-over primary forests, single trees left on pastures). Although most of the existing secondary forests in various stages of development are small patches of less than 10 ha, their total estimated area represents a significant potential forest resource for the future.

Table 2. Decline of the Livestock Sector after 1979 and its impact on secondary forests (based on Ortíz Valverde, 1996)

Policy aspects	Impact on secondary forests
• Less credit available for the livestock sector • Real interest rates increased to 16.4% in 1990	• Significant reduction of the number of livestock
• Decreased demand for meat in the USA led to 13% decrease in meat exports	• Abandonment of 400,000 ha of pastures between 1984 and 1994
• 15% decrease in international meat prices between 1986 and 1994	• Secondary forests increased from 230,000 ha in 1984 to 425,000 ha in 1994

Forest policy

The first Forest Law in Costa Rica was created in 1969, regulating the use of natural forests and establishing the first incentive program for reforestation. Some of the main elements of this Law and its indirect implications for secondary forests are summarized in Table 3.

Table 3. Implications of the first Forest Law (No. 4465, 1969 – 1986)

Policy	Impact
· Elimination of natural forest was permitted for land colonization, agriculture and livestock raising · Restriction of use of private forests by the Forest Administration was possible · Income tax deduction mechanisms as an incentive for reforestation · Secondary forests did not qualify as forests	· Deforestation of large areas with low agricultural potential · Insecure land tenure of private forest land favored conversion of forests to other uses · Incentives only for plantations and for large companies whose primary objective was tax deduction = disincentive for primary and secondary forest

The alarming rate of deforestation, which reached levels of 60,000 ha per year during the 1980's prompted the Costa Rican Government to issue a Second Forest Law in 1986, with the objective of regulating logging in natural forests and of promoting reforestation through a strong incentive program. Table 4 presents relevant policy aspects of this Law and their impact on primary and secondary forest management.

One of the negative effects of this second Forest Law was the excessive bureaucratic requirements for the management of natural forests. In addition, illegal logging continued and natural forests were not managed in a sustainable way.

Table 4. Implications of the second Forest Law (No. 7174, 1986 – 1996)

Policy	Impact
• Logging in natural forests required management plans approved by the Forest Administration • Certificado de Abono Forestal (CAF) as a direct financial incentive for plantation establishment (approx. $ 600/ha) • In 1992: CAF for natural forest management (approx. $ 400/ha) with emphasis on harvesting activities; secondary forests were not considered	• Strong emphasis on plantations was detrimental to secondary forests - secondary forests were not considered in CAF program - Secondary forests were cut to establish plantations • Administrative requirements for cutting permits in natural forests and high cost of management plans favored illegal logging • Easy permits for cutting trees on pastures favored illegal conversion of forest into pasture and led to loss of seed sources for secondary forest development

In 1995, the Certificate for Forest Protection (CPB) was created as an incentive to conserve and protect forests without using them. Due to the existence of extensive areas of secondary forests in the dry zone of Guanacaste, the CPB was applied not only to logged primary forests but also to secondary forests, thus paving the way for the future consideration of secondary forests in the current Forest Law. This Law, which was created in 1996, sought to liberate plantation management while prohibiting land use changes on forested land and obliging forest managers to apply the national criteria and indicators for forest sustainability, that were developed from the baseline provided by the Forest Stewardship Council (FSC, 1996). Table 5 presents some of the important elements of this current Law and its implications for secondary forest development and management.

Table 5. Implications of the new Forest Law (No. 7575, 1996)

Policy	Impact
• Prohibition of land use changes in forests • Unclear and disputed definition of the term "forest": fragments of < 2 ha are not considered ecologically viable and are excluded from the definition • No mention or definition of secondary forests • Payment of environmental services of forests through a tax on gasoline. "Natural regeneration on bare lands" qualifies for CPB	• Protection of forests from land use changes implies devaluation of forest land due to use restrictions: - Once secondary forests reach the stage of development where they qualify as forests, they have to be maintained as forests forever - In order to intervene secondary forests (silvicultural treatments, harvesting), a costly management plan is required • Due to abundance of small forest fragments, their elimination means an important loss of seed sources for secondary forest development • Financial incentives are available for the development of new secondary forests, but not for the management of existing ones

Agricultural policy related to banana production

In the early nineties, bananas were the main export crop of Costa Rica and the number one foreign income earner. Subsequently, banana production was considered a national priority and agricultural policy strongly favored the expansion of areas under banana cultivation. In order to establish new banana plantations, primary as well as secondary forests in the Northern and Atlantic Regions were eliminated. On land destined for banana cultivation, forest patches of 50 ha and less were commonly cleared in order not to obstruct aerial fumigation of the plantations. In 1991, the Minister of Agriculture publicly justified this clearing of secondary forests by essentially declaring them of no value (La Nación, December 8, 1991). In 1993, the expansion of banana production stopped when the European Community established import quota for bananas from Latin America. By 1995, tourism had surpassed bananas as the main source of foreign income and the promotion of eco-tourism became a national priority.

CONCLUSIONS AND RECOMMENDATIONS

The development of more than 400,000 ha of secondary forests in the past 15-20 years is a indirect result of a decrease in demand for beef in the United States, lower prices for meat in export markets and subsequent changes in the credit and subsidy policy for the livestock sector in Costa Rica. It clearly demonstrates the long-term environmental impact that a strong dependence on a single market for export products can have on a country. Similarly, the example of banana production shows that land use policy in Costa Rica has often been short-sighted without consideration of the long-term negative effects on natural resources and the environment, especially on the existence of primary and secondary forests. Although the banana "boom" lasted only a few years, significant areas of forest have been irrevocably destroyed. Secondary forests always were and still are competing with other land use options, such as livestock raising, banana cultivation and plantation establishment. Policies in the past generally favored the latter options because they were considered more productive. This is in part due to the lack of knowledge about the potential of secondary forests to generate income while maintaining an ecologically stable environment in areas not appropriate for agriculture.

Secondary forests developed in spite of unfavorable forest policy and even today, when they are the most abundant forest resource in the country, policy makers are slow to recognize their productive potential. This is reflected in the current Forest Law which takes a first step towards the promotion of the development of new secondary forests but still does not provide the legal framework for managing them. The current Law makes no distinction between primary and secondary forests in terms of the legal requirements for their management. The existing legal framework, including criteria and indicators for sustainability, is not totally applicable to secondary forests. Primary forests are an existing, mature resource, where the first intervention is usually a harvesting operation. In this sense, secondary forests resemble plantations more than primary forests: both are new forest resources which develop on abandoned land; the only difference is the mode of establishment (planting versus natural regeneration). In both cases, the first interventions are silvicultural treatments to favor the growth of desirable trees.

The application of the legal restrictions developed for primary forests to secondary forests actually constitutes a major disincentive for landowners who are considering forestry as a land use option. In order to make secondary forests more attractive to land owners, forest policy has to be less restrictive and allow the same flexibility as for the management of plantations. A legal framework has to be established that takes into consideration the specific characteristics and dynamics of these forests, including criteria and indicators for sustainability. For the same reasons, management plans for secondary forests will have to be quite different from those for primary forests, especially in view of potentially different management systems (for example: monocyclic versus polycyclic). The establishment of criteria and indicators of sustainability may allow for the future application of the payment of environmental services to managed secondary forests which would constitute a further incentive for their owners.

In order to generate a sound technical base for the sustainable management of secondary forests, research in this area has to be intensified taking into account economic aspects. Furthermore, research efforts should also consider wood characteristics and potential uses of secondary forest species, including product development.

Finally, there is an urgent need to protect seed sources for the establishment of new secondary forests, either through restrictions on the harvesting of trees on pastures or through the modification of the legal definition of forests to protect small, fragmented forest patches from being eliminated.

REFERENCES

Centro Científico Tropical (CCT), World Resources Institute (WIR). 1991. La depreciación de los recursos naturales en Costa Rica y su relación con el sistema de cuentas nacionales. CCT, San José, Costa Rica; WIR Washington, D.C.

Fedlmeier, C. 1996. Desarrollo de bosques secundarios en zonas de pastoreo abandonadas en la Zona Norte de Costa Rica. Tesis de Doctorado University of Göttingen, Germany.

Finegan, B. 1992. El potencial de manejo de bosques húmedos secundarios neotropicales de las tierras bajas. Colección silvicultura y manejo de bosques naturales no. 5. Trad. por R. Luján. CATIE. Serie Técnica. Informe Técnico no. 188. 29 p.

Forest Stewardship Council (FSC). 1996. Principios y criterios para el manejo de bosques. Documento No. 1.2. FSC, Oaxaca, México

Ortíz Valverde, R. 1996. Bosque secundario por abandono de pastizales en la Región Huetar Norte de Costa Rica: análisis de algunos criterios económicos y ambientales. Masters Thesis, Universidad Nacional, Heredia, Costa Rica.

A PANTROPICAL PERSPECTIVE ON THE ECOLOGY THAT UNDERPINS MANAGEMENT OF TROPICAL SECONDARY RAIN FORESTS

T C Whitmore
Geography Department
Cambridge University Cambridge CB2 3EN England

ABSTRACT

Secondary forests develop on sites that have been completely cleared, and are quite distinct from logged or otherwise disturbed primary forests. Species composition and rate of secondary succession depends on the amount of site degradation that followed clearance. On the least degraded sites coppice shoots and seed stored in the soil are important components of the regrowing forest. Widespread natural, and now human, disturbances mean that secondary forests are very extensive across the tropics. They are valuable to rural people and, increasingly, as sources of commercial timber. The perpetuation of secondary forests requires repetition of the massive disturbances that create them. Tree species differ in their seedling shade tolerance from obligate light-demanders to extreme shade-tolerators. Strongly light-demanding species grow fast and have useful pale light timber. The establish on open sites. Within them is a subset of species, the pioneers, that require full light for both germination and establishment. Forest succession has 4 phases: herbs (Phase 1) are replaced at 1-3 years by short-lived pioneers (Phase 2). These are replaced at 10-15 years by other strong light-demanders, Phase 3, themselves replaced at 75-150 years by a self perpetuating Phase 4 canopy of shade-tolerants. In the neotropics Phase 3 species establish as a layer below Phase 2, and consist of both pioneers and other strong light-demanders. They are released as the Phase 2 canopy becomes moribund. Phase 3 forests are particularly extensive in America, which has numerous big pioneer species. The sharp distinction between Phases 2 and 3 has not been reported from Africa or Asia.

Monocyclic silviculture, clear-cutting in one cycle, is necessary to perpetuate secondary forests. A seed source must be retained and fruit dispersing animals assisted. Secondary forests have roles to play in timber production, hydrology, climate amelioration and biodiversity conservation. Landscape-scale planning is needed to maximise the goods and services they provide.

INTRODUCTION

This paper aims to set out a framework on tropical secondary rain forests, from a pantropical perspective: what is known and generally agreed, what is still controversial, and what appear to be topics that need investigation.

Tropical secondary forests have been much less studied than primary (climax) forests. Nevertheless, much has been written. No attempt is made to provide a full review. Coverage is representative rather than comprehensive, but should give access to the literature.
The discussion is confined to tropical rain forests. Tropical seasonal forests and forests of even drier climates (e.g. thorn forests) are not covered. There are important differences which Ewel (1977) summarized as patchy rather than continuous canopy regrowth, greater resilience (viz rate of recovery) but less resistance to environmental perturbations, and with regrowth from coppice more important than from seed.

SECONDARY AND PRIMARY FORESTS

Following Corlett (1994, 1995) the term ‘secondary forests’ is restricted to forests which have reoccupied a site after clearance. Forests resulting from regrowth after selective logging or other disturbance are excluded; in them part of the original forest survives.

Primary forests may be variously altered, but if the site is not completely cleared of trees they are different from secondary forests. They may be logged or may be depleted near settlements by progressive culling of useful plants. Disturbance may continue for a long time, as for example at Luquillo, Puerto Rico which, from European settlement to the 1940s, suffered agroforestry, selective logging, charcoal production and silvicultural treatment (García-Montiel & Scatena 1994), as well as hurricanes.

Sometimes forests are simply cleared and secondary forest allowed to grow. Alternatively, burning may follow clearance, or burning then growth of one or more crops or of pasture. This sequence progressively degrades the site by deterioration of the soil in various ways: by compaction; loss of organic matter and consequent loss of cation exchange capacity; and loss of nutrient cations and consequent acidification and solubilisation of aluminium which then becomes toxic to many plants.

The rate of forest recovery decreases as degradation increases. The floristic composition of the early stages of a secondary forest also depends on the amount of site degradation, a fact well known to skilled swidden farmers. This is because coppice shoot regrowth from cut stumps and from roots diminishes as disturbance increases. So does the amount of seed in the soil; for example Ewel *et al.* (1981) found a reduction by burning from 8000 to 3000 seeds and a reduction from 67 to 37 species m^{-2}. Thus, the secondary forest becomes increasingly reliant on seeds transported in and composed of species that can withstand degraded soils. In the absence of seed sources of primary species to replace it secondary forest succession may be impoverished or totally arrested, examples will be given below. This regressive sequence has been repeatedly documented, e.g. for French Guiana (de Foresta 1983, Maury-Lechon 1982), Kalimantan (Kartinawata *et al.* 1980), Malaya (Wyatt-Smith 1955), and Venezuelan caatinga (Uhl *et al.* 1982). The least site degradation occurs where the forest is simply clear cut and then allowed to regenerate. In this case the regrowth is likely to have a strong coppice component and therefore considerable floristic similarity to the previous forest. An example is the Bajo Calima forest, Colombia, felled for pulp (Faber-Langendoen 1992).

Logged primary forest is not the same as secondary forest (*pace* Brown & Lugo 1990). It is more complex structurally, floristically and spatially. It consists of patches of primary forest, a few untouched but most heterogeneously thinned by the felling and damaging of trees, and with the forest floor variously intact. These patches are interdigitated with fingers of secondary forest grown up along roads and skid tracks where the soil was bared. The patches retain species of the primary forest, from seedling size upwards, and its litter layer, superficial roots, mycorrhiza and soil seed bank.

Logged and relogged primary forests are becoming very extensive, especially in Asia. Their silviculture, harvesting and management present different challenges from primary forest itself, and should now become a focus of research. In America and Central Africa by contrast the timber industry is still focused on primary forest.

Primary forests, both pristine and logged, contain a mixture of numerous climax species (see below) which have a wide range of kinds of timber and growth rates. For these forests polycyclic silviculture is the most appropriate. The ecologically very different secondary forests are best managed by a monocyclic system, as will be described below.

Thus it cannot be stated too strongly that in ecology and appropriate management primary and secondary rain forests are very different.

OCCURRENCE OF SECONDARY RAIN FORESTS

Massive natural disturbances to tropical moist forests, including rain forests, are now known to be very extensive (Whitmore & Burslem 1998). The disturbance factors include fire, wind and human activity and may either damage or destroy the primary forest. In the latter case secondary forests develop. Modern human activity has created huge areas of secondary forests so the light-demanding tree species which they contain are even more widespread and abundant than originally when they were confined to naturally disturbed sites. One example is `*Adinandra* belukar' (Holttum 1954), the secondary forest dominated by *Adinandra dumosa* and *Ploiarium* *alternifolium* that today covers hundreds of km^2 of the southern tip of the Malay peninsula, a result of site degradation 100-80 years ago by farming for gambir (*Uncaria gambir*) and then pineapples. The failure of primary dipterocarp rain forest to re-establish after so long is likely to be due to the absence of seed sources.

ECONOMIC IMPORTANCE OF SECONDARY RAIN FORESTS

Secondary forests are starting to be valued for their timber, Costa Rica being a prime example, and this can only increase as primary forests are progressively exhausted. Secondary forest tree species mostly have soft leaves with few chemical defences, and are attractive to browsing animals). Local people have for a long time valued secondary forests as sources of animals for hunting and for minor forest products. Swidden farmers often enhance the usefulness of `bush fallow' by planting useful species or species that attract animals. Secondary forests have a role to play in biodiversity conservation as is elaborated later (section 9).

FOREST SUCCESSION

In simple terms forest succession is very well known. The trees which colonise open ground are light-demanders. They have a high light requirement for establishment and growth and do not regenerate below a closed canopy. Beneath these trees shade-tolerant or climax species establish and, as the colonisers die creating canopy gaps, these grow up to replace them. Thus there is a floristic succession, back to a forest of shade-tolerants that can regenerate *in situ* in shade so form a self-perpetuating climax forest. At the last stages of this succession a few of the colonizing light-demanders may remain as scattered big old trees in a matrix of climax species. Examples are *Araucaria cunninghamii* (hoop pine) in Queensland and *Swietenia macrophylla* (mahogany) and *Ceiba pentandra* (kapok) in America.

Secondary succession is the term used to describe regrowth on a site previously occupied by vegetation. Primary succession by contrast occurs on new surfaces such as volcanic deposits, river banks and land slips. It also involves light-demanding tree species, perhaps including or consisting of a subset adapted to raw soil, but arriving only from off the site as there is no soil seed bank. There is no contribution by regrowth of coppice shoots. The most extensive primary successional rain forests are probably those of Amazonian Peru developing on fresh riverine alluvium (Salo *et al.* 1986). In many respects, including management considerations, primary and secondary successions have no differences.

Persistence of secondary forests depends on recurrence of the massive disturbances that create them. This has implications for management which will be discussed below (section 8).

In the course of succession there is a rapid increase in biomass, which slows down at about 15-20 years age (Brown & Lugo 1990). Leaf biomass and leaf area index are quickly restored in c. 5 years, as are twig, branch and fine root biomass (Brown & Lugo 1990). Nutrients are most concentrated in these parts, hence during this period above ground biomass nutrients return close to their former levels (there are few hard data, but see e.g. Harcombe 1977, Williams-Linera 1983, Whitmore 1998, Fig.8.3) and carbon sequestration is rapid. Later, bole wood is the main addition, and roots continue to grow, so carbon sequestration continues, but because boles have low nutrient concentrations, nutrient accumulation slows down.

Leaf life of pioneer species is typically short and leaves are soft and without protective chemicals so they decay quickly. Thus there is rapid nutrient cycling within secondary forest ecosystems.

ECOLOGICAL SPECIES GROUPS

It is commonplace that tree species differ in their light requirement for regeneration, i.e. in their seedling shade tolerance. There is a spectrum of species, well expressed in rich tropical floras, from obligate light-demanding species to extremely shade-tolerant ones. This is exemplified by the 12 common big tree species in the lowland rain forest of Kolombangara in the Solomon Islands, Table 1. Successful regeneration occurs in big gap, small gap and no gap along this species spectrum. The species that successfully establish on open sites, viz those that comprise secondary forest, are light-demanders. Later successional climax species variously shade tolerant. Light-demanders have a syndrome of characters that include copious small seeds capable of dormancy, well-dispersed by animals or wind, rapid growth, and low density, pale, non-durable timber. By contrast, shade-tolerant species have fewer, larger seeds, often with no capacity for dormancy, slow growth, and high density, dark, commonly siliceous but durable timber. There are exceptions to these broad generalisations. An important one is that some fast growing light-demanders have heavy, dark, durable timber, e.g. *Casuarina* of Asia and *Milicia* spp. (iroko) of Africa.

One group of extreme light-demanders can be recognised which differs qualitatively in requiring full light for both seed germination and seedling establishment (Swaine & Whitmore 1988). These species are therefore unable to regenerate below a canopy, so cannot perpetuate *in situ*. All other characters along the spectrum from strong light-demanders to strong shade-tolerators are quantitative, and vary continuously. The subgroup, distinguished by possession of these two different characteristics can be called pioneers and contrasted with the rest, which can be called climax species. The latter group is much more heterogeneous and includes all degrees of shade tolerance.

Table 1 Regeneration behaviour of the 12 common big tree species, Kolombangara, Solomon Islands (Whitmore 1998)

Group	Species	Conditions to establish	Conditions to grow up
Climax	*Dillenia salomonensis*	High forest	High forest
	Maranthes corymbosa	High forest	High forest
	Parinari salomonensis	High forest	High forest
	Schizomeria serrata	High forest	High forest
	Calophyllum peekelii	High forest/ small gaps	High forest/ small gaps
	Calophyllum neoebudicum	High forest	High forest/ gaps
	Pometia pinnata	High/disturbed forest	High forest/ ? small gaps
	Elaeocarpus angustifolius	High forest	Gaps
	Campnosperma brevipetiolatum	High forest/ gaps	Gaps
	Terminalia calamansanai	High forest/ gaps	Gaps
Pioneer	*Endospermum medullosum*	Mostly gaps	Gaps
	Gmelina moluccana	Mostly gaps	Gaps

Pioneer species vary in the age and hence the size that they reach and can arbitrarily be divided into three groups, small, medium and large, Table 2. In all tropical floras pioneers are a minority of species and many families have no pioneer species. They have naturally wide geographical ranges, least so in Asia where their dispersal, although efficient, has been hampered by sea barriers.

Forests of the larger pioneers are commercially attractive. Asia again differs from Africa and America. It has fewer species and fewer forests of these larger pioneers, see Table 2. In Central Africa *Aucoumea klaineana* (okoume) forms extensive secondary forests grown up on abandoned farms (Richards 1996) which are currently focus of a major timber industry. In West Africa *Terminalia ivorensis* and *T.superba* are also sometimes gregarious (M.D.Swaine *pers. comm.*).

America has extensive secondary forests of a range of species, identified by * on Table 2 and occurring singly or in small mixtures. They occur either on land clearcut but not farmed (for example in Costa Rica), or on abandoned pasture or swidden fields, or as a result of silvicultural experiments (Curua Una, Brazil, Palcazu, Peru, see Finegan 1992).

Asia does not have extensive forests of these larger, commercially useful pioneers, except *Eucalyptus deglupta* on riverine alluvium in eastern Malesia, and *Paraserianthes falcataria* and *Octomeles sumatrana* on volcanic effluvia in Papua (Whitmore 1984).

Forests of introduced, naturalised light-demanders occur in Asia, namely scattered across Indonesia the small pioneer *Piper aduncum*, and *Paraserianthes falcataria* in parts of Malaysia and which in Singapore forms the main secondary forest of mesic sites mixed with the other exotics *Manihot glaziovii* and *Spathodea campanulata* (Corlett 1988).

Pioneers are a distinctive subset of light-demanders in their obligate requirement of full light for both germination and seedling establishment. To foresters other characters of light-demanding species are more important. Modern markets favour low density, pale timber. Rapid growth and quick response to canopy opening and natural occurrence in pure stands without succumbing to pests and diseases are all useful in silviculture, as are the small, copious, storable seeds that most possess. So, to foresters the whole group of light-demanding big trees is of interest. Examples of climax species of this group are listed in Table 3. These usually germinate and establish below a canopy, but can and sometimes do so in the open. Pure stands of Cavanillesia platanifolia and Swietenia macrophylla regrown on old clearings have been reported, the latter from eastern Panama and adjoining Colombia (Budowski 1970).

Table 2 Some common rain forest pioneer tree species (Whitmore 1998, Table 7.4)

Stature	Neotropics	Africa	Eastern tropics
Small, 2-7.9 m tall	*Cordia nitida* *Ocotea atirrensis* some *Piper* *Vernonia patens* *Vismia baccifera*	*Ficus capensis* *Leea guineensis* *Phyllanthus muellerianus* *Rauvolfia vomitoria*	*Commersonia bartramia* *Glochidion* spp. *Macaranga*, » 100 spp. some *Mallotus* spp. some *Melastoma* spp. *Phyllanthus* spp. *Pipturus* spp. *Trichospermum*, 8 spp.
Medium, 8-29 m tall	*Trema* *Alchornea triplinervia* * *Cecropia*, c. 100 spp. *Cordia* spp. * *Jacaranda copaia* *Muntingia calabura* * *Ochroma lagopus* * *Schefflera (Didymopanax) morototoni*	*Trema* *Anthocleista nobilis* *Psydrax arnoldiana* *Cleistopholis patens* *Macaranga* *Maesopsis eminii* *Musanga cecropioides* few *Spathodea campanulata* *Vernonia conferta* *Vismia guineensis*	*Trema* *Acacia aulacocarpa* *Acacia mangium* *Adinandra dumosa* *Alphitonia petrei* *Anthocephalus*, 2 spp. *Macaranga* spp. *Octomeles sumatrana* *Ploiarium alternifolium*
Large, >30 m tall	*Ceiba pentandra* *Cedrelinga catenaeformis* * *Goupia glabra* * *Laetia procera* * *Vochysia ferruginea* * *Vochysia hondurensis* *Vochysia maxima*	*Ceiba pentandra* *Lophira alata* *Milicia excelsa* *Milicia regia* *Nauclea diderrichii* *Ricinodendron heudelotii* *Terminalia ivorensis* *Terminalia superba*	*Eucalyptus deglupta* *Paraserianthes falcataria*

* these species form extensive forests

FLORISTICS OF FOREST SUCCESSION

Four phases of succession can be identified (Finegan 1996). The first phase is a dense growth of herbs, shrubs and climbers that rapidly occupies the site. This is replaced by Phase 2, fast growing small pioneers which quickly emerge and form a continuous woody canopy in less than three years and under whose shade the species of Phase 1 mostly disappear. The even-aged population of small pioneers lives only for 10-30 years. It is replaced by the third phase of succession, big light-demanders. Some of these are larger pioneers that established simultaneously with the small pioneers in full light, others are strongly light-demanding climax species and came in during the first three years. Many observations in the neotropics show that the strong light-demanders of Phase 3 have some shade tolerance and form a monolayer below the obligately heliophile, faster growing, Phase 2 small pioneers (which themselves become moribund, grow slowly and soon die if overtopped). As the small pioneers die off and their canopy opens these Phase 3 species are released and grow fast. Their population is also approximately even-aged. They live perhaps 75-150 years, though there are few hard data. For forestry purposes Phase 3 species are one single group, and indeed apart from their establishment ecology the two component guilds cannot be told apart.

Table 3 Strongly light-demanding climax trees that reach timber size

Neotropics	Africa	Eastern tropics
Cavanillesia	*Entandrophragma*	*Anisoptera thurifera*
Cedrela	*Triplochiton*	*Artocarpus*
Cordia		*Campnosperma*
Simarouba amara		*Dyera*
Swietenia		*Elaeocarpus angustifolius*
		Endospermum
		Shorea red meranti group
		Terminalia calamansanai

Phase 4 climax species establish progressively below Phases 2 and 3. Small gaps begin to form as Phase 3 trees dies, and Phase 4 juveniles are released and grow to full height, so that eventually a shifting mosaic steady state forest, reproducing by gap-phase replacement, is re-established. The degree to which this has the composition of the original forest depends on the presence of seed trees within dispersal range, and the presence of dispersers. In Hongkong and Singapore it has been found that the new climax forests contain only the subset of Phase 4 species with small seeds, because dispersers of big seeds (e.g. birds with a large gape) have become locally extinct. In Singapore even after 30-100 years only a small fraction of the primary forest trees have spread out from relict patches into the regrowth forest that now surrounds them (Corlett 1991, Corlett & Turner 1997). Krakatau island, over a century since its eruption, and fifty years since canopy closure, still has a species-poor forest of mainly pioneer species (Whittaker et al. 1989).

The later stages of succession have been less fully studied than the early ones. It is not known to what extent the floristically different early successional stages of degraded sites (see above) converge and become similar in later years of the succession. The growth rate in response to a canopy gap may change as a seedling grows in size. For example, the rank order of response of 12 species on Kolombangara as seedlings (Table 1) has altered by the time they are 5-10 cm diameter and continues to change to 70 cm diameter. Change in successional status with increasing size has also been shown in Queensland (Thompson et al. 1988). Such changes make it impossible to predict the later stages of succession from growth measurements in the early stages.

The development of a distinct monolayer of Phase 3 light-demanders below small, short-lived Phase 2 pioneers has not been observed outside the neotropics. In Asia there are few larger pioneers (Table 2), though numerous strongly light-demanding climax species do occur (Table 3). Africa, however, has numerous larger pioneers (Table 2). The existence of a subset amongst pioneers with slower height growth and greater shade tolerance is interesting, and it would be valuable to confirm its reality by detailed autecological and ecophysiological studies. It would be very curious if the guild was restricted to the neotropics. Again, further study is clearly needed.

The canopy top of Phases 2 and 3 secondary forests are smooth without emergents and grey on aerial imagery, so secondary forests are easily mapped. They have a higher proportion of deciduous species. Phase 4 primary or climax forests have a darker, billowing canopy, often with emergents. There is another contrast: climax canopies are usually species-rich and secondary canopies are species-poor, consisting in any one place of just one or a few species of what is everywhere a species-poor secondary tree flora. It is not yet known what causes the species-poverty of secondary forest canopies. It could be selective germination from the soil seed bank, or selective establishment on the particular microsites occurring at a given location (e.g. Uhl et al. 1981). It could reflect spatial heterogeneity within the soil seed bank (about which little is known), or it could reflect the vagaries of dispersal to the site by which ever species within range happened to be fruiting at the appropriate time.

Finally, it should be noted that this model of succession does not apply in heath forest or upper montane rain forest, both of which formations lack pioneer tree species. On extremely degraded sites in Singapore and southern Malaya *Adinandra belukar* develops (see above), which lacks the normal pioneer species. It has physiognomic similarities with heath forest, which also occurs on poor soils (Turner & Tan 1991). *Adinandra* and the other trees that it consists of are the natural climax species of poor thin soils (Corlett 1995).

Arrested succession

Vine tangles can delay forest succession. They are common across the Eastern tropics but have not been reported from elsewhere, except in Suriname where a climber carpet was noted twelve years after harvesting of 200m^3/ha of timber (de Graaf 1986, Fig. 2.11). They are a serious problem for the forester. Trees establish below the carpets of woody and wiry climbers that sometimes quickly cover open spaces and eventually carry up the carpet and break through it. The trees often have kinks in their trunks that reveal this history, for example the former Kemehang forest of Peninsular Malaysia (Whitmore 1998, Fig.7.42). What leads to the development of climber carpets remains unknown. In the Solomon Islands *Merremia* spp. (Convolvulaceae) smother logging areas, but not forest opened by cyclones. Sabah has some forests infested by *Merremia* and *Mezonevron* (Caesalpinaceae) but others without them. Some pioneer trees outgrow climbers by shedding branches or leaves or, in the case of *Cecropia* and some *Macaranga*, by harbouring symbiotic ants that nip off the tips of vine shoots as these attempt to climb on board (Ewel 1983).

Succession can also be arrested by fern brakes. For example *Dicranopteris* in Malesia can, on hot, dry, degraded soils, form inpenetrable tangles. One such brake studied at Kepong was not replaced by trees for 13 years (Kochummen & Ng 1977). *Chromolaena odorata*, a sprawling semi-woody American shrub is still spreading across Africa and Asia. It forms a prolonged Phase 1 successional canopy. Farmers like it because it concentrates nutrients (Baxter 1995) and is easily cut and burned. *Lantana camara* is another neotropical shrub that has become an aggressive weed in many parts of the tropics, notably in Queensland. In the slightly seasonal and monsoon tropics of continental southeast Asia a secondary forest of sprawling bamboos may develop after forest clearance. In some places trees are unable to grow through these thickets, which therefore persist indefinitely. Huge areas of bamboo thicket were created in the Vietnam War by the American aerial spraying of the herbicide Agent Orange.

SILVICULTURE OF SECONDARY FOREST

- Monocyclic silviculture, clear cutting of all harvestable trees in one operation, is necessary in order to recreate the open conditions in which secondary forests establish. There are a number of simple rules that should be followed.

- Minimise damage to the forest floor to reduce erosion and to maintain water infiltration capacity, the nutrient-capturing superficial root mat and the soil seed bank.

- Minimise soil compaction. Trees do not encounter compact soil in nature and many cannot cope with it. Growth is prevented or reduced.

- Most light-demanders have timber that decays rapidly and may be quickly stained by fungi. Remove and process the timber quickly.

- Ensure a seed source remains. This is especially important where the forest occurs as small parcels in agricultural land as the nearest seed sources may be beyond dispersal distance.

- Most species have fruits adapted to generalist frugivores, for example small and rich in sugars (Snow 1981) so show some flexibility in dispersal between birds, bats and other mammals (e.g. civets). But dispersers are needed. They are aided by provision of perch trees (Guevara et al. 1986), and many will not cross open ground but require a continuous woody canopy (as has been shown well near Manaus, Bierregaard & Stouffer 1997).

THE FUTURE

Secondary forests are set to increase. They are an increasing fraction of the anthropogenic landscapes that are progessively replacing primary rain forests. This has reached an advanced stage in Costa Rica, for example.

Acceptance of their timbers will increase. Technology to utilise small pieces of wood (using modern glues and finger-jointing) is gaining acceptance, so small trees are becoming increasingly utilisable. Before long Phase 2 successional forests may become commercially attractive. Continuing removal of high volumes of timber on relatively short cutting cycles makes ecosystem nutrient depletion more likely than in primary forests where a lower fraction is harvested at longer intervals. Nutrient depletion depends on local soil and bedrock conditions and aerial inputs so is site-specific. Data will need to be collected, and specific nutrients may need to be added. There is, to coin a phrase, no such thing as a `free lunch'.

Secondary forests have a role to play in provision of forest services, namely the hydrological cycle, the carbon cycle and climate amelioration. They play a role in biodiversity (gene pool, species and ecosystem) conservation that only slightly overlaps that of primary forests. They are less species-rich than primary forests and more of their tree species have wide geographical ranges. They consist of a set of plant and animal species that is conserved by the periodic massive destruction of the forest, followed by its regrowth. At landscape scale these seral (Phase 2 and 3) forests contain one part of a region's biodiversity whose persistence necessitates periodic mayhem. Monocyclic silviculture provides this. By contrast, to maintain the climax (Phase 4) forests polycyclic (selection) silvicultural systems that mimic single or small-group treefall, and like them lead to gap-phase replacement, are the appropriate tool for maintaining biodiversity. For example, heavy human ecosystem disturbance is needed to perpetuate the Swietenia and Aucoumea forests of the Amazon and Central Africa respectively, in contrast to the much gentler intervention needed to maintain the biodiversity of most of the world's tropical rain forests. To conflate the two kinds of forests as Rice *et al.* (1997) recently did is a mistake.

Landscape-scale planning is needed if both seral and climax forests are to make their maximal contribution to provision of forest goods and services, including biodiversity conservation. Contiguity of forest patches or their linking by corridors seems to be useful (Laurance & Bierregaard 1997). Land use planning, further data on dispersal and dispersers, research on climber biology, on nutrient budgets, and further probing of the autecology of different Phase 3 light-demanding tree species seem to be the salient points for further investigation.

ACKNOWLEDGEMENTS

Warm thanks are due to the organisers of the Symposium for enabling my participation and to B.Finegan for many discussions on the biology of light demanding tree species.

REFERENCES

Baxter, J. (1995). Chromolaena odorata, weed for the killing or shrub for the tilling? Agroforestry Today 7, 6-8.

Bierregaard, R.O.Jr. & Stouffer, P.C. (1997). Understory birds and dynamic habitat mosaics in Amazonian rain forests. In Laurance, W.F. & Bierregaard, R.O.Jr. (eds.) (1997). Tropical forest remnants. University of Chicago Press, Chicago.

Brown, S. & Lugo, A.E. (1990). Tropical secondary forests. Journal of Tropical Ecology 6, 1-32.

Budowski, G. (1970). The distinction between old secondary and climax species in tropical Central American lowland forests. Tropical Ecology 11, 44-8.

Corlett, R.T. (1988). The naturalized flora of Singapore. Journal of Biogeography 15, 657-63.

Corlett, R.T. (1991). Plant succession on degraded land in Singapore. Journal of Tropical Forest Science 4, 151-61.

Corlett, R.T. (1994). What is secondary forest? Journal of Tropical Ecology 10, 445-7.

Corlett, R.T. (1995). Tropical secondary forests. Progress in Physical Geography 9, 159-72.

Corlett, R.T. & Turner, I.M. (1997). Long-term survival in tropical forest remnants in Singapore and Hong Kong. In Laurance, W.F., Bierregaard, R.O. Jr. (eds.) Tropical forest remnants. University of Chicago Press, Chicago.

de Foresta, H. (1983). Hétérogénéité de la végétation pionnière en forêt tropicale humide: exemple d'une coupe papetière en forêt guyanaise. Acta Oecologica 4, 221-35.

de Graaf, N.R. (1986). A silvicultural system for natural regeneration of tropical rain forest in Suriname. Agricultural University, Wageningen.

Ewel, J. (1977). Differences between wet and dry successional tropical ecosystems. Geo-Eco-Trop 1, 103-17.

Ewel, J. (1983). Succession. In Golley, F.B. (ed.) Tropical rain forest ecosystems. A, Structure and function. Elsevier, Amsterdam.

Ewel, J., Berish, C., Brown, B., Price, N. & Raich, J. (1981). Slash and burn impacts on a Costa Rican wet forest site. Ecology 62(3), 816-29.

Faber-Langendoen, D. (1992). Ecological constraints on rain forest management at Bajo Calima, western Colombia. Forest Ecology and Management 53, 213-44.

Finegan, B. (1992). The management potential of neotropical secondary lowland rain forest. Forest Ecology & Management 47, 295-321.

Finegan, B. (1996). Pattern and process in neotropical secondary rain forests: the first hundred years of succession. Trends in Ecology and Evolution 11, 119-24.

García-Montiel, D.C. & Scatena, F.N. (1994). The effect of human activity on the structure and composition of a tropical forest in Puerto Rico. Forest Ecology and Management 63, 57-78.

Guevara, S., Purata, S.E. & van der Maarel, E. (1986). The role of remnant forest trees in tropical secondary succession. Vegetatio 66, 77-84.

Harcombe, P.A. (1977). The influence of fertilization on some aspects of succession in a humid tropical forest. Ecology 58, 1375-83.

Holttum, R.E. (1954). Adinandra belukar. Malayan Journal of Tropical Geography 3, 27-32.

Kartinawata, K., Riswan, S. & Soedjito, H. (1980). The floristic change after disturbance in lowland dipterocarp forest in East Kalimantan, Indonesia. Tropical Ecology and Development, 47-54.

Kochummen, K.M. & Ng, F.S.P. (1977). Natural plant succession after farming at Kepong. Malaysian Forester 40, 61-78.

Laurance, W.F. & Bierregaard, R.O.Jr. (eds.) (1997). Tropical forest remnants. University of Chicago Press, Chicago.

Maury-Lechon, G. (1982). Régénération forestière en Guyane Française: recrû sur 25 ha de coupe papetière en forêt dense humide (Arbocel). Revue Bois et Forêts des Tropiques. 197(3), 3-21.

Rice, R.E., Gullison, R.E. & Reid, J.W. (1997). Can sustainable management save tropical forests? Scientific American April 1997, 34-9.

Richards, P.W. (1996). The tropical rain forest. 2nd edn. Cambridge University Press, Cambridge.

Salo, J., Kalliola, R., Häkkinen, I., Mäkinen, Y., Niemalä, P., Puhakka, M. & Coley, P.D. (1986). River dynamics and the diversity of Amazon lowland forest. Nature 322, 254-8.

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

Swaine, M.D. & Whitmore, T.C. (1988). On the definition of ecological species groups in tropical rain forests. Vegetatio 75, 81-6.

Thompson, W.A., Stocker, G.C. & Kriedemann, P.E. (1988). Growth and photosynthetic response to light and nutrients of Flindersia brayleyana F. Muell., a rain forest tree with broad tolerance to sun and shade. Australian Journal of Plant Physiology 15, 299-315.

Turner, I.M. & Tan, H.T.W. (1991). Habitat-related variation in tree leaf form in four tropical forest types on Pulau Ubin, Singapore. Journal of Vegetation Science 2, 691-8.

Uhl, C., Clark, K., Clark, H. & Murphy, P. (1981). Early plant succession after cutting and burning in the upper Rio Negro region of the Amazon basin. Journal of Ecology 69, 631-649.

Uhl, C., Jordan, C., Clark, K., Clark, H. & Herrera, R. (1982). Ecosystem recovery in Amazon caatinga forest after cutting and burning, and bulldozer clearing treatments. Oikos 38, 313-20.

Whitmore, T.C. (1984). Tropical rain forests of the Far East. 2nd ed. Clarendon, Oxford.

Whitmore, T.C. (1998). An introduction to tropical rain forests. 2nd ed. Clarendon, Oxford.

Whitmore, T.C. & Burslem D.F.R.P. (1998). Major disturbances in tropical rain forests. In Newbery, D.M., Prins, H.H.T. & Brown, N.D. (eds.) Dynamics of tropical communities. Blackwell Science, Oxford.

Whittaker, R.J., Bush, M.B. & Richards, K. (1989). Plant recolonisation and vegetation succession on the Krakatau islands, Indonesia. Ecological Monographs 59, 59-123.

Williams-Linera, G. (1983). Biomass and nutrient content in two successional stages of tropical wet forest in Uxpanapa, Mexico. Biotropica 15, 275-84.

Wyatt-Smith, J. 1955. Changes in composition in early natural plant succession. Malayan Forester 18, 44-9.

FOREST DEVELOPMENT AS A BASIS FOR MANAGEMENT; TREE ARCHITECTURE AND TREE TEMPERAMENTS

H. F. M. Vester
Tropenbos-Colombia. A.A. 036062, Bogotá, Colombia

ABSTRACT

This paper gives a description of the natural forest development in terms of tree development as observed in tropical rain forest after slash and burn agriculture and proposes this development as a principle for forest management. Different phases of forest development are characterized, both for their natural and architectural characteristics as for their potential in providing products for human consumption, directly or indirectly. Because of natural changes in species composition during forest development, management of secondary forest should result in a changing composition of forest products. To be able to manage the developing forest with its changing composition and thus product characteristics, knowledge on the life history and temperament of trees is necessary. In this paper tree architecture is used to describe life history, and temperaments of trees, in a holistic approach, because tree form is the result of the many influences and reactions during the life of a tree. Both experimental and additional basic research on the relation between architecture and forest development are needed to enhance the possibilities of establishing wise forest management.

INTRODUCTION

The area of primary forests is dramatically decreasing (Myers, 1988), and together with it a great number of species is in danger of extinction, mainly due to habitat destruction (Wilson, 1992). In order to prevent greater loss of species, the use of secondary forests is proposed as an alternative to the use of primary forests (e.g. Lammerts van Bueren & Duivenvoorden, 1996). This policy leads easily to large scale monocyclic wood harvesting operations (Whitmore, this volume) and does not consider the fact that natural early forest development phases are usually of small scale and distributed in a mosaic of older development phases in the tropical rainforest biome (Oldeman, 1990). Maintenance of large areas of secondary forest in early stages of forest development for the production of cheap timber must have implications for the succession and evolution in the biome. One of the most obvious results is the reduction in species richness (Wilson, 1992) but also unexpected effects can be awaited e.g. formation of new species within groups of pioneers (Gómez Pompa, 1971), possibly complicating weed control. Moreover, nutrient stocks, and species richness in the ecosystem are drastically reduced in secondary forest compared to mature forests (Jordan, 1989). Therefore, secondary forests should be treated as damages in ecosystems and not as timber mines.

In this paper, secondary forests are treated as forests in a process of recovery, developing after a major impact, such as clearing for agriculture. This leads to the following question: "How can we use secondary forests permitting the recovery process to proceed ?" This is probably the greatest challenge for mankind, because land-use and management are characterized by conserving certain developmental or successional phases because they provide certain products. Even management objectives for natural vegetation are directed to conservation of the present state, usually not to conservation of natural dynamics.

The objective of this paper is to give an architectural description of the natural process of forest development after slash and burn agriculture as a basis for management of this development. This is a point of departure. I will not prove nor discuss if mimicking the natural system (Uhl et al., 1990; Gómez Pompa, 1991; Del Amo R., 1991; Galindo Leal & Bunnell, 1995) is the best way to come to sustainable management. Evolution itself is the proof that life changes at every level of organization according to its own rules, maintaining the earth covered with life in changing forms for millions of years.

First, I will outline the regularities in forest development at a time scale of about 40 years. These regularities are fit into a model which is the result of seven years of research in the Colombian Amazon, observing permanent plots in a chrono-sequence, and studying the autoecology of the most important species growing in the secondary forest (Vester, 1997; Vester, unpubl.). The model confirms the theory of forest dynamics outlined by Oldeman (1990) and follows this author's terminology.

Secondly, I will derive from the forest development model different species roles. These roles are expressed in the relation of the life history of the species (in terms of tree architecture) with the developing forest. Species fitting these roles are both part of the regenerating forest and potentially producers of products for human use. Each species is present during a certain period in the recovery of the forest. The products it produces can be available during part of its life cycle, or at its death. Many species do not provide products that are directly useful for humans or produce benefits only after some length of time, during which a mono-culture of this species would be useless to humans.

In general terms one can say that species with the same role can replace each other, and that at any moment species with different roles are present together. Here is the key to manipulation of the composition. In theory one could replace a species with a certain role and undesired characteristics by a species with the same role but useful characteristics. One could even reconstruct a forest based on roles, provided that all included roles form a chronological sequence similar to natural succession in a given area.

However, any level of organization in nature follows its own rules, which means that the rules of trees cannot just be summed up to form the rules of a forest, like a "Frankenstein" monster.

The vegetation and its regeneration in one site, have been formed during many ages, in an accumulation of different elements, some very old, some more recent. Thus replacement of a forest ecosystem by a complete set of new species though similar roles would be a monster out of control. It is impossible to include every aspect of tree interaction in a description of a species role.

The temperament of a tree is a concept that helps to order part of the knowledge about tree behavior and interactions. My focus on tree temperament is based on architectural development. I will explain the role of tree architecture in tree temperament, rather than give a recipe for identifying temperaments.

Forest development after slash and burn agriculture.

Vester (1997; Vester & Cleef, 1998) described the development of secondary forest near Araracuara in the western Amazon region (0°37′ S and 72°27′W up to an age of 35 years. These descriptions are based on seven forest transects with profiles, five of which (with a surface of 50 x 10 m) were repeatedly assessed. Between 1990 -1991 (Vester & Saldarriaga, 1993; Vester & Cleef, 1998) a first description took place, between 1993 and 1994 a second (Vester, 1997), and in 1997 a third (Vester, unpublished). Description of these transects included: Dbh, tree position, total height, height to the first living branch, height to the first fork, height of the crown periphery, crown projection, and a profile of the tree showing its architectural features, i.e. architectural model (cf. Hallé et al, 1978) and reiteration pattern (cf Oldeman, 1974a). The transects were all selected in secondary forests on the lower terrace of the Caquetá river, described by Duivenvoorden & Lips (1993) as a nearly flat, poorly dissected terrace with typic paleudults (haplic alisols). The well drained paleudults on these terraces are mostly used for slash and burn agriculture.

Many characteristic species and genera (e.g. *Cecropia spp., Vismia japurensis, Vismia macrophylla, Jacaranda copaia, Miconia* spp., *Inga* spp., *Goupia glabra*) in the transects were also important in secondary forests reported from other sites in western Amazonia (Saldarriaga, 1994; Walschburger & von Hildenbrand, 1991), so that, taking into account that the architectural development is species specific and often generically similar (Hallé *et al.*, 1978), the general features of forest development derived from these transects can be extrapolated to a larger area in western Amazonia. Saldarriaga (1994) argues that species composition is probably an incidental characteristic of secondary forests, because he found that species composition in secondary forests of the same age can be very different. However, the examples he mentions are of mature forest species (i.e. *Protium* sp. *Caryocar gracile* Wittm. and *Cedrelinga* sp.). Moreover, in the present paper forest development is expressed in tree roles, where different species can fit in, thus offering a more general model.

The forest development phases recognized in Araracuara are characterized using the general scheme of forest patch development by Oldeman (1990) based on architectural characteristics. This model is similar to the one described by other authors, e.g. Peet & Christensen, (1987) for forests with a smaller number of species and tree roles, resulting in a smaller resolution (i.e. less phases), and Finegan (1996) for secondary tropical rain forests, putting a heavy accent on compositional change, and also offering a smaller resolution.

Innovation phase

According to Oldeman (1990), this is the relative short period in which stumps, roots and other plant parts start to resprout and seeds germinate (Fig. 1A). The floristic composition of the forest patch for the next 40 years is determined to an extensive degree in this development phase (e.g. Finegan, 1996). Peet & Christensen (1987) call this phase the establishment phase, Finegan (1996) calls it phase one, the phase where herbs are determining the vegetation aspect.

Aggradation phase

This phase starts as soon as the woody vegetation gets closed (Fig. 1B). All tree crowns are expanding and there is a strong interaction between the crowns (Oldeman, 1990). This interaction between crowns is usually called competition because the trees are using the same limited resources, such as light and nutrients. However, because of the importance of spatial and temporal aspects in both the distribution of these resources and the patterns of tree development (Hallé *et al.*, 1978), I prefer to use the term crowding (Begon et al., 1986; Vester, 1997) in stead of competition. Dynamics in this phase are very strong, i.e. changes are remarkable between two consecutive years. In Araracuara, but also in San Carlos de Rio Negro (Saldarriaga, 1994) this phase is characterized by trees of the genus *Vismia*. Some species manage to reach a tree of the present architecture (Oldeman, 1990; Vester, 1997), others die before that. Hence, for many species in this phase a thinning process takes place, some however manage to reproduce. Therefore, the term "thinning phase" applied by Peet & Christensen (1987), comes short in characterizing this development phase. Finegan (1996), characterizes his "phase two" which corresponds with our aggradation plus biostatic 1 phase by canopy dominance of short lived pioneers.

Pioneer biostatic phase I

In the biostatic phase, the canopy of the forest is formed by trees of the present (Fig. 1C). These trees do not expand anymore, they have reached their maximum height and do not extend their crowns any further (Oldeman, 1990). The forest enters in a period of relative low dynamics, in the sense of expanding crowns. All potential trees in the under growth are suppressed in their growth by the trees of the present in the canopy.

In secondary forest this biostatic phase is formed by pioneer trees. The forest in that case has not reached its maximum height, but there is a period of relative rest in the development. Potential trees of primary forest species in the under growth will continue their height growth and are little affected by the canopy pioneers until they reach just below their crowns, the zone of heavy shade (cf. Alexandre, 1984). In most situations the pioneer biostatic phase does not last a long time. In Araracuara it lasted from 10 to about 30 years. This phase is characterized by *Inga* spp., *Miconia poeppigii, M. myriantha* and *Jacaranda copaia* in the canopy and several species of *Miconia* forming a set of trees of the present in the under growth. In the terminology of Peet and Cristensen (1987) this phase corresponds to the transition phase, though it clearly has characteristics of their "steady state". These authors do not recognize that pioneer trees can form a temporary "steady state".

Reorganization phase

Trees in the canopy of trees of the present start to die (Fig. 1D). In the Araracuara situation, the trees of the present in the canopy started to die at about 30 years. The potential trees in the under growth rapidly take over the positions in the canopy, and many trees showing still potential to grow higher and form a canopy at greater height. Most important species among these trees are *Guatteria* spp., *Goupia glabra, Casearia arborea* and *Clathrotropis macrocarpa*. Because of a difference in the moment at which individual trees die, the release of the undergrowth is also different. This accentuates spatial differences in large eco-units such as abandoned agricultural fields. Also, the limits between eco-units get vaguer due to reorganization. This phase also would be within the transition phase according to Peet & Christensen.

After the reorganization phase there will be a second biostasis, whose canopy is formed by *Guatteria* spp, *Goupia glabra, Clathrotropis* macrocarpa and *Casearia arborea*, according to the forest plots which were examined. The diversity in this canopy will probably be much higher, but these species were found characteristic for mature forests over a large area along the Caquetá (Duivenvoorden & Lips, 1993 and 1995). This second biostatic phase corresponds to Finegan's (1996) 3th phase.

Life histories

An organism's life history is its lifetime pattern of growth, differentiation, storage and reproduction (Begon *et al.*, 1986). Because of the importance of spatial and temporal aspects in development, survival and reproduction, the life history of trees was described according to architectural characteristics (Oldeman & van Dijk, 1991; Vester, 1997). The architecturally distinctive life cycle stages, potential tree, tree of the present and tree of the past (Hallé *et al.*, 1978; Oldeman, 1990; Vester, 1997) were related to architecturally distinctive forest development phases (Table 1). Many trees obtain sexual maturity before reaching the tree of the present stage. Though this sexual maturity is important, the major reproduction effort is reached in when the trees obtain a tree of the present form.

Life histories of tree species as exemplified in Table 1 do not include information about the relative position which species take in the forest. Such information would according to Whittaker et al. (1973) indicate the niche of the species, and according to Oldeman (1974b) the ecotope. In fact, information about the relative position of a tree species to other trees during its life cycle is indicative for inherited patterns of reactions to its environment, being part of the temperament of a tree (Oldeman & van Dijk (1991)). For proper understanding of the temperament of a tree, a more detailed knowledge of the reactions of species towards its environment is required.

Management suggestions derived from forest architecture and life histories

During each phase in the development of the forest, different forest products are available. Forest use should be adapted to this fact of nature. The land use principle that most closely imitates this natural characteristic is shifting cultivation in its original form with long fallow periods. During the fallow period fruits are harvested, and many game animals are attracted to the recovering forest, thus forming a well of proteins (van der Hammen, 1991). The innovation phase is variable, because its composition depends very much on (former) land use. In fact, shifting cultivation is in the first place a change in composition of the innovation phase. Some shifting cultivation systems include long living fruit trees, thus influencing the composition of other development phases as well (Vélez O., 1991).

The products in the innovation phase are tubers, fruits, fibers and leaves from a variety of herbs (e.g. Zea maiz), climbers (e.g. Passifloraceae, Cucurbitaceae) and small, fast growing trees (e.g. Manihot esculenta Crantz). Obviously there is a relation between plant (and thus product) and soil type, influencing the possible combinations during forest development.

In the aggradation phase, some small trees and palms (e.g. Pourouma cecropifolia, Bactris gasipaes, Couma macrocarpa) still produce fruits, but in general the vegetation is characterized by potential trees of fast growing species. Also poles of soft wood are produced. In this development phase a lot of young trees can not and must not provide products, investing in height growth for later production of fruits or timber.

The first pioneer biostatic phase produces fruits of different kinds of trees, mostly small berry-like fruits consumed by birds, fuelwood and timber of fast growing species, e.g. Jacaranda copaia (Vester, 1997) and Cordia alliodora and Vochysia ferruginea (Herrera et al., this volume). Poles of more durable species are produced.

In the reorganization phase, dead wood is the food of many insects and fungus. A later reorganization phase with hard wood trees provides nesting to bees and several bird species.

Later biostatic and reorganization phases also provide niches for epiphytes and lianas, thus producing e.g. ornamental plants (e.g. Orquideaceae, Bromeliaceae), fibers (e.g. *Heteropsis jenmanii*, PRORADAM, 1979) and fruits (e.g. *Oenocarpus bataua, Poraquieba serica*).

To conserve the succession pattern it is important not to optimize any of the products related to a certain phase, this would brake the succession, i.e. potential trees must be present in every development phase, for production in later phases. Still, there is a lot of manipulation for increased production possible.

The composition of the forest can be influenced by putting in species with desired characteristics, just like in the shifting cultivation system. Care must be taken that temporal and spatial organization of the forest permits succession, and thus a continued forest cover. In harvesting timber for instance, it is important that potential trees of species that determine the architecture of later forest phases can continue their development. This means that no management action must include the elimination of the complete vegetation. If the complete vegetation is removed, the process must start again. In case of removal of species that characterize the early phases of forest development there is a different starting point for other species. Long living tree species are less represented in the seed bank, and need crowding in their early development to obtain their usual form. Taking the crowding situation away may result in a lower forest canopy, and subsequent influences on later stages of development.

Temperaments

Theoretically one could reconstruct forests using species roles with spatially explicit information. This would result in a very general simulation of forest structure and composition. As soon as tree crowns are close to each other the predictability of such a model diminishes. To be able to predict how trees of different species interact it is necessary to understand how different branching patterns are compatible. Here follows a first set of principles that helps to explain the relation between tree temperament and tree architecture.

Usually the temperament is expressed as the reaction of a tree to different light environments, soil conditions and climate (Oldeman & van Dijk, 1991). Because reactions of a tree to a variety of interacting factors is visible in its architecture, the temperament of a tree was used by these authors to relate architectural properties with environmental properties. Vester (1997) worked out a still closer relation between tree architecture and environment focusing on the growth interaction of neighboring tree crowns. Here follows a synopsis of this relation.

Trees face an important trade-off which is reflected in their organization. The energy and matter that the plant takes up from its environment can be invested in either height growth or reproduction. The extreme example of this trade-off is the model of Holttum (Hallé & Oldeman, 1970; Hallé *et al.*, 1978), an orthotropic, unbranched axis with terminal inflorescence. Axes with axillary flowers can do both at the same time, extending and reproducing.

The rate of height growth must be high for trees that both need much light for their photosynthesis and are adapted to growing in a situation surrounded by other fast upward growing trees, i.e. crowding (Vester, 1997). This kind of tree will show a preferential orthotropic organization.

Leaf size reflects branching degree, according to Corner's rules (Hallé et al., 1978). Given a certain photosynthetic system, an architecture with high branching degree is more efficient in crowding then an architecture with low branching degree. In case of shading of part of a tree, a branched system has the advantage of regeneration, whereas a leaf of similar size would only have the option to function or not. Therefore sparsely branched trees must develop before highly branched trees with similar photosynthetic systems.

One single axis (Holttum's, Chamberlain's and Corners models) is used for gaining height, but at the risk of losing the apical meristem and without alternatives in case of being shaded. Hence it is mostly found in trees that do not need so much light and are found in the undergrowth. In plants that need much light, this architecture can only be found in the early stages of development or in trees that reach a certain height where they can reproduce before most other trees in their habitat reach the same height.

Branching without axial differentiation (Leeuwenberg's, Rauh's, Scarrone's and Attims' models) distributes the height growth function over different meristems, spreading also the risk of damage and sub-optimal functioning. The lack of differentiation is often a concession to light interception. The availability of many meristems to replace the leader is only useful if fast adjustment is necessary, i.e. in a situation of directly interacting crowns.

Branching with differentiation (Massart's, Aubréville's, Prévost's, Nozeran's Fagerlind's Roux's Petit's and Mangenot's models) provides a large surface able to intercept light and one meristem ensuring height growth. The risk of insufficient energy is reduced, but reaction to meristem damage or an unfavorable position, i.e. adjustment is slow. These tree forms are often found starting their life in the under growth.

Many tree species which fit in the architectural models with differentiation can easily change the differentiation of their branches. Trees with this architecture are found among pioneer trees. The degree of differentiation is a measure of their successional status (Vester, 1997). For models with mixed axes (Troll's, Champagnat's and Mangenot's) there is also a strong relation between the degree of differentiation and successional status, which can be assessed by the place of insertion of the relay axis (Vester, 1997).

Recommendations and future lines of research

One of the obstacles in the design of management systems based on natural processes is the lack of knowledge on the autecology of many species, specifically trees species. Most attention is driven to useful species and species in extinction. The architecture of trees and their temperaments, gives a solid base for the extension of existing knowledge of species through their evolutionary relation to other species (Vester, 1997). This area of research should have more attention of basic researchers.

The design of forests with multiple products during their development to mature forests is partially realized in many home gardens (e.g. Torquebiau, 1992). Only partially, because the mayor attention is on just one development phase (i.e. biostasis) as Torquebiau (1992) signals in his revision. Also argoforestry systems come close to this idea, but are less dynamic and further away from the natural forest ecosystem, simply because their principle is the spatial and temporal arrangement of useful crops, not the adaptation of a natural system to human needs. In general, management focuses on optimal use of space and short term profit, even multistrata agroforestry systems are designed to optimize these factors. Long term development is not interesting form the productive point of view. However, long term processes and long living organisms have important functions in the regulation of ecosystems (Neugebauer et al., 1996) and should be included, though not directly profitable.

The integration of production and conservation, including saving for the future in management systems, seems opposed to modern market thinking, where optimization and fast production cycles are keywords. And effectively, most examples of management systems that come close to the ideas mentioned above are found at the agricultural frontier. However, market systems have a shorter evolutionary history than ecosystems and man must apparently find new ways to reconcile ecosystem functioning and the interchange of their products. Some ideas about alternative society and market organization that consider a healthy ecosystem functioning were outlined by F. Vester (1980).

ACKNOWLEDGEMENTS

The author wants to thank the organization of the conference for their invitation and financial support. Also the foundation TROPENBOS is acknowledged for its contribution in the traveling costs. The foundations HET KRONENDAK, TROPENBOS and ICETEX are greatly acknowledged for their financial support in the years 1990 - 1997 during which this research was carried out. I thank Prof. R.A.A. Oldeman for his stimulating discussions, many of which took form in this text. The anonymous reviewers of this paper are acknowledged for their suggestions on terminology and literature.

REFERENCES

Alexandre, D.Y.,1984: Strata in tropical rain forest at Taï (Ivory Coast). In: Chadwich, A.C. & Sutton, S.L. (eds.) Tropical rain forests: The Leeds symposium. Leeds Philosophical and literary society, Leeds. pp. 15-24.

Amo R., S. del, 1991: Management of secondary vegetation for artificial creation of useful rain forest in Uxpanapa, Veracruz, México - An alternative between transformation and modification. In: Gómez Pompa, A., Whitmore, T.C. & Hadley, M. (eds.): Rain forest regeneration and management. MAB series vol 6. UNSECO & Parthenon, Paris. pp. 343-350.

Begon, M., Harper, J.L & Townsend, C.R., 1986: Ecology, Individuals, populations and communities. Blackwell scientific publications, Boston. Second edition 1990. 945 pp.

Duivenvoorden, J.F. & Lips, J.M., 1993: Ecología del paisaje del Medio Caquetá. Estudios en la Amazonía Colombiana 3, Tropenbos - Colombia, Santa Fé de Bogotá. 301 pp. + maps.

Duivenvoorden, J.F. & Lips, J.M., 1995: A land-ecological study of soils, vegetation, and plant diversity in Colombian Amazonia. The TROPENBOS Foundation, Wageningen. 438 pp.

Finegan, B., 1996: Pattern and process in neotropical secondary rain forests: the first 100 years of succession. TREE 11(3):119-123.

Galindo, Leal, C. & Bunnell, F. L., 1995: Ecosystem management: Implications and opportunities of a new paradigm. The forest chronicle 71(5): 601-606.

Gómez Pompa, A., 1971: Posible papel de la vegetación secundaria en la evolución de la flora tropical. Biotropica 3(2): 125-135.

Gómez-Pompa, A. & Vázquez- Yanes, C., 1985: Estudios sobre la regeneración de selvas en regiones calido-húmedas de México. In: Gomez-Pompa, A & del Amo R., S. Investigaciones sobre la regeneración de selvas altas en Veracruz, México. II. Instituto Nacional de investigaciones sobre recursos bioticos. Editorial Alhambra Mexicana. pp.1-25.

Gómez -Pompa, A., 1991: Learning from traditional ecological knowledge: insights from Mayan silviculture. In: Gómez Pompa, A., Whitmore, T.C. & Hadley, M. (eds.): Rain forest regeneration and management. MAB series vol 6. UNSECO & Parthenon, Paris. pp. 335-341.

Hallé, F., Oldeman, R.A.A. & Tomlinson, P.B., 1978: Tropical trees and forests; an architectural analysis. Springer, Heidelberg. 441 pp.

Hammen, M.C. van der, 1991: El manejo del mundo. Naturaleza y sociedad entre los Yukuna de la Amazonia Colombiana. Sec. de. 1992. Estudios en la Amazonia Colombiana 4. Tropenbos Colombia, Bogotá. 376 pp.

Jordan, C.F., 1989: An Amazonian rain forest. The structure and function of a nutrient stressed ecosystem and the impact of slash and burn agriculture. MAB series vol 2. UNESCO and Parthenon, paris. 176 pp.

Lammerts van Bueren, E.M. & J.F. Duivenvoorden, 1996: Towards priorities of biodeversity research in support of policy and management of tropical rain forests. The Tropenbos Foundation, Wageningen. 35 pp.

Myers, N., 1988: Tropical forests and their species. In: Wilson, E.O. (de.): Biodiversity. National Academic Press, Washington. p. 28-35.

Neugebauer, B. Oldeman, R.A.A. & Valverde, P., 1996: Key principles in ecological silviculture. In: Fundamentals of organic agriculture. IFOAM., Ökozentrum Imsbach, Tholey-Theley. Pp. 153-175.

Oldeman, R.A.A., 1974 a: L'architecture de la forêt Guyanaise. Mémoires ORSTOM No. 73. ORSTOM, Paris. 204 pp.

Oldeman, R.A.A., 1974 b: Ecotopes des arbres et gradients écologiques verticeaux en forêt Guyanaise. La Terre et la Vie 28(4): 486-520.

Oldeman, R.A.A., 1990: Forests: elements of silvology. Springer Verlag, Berlin. 624 pp.

Oldeman, R.A.A. & Dijk, J. van, 1991: Diagnosis of the temperament of tropical rain forest trees. In: Gómez Pompa, A., Whitmore, T.C. & Hadley, M. (eds.): Rain forest regeneration and management. MAB series vol 6. UNSECO & Parthenon, Paris. pp. 21-65.

Peet, R.K. & Christensen, N.L., 1987: Competition and tree death. BiosScience 37(8):586-595.

Saldarriaga, J.G., 1994: Recuperación de la selva de "Tierra Firme" en el alto río Negro, Amazonia Colombiana-Venezolana. Estudios en la Amazonía Colombiana 5. Tropenbos-Colombia, Bogotá. 201 pp.

Uhl, C., Nepstad, D., Buschbacher, R., Clark, K., Kauffman, B, Subler, S., 1990: Studies of ecosystem response to natural and anthropogenic disturbances provide guidelines foir designing sustainable land-use systems in Amazonia. In: Anderson, A.B. (ed.): Alternatives to deforestation: steps toward sustainable use of the Amazon rain forest. Columbia University Press, New York. pp. 24-42.

Vélez O., , G.A., 1991: Los frutales Amazónicos cultivados por las comunidades indígenas de la región del Medio Caquetá (Amazonia Colombiana). Colombia Amazonica 5(2): 163-193.

Vester, F., 1980: Neuland des denkens. DTV, Stuttgart 544 pp.

Vester, H.F.M., 1997: The trees and the forest. The role of tree architecture in canopy development; a case study in secondary forests (Araracuara, Colombia). Phd thesis Universtity of Amsterdam. Eburon P&L, Delft. 180 pp.

Vester, H.F.M. & Cleef, A.M., 1998: Tree architecture and secondary tropical forest development - A case study in Araracuara, Colombian Amazonia. Flora 193,: 75-97.

Walschburger, T. & Hildebrand, P. von, 1991: The first 26 years of forest regeneration in natural and man-made gaps in the Colombian Amazon. In: Gómez Pompa, A., Whitmore, T.C. & Hadley, M. (eds.): Rain forest regeneration and management. MAB series vol 6. UNSECO & Parthenon, Paris. pp. 257-263.

Wilson, E.O., 1992: The diversity of life. Norton & Company, New York. 424 pp.

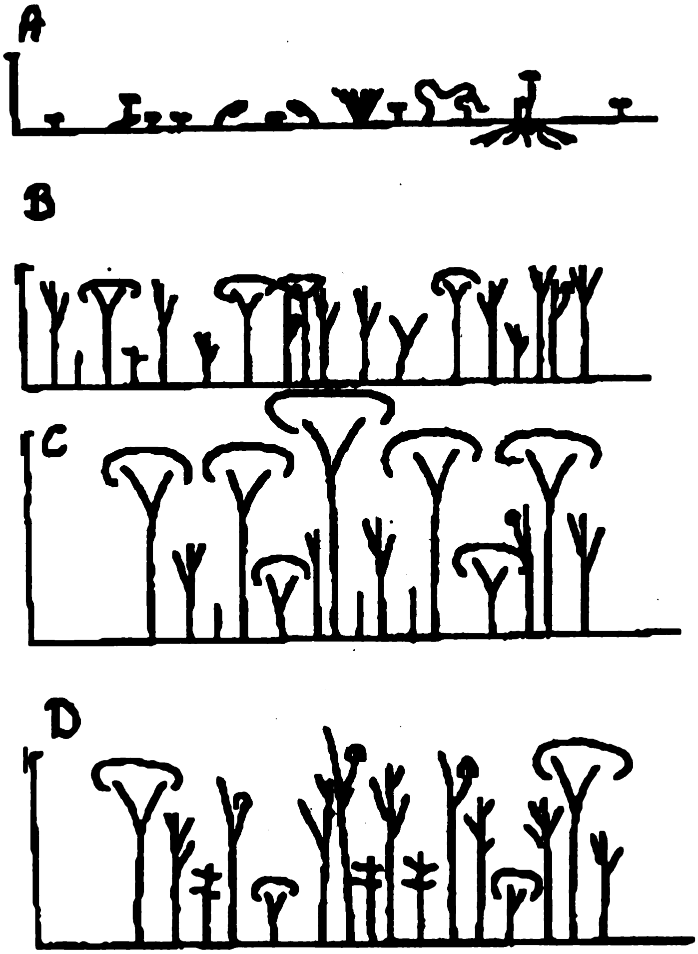


Fig.1. Synopsis of forest development in secondary forests near Araracuara, Colombia A.Innovation phase (c. year 0-1). B. Aggradation phase (c. year 1-8). Trees of the present of *Vismia* spp. C. Biostat with pioneer trees (c. year 10-30). Trees of the present in the canopy: *Miconia* spp., *Inga* spp. And *Jacaranda copaia* of the present in the under growth: *Miconia* spp. D. Reorganization phase (c. Year 30 – 40). Most important tree canopy: *Goupia glabra, Clathrotropis macrocarpa, Laetia procera, Guatteria* spp.

Table 1. Life histories of selected secondary forest tree species from tropical lowland rainforest near Araracuara, Colombia related to forest development phases. Trees of the present determine the architecture of the forest (Oldeman, 1990). Development stage "trees of the past" includes suppressed trees, being those trees which show architectural signs trees of the past, although the tree has not passed through its tree of the present stage.

Forest Biostatic development phase life cycle	Innovation phase	Aggradation phase	Pioneer biostatic I phase	Reorganisation phase	Pioneer II phase
Potential tree	*Vismia glaziovii* *Miconia minutiflora* *Visma japurensis* *Vismia macrophylla* *Miconia poeppiggi* *Miconia poeppigii* *Miconia myriantha* *Jacaranda copaia* *Inga alba* *Inga thibaudiana* *Inga punctata* *Piper arboreum* *Miconia prasina* *Guatteria trichoclonia* *Guatteria stipitata* *Clathrotropis macrocarpa* *Goupia glabra* *Trymatococcus amazonicus* *Casearia arborea*	*Vismia japurensis* *Vismia macrophylla* *Miconia poeppigii* *Miconia myriantha* *Inga alba* *Inga tribaudiana* *Inga punctata* *Mioonia prasina* *Guatteria trichoclonia* *Guatteria stipitata* *Clathrotropis macrocarpa* *Goupia glabra* *Trymatococcus amazonicus* *Casearia arborea*	*Guatteria trichoclonia* *Guatteria stipitata* *Clathrotropis macrocarpa* *Gloupia glabra* *Trymatococcus amazonicus* *Casearia arborea*	*Guatteria trichoclonia* *Guatteria stipitata* *Clathrotropis macrocarpa* *Goupia glabra* *Trymatococcus amazonicus* *Casearia arborea*	
Tree of the present		*Vismia glaziovii* *Miconia minutflora*	*Visma japurensis* *Visma macrophylla* *Miconia poeppigii* *Inga alba* *Inga thibaudiana* *Piper arboreum* *Miconia prasina*	*Guatteria trichoclonia* *Guatteria stipitata* *Clathrotropis macrocarpa* *Goupia glabra* *Trymatococcus amazonicus* *Casearia arborea*	
Tree of the past or Suppressed tree		*Vismia glaziovii* *Miconia minutiflora* *Vismia japurensis* *Vismia macrophylla*	*Vismia japurensis* *Vismia macrophylla*	*Visma japurensis* *Vismia macrophylla* *Miconia myriantha* *Inga alba* *Inga thibaudiana* *Inga punctata* *Piper arboreum* *Miconia prasina*	

SECONDARY SUCCESSION IN THE EASTERN AMAZON: STRUCTURAL CHARACTERIZATION AND DETERMINANTS OF REGROWTH RATES

Joanna M. Tucker
Department of Latin American Studies,
University of Arizona, Tucson, Arizona, USA

Eduardo S. Brondizio, Emilio F. Moran
Anthropological Center for Training and Research on Global Environmental Change
Indiana University
Bloomington, Indiana, USA

INTRODUCTION

Secondary forest succession contributes an important role to sustainable agriculture in Amazonia. The majority of Amazonian farmers practice small-scale shifting cultivation, otherwise known as slash-and-burn agriculture, which incorporates secondary forest growth into the agricultural system. As a consequence of shifting cultivation and a growing trend toward pasture development in Amazonia, large areas of rain forest have been transformed into secondary vegetation. This paper explores secondary forest succession in the region surrounding the town of Igarapé-Açu in the eastern Amazon. In this region, farmers have come to depend on secondary forests as a source of cultivable land. Besides areas under agricultural production, practically the entire landscape of this region is covered by various stages of secondary growth.

Secondary succession is also a source of many important products like fruits, nuts, oils, medicinal plants, animal game, building materials, and timber harvested by local people. The relevance of secondary succession to food production, as well as its role in the process of reforestation of degraded lands calls for a closer examination of forest regrowth in the Amazon.

The goals of this paper are to describe the structural advancement of secondary succession in Igarapé-Açu and identify factors which influence the rate of forest regrowth. We identify physiognomic characteristics of regrowth stages and investigate how land use and local environmental factors influence the rate of succession. First, we characterize the study area and explain our research methods. Then we summarize the structural features of each age class that was sampled. Next, we discuss the process of succession observed in Igarapé-Açu and consider the factors which impact the rate of succession using specific examples from the research.

STUDY AREA

The research for this paper was conducted in the area surrounding the town of Igarapé-Açu in the Bragantina Region of the eastern Brazilian Amazon within the state of Pará. Igarapé-Açu sits about 100 km east of Belém between 0° 45′ and 1°39′ latitude south and 46°16′ and 48°15′ longitude west (Figure 1). Other recent studies on secondary succession in the Bragantina Region include Dantas (1989), Denich (1991), Salomão (1994), Watrin (1994), and Vieira *et al.* (1996). This region is an important site for studying regrowth because of its history of more than 100 years of agriculture and the prevalence of secondary forest. Rainfall in Bragantina normally ranges from 2200 to 2800 mm with a dry period from September to November. The mean annual temperature of the region is 25°C, and according to Köppen's climate classification system (1936), the Bragantina Region is predominantly type Ami[1] (Denich 1991).

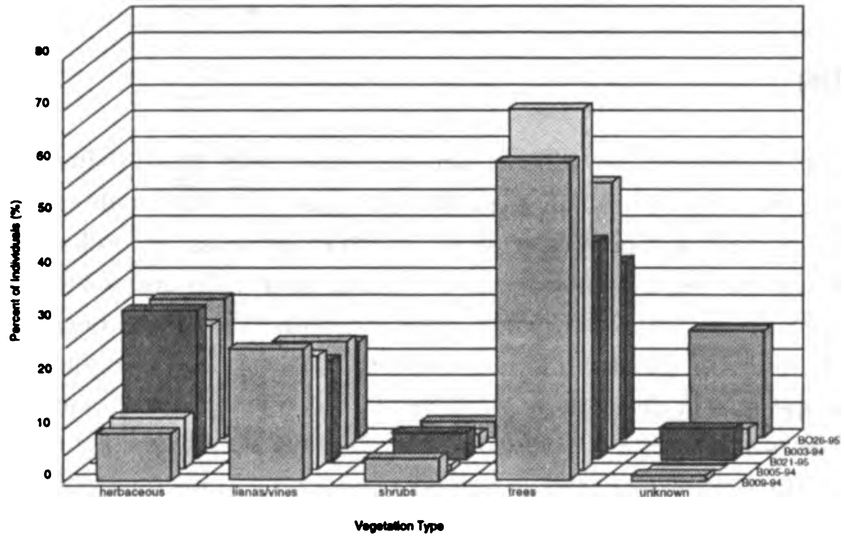


Figure 1

Life Form in Igarape-Acu
0-5 years of succession

Of the almost 1 million hectares of dense tropical forest that covered the Bragantina Region at the beginning of the century, less than 2% remained by 1960 (IBDF/SUDAM 1988 in Salomão 1994, Penteado 1967). Besides gallery forest that remains along the edges of waterways, the landscape is largely characterized by agricultural crops, pasture, and fallow vegetation in various

---

[1] Ami refers to a climate characterized by high precipitation and a short dry period including at least on month with rainfall below 66 mm.

stages of development. In recent years, the area under tree plantations, such as rubber, oil palm, and cacao has expanded. The dominant soil type in Bragantina is sandy Oxisol, or Latossolo Amarelo (Yellow Latosol) in the Brazilian Classification. Spodosols and Entisols can also be found (Vieira *et al.* 1967). Yellow Latosol often exhibit extreme nutrient deficiencies with relatively high concentrations of iron and aluminum, and they are acidic with pH between 4.5 and 5.5. In terms of physical characteristics, they normally display a granular and sandy structure which may leach nutrients quickly when denuded (Brady 1974).

Settlement History

Colonization of the Bragantina Region began during the second half of the 19th century. During the rubber-boom (1870-1910) the population of Belém, the capital city of Pará, grew rapidly. At that time Belém imported most of its food from other Brazilian provinces (Penteado 1967). To increase self-sufficiency, the state government invested its profits from the rubber boom in a colonization program, intended to create a local zone of agricultural production. Between 1883 and 1908 a railroad was built to facilitate the flow of goods from the frontier to the capital city (Penteado 1967), and to encourage agriculture, governing authorities offered land, agricultural instruments, seeds and monetary aid to new settlers (Moran 1981). By 1960, Bragantina supplied a quarter of all the rice, beans, manioc, and corn produced in the state of Pará (Vieira *et al.* 1996). Igarapé-Açu, the focus of this paper, was founded in 1897 (Denich 1991).

Small-Scale Agriculture

The traditional system of small-scale shifting agriculture endures as the dominant land use scenario in the Bragantina Region. The predominant cropping system employs a consortium of manioc, beans, corn, and/or rice (Denich 1991). Normally, farmers manually clear an area of secondary vegetation (usually one to two hectares in size) during the dry season. After the slash is sufficiently dried, they burn the area. Nutrients from the ash then become available to crops which are planted at the start of the rainy season. Burning also kills parasites, insects, fungi, nematodes, and pathogenic bacteria (Nye and Greenland 1960). After one or two years of cultivation, due to leaching of nutrients and weed invasion, the costs of maintaining the crop (i.e. fertilizer inputs, labor) exceed the benefits. The farmer then abandons his plot and clears a new area. Subsequently the forest regenerates, sometimes vigorously. The fallow stage of the cycle of shifting cultivation facilitates recuperation of the soils after abandonment: it restores organic matter and major nutrients to the soil, checks erosion, and draws water and nutrients from the lower soil depths as its age permits (Nepstad 1991, Smith 1982). Due to land shortage, Bragantina farmers are lucky to find land with five to six years of secondary growth to clear for their crops (Penteado 1967).

Land Use

The municipality of Igarapé-Açu utilizes 96.8% of their productive land in agriculture, 2.6% in pasture, and 0.6% in other uses. Manioc, beans, corn, rice, and passion fruit (*maracujá*) constitute Igarapé-Açu's majority agricultural products (Denich 1991). Since the 1980s, the sale of properties too residents in Belém has precipitated land concentration and an exodus of small farmers from the region. With the resulting expansion of large land holdings, pasture has become the fastest growing land use type in the Igarapé-Açu area since 1984. The local extension agency, Empresa Brasileira Assistência Técnica e Extensão Rural (EMATER), predicts that in the future the region will be dominated by pasture, and more resources will be directed to oil palm and passion fruit.

METHODS

Nested Sampling Strategy

The present study employs a nested sampling strategy organized by region, site, plot, and subplot to collect field data. The region, Bragantina, refers to the highest level and indicates the larger study area being represented. A site corresponds to the vegetation stand (fallow or mature forest) selected for sampling. Several tiers of information are gathered at each site: land use history, location (with a GPS or Global Positioning System device), vegetation inventory, and soil samples. To characterize the vegetation, plots are distributed at the site in a stratified random fashion, and subplots are nested within them. Plots are designed to inventory all trees at a particular site, whereas subplots are used to inventory saplings, seedlings, and herbaceous species.

Study Sites

To facilitate sampling, sites were grouped according to vegetation age classes as follows: 0-5 years, 5-10 years, greater than 10 years, and mature forest. An adequate number of representative samples were chosen from each age class to achieve a well-represented chronosequence. Landsat TM satellite images were used as a reference to ensure even spatial distribution of sample sites throughout the region. The farmer's permission to conduct field research on his property was attained prior to any final site selection.

Sixteen sites from Igarapé-Açu sampled during 1994 and 1995 are examined in this paper. Only one mature forest site was sampled due to the scarcity of primary forest in the region. Of the fallowed sites, five belong to the 0-5 year age class, four to the 6-10 year age class, and six to the older than 10 year age class. Altogether, the vegetation sampled range between 2.5 and 35 years since abandonment. All secondary forest sites included in this analysis were cleared manually and burned before planting, and they had been cleared more than once in their history.

Table 1. **Summary of Igarape-Acu Sample Sites**

Site No.	Site Vegetat	Land Use Type	Land Use History	Sampling Methods			
				Plot	Area (m2	Subplot	Area (m2)
B009-94	SS(2.5yrs)	Swidden agriculture	1984-corn, manioc, beans, rice; 1986-fallow; 1991-corn, manioc; 199	none		5*(10x2m)	100
B005-94	SS(3yrs)	Swidden agriculture/pas	1990-manioc, corn, rice; 1991-pasture; 1992-fallow	none		5*(10x2m)	100
B021-95	SS(3yrs)	Swidden agriculture	1991-crop; 1992-fallow	10*(10x15m)	1500	10*(5x2m)	100
B003-94	SS(4.5yrs)	Swidden agriculture	1989-beans, manioc, corn; 1990-fallow	none		5*(10x2m)	100
B026-95	SS(4.5yrs)	Swidden agriculture	1960?-crop; 1991-manioc	10*(10x15m)	1500	10*(5x2m)	100
B025-95	SS(6yrs)	Swidden agriculture	1988-manioc, beans; 1989-fallow	10*(10x15m)	1500	10*(5x2m)	100
B010-94	SS(8yrs)	Swidden agriculture	1985-beans, manioc, corn; 1986-fallow	10*(10x15m)	1500	10*(5x2m)	100
B027-95	SS(8yrs)	Swidden agriculture	1965?-crop; 1986-manioc	10*(10x15m)	1500	10*(5x2m)	100
B004-94	SS(10yrs)	Swidden agriculture	1983-corn,beans, manioc; 1985-fallow	10*(10x15m)	1500	10*(5x2m)	100
B001-94	SS(14yrs)	Swidden agriculture	1979-beans, manioc, corn; 1980-fallow	10*(10x15m)	1500	10*(5x2m)	100
B011-94	SS(15yrs)	Swidden agriculture	1978-rice, manioc, corn; 1980-fallow	10*(10x15m)	1500	10*(5x2m)	100
B006-94	SS(19yrs)	Swidden agriculture	1960s-manioc; 1960's-fallow; 1974-cotton; 1975-fallow	10*(10x15m)	1500	10*(5x2m)	100
B002-94	SS(20yrs)	Swidden agriculture	1974-manioc, corn; 1975-fallow	10*(10x15m)	1500	10*(5x2m)	100
B024-95	SS(25yrs)	Swidden agriculture	b/f 1970-agave for rope	10*(10x15m)	1500	10*(5x2m)	100
B020-95	SS(35yrs)	Swidden agriculture	1960-rice, manioc, corn; 1961-fallow	10*(10x15m)	1500	10*(5x2m)	100
B006-94	Dense Fores	Logging	1984-logged	10*(10x15m)	1500	10*(5x2m)	100

Most of the sites in Igarapé-Açu were cultivated for 1-2 years, and all but two successional sites were previously planted with a combination of manioc, beans, and corn or rice. Only one site previously planted in pasture area was sampled (see Table 1).

Farm-Level Interviews

In-depth land use (farm-level) interviews with the land owner, or tenant, were conducted at each sample site. Questions were asked to ascertain when the forest or secondary growth was last cut, when it was burned, the length of prior fallow periods, what cultivation and management techniques were employed (such as clearing procedures and fertilizer use), what crops/pasture were grown, yields, the time since the land was abandoned, and other pertinent information about the land use history. In most cases, although the sites experienced a long history of settlement and cultivation in Igarapé-Açu, land use histories are limited to the last two or three cultivation cycles.

Vegetation Inventory

In this study, trees refer to plant individuals with dbh (diameter at breast height) $\geq$ 10 cm. Saplings are those with dbh < 10 cm but $\geq$ 2 cm dbh or 2 m height, and herbaceous plants are classified as those under 2 cm dbh. In fallows with trees, ten 10 x 15 meter plots were randomly located along a randomly-oriented transect within the forest stand. Inside each plot, all trees were identified and measured for diameter, stem height (height to the first major branch), and total height. Height was estimated upon consensus of two or three observers using a three to five meter long rod as a guide. Within each plot, a sub-plot of 5 x 2 meters was randomly placed in which saplings were measured for diameter and total height, and all species less than 10 cm dbh were counted and identified. If the number of individuals within the sub-plot were uncountable (such as in the case of grasses), percent coverage was estimated.

In fallows with few if any trees (0-5 years), five 10 x 2 meter plots were distributed similarly as above. Each of these plots were divided into five 2 x 2 meter subplots. In each subplot the same procedures were carried out as in the 5 x 2 meter subplots mentioned above. In 1995, a slightly different procedure was followed: sites with few if any trees were sampled in the same way as sites with trees. In all cases, the total area sampled for 0-5 year fallows was 100 m2, but the new method facilitates easier plot by plot comparison between the younger and older sites. Plot sizes are summarized in Table 1.

A forest profile was drawn for each successional stage to provide a visual representation of vegetation structure and composition. Only individuals of at least 2 cm diameter were included.

---

[2] Unknown refers to species not found in available lists which describe vegetational life form.

Species identification was done in the field by an experienced field botanist and plant samples were collected, in the case of uncertainty, and later identified by an herbarium technician at the EMBRAPA (Empresa Brasileira de Pesquisa Agropecuária)or the Museu Goeldi Herbarium in Belém.

Soil Samples

In each inventoried site, soil samples were collected with a soil auger at 20 cm intervals to one meter depth. One sample was taken per site. Soil samples were delivered to the tropical soil laboratories at Centro de Pesquisa Agropecuária do Trópico Umido da Empresa Brasileira de Pesquisa Agropecuária (EMBRAPA/CPATU) in Belém, Pará, Brazil, where chemical and physical analysis of the soil was completed.

RESULTS

Igarapé-Açu: A Structural Analysis of Successional Age Classes

The following section organizes stages of succession into three major age categories: 0-5 year fallows, 6-10 year fallows, and >10 year fallows, and examines the structural characteristics of each stage and of primary forest in the area surrounding the town of Igarapé-Açu. Using age to aggregate fallow sites into stages of secondary growth helps isolate variant rates of succession, and to observe the progression of development.

0-5 Year Age Class

For the 0-5 year age class, Figure 1 expresses regeneration according to plant type: grasses, forbs, lianas and vines, shrubs, trees (saplings and seedlings), and unknown[2]. During the first five years of succession, trees species constitute the greatest number of individuals of all the vegetation types, ranging from 33%[3] to 68% of all individuals. Within an area of 100 m^2, as many as 46 different tree species are found in a four and a half year old fallow. Lianas and vines, the second most common vegetation type colonizing abandoned fields, make up about one-fourth of the individuals, while very few shrubs are present (only as much as 4%). Herbaceous plants generally constitute around 26% of the vegetation.

During the first five years of succession, the density of saplings ($\geq$ 2cm dbh) is low - between zero and four and a half percent of all individuals. Table 2 indicates high structural variation among early secondary succession sites which occurs due to specific land use history and environmental conditions. The mean height for 0-5 year fallows is 2.87 meters, and the tallest saplings stand 4.5 meters tall, except for the rapid growing pioneer species, *Cecropia palmata*

---

[3] The 33% may in reality be higher because at this site (B026-95) there is a higher percentage of unknowns (20%) which could be tree species.

[4] Basal area includes only saplings, and therefore, reflects the presence of woody plants, mostly tree species, as opposed to herbaceous vegetation.

Table 2. Igarape-Acu – Structural Characteristics

Age (yrs)	Site	Basal area (m2/ha) Total	Basal area (m2/ha) Sapling	Basal area (m2/ha) tree	Average Total height (m)	Maximum Total height (m)	Standard Dev. Total height (m)	Mode Total height (m)	Average DBH (cm)	Maximum DBH (cm)	Estándar Dev DBH (cm)	Mode DBH (cm)
	0-5 yrs											
2.5	B009-94	1.22	1.22	-	2.4	3.5	0.49	2	2.58	4	0.49	2
3	B005-94	-	-	-	-	-	-	-	-	-	-	-
3	B021-95	0.28	0.28	-	3	3.5	0.38	3	2.04	2.2	0.07	2
4	B026-95*	2.7	2.7	-	3.85	8	1.09	3	2.68	5.5	0.82	2
4.5	B003-94	1.08	1.08	-	2.43	4.5	0.68	2	2.59	4.4	0.72	2.2
	avg	1.045	1.045	0	2.2825	3.75	0.49	2	2.463	2.925	0.345	1.5
* the height meter total height max belongs to Cecropia obtusa												
	6-10 yrs											
6	B025-95	15.82	9.6	6.22	11.14	16	2.22	10	14.72	31.3	4.63	10.5
8	B027-95	12.78	11.02	1.78	8.41	13	2.52	9	11.93	16.3	1.98	10
8	B010-94**	8.19	4.78	3.41	7.43	10.5	1.27	7	10.46	16	0.99	10
10	B004-94	16.44	12.52	3.92	9.95	13	1.51	9	11.63	16.7	1.87	10
	avg	13.3075	9.48	3.8275	9.233	13.125	1.68	8.75	12.185	20.075	2.368	10.125
**excludes two Maximiliana maripa palms from the analysis due to divergent DBHs of 34.2 cm and 35.1 cm. These palms are left over from prior vegetation cover and are therefore not directy a part of the successional vegetation												
	>10 yrs											
14	B001-94	16.68	10.7	5.98	8.98	13	1.74	9	11.81	21	2.55	10
15	B011-94	14.05	7.85	6.4	8.75	13	1.9	9	14.44	25.5	4.77	10
19	B006-94***	18.72	12.04	6.68	11.22	15	2.01	10	14.59	24.6	3.89	10
20	B002-94****	22.85	13.14	9.71	11.04	18	2.45	11	13.04	38	5.24	10
25+	B024-95	21.52	1.88	19.64	15.69	25	2.98	15	18.52	45.9	7.11	11.4
35	B020-95	21.47	9.54	11.93	13.21	18	2.4	16	14.44	28	4.17	10.5
	avg	19.212	9.158	10.053	11.478	17	2.25	11.67	14.47	30.5	4.62	10.317
***excludes six Maximiliana maripa palms from the analysis due to outlier DBHs												
****excludes two Maximiliana maripa palms from the analysis due to outlier DBHs												
	Forest											
dense	B008-94	43.74	6.93	36.81	18.94	33	5.47	14	20.97	65.2	11.13	10
forest	avg	43.74	6.93	36.81	18.94	33	5.47	14	20.97	65.2	11.13	10
Only tree with DBH>10 cm to calculate height and dbh.												

which is 8 meters (site B0021-95). Stem diameter averages 2.46 cm with a maximum dbh of 5.5 cm in a four year old fallow. With regard to basal area, 0-5 year old fallows support an average 1.33 m^2/ha, ranging from zero to 2.7 m^2/ha[4].

6-10 Year Age Class

The 6-10 year stage of secondary succession in Igarapé-Açu manifests a clear advance in structural development. Saplings dominate the forest stand in terms of density and basal area, and herbaceous vegetation declines. Structure varies significantly among 6-10 year fallows due to the initial rate of colonization and other influences like original floristic composition, land use history, soil fertility, and neighboring vegetation (Table 2). Mean total height of trees varies from 7.43 meters to 11.14 meters. The tallest trees form a canopy at 10 to 16 meters. The average dbh for trees in 6-10 year fallows is 12.19 cm, while three out of the four sites sampled had a maximum diameter around 16 cm.

In fallows 6-10 years old, the number of saplings per 100 m^2 ranges from 73 to 125 individuals, or 7.7-14.5% of the vegetation under 10 cm dbh. Two fallows (sites B027-95 and B010-94), have a relatively larger number of saplings of which the majority (77-91%) are less than six meters tall. On the other hand, sites with comparatively fewer saplings (sites B025-95 and B004-94) have a higher percentage of saplings above six meters (as much as 54%). Fewer saplings seem to indicate a more advanced stage of succession. Tree density varies from 153 to 407 individuals/ha. A similar study done by Salomão (1994) at Peixe-Boi, located about 35 km southeast of Igarapé-Açu, found 336 trees/ha in fallows 10 years of age.

Between six and ten years, total basal area ranges from 8.19 m^2/ha to 16.44 m^2/ha. Tree basal area is 1.76 to 6.22 m^2/ha and sapling basal area ranges between 4.78 m^2/ha and 12.52 m^2/ha. At every site saplings contribute more to the total basal area than trees (58-86%).

Greater than Ten Year Age Class

Height and basal area change relatively little between eight and 20 years of fallow (Table 2). In fallows near 15 years of age, mean total height for trees is below 9 meters, but after 20 years, fallows display mean total tree height between 11 and 16 meters. Emergents in fallows older than 10 years stand between 13 and 25 meters tall. The canopy rises taller with age: at 15 years it forms near 10 meters, around 20 years at 15 meters, and between 25 and 35 years it extends about 18 meters high. The average diameter of trees during the greater than 10 year stage of succession varies between about 12 cm and 14.5 cm, except for one site with an average dbh of 18.52 cm (site B024-95). By 20 years, maximum dbh is 38 cm and after 25 years, trees as large as 45.9 cm dbh were found.

At Igarapé-Açu, saplings constitute anywhere from 2.8% to 18.1% of the total number of individuals less than 10 cm dbh. Generally, fallows older than 10 years have about 76 saplings per 100 m^2; however, the population may be as low as 18 individuals or as high as 114 individuals per 100 m^2 . Tree density ranges from 353 to 673 individuals/ha. Salomão (1994) sampled 20 year fallow at Peixe-Boi with 522 trees/ha. Both sapling and tree density vary widely during >10 year succession due to the wide age category and the various levels of development.

Tree basal area before the twentieth year is approximately 6.35 m^2/ha, but after twenty years, it jumps to 10-20m^2/ha. Sapling basal are ranges from about 7.65 to 13.14 m^2/ha with the exception of 1.88 m^2/ha (site B024-95). The contribution of trees to the total basal area varies from 16% to 91%. Trees contribute to the majority of total basal area after 20 years.

Mature Forest

The primary forest site represents a dense forest outside of Igarapé-Açu . The sampled area experienced some selective logging, therefore depleting the larger structural elements of the forest (a site with the least disturbance was selected). Trees in this mature forest exhibit a mode total height of 14 meters (Table 2). Mean total tree height is 18.94 meters, and the canopy forms around 30 meters. Emergents reach 33 meters, and average tree dbh in the mature forest is about 30 cm with a maximum of 65.2 cm.

Density of saplings in mature forest is 45 individuals per 100 m^2 , or about 10% of the vegetation less than 10 cm dbh. Tree density is 833 individuals per hectare. Salomão (1994) found a tree density of only 439 individuals/ha in Peixe-Boi. Pires et al. (1953) inventoried a terra firme forest near Castanhal, Pará, only 30 km southeast of Igarapé-Açu, which exhibited 423 individuals/ha (Campbell *et al.* 1986). The larger sample size used by these authors (one hectare and 3.5 hectares respectively) may provide a more accurate measure of tree density than our study.

Total basal area for mature forest in Bragantina is 43.74 m^2/ha: saplings 6.93 m^2/ha and trees 36.81m^2/ha. Nearby in Peixe-Boi, Pará, basal area is lower - sapling basal area in primary forest is 4.4 m^2/ha while tree basal area is 23.3 m^2/ha (Salomão, 1994). Again, the sample size used in this study, 1500 m^2, may have been too small to accurately represent the basal area of a primary forest in this region, or our divergent figures may be indicators of logging.

Early succession exhibits distinct characteristics, whereas succession between six and twenty years displays more similarities than differences. Structural features of the 11-19 year old fallows in Igarapé-Açu tend to overlap with the 6-10 year age class. After about 19 years of succession, structural features differ more noticeably from the younger fallow vegetation. Within each age class, basal area, height, and density vary depending on land management history, clearing size, soil conditions, and original vegetation, among other factors. Figures 2 and 3 summarize these changes in height and basal area over time with the data aggregated into five year interval age classes.

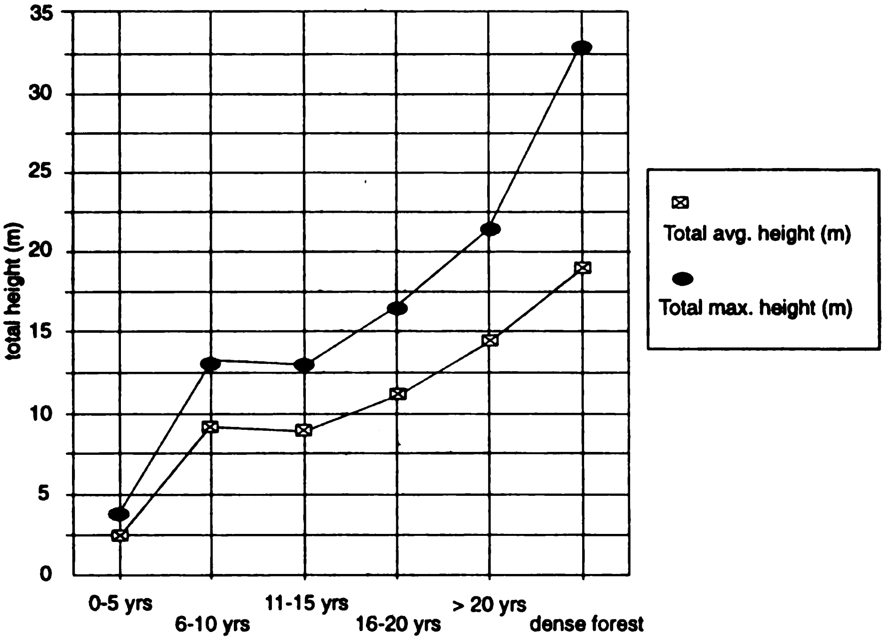


Figure 2
Change in Height by Age Class

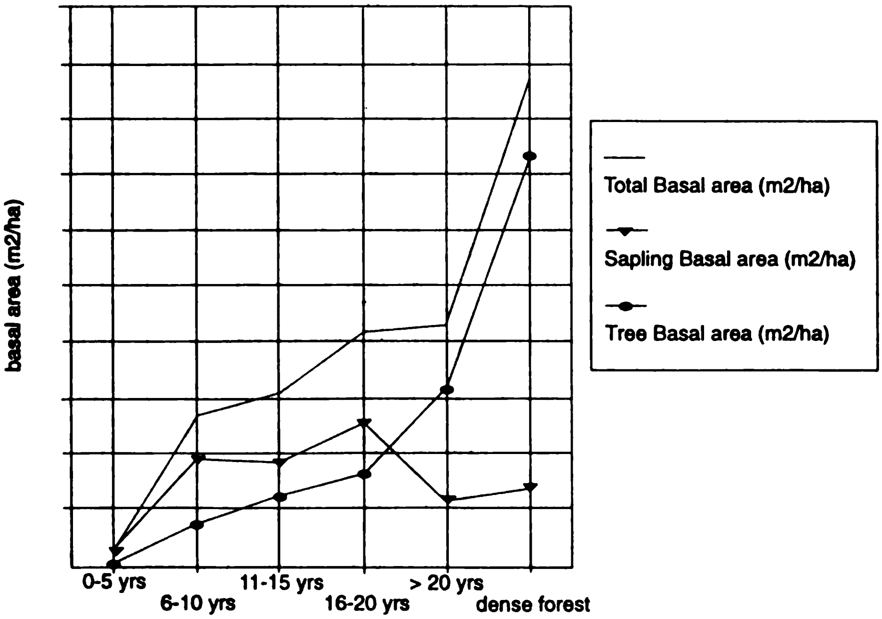


Figure 3
Change in Basal Area by Age Class

DISCUSSION

The Successional Process in Igarapé-Açu

Secondary succession in Igarapé-Açu follows a clear pattern of development. During crop or pasture use, burning and weeding hold back succession, but once the field has been abandoned, forest recovery continues unimpeded. Mechanisms of establishment and colonization, like seed dispersal, sprouting, migration, and germination from the seed bank, determine the speed of tree establishment and forest regrowth. At first, few if any trees are present, and herbs and seedlings are the dominant vegetation type. In general, sapling density increases until about 8 years (around 125 individuals/100 m^2), and then decreases gradually as the fallow ages and shade from the canopy thins the understory (see Figure 4). Tree density and diameter both increase consistently with age and development (see Figure 4 and Figure 5). Height increases rapidly during the first six years and then experiences a lull in height accumulation until about 20 years of regrowth (see Figure 6). An important trend during successional development is the general increase in the standard deviation, indicating an increasing diversity in forest and plant structure with age. Total basal area increases over the long term, at first increasing rapidly then slowing its pace after about 10 years (see Figure 7). The growth pattern for tree basal area is similar, but generally more gradual. Sapling basal area increases dramatically until about six years and then remains fairly constant until 20 years when slow-growing mature forest species occupy the area, and shade from the fuller canopy eliminates light demanding saplings. Changes in basal area reflect a delicate balance between tree and sapling basal area. Initially saplings contribute more

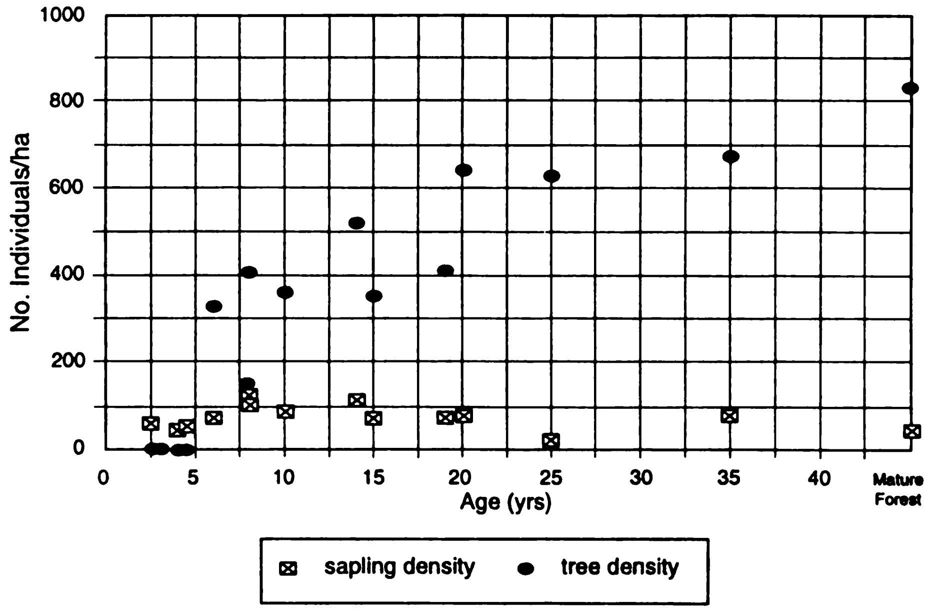


Figure 4
Density Change in Succession
Igarape-Acu

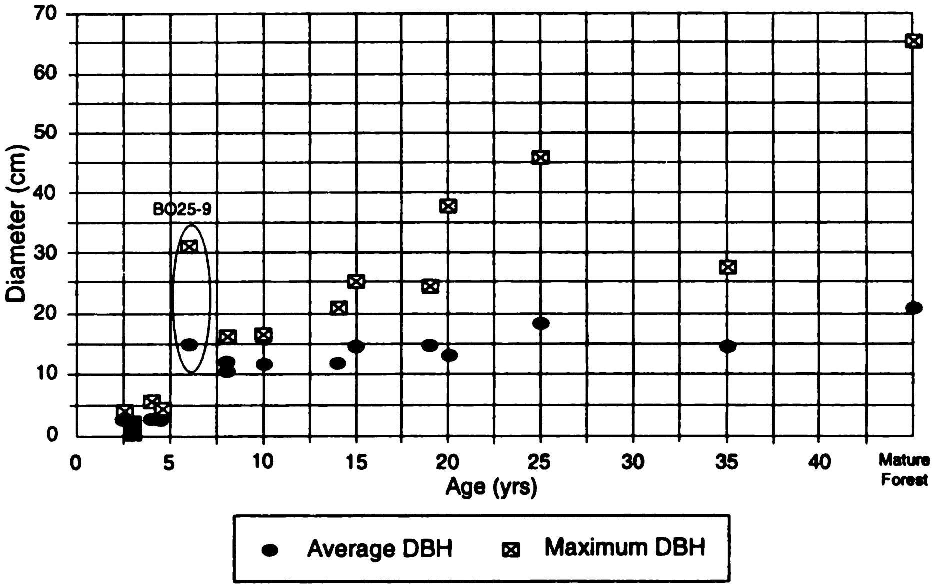


Figure 5
Diameter Change in Succession
Igarape-Acu

to total basal area until shade from the canopy relegates the them to a subordinate level and trees dominate. In Igarapé-Açu, this transition does not occur until after 20 years of fallow.

The slowing of height and basal area accumulation between six and twenty years of fallow may indicate a transitional period in forest development and calls for more research. The variation in structural parameters in the 6-10 year age class overlaps with the variation found in the greater than 10 year age class until 20 years (Table 2). Saldarriaga (1985) found that the rate of biomass accumulation declines after ten years of fallow because a high percentage of pioneer species die off within 20 years and are replaced with slow growing mature forest species. This may help explain our findings in Bragantina as well.

The slowing of plant growth, or lull, between approximately six and twenty years has important management implications. If little change occurs between seven and twenty years then farmers may be able to shorten the fallow cycle without sacrificing the amount of ash or nutrient input (the result of biomass burning). However, the impacts of shortening the fallow cycle on species composition and diversity also need to be considered as a possible trade-off. Other authors have demonstrated that shortening the fallow cycle significantly reduces species diversity, and therefore damages the forests ability to recover over the long term and implies potential species loss (Vieira, *et al.* 1996).

Factors Influencing Regrowth

Besides environmental factors, such as soil properties, original vegetation, and surrounding landscape, different human factors either speed or retard forest succession. Farmers direct the path of regrowth through burning, clearing size, repetition or frequency of land use, duration of land use, technology employed, external inputs like fertilizers, use sequence, and cropping regime. These variables influence regrowth mechanisms in various ways by affecting the soil seed bank, sprouting, migration, dispersal of species by animals and wind, and seed and seedling survival. Successional studies void of the human dimension therefore ignore a key dimension of reforestation. Structural variation among sites within the same age group help isolate factors, both human and environmental, which influence the rate of succession. The following explores three site by site comparisons which pinpoint various factors that impact forest regrowth in Igarapé-Açu.

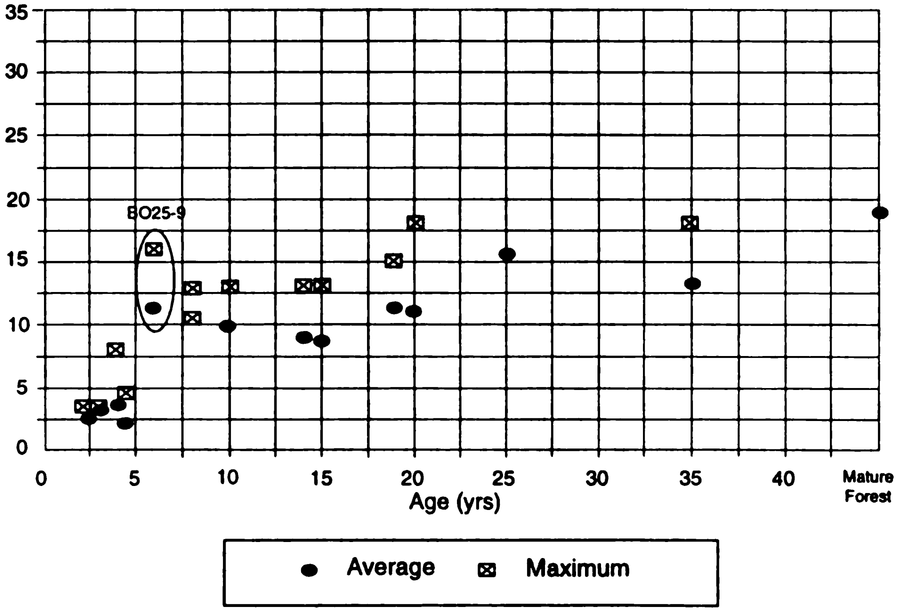


Figure 6
Total Height Change in Succession
Igarape-Acu

Specific Case Examples

1.

Land use choices play a critical role in the growth of saplings in early secondary succession. In particular, researchers have pointed out that pasture weakens the land's ability to recover (Uhl, *et al.* 1988, Nepstad et al. 1991). In most cases in Amazonia, pasture management involves frequent burning, overstocking, and large areal extent exhausts the land — practices which tends to slow forest regeneration. The abandoned pasture site (B005-94) in our sample supports the idea that pasture hinders secondary succession. The site is exceptionally dominated by grasses: 18 of the 25 subplots having at least 70 percent ground cover of grasses. *Brachiaria humidicola* and *Paspalum conjugatum* still dominate the area three years after abandonment (each of the twenty-five 2 x 2 meter subplots had an average grass cover of 71%). The other similarly aged fallows exhibit no such dominance by grasses. Moreover, the previously pastured site is the only 0-5 year fallow with no saplings. In general, the prevalent practice of clearing extensive areas (often more than 100 hectares) for pastureland restricts seed dispersal, especially since about 90% of the native forest species in Paragominas, Para, Brazil, have fruits that are dispersed by birds, bats, and/or mammals, and many of these animals refuse to move into large clearings (Uhl, et al. 1988). Furthermore, soil compaction from cattle and from bulldozer use, common to pasture clearing and cleaning, hinders germination and root penetration. Bulldozers also scrape away topsoil which holds the majority of the seeds of woody species and leaves only the deeper seed bank which is dominated by weedy species. Thus the microclimatic conditions and extensive forest clearings created by typical pasture management practices tend to restrict forest regeneration, as exemplified by site B005-95.

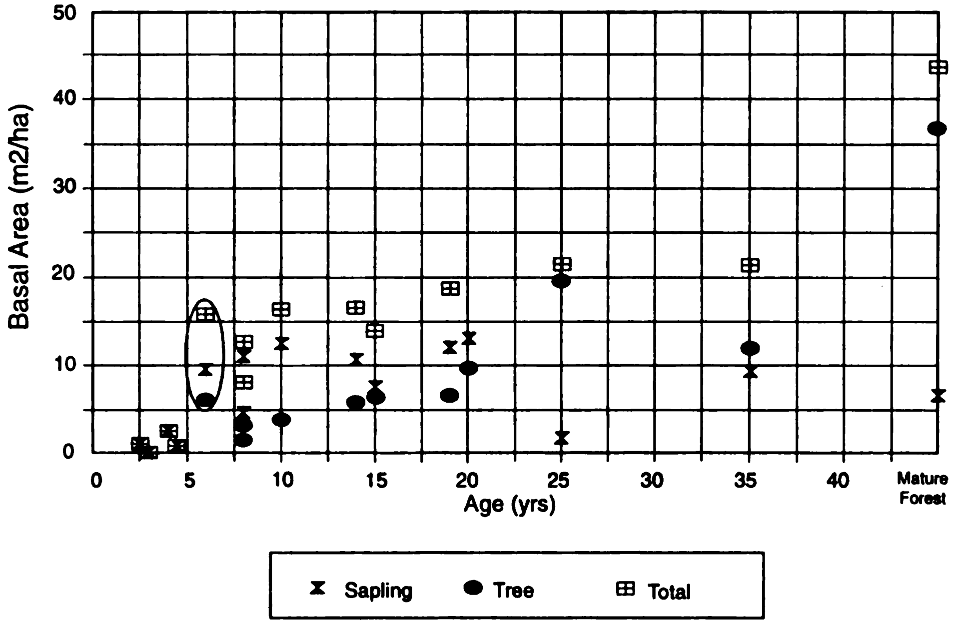


Figure 7
Basal Area Change in Succession
Igarape-Acu

2.

The length of the fallow cycle, another aspect of land use history, is also expected to impact the rate of tree establishment and growth. The longer the fallow period between crops the more time for the vegetation to recover to a level where edaphic conditions and nutrient cycling more resemble a mature forest. Also, older secondary forests attract more mature forest species, and thus develop a more diverse seed bank. Therefore, the conditions for forest regrowth will be more favorable the longer the field is left fallow. Sample site B026-95, a four year old fallow, experienced a fallow period of about 40 years prior to the cultivation and harvest of manioc. A presumably more diverse seed bank left over from the old fallow and recovered edaphic conditions contribute to the higher level of development at site B026-95 in comparison with other sites of about the same age. Total height and diameter (both average and maximum) are superior, and this four year old fallow has over twice as much basal area as a four-and-a-half year fallow which was planted in beans, corn, and manioc following a fallow period of only about six years (Table 2). A longer fallow period not only increases regrowth potential but may also improve conditions for crops, increasing production.

3.

Unexpectedly, the youngest fallow in the 6-10 age class (B025-95), only six years old, has the highest mean (14.72 cm) and maximum (31.3 cm) dbh as well as the greatest mean (11.14 m) and maximum (16 m) heights (Table 2). It also exhibits the largest tree basal area of all 6-10 year old sites. The site's last cropping cycle is very similar to the other sample sites in the same age class (see Table 1), but its soil is unique (see Table 3) and may help to explain the abnormally quick forest recovery at the site. It exhibits a very rocky soil with relatively high potassium content in addition to a relatively high percentage of clay for the region (18% in the first 20 cm). Clayey soils tend to hold the nutrients and minerals long enough for nutrient uptake to occur (Jordan 1985). One of the possible explanations is that the combination of rocks and clay promotes favorable water holding capacity and percolation. Since nutrients are often tied up in the soil solution - a mixture of water and other substances - water holding capacity is not only important in terms of water availability, but also in terms of nutrient availability. Moreover, the rocky texture of the soil resists compaction and is likely to instigate better drainage, better aeration, and hence better plant growth. The relatively higher potassium content in the soil's first 20 centimeters may also have played a role in the fallow's quicker rate of regrowth. More research is needed to understand the relationship between rates of regrowth and soil properties in the humid tropics.

CONCLUSIONS

By comparison of similarly aged fallowed sites, we have confirmed that succession is highly impacted by land use history as well as soil characteristics. Pasture restricts tree species establishment due to high root competition from grasses, soil compaction, clearing size, and reduced the habitat for seed dispersers. As a function of land management, the length of the past fallow periods also impacts regrowth. Longer fallow periods, improve edaphic conditions and enrich the seed bank - two important factors in colonization and tree species establishment. Physical characteristics of the soil play a third crucial role in the rate of succession, but are relatively uncontrollable by small farmers. More research of the affects of physical properties of

Table 3. Chemical and Physical Soil Analysis - sites from the 6-10 year age class in Igarape-Acu

Region	Site No.	Age (years)	Depth (cm)	pH	Al Meq/100g	CA+MG Meq/100 g	K	P ppm	M.O %	N %	C %	C/N	Coarse sand(%)	Fine sand(%)	silt %	clay %
Bragantina	B025-95	6	0-20	4.8	1	0.80	0.10	1	2.72	0.04	1.58	39.5	31	32	19	18
Bragantina	B025-95	6	20-40	4.8	1	0.40	0.05	1	1.74	0.05	1.01	20.2	28	31	17	24
Bragantina	B025-95	6	40-60	4.8	0.9	0.40	0.04	1	1.05	0.04	0.61	15.25	28	30	18	24
Bragantina	B025-95	6	60-80													
Bragantina	B025-95	6	80-100													
Bragantina	B027-95	8	0-20	4.8	0.6	0.70	0.05	1	1.58	0.05	0.92	18.4	43	28	21	8
Bragantina	B027-95	8	20-40	5.1	0.7	0.40	0.03	1	1	0.05	0.58	11.6	35	27	28	10
Bragantina	B027-95	8	40-60	5.1	0.7	0.60	0.03	1	0.7	0.04	0.41	10.25	34	25	19	22
Bragantina	B027-95	8	60-80	5.3	0.8	0.70	0.04	1	0.6	0.02	0.35	17.5	33	24	17	26
Bragantina	B027-95	8	80-100	5.2	0.9	0.80	0.04	1	0.58	0.02	0.34	17	33	23	18	26
Bragantina	B010-94	8	0-20	5.3	0.6	0.80	0.02	2	2.45	0.05	1.42	28.4	55	27	10	8
Bragantina	B010-94	8	20-40	5	0.8	0.70	0.02	1	0.72	0.04	0.42	10.5	44	24	2	30
Bragantina	B010-94	8	40-60	4.8	1	0.50	0.02	1	1.19	0.04	0.69	17.25	38	23	7	32
Bragantina	B010-94	8	60-80	4.9	0.8	0.50	0.02	1	0.59	0.04	0.34	8.5	38	23	6	33
Bragantina	B010-94	8	80-100	5	0.8	0.70	0.01	1	0.79	0.04	0.46	11.5	39	22	7	32
Bragantina	B004-94	10	0-20	4.2	1	0.40	0.02	2	2.38	0.07	1.38	19.71429	29	45	15	11
Bragantina	B004-94	10	20-40	4.2	0.8	0.20	0.04	1	1.52	0.04	0.88	22	6	27	7	27
Bragantina	B004-94	10	40-60	4.5	0.9	0.30	0.03	1	0.77	0.05	0.45	9	26	42	9	23
Bragantina	B004-94	10	60-80	4.7	1	0.30	0.03	1	0.19	0.05	0.11	2.2	25	39	6	26
Bragantina	B004-94	10	80-100	4.7	0.8	0.40	0.04	1	0.96	0.05	0.56	11.2	27	40	11	22

soil on the rates secondary succession in the Amazon is desperately needed to understand their role in forest regeneration. Land use decisions which increase the rate of succession can help.

In this paper density, diameter, height, and basal area were used as indicators of regrowth. Forest regrowth was found to be fairly intense during the first six years and then noticeably slowed until about 20 years after abandonment. These findings can be used in a meaningful way by Amazonian farmers in their decisions about when to reclear secondary vegetation for agriculture. If planted crops receive the same nutrient input from a 6 year and a 19 year fallow, shorter fallow periods may help relieve land pressure without sacrificing yields. However, as we showed in the second site by site comparison, fields left fallow for longer periods of time exhibit a slightly faster rate of regrowth. Both of these factors need to be weighed accordingly, and more information about how shorter fallow periods affect species diversity is crucial.

Using age classes to examine the process of secondary forest succession facilitates the comparison of rates of secondary succession among fallows and allows researchers to identify factors which influence successional rates. Nevertheless, significant differences between fallows of about the same age due to variations in land use history, original vegetation, neighboring vegetation, and soil characteristics which impact fallow development restricts the ability to predict regrowth patterns based on age classes.

REFERENCES

Brady, N. C. 1974. *The Nature and Properties of Soils.* MacMillan Publishing Co., Inc., New York.

Campbell, D. G., Daly, D. C., Prance, G. T. and Maciel, U. N. 1986. Quantitative Ecological Inventory of Terra Firme And Várzea Tropical Forest on the Rio Xingu, Brazilian Amazon. *Brittonia,* 38(4): 369-393.

Dantas, M. 1989. *Studies on Succession in Cleared Areas of Amazonian Rain Forest.* Ph.D. Dissertation: Oxford University, Oxford.

Denich, M. 1991. *Estudo da Importâcia de uma Vegetação Secundária Nova para o Incremento da Produtividade do Sistema de Produção na Amazônia Oriental Brasileira.* Ph.D. Dissertation: Departamento de Ciências Agrárias da Universidade Georg August de Göttingen. EMBRAPA/CPATU, Belém, Brasil.

Jordan, C. F. 1985. Soils of the Amazon Rainforest. In G. T. Prance & T. E. Lovejoy (eds.), *Key Environments: Amazonia.* Pages 83-94. Pergamon Press, New York.

Moran, E. F. 1981. *Developing the Amazon.* Indiana University Press, Bloomington, Indiana.
Nepstad, D. C., Uhl, C. and Serrão, E. A. S. 1991. Recuperation of a degraded Amazonian landscape: forest recovery and agricultural restoration. *Ambio* 20(6): 248-255.

Nye, P.H. and Greenland, D.J. 1960. The Soil Under Shifting Cultivation. *Technical Communication No. 51.* Harpenden, U.K.: Commonwealth Agricultural Bureaux of Soils.

Penteado, A. R. 1967. *Problemas de Colonização e de Uso da Terra na Região Bragantina do Estado do Pará.* Tese de doutorado apresentada à cadeira de Geografia do Brasil da Faculdade de Filosofia, Ciências e Letras da Universidade de São Paulo.

Salomão, R. 1994. *Estimativas de biomassa e avalição do estoque de carbono da vegetação de florestas primárias e secundárias de diversas idades (capoeiras) na Amazônia oriental, Municipio de Peixe-Boi, Pará.* Master's thesis: Universidade Federal do Pará, Belém.

Saldarriaga, J. G. 1985. *Forest Succession in the Upper Rio Negro of Colombia and Venezuela.* Ph.D. Dissertation, University of Tennessee.

Smith, N. J.H. 1982. *Rainforest Corridors: The Transamazon Colonization Scheme.* University of California Press, Los Angeles, California.

Uhl, C., Buschbacher, R. and Serrão, E. A. S. 1988. Abandoned pastures in eastern Amazonia. I. patterns of plant succession. *Journal of Ecology* 76: 663-681.

Vieira, I. C. G.; Nepstad, D. C., Salomão, R. P., Roma, J. C. and Rosa, N. A. R. 1996. Região Bragantina: as florestas secundárias após um século de agricultura na Amazônia. *Ciência Hoje.*

Vieira, L.S.; Santos W.H.P.; Falesi, I. And Oliveira, J.P.S. 1967. Levantamento de Reconhecimento dos Solos da Região Bragantina Estado do Pará. Instituto de Pesquisa e Experimentação do Norte, Belém. *Boletim Técnico* No. 47.

Watrin, O. S. 1994. *Estudo da Dinamica na Paisagem da Amazônia Oriental Através de técnicas de geoprocessamento.* Master's Thesis: INPE, São José dos Campos, São Paulo.

DINÂMICA DE CRESCIMENTO E REGENERAÇÃO NATURAL DE UMA FLORESTA SECUNDÁRIA NO ESTADO DO PARÁ

Lia C. de Oliveira
Depart. de Ciências Florestais, Faculdade de Ciências Agrárias do Pará, Belem, Pará, Brazil

ABSTRACT

Management of secondary forests is an option for alternative land use which is becoming important in both the Brazilian and international contexts, as the number of abandoned areas increases due to shifting agriculture, extensive pasture and intensive and uncontrolled logging. This paper is an analysis of the dynamics of growth and natural regeneration of a 48 hectare area of secondary forest of about fifty years in age, situated on the Tapajos plateau, in Belterra, municipality of Santarem, Para. The study was based upon a continuous forest inventory using 12 permanent sample plots of 0,25 ha, carried out over a period of 10 years. Results show that the population, at present, has 88 species, 75 genera and 38 botanical families. The ecological group of long-lived intolerants dominated the upper forest with 61% of number, 84% of the basal area and 94% of the total volume, amongst these Jacaranda copaia, Vochysia maxima and Didymopanax morototoni, all commercial species, are the most abundant. Over the period monitored, the averages of periodic annual increment in diameter for the tree strata, were 0,44 cm yr^{-1}*. The long-lived intolerants had diameter increment significantly greater than the other groups of species. The stand has maintained a positive balance in the last ten years with the number of new trees being higher than mortality in the tree population. The quantity and distribution of rainfall influenced, in a determining way, the natural regeneration. The rates of growth oscillated throughout the year according to the quantity of rainfall in the region. This influence occurred, on a greater scale, among the light-demanding species.*

INTRODUÇÃO

As florestas tropicais vêm sendo reduzidas a um ritmo acelerado nas últimas décadas. Grande parte desta redução foi devida ao aumento da demanda por produtos florestais, aliada a constante conversão dos ecossistemas primários em outras formas de uso da terra, especialmente nas nações em desenvolvimento da América Latina. Durante o período de 1981 a 1992 a média anual de desmatamento nesta região foi de 0,9%, resultando na perda de 8,3 milhões de ha por ano (FAO, 1992).

De maneira simultânea ao recuo das florestas primárias da América tropical, as áreas de sucessão secundária, que cobrem 1.200.000 km^2, vêm crescendo a uma taxa aproximada de

15.000 km^2 por ano (SIPS, 1993). Este importante processo de recuperação do ecossistema florestal se inicia com uma vegetação herbácea e arbustiva, que acaba por criar condições propícias para dar início a uma nova vegetação arbórea denominada floresta secundária.

Neste trabalho, foi considerada a definição proposta por FINEGAN (1992b), onde compreende-se como floresta secundária toda a vegetação lenhosa que se desenvolve através do processo de sucessão secundária em áreas que são abandonadas, depois que sua vegetação original é destruída pela atividade antrópica.

A maior parte das florestas secundárias do trópico úmido é proveniente da agricultura migratória e pastagens abandonadas. Na América do Sul, a extensão de florestas secundárias regenerando em áreas agrícolas abandonadas é da ordem de 83 milhões de ha (FAO, 1985). Na Amazônia brasileira, estima-se que pelo menos 400.000 ha são deixados anualmente em pousio pela atividade da agricultura migratória (YARED & BRIENZA JR., 1989).

SERRÃO & TOLEDO (1989) estimam que cerca de 10 milhões de hectares de pastagens formadas na Amazônia, nos últimos 25 anos, atingiram avançados estágios de degradação originando vegetação secundária.

A grande extensão de áreas de florestas secundárias existentes na Amazônia, aliada ao pouco conhecimento científico desse tipo de vegetação, justifica a necessidade de estudos que possam contribuir para determinar parâmetros para o seu manejo. Com isso, as florestas secundárias poderiam servir como uso alternativo da terra, diminuindo a pressão de desmatamento sobre as florestas primárias e proporcionando renda adicional aos produtores agrícolas.

O presente trabalho visa contribuir para o conhecimento das florestas secundárias através da análise da composição florística e dinâmica de um povoamento, com aproximadamente 50 anos de idade, localizado no município de Belterra - PA.

MATERIAL E MÉTODOS

Características Gerais da Área

O estudo foi realizado em uma área de 48 ha de floresta secundária situada entre 02°17″ e 02°59″ de latitude Sul e 54°36″ e 54°78″ de longitude Oeste, no município de Belterra, Pará - Brasil, cuja altitude é de aproximadamente 175 m.

O clima da região é do tipo Ami pela classificação de Köppen. A temperatura média anual é 24,8°C, com uma umidade relativa em torno de 90%. A precipitação gira em torno de 1915 mm/ano com as maiores taxas ocorrendo de dezembro a maio.

O solo predominante na área é o Latossolo Amarelo Distrófico, textura muito argilosa, com manchas de Latossolo Amarelo Húmico Antropogênico (terra-preta-do-índio).

A área experimental foi desmatada em 1934 pela Companhia de Motores Ford para o estabelecimento de um plantio homogêneo de seringueira (*Hevea* sp.). No final dos anos 40 o plantio foi sendo gradualmente abandonado. A floresta então regenerou naturalmente nas entrelinhas da plantação. Atualmente, após cerca de 50 anos de abandono, bem poucos exemplares de *Hevea* sp. são encontrados no povoamento e a área apresenta-se como uma capoeira alta, dominada por espécies arbóreas pioneiras de rápido crescimento.

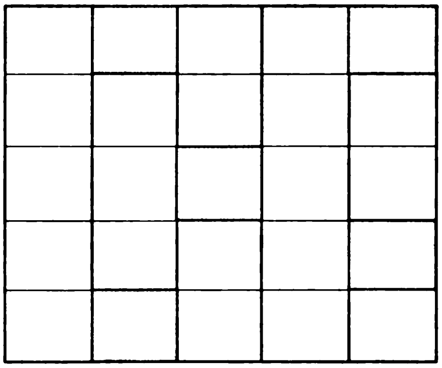
Monitoramento do Estrato Arbóreo

O monitoramento do estrato árboreo foi realizado através de inventário florestal contínuo. Foram instaladas 11 parcelas permanentes de 0,25 ha cada (50 x 50 m), distribuídas aleatoriamente na área experimental. Cada parcela foi subdividida utilizando-se piquetes de demarcação, em 25 sub-parcelas de 10 m x 10 m onde foram medidas todas as árvores com DAP Ú 5 cm (Fig. 1). Cada árvore foi individualmente identificada e etiquetada. Além da medição do diâmetro, foram feitas observações quanto a classe de identificação do fuste (CIF), iluminação e forma da copa, grau de aproveitamento comercial do fuste e presença e efeito de cipós na árvore. As parcelas foram instaladas e medidas em 1983, com medições posteriores em 1985, 1987, 1991 e 1993, perfazendo um total de dez anos de observações.

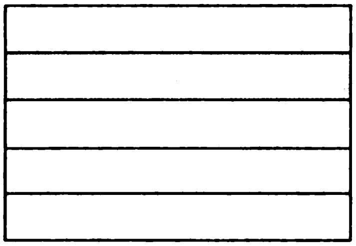
As espécies encontradas na área foram divididas em grupos ecológicos, de acordo com a classificação proposta por FINEGAN (1992a). Os grupos foram: Heliófilas Efêmeras, Heliófilas Duráveis, Esciófitas Parciais e Esciófitas Totais.

Monitoramento da Regeneração Natural

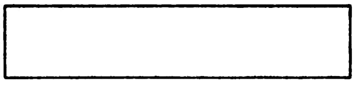
Para avaliar a quantidade, a qualidade e o crescimento da regeneração natural, foram instaladas, de forma aleatória dentro de cada parcela de monitoramento arbóreo, 5 sub-amostras de 0,0025 ha (5 m x 5 m) para medição de varas e dentro destas, foi sorteada uma faixa de 0,0005 ha (1 m x 5 m) para medição de mudas, perfazendo um total de 55 sub-amostras para o monitoramento de varas e 55 sub-amostras para o monitoramento de mudas (Fig. 1). Foram consideradas como varas todas as árvores com 2,5 cm £ DAP < 5,0 cm, a variável medida foi o diâmetro. Foram consideradas como mudas toda a regeneração com altura superior a 30 cm e que não atingiram 2,5 cm de diâmetro, a variável medida foi a altura.



parcela de 50 m x 50 m
mediçao de árvores



Sub-amostra para medição de varas:5 m x 5 m



Sub-amostra para medição de mudas:
5 m x 1 m

Figura. 1: Esquema de uma parcela permanente de inventário florestal contínuo

Foram realizadas sete coletas de dados de campo nos seguintes meses: janeiro abril, agosto e dezembro de 1992 e março, junho e outubro de 1993.

RESULTADOS E DISCUSSÃO

Composição Florística

O povoamento apresentou 88 espécies, pertencentes a 75 gêneros e 38 famílias botânicas. O grupo com maior número de representantes foi o das esciófitas parciais, que apresentou 27 espécies (30,7% do total). O segundo maior grupo foi o das heliófilas duráveis com 24 espécies (27,3%), seguido das heliófilas efêmeras com 23 espécies (26,0%) e das esciófitas totais com 14 espécies (15,9%).

A presença de 41 espécies esciófitas ou tolerantes no povoamento pode ser explicada pelo adiantado estágio de sucessão em que se encontra a floresta, que já apresenta, em vários pontos, o dossel parcialmente fechado pelas espécies heliófilas, gerando condições ambientais e ecológicas favoráveis ao desenvolvimento deste grupo. Outro fator que pode ter contribuído é a existência de áreas de floresta primária nas cercanias do povoamento que vêm funcionando como fonte de sementes.
As espécies que compõem a vegetação da área estudada estão relacionadas na Tabela 1 (em anexo), na qual apresentam-se também os grupos ecológicos e as classes de tamanho nas quais as espécies ocorreram.

Quanto ao aspecto dinâmico, pôde-se observar o surgimento de 4 novas famílias, 12 novos gêneros e 13 novas espécies, em um período de 10 anos. Isso indica um aumento em torno de 2,2% ao ano na diversidade de espécies. Esse aumento na diversidade da composição florística é característico de povoamentos jovens, onde a entrada de novos indivíduos é consequência natural do processo de sucessão a que estão sujeitos.

Valores semelhantes para aumento de diversidade foram obtidos por CROW (1980) em povoamentos secundários, com mais de 30 anos, na região de Luquillo, em Porto Rico, onde foram encontradas 71 espécies/ha com um crescimento de 2,3%/ano na diversidade.

Estrutura da floresta: número de árvores, área basal e volume/ha

O número de árvores, área basal e volume por ha, de acordo com o grupo ecológico, registrados na última medição, realizada em 1993, são mostrados na Tabela 2.

TABELA 1 : Lista de espécies ocorrentes na floresta secundária - Quarubal em Belterra, Santarém - Pa.

				Classes de Tamanho		
GE.	Nome Científico	Nome Vulgar	Família	I	II	III
EP	*Aspidosperma desmanthum* Benth	Araracanga	Apocinaceae			X
EP	*Astronium lecointei* Ducke	Muiracatiara	Anacardiaceae	X	X	
EP	*Bowdichia nitida* Spruce	Sucupira	Leguminosae			X
EP	*Brosimum discolor* Schott	Muirapinima	Moraceae	X		X
EP	*Byrsonima crispa* Juss.	Muruci-da-mata	Malpighiaceae	X		
EP	*Casearia favitensis* H. B. K.	Caneleira	Flacourtiaceae	X	X	X
EP	*Connarus* sp. L.	Connarus	Connaraceae	X		
EP	*Copaifera martii* Hayne	Copaibarana	Leguminosae			X
EP	*Diplotropis purpurea* (Rich.) Amsh.	Sucupira-preta	Leguminosae	X	X	X
EP	*Endopleura uchi* (Huber) Cuatr	Uxi-liso	Humiriaceae	X		X
EP	*Eschweilera amara* Ndz.	Matamata-verm.	Lecythidaceae	X		
EP	*Eschweilera odora* (Poepp.) Miers	Matamata-branco	Lecytidaceae		X	X
EP	*Eugenia* sp. L.	Eugenia	Myrtaceae	X		X
EP	*Guarea kunthiana* A. Juss.	Andirobarana	Meliaceae	X		
EP	*Holopyxidium jarana* Ducke	Jarana	Lecythydaceae	X		X
EP	*Hymenaea courbaril* L.	Jutai-açu	Leguminosae	X		
EP	*Hymenaea parvifolia* Huber	Jutai-mirim	Leguminosae	X		
EP	*Licania heteromorpha* Benth.	Macucu	Chrysobalanaceae			X
EP	*Licania* sp. Aubl.	Licania	Chrysobalanaceae			X
EP	*Licaria canella* (Meissn.)Kosterm	Louro-preto	Lauraceae	X	X	X
EP	*Luehea speciosa* Willd.	Açoita-cavalo	Tiliaceae	X		
EP	*Maytenus pruinosa* Reiss.	Chichua	Celastraceae	X		
EP	*Neea* sp. Ruiz et Pav.	Neea	Nyctaginaceae	X		X
EP	*Pithecelobium cauliflorum* Mart.	Ingarana	Leguminosae	X		
EP	*Polygala spectabilis* DC.	Quemembeca	Polygonaceae			X
EP	*Protium apiculatum* Swartz	Breu	Burseraceae	X	X	X
EP	*Saccoglottis* sp. Mart.	Uxirana	Humiriaceae	X	X	X
EP	*Sahagunia racemifera* Huber	Janita	Moraceae	X	X	X
EP	*Siparuna decipiens* A. DC.	Capitiu	Monomiaceae	X	X	X
EP	*Sloanea froessi* C.E. Smith	Urucurana	Elaeocarpaceae	X	X	X
EP	*Swartzia stipulifera* Harms	Gombeira	Leguminosae	X	X	X
EP	*Trattinickia rhoifolia* Willd.	Breu-sucuruba	Burseraceae	X		
EP	*Virola cuspidata* Warb.	Ucuuba-vermelha	Myristicaceae			X
EP	*Vismia cavennensis* Pers.	Lacre-branco	Guttiferae	X		X
EP	*Vitex triflora* Vahl	Tarumã	Verbenaceae	X		X
ET	*Ambelania grandiflora* Huber	Culhão-de-bode	Apocynaceae			X
ET	*Couepia bracteosa* Benth	Pajurá-da-mata	Chrysobalanaceae			X
ET	*Coussarea paniculata* A. Rich.	Caferana	Rubiaceae	X	X	X
ET	*Duguetia echinophora* R. E. Fries	Envira-surucucu	Annonaceae	X		X
ET	*Eugenia lambertiana* DC.	Goiabinha	Myrtaceae	X	X	
ET	*Eugenia patrissi* Vahl.	Araçarana	Myrtaceae	X		X
ET	*Guarea* sp. Allem.	Guarea	Meliaceae	X	X	
ET	*Homalium* sp. Jacq.	Homalium	Flacourtiaceae	X	X	
ET	*Lacistema agregatum* Rusby	Mata-calado	Lacistemaceae	X	X	X
ET	*Mabea* sp. Aubl.	Mabea	Euphorbiaceae	X		X
ET	*Malouetia* sp. A. DC.	Malouetia	Apocinaceae	X	X	
ET	*Myrcia* sp. DC.	Murta	Myrtaceae	X	X	X
ET	*Ouratea aquatica* Engl.	Pau-de-cobra	Ochanaceae	X	X	X
ET	*Phyllanthus nobilis* Muell. Arg.	Aquiqui	Euphorbiaceae	X		

TABELA 1 : Continuação.

GE.	Nome Científico	Nome Vulgar	Família	Classes de Tamanho I	II	III
ET	*Poecilanthe effusa* Ducke	Amarelinho	Leguminosae	X	X	
ET	*Psychotria deflexa* DC.	Pimenta-de-jacú	Rubiaceae			X
ET	*Rinorea macrocarpa* Aubl.	Canela-de-velho	Violaceae	X	X	X
ET	*Sapindus saponaria* L.	Saboneteira	Sapindaceae	X		
ET	*Theobroma speciosum* Will.	Cacau-da-mata	Sterculiaceae	X		
HD	*Apuleia molaris* Spruce et Benth	Amarelão	Leguminosae	X		
HD	*Bellucia* sp. Neck.	Muuba	Melastomataceae	X		X
HD	*Cordia bicolor* A. DC.	Freijo-branco	Boraginaceae		X	X
HD	*Didymopanax morototoni* (Aubl) D. et Panch	Morototo	Araliaceae	X	X	X
HD	*Dipteryx odorata* Willd.	Cumaru	Leguminosae			X
HD	*Enterolobium maximum* Ducke	Fava-bolacha	Leguminosae	X		
HD	*Guatteria poeppigiana* Mart.	Envira-preta	Annonaceae	X	X	X
HD	*Hevea* sp. Aubl.	Seringueira	Euphorbiaceae	X	X	X
HD	*Hymenolobium excelsum* Ducke	Angelim-da-mata	Leguminosae	X		
HD	*Inga heterophylla* Willd.	Inga-xixi-vermelho	Leguminosae			X
HD	*Inga* sp. Scop.	Inga	Leguminosae	X	X	X
HD	*Jacaranda copaia* (Aubl.) D. Don.	Parapara	Bignoniaceae	X		X
HD	*Miconia* sp. Ruiz et Pav.	Papaterra	Melastomataceae	X	X	X
HD	*Ocotea acutangula* Mez	Canela	Lauraceae			X
HD	*Ormosia discolor* Spruce et Benth	Tento-folha-graúda	Leguminosae	X	X	
HD	*Ormosia* sp. Jack	Tento	Leguminosae	X		X
HD	*Parkia pendula* Benth	Fava-bolota	Leguminosae			X
HD	*Piptadenia suaveolens* Miq.	Faveira-folha-fina	Leguminosae	X		X
HD	*Pithecelobium racemosum* Ducke	Angelim-rajado	Leguminosae	X	X	X
HD	*Qualea* sp. Aubl.	Mandioqueira	Vochysiaceae	X		
HD	*Sclerolobium chrysophyllum* Poepp & Endl.	Taxi-vermelho	Leguminosae	X		
HD	*Sclerolobium guianensis* Benth	Taxi-branco	Leguminosae	X		X
HD	*Sclerolobium* sp. Vog.	Taxi	Leguminosae	X		X
HD	*Simaruba amara* Aubl	Marupa	Simarubaceae	X		X
HD	*Stryphnodendron pulcherrimum* Hachr.	Fava-barbatimão	Leguminosae			X
HD	*Tachigalia myrmecophyla* Ducke	Taxi-pto-f.graúda	Leguminosae	X		
HD	*Talisia longifolia* (Benth) Radlk	Pitomba	Sapindaceae	X	X	X
HD	*Tapirira guianensis* Aubl.	Tatapiririca	Anacardiaceae	X	X	X
HD	*Terminalia amazonica* Exell.	Cuiarana	Combretaceae	X		
HD	*Vochysia maxima* Ducke	Quaruba-verdadeira	Vochysiaceae	X	X	X
HE	*Cecropia leucoma* Miquel	Embauba-branca	Moraceae	X		X
HE	*Pourouma longipendula* Ducke	Embaubarana	Moraceae	X		X
HE	*Vismia japurensis* H.G. Reich.	Lacre-vermelho	Guttiferae	X	X	X
HE	*Vismia* sp. Vand.	Vismia	Guttiferae	X		X

GE: Grupo Ecológico; EP: Esciófita Parcial; ET: Esciófita Total; HD: Heliófila Durável; HE: Heliófila Efêmera; I: Árvore (DAP ≥ 5,0 cm); II: Varas (2,5 > DAP < 5,0 cm); III: Mudas (H ≥ 30 cm e DAP < 2,5 cm).

TABELA 2: Número de árvores, área basal e volume por hectare e por grupo ecológico, registrados em 1993, em uma floresta secundária em Belterra, Santarém - Pa..

Grupos	N/ha	%	AB (m^2 ha^{-1})	%	Vol (m^3 $há^{-1}$)	%
Escióftas Totais	237,8	22,2	1,5	7,6	2,4	1,8
Escióftas Parciais	147,6	13,8	1,1	5,6	2,8	2,2
Heliófilas Duráveis	648,7	60,5	16,6	83,8	121,7	93,5
Heliófilas Efêmeras	37,5	3,5	0,6	3,0	3,2	2,5
Total	1071,6	100,0	19,8	100,0	130,1	100,0

* Para o cálculo do número de árvores e área basal foram consideradas todas as árvores com DAP ≥ 5 cm, para o cálculo do volume, apenas as com DAP ≥ 20 cm.

No último inventário, realizado em 1993, o povoamento apresentou em torno de 1.072 árvores por hectare, aproximadamente 20 m^2 ha^{-1} de área basal e 130 m^3 ha^{-1} de volume total.

Estes valores são compatíveis com os obtidos por diversos autores em outras florestas secundárias tropicais. CROW (1980), considerando todas as árvores com DAP ≥ 4,0 cm, em um povoamento secundário com aproximadamente 30 anos em Porto Rico, observou a presença de 1.015 indivíduos/ha com área basal de 35,7 m^2 ha^{-1}. ULH & MURPHY (1981) estudando florestas secundárias com aproximadamente 60 anos, em São Carlos na Venezuela, observaram a presença de 518 árvores com DAP ≥ 10 cm, por hectare.

Pode-se observar na Tabela 2, que o povoamento apresenta uma dominância de espécies heliófilas duráveis, tanto em termos de número, como em área basal e volume, apresentando aproximadamente 61% do número total de árvores e 84 e 94% da área basal e volume total da população, respectivamente.

As espécies escióftas totais e escióftas parciais, características de povoamentos primários, já começam a se destacar, apresentando juntas 36% do total de árvores, 13,2% da área basal e 4% do volume por hectare do povoamento. A maioria das árvores destes dois grupos apresenta diâmetros inferiores a 20 cm e está concentrada no sub-bosque, sob a sombra das espécies heliófilas.

As espécies heliófilas efêmeras, características das primeiras fases de sucessão estão pouco representadas, uma vez que, no atual estágio do povoamento, o dossel já apresenta-se parcialmente fechado dificultando a germinação e desenvolvimento das espécies deste grupo

Na tabela 3 estão relacionadas as sete espécies mais importantes na estrutura horizontal da floresta.

No grupo das heliófilas duráveis, encontram-se seis das mais abundantes espécies do povoamento, que representam juntas aproximadamente 64% do número e 85% da área basal total. *Miconia* sp. com 328,7/ha, *Myrcia* sp. com 190,5/ha e *Bellucia* sp. com 118,2/ha dominam o estrato médio da floresta, apresentando indivíduos cujo diâmetro varia entre 10 e 30,0 cm.

TABELA 3: Representação das 7 espécies (DAP ≥ 5,0 cm) mais importantes na estrutura horizontal de uma floresta secundária em Belterra, Santarém - Pa.

Grup Ecol.	Espécies	Família	Nº de Arv./ha	AB (m^2 ha^{-1})	Freq(%)	IVI
HD	*Miconia* sp.	Melastomataceae	328,7	3,50	93,5	58,6
HD	*Jacaranda copaia*	Bignoniaceae	105,1	4,74	50,2	38,8
ET	*Myrcia* sp.	Myrtaceae	190,5	1,26	74,9	33,8
HD	*Bellucia* sp.	Melastomataceae	118,2	2,71	45,4	29,7
HD	*Vochysia maxima*	Vochysiaceae	55,3	2,83	32,0	22,9
HD	*Didymopanax morototoni*	Araliaceae	42,9	1,53	28,0	15,2
HD	*Tapirira guianensis*	Anacardiaceae	37,5	1,63	24,7	14,7

EP: esciófita parcial, ET: esciófita total HD: heliófila durável, HE: heliófila efêmera.

As espécies *Jacaranda copaia, Vochysia maxima,* e *Didymopanax morototoni,* além da importância ecológica para a estrutura do povoamento, destacam-se por serem comercializadas no mercado interno e externo. Dentre estas, a *Vochysia maxima* possui grande importância fitossociológica e silvicultural por apresentar abundante regeneração natural e distribuição uniforme em todas as classes diamétricas.

Potencial de Aproveitamento Comercial

O número de árvores, área basal e volume por ha, de acordo com o potencial de aproveitamento comercial, registrados na última medição, realizada em 1993, são mostrados na Tabela 4.

TABELA 4: Número de árvores, área basal e volume por hectare e por grupo de utilização, registrados em 1993, em uma floresta secundária em Belterra, Santarém - Pa.

Grupos	Nº Arv./ha	AB (m^2 ha^{-1})	Vol (m^3 ha^{-1})
Comerciais + Potenciais	325,5 (30,4%)	11,9 (59,9%)	104,5 (80,3%)
Demais Espécies	746,9 (69,6%)	7,9 (40,1%)	25,6 (19,7%)
Total	1072,4 (100 %)	19,8 (100 %)	130,1 (100 %)

* Para o cálculo do número de árvores e área basal foram consideradas todas as árvores com DAP ≥ 5 cm, para o cálculo do volume, apenas as com DAP ≥ 20 cm.

As espécies utilizáveis, embora representem apenas em torno de 30% do número total de árvores por ha, contribuem com aproximadamente 60% da área basal e 80% do volume total do povoamento. Isso indica a presença de um maior número dessas espécies nas classes de diâmetro mais elevadas (DAP ≥ 20 cm). Tendência inversa se observa em relação as demais espécies que apresentam aproximadamente 70% do número, 40% da área basal e apenas 20% do volume total do povoamento, devido a maior concentração dos indivíduos deste grupo nas classes de diâmetro inferiores (DAP ≥ 20 cm).

A dominância de espécies comercializáveis tem sido observada em diversos povoamentos secundários ao longo da região neotropical. SIPS (1993) ressalta a abundância e o rápido crescimento de espécies heliófilas utilizáveis em bosques secundários úmidos na Costa Rica. HERRERA (1990) observou que em povoamentos com 15 anos na Costa Rica, 80% da área basal e 84% do volume total era composto por espécies comercializáveis (18,0 m^{2} ha^{-1} e 96 m^{3} ha^{-1}). Em povoamentos com 25 anos, esses valores subiam para 85% e 89% (20,0 m^{2} ha^{-1} e 183 m^{3} ha^{-1}), respectivamente.

O povoamento apresenta 20 espécies atualmente comercializadas no mercado de madeiras, entre elas, destacam-se em termos de volume *Jacaranda copaia* (Parapará) com 39,7 m^{3} ha^{-1}, *Vochysia maxima* (Quaruba-verdadeira) com 30,9 m^{3} ha^{-1} e *Didymopanax morototoni* (Morototó) com 12,1 m^{3} ha^{-1}. Algumas dessas espécies não são utilizadas pelas indústrias madeireiras tradicionais (serrarias) por serem consideradas como madeiras leves, de baixa densidade, todavia, podem ser grandemente aproveitadas nas indústrias de compensado e laminado e para a fabricação de polpa e papel.

Além das espécies de valor comercial para serraria, a floresta estudada apresenta também 14 espécies com potencial para lenha, carvão, caixaria, construções rurais, etc. Dentre estas espécies, merecem destaque *Tapirira guianensis* (Tatapiririca) com 11,0 m^{3} ha^{-1}, *Guatteria poeppigiana* (Envira-preta) com 0,7 m^{3} ha^{-1} e *Sclerolobium guianensis* (Taxi-branco) com 3,6 m^{3} ha^{-1}

Incrementos em Diâmetro

As taxas de incremento em diâmetro para os grupos ecológicos de espécies do povoamento são mostradas na Tabela 5.

A média do incremento periódico anual em diâmetro considerando todas as espécies com DAP ≥ 5,0 cm, foi de 0,40 cm ano^{-1}. As espécies heliófilas apresentaram incremento em DAP significativamente superior as esciófitas

TABELA 5: Comparação entre o incremento médio anual em diâmetro (IPA) por grupo de espécies entre 1983-1993. Árvores sobreviventes (CIF = 111), em uma floresta secundária em Belterra, Santarém - Pa.

Grupos ecológicos	Nº absoluto de Arv.	IPA médio (cm)
Heliófila durável	1076	0,45 a
Heliófila efêmera	57	0,45 a
Esciófita parcial	129	0,36 b
Esciófita total	167	0,32 b
Total das espécies	1429	0,40

* Medias seguidas pela mesma letra não apresentam diferença significativa de acordo com o teste SNK ao nível de 0,05 de probabilidade

O maior crescimento médio anual em diâmetro das espécies heliófilas, em relação a outros grupos ecológicos, foi também observado por SWAINE (1990) em florestas primárias de Ghana, onde as espécies heliófilas apresentaram incremento de 0,4 cm ano^{-1}, bastante superior as demais espécies esciófitas ou tolerantes que variaram em torno de 0,1 a 0,2 cm ano^{-1}.

Dentre as espécies do povoamento, *Vochysia maxima* foi a que apresentou a maior taxas de incremento periódico anual em diâmetro, com média de 1,8 cm ano^{-1}. Esse valor é aproximadamente 4,0 vezes superior ao crescimento das demais espécies heliófilas duráveis cujo IPA médio foi de 0,45 cm ano^{-1}.

Elevados valores de IPA em diâmetro para o gênero *Vochysia* também foram observados por HERRERA (1990) em uma floresta secundária com 25 anos na Costa Rica, onde este autor encontrou taxas de incremento para *Vochysia ferruginea* em torno de 1,0 cm ano^{-1}.

Ingressos e Mortalidade

Para o propósito deste estudo, ingressos serão considerados como árvores que atingiram o diâmetro mínimo de 5,0 cm entre duas medições subsequentes e mortalidade como o número de árvores encontradas mortas na época de cada medição.

As causas da mortalidade natural em florestas raramente tem sido examinadas em detalhe. Tempestades, fungos patógenos, herbívoros, condições ambientais adversas como grandes períodos de estiagem, senescência natural, ou ainda uma combinação desses fatores, têm sido apontados como possíveis causas da mortalidade de árvores em florestas tropicais que não sofrem interferência humana (LIEBERMAN et al. 1985).

PUTZ *et al.* (1983), LIEBERMAN et al. (1985) e SWAINE & HALL (1983) comentam que as espécies pioneiras, características das florestas secundárias, possuem, de maneira geral, maiores taxas de mortalidade que as espécies primárias devido ao curto tempo de vida geneticamente controlado e a menor densidade da madeira que torna as árvores mais vulneráveis a ventanias e tempestades tropicais devido a baixa resistência dos troncos.

As taxas de mortalidade e ingressos encontradas no povoamento são apresentadas na Tabela 6. Considerando todo o período monitorado, a floresta apresentou um balanço positivo, sendo o número de árvores mortas aproximadamente 49,2 ha^{-1} ano^{-1} e o número de ingressos de 53,2 ha^{-1} ano^{-1}. Em termos percentuais estes valores indicam que a cada ano a floresta aumenta 5,2% o número total de árvores da população, e perde 4,8% por mortalidade, o que gera, em termos líquidos, um ganho de aproximadamente 0,4 %/ano.

TABELA 6: Taxa anual de mortalidade (TAM) e Ingressos (TAI) por grupo ecológico de espécies (DAP ≥ 5,0 cm) em uma floresta secundária em Belterra, Santarém - Pa.

Grupo Ecológico	Mortalidade		Ingressos	
	Nº/ha	(%)	Nº/ha	(%)
Esciófitas Totais	7,9	(5,5%)	17,5	(12,1%)
Esciófitas parciais	3,3	(4,1%)	10,1	(12,6%)
Heliófilas duráveis	35,7	(4,7%)	24,1	(3,2%)
Heliófilas efêmeras	2,3	(5,0%)	1,5	(3,2%)
Total das espécies	49,2	(4,8%)	53,2	(5,2%)

.(%) - Porcentagem anual de mortalidade e ingressos = porcentagem do montante de árvores vivas no primeiro ano de cada período/nº de anos do intervalo.

No atual estágio de sucessão do povoamento, ainda se observa uma intensa dinâmica entre a entrada e saída de indivíduos. Apesar da tendência ao balanço negativo observado no grupo das heliófilas efêmeras e duráveis, não há evidência que algum grupo ecológico esteja em declínio. Durante os dez anos de observação, as espécies esciófitas totais e parciais apresentaram taxa de ingresso bastante superior a de mortalidade. As elevadas taxas de ingressos nestes dois grupos indicam o avançado estágio sucessional do povoamento, cujo sub-bosque já apresenta os requerimentos de sombra e umidade necessárias para beneficiar estas espécies.

População de varas (2,5 > DAP < 5,0 cm)

O povoamento, de maneira geral, apresentou em média 1.194 varas/ha. Desse total, 498,0/ha (42%) pertencem ao grupo das espécies heliófilas e 696,0/ha (58%) ao grupo das esciófitas (Tab 7).

TABELA 7: Número de varas/ha (2,5 > DAP < 5,0 cm) por grupo ecológico a cada medição em uma floresta secundária em Belterra, Santarém - Pa.

Grupo	Jan/92	Abr/92	Ago/92	Dez/92	Mar/93	Jun/93	Out/93	Média
Heliófilas	545,5 a	524,0 a	524,0 a	502,0 a	473,0 a	451,0 a	466,0 a	498,0 a
Esciófitas	749,0 b	720,0 b	713,0 b	713,0 b	691,0 b	676,0 b	611,0 b	696,0 b
Total	1294,5	1244,0	1237,0	1215,0	1164,0	1127,0	1077,0	1194,0

Médias seguidas pela mesma letra não apresentam diferença significativa de acordo com o teste U Mann-Whitney (P < 0,05).

O número de varas permaneceu praticamente estável durante todo o período de observação nos dois grupos ecológicos, sendo o número de esciófitas significativamente superior ao das heliófilas.

Não houve diferença significativa no crescimento em diâmetro entre os grupos ecológicos ao longo do período de observação. O incremento médio em DAP das espécies heliófilas foi de 0,19 cm ano^{-1} e das esciófitas 0,18 cm ano^{-1} (Tab. 8).

TABELA 8: Crescimento em diâmetro de varas (2,5 cm > DAP < 5,0 cm) por grupo ecológico em uma floresta secundária situada em Belterra, Santarém - Pa.

Grupos de espécies	Média anual de crescimento (cm ano^{-1})
Heliófilas	0,19 a
Esciófita	0,18 a

Médias seguidas pela mesma letra na posição horizontal não apresentam diferença significativa de acordo com o teste S.N.K. (P = 0,05).

Os valores de crescimento nos dois grupos ecológicos permaneceram praticamente constantes durante os 21 meses de acompanhamento, exceto no período de agosto a dezembro de 1992, quando ambos apresentaram uma queda acentuada no incremento em DAP.

Este período coincide com a estação de menor precipitação pluviométrica na região, por isso, acredita-se que a queda no incremento esteja associada a estação seca, que no ano de 1992, foi bastante severa durante os meses de julho a dezembro, com uma média mensal inferior a 40 mm (Fig. 2).

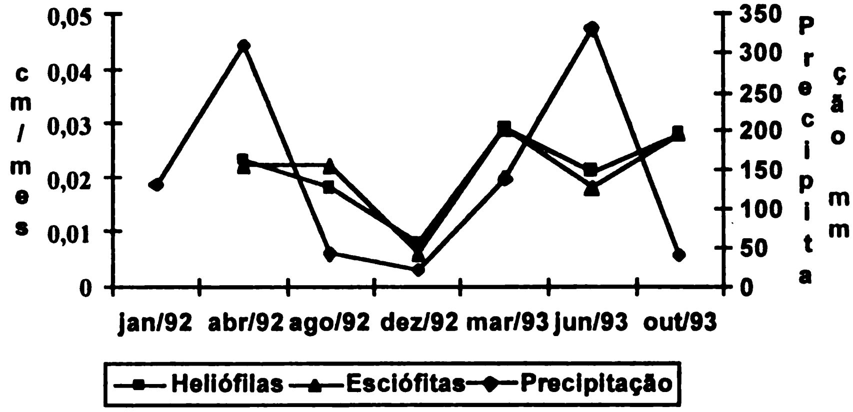


Figura 2: Influência do regime de precipitação pluviométrica no incremento em diâmetro de varas (2,5 cm > DAP < 5,0 cm), por grupo ecológico, em uma floresta secundária situada em Belterra, Santarém - Pa.

LOJAN (1965) demostrou que a quantidade e a duração do período de chuvas exerce grande influência no crescimento das árvores e na da regeneração natural. Segundo este autor, a maioria das espécies tropicais crescem a um ritmo maior durante o período chuvoso e menor durante o período seco, GLOCK & AGERTER (1962) obtiveram coeficientes de correlação variando entre 0,4 e 0,8 para a associação entre precipitação e o crescimento vegetal e afirmaram ser a água um dos principais fatores limitantes do crescimento.

População de mudas (H ≥ 30 cm e DAP < 2,5 cm)

O estoque médio de mudas com altura igual ou superior a 30 cm e diâmetro inferior a 2,5 cm foi de aproximadamente 49.366/ha. Deste total, 11.683 (23,7%) era composto de espécies heliófilas e 37.683 (76,3%) de espécies esciófitas ou tolerantes (Tab. 9).

As médias apresentaram-se pouco variáveis durante os 21 meses de observação, sendo o grupo das esciófitas significativamente superior as heliófilas durante todo o período, de acordo com o teste de U de Mann-Whitney.

TABELA 9: Número de mudas/ha (H ≥ 30 cm e DAP < 2,5 cm) por grupo ecológico, presentes a cada medição, em uma floresta secundária em Belterra, Santarém - Pa.

Grupo	Jan/92	Abr/92	Ago/92	Dez/92	Mar/93	Jun/93	Out/93	Média
Helióf.	11.527 a	11.746 a	12.182 a	11.481 a	11.382 a	11.636 a	11.891 a	11.683 a
Escióf.	37.200 b	38.364 b	38.182 b	36.800 b	37.164 b	37.746 b	38.327 b	37.683 b
Total	48.727	50.110	50.364	48.218	48.546	49.382	50.218	49.366

Médias seguidas pela mesma letra não apresentam diferença significativa de acordo com o teste U Mann-Whitney ($P < 0,05$).

A abundância de mudas em florestas, quer sejam primárias ou secundárias, parece variar grandemente com os tipos florestais. Segundo NICHOLSON (1965), em uma típica floresta de planície de Dipterocarpaceas, o número de mudas por hectare, normalmente varia em torno de 24.700 a 49.400. Em florestas primárias exploradas nas Filipinas, o número de mudas (30 cm de altura a 5 cm de DAP) variou entre 31.200 a 123.000/ha (TOMBOC & BRUZON, 1979).

As espécies heliófilas apresentaram incremento em altura de 10,2 cm ano^{-1}, sendo este valor estatisticamente igual ao obtido pelas espécies esciófitas, que foi de 11,0 cm ano^{-1}. Esta tendência se manteve ao longo de todo o período de estudo (Tab 10)

TABELA 10: Crescimento em altura de mudas (H ≥ 30 cm e DAP < 2,5 cm) por grupo ecológico, em uma floresta secundária em Belterra, Santarém - Pa.

Grupos de espécies	Média anual de crescimento (cm ano^{-1})
Heliófilas	10,2 a
Esciófita	11,0 a

Médias seguidas pela mesma letra na posição horizontal não apresentam diferença significativa de acordo com o teste S.N.K. ($P = 0,05$).

O crescimento da regeneração natural, principalmente na fase de mudas, é bastante irregular e comparações entre taxas de incremento são pouco satisfatórias devido a diferenças entre sítios, parâmetros avaliados e métodos de investigação. Todavia, parece claro para muitos autores, que este crescimento é essencialmente dependente dos suprimentos de água e da quantidade de radiação luminosa que atinge o solo da floresta (LOJAN, 1965; GLOCK & AGERTER, 1962).

As taxas mensais de crescimento em altura sofreram uma queda acentuada durante a estação seca (julho a dezembro/1992). As mudas de ambos os grupos ecológicos cresceram a um ritmo maior durante o período chuvoso e diminuiram seu incremento durante os meses de menor precipitação, o que indica ser a água um dos principais fatores limitantes do crescimento (Fig. 3).

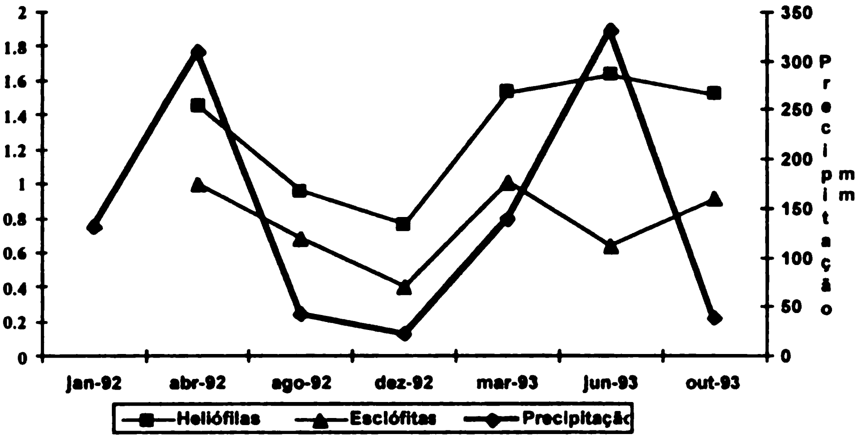


Figura 3: Influência do regime de precipitação pluviométrica no incremento em altura de mudas (H ≥ 30 cm e DAP < 2,5 cm), por grupo ecológico, em uma floresta secundária em Belterra, Santarém - Pa.

CONCLUSÕES

- O crescimento da diversidade no povoamento secundário estudado parece ocorrer de forma bem mais dinâmica do que em florestas primárias. Todavia, apesar do número de espécies ter aumentado em torno de 20% no período de 10 anos, a composição florística da floresta secundária ainda se apresenta bem menos diversificada do que a observada em povoamentos primários da região, ocorrendo a predominância de apenas três a quatro espécies em cada grupo ecológico;

- As espécies heliófilas duráveis dominam o povoamento em termos de número de árvores, área basal, volume. Isso indica que, o processo de sucessão secundária ainda esta em andamento e que, provavelmente, ainda serão necessárias algumas décadas para que a floresta atinja o estado maduro;

- As espécies comerciais representam uma grande proporção da área basal e do volume do povoamento, permitindo, atualmente, o seu aproveitamento comercial. O manejo de florestas como a estudada, pode ser uma opção adicional para aumentar a renda de pequenos proprietários rurais;

- As espécies heliófilas duráveis apresentaram crescimento em DAP significativamente superior aos demais grupos de espécies do povoamento. Dentro deste grupo, destaca-se *Vochysia maxima* que apresentou taxas de incremento periódico anual em diâmetro aproximadamente quatro vezes superior as demais espécies do grupo. O rápido crescimento, boa formação de fuste e abundante regeneração natural fazem da *Vochysia maxima*, uma espécie recomendada para ser manejada através de regeneração natural.

- No atual estágio de desenvolvimento da floresta, não há evidências de que nenhum grupo ecológico esteja em declínio. A média anual de ingressos foi superior a de mortalidade durante o período estudado, indicando que o povoamento, de maneira geral, vem apresentando um balanço positivo em termos de número de árvores/ha;

- A quantidade e a distribuição da precipitação pluviométrica influenciam de maneira marcante a regeneração natural. No estrato de varas, a diminuição da precipitação ocorrida no período de secas da região praticamente paralisou crescimento em diâmetro. No estrato de mudas, observou-se a diminuição dos incrementos em altura nos dois grupos ecológicos, durante o mesmo período.

REFERÊNCIAS

CROW, T.R. A rainforest chronicle: a 30-year record of change in structure and composition at El Verde, Puerto Rico. Biotropica, Ohio-U.S.A., v.12, n.1, p.42-55, 1980.

FINEGAN, B. Bases ecologicas de la silvicultura y la agroforesteria. Turrialba-Costa Rica: Centro Agronomico Tropical de Investigacion y Ensenanza-CATIE, 1992a. 153p. (Mimeogr.).

_______ El potencial de manejo de los bosques húmedos secundarios neotropicales de las tierras bajas. Coleccion Silvicultura y Manejo de Bosques Naturales, Turrialba-Costa Rica, n. 5, p.1-29, 1992b.

FOOD AGRICULTURE ORGANIZATION - FAO. Intensive multiple-use forest management in the tropics, FAO. Forest Paper, n.55, 180p., 1985.

_______.The forest resources of the tropical zone by main ecological regions. Forest Resources Assessment 1990 Project, Rome, 30p., 1992.

GLOCK, W., AGERTER, S.R. Rainfall and tree growth. In KOSLOWSKI T.T Tree Growth. New York: Ronald Press, 1962, p. 23-53.

HERRERA, R.E. Evaluación financiera del manejo del bosque_natural secundario en cinco sitios en Costa Rica. Turrialba, Costa Rica. Universidad de Costa Rica/CATIE, 1990. 120p. Dissertação Mestrado - Universidad de Costa Rica y el Centro Agronomico Tropical de Investigacion y Ensenanza-CATIE, 1990.

LIEBERMAN, D. , LIEBERMAN, M., HARTSHORN, G., PERALTA, R. Growth rates and age size relationships of lowland tropical wet forest trees in Costa Rica. Journal of Tropical Ecology, Cambridge-England, n.1, p.97-109, 1985.

LOJAN, L. Aspectos del crescimiento diamétrico quincenal de algunos árboles tropicales. Turrialba, Turrialba-Costa Rica, v.15, n.3, p.231- 237, 1965.

NICHOLSON, D. I. A review of natural regeneration in the dipterocarp forest of Sabah. The Malasian Forester, Malásia, n.28, p.4-26, 1965.

PUTZ, F.E., COLEY, P.D., MONTALVO, A., AIELLO, A. Snapping and uprooting of trees: structural determinants and ecological consequences. Canadian Journal of Forest Research. Canadá, n.13, p.1011-1020, 1983.

SERRÃO, E.A.S., TOLEDO, J.M. A procura de sustentabilidade em pastagens amazônicas. IN ANDERSON, A.B. Alternatives to deforestation: coexistence of humans and the Amazon Forest. New York, 1989.

SIPS, P.A. Polycyclic Multi-Purpose Management of Tropical Secondary Rainforests. In: AN INTERNATIONAL SYMPOSIUM OF MANAGEMENT AND REHABILITATION OF DEGRADED LANDS AND SECONDARY FOREST IN AMAZONIA, 1993, Santarém, Pará, Brasil. Tropical Forestry Program, Internacional Forestry. Washington: U.S.A. Department of Agriculture - Forest Service (no prelo)

SWAINE, M.D., HALL, J.B. Early succession on cleared forest land in Ghana.Jounal of Ecology, Oxford-England, v. 71, p.601-627, 1983.

SWAINE, M.D. Population dynamics of a moist tropical forest at kade, Ghana. In: ATELIER SUR LÁMÉNAGEMENT ET LA CONSERVATION DE LÉCOSYSTÈME FORESTIER TROPICAL HUMIDE. ACTES, Cayenne-Guyane Francaise, p.40-61, 1990.

TOMBOC, C.C., BRUZON, J.B. Ten-year dynamics of logged-over forest in Surigao del Sur. Sylvatrop Philippines Forest Research, Surigao del Sur - Philippines, v.4, n.3, p.103-122, 1979.

UHL, C., MURPHY, P.G. Composition, structure and regeneration of a tierra firme forest in the amazon basin of Venezuela. Tropical Ecology, Varanasi-India, v. 22, n.2, 1981.

YARED, J.A.G., BRIENZA JUNIOR, A atividade florestal e o desenvolvimento da Amazônia. Pará Desenvolvimento, Belém-Brasil, v.25, p.60-64, 1989.

DINÂMICA DE SEMENTES E REGENERAÇÃO VEGETATIVA EM FLORESTAS SUCESSIONAIS DA AMAZÔNIA ORIENTAL

Ima Célia Guimarães Vieira
Museu Paraense Emilio Goeldi, Departamento de Botânica
C.P. 399, Belém (PA), CEP 66.040-170

John Proctor
University of Stirling
Dept. of Biological and Molecular Sciences
Stirling FK9 4LA, Scotland, UK

ABSTRACT

We evaluated seed bank, seed rain and regeneration from seedlings and sprouts in secondary forests of 5, 10 and 20-years-old following shifting cultivation and a remnant primary forest in the Bragantina region, Pará, Brazil. The seed bank was evaluated in four soil samples of 20 cm x 20 cm taken to a depth of 0-5 cm, and 5-10 cm in three 0.04-ha (5 m x 50 m) plots of each forest age class. To evaluate annual seed rain four seed traps of 1 m^2 *were located in each plot. All plants* $\geq$ *1 m tall and < 5 cm dbh were identified and counted in two random 1m x 5 m subplots in each plot and a distinction was made between seedlings and sprouts. Large plants (*$\geq$ *5 cm dbh) in the same plots were identified and examined for evidence of cutting and resprouting. The studies showed: the largest seed bank (0-5 cm) in the 5-years-old forest (1190 ± 284 seeds* m^{-2}*) and a decrease with age to 137 ± 19 seeds* m^{-2} *in the primary forest; the highest seed rain in the 5-years-old forest (883 ± 230 seeds* m^{-2}*) and least in the primary forest (220 ± 80). Larger plants (*$\geq$ *5 cm dbh) had more individuals and species regenerated from sprouts than from seeds. The smaller individuals (*$\geq$*1m tall, < 5 cm dbh) in the 5-years-old forest arose mainly from sprouts, but these in the older secondary forests arose mainly from seeds. Sprouting is the main source of regeneration for the most abundant species along the chronosequence.*

INTRODUÇÃO

Em geral, as fontes de regeneração de plantas após o uso repetido da terra para cultivo baseado na agricultura migratória são pouco conhecidas. Este trabalho apresenta uma análise destas fontes na Região Bragantina, no nordeste da Amazônia, onde cerca de 90% da floresta primária já foi retirada, e a maior parte da terra sofreu pelo menos oito ciclos de corte, queima e abandono. Analisamos o banco de sementes do solo e a chuva de sementes em florestas secundárias de 5, 10 e 20 anos e em uma floresta primária, e a regeneração de plântulas e brotações nas florestas secundárias, e avaliamos a importância relativa dessas fontes de regeneração para a recuperação de florestas.

ÁREA DE ESTUDO

A Região Bragantina (0° 45′ - 1° 39′ S and 46° 16′ - 48° 15′ W) (Fig. 1) é a mais antiga fronteira agrícola na Amazônia (Oliveira, 1983). A colonização ocorreu durante os primeiros anos do século passado, quando milhares de imigrantes da Europa (principalmente espanhóis, portugueses e franceses) e do nordeste do Brasil foram trazidos para se tornarem produtores (Penteado 1967). O sistema de cultivo era baseado na agricultura migratória e a maioria das terras foi posteriormente abandonada, transformando-se em florestas secundárias ou *capoeiras*.

A região apresenta um relevo suave, com elevações que não ultrapassam os 50 m. A temperatura média anual é de cerca de 25,5°C e a precipitação anual é de cerca de 2.300 mm. A maior parte da precipitação ocorre de janeiro a março e há um período de seca de setembro-novembro (com menos de 150 mm de precipitação). Os solos (incluindo aqueles sob as parcelas estudadas) são predominantemente oxisols e têm composição química e física semelhantes (Vieira 1996).

As áreas de florestas secundárias foram selecionadas após entrevista com residentes locais (Vieira 1996), sob o critério de terem sido utilizadas intensivamente durante pelo menos oito ciclos de agricultura migratória com culturas anuais, e não terem sofrido aplicação de herbicidas ou fertilizantes.

MATERIAIS

Banco de sementes no solo

Quatro amostras de solo de 20 x 20 cm foram coletadas aleatoriamente em cada parcela de 250 m^2 nas florestas secundárias e ao longo de cada uma de três parcelas de 1 ha estabelecidas aleatoriamente na floresta primária, a profundidades de 0-5 cm e 5-10 cm (total de 12 amostras para cada classe etária de floresta e profundidade de solo). Todas as amostras foram espalhadas separadamente com profundidades de cerca de 3 cm em bandejas de 25 x 40 cm, sendo mantidas úmidas e bem ventiladas ao ar livre, sob uma cobertura telada. As amostras foram examinadas a cada 7 dias nos primeiros dois meses, e a cada 14 dias após este período. Os solos foram revirados nas bandejas após quatro meses e observados por mais dois meses. Todas as plântulas eram identificadas assim que emergiam.

Chuva de sementes

Quatro coletores de sementes (tecido esticado em moldura de madeira) de 1 m² foram colocados aleatoriamente dentro de cada parcela a cerca de 1 m do solo. Os coletores foram visitados a cada 14 dias, no período de 1 de Abril de 1993 a 31 de março de 1994. Todas as sementes visíveis e saudáveis eram contadas e retiradas, e as sementes não identificadas foram colocadas para germinar em casa de vegetação. Fezes de animais e diversos resíduos encontrados nos coletores foram colocados em câmara de germinação (FANEM model 347) com bastante luz e temperatura constante de 30°C. Cada plântula que surgia era contada e identificada.

Plântulas e brotações

Em cada parcela foram numeradas todas as plantas (≥ 5 cm dap) (Vieira 1996) e verificada a ocorrência de brotações. Plantas menores (< 5 cm dap e ≥ 1 m altura) foram amostradas a partir de duas sub-parcelas aleatórias de 1 x 5 m, em cada uma das três repetições de parcelas em cada classe de idade das florestas. Após a identificação as plantas menores foram contadas, sendo feita a distinção entre aquelas originadas por sementes ou brotação de tocos e raízes, através da observação das partes mais velhas da planta. Frequentemente era necessário remover o solo em volta das plantas para checagem da sua origem. Embora tenham sido encontrado brotações de raízes e tocos, estes não foram registrados separadamente.

RESULTADOS

Banco de sementes no solo

A densidade de sementes germinadas foi significativamente diferente entre as classes de idade de florestas nas duas profundidades (F=19,39 para 0-5 cm e 30,88 para 5-10 cm; df=3, p< 0.001) (Tabela 1). O maior número de germinações foi encontrado no solo 0-5 cm da floresta de 5 anos de idade (1190 ± 284 sementes m^{-2}) e decresceu conforme aumentava a idade da floresta, até atingir 137 ± 19 sementes m^{-2} na floresta primária (Tabela 1). A densidade de sementes encontrada no solo a 5-10 cm foi cerca de metade daquela encontrada a 0-5 cm (Tabela 1). Entre 30% e 40% das sementes germinaram após quatro semanas, ocorrendo um pico de germinação após o reviramento do solo com 16 semanas.

As sementes mais comuns foram de herbáceas (incluindo gramíneas) (Figura 1), que sofreram um decréscimo com o aumento na idade da floresta, correspondendo a 78% do total de sementes das florestas de 5 anos e a 43% na floresta primária. O número de espécies herbáceas foi maior nas florestas secundárias (27-36 espécies) do que na floresta primária (23). A proporção de sementes e espécies de árvores aumentou com a idade da floresta (Figura 1).

As espécies mais numerosas no banco de sementes das florestas secundárias foram as herbáceas *Borreria verticillata* (Rubiaceae) > *Cyperus luzulae* (Cyperaceae) > *Lindernia crustacea* (Scrophulariaceae) > *Borreria latifolia* (Rubiaceae), > que a árvore *Cecropia palmata* (Moraceae) > o arbusto *Clidemia hirta* (Melastomataceae). Na floresta primária *Cecropia palmata* > *Clidemia hirta* > o capim *Paspalum conjugatum* (Gramineae) foram as mais abundantes.

Chuva de sementes

No período de um ano, foram encontrados nos coletores estabelecidos nas florestas secundárias de 5 anos um total de 10.591 sementes de pelo menos 70 espécies, 6.320 sementes de pelo menos 93 espécies nas florestas de 10 anos, 6.170 sementes de pelo menos 104 espécies nas florestas de 20 anos de idade e 2.641 sementes de pelo menos 134 espécies na floresta primária. Permaneceram sem identificação de 2% a 6,6% das espécies de sementes encontradas nas florestas secundárias e 21,4% das sementes na floresta primária. O maior número médio de sementes foi encontrado na floresta de 5 anos de idade (883 ± 230 sementes m^{-2} ano^{-1}), que é significativamente diferente ($p<0.05$) da floresta primária (220 ± 80 sementes m^{-2} ano^{-1}) (Tabela 1).

Tabela 1. Número médio de sementes (m^2 ± SE), número de espécies e diversidade do banco de sementes (amostra de 0,48 m^2) e da chuva de sementes (12m^2), em florestas secundárias de 5, 10 e 20 anos e floresta primária, na Região Bragantina, Pará, Brasil. Os valores médios seguidos por diferentes letras, nas mesmas linhas, são significativamente diferentes de acordo com o teste de Tukey, $p<0,05$.

	Classe de idade das florestas (anos)			
	5	10	20	Floresta primária
Banco de sementes no solo				
Número médio de sementes				
0-5 cm	1190 ± 284a	547 ± 42b	450± 56.7b	137 ± 19c
5-10 cm	411± 78.2a	260 ± 6.2ab	162 ± 20.5b	64 ± 10.4c
No. de espécies	60	63	70	54
Diversidade de espécies (H')	1.20	1.30	1.42	1.31
Chuva de sementes				
Número médio de sementes ano^{-1}	220 ± 80b	883 ± 230a	527 ± 122ab	514 ± 169ab
No. de espécies	70	93	104	134
Diversidade de espécies (H')	0.91	1.19	1.09	1.35

Poucas espécies dominaram a chuva de sementes em cada classe de idade. Na floresta de 5 anos de idade *Cecropia palmata*, *Miconia* sp., *Myriaspora* sp. e *Vismia guianensis* corresponderam a

71% de todas as sementes. Na floresta de 10 anos de idade, *Cecropia palmata, Clidemia hirta, Inga* sp., *Vismia guianensis* e *Zanthoxylum rhoifolium* foram responsáveis por 66% de todas as sementes e na floresta de 20 anos de idade, *Cecropia palmata, Didymopanax morototoni, Vismia guianensis* e *Zanthoxylum rhoifolium* foram responsáveis por 70% de todas as sementes que caíram nos coletores.

Brotações e plântulas

A proporção de todos os indivíduos (= 1 m altura, < 5 cm dap) originados por brotação declinou de 54% na floresta mais jovem (5 anos) para 19,3% na floresta de 10 anos e alcançou 27,6% na floresta de 20 anos de idade. Embora nas florestas secundárias mais jovens sementes e brotações tenham a mesma importância, nas florestas secundárias mais velhas (florestas com 10 e 20 anos de idade) as sementes passam a ter maior importância. Por outro lado, plantas maiores (≥ 5 cm dap) têm mais indivíduos e espécies que regeneraram por brotação do que de sementes, em todas as classes de idade de florestas (Tabela 2).

Os números médios de brotações m^{-2} (= 1 m altura, < 5 cm dap) não eram significativamente diferentes entre classes de idade de florestas. O maior número de espécies originadas por brotação foi encontrado na floresta de 20 anos de idade (36 espécies) (Tabela 2).

Tabela 2. O número de espécies e densidade média de sementes e brotações de duas classes de tamanho (≥ 1 m altura, <5 cm dap e ≥ 5 cm dap) em florestas secundárias de 5, 10 e 20 anos de idade na Região Bragantina, Pará, Brasil.

Origem	Características	Classes de idade das florestas (anos)		
		5	10	20
≥ 1 m altura, < 5 cm dap				
Plântulas	no. de espécies*	36	58	48
	densidade m^{-2}	4.6 (1.4-7.5)	14.7 (7.7-25.5)	11.5 (6.6-16.4)
Brotaçãos	no. de espécies *	37	19	28
	densidade m^{-2}	5.4 (4.3-6.1)	3.5 (0-7.5)	4.4 (2.9-5.6)
≥ 5 cm dap				
Sementes	no. de espécies *	4	13	13
	densidade 250 m^{-2}	3.3 (1-7)	7.3 (3-10)	9 (5-13)
Plântulas	no. de espécies*	18	25	31
	densidade 250 m^{-2}	21.3 (10-34)	32.3 (21-44)	38 (32-44)

* Algumas espécies foram encontradas com as duas formas de regeneração.

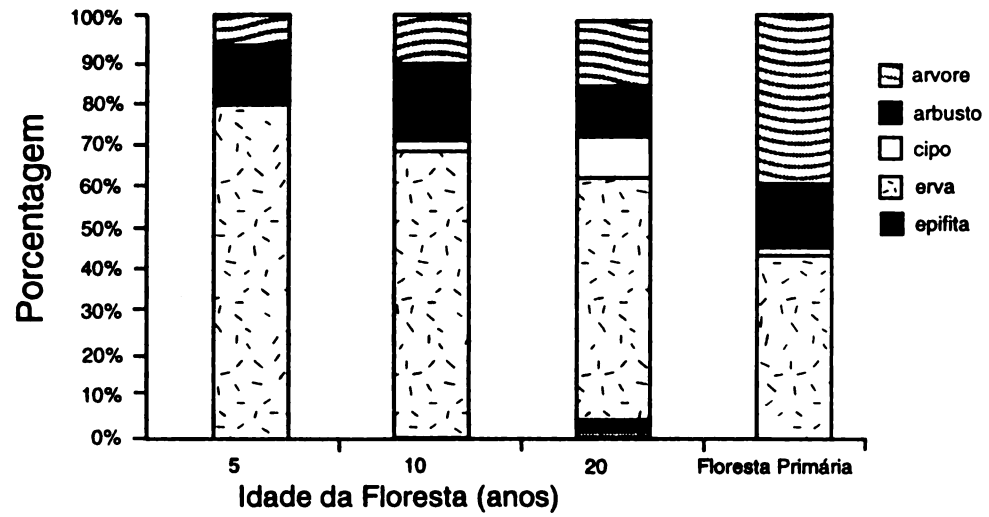


Figura 1. Porcentagem de formas de vida encontradas no banco de sementes de florestas secundárias de 5, 10 e 20 anos de idade e em florestas primárias na Região Bragantina, Pará.

DISCUSSÃO

O banco de sementes da floresta primária na Bragantina estão dentro do intervalo (55-860 sementes m^{-2}) registrado em outras florestas tropicais (Guevara & Gomez-Pompa 1972; Hall & Swaine 1980; Uhl *et al.* 1981, 1982a; Putz 1983; Uhl & Clark 1983; Putz & Appanah 1987) e eram principalmente de espécies lenhosas. Da mesma forma, o número de espécies presentes no banco de sementes da floresta primária (54) e florestas secundárias (60-70) estavam dentro do intervalo registrado por Garwood (1989), Skoglund (1992) e Young *et al.* (1987), de 4 - 79 para floresta primária e 8 - 67 para floresta secundária.

Das 96 espécies encontradas no banco de sementes de florestas secundárias 14 eram árvores, sendo quatro espécies pioneiras que também ocorreram na floresta primária *(Annona densicoma, Casearia decandra, Cecropia palmata, Croton matourensis)* e duas eram tolerantes à sombra *(Neea* sp. e *Trichilia* sp.). Em pastagens degradadas próximas a Paragominas, Pará apenas duas espécies arbóreas pioneiras foram encontradas no banco de sementes (Nepstad et al. 1996), e o mesmo número em uma floresta secundária de 5 anos na Bragantina (Denich 1991).

Quantificações da chuva de sementes na sucessão vegetal tropical são raras (Young *et al.* 1987). Neste estudo foram coletadas mais sementes em florestas secundárias do que em floresta primária (883, 527 e 514 sementes m^{-2} ano^{-1} para florestas secundárias de 5, 10 e 20 anos de idade, respectivamente, e 220 sementes m^{-2} ano^{-1} para floresta primária). Young *et al.* (1987) encontraram o mesmo padrão na Costa Rica, mas registraram valores maiores para florestas secundárias de 3 e 11 anos de idade (3366 e 3700 sementes m^{-2} ano^{-1}, respectivamente) e para floresta primária (1233 sementes m^{-2} ano^{-1}). Na Bragantina, o número de espécies aumentou de 69 na floresta de 5 anos de idade para 133 na floresta primária. Young *et al.* (1987) registrou mais espécies na chuva de sementes na vegetação mais nova do que na floresta primária (75 vs. 48), mas utilizaram apenas metade da área total de coletores na floresta primária.

Na Bragantina, a chuva de sementes desempenha um papel importante na regeneração de florestas devido à grande quantidade de sementes que caem das plantas sucessionais, e também por ser provavelmente a responsável pelo grande banco de sementes encontrado nas florestas secundárias. Nas florestas de San Carlos, Venezuela, onde foi encontrado um menor número de espécies na chuva de sementes durante um ano, do que nos primeiros 4-5 cm de solo, a chuva de sementes provavelmente contribui com apenas uma pequena proporção da regeneração após distúrbio (Uhl & Clark 1983). Entretanto, em um estudo na Costa Rica, a chuva de sementes foi mais importante em regenerações jovens, onde o número de espécies na chuva de sementes durante um ano foi equivalente ou maior do que o encontrado no solo (Young *et al.* 1987).

Em geral na Bragantina, a maioria das áreas abertas são cultivados imediatamente após a queima, sem a remoção de tocos. Consequentemente, a regeneração inicial potencial do banco de sementes e de brotação no pousio é alta. De 81% a 86% dos indivíduos e 68% a 81% das espécies ≥ 5 cm dap aparecem principalmente por brotação. Os indivíduos menores (≥ 1m altura, < 5 cm dap) na floresta de 5 anos de idade surgem principalmente por brotação, porém nas florestas secundárias mais velhas estes se originam principalmente de sementes. Aparentemente as florestas secundárias são compostas inicialmente por brotação, com novas plantas chegando através de sementes, conforme a floresta envelhece. A porcentagem de plantas < 5 cm dap que rebrotam na floresta mais jovem foi alta, porque as brotações não atingiram a categoria de maior tamanho. Uhl *et al.* (1982a), trabalhando em San Carlos na Venezuela, observaram em uma floresta de 3 anos de idade que 54% dos indivíduos ≥ 5 cm de altura eram brotações, enquanto na floresta de 5 anos de idade, na mesma área, apenas 17% originaram-se de brotações (Uhl & Jordan 1984). Em trabalho anterior, em San Carlos, havia sido demonstrado que a brotação era a forma mais comum de regeneração após o corte de florestas (Uhl *et al.* 1981), com 6,37 brotações m^{-2} vs apenas 0,95 plântulas m^{-2} (todos os indivíduos ≥ 5 cm altura). No estudo de Denich (1991), em florestas secundárias de 5 anos de idade na Região Bragantina, a maioria dos indivíduos originaram de brotação.

Na Bragantina, enquanto as espécies pioneiras predominaram sobre as plântulas de espécies secundárias, as brotações incluíram algumas espécies de floresta primária como *Andira retusa, Couratari guianensis, Eschweilera pedicelata, Guatteria poeppigiana, Saccoglotis guianensis, Swartzia racemosa,* e *Talisia subalbens*. Várias delas não apresentaram ou estavam pouco presentes na chuva e banco de sementes, podendo a brotação representar sua única forma de regeneração nas florestas secundárias. Não resta dúvida de que um grande número de espécies lenhosas regeneraram por brotação em florestas secundárias da Bragantina.

CONCLUSÕES

As espécies arbóreas pioneiras mais abundantes em todos os estágios sucessionais amostrados têm um grande banco e chuva de sementes e podem rapidamente recolonizar novas áreas abertas através de sementes, enquanto outras pioneiras e algumas espécies primárias estão presentes em florestas secundárias devido apenas à sua capacidade de resistir a repetidas derrubadas e queimas, através da regeneração à partir de brotação. Devido à demonstrada importância de brotação parece que a estrutura básica da floresta ou a presença de certas espécies de árvores ao longo da cronosequência depende deste fenômeno.

RECOMENDAÇÕES E FUTURAS LINHAS DE PESQUISA

Nossos estudos intensivos de ecologia de florestas secundárias tem 6 anos e são desenvolvidos no Estado do Pará, Amazônia oriental, Brasil. Esses estudos visam avaliar as interações entre remanescentes de florestas primárias e secundárias e o fluxo de propágulos e movimentação de animais dispersores de sementes. Em breve iniciaremos um grande projeto dentro do programa LBA, do qual participam pesquisadores americanos e brasileiros, que avaliará os ciclos biogeoquímicos em diferentes tipos de floresta e de uso da terra na Amazônia, que possibilitará dimensionar os níveis de degradação da região. Como recomendação podemos indicar o estudo das florestas secundárias do ponto de vista da sua utilização pelas comunidades locais, visando o manejo dos recursos florestais, principalmente lenha , carvão e plantas medicinais.

REFERÊNCIAS

Denich, M. 1991. *A Importância de uma Vegetação Secundária Nova para o Incremento da Produtividade do Sistema de Produção na Amazônia Oriental Brasileira.* EMBRAPA /CPATU- GTZ, Belém- Pará.

Garwood, N.C. 1989. Tropical soil seed banks: a review. Pp. 149-202 in Leck, M.A.; Parker, V.T. & Simpson, R.L. (eds). *Ecology of Soil Seed Banks* Academic Press, London.

Guevara, S. & Gomez-Pompa, A. 1972. Seeds from surface soils in a tropical region of Veracruz, Mexico. *Journal of the Arnold Arboretum* 53: 312-335.

Hall, J.B. & Swaine, M.D. 1980. Seed stocks in Ghanaian forest soils. *Biotropica* 12: 256-263.

Nepstad, D.C.; Uhl, C.; Pereira, C. & Silva, J.M.C. 1996. A comparative study of tree establishment in abandoned pasture and mature forest of eastern Amazonia. *Oikos* 76: 25-39.

Oliveira, A.E. 1983. Ocupação Humana. In: *Amazônia, Desenvolvimento, Integração e Ecologia* (Salati, E.; Schubart, H.O.R.; Junk, W. & Oliveira, A.E., eds.) Ed. Brasiliense-CNPq, São Paulo, p. 144-323.

Penteado, A.R. 1967. *Problemas de Colonização e de Uso da Terra na Região Bragantina do Estado do Pará*. Universidade Federal do Pará, Coleção Amazônia, Série José Veríssimo, Pará.

Putz, F.E. & Appanah, S. 1987. Buried seeds, newly dispersed seed, and the dynamics of a lowland forest in Malaysia. *Biotropica* 19: 326-33.

Putz, F.E. 1983. Treefall pits and mounds, buried seeds, and the importance of soil disturbance to pioneer trees on Barro Colorado Island, Panama. *Ecology* 64: 1069-1074.

Skoglund, J. 1992. The role of seed banks in vegetation dynamics and restoration of dry tropical ecosystems. *Journal of Vegetation Science* 3: 357-360.

Uhl, C. & Clark, K. 1983. Seed ecology of selected Amazon basin successional species. *Botanical Gazette* 144: 419-425.

Uhl, C.; Clark, H. & Clark, K. 1982a. Successional patterns associated with slash-and-burn agriculture in the upper Rio Negro region the Amazon basin. *Biotropica* 14: 249-254.

Uhl, C. ; Clark, K.; Clark, H. & Murphy, P. 1981. Early plant succession after cutting and burning in the upper Rio Negro region of the Amazon basin. *Journal of Ecology* 69: 631-649.

Vieira, I.C.G. 1996. *Forest Succession after Shifting Cultivation in Eastern Amazonia*. PhD. Thesis, University of Stirling, Scotland, 215 pp.

Young, K.R.; Ewel, J.J.; Brown, B.J. 1987. Seed dynamics during forest succession in Costa Rica.. *Vegetatio* 71: 157-173.

DYNAMICS OF A TROPICAL SECONDARY FOREST IN AMAPÁ STATE, BRAZIL

Guilherme Luís Augusto Gomide
Doctoral Programme, Paraná Federal University, Curitiba, Brazil
Carlos Roberto Sanquetta
Associate Professor, Paraná Federal University, Curitiba, Brazil
José Natalino Macedo da Silva
Senior Researcher, EMBRAPA/CPATU, Belém, Brazil

RESUMEN

Fueron estudiadas las variaciones en la composición florística, la estructura horizontal y la dinámica (ingreso, crecimiento y mortalidad) de un bosque tropical secundario sometido a una tala rasa en 1982, durante un período de 11 años, a través de un inventario contínuo. La primera medición ocurrió en 1985 y las mediciones siguientes en 1986, 1988, 1994 y 1996. El área está localizada en el cerro Felipe, Estado del Amapá, Brasil (52^{0} 20" W 00^{0} 55" S). Se siguieron todos los árboles con más de 10 cm de DAP (clase arbórea), las "varas" con diámetros comprendidos entre 2.5 y 4.9 cm, y las "mudas" con diámetros menores a 2.5 cm y altura superior a 30 cm. Los árboles fueron divididos en tres grupos de comercialización: Especies comerciales, especies potencialmente comerciales, especies no comerciales. En el período observado el bosque presentó un incremento del 217% en la abundancia de individuos. En cuanto a los grupos de comercialización, fue observado un aumento positivo en el número de individuos, pasando el grupo de las especies comerciales de 3 % en 1985 a 9 % en 1996, el grupo de las especies con potencial de comercialización de 4 % en 1985 a 18 % en 1996, mientras que el grupo de las especies no comerciales disminuyó de 92 % en 1985 a 71 % en 1996. Entre 1985 y 1996, el bosque presentó un aumento en área basal de 3.3 a 28.7 m^2/ha. Analizando todo el período, el bosque secundario presentó un balance positivo, donde el número de árboles muertos fue de aproximadamente 111 /ha/año y el número de ingresos fue de 264 /ha/año. Todos los grupos comerciales crecieron en lo que respecta a la abundancia, área basal y volumen. El grupo de las especies no comerciales fue el que presentó la mayor tasa de mortalidad durante todo el período observado y el grupo de las especies con potencial de comercialización la mayor tasa de ingreso.

INTRODUCTION

According to FAO, the annual deforested area of tropical forests in Brazil at the beginning of the 1980´s, was estimated in 13.600 km^2, i.e., approximately 0.4% of its total land area. In 1989, these values jumped abruptly to 50.000 km^2, or about 2.3% of the Brazilian territory. However, as reported by IBGE (cited in EMBRAPA, 1994), recently there is a trend of diminishing deforestation rates. The total area deforested decreased from 2.5 million ha/year in 1988 to 0.9 million ha/year in 1991. The main causes of the reduction in the deforestation rates in the Brazilian tropical region are the international concern on the matter and the political pressure on the Brazilian government, as well as the environmental activism in the country. The resulting consequences are that the environmental legislation has been turned more strict and decision-makers have considered sustainable forest management as a high national priority.

Human activities in tropical Brazil have led to conversion of forestland to agriculture, pasture or other land use. A large portion of these areas have been abandoned and reverted into forest. These secondary forests, due to the large area they occupy in the Amazon region and other Brazilian ecosystems, as well due to their unique characteristics, have attracted the attention of many researchers in terms of studying rates of recovery in species diversity and stand structure, as well as primary production and their role in the environmental services at the local, regional and global scales. Therefore, this study was carried out with the objective of complementing the available information by analyzing changes in floristic composition and stand structure, as well as tree recruitment, mortality and growth during an 11-year period.

STUDY SITE

The study was carried out in a secondary forest following clear felling of the original vegetation. The area belongs to Jari, a pulp and paper manufacturer which established a 112 ha experiment in cooperation with the Brazilian agency EMBRAPA/CPATU in order to monitor forest succession. The area is located in Amapá State, Brazil (52°20"W and 00°55"S), at an approximate elevation of 150 m. Soils are oxisols, and the regrowth forest grows on gentle topography.

DATA COLLECTION

Forest succession was monitored by means of continuous forest inventory. The site was abandoned in 1982 and first measured in 1985, with remeasurements in 1986, 1988, 1990, 1994, and 1996. We classified all woody species sampled in three size classes: trees (over 5 cm DBH), poles (2.5 cm > DBH < 4.9 cm), and saplings (DBH > 2.5 cm and height over 30 cm). For trees 8 plots of 50 m x 50 m (0.25 ha) were randomly established in the 112 ha experimental stand, which was subdivided into 25 subplots of 10 m x 10 m (100 m^2) each. Poles were sampled in 5 quadrats of 5 m x 5 m (0.0025 ha) located inside 5 randomly selected subplots. Saplings were sampled in 0.000625 ha plots nested within the pole quadrats. The DBH of trees and poles was measured and identified, when possible, to species. Species were classified in three commercial groups in accordance with their wood quality and utilization: Group I: commercial species; Group II: species that might become commercial in the future; Group III: currently non-commercial species.

DATA ANALYSIS

The data was analyzed in terms of floristic composition, horizontal structure, bole volume, and diameter distribution, at the beginning and end of the 11-year period. Recruitment, growth (bole annual periodic increment), and mortality was recorded in four periods: 1985 to 1988; 1988 to 1990; 1990 to 1994 and 1994 to 1996. Mortality was considered the number of trees that died between two consecutive measurements. The annual mortality rate (AMR) was obtained by dividing the number of trees that died during a given period by the number of year considered. Recruitment was assessed as the number of trees that attained the threshold measurement DBH during a given period of time. The annual recruitment rate (ARR) was calculated by the ratio of number of the average number of recruits that appeared during all the inventories and the average number of trees at the beginning of each time interval of measurement. The annual increments in DBH, basal area and outbark bole volume were calculated by the difference of these values at each period of observation.

RESULTS AND DISCUSSION

FLORISTIC COMPOSITION

Mean tree density in 1985 was calculated as 741 trees/ha. These trees belonged to 34 families, 55 genera and 76 species. Among the trees recorded in the plots just 13 individuals were identified only to the family level, 20 at the genus level and 9 could not be identified. The families with larger number of species were Mimosaceae, with 12 species, Moraceae with 9, and Sapotaceae with 6 species identified. In relation to the number of individuals, Moraceae was the most numerous family, mainly due to the remarkable presence of the pioneer *Cecropia* (*C. obtusa*, with 133 trees/ha, and *C. sciadophylla*, with 188 trees/ha). Regarding the commercialization groups, 13 species were classified as commercial, 28 species were potentially commercial, and 35 were considered as non-commercial species (3 %, 92 %, and 4 % of the total number of individuals, respectively). In 1985, the forest was dominated by pioneer tree species. This predominance was more remarkable for the sapling and pole size classes. Among the 2830 poles/ha that occurred in the forest, 77% belonged to *Cecropia* and among the 25792 saplings/ha, 22% were *Goupia glabra* and 20% were *Cecropia*. Fourteen years after clear-felling, the results of a new inventory demonstrated considerable alteration in floristic composition (TABLE 1).

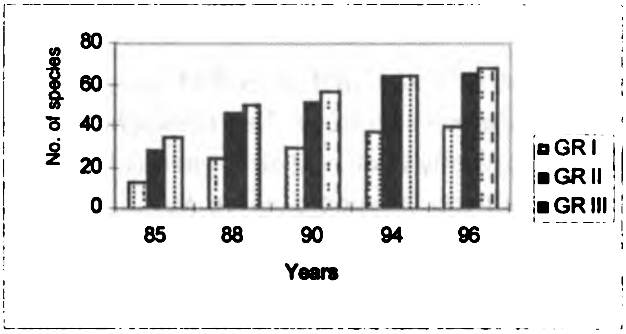
TABLE 1 –Changes in floristic composition in the tree size class during 1985 and 1996.

	Calendar year	
	1985	1996
No. Families	34	42
No. Genera	55	109
No. Species	60 + 16*	141 + 33*

* Non-identified

During 1985 and 1996, 105 new species appeared and 7 species disappeared in the tree size class. The families that had the greatest number of species in 1996 were Mimosaceae (19 species), Moraceae (17), Caesalpinaceae (13), Fabaceae (12), and Lauraceae (10.). The Moraceae still had the greatest number of individuals, especially (*Cecropia obtusa* with 246 trees/ha, and *C. sciadophylla* with 915.5 trees/ha. In relation to the commercialization groups, there was a positive evolution in relation to 1985, with 40 species classified as commercial, 66 species as potentially commercial, and 68 species as non-commercial (Figure 1).

FIGURE 1 – Changes in number of species per commercial group during 1985 and 1996.



DENSITY

TABLE 2 shows the changes in tree density in the forest during 1985 and 1996, 3 and 14 years after clear-felling, respectively. There was a change in tree density from 741 stems/ha to 2353 stems/ha. In 1985, the non-commercial species represented 92 % of the total density, whereas in 1996 their representation diminished to 71 %. Overall, there was an increase in the abundance of valuable woody species.

TABLE 2: Changes in tree density, basal area and volume by commercialization groups during 1985 and 1996.

Group	1985						1996					
	No. Stems/ha		BA (m^2/ha)		V (m^3/ha)		No. Stems/ha		BA (m^2/ha)		V (m^3/ha)	
I	25.5	3.37%	0.076	2.3%	0.00	0.0%	223.0	9.48%	1.29	4.5%	1.40	3.5%
II	31.5	4.25%	0.210	6.3%	0.18	3.6%	438.5	18.64%	2.32	8.1%	0.96	2.4%
III	684.5	92.31%	3.056	91.4%	4.79	96.4%	1691.5	71.89%	25.14	87.4%	37.2	94.2%
Total	741.5	100 %	3.340	100 %	4.97	100 %	2353	100 %	28.74	100%	40.27	100 %

BA = basal area;

V = outbark stem volume.

In 1985, *Cecropia sciadophylla* and *Cecropia obtusa* showed the highest tree density, with 375.5 and 265.5 trees/ha, respectively, thus corresponding to 86 % of the total tree density. Following these two species was *Dipteryx odorata* and *Inga alba*, which showed densities of 9.0 and 6.5 trees/ha, respectively. TABLE 3 shows the numbers of saplings and poles recorded in the inventories carried out in 1985 and 1996. The number of poles was calculated at 2830 in 1985, which decreased to 1380 in 1996. The same phenomenon happened for saplings, which decreased from 25792 stems/ha to 5042 stems/ha. This sharp reduction in number of young trees is attributed to the intense competition for light initiated by canopy closure. It is interesting to note that decreases in pole and sapling density were pronounced for the non-commercial pioneer species. It was also noticed that the number of species that appeared only as saplings and poles diminished from 57 in 1985 to 11 in 1996, as result of the ingrowth into the tree size class. In the pole size class, *Cecropia* had the greatest number of individuals, with 2180 stems/ha, followed by *Apeiba burchellii,* with 110 stems/ha, as well as *Inga* spp., with 100 stems/ha. In the sapling size class, the pioneer species *Goupia glabra*, *Cecropia sciadophylla*, and *Cecropia* spp., had densities of 5750, 3958, 1375, and 1333 saplings per hectare, respectively.

In 1996 in the tree size class, the most abundant species were *Cecropia sciadophylla*, with 915 stems/ha, followed by *Cecropia obtusa* and *Laetia procera*, with 246 and 130 stems/ha, respectively. In pole size class, *Goupia glabra* had the greatest abundance, with 200 stems/ha (14 % of the total density). It was followed by *Siparuna decipiens*, with 110 poles/ha and *Xylopia nitida*, with 100 poles/ha. In the sapling size class, the species of greatest abundance was *Goupia glabra*, with 916 stems/ha (18 %), followed by *Pouteria*, with 375 stems/ha and *Siparuna decipiens*, with 250 stems/ha.

TABLE 3: Change in sampling and seedling densities by commercialization groups during 1985 and 1996.

Group	1985				1996			
	No. Saplings/ha		No. Poles/ha		No. Saplings/ha		No. Poles/ha	
I	7000	27.0%	240	8.5%	875	17.4%	360	26.1%
II	2166	8.4%	100	3.5%	1167	23.1%	540	39.1%
III	16625	64.4%	2490	88.0%	3000	59.5%	480	34.8%
Total	25792	100 %	2830	100%	5042	100%	1380	100%

DOMINANCE

The total basal area of the forest in 1985 was 3.3 m²/ha. *Cecropia* alone accounted for 2.44 m²/ha, about 73 % of the stand basal area. The species with larger basal areas were *Cecropia sciadophylla*, *Cecropia obtusa*, *Geissospermum sericeum*, and *Rinorea guianensis*. *G. sericeum* and *Rinorea guianensis* occurred in larger DBH class in 1985, in contrast with *Cecropia*, whose dominance was determined by the huge density attained at the beginning of succession.

During 1985 and 1996, the change in basal area was of 25.4 m²/ha, from 3.34m²/ha in 1985 to 28.74m²/ha in 1996. This great variation in only 11 years was due to the rapid growth and the great abundance of the pioneer species that found a favorable environment to their establishment and development in the beginning of succession. In 1996, *Cecropia sciadophylla* and *Cecropia obtusa* still dominated the forest.

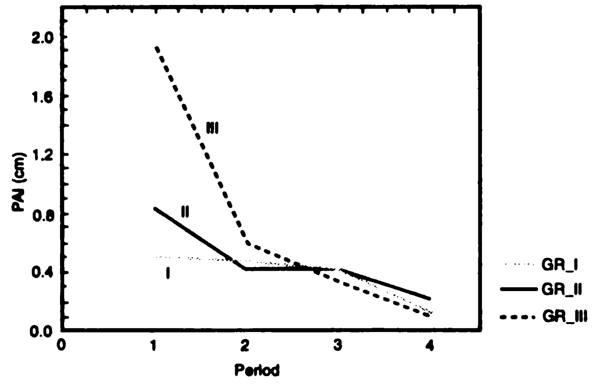
STEM VOLUME

TABLE 2 also shows the stem volumes (assessed only for stems > 20 cm DBH) calculated for 1985 and 1996. In 1985, only 5 species had individuals with DBH larger than 20 cm. They were: *Pouteria laurifolia*, *Aspidosperma oblongum*, *Geissospermum sericeum*, *Pouteria* sp., and *Rinorea guianensis*. The total stem volume in 1985 was calculated to be 4.97 m³/ha, and 96 % of it belonged to the species of the non-commercial species group and the remainder to potentially commercial species. In 1996, stem volume increased to 40 m³/ha, which corresponded to an increase of 710% in relation to the volume calculated for 1985. The species that presented larger volumes were *Cecropia sciadophylla*, *Cecropia obtusa*, *Inga alba*, and *Didymopanax morototoni*, being the species of the *Cecropia* responsible for 88% of the total volume.

STEM GROWTH RATES

As seen in FIGURE 2, the average annual periodic increment (PAI) in diameter of the trees was 0.60 cm/year, considering all individuals over 5 cm DBH. The species that composed the group II of commercialization showed the fastest diameter growth (0.63 cm/year), but for groups I and II no significant difference was noticed in terms of diameter growth. Another fact revealed by the data was the decrease in diameter growth rates with time as result of increasing competition. During the first period of observation (1985-1988), the average rate was 1.93 cm/year, which decreased to 0.34 cm/year within the last two years. The reduction in growth rate was more remarkable for group of commercialization III, which further indicates the progressive decline of the pioneers.

Figure 2: Changes in PAI of stem growth by commercialization group over time.



BASAL AREA AND STEM VOLUME GROWTH RATES

The basal area growth rates during 1985 and 1996 are shown in FIGURE 3 and FIGURE 4. The increment rate in basal area was about 2 m^2/ha/year, which changed from ca. 6 m^2/ha/year in the first census to less than 1 m^2/ha/year in the last census. This trend was similar to stem diameter growth rates, reflecting canopy closure and competition. The change in basal area growth in terms of commercialization groups was also similar to diameter growth. Basal area growth increased with increasing DBH classes up to diameter class 3 (15-20 cm) and then decreased systematically. This finding was noticed for the period 1985-1990, for the period 1990-1996, as well as for the period 198-1996. Average volume growth for 14 years was 3.53 m^3/ha/year.

FIGURES 5 and 6 show the stem volume increment. The increment in stem volume increased from the first period (1985-1988) to the second (1988-1990), and tended to decrease for the third and fourth periods of observation. In terms of volume growth per diameter classes, it was observed a decrease in PAI with increasing DBH for all time periods.

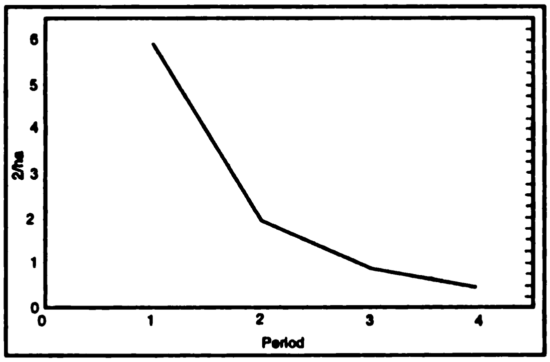


Figure 3:Change in basal area PAI with time

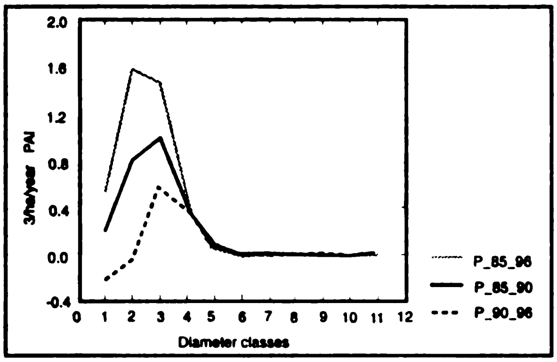


Figure 5: Change in volume PAI with time

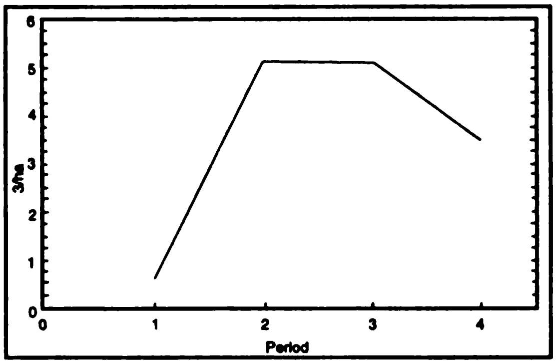


Figure 4: Mean basal area PAI per DBH class

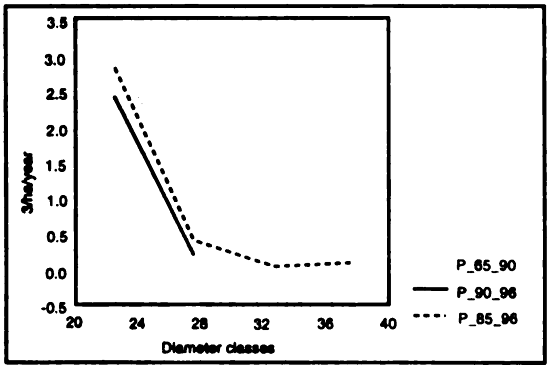


Figure 6: Mean volume PAI per DBH class

RECRUITMENT AND MORTALITY RATES

The mortality and recruitment rates during 1988 and 1996 are presented in TABLES 4 and 5. The mortality rate during the study period 1985-1996 was estimated at 111 trees/ha/year which represented about 5% of the initial number of trees in 1985. Most of the dead stems (97 %) belonged to group III (non-commercial species). The annual mortality rate varied with time, but no apparent trend was found. AMR was low during the first three years of succession, increased abruptly during the next two years, decreased two years later, and increased considerably during the final two years. The annual recruitment rate was about 263 trees/ha/year, corresponding to 14 % of the initial number of trees (in 1985). Recruitment rate was greater for the group of commercialization III, which includes most of the "typical" pioneer species. Most trees were recruited immediately after disturbance (during 1985-1988). Recruitment rates were nearly constant from 1988 to 1996. Recruitment rates were always greater than mortality rates for commercial groups I and II. On the contrary, for group II this happened only for the beginning of the secondary succession. After 1988, mortality rates were remarkably greater than recruitment rates for this group of commercialization. This finding in connection with the fact that the number of saplings and seedling of group I are diminishing in the forest, indicates the beginning of the decline of the pioneer species. TABLE 6 shows a summary of the forest dynamics during the 14 years of succession.

TABLE 4: Annual mortality rate (amr) per cmmercialization group in diferent time periods

GROUP	1985 – 1988		1988 - 1990		1990 - 1994		1994 - 1996		1985 - 1996	
	No./ha.year^{-1}	%	No./ha.year^{-1}	%	No./ha.year^{-1}	%	No./ha.year^{-1}	%	No./ha.year^{-1}	%
I	0.88	3.50	0.89	1.10	1.10	1.00	2.00	1.10	1.14	4.47
II	0.71	2.20	2.44	2.00	1.10	0.70	3.71	1.00	1.70	5.40
III	12.01	1.80	178.44	7.30	95.58	4.30	204.00	10.30	108.88	5.90
Average	13.60	1.86	181.78	6.80	97.79	3.90	207.7	8.30	111.22	5.28

TABLE 5: Annual recruitment rate (ARR) per commercialization group in diferent time periods.

GROUP	1985 – 1988		1988 - 1990		1990 - 1994		1994 - 1996		1985 - 1996	
	No./ha.year^{-1}	%	No./ha.year^{-1}	%	No./ha.year^{-1}	%	No./ha.year^{-1}	%	No./ha.year^{-1}	%
I	21.00	91.30	13.8	66.20	20.40	19.20	20.90	11.20	19.27	19.46
II	32.50	110.00	23.10	19.90	49.10	30.00	47.70	13.30	39.20	23.53
III	651.00	100.00	62.40	3.00	42.20	2.30	47.40	2.90	205.12	13.36
Average	704.50	100.20	99.30	4.40	111.70	5.30	116.00	5.30	263.59	14.63

TABLE 6: Changes in tree density, basal area, volume and number of species during 1985 and related dynamic components.

Group	1985				1996				1985 – 1996		
	N trees/ha	V	BA	sp	N trees/há	V	BA	sp	ARR	AMR	DBHPA
I	25.5	0.00	0.076	13	223.0	1.40	1.291	40	19.27	1.14	0.46
II	31.5	0.18	0.210	28	438.5	0.96	2.316	66	39.20	1.70	0.44
III	684.5	4.79	2.066	35	1691.5	37.91	25.136	68	205.12	108.8	0.63
Total	741.5	4.97	2.949	76	2353.0	40.27	28.744	174	263.59	111.22	0.60

V = Volume (m^3/ha); BA = basal area (m^2/ha); sp = number of species; ARR =annual recruitment rate; AMR = annual mortality rate (No./ha.$year^{-1}$); DBHPAI = DBH growth rate (cm/year).

CONCLUDING REMARKS

In the present study, the clear-cut area was rapidly recolonized by forest vegetation. The secondary succession during 14 years led to a species richness values that were very close to those found in surrounding primary forest. The basal area of the forest after 14 years also attained a level comparable to values found in some primary forests. This quick rehabilitation of the tree community is attributed to the absence of fire, the existence of abundant seed sources from neighboring old-growth forest, and the vital attributes of earlier colonizers as well, namely sprouting and germination from the seed bank. In spite of the high recovery potential of this forest, stand structure and its timber stocking are obviously completely different from the primary forest. The valuable commercial species are just starting to appear as they account for a very small fraction of the stand basal area. It is quite probable that several decades will be necessary to "transform" this secondary forest dominated by non-commercial pioneers into a commercially valuable forest.

REFERENCES

EMBRAPA. 1994. Atlas do meio ambiente do Brasil, Brasilia, Ed. Terra viva, 138p.

ACKNOWLEDGEMENTS

The authors wish to express their gratitude to JARI CELULOSE S.A. for providing all facilities and partial financial support to this study.

CARACTERIZACION FLORISTICA Y ESTRUCTURAL DE TRES ESTADOS SUCESIONALES DEL BOSQUE DE COLINAS BAJAS DEL BAJO CALIMA, COLOMBIA

Gonzalo De las Salas, Adriana García, Alejandro Ayala.
Universidad Distrital Francisco José de Caldas, Bogotá, Colombia.

ABSTRACT

We characterized stand structure and floristic composition of woody components of a rain forest at Bajo Calima (8, 18 years old and a primary, but nevertheless altered forest site) in the Colombian Pacific Bioregion (27°C, 7600mm/yr; dystrophic soils). Basal area, volume, richness diversity parameters (expressed as alpha and beta indices) and Importance Value Index (IVI) were calculated. The most abundant families surveyed were: Melastomataceae (25%), Sapotaceae (26%), Hypericaceae (23%) and Rubiaceae (18%). We also identified the genera Miconia, Eschweilera, Inga *and* Otoba *as the most representative. Sixty six percent of the IVI is conformed by 14, 18 and 20 woody species in 8 and 18 years old secondary stands and in the primary forest stand, respectively. The high floristic similarity betwen stands can be explained by the high dominance of five species* Licania chocoensis, Guattenia calimensis, Eschweilera amplexifolia, Otoba lehmanii, Brosimum utile. *The basal area of the secondary stands surveyed accounts for only one third (8 years old) and one half (18 years old) of the value registered by the old-growth stand. Observed levels of natural regeneration indicate that seedlings and saplings play a significant role in the maintenance of the diversity of "climax" species. The importance of carrying out dynamic studies (growth, mortality, phenology, seedling ecology), which permit a better identification of silvicultural sustainable management options, is pointed out. It is concluded that ecological research can cast light on the growth dynamics of valuable woody species in this area and generate local or regional models transferable to social forestry projects.*

INTRODUCCIÓN

El interés publico hacia la conservación del bosque tropical ha aumentado en los últimos 30 años, mientras que la aplicación de su manejo sistemático ha disminuido o no se ha realizado. En ese mismo período la investigación de ecosistemas boscosos tropicales se ha incrementado notablemente pero muy pocos de sus resultados se han incorporado a la práctica. Ello debido en gran parte a la dificultad de transferirlos a quienes hacen uso de los bienes y servicios de los bosques. Por otra parte, las investigaciones pocas veces han respondido a políticas de los gobiernos por conocer el estado de arte de sus recursos boscosos para utilizarlos a largo plazo en forma sostenida. Como contribución a esta preocupación algunos casos merecen mención en este contexto : (1) las investigaciones ecológicas del bosque tropical en la Isla de Barro Colorado, Panamá (Leigh, Rand y Windsor 1985), (2) las investigaciones conducidas en la estación La Selva en Costa Rica (Mc Dade, et al. 1994), así como (3) las establecidas por el CATIE en bosques secundarios en ese mismo país (Finegan 1992); las realizadas por (4) el Proyecto Guandal en el Pacífico Surcolombiano por espacio de una década (1985-1995) (Del Valle 1997), los estudios (5) de cronosecuencia de rastrojos secundarios en la Amazonía Colombo - Venezolana (Saldarriaga et al 1988) y (6) el Proyecto SHIFT (Studies on Human Impact on Forest and Flood Plains in the Tropics), uno de cuyos escenarios son los bosques secundarios de la región Bragantina en Brazil (Kanashiro y Vlek, 1995).

La investigación sobre la caracterización y el funcionamiento de los ecosistemas boscosos es fundamental para definir indicadores y criterios de sostenibilidad que orienten a las instituciones encargadas de la política forestal y de recursos naturales renovables de los paises con bosques tropicales. El objetivo del presente estudio es caracterizar la composición florística y la estructura de tres sitios representativos del Bosque de Colinas bajas de la región del Bajo Calima (Colombia), en diferentes estados de sucesión.

AREA DE ESTUDIO

Esta región corresponde a una extensa área biogeográfica denominada Bajo Calima.(3° 55´ N, 77° 07´ W) Sus características climáticas son: precipitación 7.600 mm/año y ausencia de periodos secos. El periodo de menor precipitación (200-300 mm/mes) ocurre en Diciembre - Marzo; temperatura promedio 26°C, humedad relativa 88%. El brillo solar es muy bajo, con solo 712 horas/año. La región de Bajo Calima corresponde a la formación Bosque húmedo Tropical con transición a pluvial Tropical (BmhT / BpT) del sistema de Zonas de Vida de Holdridge (1978).

El bosque ocurre sobre el paisaje denominado Colinas bajas con elevaciones entre 50 y 150m y pendientes desde moderadas (10°) a escarpadas (50°). Los suelos son distróficos (Dystropepts) con una matriz de arcillas moteadas grises y amarillas en depósitos gruesos aluviales del Terciario. El pH es ácido (4.3-5.3), muy infértiles (capacidad de intercambio catiónico menor a 10 me / 100g), muy bajas concentraciones de fósforo (menos de 10 ppm) y alta saturación de aluminio (mas del 60%) (Cannon 1985, De las Salas et al. este estudio). El área descrita fue aprovechada durante 23 años(hasta 1993) por una compañía maderera para la obtención de pulpa para papel, en "cupos" o "frentes" de 600 ha. y una superficie de aprovechamiento de 1200 ha/año. El método utilizado fue el de tala rasa dejando árboles < 13 cm de diámetro, palmas y otras especies no aceptables seguido por la regeneración natural de renuevos y brinzales sin tratamiento silvicultural. Este método permitió : i) una rápida recuperación del bosque compuesto en su mayoría por especies heliófitas en los primeros 12 años ; ii) una protección parcial de la regeneración natural y del suelo por la utilización de cables de extracción ; iii) la regeneración natural de especies climax cuyas semillas quedaron en el piso después del aprovechamiento de los árboles maduros. No obstante estas ventajas, la regeneración natural estuvo siempre perturbada por la extracción y venta de varas realizada por las comunidades nativas como medio de subsistencia.

SELECCIÓN DE SITIOS

Los sitios seleccionados para este estudio fueron ubicados en parches diferentes de antiguos frentes de aprovechamiento correspondientes a estados sucesionales de 8 y 18 años y a un bosque maduro ligeramente intervenido, el cual la compañía maderera no alcanzó a aprovechar. La edad de las sucesiones fue suministrada por exfuncionarios de la misma compañía.

CARACTERIZACIÓN DE LA VEGETACIÓN

Se caracterizó florística y estructuralmente la vegetación del Bosque de Colinas Bajas del Bajo Calima, tomando tres estados sucesionales de 8, 18 años y Bosque Primario Intervenido. Para tal efecto, se establecieron 9 parcelas de 1/10 de ha en el Bosque de Colinas Bajas (3 en cada estado sucesional). En cada parcela se realizó un inventario de todos los individuos en 10 subparcelas de 10x10 m (dap > 10cm.), 5x5 m (dap 5-10cm.) y 20 subparcelas de 2x2 m (vegetación entre 30 y 150cm. y menor de 10cm dap). Se tomaron datos de altura total (m), diámetro normal (dap en cm), forma y tamaño de las copas. Se levantó también la vegetación asociada (bejucos y lianas). Esta información se observa en el Cuadro 1.

Cuadro 1. Información Recopilada Por Unidad De Muestreo

Clases De Tamaño	Designación	Datos Recopilados	Unidad De Muestreo
de 0 - 1,5 m.	brinzal	especie, número de árboles, altura, observaciones y coordenadas	2 * 2 m.
1,5 a 3 m. < 10 de dap	latizal	especie, dap, altura total, altura de copa, estado fitosanitario, presencia o ausencia de lianas y bejucos, observaciones y coordenadas	5 * 5 m.
> 10 cm de dap	fustal	especie, dap, altura total, altura de copa, forma de copa , posición de copa, diámetro de copa, estado fitosanitario, presencia o ausencia de lianas y bejucos, observaciones y coordenadas.	10x10 m.

ANÁLISIS DE LA INFORMACIÓN

Para identificar los patrones de diversidad de las poblaciones se aplicaron los índices de (a) alfa diversidad (Shannon-Wiener y Simpson), los cuales corresponden a la diversidad dentro del hábitat o diversidad intracomunitaria; y los índices de (b) beta diversidad (coeficientes de similaridad de Jaccard y Sorenson) que dan cuenta de la abundancia relativa de especies compartidas entre sitios (Matteucci y Colma 1982 ; Magurran 1988). El Indice de Valor de Importancia (I.V.I.) para cada sitio se interpretó como la suma de la abundancia relativa, la frecuencia relativa y la dominancia relativa para todos los individuos clasificados como fustales y latizales . Este valor refleja la importancia ecológica cada especie en una muestra, mejor que cualquiera de sus tres componentes aislados. Ha sido ampliamente utilizado para caracterizar la estructura horizontal de los bosques naturales. La vegetación menor(brinzales) se caracterizó por la abundancia relativa de cada especie en los sitios y tipos de bosque estudiados y se comparó con la de fustales y latizales. Las especies leñosas inventariadas se dividieron en tres grupos : a) aceptables, como aquellas con alta demanda comercial ; b) deseables, con poca demanda comercial y mucha utilización local y c) uso desconocido (utilización local desconocida y nula o escasa demanda comercial).

RESULTADOS

Los resultados obtenidos por nosotros son parcialmente comparables con los obtenidos por otros autores en la zona (Buitrago & Montaña 1995, CONIF 1996, Forero & Ordoñez 1992, Faber - Langendoen & Gentry 1991, Niño 1989, Ladrach 1985, Mazuera 1979, Rojas 1996).

Composición florística

En el levantamiento de 0.9 hectáreas del bosque de Colinas Bajas se encontraron 106 especies, agrupadas en 38 familias y 76 géneros. De éstas, especies, 32 (30% del total) corresponden a especies aceptables, 43 (41%) a especies deseables y 31 (29%) son especies sin uso conocido. La vegetación asociada (lianas y bejucos) corresponde al 23% del total de los individuos en el bosque de 8 años, 52% en el de 18 años y 42% en el Bosque Primario Intervenido. Las familias más abundantes son Melastomataceae (25% del total de familias encontradas), Sapotaceae (26%), Hypericaceae (23%) y Rubiaceae (18%). Las palmas contribuyen en promedio con un 15% y están asociadas con paisajes altamente intervenidos (Faber - Langendoen 1989 registró 20%). En concordancia con estudios anteriores (Buitrago & Montaña 1995, Forero & Ordoñez 1992, Niño 1989), los géneros más representativos son *Miconia*, *Eschweilera*, *Inga* y *Otoba*.

Es notable el hecho de que el 66% del I.V.I. lo conforman 14 y 20 especies en el sitio de 8 años y en el Bosque Primario Intervenido respectivamente. El mismo porcentaje es cubierto por solo 8 especies en el sitio de 18 años (*Licania chocoensis*, *Otoba lehmanii*, *Miconia* sp., *Guattenia calimensis*, *Eschweilera amplexifolia*, *Matisia leptandra*, *Lucuma* sp., y *Oenocarpus bataua*. Estas especies son del dosel con excepción de la palma *Oenocarpus* que es típica del subdosel. Casi todas las especies se encuentran dentro del 66% del I.V.I. para el Bosque Primario Intervenido (BP). Resultados similares obtuvieron Guariguata *et al.* (1997) en estudios florísticos en bosques secundarios y maduros de Costa Rica.

La mayor similitud, aplicando el índice de Sorenson, se encontró entre los sitios de 8 y 18 años (63%; p = 0.05). Un índice ligeramente menor (59%; p = 0.05) arrojó la comparación entre BP y el sitio de 18 años. Estos altos valores pueden explicarse por la alta dominancia en los dos sitios de cinco especies (33% del I.V.I.) *Licania chocoensis*, *Otoba lehmanii*, *Guattenia calimensis*, *Eschweilera amplexifolia* y *Brosimum utile*.

La distribución del número de especies por clases naturales de tamaño se ilustra en el Cuadro 2. Se aprecia que el número de especies compartidas es prácticamente igual en los tres sitios: 8 años (26; 29%), 18 años (25; 35%) y bosque maduro (28; 33%). Esto sugiere que existe cierto número de especies

Cuadro 2 - Distribución del número de especies por clases naturales de tamaño Fustal (> 10cm DAP), Latizal (altura 1.5m y <10cm DAP) y Brinzal (altura 0.3-15m)

SITIO	NÚMERO TOTAL DE ESPECIES	NÚMERO DE ESPECIES EN FUSTAL	NUMERO DE ESPECIES EN LATIZAL	NUMERO DE ESPECIES EN BRINZAL	NUMERO DE ESPECIES COMUNES EN LOS TRES SITIOS
BOSQUE DE 8 AÑOS	90 (representadas en 977 individuos)	46 (representadas en 172 individuos)	72 (representadas en 429 individuos)	56 (representadas en 376 individuos)	26
BOSQUE DE 18 AÑOS	72 (representadas en 1150 individuos)	45 (representadas en 162 individuos)	51 (representadas en 310 individuos)	52 (representadas en 678 individuos)	25
BOSQUE PRIMARIO INTERVENIDO	85 (representadas en 1103 individuos)	59 (representadas en 163 individuos)	55 (representadas en 269 individuos)	63 (representadas en 671 individuos)	28

ubícuas que asegurarían su regeneración natural y contribuyen a la recuperación de sitios aprovechados a tala rasa. Su posibilidad de sobrevivencia dependerá de su temperamento ecológico, de la presencia de predatores naturales, de la ocurrencia de enfermedades endógenas y de la posibilidad de que sean cortadas (caso muy frecuente en el área de estudio) cuando alcancen el tamaño de "varas" (7-13cm de dap) o "tucas" (> 10cm dap).

Estas especies ubicadas en los tres sitios levantados para cada clase natural de tamaño, aparecen en el dosel y en el subdosel con fuerte frecuencia en la fase de regeneración natural (brinzal): *Welfia regia* (Arecaceae), *Protium nervosum* (Burseraceae), *Otoba lehmanii* (Myristicaceae), *Licania chocoensis* (Rosaceae), *Aniba* sp (Lauraceae). Esta especie, junto con *Guattenia calimensis* (Annonaceae) no aparecen en la fase de fustal (dap >10 cm) en el bosque maduro, pero son abundantes en la fase de brinzal (0.30 - 1.50 m), lo que sugiere que fueron cortadas después de su semillación. Finalmente *Brosimum utile* (Moraceae), típica especie esciófita, presenta muy pocos individuos en la fase fustal del bosque maduro y una escasa regeneración natural atribuible a su sobreexplotación. El temperamento ecológico de la mayoría de las especies del área de estudio ha sido definido en investigaciones anteriores (Ladrach y Mazuera, 1985 ; Faber-Langendoen, 1992)

Estructura diamétrica

El conocimiento y la identificación de los individuos y las especies por catego
permite identificar el estado de desarrollo del bosque, su coetaniedad y la formulación de sistemas silviculturales de manejo. Se emplea también para el cálculo de modelos de rendimiento.

La mayoría de los individuos mayores de 10 cm de dap tiende a agruparse en la clase diamétrica I (10-19.9cm). Para el sitio de 8 años, corresponde al 93%, para el de 18 años, al 74% y para el bosque primario al 50%, lo que evidencia el alto grado de intervención a que ha sido sometido este sitio.

En el Bosque Primario Intervenido se presenta una distribución relativamente uniforme de individuos a través de todas las clases diamétricas, en las especies *Otoba lehmanii, Licania chocoensis, Eschweilera amplexifolia, Protium nervosum* y *Brosimum utile*. En el caso del bosque de 18 años, se presenta un estado intermedio; aquí, especies como *Otoba lehmanii* y *Licania chocoensis* presentan individuos en la mayoría de clases diamétricas, mientras que *Guattenia calimensis* y *Miconia* sp. solo presentan individuos en las clases diamétricas inferiores. En el sitio de 8 años, *Vismia ferruginea* aparece solo en la clase diamétrica I, hecho que concuerda con otros estudios conducidos en sitios de edad similar en la misma zona.(Forero y Ordoñez, 1992 ; Mazuera, 1979). Es bien sabido que esta especie coloniza rápidamente claros originados por la caída natural de árboles grandes o por operaciones de extracción.

Area basal

Al establecer la relación entre las clases diamétricas y las áreas basales para los diferentes estados sucesionales estudiados, en el bosque de 8 años se puede observar que el 74% del área basal se concentra en los individuos ubicados en la clase diamétrica uno, con valores cercanos $2m^2$. Para el bosque de 18 años el 37% y el 26% de las áreas basales se concentran en las clases diamétricas 1 y 2, sugiriendo un bosque joven pero con individuos en transición a clases diamétricas superiores. El número de árboles por hectárea, el área basal y el volumen encontrados para los sitios estudiados se observa en el Cuadro 3.

Cuadro 3. Estructura de los sitios estudiados.

Tipo De Bosque	Dap (cm).	Nº Arboles/ha	Area Basal (m²/ha)	Volumen (m³/ha)
COLINAS BAJAS				
8 Años	>10	573	9.29	58.4
18 Años	>10	558	16.15	130.0
Primario intervenido	>10	543	27.37	287

El área basal del sitio de 8 años es 1/3 de la del bosque primario intervenido, mientras que el de 18 años alcanza algo más de la mitad. Una proporción similar fue encontrada para esta misma región por Faber - Langendoen (1992) en los bosques secundarios de similar edad (16-18 años). En la zona baja tropical del norte de Costa Rica, Guariguata *et al* (1997) encontraron valores de área basal (fustes > 10cm dap) 15% por debajo de la de sitios de bosque maduro. Esto sugiere que los bosques costarricenses tendrían un mayor poder de recuperación que los sitios talados del Bajo Calima. La razón podría encontrarse en el hecho de que aquellos se ubican en suelos de origen volcánico reciente, a la singularidad de las especies que conforman estos sitios, o a otras causas de sitio que están por investigarse.

CONCLUSIONES

La rápida recuperación de áreas sometidas a tala rasa en este estudio depende más de procesos de semillación *"in situ"* que de la acción de dispersores. Este hecho podría atribuirse a que la fauna capaz de dispersar frutos y semillas necesita amplios territorios, hoy muy disturbados por la permanente extracción de madera. Los levantamientos efectuados en las parcelas de regeneración natural indicaron que los renuevos y los brinzales juegan un papel muy significativo en el mantenimiento de la diversidad de especies "clímax" en estos bosques secundarios.

Se identificaron especies que hacen presencia solamente en las clases diamétricas inferiores : Sangre gallina (*Vismia ferruginea*), Yarumo (*Cecropia sp*), lo que sugiere su escasa longevidad o su lento crecimiento. Otras especies como Cargadero (*Guatteria calimensis*), no aparecen en clases diamétricas intermedias (20-40 cm), hecho que indica su desaparición debido al aprovechamiento de varas y tucas entre otras razones.

Este estudio desarrollado en fases sucesionales de 8, 18 años y Bosque Primario Intervenido, confirma la hipótesis propuesta por Faber Langendoen (1992), quien afirma que las especies clímax necesitan un largo tiempo de recuperación (más de 30 años); los resultados muestran que los ejemplares del dosel superior corresponden en su gran mayoría a especies heliófitas y heliófitas durables; las esciófitas parciales (más longevas) se agrupan en el subdosel.

Investigaciones previas realizadas en la misma región (Ladrach y Mazuera, 1985) apoyan nuestras observaciones. Ellos identificaron 18 especies heliófitas de los géneros *Cecropia* (cuatro especies), *Isertia* (una especie), *Miconia* (seis especies), *Ochroma* (una especie), *Pourouma* (dos especies), *Psychotria* (una especie) y *Vismia* (tres especies). Por su parte, Fdaber-Langendoen (1992) observó que especies "clímax" como *Mabea occidentalis, Guatteria* sp., *Macrolobium archerii* y las palmas *Orbygnia cuatrecasana y Amandra decasperma,* eran dominantes en el subdosel antes de la explotación del bosque primario, mientras que *Goupia glabra* (heliófita) era escasa. Estas especies, junto con otras identificadas en nuestros inventarios (*Brosimum utile, Calophyllum mariae, Protium nervosum, Manilkara bidentata, Pouteria* sp., *Licania chocoensis, Eschweilera amplexifolia, Otoba lehmanii y Welfia regia*) probablemente estarán por muchas décadas presentes en el dosel y en el subdosel. La permanencia de las especies del dosel identificadas en nuestro estudio dependerá : de la luz lateral que reciban los ejemplares juveniles, de las tasas de mortalidad de la regeneración natural, del grado de protección del bosque primario remanente como fuente semillera y de la presencia de claros. Esto último, apoyado en los resultados de otros investigadores (Foster y Brokaw, 1982 ; Hartshorn 1978, 1980), quienes concluyen que la mayoría de las especies del dosel en el bosque húmedo tropical dependen de claros para regenerarse y desarrollarse.

El área basimétrica (27 m^2/ha, dap $\geq$ 10 cm.) del bosque primario intervenido es baja comparada con la de otros bosques tropicales lluviosos. Sin embargo, recuperaría su valor inicial 30 años después de la explotación (Faber-Langendoen, 1992). El lento crecimiento de las especies del dosel y del subdosel con alta demanda comercial y la contínua extracción de madera del bosque remanente por los nativos, hacen muy imprecisa esta apreciación.

La dinámica de las especies heliófitas durables (tasas de incremento diamétrico, y mortalidad, patrones de dispersión, manejo de la regeneración natural, estudios fenológicos, entre otros), es una prioridad de investigación en el Bajo Calima, ya que de su manejo adecuado dependería la recuperación de extensas áreas taladas. Los resultados podrían generar modelos locales de silvicultura comunitaria.

Reconocimientos: Este trabajo se realizó con el apoyo financiero del Instituto de Hidrología, Meteorología y Estudios ambientales de Colombia.

REFERENCIAS

Buitrago, A y Montaña ,A, 1995. Análisis de fitocenosis de un bosque intervenido en las terrazas disectadas del Bajo Calima, Buenaventura, Colombia. Tesis de grado Universidad del Tolima.

Cannon P. 1985. Comparative analysis of the soils in the Bajo Calima concession in the primary forest and after clear-cutting. In: Ladrach, W. (ed): Investigación forestal en la concesión del Bajo Calima, 9°informe anual. Cartón de Colombia S.A. Cali. Colombia

CONIF. 1996. Investigación forestal del Pacífico Colombiano. Serie técnica N° 33. Santa fe de Bogotá. 175 p.

Del Valle J.I. 1997. Silvicultura en los Bosques de Guandal del Pacífico surcolombiano. En : Sabogal,C., Guariguata,M. y Camacho, M. (eds) : Seminario taller "Experiencias prácticas y prioridades de investigación en silvicultura de Bosques naturales en América Tropical." CIFOR/CATIE/INIA. Pucallpa, Perú.

Faber - Langendoen, D . F . 1989. Combining conservation and forestry in a Colombian rain forest: an Ecological assessment. PhD dissertation. Universidad de St. Louis. Missouri. USA. 284 p.

Faber - Langendoen & Gentry, A. 1991. The structure and diversity of rain forest at Bajo Calima, Chocó region, Western Colombia. Biotropica 23: 2-11.

Faber - Langendoen, D. 1992. Ecological constraints on rain forest management at Bajo Calima, western Colombia. Forest Ecology and Management. 53 :213-244.

Finegan, B. 1992. The management potential of neotropical secondary lowland rainforest. Forest Ecology and Management. 47: 295-321.

Foster, R.B. y Brokaw, N.V.L. 1982. Structure and history of the vegetation of Barro Colorado Island. Pp 67-81.In : E.G. Leigh, A.S. Rand y D.M.

Forero, L.A. y Ordoñez, H. R. 1992. Estudio ecológico estructural del bosque de segundo crecimiento (5 a 20 años de edad) en el Bajo Calima, Buenaventura, Valle, Colombia. Tesis Ingeniería Forestal Universidad del Tolima.

Guariguata, M.R., Chazdon, R.L., Denslow, J.S., Dupuy, J.M. & Anderson, L. 1997. Structure and floristics of secondary and old-growth forest stands in lowland Costa Rica. Plant Ecology 132 : 17-120.

Hartshorn, G.S. 1978. Tree falls and tropical forest dynamics. Pp 617-638. In : P.B. Tomlinson y M.H. Zimmerman (eds) : Tropical trees as living systems. Cambridge Univ. Press. London.

Hartshorn, G.S. 1980. Neotropical forest dynamics. Biotropica 12 (suppl.): 23-30

Holdridge, L.R. 1978. Ecología basada en Zonas de vida. Traducción de H. Jiménez. IICA. Serie libros y materiales educativos N° 34. 216 p.

Kanashiro, M. & Vleck, P.L. 1995. Secondary forest and fallow vegetation in Eastern Amazon region; Function and management. In: II SHIFT - Workshop Cuiaba. July 10-14 1995. Univ. Fed. Mato Grosso. CNPq / IBAMA / BMBF / DLR.

Ladrach, W.E. 1985. Investigación forestal en la concesión del Bajo Calima. 9° informe anual. Cartón de Colombia S.A. Cali. Colombia.

Ladrach, W.E. y Mazuera, A.E. 1985. Origen y características de la regeneración natural en un bosque lluvioso tropical después de la tala rasa. En: W.E. Ladrach (ed) : Investigación forestal en la concesión del Bajo Calima. Noveno informe anual. Cartón de Colombia S.A. Cali. Colombia.

Leigh, E.J., Rand, A.S. y Windsor, D.M. (eds) 1985. The Ecology of a Tropical Forest.: seasonal rhythms and long-term changes. Smithsonian Institution Press. Washington, D.C. 468 p.

Matteucci, S . y Colma , A. 1982. Metodología para el estudio de la vegetación. Organización de los Estados Americanos . Programa regional de desarrollo científico y tecnológico. Washington D.C. 168 p.

Magurran, A.E. 1988. Ecological diversity and its measurement. Princeton Univ. Press. New Jersey.

Mazuera, H. 1979.Composición y crecimiento de la regeneración natural de 4 a 15 años de edad en la concesión del Bajo Calima. Informe de investigación forestal N° 46. Cartón de Colombia S.A. Cali. Colombia

Mc Dade, L.A., Bawa, K.S., Hespenheide, H.A. & Hartshorn, G.S. (eds) 1994. La Selva; Ecology and natural history of a neotropical rainforest. University of Chicago Press. Chicago. 451.

Niño L. 1989. Los bosques de la subregión central del Anden Pacifico Colombiano; estado actual del conocimiento. Convenio CONIF - Holanda. Documento base. Serie de Documentación N° 14, Bogotá, Colombia.

Rojas, G. 1996. Caracterización estructural de los bosques del Bajo Calima. Buenaventura - Colombia. Universidad del Tolima. Facultad de Ingeniería Forestal, Ibagué. Colombia.

Saldarriaga, J.G., West, D.C., Tharp, M.L. & Uhl, C. 1988. Long-term chronosequence of forest succession in the upper Río Negro of Colombia and Venezuela. Journal of Ecology. 76: 938-958.

ECOLOGY AND SILVICULTURE OF OAK AND MIXED-OAK FORESTS IN THE SIERRA DE MANANTLAN, MEXICO: SEEKING FOR A SUSTAINABLE FOREST MANAGEMENT IN A BIOSPHERE RESERVE

Miguel Olvera Vargas, Blanca L. Figueroa Rangel
Universidad de Guadalajara. Centro Universitario de la Costa Sur. Instituto Manantlán de Ecología y Conservación de la Biodiversidad. Apartado Postal No 108. C.P. 48900. Autlán de Navarro, Jalisco. MÉXICO.

ABSTRACT

Oak woodlands (Quercus FAGACEAE) are one of the most abundant and diverse ecosystems in México. The Quercus genus is widely distributed in temperate areas represented by approximately 200-250 species. In the Sierra de Manantlán Biosphere Reserve (SMBR), in western México, Quercus embodies the fourth most abundant tree genus with approximately 34 species forming part of different vegetation types (oak forest, pine-oak forest, cloud forest and semideciduous dry forest) located over a diverse spectrum of environmental variables. With the aim to set the basis for a sustainable forest management of secondary oak and mixed-oak forests in the SMBR, the present study was started in 1991 when 60 circular permanent plots (500m^2 each) were established over different oak and mixed-oak forests. Stand structures, species composition, regeneration patterns, diameter growth, and their relation to physical site conditions were registered and analyzed. Different oak communities were discerned according to floristic composition and stand structure using multivariate methods. The results showed that oak regeneration is not being successful while more shade-tolerant species are replacing them. According to the diameter growth estimated for adults, a rotation length of 120 yr is suggested. We propose the application of two cutting methods for the management of these forests: Shelterwood Method for the monodominant oak community and Selection Cuttings for mixed-oak communities. However, the latter could not be profitable nor successful if it is implemented only for oaks.

INTRODUCTION

The highlands of México are probably the center of diversity for the genus *Quercus* in the western hemisphere. Oak forests (*Quercus* FAGACEAE) are among the most prominent vegetation types in the country with nearly 200 to 250 species already described, of which 86 are endemic to México. In the Sierra de Manantlán, Biosphere Reserve (SMBR) 34 oak species have been registered (Vázquez-García et al., 1995) growing in a wide spectrum of forest ecosystems mainly differentiated in two types: (1) Dry oak forest (400-1500 meters above sea level), characterized by deciduous trees reaching 15 m; the main species being *Quercus castanea*, *Q. glaucescens*, *Q. magnolifolia*, and *Q. rugosa*. (2) Subdeciduous oak forest (above 1500 m a.s.l.), characterized by Subdeciduous trees ranging in height from 20 to 35 m and dominated by *Quercus crassipes*, *Q. candicans*, *Q. acutifolia*, and *Q. laurina* (Cuevas et al., 1997).

These ecosystems are basically secondary forests as a result of intensive anthropogenic manipulations in which, many of the present stands, became established after heavy cuttings (basically clearcuttings), intensive wildfires and other man-related disturbances. In some cases,these events have promoted advance regeneration resulting in a mosaic of stands with different species composition and structures. Apparently, during former forest management executions undertaken in the area, a common practice was to deplete growing stocks of good quality trees while leaving the smallest or most deformed trees, not only in oak forests, but also in areas with other commercial tree species (mainly pines). These historical circumstances led to the replacement of the former vegetation and to the development of a highly fragmented secondary forest with ecologically complex stands, variable in structure, species composition and wood quality, making investment in many of them unjustified or marginal.

In spite of having a wide distribution along the national territory with a relatively high number of species, there have been only a few oak-related silvicultural research projects. This fact is reflected in the reduced number of scientific publications which are mostly linked to topics such as wood-structure, taxonomy and species-distribution, and only a few ones have been conducted to understand the ecological processes that underline these important ecosystems. Under the above scenario the present project considered the following objectives:

OBJECTIVES

i. To identify the floristic composition associated to secondary oak and mixed-oak forests in the Sierra de Manantlán, México.

ii. To identify stand characteristics which play a major role in the dynamic of secondary oak and mixed-oak forest (i.e. stand structures, regeneration patterns, diameter growth and physical site conditions).

iii. To define silvicultural systems of management, applicable to secondary oak and mixed-oak forests in the Sierra de Manantlán Biosphere Reserve.

METHODS

Study area

The SMBR is a protected area of 139,000 hectares established by governmental decree in 1987. It is internationally recognized as a floristic treasure house (McNeely *et al.*, 1990) and officially accepted within the UNESCO-MAB program. The SMBR belongs to the northwestern portion of the Sierra Madre del Sur. (19° 24° 32″ -19° 31° 02″ N; 104° 01° 09″ -103° 57° 44″ W) localized between the states of Jalisco and Colima in western México. Due to its geographical position in the transition zone between the Neartic and Neotropic and its closeness to the Pacific Ocean (50 km inland), it is a place distinguished by an outstanding richness of flora and fauna (Vázquez-García *et al.*, 1995). The landscape of the SMBR is characterized by its markedly folded topography and craggy physiography commonly constituted by steep slopes and ravines. The slope's range shows high variability as well, but it generally departs from 10 to 60%, albeit steep-side ravines with slopes higher than 90% are also very common. The altitude goes from approximately 400 m a.s.l. at Casimiro Castillo to 2860 m a.s.l. at Cerro La Bandera (Cuevas *et al.*, 1997), where a high floristic variation as well as a high variety of habitats converge. Over the highlands of the Sierra, woody-species such as oaks (Quercus spp), pines (Pinus spp), firs (Abies spp) as well as montane mesophytic forest species (generally integrated up to 200 different woody-tree species), are very common (Vázquez-García *et al.*, 1995). However, the main percentage of economic potential from lumber (e.i. oak forest, pine forest and montane mesophytic forest) roughly stretches between 1000 and 2400 m a.s.l. The Sierra de Manantlán lies within two hydrographic regions: RH15 and RH16 (INEGI, 1986), contributing significatively to the irrigation of the surrounding agricultural valleys on which sugar cane, maize and other important crops and fruits are cultivated.

Forest management background

The SMBR has a long forest management background; apparently its ecosystems have been under human influence since pre-Hispanic times. However, limited written evidence exists to support these judgements. Presently there are approximately 31 ejidos and rural communities with a population of approximately 9,000 inhabitants living inside the Reserve, and around 32,000 in the area of influence exerting great pressure into the area. Recently, much of the land has been cleared and turned into pasture or cultivation fields and the remaining stands have been repeatedly logged for timber and fuelwood or for the gathering of non-woody products. There is little information about the former forest operations in the area. Detailed records rarely go back as far as 15 years, but comments from local observers and supplemented by field testimony have indicated that "commercial" forest logging operations in the area were started by a transnational company, the "Colima Lumber", in the early 1900s.

Permanent plot sampling

The data set of this study was derived from sixty circular permanent plots of 500 m² each (0.05 ha), established selectively in several oak forest associations: 32 were installed in 1991 and 28 in 1994. A second remeasurement was undertaken in 1997 on the first 32 initial plots. A detailed methodology for the selection, establishment and survey of the permanent plots is fully described in Olvera *et al.* (1996).

Site characteristics

In each plot the following site characteristics were considered: altitude (m a.s.l.), canopy openness (%), humus layer thickness (cm), litter depth (cm), slope (%), herbaceous cover (%) and shrub cover (%). Canopy openness was evaluated using hemispherical photography. An average measure was obtained from eight photos taken in subplots of 1 m² (four perpendicular to the slope and four parallel to the slope), located at the center of the 500 m². Photographs were taken with a camera Canon Ti70 and a Canon 7.5mm/5.6 fisheye lens.

Tree characteristics

All woody-tree species found inside each 500 m² plot were ranked into three sampling categories. a) seedlings (individuals ≤ 1.30 m height); they were surveyed and recorded into eighth plots of 1 m², b) saplings (individuals > 1.30 m height < 5 dbh), they were monitored inside a sub-plot of 50 m² (4 m radius) installed at the center of the 500 m², c) adults (individuals ≥ 5 cm dbh), they were monitored within the 500 m² (12.7 m radius) plot; every adult was individually numbered and tagged.

- For adults we considered the following variables: species composition, diameter over bark at 1.30 m measured to the nearest millimeter, total height, total commercial pole height, bark thickness, canopy crown class (dominant, codominant, intermediate and overtopped), biological condition (alive or death), visible damage (classified into 13 different types) (Olvera et al., 1996) and stem forking condition.

- For saplings and seedlings we consider only number of individuals, species and total height.

Data analysis

Data analysis was organized into three parts: The first was to know the different species associations present in the 60 plots and their relation with site characteristics. We used TWINSPAN (Two-Way Indicator Species Analysis) to group the plots into classes based on their floristic composition (Hill, 1979), considering presence/absence data. An average of some site characteristics was computed by community type. The program HEMIPHOT (ter Steege, 1994) was used to derive estimations of canopy openness in percentage.

The second part was undertaken to describe the actual forest stand structure of the permanent plots by means of their diameter distributions and diameter increments.

Finally, the third part was undertaken to have an insight of the stand regeneration, a simple linear regression model was computed, with canopy openness as the independent variable, and the seedling density of each species as the dependent variable. A "t" test for independent variables was used to test the hypothesis of difference in seedling species abundance in relation to canopy openness.

RESULTS AND DISCUSSION

Oak and mixed-Oak forest composition

Seven community types distinguished from TWINSPAN at the 3rd level of division represented canopy species composition. The synoptic cover-abundance value which is the product of frequency and abundance (van der Maarel et al., 1987) was calculated for each tree species present in the 60 plots (Table 1). According to the results the communities were named as: 1. *Quercus laurina* community, 2. *Quercus rugosa* community, 3. Mixed-oak community (*Q. candicans*, *Q. castanea* and *Q. crassipes*), 4. *Quercus castanea community*, 5. *Quercus crassipes-Quercus castanea* community, 6. *Quercus crassipes-Pinus leiophylla* community and 7. *Quercus crassipes* community.

Table 1. Cluster structure of the mixed-oak forests in Cerro Grande with synoptic cover-abundance values for species in the 60 plots. The average of some site characteristics by community is shown at the bottom of the table.

COMMUNITY TYPE	1	2	3	4	5	6	7
CLUSTER SIZE	14	17	6	3	2	4	14
A. religiosa var. *emarginata*	0.6	0.0	0.0	0.0	0.0	0.0	0.0
A. religiosa var. *religiosa*	0.0	0.0	0.0	0.0	0.0	0.0	0.1
Acacia pennatula	0.0	0.0	0.0	2.0	0.0	0.0	0.0
Alnus jorullensis	0.0	0.0	0.8	0.0	3.0	4.2	3.7
Arbutus xalapensis	0.2	0.9	0.8	0.0	1.5	0.2	0.0
Carpinus sp.	0.0	0.1	0.0	0.0	0.0	0.0	0.0
Clethra sp.	0.9	0.0	0.0	0.0	0.0	0.0	0.0
Comarostaphylis discolor	0.0	0.8	0.0	0.0	0.0	0.0	0.0
Cornus excelsa	1.2	0.3	1.0	0.0	0.0	0.0	0.0
Fraxinus uhdei	0.1	0.6	0.0	0.0	0.0	0.0	0.0
Garrya laurifolia	1.7	0.6	0.0	0.0	0.0	4.0	0.0
Ilex brandegeana	1.1	0.1	0.0	0.0	0.0	0.0	0.0
Litsea glaucescens	0.0	0.3	0.0	0.0	0.0	0.0	0.0
Oreopanax xalapensis	1.0	0.1	0.0	0.0	0.0	0.0	0.0
Picramnia guerrerensis	0.0	0.0	0.0	0.3	0.0	0.0	0.0
Pinus leiophylla	0.1	0.4	0.2	0.0	0.0	4.7	1.2
Pinus pseudostrobus	0.0	0.0	0.0	0.0	0.0	0.0	0.7
Prunus serotina	0.1	0.0	0.1	0.0	0.0	2.0	3.8
Quercus candicans	1.5	1.3	4.5	0.0	3.0	0.0	0.0
Quercus castanea	0.3	2.1	4.6	6.0	6.0	2.0	0.0
Quercus crassipes	0.0	0.0	4.5	0.0	7.0	6.7	8.3
Quercus laurina	4.2	0.0	0.0	0.0	0.0	0.0	0.0
Quercus obtusata	0.0	0.0	0.0	2.0	0.0	0.0	0.0
Quercus rugosa	0.5	2.8	0.6	0.0	1.5	1.5	0.1
Styrax argenteus	3.2	0.0	0.0	0.0	0.0	0.0	0.0
Symplocos citrea	2.8	0.9	0.2	0.0	0.0	0.0	0.0
Ternstroemia lineata	6.2	6.5	0.1	0.0	0.0	0.0	0.0
Xylosma flexuosum	0.1	0.4	0.1	0.0	0.0	0.0	0.0
Zinowiewia concinna	0.1	0.0	0.0	0.0	0.0	0.0	0.0
Altitude (m a.s.l)	2200	2187	2110	2033	2125	2300	2259
Canopy openness (%)	3.4	7.9	12.8	15.8	15.7	7.3	5.7
Herbaceous cover (%)	10	20	30	50	30	40	35
Litter depth (cm)	4.5	4.5	4.5	1.6	4.5	4.6	3.7
Shrub cover (%)	2.1	3.2	5.0	3.3	0.0	0.0	0.3
Slope (%)	38	31	33	21	30	59	23
Thickness of the humus layer (cm)	2.5	2.2	3.5	1.0	1.7	3.1	2.0

Structure of oak and mixed-oak forests

When the diameter distribution range of each of the seven oak and mixed-oak communities were compared they were mostly representatives of young stands (Fig 1), which are characterized by trees of relatively small diameter and moderate density. In most cases, stands of stem size distribution skewed to small individuals (except community 4) particularly in stands where species composition was more diverse. Generally, the number of trees per diameter size gradually decreased at different rates while increasing the diameter size. However, most of the plots showed the classical negative exponential diameter distribution, a typical pattern expected in uneven-aged stands (Leak, 1965) characteristic of shade-tolerant species (Fig. 1).

Communities dominated by *Q. crassipes* (communities 5, 6 and 7) had a similar diameter distribution pattern, either in mixed-oak canopies or in monodominant ones. Such a pattern characterized this species with a good recruitment and probable successful self-replacement. However considering the 60 plots, no clear pattern showed up among the main stand attributes (e.g., stocking density and mean diameter size) which are normally stand parameters used to design silvicultural management programs (Fig. 1).

Diameter Growth Patterns

Diameter increment did not show a linear pattern in relation to mean diameter (e.g. big increments related to big diameters), although there was a clear variation among the plots in relation to diameter increments (from 0.4 to 1.6 cm)(Fig. 2). The regression linear model for this data was not significant ($r^2=0.001$, $P=0.82$). This finding differed from the results reported by Perry (1985) and Tanaka (1988), in which they described a positive linear relationship between periodic increment and the diameter size of the tree within any given social stratum.

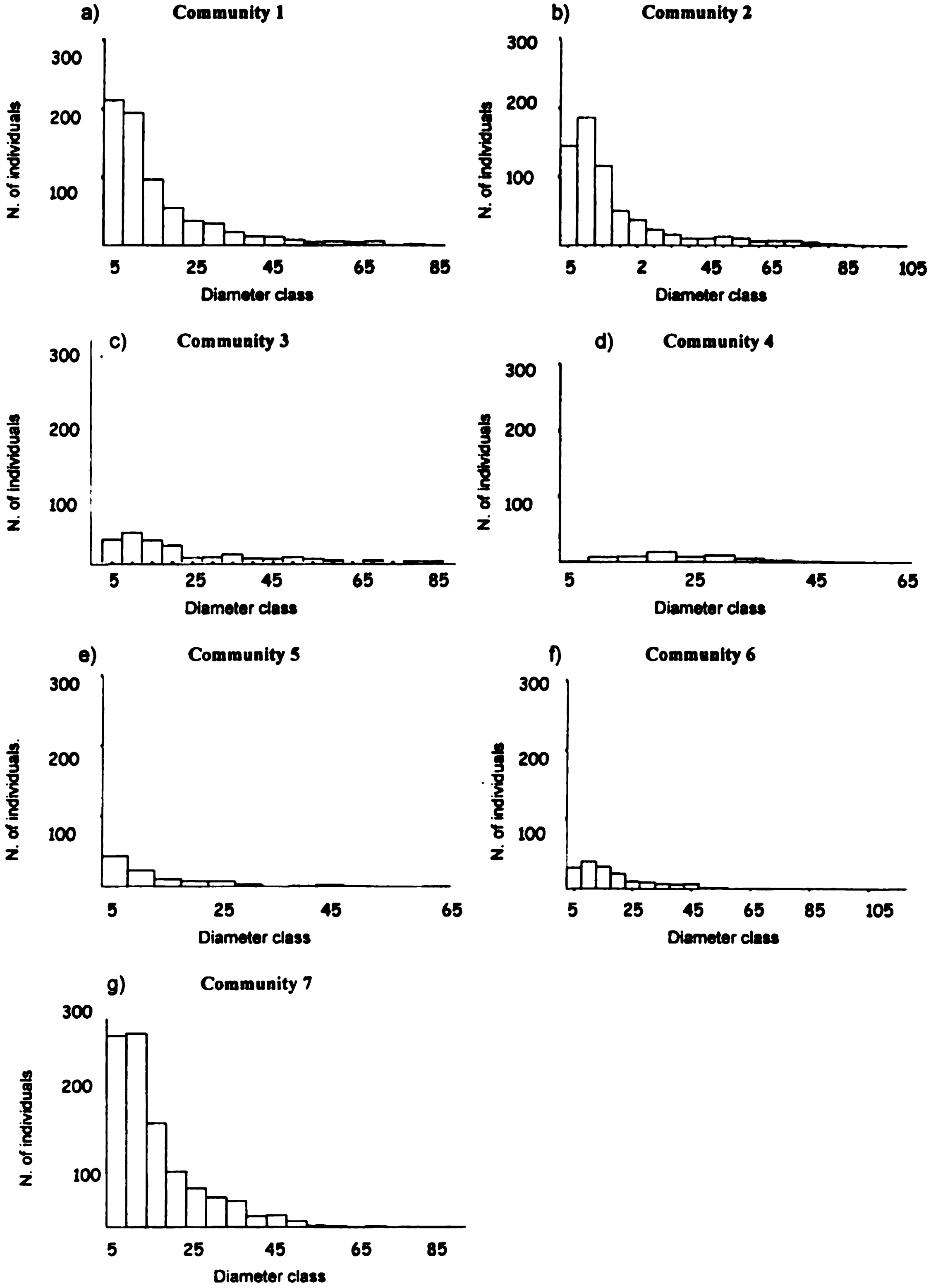


Figure 1. Diameter distributions of the seven oak communities

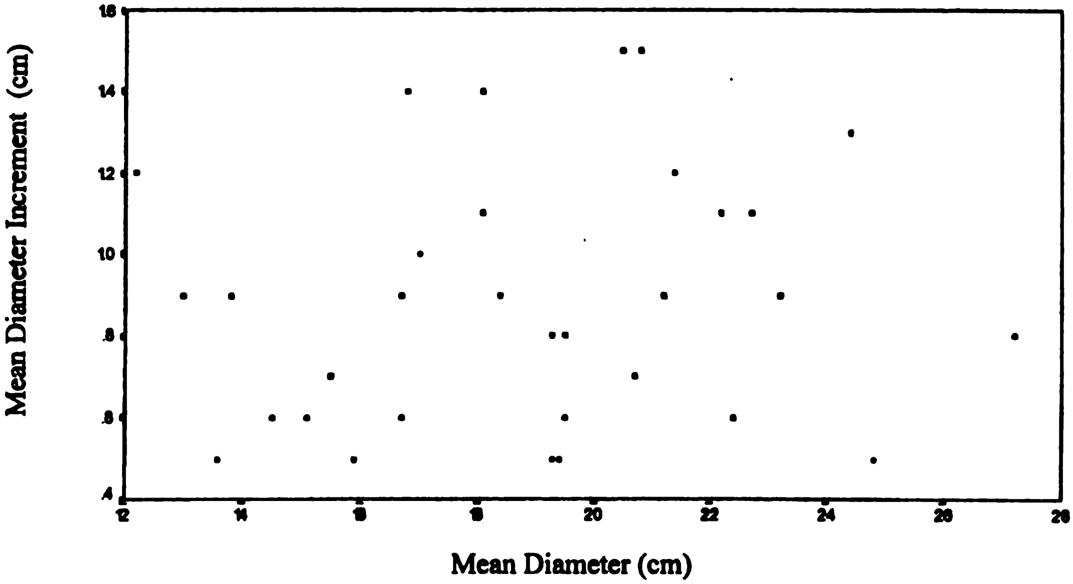


Figure 2. Mean Diameter Increment-Mean Diameter relationship

We assumed that these diameter-increment dissimilarities were due to differences in some site characteristics such as slope and canopy openness among the permanent plots, and to different diameter growth capabilities among species (Table 2). Another reason of the non-linearity relationship displayed by the diameter increment was probably due to the short time-span between measurements, or that the sample sizes (number of permanent plots or number of trees by diameter-class) did not include the full range of diameter increment present in the study area. Probably if we try with other predictor variable (canopy openness, basal area, density) we could find a clearest linear pattern.

Table 2. Mean Diameter Increment of some species in Secondary Oak and Mixed-Oak forest stands in the Sierra de Manantlán from 1991 to 1994

SPECIES	Dg (cm)
Alnus jorullensis	1.0±0.3
Arbutus xalapensis	1.0±0.4
Comarostaphylis discolor	0.8±0.4
Garrya laurifolia	1.5±1.0
Oreopanax xalapensis	1.9±2.1
Pinus leiophylla	2.3±0.7
Pinus pseudostrobus	3.1±2.4
Prunus serotina	0.8±0.1
Quercus candicans	0.9±0.3
Quercus castanea	0.9±0.3
Quercus crassipes	0.6±0.05
Quercus rugosa	1.2±0.3
Symplocos citrea	0.8±0.6
Ternstroemia lineata	0.8±0.1

Dg = Diameter increment (91-94)

Regeneration patterns in relation to canopy openness

The relationship between seedling density and canopy openness was not linear for any species, except for Prunus serotina (r^2=0.29, P=0.0). It has been seen that understory composition showed local dominance by different species and, such heterogeneity can be a result of different tree dispersal patterns. This brings canopy heterogeneity, which produces complex gradients of light at the forest floor (Cho and Boerner, 1991). In the present study we could see that every *Quercus* species requires a specific amount of canopy openness and, according to our results, *Q. crassipes* and *Q. castanea* required larger canopy gaps and *Q. laurina* and *Q. rugosa* required small openings for successful establishment (Table 3).

Table 3. Presence of seedling species in the 60 plots related to mean canopy openness.

SPECIES	MEAN CANOPY OPENNESS (%)	NUMBER OF PLOTS
Cornus excelsa	5.14	17
Garrya laurifolia	6.21	38
Oreopanax xalapensis	3.99	22
Prunus serotina	6.57	23
Quercus candicans	6.41	15
Quercus castanea	13.0	15
Quercus crassipes	8.16	17
Quercus laurina	2.90	13
Quercus rugosa	6.20	9
Styrax argenteus	4.00	25
Symplocos citrea	4.21	11
Ternstroemia lineata	6.00	31
Xilosma flexuosum	10.18	13

Canopy openness in the stands is related to crown density, species composition and number of individuals. Oak density decreases with increasing basal area, which in turn is associated with reduced light on the forest floor (Johnson, 1992). Plots in which *Q. crassipes* and *Q. castanea* dominated the canopy showed smaller stems than those of other species, their crowns were smaller and more light entered the forest floor. In contrast, *Q. candicans* and *Q. laurina* had bigger stems which implied more basal area (Figueroa-Rangel, 1995) and less light entering to the forest.

Silvicultural alternatives of management

To define the potential alternatives of management, we considered the forest association discerned by TWINSPAN (Table 1), the structure of each community (Fig. 1) and the regeneration pattern in relation to canopy openness. Therefore each community should receive different silvicultural treatments and cutting methods to conduct them towards a desirable condition. However, in order to facilitate the forest management strategy, it would be more appropriated the implementation of only two management alternatives. One under an even-aged management (shelterwood cuttings) and another under uneven-aged management (selection cuttings). It is important to consider that the oak community number 3 (Table 1) dominated by Q. candicans in which mesophytic species were associated, should not be managed under a timber production perspective, once the particular species associations and restricted range of distribution might not sustain its management.

a) Shelterwood method (technical and ecological fundamentals)

Oaks are characterized as shade-tolerant to mid-tolerant species (McGee, 1981; Jokela and Sawtelle, 1985; Crow, 1988; Kolb et al., 1990; Quintana-Ascencio and González-Espinosa, 1993). This particular shade tolerance behavior enable them to establish and grow beneath close canopies which facilitate the implementation of both even and uneven-aged management systems. However, the best cutting alternative for communities 4, 5, 6 and 7 could be the shelterwood method. The ecological and technical foundations to recommend a shelterwood cutting method strategy are:

1) Shelterwood cuttings of low intensity might be carried out in the initial phase of the management activities. During this phase, only those overtopping and all badly-shape or crocked trees may be removed, although oak species must be removed with a low intensity, because it is important to keep stands dominated by oak-species.

2) Stocking density does not necessarily need to be maintained high, only trying to keep the necessary number of trees to achieve an adequate stand canopy cover according to particular oak-species requirement for light.

3) We consider that there is not need to apply early thinnings on oak species, firstly because we did not observe high density in the stands, which could represent a risk of mortality due to competition. Secondly, because their mid-shade tolerance characteristics enables them to grow beneath closed canopies.

4) Partial cuttings might be leaded toward those abundant and conspicuous species associated to these communities such as *T. lineata* and *P. serotina* and occasionally *Abies religiosa*. However, it would be important to keep the mixture of species in order to provide the opportunity to apply intermediate cuttings on these tree species before the final harvest over oak is reached. Apparently, the oak associations with these secondary species have little influence on oak diameter growth and, at the same time, they might provide favorable stand conditions for oak regeneration in their first developmental stages. Oaks could be partially harvested until they begin to compete among themselves, either in the canopy or in the medium stratum.

Rotation Period

In previous studies, Olvera and Moreno (1992) and Moreno et al., (1995) suggested an 80 yr rotation period for oaks (independently of the oak species) to attain a 45 cm mean diameter in Cerro Grande, Sierra de Manantlán. Based on actual diameter growth estimations, we consider that an 80 year rotation period, it is not possible to attain the mean diameter previously programmed. The rotation period will be in function of each particular species, due to the differences in their diameter increments (Table 2). Therefore, it should be extended to a minimum of 120 years, that means 40 years more than the previously estimated, but it is imperative to undertake additional research strategies to make more reliable these estimations. One important alternative will be the development of growth models for the estimation of rotation lengths.
In this respect, if one wants to profit from the harvesting of these oaks stands other species present in the medium stratum (such as *T. lineata* or *P. serotina*) could be considered, as they are also appreciated in the construction industry or as a source of minor forest products.

b) Selection cuttings

It is important to mention that the study area is located in a protected area, a Biosphere Reserve, therefore it is necessary to set a balance between conservation and production objectives, which in many cases are mutually exclusive. Under this scenario, the Selection Cuttings Method could be the most appropriate to be implemented on the communities 1 and 2, because uneven-aged systems might be more compatible to undertake multiple-objective management. Uneven-aged management is also more compatible when leading with different range of light-tolerance and species composition (Alexander, 1986). As our results showed, Communities 1 and 2 (Table 1) included different species mostly characterized as shade-tolerant with oak species dominating the canopy; these communities also showed irregular stand structures (Fig. 1) and more diverse species composition than the other communities. However, due to the scarce oak presence, their low diameter growth, and their location in the "Core Area" of the Reserve, we consider that the implementation of this method is not profitable both economically and socially.

FUTURE LINES OF RESEARCH

Future lines of research for this project will consider:
- To construct growth models for the different oak species.
- To determinate the effect of controlling burning on the regeneration establishment
- To determinate the effect of partial cuttings on diameter growth and regeneration establishment.
- To quantify the effect of environmental factors on tree and stand growth.

ACKNOWLEDGEMENTS

The authors want to thank M.Sc. Carlos Palomera García for his help in the english correction of the manuscript. To the people from El Terrero in the Sierra de Manantlán for their help and assistance in the development of this project, and to Dr. Bryan Finegan and the WWF for their support to attend this meeting. The Universidad de Guadalajara, México and the United Kingdom's Department for International Development (DFID) supported financially this project.

REFERENCES

Alexander, R. R. 1986. Silvicultural systems and cuttings methods for ponderosa pine forests in the front range of the central Rocky Mountains. USDA For. Serv. Gen. Tech. Rep. RM-128, 22 p.

Cho, D.S. y R.E.J. Boerner. 1991. Canopy disturbance patterns and regeneration of Quercus species in two Ohio old-growth forests. Vegetatio 93:9-18

Crow, T.R. 1988. Reproductive mode and mechanism for self-replacement of Northern Red Oak (Quercus rubra)- a review. Forest Science. 34(1):19-40.

Cuevas-Guzmán, R., B. Benz and E. Jardel. 1997. Sierra de Manantlán Region and Biosphere, México. In: WWF and IUCN (1994-1997). Centers of Plant Diversity. A guide and strategy for their conservation. 3 volumes. IUCN Publications Units. Cambridge, U.K. pp. 148-152.

Figueroa-Rangel, B.L. 1995. Ecology of mixed-oak forests in Cerro Grande, Sierra de Manantlán, Jalisco, México. M. Sc. Thesis. Wageningen Agricultural University. The Netherlands. 99 p.

Hill, M.O. 1979. DECORANA - A FORTRAN program for Detrended Correspondence Analysis and Reciprocal Averaging. Cornell University, Ithaca, NY.

INEGI. 1986. Cartas hidrográficas E13-2-5.

Johnson, P.S. 1992. Oak overstory reproduction relations in two xeric ecosystems in Michigan. For. Ecol and Manage. 48:233-248

Jokela, J.J. and R.A. Sawtelle. 1985. Origin of oak stand on the Springfield plain: A lesson on oak regeneration. In: J.O. Dawson and K.A. Majerus (eds). Proc. Fifth Central Hardwood Forest Conference. Univ. of Illinois. 299 p.

Kolb, T.E., K.C. Steiner, L.H. McCormick y T.W. Bowersox. 1990. Growth response of northern red-oak and yellow-poplar seedling to light, soil moisture and nutrients in relation to ecological strategy. For. Ecol and Manage. 38:65-78

Leak, W.B. 1965. The J-shaped Probability Distribution. Forest Science 11(4):405-409.

McGee, C.E. 1981. Response of white oak to release. Res. Note SO-273. New Orleans, LA. USDA For. Serv. Southern For. Exp. Station. 4 p.

McNeely, Jeffrey A., Kenton R. Millere, Walter V. Reid, Russell A. Mittermeier and Timothy B. Werner. 1990. Conserving the world's biological diversity. IUCN, Gland, Switzerland; WRI, CI,

WWF-US, and the World Bank, Washington, D.C. 193 p.

Moreno G. S., M. Olvera Vargas y B.L. Figueroa R. 1995. Sistemas Silvícolas para Encinares en Cerro Grande, Sierra de Manantlán. In: Marroquín, J. (ed.). Memorias del III Seminario sobre

Utilización de Encinares. 4-6 de noviembre de 1992. Facultad de Ciencias Forestales. Universidad

Autónoma de Nuevo León. Reporte Científico Número Especial 15. pp. 301-319.

Olvera Vargas, M. y S. Moreno G. 1992. Estructura y Regeneración de Encinares en la Sierra de Manantlán, Jalisco. In: Martínez A., B. (ed.). Memorias del Primer Foro Nacional sobre Manejo

Forestal Integral. 10-11 de octubre de 1991. Universidad Autónoma de Chapingo. División de Ciencias Forestales. pp. 403-409.

Olvera Vargas, M., S. Moreno G, y B.L. Figueroa R. 1996. Sitios permanentes para la investigación silvícola: Manual para su establecimiento. Universidad de Guadalajara. Centro Universitario de la Costa Sur. Instituto Manantlán de Ecología y Conservación de la Biodiversidad. 55 p.

Perry, D.A. 1985. The competition process in forest stands. In: Attributes of trees as crop plants. M.G.R. Cannel and J.E. Jackson, eds. Institute of Terrestrial Ecology, Abbots Ripton, Hunts, England pp. 481-505.

Quintana-Ascencio, P. F. y M. Gonzalez-Espinosa. 1993. Afinidad fitogeográfica y papel sucesional de la flora leñosa de los bosques de pino-encino de los altos de Chiapas, México. ActaBotánica Mexicana 20.59-75

Tanaka, K. 1988. Effects of stand density on the increments of trees in an even-aged pure stand. In: Ek, A.R., Shifley, S.R. and Burk, T.E. eds. Forest growth modeling and prediction. Proceedings of the IUFRO conference, Gen. Tech: Rep. NC-120. August 23-27, 1987. Minneapolis, Minnesota. pp. 644-651

ter Steege, H. 1994. HEMIPHOT: a programme to analyze vegetation indices, light and light quality from hemispherical photographs. Tropenbos Document 3. The Tropenbos Foundation. Wageningen, The Netherlands. 44 p.

van der Maarel, E., Espejel, I. & Moreno-Casasola, P. 1987. Two step vegetation analysis based on very large data sets. Vegetatio 68:139-143.

Vázquez-García, J.A., Cuevas-Guzmán, R., Cochrane, T.S., Iltis, H.H., Santana-Michel F.J. & Guzmán-Hernández, L. 1995. Flora de Manantlán. SIDA Botanical Miscellany No. 13. U.S.A. 312 p.

CONTRIBUTION OF SPROUTS TO FOREST RECOVERY AFTER SLASH-AND-BURN AGRICULTURE IN EASTERN PARAGUAY

Ludwig Kammesheidt
Institut für Waldbau, Abt. II: Waldbau der Tropen, Universität Göttingen, Büsgenweg 1, D-37077 Göttingen, Federal Republic of Germany

ABSTRACT

The role of tree sprouts in the recovery of tropical moist forest in Eastern Paraguay after swidden agriculture was examined in 2-15 yr old forest fallows and compared with sprouting in mature forest. The proportion of stems of sprout origin, as individuals arising from stumps or lower parts of live stems (R ≤1 m), in the stem density declined from 59.5% (stems 1 - 4.9 cm DBH) and 21.0% (stems ≥ 5 cm DBH) in the young regrowth stands (2-5 yr old) to 32.9% and 19.6%, respectively in the older regrowth stands (10 and 15-yr old). Sprouts were absent in the mature forest. Out of 58 species sampled in the regrowth stands, 28 occured both as resprouts and seed regeneration, 7 were only found as resprouts, and 23 were only present as seed-established individuals. No significant relationship was found between the successional status or the growth form of species and apparent resprouting capacity. Seed-established individuals of Trema micrantha were predominant in the two and three year old regrowth stands. In the more advanced successional stages, T. micrantha *was replaced by* Cecropia pachystachia *and other secondary species. Species richness increased during succession. Floristic similarity to the mature forest, calculated with the qualitative Soerensen index, increased from 0.45 (1-4.9 cm DBH) in the young regrowth stands to 0.52 in the older regrowth stands. In the tree stratum (≥ 5 cm DBH), however, floristic composition approached only 0.28 in the younger regrowth stands and 0.44 in the older regrowth stands, respectively that of the mature forest.*

INTRODUCTION

Initial floristic composition in disturbed tropical forest is mainly determined by the soil seed bank, advance regeneration, and the resprouting capacity of stumps. In recent times, sprouting has been studied in natural forests after hurricane disturbance (Yih *et al.* 1991; Basnet 1993; Bellingham *et al.* 1994), after fire disturbance (Kauffman 1991), or as a component of regeneration after natural gap creation (Putz & Brokaw 1989; Matelson *et al.* 1995).

In neotropical forests, sprouting is the most common means of regeneration after forest cutting, but burning reduces the amount of sprouts (Uhl *et al.* 1981; Uhl & Jordan 1984). Moreover, repeated weeding and prolonged cultivation lead to a steady decline in, or even to the complete exhaustion of, the resprouting capacity of trees (Uhl *et al.* 1982a; de Rouw 1993). However, except for the work of Saldarriaga *et al.* (1988), who studied sprout density in 9 to 80-years old forest fallows and mature forest stands, the long-term role of sprouts in the overall recovery process after slash-and-burn agriculture is not well documented.

This paper describes resprouting in different-aged forest fallows and mature forest in Paraguay with the following objectives: (1) to determine the proportion of sprouts in stem density and basal area with successional age, (2) to study the role of sprouts in canopy recovery, (3) to investigate the resprouting ability of tree species of different successional status and growth form, and (4) to determine the contribution of sprouts to the restoration of species diversity.

STUDY AREA

This research was conducted in the District of Choré (24° 06′-17′ S, 56°22′-34′ W), Department of San Pedro, in the Eastern Region of Paraguay. The terrain is gently undulating and ranges from 80 to 230 m asl. Mean annual rainfall is about 1300 mm. The dry season with monthly precipitation of < 60 mm lasts from May to August. Mean annual temperature is 22.4° C.

Forest formation and geology

Hueck (1966) describes most of the forests of the Eastern Region as part of the formation that includes 'subtropical, deciduous and mesophytic forests of South-eastern Brazil'; in some parts, this forest shows a high proportion of evergreen tree species. The canopy is 25-30 m tall. In the past, this type of forest covered vast areas between the Paraguay and Paraná river; the study area is situated at the westernmost edge of the present distribution of this vegetation type. The parent material consists mainly of fluvio-glacial sandstone which is deeply weathered. Soils are Oxisols composed mostly of quartz sand with low percentages of clay down to a depth of 1 m (de Olivéira & Burgos 1995). Our knowledge about the structure and species composition of this fast-dwindling forest resource is still very scanty. The only detailed floristic study to date was published by Stutz de Ortega (1987).

Colonization and farming practices

Modern colonization of the study area began in the late 1960s. At that time, the area was densely covered by forests, except some small patches of savanna along creeks. Early settlers received 15 - 20 ha of pristine forest for cultivation from a government programme. But with time, areas allocated to farmers decreased to 3 - 10 ha. At the time of this study (1988), mature forests had diminished to some 10%. Secondary forests of various ages occupied about 20-30% of the entire area.

Cash crops are tobacco (*Nicotiana tabacum*) and cotton (*Gossypium* sp.). Due to the higher market price, farmers plant tobacco in the first year after forest clearance. However, after tobacco cultivation soil fertility is reduced to a degree which does not allow further agricultural use of this plant. Thus, farmers usually shift to cotton cultivation. After three years the soils may require a fallow of ten to fifteen years to regain fertility. Nonetheless, small farmholders often cut the regrowth long before fertility is fully restored. In the second farming period, the soil condition restricts cultivation to food crops such as cassava (*Manihot esculenta*). The decreasing productivity of the sites is indicated by the accelerating tendency of converting crop fields into pasture.

METHODS

Site selection

A chronosequence of study sites was selected by interviewing farmers. The oldest regrowth found had been abandoned fifteen years before the study. Another regrowth stand was dated at 10 yr. Younger regrowth stands 2-, 3-, 4- and 5 yr old were also identified. In the stand selected as mature forest large size trees and lianas were found and no signs of human disturbance (e.g. stumps, charcoal) were observed. Additional criteria for site selection was that the regrowth stands were all similar in topography, distance to mature forest, and site history. All regrowth stands, ranging from 0.2 - 1.5 ha in size, were located in the upper part of the undulating landscape (c. 200 m asl.). Mature forest was within 100-150 m and in all forest fallows tobacco and cotton were cultivated for a period of three years prior to abandonment. Tall residual trees or palms of the original forest were not found within the regrowth stands.

Sample size and sampling design

All sample plots were 10 x 50 m (500 m^2). Eight plots were established randomly in the mature forest. Four plots were laid down in each of the 10-yr and 15-yr old forest fallows, hereafter lumped together as older regrowth stands. Young forest fallows were found particularly small in scale (0.2 - 1 ha). Thus two plots were established in each of the two-, three-, four- and five year old forest fallows and hereafter combined as young regrowth stands. Hence, sample area in each of the three stand types was 0.4 ha (n = 8 plots).

Parameters measured

In each sample plot (500 m^2) all trees, shrubs and palms were measured and identified down to 5 cm DBH (diameter at breast height = 130 cm), hereafter referred to as tree stratum. Woody plants, 1.0 - 4.9 cm DBH, excluding lianas, were sampled in a central strip of 2 x 50 m (100 m^2) within each plot, hereafter referred to as sapling stratum. Sprouts emerging from stumps and lower parts of live stems ($\leq$1m) were measured and identified in both strata; the number of sprouts per stump were counted. The diameter of resprouting stumps was measured at the stem base. The height of trees $\geq$ 5 cm DBH was measured either with a telescoping measuring pole or a Blume-Leiss altimeter to the nearest meter.

Categorization of species

Species were categorized according to successional status. Pioneers were found exclusively in the regrowth stands where they are capable of forming nearly pure stands at initial stages. Secondary species occured both in regrowth forest and in mature forest, but predominantly in the former. Primary species were found mainly in mature forest. Moreover, species were categorized into growth forms defined as maximum attainable height: (1) large trees > 20 m tall, (2) medium-sized trees are in the range of 10 - 20 m in height, and (3) small trees < 10 m tall. Species denoted as 'shrub' are small woody plants which branch near ground level into several main stems.

Data analysis

The structural dominance of resprouting species in regrowth stands and mature forest was calculated with the Importance Value Index (IVI), as the average of relative density, frequency and basal area; in the sapling stratum (1 - 4.9 cm DBH) only relative density and frequency were considered. IVI values of both strata were divided by two to give the mean value of the individual species. The G-test (Sokal & Rohlf 1981) was used to test if resprouting depended on (1) the successional status or (2) the growth form of the species. The *t*-test was applied to test for differences in the mean number of species per plot between stand types. Level of significance was set at $\alpha = 0.05$. Species diversity within stand types was calculated by using the Shannon-Wiener H' value and evenness value (Magurran 1988). Floristic similarity between stand types was calculated with the qualitative index of Sorensen, considering the species common to both sites, and with the quantitative index, which accounts either for the relative abundance or relative basal area of shared species (Magurran 1988).

RESULTS AND DISCUSSION

Stem density and basal area

Stem density varied most widely in the young regrowth stands, suggesting that chance and time of establishment are predominant factors (Table 1). In the sapling stratum (1 - 4.9 cm DBH) mean stem density declined sharply with age. In contrast, in the tree stratum (≥ 5 cm DBH) stem density increased and approached the value of mature forest. Sprouts were not found in the mature forest. In the sapling stratum of the young regrowth stands, sprouts accounted for approximately 60% of the total stem number, while in the older regrowth stands roughly one third of all stems were of sprout origin. In the tree stratum stem density and percentage of sprouts was more similar. The decreasing share of sprouts in the basal area during succession and, the relatively high sprout density in the older regrowth stands indicates that with time individuals established by seeds become more dominant in the stand structure. Saldarriaga *et al.* (1988) observed a similar trend along a chronosequence of 9 to 80 yr old regrowth stands on Oxisols of *tierra firme* in Venezuela and Colombia.

Table 1. Stem density per plot, basal area (m^2 ha_{-1}) and proportion of sprouts (%) in successional stages and mature forest (Abbreviations for stages: YRS = young regrowth stands, 2-5-yr old; ORS = older regrowth stands, 10 and 15-yr old; MF = mature forest)

	1 - 4.9 cm DBH/100 m^2					DBH ≥ 5 cm/500 m^2					
Stage	*n*	min	max	mean ± SD	sprouts	min	max	mean ± SD	sprouts	m^2 ha^{-1} *	sprouts
YRS	8	39	88	68.0±16.8	(59.5)	12	43	29.8±11.3	(21.0)	3.2	(30.5)
ORS	8	12	61	40.3±15.7	(32.9)	24	40	34.4±5.2	(19.6)	9.1	(19.9)
MF	8	19	37	30.8±6.0	-	29	38	33.9±3.4	-	24.7	-

* trees ≥ 5 cm DBH

Number of sprouts and non-sprouts in successional stands

Species were classified as 'pioneer' or 'non-pioneer', the latter group includes all secondary and primary species (see Methods; Fig. 1). In the study area, *Trema micrantha*, *Cecropia pachystachia* and *Solanum granuloso-leprosum* are typical pioneer species. Two and three years after farm abandonment stems ≥ 5 cm DBH were predominantly seedlings of *T. micrantha* which presumably emerged from the soil seed bank. In the sapling stratum mainly sprouts of non-pioneer species were found. In the tree stratum of the four and five-year old forest fallows, the percentage of sprouts increased while it declined in the sapling stratum. Only a tiny fraction of the overall number of individuals in both strata were represented by seed-established pioneers. *C. pachystachia* was the only pioneer species which persisted in this successional stage. In the first few years of succession, in general, sprouts ≥ 5 cm DBH represented an increasing proportion on the total number of stems (from 7.4% in year 2 to 33.8% in year 5), whereas the percentage of sprouts < 5 cm DBH decreased steadily (from 72.0% in year 2 to 47.8% in year 5). In the more advanced successional stages, ten and fifteen years after farm abandonment, seed-established pioneer species continued to play a minor role in species composition. Sprouts of non-pioneer species showed a declining proportion on the total stem density in both strata. The small number of resprouting pioneer species emerged either from randomly cut or fallen individuals. As in the four and five year old regrowth, no seedlings of pioneer species were recorded in the sapling stratum.

Uhl & Jordan (1984) found that the stem density of seed-established pioneer species > 2 m tall culminated two to four years after cutting and burning in Amazonian Venezuela, and sharply declined thereafter, whereas the sprout density, as in the tree stratum of this study, increased up to the fifth year after disturbance. No other study in regrowth stands, however, monitored the dynamic of seed-established pioneers, sprouts and non-sprouts of non-pioneer species in more advanced successional stages.

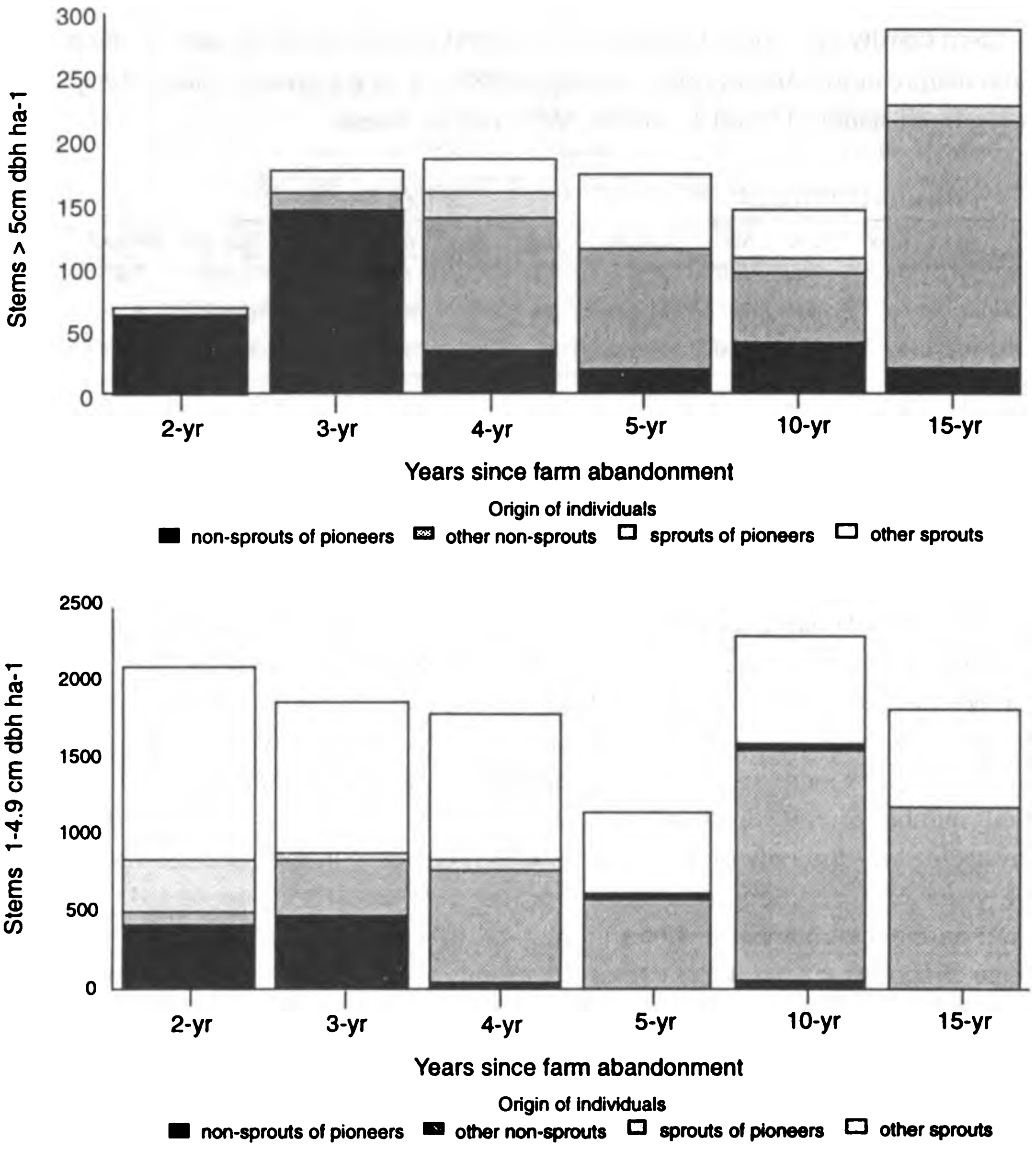


Fig. 1a-b. Number of sprouts and non-sprouts of pioneers and non-pioneers (in the legend given as 'other') in successional stands following slash-and-burn agriculture in Eastern Paraguay.

Diameter class distribution of the most abundant resprouting species

In the time span covered by the chronosequence no sprout reached 20 cm DBH, whereas some non-sprouts did (Table 2). Out of 58 species sampled in the regrowth stands, 28 occured both as resprouts and seed regeneration, 7 were only found as resprouts, and 23 were only present as seed-established individuals. However, with a larger sample size the overall number of resprouting species might have been increased.

Table 2. Diameter distribution of the most abundant resprouting species in the regrowth stands; number of non-sprouts in parentheses; Importance value index (IVI= rel. frequency + rel. density + rel. basal area) in regrowth stands (RS) and mature forest (MF).

Species (Family)	Successional status	Growth form	Diameter class (cm) 0-5	5-10	10-15	15-20	>20	Sprouts ha^{-1}	IVI-RS	IVI-MF
Peltophorum dubium (Sprengel) Taub. (Caesalpinaceae)	secondary	large tree	575 (175)	2 (28)	3 (19)	5 (8)	- (4)	585	25.0	-
Chrysophyllum gonocarpum (Mart.&Eich.) Engl. (Sapotaceae)	primary	medium-sized tree	218 (43)	3 (4)	- (3)			221	6.8	15.3
Trema micrantha (L.) Blume (Ulmaceae)	pioneer	small tree	174 (506)	- (86)				174	20.1	-
Inga uruguensis Hook. & Arn. (Mimosaceae)	secondary	medium-sized tree	144 (106)	5 (22)	10 (19)	4 (10)		163	21.8	-
Achatocarpus sp. (Achatocarpaceae)	secondary	shrub	138 (68)					138	8.7	0.8
Inga marginata Willd. (Mimosaceae)	secondary	small tree	120 (350)	5 (19)	- (4)			125	11.8	1.4
Balfourodendron riedelianum (Engl.) Engl. (Rutaceae)	primary	large tree	120 (232)	- (2)	- (5)			120	6.0	12.8
Citrus aurantium L. (Rutaceae)	primary	small tree	120 (68)	- (1)	- (3)			120	3.5	6.0
Machaerium minutiflorum Tul. (Fabaceae)	secondary	medium-sized tree	100 (494)	6 (23)	4 (12)			110	17.5	3.0
Cordia trichotoma (Vell.) Arráb. (Ehretiaceae)	secondary	large tree	88 (38)	1 -	- (3)			89	4.0	0.8
Cedrela fissilis Vell. (Meliaceae)	secondary	large tree	69 (44)	6 (9)	1 (5)	2 (2)		78	17.9	3.3
Nectandra angustifolia Nees. Et. Mart. (Lauraceae)	primary	medium-sized tree	56 (68)	3 (5)	1 (8)	4 (4)	- (9)	73	10.7	5.0
Cecropia pachystachia Trécul (Moraceae)	pioneer	medium-sized tree	50 (69)	5 (9)	14 (28)	3 (6)	- (6)	72	21.3	-
Acacia polyphylla DC. (Mimosaceae)	secondary	medium-sized tree	32 (19)	4 (4)	14 (1)	5 (1)		55	9.5	-

Peltophorum dubium, a fairly rare light-demanding species of the upper canopy of mature forest, was by far the most abundant resprouting species. *Chrysophyllum gonocarpum* which also showed a high sprout density is a common representative of the mid-canopy in undisturbed forests. In both species sprouts mainly derived from small to medium-sized stumps (*P. dubium*: *n* = 130, diameter range = 3 - 57 cm, mean = 18.0 cm, SD = 10.4; *C. gonocarpum*: *n* = 26, diameter range = 8 - 25 cm, mean = 16.8 cm, SD = 3.5), suggesting that there were suitable conditions for their seed establishment some years before slash-and-burn activities began. *Inga uruguensis* and, above all, *T. micrantha* are typical components of early successional stages and also regenerate vigorously by sprouts. *Achatocarpus* sp. was the only shrub among the most abundant resprouting species. All other species of this growth form occured rarely in forest fallows and mature forest, both as non-sprouts and sprouts. Resprouting individuals of *Inga marginata* accounted only for a small percentage of the overall regeneration of this species. Seeds of *I. marginata* were presumably brought in by birds or mammals. Regeneration of *Citrus aurantium* was mainly represented by sprouts. *Balfourodendron riedelianum* is one of the most abundant species in the upper canopy of the mature forest. In the secondary stands, this wind-dispersed species was mainly represented by seedlings. *Machaerium minutiflorum*, *Cordia trichotoma* and *Cedrela fissilis* are typical light-demanding species that occured rarely in mature forest. Regeneration of the large tree species *C. trichotoma* and *C. fissilis* was mainly of sprout origin, whereas in *M. minutiflorum* seedlings were dominant. The regeneration of the primary species *Nectandra angustifolia* and the pioneer species *C. pachystachia* derived mainly from seeds, while individuals of *Acacia polyphylla* occured mostly as sprouts.

No significant relationship was found between the successional status or the growth form of species and the ability to resprout ($p = 0.48$; $p = 0.63$). Putz & Brokaw (1989) measured sprouts at all levels above ground on Barro Colorado Island, Panama, and found that understory or lower canopy species were more often of sprout origin than large species; pioneer species tended not to resprout. In this study, the most abundant resprouting species, *Peltophorum dubium*, is a large light-demanding tree, whereas the second most abundant resprouting species, *Chrysophyllum gonocarpum*, is a shade-tolerant representative of the mid-canopy. Typical pioneer species rarely resprout after natural stem break in the crown and upper stem zone, whereas cut trees resprout frequently (pers. observation).

Height distribution

In the young regrowth stands, approximately 80% of all sprouts that occured were in the upper two height classes, whereas only 49% of non-sprouts were recorded there (Fig. 2a). Stems of three pioneer or early secondary species, *C. pachystachia*, *I. uruguensis* and *A. polyphylla* accounted for 75% of all sprouts in the upper two height classes. In the older regrowth stands, sprouts nearly lost their leading position in height growth (Fig. 2b). Mean height of sprouts ($\bar{x}$ = 11.5 m; SD = 2.8; *n* = 54) and non-sprouts ($\bar{x}$ = 11.1 m; SD = 2.2; *n* = 221) was similar; sprouts were evenly distributed in the upper two height classes. No resprouting species was dominant in the canopy of the more advanced successional stages. During succession an increasing number of individuals grew into the upper height classes, thinning out slower growing species. This dynamic process is illustrated by the height class distribution: in the young regrowth stands 44.5% of all trees were recorded in the lower height class (< 7.5 m), while in the older regrowth stands only 13.8% occured there. The height class distribution of trees in the mature forest is approximately normal (Fig. 2c). Most individuals occured in the 10-m and 15-m height class. Only a small proportion (0.7%) of all trees were taller than 22.5 m. The maximum height recorded was 27.0 m.

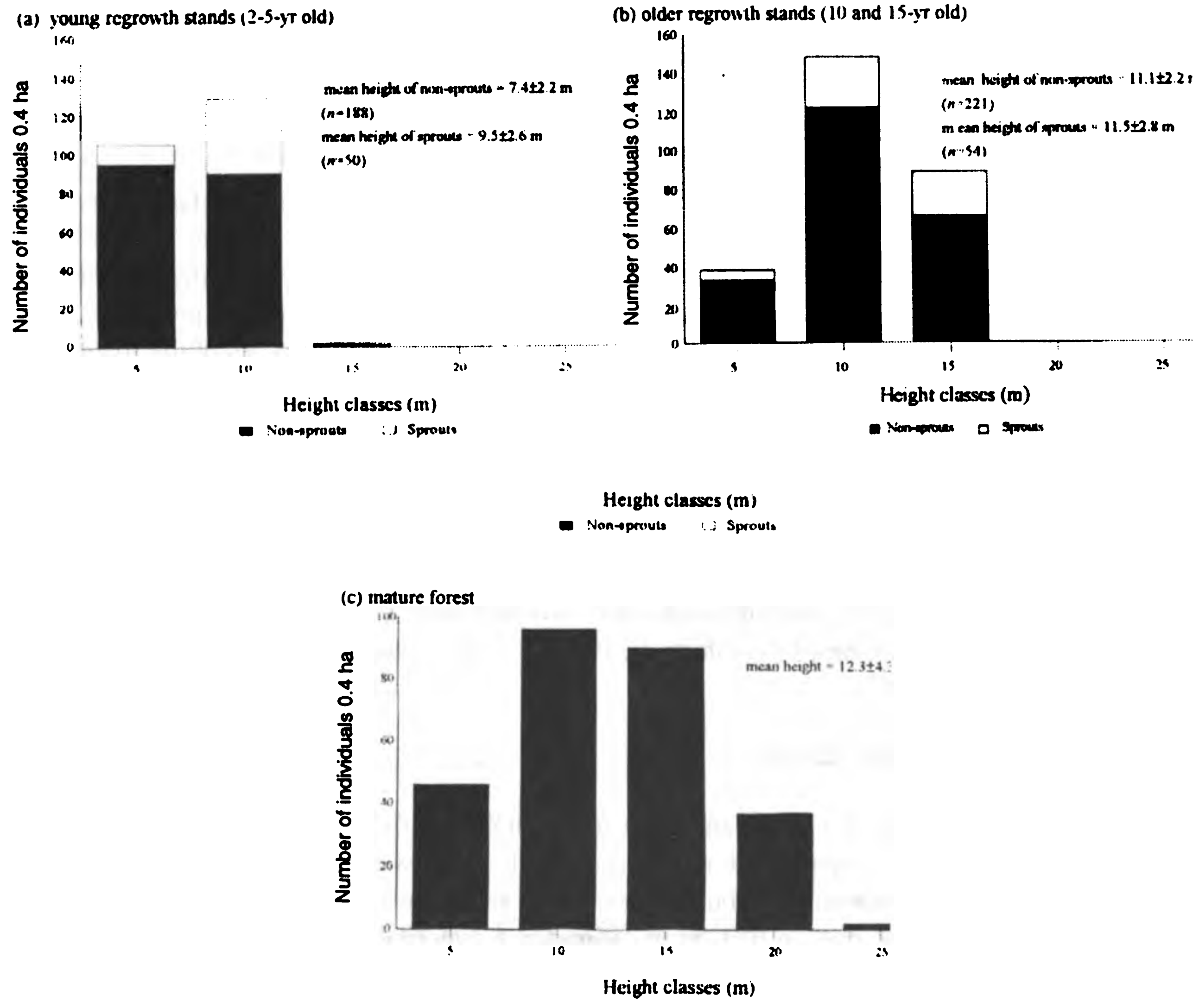


Fig. 2a-c. Height class distribution of sprouts and non-sprouts (DBH ≥ 5 cm; meanGSD) in successional stages and mature forest in Eastern Paraguay.

The fact that there were no resprouted trees > 20 cm DBH (Table 2), whereas some seed-established trees passed this diameter, and that 81% of the tallest trees (≥ 12 m ht; *n* = 16) in the young regrowth stands were of sprout origin, while only 25% of the tallest trees (≥ 16 m ht; *n* = 16) in the older regrowth stands were of sprout origin provides some hints about the growth dynamic of coppice shoots. Uhl & Jordan (1984) measured the diameter and height increment of seed and sprout-established stems of primary species in a cut and burnt site three to five years of age. Diameter increment was slightly faster in seedlings than in sprouts, whereas height increment was faster in sprouts. Stocker (1981) found 23 months after felling and burning that seed-established pioneer species generally grew faster than species regenerating vegetatively. Uhl *et al.* (1982b) report that tree sprouts accumulated much greater biomass than tree seedlings three years after cutting and burning. They attributed this to the large root photosynthate reserves in cut trees. With time, however, these reserves may become exhausted, resulting in slower growth rates of sprouts.

Species diversity

In the sapling stratum, the slightly higher species number per plot in the successional stands compared to the mature forest may be due to the sparse canopy of secondary tree species in regrowth stands permitting more species to thrive below (Table 3). This trend was also reflected by the species richness per successional stage. In the tree stratum, species number per plot and species richness increased strikingly with stand age but did not reach the values of the mature forest. The mean number of species differed significantly between the younger regrowth stand and older regrowth stand ($t = 3.09$, df = 14, $p < 0.01$) as well as between the younger regrowth stand and the mature forest ($t = 4.47$, df = 14, $p < 0.001$). However, no significant differences were found in the sapling stratum ($p > 0.12$). Similar to this, Guariguata *et al.* (1997) found in regrowth stands (10-18 yr old) in Costa Rica a consistently lower tree species richness compared to mature forest, while sapling size classes showed much less difference. As in the sapling stratum, the proportion of resprouting species declined with time. During succession, evenness and H′ values steadily increased in both strata, indicating that species become more similar in their abundance pattern.

Floristic similarity between stands

Floristic similarity between the young and older regrowth stands based on the qualitative index, showed that many species were found in both sites (Table 4). However, similarity based on the quantitative indices, considering the abundance or basal area of species found in both sites, was much lower. This may be due, in part, to the abundance pattern in early stages of succession which were characterized by a few dominant species. These species were either absent or rare in more advanced successional stages, suggesting a high turn-over rate. As time elapses from farm abandonment, similarity with the mature forest increased in all indices. However, the quantitative similarity indices lag considerably behind the qualitative index. As in the study of Guariguata *et al.* (1997), similarity indices between regrowth stands and mature forest were higher for saplings than for trees. Overall, the values of similarity suggest that restoration of species composition will require a long time. Sprouting species generally were recorded either in much smaller or much higher numbers in regrowth stands than in mature forest. We can thus deduce that sprouts probably do not speed up this process.

Table 3. Species number per plot, species richness (S), Shannon-Wiener index H', and evenness in successional stages following slash-and-burn agriculture and mature forest in Paraguay; number of resprouting species in parentheses. Abbreviations as in Table 1.

		1 - 4.9 cm DBH/100 m^2								DBH ≥ 5 cm/500 m^2			
Stage	*n*	min	max	mean ± SD	S	H' [1]	Evenness [2]	min	max	mean ± SD	S	H'	Evenness
YRS	8	8	17	13.3±3.2	39 (34)	1.79	0.49	2	10	5.8±3.5	19 (8)	2.14	0.73
ORS	8	6	20	14.0±4.3	44 (19)	2.33	0.62	9	16	12.8±2.1	33 (13)	2.84	0.81
MF	8	9	15	12.6±2.6	37 -	2.34	0.65	14	17	15.9±1.1	42 -	3.09	0.83

[1] $H' = -Sp_i \ln p_i$ where p_i = proportion of individuals of species i in the community (Magurran 1988)

[2] $E = H'/H_{max}$; H_{max} indicates a situation where all species are found equally abundant

Table 4. b-Diversity between stands based on the qualitative Soerensen index (C_S); the quantitative indices are considering (1) the lower sum of individuals found in both sites (C_N), and (2) the lower sum of basal area of species in common (C_{BA}).

β-Diversity	1-4.9 cm DBH		≥ 5 cm DBH		
between stands	**C_S 1**	**C_N**	**C_S**	**C_N**	**C_{BA}**
young regrowth stands/older regrowth stands	0.67	0.37	0.89	0.38	0.36
young regrowth stands/mature forest	0.45	0.11	0.28	0.06	0.02
older regrowth stands/mature forest	0.52	0.15	0.44	0.17	0.16

[1] $C_S = 2j/(a+b)$; Magurran (1988)

where j = the number of species common to both sites
a = the number of species in site A, and
b = the number of species in site B

CONCLUSIONS AND FUTURE LINES OF RESEARCH

In this study, sprouts played an important role in forest restoration during initial successional stages, but the abundance of sprouts declined in more advanced stages. These results suggest that on the one hand, natural senescence of sprout-established individuals increased, and on the other that a progressive immigration of climax species occured. Given the absence of further disturbance, the rate of forest recovery in terms of stem density, basal area and height class distribution of trees was found to be high, while the restoration of the species composition, even under the favourable conditions of the study area with forest fragments at short distance, progresses much slower. However, the long-term viability of sprouts in secondary forests is not well studied. Due to its ecological importance this process deserves more attention.

ACKNOWLEDGEMENTS

This study was funded by the German Agency for Technical Cooperation (GTZ). I am grateful to V. Kohler, J. Pretzsch, C. Benitez and J. Davalos for their assistance during the field phase. I thank N.V.L. Brokaw, S. Stevens Hummel, B. Finegan and M. Guariguata and two anonymous reviewers for their comments on earlier versions of this manuscript.

REFERENCES

Basnet, K. 1993. Recovery of a tropical rain forest after hurricane damage. Vegetatio 109:1-4.

Bellingham, P.J., Tanner, E.V.J. & Healey, J.R. 1994. Sprouting of trees in Jamaican montane forests, after a hurricane. Journal of Ecology 82:747-758.

De Olivéira, J.B. & Burgos, S.M. 1995. Sistema de clasificación de la aptitud agro-ecologica de la tierra (S.C.A.A.T.) para la Region Oriental del Paraguay. Universidad Nacional de Asunción, Asunción. Paraguay.

de Rouw, A. 1993. Regeneration by sprouting in slash and burn rice cultivation, Taï rain forest, Côte d'Ivoire. Journal of Tropical Ecology 9:387-408.

Guariguata, M.R., Chazdon, R.L., Denslow, J.S, Dupuy, J.M. & Anderson, L. 1997. Structure and floristics of secondary and old-growth forest stands in lowland Costa Rica. Plant Ecology 132:107-120.

Hueck, H. 1966. Die Wälder Südamerikas. G. Fischer-Verlag, Stuttgart.

Kauffman, J.B. 1991. Survival by sprouting following fire in tropical forests of the eastern Amazon. Biotropica 23:219-224.

Magurran, A.E. 1988. Ecological diversity and its measurement. Croom and Helm, London.

Matelson, T.J., Nadkarni, N.M. & Solano, R. 1995. Tree damage and annual mortality in a montane forest in Monteverde, Costa Rica. Biotropica 27:441-447.

Putz, F.E. & Brokaw, N.V.L. 1989. Sprouting of broken trees on Barro Colorado Island, Panama. Ecology 70:508-512.

Saldarriaga, J.G., West, D.C., Tharp, M.L. & Uhl, C. 1988. Long-term chronosequence of forest succession in the upper Rio Negro of Colombia and Venezuela. Journal of Ecology 76:938-958.

Sokal, R.R. & Rohlf, F.J. 1981. Biometry. Freeman, San Francisco, California. 859 pp.

Stocker, G.C. 1981. Regeneration of a North Queensland rain forest following felling and burning. Biotropica 13:86-92.

Stutz de Ortega, L.C. 1987. Etudes floristique de divers stades secondaires des formations forestières du Haut Paraná (Paraguay Oriental - Structure, composition floristique et régénération naturelle:comparaison entre la forêt primaire et la forêt sélectivement exploitée. Candollea 42:205-262.

Uhl, C., Clark, K., Clark, H. & Murphy, P. 1981. Early plant succession after cutting and burning in the upper Rio Negro region of the Amazon basin. Journal of Ecology 69:631-649.

Uhl, C., Clark, H., Clark, K. & Maquirino, P. 1982a. Successional patterns associated with slash-and-burn agriculture in the upper Rio Negro region of the Amazon basin. Biotropica 14:249-254.

Uhl, C., Jordan, C., Clark, K., Clark, H. & Herrera, R. 1982b. Ecosystem recovery in Amazon caatinga forest after cutting, cutting and burning, and bulldozer clearing treatment. Oikos 38:313-320.

Uhl, C. & Jordan, C.F. 1984. Succession and nutrient dynamics following forest cutting and burning in Amazonia. Ecology 65:1476-1490.

Yih, K., Boucher, D.H., Vandermeer, J.H. & Zamora, N. 1991. Recovery of the rain forest of southeastern Nicaragua after destruction by hurricane Joan. Biotropica 23:106-113.

LARGE-SCALE FACTORS INFLUENCING FOREST SUCCESSION IN NW ARGENTINA SUBTROPICAL FORESTS

Héctor Ricardo Grau

Dept of Geography. Campus Box 260. University of Colorado, 80309, Boulder, Colorado, USA.
Laboratorio de Investigaciones Ecológicas de las Yungas. Universidad Nacional de Tucumán, Tucumán, Argentina.

ABSTRACT

I evaluate the effects of two large-scale ecological processes on forest succession in subtropical montane forests of NW Argentina: exotic plant invasion and fire-mediated climatic change. In the lowlands, patterns of secondary succession are influenced by the presence of exotic species. For example, secondary forests that developed on abandoned fruit plantations are often dominated by the Southeast-Asian trees Ligustrum *spp. and* Morus *spp., and grazed areas are often dominated by the North American tree* Gleditzia triacanthos. *While many native secondary forests are characterized by the abundance of highly valuable timber species such as* Cedrela lilloi, Juglans australis, *or* Tipuana tipu, *exotic-dominated forests lack commercial value. In the highlands, native* Alnus acuminata *forests have expanded over grasslands during the last decades.* Alnus *forest expansion seems to be associated to fires that occurred during relatively wet multi-year periods, which in turn is associated to the increase in precipitation and in precipitation variability during the 20th century. Both examples emphasize the importance of regional-scale processes influencing the distribution, economic value and ecological functions of neotropical montane secondary forests.*

INTRODUCTION

The main causes of vegetation dynamics are site availability, species availability and differential species performance. Site availability is controlled by the disturbance regime. Species availability is due to the existence of species potentially able to colonize an area, within a dispersal distance. Differential species performance is controlled by many factors including ecophysiology, life history, demography, competition, and other interspecific interactions (Pickett et al. 1987). Most studies in tropical forest succession focus on the differential species performance and ecological changes at the scale of the forest stand (Brown & Lugo 1990, Corlett 1995). Disturbance regimes are typically studied as factors that influence the conditions for early succession (e.g. soil, presence of a seed/seedling bank, patch size), but the temporal dimension of these regimes (e.g., frequency) is usually neglected. Climatic conditions are also assumed to be generally stable at the temporal scales of typical studies on plant succession .

If the interaction among species availability, disturbance regime, and climatic change are important factors controlling tropical forest succession, they should be considered for management recommendations. But despite a landscape perspective is often mentioned as the proper scale for addressing secondary forest processes (see for example, Brown & Lugo 1990), ecological recommendations for management typically focus on stand-scale ecological processes (Finegan 1992, 1997).

During the last two decades, ecology as a science has become aware of the importance of large-scale phenomena influencing plant community dynamics. Both modeling studies (Overpeck et al. 1990, Suffling 1995) and paleontological records (Walker & Chen 1987, Gajewski 1987) suggest that climatic changes, even relatively small, can produce significant short-term changes in forest dynamics. Important vegetation changes can derive even from relatively small climatic changes, specially when they are mediated by fire. In many ecosystems, native species availability for site colonization is being severely altered due to the widespread introduction of exotic plants. Such pattern is more evident in early successional stages (Bingelli 1996). These factors interact with land-use and land-cover changes, which is probably the single most important component of global environmental change (Vitousek 1994). In this paper I show how two global phenomena (exotic species invasions and climatic change) can produce significant changes in forest succession in subtropical Argentina. I expect that the ideas suggested here are worth to be tested in lower latitude ecosystems.

STUDY AREA

This work reports results of studies carried out in two elevational zones of the subtropical montane forests of Northwest Argentina, or Argentine *Yungas*: the upper montane forests (1600-2700m), and the lower montane forest (most of my examples refer to study sites between 600 and 1100m). The region is located between 22^{O} and 28^{O} S. This biogeographic unit is considered to be the southern limit of the neotropical montane forests that occur along the eastern slopes of the Andes. In fact, Argentine Yungas share most of their plant genera, and several species with the tropical Andean forests of lower latitudes (Cabrera & Willink 1980).

Climatically, the region is characterized by pronounced seasonal variations in precipitation. Winter (June to September) is the dry season, where about 80% of the annual rainfall occurs in the summer months (November to March). At 600 m elevation, mean annual temperature oscillate between 19° and 20° C., whereas in the upper montane forest, mean annual temperature decreases with altitude (for example at 1500m elevation is 14° C).

In the upper montane forest, dominant disturbances are grazing and surface fires. Below 1500 m fire is not frequent, as treefall gaps and landslides became the dominant natural disturbances. Below 1000 m elevation, many areas have been transformed to agriculture and pastures, and most forests surrounding agricultural and urban areas can be considered "typical" secondary forests. The difference in disturbance regime along the elevational gradient is correlated with important changes in tree species diversity. Below 1600 m elevation, where fire is not frequent, forests usually have around 20 species of trees per hectare; whereas above 1800 m elevation, where fire is the dominant disturbance agent, forest stands typically have between 1 and 4 species per hectare, and are clearly dominated by just one or two species of which *Alnus acuminata* and *Podocarpus parlatorei* are the more common (Grau & Brown 1995a).

EXOTIC PLANT INVASIONS IN THE LOWER MONTANE SECONDARY FORESTS

Post-agriculture forest succession in the lower montane forests seems to be strongly influenced by the characteristics of the pre-abandonment use and its relationship with species availability and seed dispersal. Succession over herbaceous fields is reported to be dominated by wind-dispersed tree species (ordered from shorter to longer longevity): *Tecoma stans*, *Heliocarpus popayanensis*, *Jacaranda mimosifolia*, *Anadenanthera macrocarpa*, *Tipuana tipu*, *Parapiptadenia excelsa*, and *Cedrela lilloi* (Grau et al. 1997). After 50 years of succession, the first three species show very high mortality, and their abundance decreases. The first four species are typical pioneer trees with soft wood, and less than 15m height at maturity. In contrast, *T. tipu*, *P. excelsa* and *C. lilloi* can live several hundreds years, and can reach more than 30 m height and more than 1 m DBH. These species have medium to high-density wood, and are valuable timber species. They can be considered long-lived pioneers or durable light-demanding species. Probably due to their longevity, these species are frequent components of old-growth forests, where the short-lived pioneers are absent (Grau & Brown 1998).

Succession over abandoned fruit plantations follows a different floristic pattern. In these conditions, in addition to the above mentioned pioneer trees, animal-dispersed species become more important. For example, the native light-demanding treelet *Solanum riparium*, plus many shade-tolerant species such as *Phoebe porphyria*, *Myrsine laetevirens*, *Cupania vernalis*, and several Myrtaceae species (Grau et al. 1997). This floristic pattern can be attributed to dispersal facilitation by the remaining fruit trees by providing perches for animal dispersal as has been observed in secondary successions on different ecosystems (for example, Mc Donnel & Stiles, 1983, Guevara et al. 1986). Besides their evident animal-dipersal syndrome (fleshy fruits), these species have been documented to be dispersed by birds (Aragón 1998), and bats (Iudica and Bonaccorso 1997). But the most striking differential characteristic reported for successions over abandoned fruit plantations is the dominance of exotic species. The two most important species are *Morus alba*, and *Ligustrum lucidum*, which in some secondary forests rank first in density and basal area. Other common exotic species in post-agriculture secondary forests of NW

Argentina are *Morus nigra, Psidium guajaba, Ligustrum sinensis, Citrus aurantium, Syagrus romanzofiannum, Bahuinia candicans,* and *Prunus persica*. (Grau et al. 1997, Grau & Aragón 1998). Most of the exotic trees are "escaped" ornamental and fruit plants, originally used for landscaping, providing shade, and for fruits. None of these exotic trees, nor the native bird/bat-dispersed species have commercial timber.

Secondary succession in previously grazed pastures is dominated by species whose fruits have hard endocarps or seed protection, such as different native treelet species of *Acacia, Celtis, Fagara* and *Xylosma,* and the large long-lived tree *Juglans australis* (Chalukian 1992, Grau et al. 1997). In other situations, early successions are dominated by the North-American exotic tree *Gleditzia triacanthos,* the tropical treelet *Psidium guajaba* or the European spiny shrubs *Pyracantha coccinea* and *Crataegus oxyacantha* (Grau & Aragón 1998). With the exception of *J. australis* (a valuable timber species), the other species are only used as firewood.

Type of past land use seems less important as the abundance of exotic plants present in the landscape increases. For example, in areas of abandoned herbaceous crops surrounded by abundant *Ligustrum* trees, this species invades during early in succession (Grau & Aragón 1998). In heavily grazed pastures, the exotic spiny shrubs *Crataegus oxyacantha* and *Piracantha coccinea,* "facilitate" forest recovery by providing perches for seed dispersal, and mechanical protection against browsing. Landslides, which are usually colonized by native wind-dispersed species, also are colonized by *Morus alba* in the proximity of human-transformed landscapes (Grau & Brown 1995 b). In addition, secondary forests dominated by *Ligustrum* spp. show a very slow pattern of species replacement. Considering that *Ligustrum* spp. are relatively shade tolerant and show resprouting ability, replacement of successional communities by native species is expected to take several tree generations (Aragón 1997). In many situations, the dominant tree colonizing these sites is the exotic *Ligustrum sinensis* (Malizia & Greslebin 1998).
In conclusion, secondary forest composition in the region is affected by the availability of exotic plants in the landscape. Since this is a positive feedback process (the increase of exotic-dominated secondary forests increases the chances to colonize future disturbances), probably many secondary forests in the future will be severely influenced by exotic plant invasions at a regional scale. In turn, this will strongly influence both the economic and ecological value of NW Argentina secondary forests.

CLIMATE, FIRE, AND FOREST EXPANSION IN THE UPPER MONTANE FORESTS

The most evident pattern of forest succession in the upper montane forests of the study region during the last decades has been the expansion of *Alnus acuminata* dominated forests over grasslands. This phenomenon seems to be generalized at a regional scale, as suggested by the examination of sequential photographs (Grau 1985). *Alnus acuminata* stands (many of which appear to be recently established) are probably the most widespread in the region, covering millions of hectares (Bell 1991). *Alnus* trees initiate forest succession by providing perches for bird-dispersed trees such as *Podocarpus parlatorei*, and probably by improving soil fertility through fixation of atmospheric Nitrogen (Grau 1985, Grau & Pacheco 1997). At the lower lever of the upper montane forest (1600-2000m), an analysis of forest chronosequence suggest that succession seems to proceed from *Alnus* to *Podocarpus* forests, and eventually to more diverse forests dominated by *Ilex argentina, Cedrela lilloi, Juglans australis, Prunus tucumanensis, Sambucus peruviana, Blepharocalyx salicifolius and Myrcianthes mato* (Arturi et al., in review). The young stands dominated by *Alnus* and *Podocarpus* are also of high economic value. *Podocarpus* forests are particularly valuable both for timber and paper-pulp production. The *Alnus* forests are also exploited for intermediate-quality timber, and provide a landscape for productive silvopastoral systems (Molinillo & Vides-Almonacid 1989, Brown & Grau 1993). As a consequence, the successional processes controlling the relative importance of grasslands and forests at this elevational level, have a direct impact on management and conservation.

Different hypotheses have attempted to explain this expansion of *Alnus*. Changes in land use is one probable explanation. Grau (1985) suggests that increasing availability of industrial fuel may have lead to a decrease in firewood extraction, which in turn released human pressure over the tree resource. He also suggests that decreases in human-caused fires to promote palatability of pasture grasses may have favor tree invasion in these grasslands. On the other hand, Molinillo and Vides-Almonacid (1989) showed that *Alnus* establishment is enhanced by intermediate intensities of cattle grazing and is associated to soil factors. *Alnus* seedlings need bare soil and reduced competition with grasses to establish. But the regional scale of the expansion, despite different management practices, suggests that regional factors are also playing an important role on forest dynamics at this elevation.

Climatic change is a factor that needs to be explored further. The single most evident climatic change during the 20th century has been an increase in precipitation throughout the region (Fig 1a). Interestingly, precipitation during the last decades seems to be the highest over the last two centuries, according with dendroecological reconstruction (Villalba *et al.*, in review). An increase in rainfall could have affected forest establishment in two ways. One is by increasing the chances of seedling establishment due to enhanced soil moisture. In support of this hypothesis, Bell (1991) showed that *Alnus* forests tend to occur in soils with higher moisture than grasslands. The other is that rainfall can enhance tree invasion by reducing fire frequency and intensity. In support of this hypothesis, my preliminary data suggest that fire occurs mostly during dry years (Fig 1a).

Another way to relate climatic change with forest expansion is to focus not on the precipitation trends but on their inter-annual variability. Figure 1b also shows that along with the increase in precipitation, there has been an increase in the interval of precipitation in short term periods (3-5 years), implying that there are more chances to find wet years (maximizing fuel production),

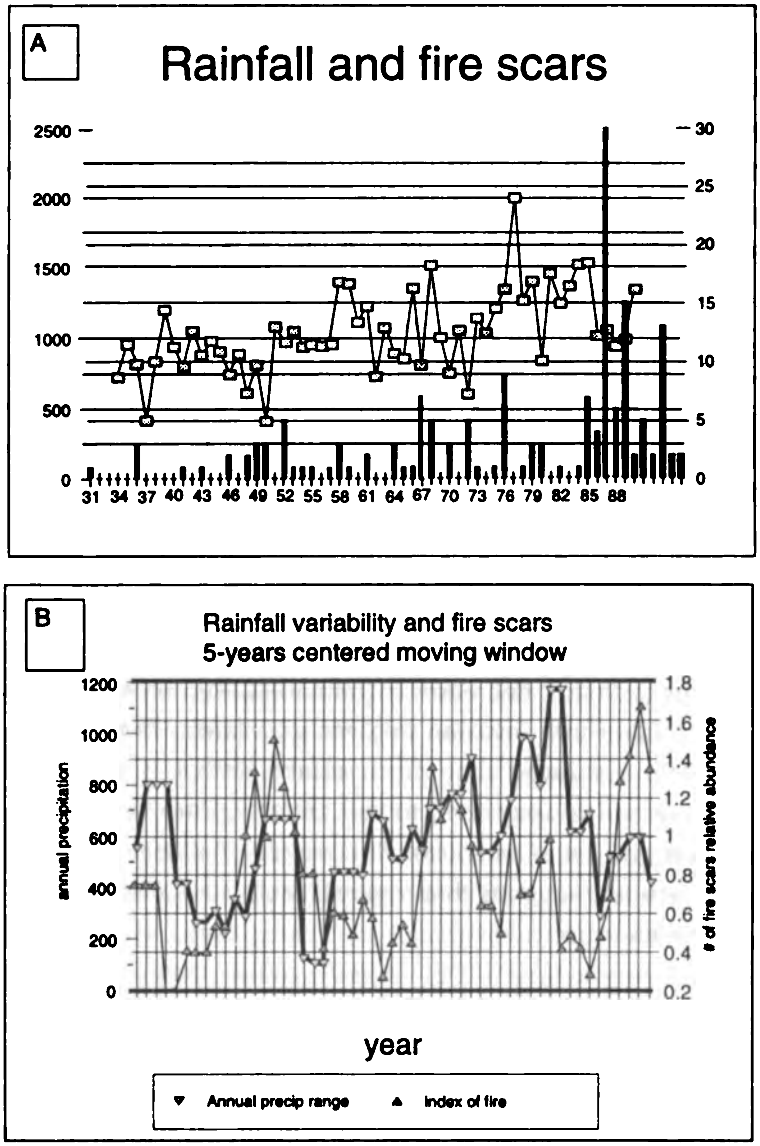


Figure 1: Precipitation and fire regime in montane forests of NW Argentina. In Figure 1a, continuous line is annual of Concepción (27° 43′ S) between 1934 and 1990. The figure shows an increasing trend in annual rainfall in during the period. Bars indicate fire events recorded as fire scars in Alnus acuminata trees in a 70-wedges sample taken at the locality of La Banderita (1800 m; 27° 46′). Density of fire are clustered around relatively dry periods (1948-1950; 1967; 1972; 1987-1989). In Figure 1b, one line is an index rainfall variability (5-years moving window range = maximum - minimum during the 5-years period centered in each year). The other line is the 5 years moving window summation of the annual percentage of fires. The figure shows a consistent association between periods with high rainfall variability and density of fire events.

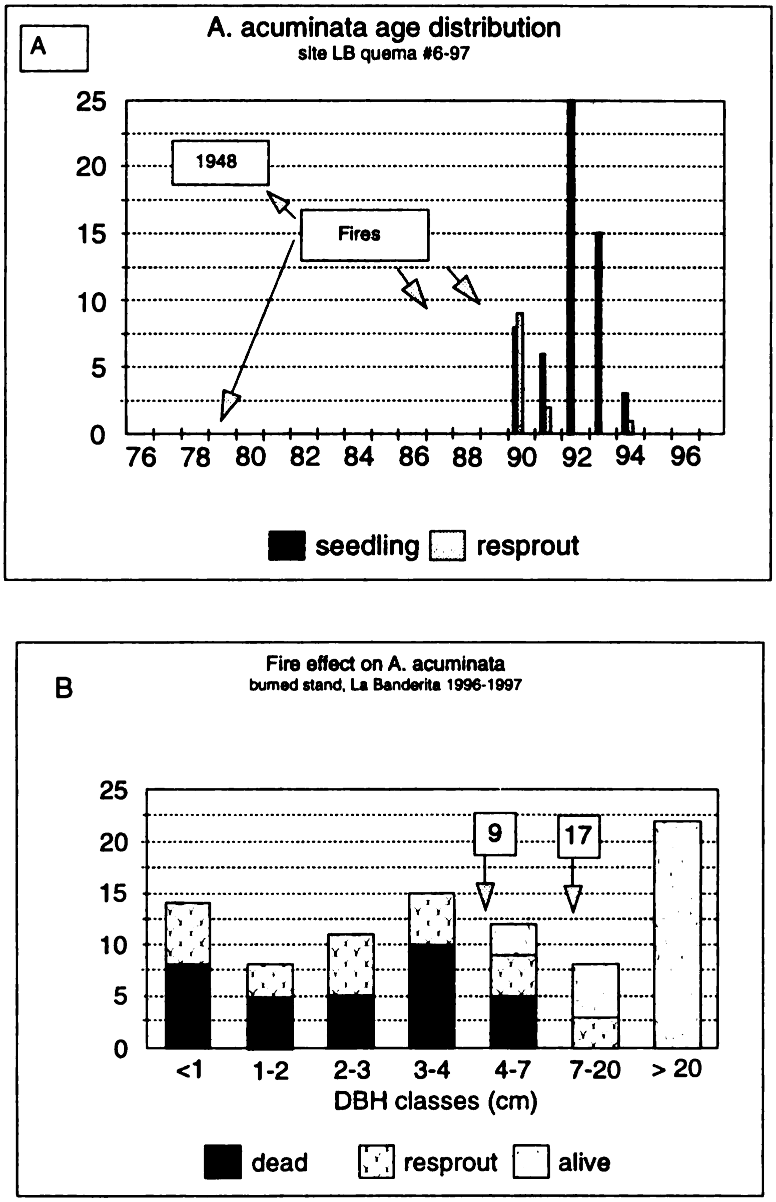


Figure 2: Effects of fire on *Alnus acuminata* tree establishment (2a) and mortality (2b), in the site La Banderita (1800 m; 27°, 46' S). In Fig 2a, arrows indicate fire dates, dated using fire scars in *Alnus acuminata* trees surrounding the plot. Frequency distributions of establishment dates (estimated using increment borer samples), show that most seedlings and resprouts recruit during the three years following a fire. In Fig 2b, arrows indicate estimated age (on the basis of diameter-age regressions) of trees affected by a fire occurred in July 1996. The plot was remeasured one year later. It can be observed that most trees older than 10 years were not affected by fire. While most younger trees were affected, about 25% of them resprouted.

followed by dry years (maximizing fire probability, thus decreasing grass competition with tree seedlings), followed again by wet years (maximizing chances of tree establishment). In support of this explanation lies the fact that age distribution of *Alnus* saplings reveal that fire facilitate tree invasion over grasslands, since trees establish mostly within three years after fire (Fig 2a). In addition, *Alnus* trees seem to be fairly resistant to fire. Studying the results of one fire, I observed (Fig. 2b) that a proportion of trees of all sizes (including saplings of about 1 cm DBH) were able to resprout after a fire; whereas most trees older than 15 years, survived fire.

DISCUSSION

I have presented two examples of regional scale processes controlling forest succession in Northwest Argentina. While most current research on tropical secondary forests focus on few-hectare scales (Brown & Lugo 1990, Corlett 1995), the examples shown above emphasize the importance of studying and (eventually) taking decisions at a landscape scale.

In lowland areas, exotic plant invasions are altering native species availability during secondary forest succession. In particular, exotic species such as *Ligustrum* spp., *Morus* spp., and *Gleditzia triacanthos*, are replacing the native species in secondary stands. In general, these exotic species are commercially less valuable than the native pioneers such as *Cedrela, Juglans, Tipuana,*and *Parapiptadenia*. In addition to altering the economic value of the forest, the invasion of exotic species may affect the diversity and function aspects of secondary forests there. The invasion by exotic plants is a generalized phenomenon in most terrestrial ecosystems. Tropical forests, however, is the biome least affected by invasions (Bingelli 1996). This may be due to an intrinsic resistance of tropical forests to invasion. But also may be due to the fact that opportunities for invasions in non-tropical environments have had more time to occur, due to the fact that most tropical environment have been transformed to agriculture more recently than temperate ecosystems. As land-use changes and exchange of plants from different tropical areas increases, successful invasions are also likely to increase. In the upper montane forests, climatic change (probably interacting with land-use changes) seems to be controlling the relative presence of forest and grasslands, currently leading to an increase in forest cover.

The influence of fire in Neotropical upper montane forests has been suggested as a very important factor controlling their altitudinal distribution (Ellenberg 1979, Kessler & Driesch 1993, Young 1993). The interaction among climate, land-use, and fire, can be a determinant factor on the future economic and ecological value of these ecosystems. In lowland tropical forests, fire is a less frequent type of disturbance, but is not totally absent. In fact, most tropical forests are occasionally affected by fire (Goldammer 1993). Under shifting agriculture, fires can "escape" when meteorological conditions are favorable. Recent extensive fires related to El Niño in tropical Southwestern Asia suggest that high-frequency rainfall variability can play a key role in controlling fire spread (Brown 1998), as it seems to be the case in our Argentine examples.

Increases in climatic variability at different temporal scales seems to be a global trend (Karl *et al.* 1995, Mann *et al.* 1995) and its influence on forest dynamics and distribution should be considered.

Both climate-mediated fires and exotic plant invasions are essentially biophysical processes but they are closely connected to human activity. Although climatic conditions seem to play a key role in fire spread, most fires in tropical environments are human-caused. Fuel loads and fuel moisture are also strongly dependent of management practices such as grazing and forest exploitation (Kaufman & Uhl 1990). Also, exotic plant invasions are inextricably linked to human activities. As in this study, most exotic trees throughout the world are "escaped" ornamental trees, but occasionally economically valuable trees (Bingelli 1996).

RECOMMENDATIONS AND RESEARCH PRIORITIES

The main recommendation emerging from this work is that management guidelines at a forest-stand scale would benefit from knowledge of larger-scale processes. For example, projects aiming to predict succession trends based on current vegetation patterns, should be aware that in the following decades (when the results of the research should be transferred to management practices), the dominant species in successional forests, could be very different. Species availability can be largely affected by the invasion of exotic species. In landscapes where fire is the dominant disturbance (for example in savanna-like ecosystems or in shifting-agriculture/secondary forests mosaics), climatic changes at the scale of inter-annual variability controls fuel availability and moisture, and consequently it could have an effect on fire intensity and area more important than the management practices regulating fire ignition.

The emphasis on large-scale processes opens interesting opportunities for applied research. A common problem of stand-scale oriented research is that many situations it is highly idiosyncratic. A management model developed for a particular forest is hardly extrapolable to other situations with slightly different ecological and economic conditions (e.g., environment, species composition, access to market, education level). In contrast, research on large-scale processes by definition should affect a larger number of management units. Consequently the cost/benefit relationship of research on large-scale processes affecting forest dynamics is likely to be more efficient.

Understanding the relationship between fire and climatic variables is limited by the availability of long term records. Recent methodological progresses provide the opportunity to study such relationships at relevant ecological scales. Dating fire scars by counting tree rings (Arno & Sneck 1977, Mc Bride 1983), is the most used method in temperate ecosystems for assessing fire periodicity. In many tropical ecosystems this method is limited by the absence of species with reliable annual rings. However, the use of fire scars in *Alnus acuminata* as mentioned here, can also used in montane forests of Bolivia and Perú at latitudes as low as 12°. It is likely that montane and lowland areas with distinct rainfall seasonality, have species with reliable tree-rings. The search for species useful for dating fires in tropical ecosystems can open the way to assess fire regimes at multidecadal scales and relate them to climatic records. Satellite images also provide increasing possibilities for studying fire regime. Landsat MSS images (90 m x 90 m pixel) already have more than 20 years of records, Whereas Landsat TM and SPOT images with pixels smaller than 30 m x 30 m have already more than 10 years of records. The spatial resolution provided by satellite imagery, together with the temporal span provided by dendroecological methods, combines the information needed to accurately describe (predict and manage) temporal and spatial patterns of fire regime, and its relationship with both climatic, topographic and anthropic variables.

As said before, plant invasions and fire regimes are influenced by social factors. Assessing both the interaction and the relative importance of biophysical and social factors controlling ecological processes is relevant for the ecology and management of tropical secondary forests. Interdisciplinary efforts in this direction, probably have the highest chance of success in predicting the future of tropical forests, the goods and services they produce, and the fate of the people depending on these resources.

Acknowledgments

Research presented here were supported by grants from National Science Foundation, National Geographic Society, Biogeography Specialty Group of the Association of American Geographers, Sigma Xi, Fulbright commission, Encyclopedia Brittannica, and CONICET, Argentina. The manuscript was improved by the comments of Alfredo Grau and Roxana Aragón.

LITERATURE CITED

Aragón, M.R. In press in A.D. Brown et al., eds. Historia Natural de la Sierra de San Javier.

Aragón, M.R. 1997. Sucesión secundaria en invasión por especies exóticas: *Ligustrum* spp y *Morus* spp. Informe beca de iniciación, CONICET. Inédito.

Arturi, M.F.; H.R. Grau; P.G. Aceñolaza & A.D. Brown. Manuscript under review. Structure and successional trends in higher montane forests of NW Argentina. Revista de Biología Tropical.

Arno, S.F. & Sneck, K.M. 1977. A method for determining fire history in conifeorus forests of the mountain west. USDA technical report 42.

Bell, D.A. 1991. Distribución del Bosque de Aliso del cerro (Alnus acuminata) en la provincia de Tucumán, Argentina. Boletín Sociedad Argentina de Botánica 27: 21-30.

Bingelli, P. 1996. A taxonomic, biogeographical and ecological overview of invasive woody plants. Journal of Vegetation Science 7: 121-124.

Brown, A.D. & Grau, H.R. 1993. La Naturaleza y el Hombre en las Selvas de Montaña. GTZ. Salta. 121 pp.

Brown, N. 1998. Out of control: fires and forestry in Indonesia. Trends in Ecology and Evolution 13: 41.

Brown, S. & Lugo, A.E. 1990. Tropical secondary forests. Journal of Tropical Ecology 6: 1-32.

Cabrera, A.L. & Willink, A. 1980. Biogeografía de America Latina. Organización de Estados Americanos. Washington DC. 121 pp.

Chalukian, S. 1992. Regeneración, sucesión y plantas invasoras en un bosque de Yungas, Salta, Argentina. Tesis de Maestría. Programa de Maestría en Manejo de Vida Silvestre, Universidad Nacional, Heredia, Costa Rica. 180 pages.

Corlett, R.T. 1995. Tropical secondary forests. Progress in Physical Geography 19: 159-172.

Ellemberg, H. 1979. Man's influence on tropical mountain ecosystems in South America. Journal of Ecology 67: 401-416

Finegan, B. 1992. The managment potential of neotropical secondary lowland rainforests. Forest Ecology and Management 4: 295-321.

Finegan, B. 1997. Bases ecológicas para el manejo de bosques secundarios en zonas húmedas del tropico americano, recuperación de la biodiversidad y producción sostenible de madera. Pages 106-119 in Memorias del Taller Internacional sobre Estado Actual y Potencial del Manejo y Desarrollo del Bosque Secundario Tropical en America Latina, Pucallpa, Perú.

Gajewski, K. 1987. Climatic impacts on the vegetation of eastern North America during the last 2000 years. Vegetatio 68: 179-190.

Goldammer, J.G. 1993. Historical biogeography of fire: tropical and subtropical. Pages 297-314 in P.J. Crutzen & J.G.Goldammer, eds. Fire in the Environment. Wiley.

Grau, A. 1985. La expansión del Aliso del Cerro (*Alnus acuminata* H.B.K. subsp *acuminata*) en el noroeste de Argentina. Lilloa 36: 237-247.

Grau, H.R. & Aragón, M.R. 1998. Arboles exóticos de la Sierra de San Javier, Tucumán, Argentina. In press in A.D. Brown et al., eds. Historia Natural de la Sierra de San Javier

Grau, H.R. & Brown, A.D. 1998. Structure and inferred dynamics of a subtrpical montane forest of NW Argentina. In press in F. Dallmeier, ed. Forest Biodiversity Measuring and Monitoring. Parthenenon Publishers, London.

Grau, H.R.; Arturi, M.F.; Brown, A.D. & Aceñolaza, P.G. 1997. Floristic and structural patterns along a chronosequence of secondary forest succession in Argentinean subtropical montane forests. Forest Ecology and Management 95: 161-171.

Grau, H.R. & Pacheco, S.E. 1997. Regeneration dynamics of *Podocarpus parlatorei* in the Argentiean Yungas. Abstracts II Southern Connection Congress. Noticiero de Biología, Sociedad de Biología de Chile 5: 103.

Grau, H.R. & Brown, A.D. 1995a. Patterns of tree species diversity along latitudinal and altitudinal gradients in the Argentinean subtropical montane forests. Pages 295-300 in S.P. Churchill, J. Luteyn, E. Forero & E. Balslev, eds. Biodiversity and conservation of Neotropical Montane Forests. New York Botanical Garden, Bronx.

Grau, H.R. & Brown, A.D. 1995b. Los deslizamientos de ladera como condicionantes de la estructura y composición de la selva subtropical de montaña. Pages 79-84 in A.D. Brown & H.R. Grau. Investigación, Conservación y Desarrollo en Selvas Subtropicales de Montaña. LIEY, Universidad Nacional de Tucumán.

Guevara, S., Purata, S. & van der Maarel, E. 1986. The role of remnant forest trees in tropical secondary succession. Vegetatio 66: 77-84.

Iudica, C. & Bonaccorso, FJ. 1997. Feeding of the bat *Sturnira lilium* on fruits of *Solanum riparium* influences dispersal of this pioneer tree in northwestern Argentina. Studies in Neotropical Fauna and its Environment 32: 4-6.

Karl, T.R.; Knight, R.W. & Plummer, N. 1995. Trends in high-frequency climatic variability in the twentieth century. Nature 377: 217-220.

Kaufman, J.B. & Uhl, C. 1990. Interactions of anthropogenic acitivities, fire, and rain forests in the Amazon basin. Pages 11-31 in J. Goldammer, ed. Fire in the Tropical Biota. Springer Verlag, Berlin.

Kessler, M. & Driesch, P. 1993. Causas e historia de la destrucción de los bosques altoandinos en Bolivia. Ecología en Bolivia 2: 1-18.

Malizia, L.R. & Greslebin, A. 1998. Regeneración de especies arbóreas bajo arbustos exóticos en la sierra de San Javier (Tucumán, Argentina). In press in A.D. Brown et al., eds. Historia Natural de la Sierra de San Javier.

Mann, M.E.; Park, J. & Bradley, R.S. 1995. Global interdecadal and century-scale climate oscillations diring the past five-centuries. Nature 378: 266-270.

Mc Bride, J.R. 1983. Analysis of tree rings and fire scars to estblish fire history. Tree-Ring Bulletin 43: 51-67.

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

Oliver, C.D. & Larson, B.C. 1990. Forest Stand Dynamics. Mc Graw-Hill. N. York. 467 pp.

Molinillo, M.F. & Vides-Almonacid, R. 1989. Uso de los recursos naturales en el bosque de Aliso de la provincia de Tucumán. Avances de Investigación, Instituto de Geociencias y Medio Ambiente 1: 1-20.

Overpeck,J.T.; Rind,D & Goldberg, P. 1990. Climate-induced changes in forest disturbance and vegetation. Nature 343:51-53

Pickett, S.T.A.; Collins, S.L. & Armesto, J.J. 1987. Models, mechanisms and pathways of succession. Botanical Review 53: 335-371.

Suffling, R. 1995. Can disturbance determine vegetation distribution during climate warming?. A boreal test. Journal of Biogeography 22: 501-508.

Villalba, R.; Grau, H.R.; Boninsegna, K.; Jacoby, G. & Ripalta, A.. Manuscript under review. Treeline chronologies and their relationship to continental atmosperic circulation in Southamerica subtropics. International Journal of Climatology

Vitousek, P.M. 1994. Beyond global warming: ecology and global change. Ecology 75: 1861-1876.

Walker, D & Chen, Y. 1987. Palynological light on rainforest dynamics. Quaternary Science Reviews 6: 77-92

Young, K.R. 1993. Tropical treelines: changes in forest structure and regeneration between two peruvian timberline margins. Artic and Alpine Research 25: 167-174.

ABUNDANCE AND DIVERSITY OF USEFUL WOODY SPECIES IN SECOND-GROWTH, OLD-GROWTH AND SELECTIVELY-LOGGED FORESTS OF NE COSTA RICA

Robin L. Chazdon
Department of Ecology and Evolutionary Biology
University of Connecticut, Storrs, CT 06269 USA

Felix G. Coe
Biology Department, Tennessee Technological University
P.O. Box 5063, Cookeville, TN 38505, USA

ABSTRACT

Tropical secondary forests are rich sources of useful species for native and traditional people. Our objective was to conduct a quantitative assessment of useful species in a series of forest stands with different land-use histories. Based on a detailed vegetation inventory of 10 tropical wet forest stands in Sarapiquí, Costa Rica, species were classified into 20 use categories. Classification was based on personal knowledge of uses of these species in SE Nicaragua and NE Costa Rica and from published ethnobotanical sources. Here, we examine results for the six most important use categories: medicine, construction, firewood, crafts, food, and timber. We sampled three size classes of woody vegetation in nested, contiguous plots along transects: trees ($\geq$ *5 cm dbh), saplings* ($>$ *1m ht,* $<$ *5 cm dbh), and seedlings* ($>$ *20 cm ht,* $<$ *1m ht). Our study included five second-growth stands (15-25 years old) that developed following pasture abandonment, three old-growth stands with no history of logging, and two recovering, selectively-logged stands (12-17 years since logging).*

Of the 459 woody taxa surveyed, 382 were identified conclusively to species—of these, 313 species (82%) had at least one use. Medicinal uses were noted for 167 species. Density of trees of medicinal species was significantly higher in the second-growth stands (740 individuals/ha) compared to old-growth (434 individuals/ha) and logged stands (542/ha; ANOVA, $P < 0.022$*). Sapling and seedling density of medicinal species did not differ significantly among forest types. The increased density of medicinal trees in second-growth was not due solely to the greater overall tree density. For both trees and saplings, relative abundance of medicinal species was* *significantly higher in second-growth (65%) compared to old-growth (48%) and selectively-logged (56%) stands. Forty-seven species had timber use; 11 of high, commercial value. For trees, second-growth stands had twice the mean density of timber species of old-growth stands; logged stands were intermediate. Timber trees showed higher relative abundance in second-growth; 35% of trees have timber value in second-growth stands, compared to 22% in old-growth stands. Sapling and seedling timber tree density did not differ significantly across forest types. Dominant tree species in second-growth, such as* Pentaclethra macroloba, Laetia procera, *and* Goethalsia meiantha *have low to moderate timber value, and are abundant in the 10-30 cm size class. Second-growth stands can also harbor abundant regeneration of high-quality, commercial timber species, with abundant saplings of* Dipteryx panamensis, Minquartia guianensis, *and* Vochysia ferruginea *in the understory.*

Non-timber uses of species for food, firewood, construction, and crafts show similar densities across forest types for trees, saplings, and seedlings. Second-growth and logged forests in NE Costa Rica are a rich source of non-timber products and show high potential for management in timber production. Ample regeneration of high-value, commercial timber species will be sustained through regional and landscape-level approaches that ensure availability of seed sources in remnant forest fragments. Our study suggests that, at least in NE Costa Rica, second-growth forests may become the primary sources of forest products in future generations.

INTRODUCTION

Throughout the world's tropical regions, secondary and degraded forests are increasing in extent and importance as old-growth forests become exploited, fragmented, or converted to agricultural uses (Brown and Lugo 1990, Whitmore 1997). The utilitarian value of tropical forests as sources of timber and non-timber products has been widely appreciated, and has been used as a strong argument for conservation and for sustainable management (Prance *et al.* 1987, Peters et al. 1989, Panayotou and Ashton 1993, Phillips *et al.* 1994). Recently, an increasing number of studies have emphasized the potential of second-growth or logged tropical forests for timber and non-timber products (Wadsworth 1987, Dubois 1990, Finegan 1992, Lugo 1992, Salick 1992, Salick et al. 1995, Toledo *et al.* 1995). Our study was motivated by the observation that tropical secondary forests and degraded old-growth forests are generally under-valued and under-appreciated, despite the wide variety of useful plant species they house (Toledo *et al.* 1992, Toledo *et al.* 1995). Yet, throughout the tropics, secondary and degraded forests will likely be the predominant forest type remaining to provide timber and non-timber resources in the future. In this regard, tropical zones are quickly following the example of forest conversion and regrowth witnessed over the last centuries in the temperate zones.

Ethnobotanical studies in the neotropics confirm that the second-growth flora is rich in medicinal species, and may be utilized far more intensively by traditional (indigenous and non-indigenous) peoples than old-growth forests in the same vicinity (Kohn 1992, Toledo *et al.* 1995, Voeks 1996). Moreover, many fast-growing second-growth tree species are recognized for their timber value (Wadsworth 1987). To date, however, no studies have compared in a rigorous, quantitative manner, the species richness and abundance of useful species found in old-growth, second-growth, and selectively-logged forests within the same region.

This study combines techniques of forest ecology and ethnobotany. We use a quantitative vegetation inventory of trees and woody regeneration (saplings and seedlings) to compare quantitatively the abundance and species richness of useful species among five second-growth stands, three old-growth stands, and two recovering, selectively-logged stands within the same regional flora. We consider 20 different categories of use, based on a detailed ethnobotanical study in the same general region (Fig. 1). These uses include timber and non-timber uses, traditional and commercial uses. In this way, we can evaluate the management potential of different types of forest cover and land-use practices for both timber and non-timber products. By including seedling and sapling size classes, our results permit an assessment of regeneration of useful species in these forests. In this paper we compare results for the six most important use categories: medicine, construction, firewood, crafts, food, and timber, based on number of species used (Fig. 1). A complete analysis of all 20 uses has been prepared by Chazdon and Coe (in review). Because our inventory was restricted to woody species, these estimates are clearly underestimates of the total abundance and richness of species of non-timber value in these forests.

MATERIALS AND METHODS

Vegetation inventory

Our study is based on a survey of woody vegetation conducted in three old-growth stands, five second-growth stands, and two recovering, selectively-logged stands (Table 1). All study areas were located in the Atlantic lowland rain forest of Sarapiquí, Costa Rica in the premontane wet forest life zone (Holdridge *et al.* 1975). Species richness, floristics and vegetation structure in six of these stands are described by Guariguata et al. (1997) and Chazdon *et al.* (1998). Forest structure, light conditions, and the soil seed bank within seven of these stands are described by Dupuy and Chazdon (1998) and Nicotra et al. (1998). Second-growth forests were 15-25 years old at the time of the vegetation census. All second-growth stands had been clear cut and four stands had been used as pastures for several years before abandonment. The selectively-logged stands were logged at about the same time as the second-growth forests began to regenerate.

In each stand, vegetation was sampled in nested, contiguous quadrats along three roughly parallel transects 100-160m in length. Trees ≥ 5 cm dbh were sampled in 10 m x 10 m quadrats (total area sampled per stand = 0.24 - 0.48 ha); saplings (stems > 1 m ht and < 5 cm dbh) were sampled in 5 m x 5 m quadrats (total area sampled per stand = 0.135 - 0.24 ha); and seedlings (stems 20-100 cm ht.) were sampled in 1 m x 1 m quadrats (total area sampled per stand = 270

Table 1. Site characteristics of eight forest stands in the Caribbean lowlands of Costa Rica

Site name	Forest type	Location (latitude; longitude)	Recent land use history	Estimated time since disturbance
Lindero Occidental	Second-growth	La Selva Biological Station (10° 26' N; 84° 01' W)	Cleared in 1971-73. Pasture for 6 years; regrowth cleared before pasture abandoned	15-17 years
Peje	Second-growth	La Selva Biological Station (10° 26' N; 84° 02' W)	Cleared in 1972-74. Pasture for 5 years; regrowth cleared before pasture abandoned	15-17 years
La Martita	Second-growth	Chilamate (10° 27' N; 84° 04' W)	Cleared in 1971-72. Pasture for 4-5 years, then abandoned	17-20 years
Cuatro Rios	Second-growth	La Virgen (10° 23' N; 84° 08' W)	Clear cut in mid 1970's for timber.	15-20 years
Sendero Holdridge	Second-growth	La Selva Biological Station (10° 25' N; 84° 01' W)	Cleared in 1950's. Pasture abandoned in 1967.	25 years
La Selva	Old-growth	La Selva Biological Station (10° 25' N; 84° 03' W)	No apparent or recorded human disturbance	
Chilamate	Old-growth	Chilamate (10° 27' N; 84° 04' W)	No apparent or recorded human disturbance	
Cay Rica	Old-growth	El Roble (10° 26' N; 84° 05' W)	No apparent or recorded human disturbance	
Intervenido	Selectively-logged	La Selva Biological Station (OTS; 10° 25' N; 84° 02' W)	Logged for more than 10 years until the late 1970's. *ca.* 3-4 stumps / ha	15-17 years
Kelady	Selectively-logged	Pueblo Nuevo (10° 29' N; 84° 09' W)	Logged for more than 10 years until the early 1980's. *ca.* 8-9 stumps / ha	12-14 years

- 480 m2). Transects did not traverse any steep slopes or known environmental gradients. Species were identified in the field by project staff assisted by an expert local naturalist; in questionable cases, leaf samples were collected, dried, and pressed, and used to identify species by comparison with specimens in the La Selva herbarium or the Costa Rican National herbarium. Vegetation data were entered into a specimen-based, relational database (Biota; Colwell 1996). Species names follow an updated list published by Robert L. Wilbur and Collaborators (McDade *et al.* 1994). A complete listing of species and their uses can be obtained upon request from the senior author or at http://viceroy.eeb.uconn.edu/useful species.

Ethnobotanical survey

Ethnobotanical uses of species found within the study areas were compiled by the second author, based on a detailed ethnobotanical study of the Garífuna people of eastern Nicaragua, who live in the same rainforest zone found in NE Costa Rica (Coe and Anderson 1996). The Garífunas are relative newcomers to the Atlantic Coast of Nicaragua. They are descendants of the Arawaks and Red Carib Islanders, who settled along the Atlantic Coast of Nicaragua after being transferred to the island of Roátan, Honduras from St. Vincent in 1797. Currently, about 1,500 Garífuna live on the Atlantic Coast of Nicaragua; their largest settlement is in Orinoco. Plants utilized by the Garífunas are of wide taxonomic diversity, distributed among 75 families, 192 genera, and 253 species. A complete listing of species and their uses is provided by Coe and Anderson (1996).

Surveys of plant uses by Garífuna informants were supplemented by published accounts of species used by other indigenous and non-indigenous peoples throughout the lowland wet forest life zone of Central America (Table 2). For broadly distributed species that are used differently in South America than in Central America, only local uses are considered here. Timber species currently used in local or international commerce in Costa Rica were considered of commercial value; others were classified as traditional value only. Commercial value of timber and non-timber forest products varies greatly among regions and countries, and is subject to market demand. Use values (high, moderate, low) were recorded for each species for each of the 20 use categories, as auxiliary fields in the species table of the Biota database (Colwell 1996). Specimen data were then export by site, size-class, and use value for subsequent tabulation and statistical analysis.

RESULTS

Species richness and uses

A total of 24,769 specimens were recorded in the vegetation inventory. These specimens represent a total of 456 species and 80 families. Of these, 382 species were conclusively identified to species. Of the total number of specimens recorded, 21,217 specimens were observed to have at least 1 use (85.7%). A total of 320 useful species were observed, comprising 167 genera and 69 families. Among these useful species, 313 were conclusively identified to species, 81.9% of the total number of identified species found within the study area. Of the 139 species with no use, 50% remain unidentified at the species or genus level. Therefore, we have likely underestimated the number of useful woody species within the study region.

Table 2. Ethnobotanical sources used to compile the database of species uses.

Coe, F. and G. J. Anderson 1996. Ethnobotany of the Garífuna of Eastern Nicaragua. Economic Botany 50: 71-107.

D'Arcy, W. G. and M. D. Correa. 1985. The botany and natural history of Panama. Saint Louis, MO, USA, Missouri Botanical Gardens.

Duke, J. A. 1972. Istmian ethnobotanical dictionary. Fulton, Maryland.

Gordon, B. L. 1982. A Panama forest and shore: natural history and Amerindian culture in Bocas del Toro. Pacific Grove, CA, USA, The Boxwood Press.

Hazlett, D. L. 1986. Ethnobotanical observations from Cabecar and Guaymi settlements in Central America. Economic Botany 40: 339-352.

Holdridge, L. R. and L. J. Poveda. 1975. Arboles de Costa Rica. Vol. 1. San Jose, Costa Rica, Centro Cientifico Tropical.

Janzen, D. H. 1983. Costa Rican Natural History. Chicago, IL, USA, University of Chicago Press.

Melendez, N. E. 1984. Plantas medicinales de Costa Rica y su folklore. San Jose, Costa Rica, Editor Universidad Nacional De Costa Rica.

Morton, J. F. 1981. Atlas of medicinal plants of middle America. Vols. 1 & 2. Springfield, IL, USA, Charles C. Thomas Publishers.

Ocampo, R. 1994. Estudio etnobotánico de las palmas empleadas por los indígenas en Talamanca, Costa Rica. 7: 16-21.

Ocampo, R. A. 1980. San Jose de Cabecar, ua comunidad en decadencia. Reporte Interno, Universidad Nacional de Costa Rica, San Jose, Costa Rica

Ocampo, R. A. 1981. La comunidad de Telire en equilibrio con la naturaleza. Reporte Interno, Museo Nacional, San Jose, Costa Rica.

Ocampo, R. A. and A. B. Vargas 1981. Nota preliminar sobre la utilización de plantas en confeccion de artesanias menores en Alto Conte, comunidad Guaymi, y la ubicacion geografica de los grupos Guaymi en Costa Rica. Reporte Interno, Museo Nacional, San Jose, Costa Rica

Pittier, H. 1978. Plantas usuales de Costa Rica, 2nd edition. San Jose, Costa Rica, Editorial Costa Rica.

Record, S. J. and R. W. Hess. 1972. Timbers of the New World. New York, NY, USA, Arno Press.

Sarkis, A. and V. Campos. 1985. Curanderismo tradicional del Costaricense. San Jose, Costa Rica, Lehman Editores.

Skutch, A. F. 1971. A naturalist in Costa Rica. Gainesville, FL, USA, University of Florida Press.

Standley, P. 1938. Flora of Costa Rica. Publ. Field Museum of Natural History, Botanical Series 18 (1-4).

Standley, P. 1946-1974. Flora of Guatemala. Vol. 24. Fieldiana, Field Museum of Natural History, Chicago, IL

Young, A. M. 1991. Sarapiquí chronicle: A naturalist in Costa Rica. Washington, D. C., Smithsonian Institution Press.

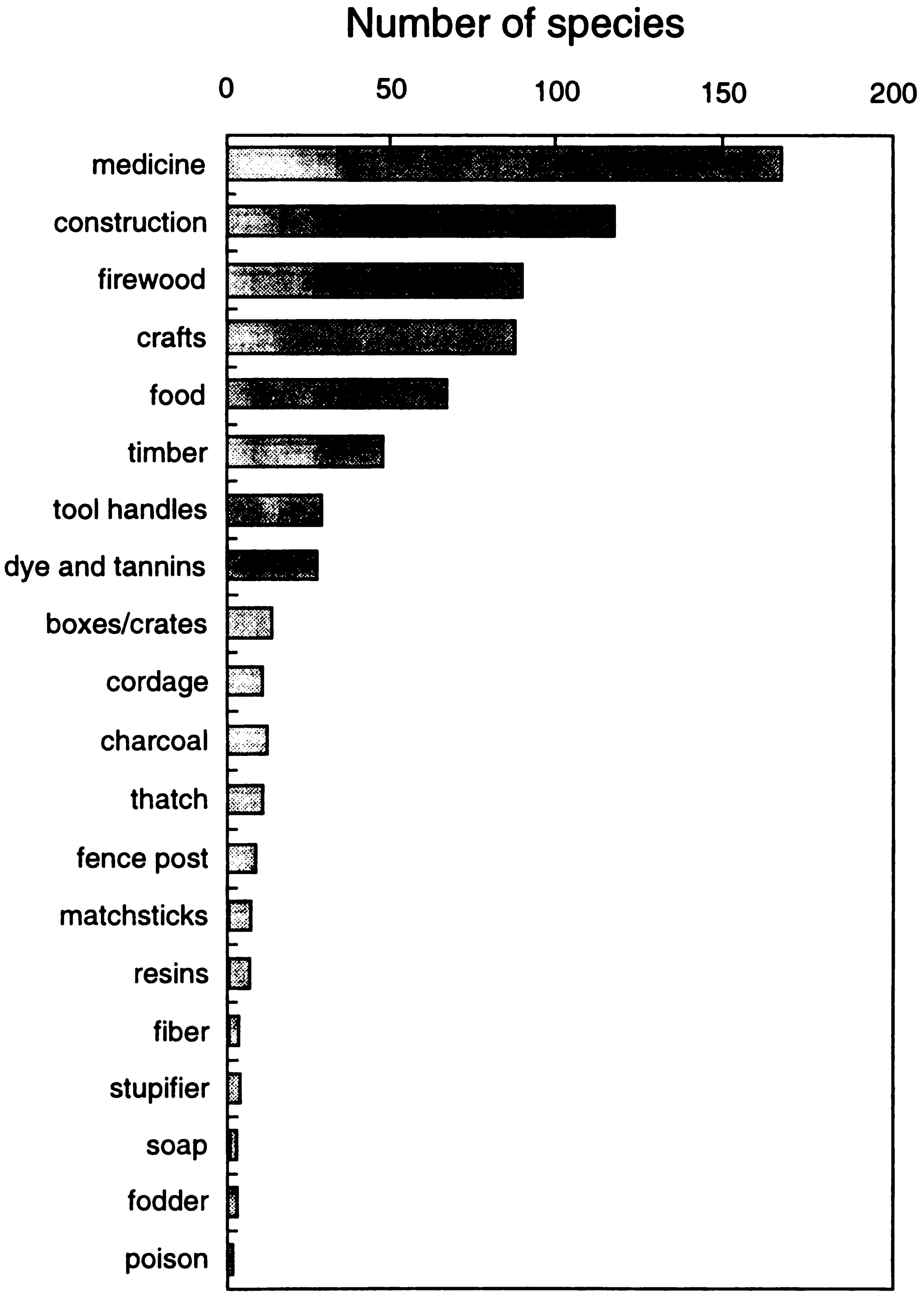


Figure 1. Species richness distribution across 20 use categories, based on the complete data base from 10 forest stands in Sarapiquí, Costa Rica.

Across the entire vegetation inventory, the use category containing the largest number of species was medicine, with 167 species (Fig. 1). Medicinal uses were followed by construction (117 species) , firewood (90 species), crafts (87 species), food (67 species), and timber (47 species). Less species-rich use categories are tool handles (28 species), dyes or tannins (27 species), boxes and crates (13 species), cordage (11 species) and thatch (10 species). The remaining eight categories contain fewer than 10 species (Fig. 1).

Species richness: taxonomic distribution

Among the 10 stands, four families dominate the species richness of useful species, a pattern that reflects the family composition within this region's woody flora (Fig. 2). The Fabaceae contained the largest number of useful species (33 species), followed by the Rubiaceae (30 species), the Melastomataceae (25 species) and the Arecaceae (23 species). The most common families of useful species were also the most common families in the study area, excluding non-woody taxa (Fig. 2 Hartshorn and Hammel 1994). Half of the useful species observed in the vegetation inventory were found in only eight plant families; these eight families composed 48% of the total number of woody species sampled. Of the 17 families with five or more species in the study area, on average, 82.75% of the species had at least one use.

Many species had multiple uses; six species had seven different uses. For example, *Pouteria campechiana* and *P. glomerata ssp. stylosa* (Sapotaceae) are used for food, medicine, tool handles, construction, firewood, charcoal and crafts. *Virola koschnyi* (Myristicaceae), a species widely used for reforestation throughout Sarapiquí, is used for timber, medicine, boxes & crates, construction, resins, and soap.

Medicinal species

For trees $\geq$ 5 cm dbh, density of medicinal species ranged from 353 to 913 stems/ha. The second-growth stands had significantly higher density of medicinal trees (mean of 740 stems/ha) compared to both old-growth (mean of 434 stems/ha) and selectively-logged stands (mean of 542 stems/ha; one-way ANOVA; $P < 0.022$; Fig. 3A). Mean medicinal sapling density ranged from 2152 stems/ha in the old-growth stands to 3483 stems/ha in the second-growth stands. In the seedling size class, mean density of medicinal species ranged from 6742 stems/ha in the second-growth stands to 9087 stems/ha in the selectively-logged stands. For these smaller size classes, forest types did not differ significantly in density of medicinal species (one-way ANOVA; $P > 0.05$).

The greater density of medicinal trees in the second-growth stands reflects both the higher total tree density and the higher relative abundance of medicinal species. In the second-growth stands, 65% of the trees $\geq$ 5 cm dbh had medicinal value, compared to 48% in the old-growth and 56% in the selectively-logged stands. Second-growth stands showed significantly higher relative abundance of medicinal trees and saplings compared to old-growth stands [Kruskal-Wallis, $P = 0.041$ (trees) and $P = 0.049$ (saplings); Fig. 3B]. Relative abundance of medicinal species did not vary significantly with stand type for seedlings (Kruskal-Wallis, $P = 0.56$).

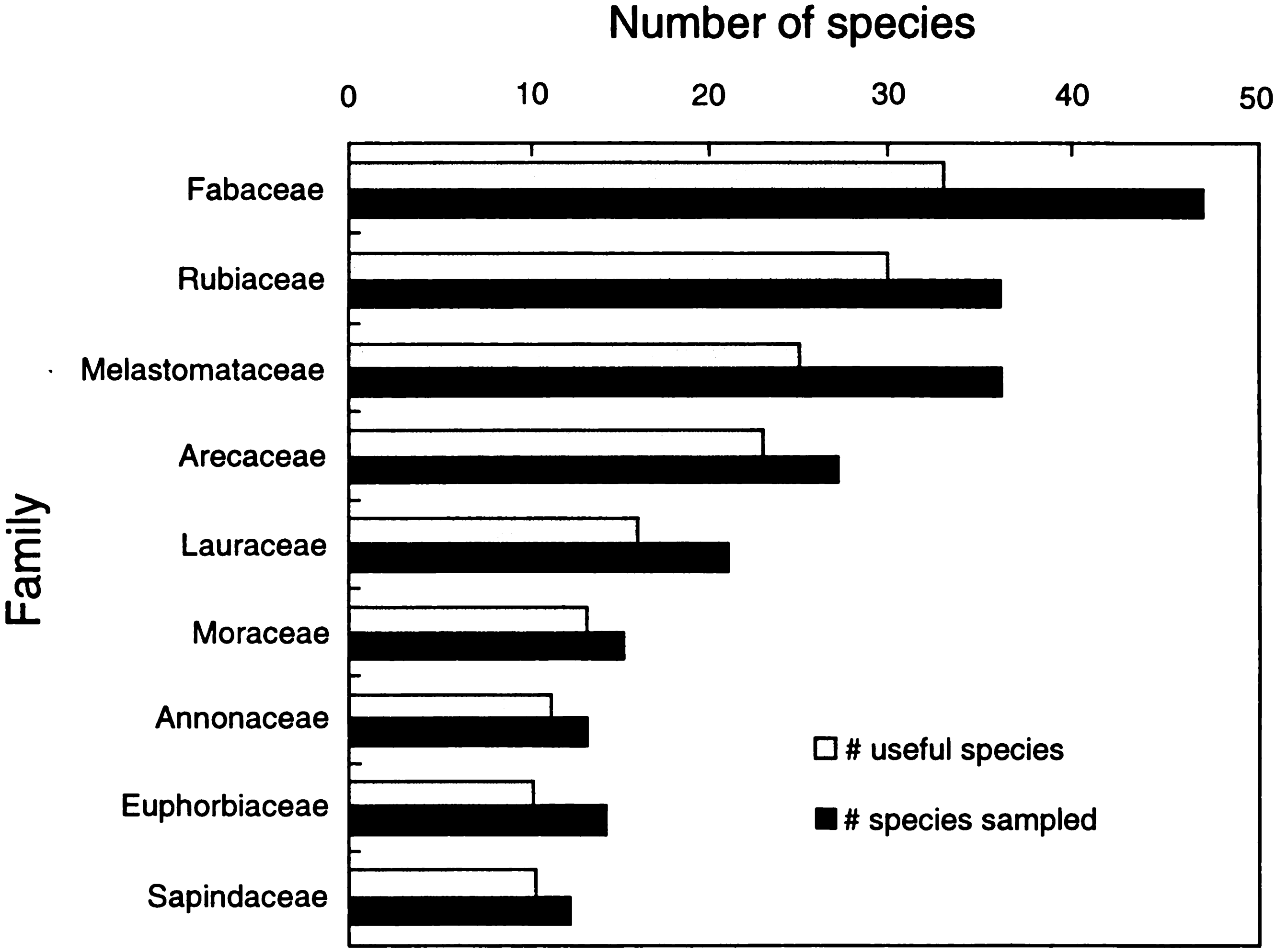


Figure 2. The familial distribution of species with at least one use and the total number of species sampled within those families. Only families with 10 or more useful species are shown. The ranking of families with useful species reflects the overall family importance in the native, woody plant flora.

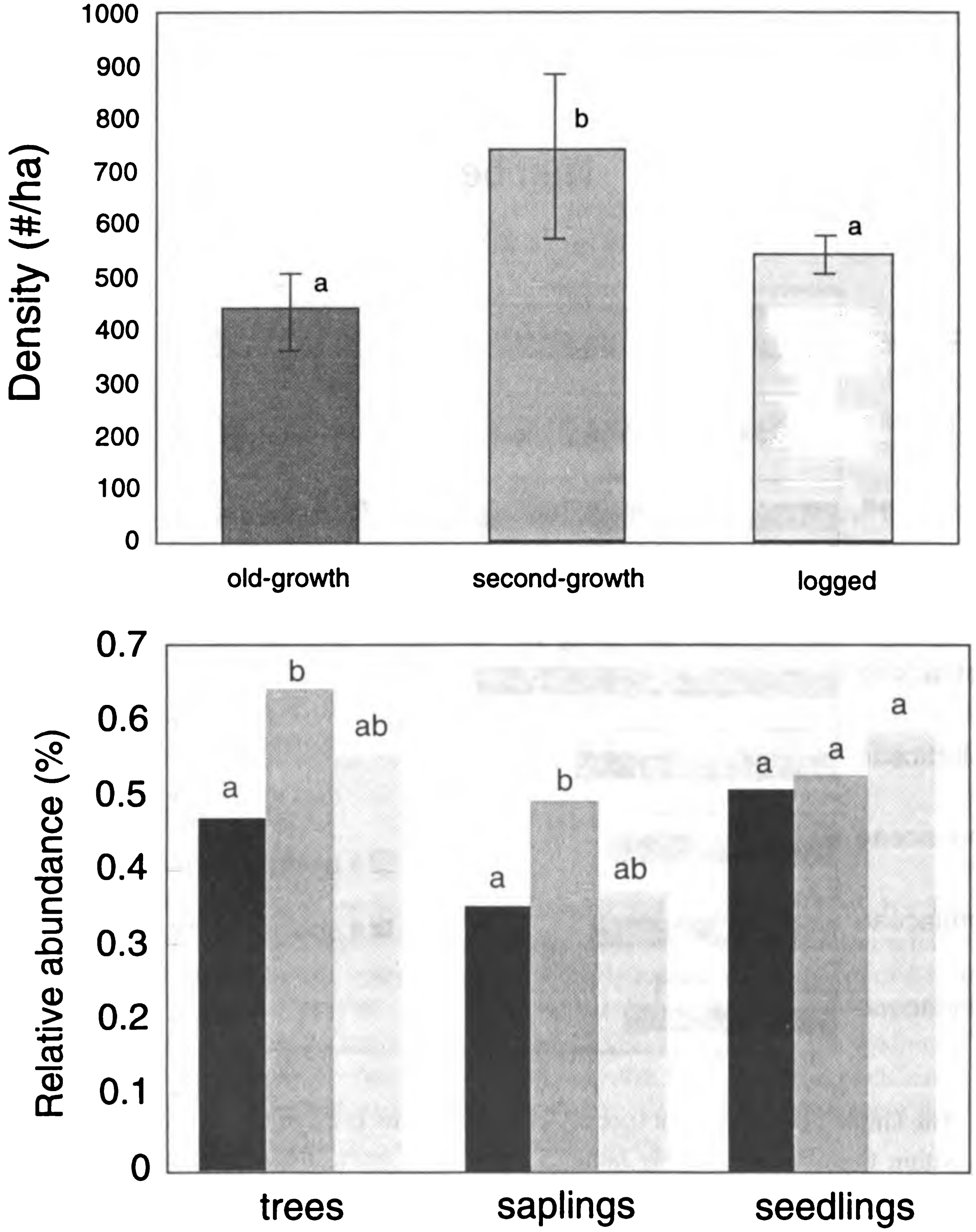


Figure 3. The A) density (#/ha) and B) relative abundance (%) of species with medicinal use in old-growth ■, second-growth ■, and logged stands . Letters indicate significantly different means across forest types (P < 0.05).

Timber species

Second-growth stands also showed significantly higher density of timber trees ≥ 5 cm dbh compared to both old-growth and selectively-logged stands (one-way ANOVA, $P = 0.002$; Fig. 4A). On average, second-growth stands contained 406 stems/ha, whereas old-growth stands contained 195 stems/ha and selectively-logged stands contained 246 stems/ha for tree species with timber value. Density of timber species in the sapling and seedling size class varied greatly across stands and did not differ significantly with stand type. Two second-growth stands showed high sapling densities, up to 1533 stems/ha in La Martita. This stand has excellent regeneration of timber species, such as *Brosimum guianensis, Dendropanax arboreus, Dipteryx panamensis, Minquartia guianensis, Pentaclethra macroloba,* and *Vochysia ferruginea*. Relative abundance of timber species was significantly higher in the second-growth stands (mean of 35%) compared to old-growth stands (mean of 22%) and logged stands (mean of 25%; Fig. 4B). Saplings and seedlings showed no significant difference in relative abundance of timber species across stand types.

Although density is a useful comparative measure, basal area is a better measure of timber volume. When only high-value (commercial) timber species are considered, no significant difference was observed in basal area of trees ≥ 30 cm dbh or between 10-30 cm dbh between second-growth and old-growth stands, although selectively-logged stands clearly showed previous removal of virtually all high-value timber (Fig. 5a). *Vochysia ferruginea*, a common second-growth canopy dominant, is a high-value timber species that contributes substantially to the basal area in several of the stands studied.

For moderate- and low-value timber species, second-growth forests showed significantly higher basal area in the 10-30 cm dbh size class, but not for stems ≥ 30 cm dbh (Fig. 5b). Enhanced timber basal area of this smaller size class in second-growth stands is largely due to the high density of small trees of moderate timber value, such as *Goethalsia meiantha, Laetia procera,* and *Pentaclethra macroloba* (Appendix 2).

Construction, firewood, crafts, and food

Of these four use categories, the highest density of stems have uses in construction of homes and furniture. Abundances of trees, saplings, and seedlings of species used for construction, firewood, crafts, or food did not differ significantly among stand types (one-way ANOVA; $P > 0.05$; Table 3). Second-growth and selectively-logged forests are similar to old-growth forests in the abundance of these non-timber products, in all three size classes examined.

Table 3. Density of non-timber species used for construction, firewood, food, and crafts in tree, sapling, and seedling size classes. Values are means ± 1 s.d. for 5 second-growth stands, 3 old-growth stands, and 2 selectively-logged stands.

Use/size class	Second -growth		Old- growth		Selectively- logged	
	mean	s.d	mean	s.d.	mean	s.d.
Construction						
tree	471.5	68.6	470.9	21.2	441.2	45.4
sapling	2031.6	576.1	2843.9	969.1	2724.8	151.4
seedling	3980.3	1254.1	6537.1	2006.7	6306.7	685.2
Firewood						
tree	402.3	65.1	335.3	26.1	409.9	33.2
sapling	1413.5	342.9	1185.8	76.2	1328.4	522.3
seedling	7134.4	1677.7	8783.9	2024.3	8960.0	1615.5
Food						
tree	201.4	119.4	268.5	28.2	236.3	38.7
sapling	1389.1	636.1	1121.3	334.0	1145.4	655.6
seedling	2772.5	664.1	3054.2	695.2	3077.2	1460.5
Crafts						
tree	213.9	90.8	263.1	55.7	209.8	4.21
sapling	1563.6	545.1	1173.5	296.9	1111.2	151.3
seedling	1804.2	715.7	2323.6	325.4	1997.6	153.8

DISCUSSION

Secondary forest regeneration in these stands has proceeded rapidly and after 15-20 years, basal area of trees ≥5 cm dbh has reached values similar to nearby old-growth stands. We recognize that these young stands represent a "best case" scenario for successful secondary forest regeneration. Several large patches of old-growth forest remain in the region and serve as important seed sources. Remnant trees of commercial timber species are found within all of the second-growth stands we studied. Moreover, these stands have been protected from harvesting and exploitation since the second-growth vegetation developed. These factors contribute to the rapid recovery of basal area and the high abundance of useful species currently found within these young stands (Guariguata et al. 1997).

Because uses and commercial value of timber and non-timber products, and patterns of secondary forest regeneration vary considerably regionally, our detailed quantitative results may not be generally applicable beyond the region of SE Nicaragua and NE Costa Rica. Our overall findings, however, echo those of Toledo et al. (1995) conducted in the humid tropics of Mexico and support the findings of Balick and Mendelsohn (1992) in Belize. Second-growth forests in the Sarapiquí region of Costa Rica are rich in useful species, and contain higher abundances of trees with medicinal and timber uses than neighboring old-growth forests (Figs. 3A,B and 4A,B). In fact, these well-developed secondary stands show a significantly greater relative abundance of medicinal species in the tree size class, suggesting differences in both species composition and tree density.

Dominant tree species in these second-growth stands have notable medicinal and timber value as well as other uses. These dominant species include *Casearia arborea, Cordia bicolor, Goethalsia meiantha, Laetia procera, Pentaclethra macroloba* (Guariguata *et al.* 1997), which all have low or moderate traditional medicinal uses (Appendix 1). With the exception of *Pentaclethra macroloba*, these species have greater total abundance in the second-growth compared to the old-growth stands in our study (Guariguata *et al.* 1997). A similar explanation supports the higher total and relative abundance of timber species in the second-growth stands. *Laetia procera, Goethalsia meiantha,* and *Vochysia ferruginea* reach high abundances in the canopy of these second-growth stands and have moderate to high timber value on the commercial market (Guariguata *et al.* 1997; Appendix 2). Voeks (1996) also observed in eastern Brazil that a greater number of medicinal species were utilized from second-growth habitats compared to old-growth forest. Medicinal species from second-growth habitats are more familiar, accessible, and may be more pharmacologically rich than species found in old-growth forests (Voeks 1996).

Non-timber uses, such as crafts, food, firewood, and construction are equally abundant in the three forest types, indicating that second-growth stands have far greater potential as managed, extractive reserves than previously thought. This tremendous potential has long been recognized by indigenous and non-indigenous peoples throughout the neotropics (Gomez-Pompa et al. 1987, Coomes 1995). Selectively-logged stands also have a high potential for management for non-timber products (Table 3) and show a high basal area of low-and moderate-quality timber in the ≥ 30 cm dbh size class (Fig. 5b).

Clearly, second-growth and recovering, logged forests of the Sarapiquí region have a high potential to be managed for extraction of non-timber products and for timber harvesting as well. The current regeneration is well stocked with species in all use categories examined, suggesting that careful harvesting and management could permit ample regeneration of a wide variety of useful species in the future.

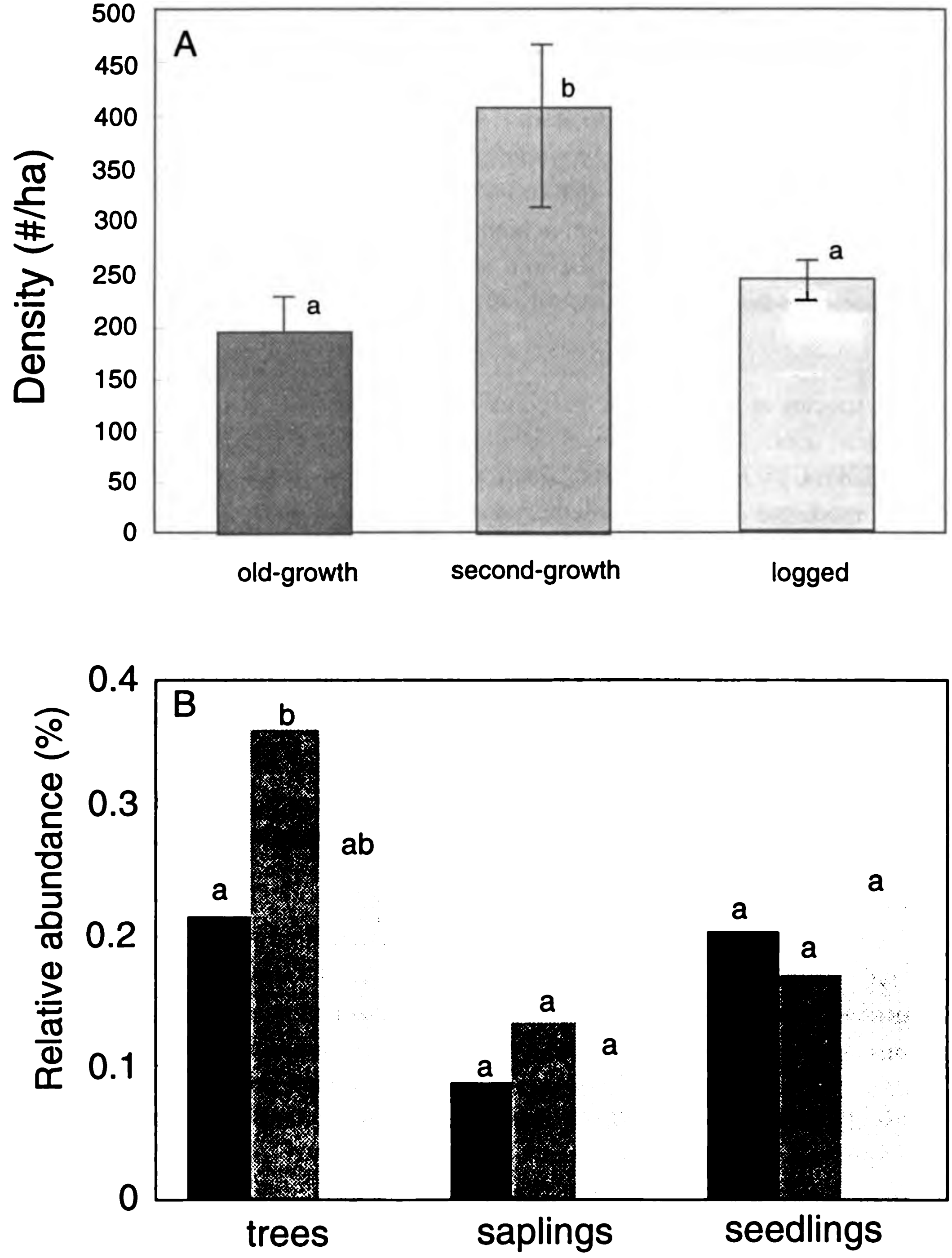


Figure 4. The A) density (#/ha) and B) relative abundance (%) of species with medicinal use in old-growth ■, second-growth ■, and logged stands . Letters indicate significantly different means across forest types ($P < 0.05$).

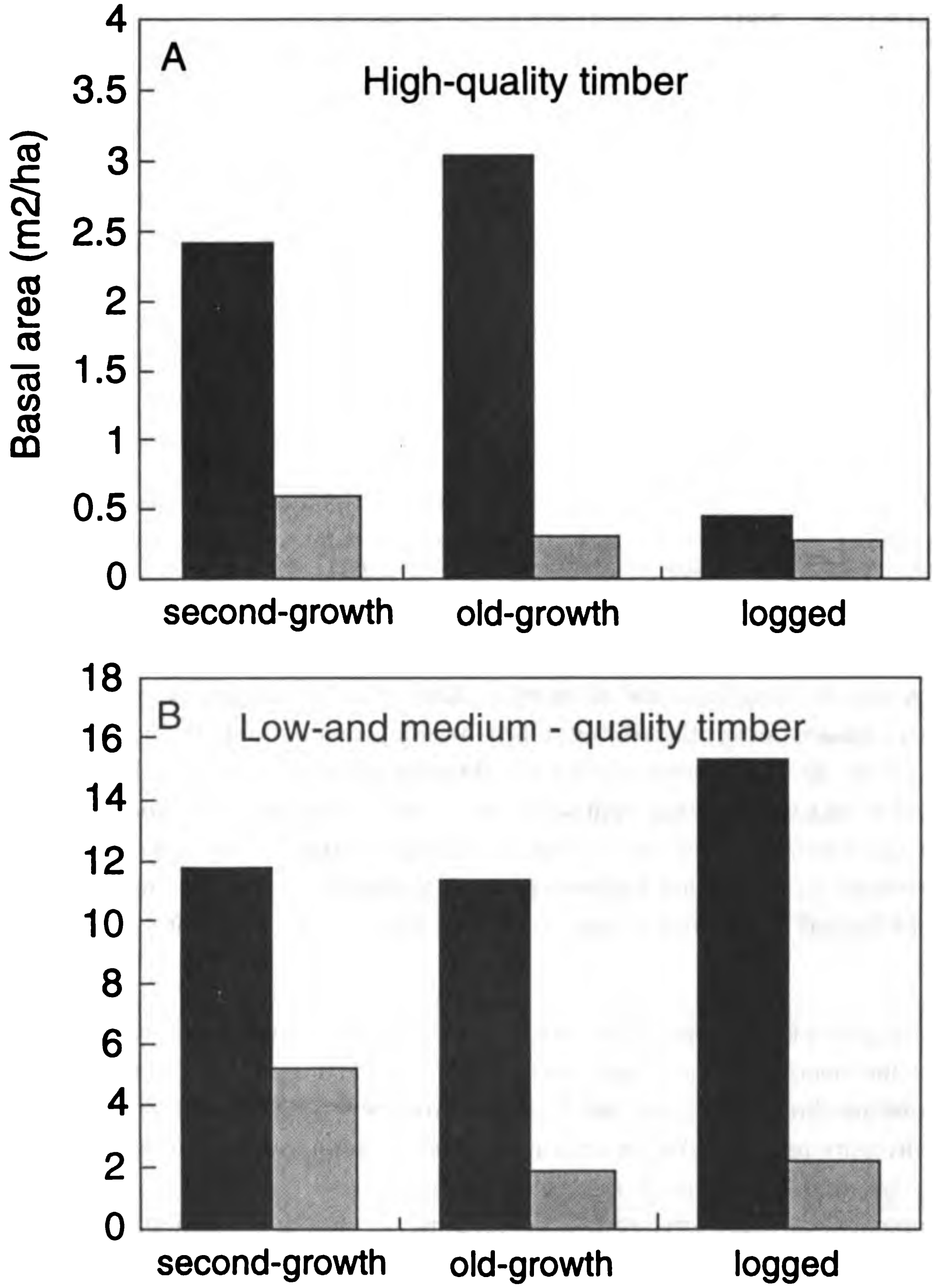


Figure 5. The basal area (m²/ha) of A) high-quality, commercial timber species and B) low- to moderate- quality timber species ≥30 cm dbh ■ and 10-30 cm dbh ■. Statistics are provided in the text. For high-quality timber species, there is no significant difference in basal area between second-growth and old-growth stands. For low- and moderate- quality timber species, second-growth stands have significantly higher basal area of trees 10-30 cm dbh.

RECOMMENDATIONS AND FUTURE LINES OF RESEARCH

We recommend that studies such as this one, be enlarged to include an assessment of the non-woody species and their uses. Many medicinal species, particularly in young second-growth, are herbaceous, and were not included in our inventory (Kohn 1992, Toledo et al. 1995, Voeks 1996). Vegetation inventory data have been gathered for many forests throughout the new- and old-world tropics and could be used to conduct similar quantitative analyses, if ethnobotanical data for the same regional flora can be obtained. Examples of forest inventory studies that are linked to ethnobotanical surveys illustrate this approach (Prance et al. 1987, Boom 1989, Bennett 1992, Phillips et al. 1994, Toledo et al. 1995). We feel that these quantitative studies will enhance forest conservation efforts and in many cases would not require new field work, if ethnobotanical data for the region are already available.

Now that we know the wealth that these second-growth and logged forests contain, the challenge is how to use this information to manage these forests for human benefit without sacrificing their biological integrity. Local people can benefit from marketing of value-added products extracted in a sustainable manner from these forests, such as crafts. Teas, salves, and other medicinal products could also be produced for local or commercial markets. These activities may boost struggling rural economies. Currently, the second-growth and degraded forests of Sarapiquí are being utilized (but not managed) primarily for extraction of timber, such as *Goethalsia meiantha* and *Cordia alliodora*. If these forests are not managed for a wider range of species and products, they may simply be destroyed in the battle for land speculation and converted to agricultural use. Future success of secondary forest regeneration within this region will be jeopardized by increasing fragmentation, degradation, and loss of source populations. Similarly, once-logged forests in this region could be managed for future timber and non-timber production.

In our view, increased knowledge of the uses of species found in these stands will increase public awareness of the need for their conservation and careful management. Old-growth stands in many countries are diminishing and will likely become increasingly protected from use as their value as biodiversity reservoirs becomes critical. The second-growth and degraded forests will, of necessity, become the focus of increasing exploitation for timber as well as non-timber products. Tropical second-growth forests have much to offer future generations and may actually be more amenable to sustainable management than old-growth forests, due to their high total and relative abundance of useful species and their more even age structure.

ACKNOWLEDGEMENTS

We thank Manuel Guariguata, Marcos Molina, Juan Dupuy, Jeannette Paniagua, Carlos Castillo, Orlando Vargas, and Carolina Gonzalez for their excellent field work and species identification. Julie Denslow helped design the forest inventory study. Anne Geissinger, and Meredith

Alexandrowicz helped with data processing and analysis, and Robert Colwell's program Biota made databasing a reality as well as a dream. The staff of La Selva and the Organization for Tropical Studies greatly facilitated this study. Funding for this research was provided by grants from the National Science Foundation and the Andrew W. Mellon Foundation.

REFERENCES

Balick, M. J. and R. Mendelsohn 1992 Assessing the economic value of traditional medicines from tropical rain forests. Conservation Biology 6: 128-130.

Bennett, B. E. 1992 Plants and people of the Amazonian rainforests. BioScience 42: 599-607.

Boom, B. 1989 Use of plant resources by the Chácabo. Advances in Economic Botany 7: 1-32.

Brown, S. and A. E. Lugo (1990) Tropical secondary forests. Journal of Tropical Ecology 6: 1-32.

Chazdon, R. L. and F. G. Coe. Quantitative ethnobotany of woody species in second-growth, old-growth and selectively-logged forests of NE Costa Rica. Conservation Biology (in review).

Chazdon, R. L., R. K. Colwell, J. S. Denslow and M. R. Guariguata. 1998 Statistical methods for estimating species richness of woody regeneration in primary and secondary rain forests of NE Costa Rica. Pp 285-308 in F. Dallmeier and J. Comiskey, eds. Forest Biodiversity Research, Monitoring and Modeling: Conceptual Background and Old World Case Studies, Parthenon Publishing, Paris.

Coe, F. and G. J. Anderson 1996 Ethnobotany of the Garífua of Eastern Nicaragua. Economic Botany 50: 71-107.

Colwell, R. K. (1996) Biota: The Biodiversity Database Manager. Sunderland, MA, Sinauer Associates, Inc.

Coomes, O. T. 1995 A century of rain forest use in western Amazonia. Forest and Conservation History 39: 108-120.

Dubois, J. C. L. 1990. Secondary forests as a land-use resource in frontier zones of Amazonia. Pp 183-194 in A. B. Anderson, eds. Alternatives to Deforestation: Steps Toward Sustainable Use of the Amazon Rain Forest, Columbia University Press, New York.

Dupuy, J. M. and R. L. Chazdon 1998 Long-term effects of forest regrowth and selective logging on the seed bank of tropical forests in NE Costa Rica. Biotropica 30 (2) (in press)

Finegan, B. 1992The management potential of neotropical secondary lowland rain forest. Forest Ecology and Management 47: 295-321.

Gomez-Pompa, A., J. S. Flores and V. Sosa 1987 The "Pet Kot": a man-made tropical forest of the Maya. Interciencia 12: 10-15.

Guariguata, M. R., R. L. Chazdon, J. S. Denslow, J. M. Dupuy and L. Anderson 1997 Structure and floristics of secondary and old-growth forest stands in lowland Costa Rica. Plant Ecology 132: 107-120.

Hartshorn, G. S. and B. E. Hammel. 1994. Vegetation types and floristic patterns. Pp 73-89 in L. A. McDade, K. S. Bawa, H. A. Hespenheide and G. S. Hartshorn, eds. La Selva: Ecology and Natural History of a Neotropical Rain Forest, University of Chicago Press, Chicago.

Holdridge, L. R., W. G. Grenke, W. H. Haheway, T. Liang and J. Tosi, J. A. 1975. Forest Environments in Tropical Life Zones. New York, Pergamon Press.

Kohn, E. O. 1992 Some observations on the use of medicinal plants from primary and secondary growth by the Runa of eastern lowland Ecuador. Journal of Ethnobiology 12: 141-152.

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

McDade, L. A., K. S. Bawa, H. A. Hespenheide and G. S. Hartshorn, eds. 1994 La Selva: Ecology and Natural History of a Neotropical Rain Forest, University of Chicago Press, Chicago.

Nicotra, A. B., R. L. Chazdon and S. Iriarte 1998 Spatial heterogeneity of light and woody seedling regeneration in tropical wet forests. Ecological Monographs (submitted ms)

Panayotou, T. and P. S. Ashton. 1992. Not by Timber Alone. Washington, D. C., Island Press.

Peters, C. M., A. H. Gentry and R. O. Mendelsohn 1989 Valuation of an Amazonian rain forest. Nature 339: 655-656.

Prance, G. T., W. Balee, B. M. Boom and R. L. Carneiro 1987 Quantitative ethnobotany and the case for conservation in Amazonia. Conservation Biology 1: 296-310.

Salick, J. 1992. Amuesha forest use and management: an integration of indigenous use and natural forest management. Pp 305-332 in K. Redford and C. Padoch, eds. Conservation of Tropical Forests: Working from Traditional Resource Use, Columbia University Press, New York.

Salick, J., A. Mejia and T. Anderson 1995 Non-timber forest products integrated with natural forest management, Rio San Juan, Nicaragua. Ecological Applications 5: 878-895.

Toledo, V. M., A. I. Batis, R. Becerra, E. Martínez and C. H. Ramos 1995 La selva util: etnobotánica cuantitativa de los grupos indígenas del trópico húmedo de México. Interciencia 20: 177-187.

Toledo, V. M., A. I. Batis, R. Becerra and R. Martínez. 1992. Products from the tropical rain forests of Mexico: An ethnoecological approach. Pp 99-109 in M. Plotkin and L. Famolare, eds. Sustainable Harvest and Marketing of Rain Forest Products, Island Press, Covelo, CA.

Voeks, R. A. 1996 Tropical forest healers and habitat preference. Economic Botany 50: 381-400.

Wadsworth, F. H. 1987. A time for secondary forests in tropical America. Pp 189-197 in J. C. Giguera Colon, F. H. Wadsworth and S. Branham, eds. Management of the Forets of Tropical America: Prospects and Techniques, Institute of Tropical Forestry, USDA Forest Service.

Whitmore, T. C. 1997. Tropical forest disturbance, disappearance, and species loss. Pp 3-12 in W. F. Laurance and R. O. J. Bierregaard, eds. Tropical Forest Remnants, The University of Chicago Press, Chicago, IL.

Appendix 1. Medicinal species, sorted by value and alphabetically by genus. Species with commercial value are noted by an asterisk before the species name. The forest types where each species was sampled are indicated by S (second-growth), O (old-growth), or L (logged).

High	
**Bactris gasipaes* Kunth Arecaceae	S
Bauhinia guianensis Aubl. Fabaceae	SOL
Callichlamys latifolia (L. C. Rich.) K. Schum. Bignoniaceae	SOL
**Calophyllum brasiliense* Cambess. var rekoi (Standl.) Standl. Clusiaceae	SOL
Cyathula achyranthoides (Kunth) Moq. Amaranthaceae	SL
Hedyosmum scaberrimum Standl. Chloranthaceae	SOL
**Hyeronima alchorneoides* Allermao Euphorbiaceae	S
Machaerium floribundum Benth. Fabaceae	SO
Piper augustum Rudge Piperaceae	SOL
Pouteria campechiana (H.B.K.) Baehni Sapotaceae	SOL
Pouteria glomerata (Miq.) Radlk. ssp. *stylosa* (Pierre) T. D. Penn Sapotaceae	SOL
Psychotria elata (Sw.) Hammel Rubiaceae	SOL
Psychotria glomerulata (Donn. Sm.) Steyerm. Rubiaceae	SOL
Psychotria poeppigiana Müll. Arg. Rubiaceae	SOL
* *Quassia amara* L. Simaroubaceae	SOL
Smilax sp.1 Smilacaceae	SOL
Smilax sp2 Smilacaceae	S
Smilax sp3 Smilacaceae	SL
Moderate	
**Carpotroche platyptera* Pittier Flacourtiaceae	SOL
**Laetia procera* (Poepp.) Eichl. Flacourtiaceae	SOL
**Licania hypoleuca* Benth. Chrysobalanaceae	OL
Andira inermis (W. Wright) Kunth Fabaceae	SO
Byrsonima crispa Adr. Juss. Malphigiaceae	SOL
Carapa nicaraguensis C. DC. Meliaceae	SOL
Cestrum megalophyllum Dunal Solanaceae	SOL
Cestrum racemosum Ruiz & Pavon Solanaceae	S
Cordia alliodora (Ruiz & Pavon) Oken Boraginaceae	SL
Dipteryx panamensis (Pittier) Record & Mell Fabaceae	SO
Dussia cuscatlantica Fabaceae	SOL
Dussia macroprophyllata (Donn. Sm.) Harms Fabaceae	SOL
Hirtella lemsii L. 0. Wms. & Prance Chrysobalanaceae	OL
Jacaranda copaia (Aubl.) D. Don Bignoniaceae	S
Myrcia splendens (Sw.) DC. Myrtaceae	SOL

Pachira aquatica Aubl. Bombacaceae	SO
Pentaclethra macroloba (Willd.) 0. Ktze. Fabaceae	SOL
Psychotria marginata Sw. Rubiaceae	S
Psychotria racemosa (Aubl.) Raeuschel Rubiaceae	SOL
Rudgea cornifolia (Kunth) Standl. Rubiaceae	S
Siparuna guianensis Aubl. Monimiaceae	SOL
Siparuna macra Standley Monimiaceae	SO
Siparuna pauciflora (Beurl.) A. DC. Monimiaceae	SOL
Siparuna grandiflora (Kunthin Humb & Bonpl.) A. DC Monimiaceae	SOL
Solanum rugosum Dunal Solanaceae	SOL
Stryphnodendron microstachyum Poepp. & Endl. Fabaceae	SOL
Symphonia globulifera L.f. Clusiaceae	SOL
Trophis involucrata W. Burger Moraceae	SOL
Trophis racemosa (L.) Urb. Moraceae	SOL
Virola koschnyi Warb. Myristicaceae	SOL
Warszewiczia coccinea (Vahl) Klotzsch Rubiaceae	SOL
Xylosma chloranthum Donn. Sm. Flacourtiaceae	S
Zanthoxylum panamense P. Wils. Rutaceae	S
Guarea grandiflora DC. Meliaceae	SO
Piper sancti-felicis Trel. Piperaceae	S
Pterocarpus hayesii Hemsl. Fabaceae	SOL

Low

Abuta panamensis (Standl.) Krukoff & Barneby Menispermaceae	SOL
Acalypha diversifolia Jacq. Euphorbiaceae	SOL
Acacia watzonii Fabaceae	L
Aegiphila sp Verbenaceae	OL
Amphitecma kennedyae (A. Gentry) A. Gentry Bignoniaceae	L
Anaxagorea crassipetala Hemsl. Annonaceae	SOL
Anaxagorea phaeocarpa Mart. Annonaceae	S
Annona amazonica R. E. Fries vel aff. Annonaceae	OL
Annona montana Macfad. Annonaceae	SOL
Apeiba membranacea Spruce ex Benth. Tiliaceae	SOL
Ardisia auriculata Donn. Sm. Myrsinaceae	SOL
Ardisia granatensis Myrsinaceae	SOL
Ardisia nigropunctata Oerst. Myrsinaceae	SO
Astrocaryum confertum H. Wendl. ex Burret Arecaceae	SO
Bertiera guianensis Aubl. Rubiaceae	SOL
Borojoa panamensis Dwyer Rubiaceae	SOL
Brosimum lactescens (Moore) C.C. Berg Moraceae	SOL

Bunchosia macrophylla Rose ex Donn. Sm. Malphigiaceae	SO
Callicarpa acuminata Kunth Verbenaceae	S
Calatola costaricensis Standl. Icacinaceae	OL
Casearia arborea (L. C. Rich.) Urb. Flacourtiaceae	SOL
Casearia commersoniana Cambess. Flacourtiaceae	SO
Casearia coronata Standl. & L. O. Williams Flacourtiaceae	S
Casearia silvestris Sw. var *silvestris* Flacourtiaceae	SOL
Cecropia insignis Liebm. Cecropiaceae	SOL
Cecropia obtusifolia Bertol. Cecropiaceae	SO
Ceiba pentandra (L.) Gaertn. Bombacaceae	S
Chamaedorea pinnatifrons (Jacq.) Oerst. Arecaceae	SL
Clethra lanata Mart. & Gal. Clethraceae	SOL
Colubrina spinosa Donn. Sm. Rhamnaceae	SOL
Compsoneura sprucei (A. DC.) Warb. Myristicaceae	SOL
Conceveiba pleiostemona Donn. Sm. Euphorbiaceae	SL
Cordia bicolor A. DC. Boraginaceae	SOL
Cordia porcata Nowicke Boraginaceae	SOL
Coussarea hondensis (Standl.) C. M. Taylor & W. C. Burger Rubiaceae	SOL
Coussarea talamancana Standl. Rubiaceae	SOL
Doliocarpus sp1 Dilleniaceae	SOL
Erythrina poeppigiana (Walp.) 0. F. Cook Fabaceae	SO
Euterpe precatoria var. *longevaginata* (Mart.) Henderson Arecaceae	SOL
Ficus colubrinae Standl. Moraceae	S
Ficus glaucescens (Liebm.) Miq. Moraceae	SO
Garcinia intermedia (Pittier) Hammel Clusiaceae	SOL
Goethalsia meiantha (Donn. Sm.) Burret Tiliaceae	SOL
Gonzalagunia bracteosa (Donn. Sm.) B. L. Robinson Rubiaceae	S
Guatteria aeruginosa Standl. Annonaceae	SOL
Guatteria diospyriodes Baill. Annonaceae	SOL
Hamelia xerocarpa 0. Ktze. Rubiaceae	S
Heisteria concinna Standl. Olacaceae	OL
Heisteria macrophylla Oerst. Olacaceae	SO
Hernandia didymantha Donn. Sm. Hernandiaceae	SOL
Herrania purpurea (Pittier) R. E. Schultes Sterculiaceae	SOL
Hernandia stenura Standl. Hernandiaceae	SOL
Lacistema aggregatum (Berg.) Rusby Flacourtiaceae	SO
Lacmellea panamensis (Woodson) Markgraf Apocynaceae	OL
Licaria triandra (Sw.) Kosterm. Lauraceae	SOL
Luehea seemannii Tr. & Planch. Tiliaceae	S
Mabea occidentalis Benth. Euphorbiaceae	SOL

Macrolobium costaricense W. Burger Fabaceae	SO
Maquira costaricana (Standl.) C. C. Berg Moraceae	SOL
Miconia appendiculata Tr. Melastamataceae	S
Miconia gracilis Tr. Melastamataceae	SOL
Miconia lateriflora Cogn. Melastamataceae	SOL
Miconia ligulata Almeda Melastamataceae	SOL
Mollinedia costaricensis Donn. Sm. Monimiaceae	O
Naucleopsis naga Pittier Moraceae	SOL
Otoba novogranatensis Moldenke Myristicaceae	SO
Ouratea curvata (St. Hil.) Engler Ochnaceae	S
Paullinia baileyi Standley Sapindaceae	SOL
Paullinia grandifolia Benth. ex Radlik. Sapindaceae	SOL
Paullinia pinnata L. Sapindaceae	SOL
Paullinia pterocarpa Tr. & Planch. Sapindaceae	O
Paullinia rugosa Benth. ex Radlk. Sapindaceae	SOL
Paullinia serjaniaefolia Tr. & Planch. Sapindaceae	SOL
Pentagonia donnell-smithii (Standl.) Standl. Rubiaceae	SOL
Perebea angustifolia (Poepp. & Endl.) C. C. Berg Moraceae	SOL
Posoqueria latifolia (Rudge) Roem. & Schult. Rubiaceae	SOL
Pourouma aspera Trecul Cecropiaceae	SOL
Pourouma minor Benoist Cecropiaceae	SOL
Protium costaricense (Rose) Engler Burseraceae	SOL
Protium glabrum Burseraceae	SOL
Protium panamense (Rose) I. M. Johnston Burseraceae	SOL
Protium pittieri (Rose) Engler Burseraceae	SOL
Psychotria brachybotrya Muell.-Arg. Rubiaceae	SO
Psychotria capacifolia Dwyer Rubiaceae	S
Psychotria chagrensis Standl. Rubiaceae	OL
Psychotria eurycarpa Standl. Rubiaceae	SOL
Psychotria luxurians Rusby Rubiaceae	OL
Psychotria officinalis (Aubl.) Raeusch. ex Sandw. Rubiaceae	SOL
Psychotria panamensis Standl. var compressicaulis (K. Krause) C. W. Ham Rubiaceae	SOL
Psychotria pilosa Ruiz & Pavon Rubiaceae	S
Psychotria suerrensis Donn. Sm. Rubiaceae	SOL
Rinorea deflexiflora H. H. Bartl. Violaceae	SOL
Rourea glabra Kunth Connaraceae	SO
Salacia megistophylla Celastraceae	SOL
Solanum arboreum Humb. & Bonpl. ex Dunal Solanaceae	SOL
Solanum novoboragensis Solanaceae	SL

Spondias mombin L. Anacardiaceae	S
Stemmadenia donnell-smithii (Rose) Woodson Apocynaceae	SOL
Stemmadenia robinsonii Woodson Apocynaceae	SL
Symplocos sp1 Symplocaceae	O
Tabernaemontana amygdalifolia Jacq. Apocynaceae	SOL
Tabernaemontana arborea Rose Apocynaceae	S
Talauma gloriensis Pittier Magnoliaceae	OL
Terminalia amazonia (J. F. Gmel.) Exell Combretaceae	SOL
Tetracera portobellensis Buerl. Dilleniaceae	S
Theobroma mammosum Cuatr. & J. Leon Sterculiaceae	S
Theobroma simiarum Donn. Sm. Sterculiaceae	SOL
Tovomitopsis nicaraguensis Oerst. Planch. & Tr. Clusiaceae	SOL
Tovomitopsis silvicola Hammel Clusiaceae	SO
Vismia baccifera Clusiaceae	S
Vismia bilbergiana Beurl. Clusiaceae	S
Vismia macrophylla Kunth Clusiaceae	S
Vismia panamensis Duchass. & Walp. Clusiaceae	O

Appendix 2. Timber species, sorted by value and alphabetically by genus. Species with commercial value are noted by an asterisk before the species name. The forest types where each species was sampled are indicated by S (second-growth), O (old-growth), or L (logged).

High (all commercial)

Calophyllum brasiliense Cambess. var *rekoi* (Standl.) Standl. Clusiaceae	SOL
Carapa nicaraguensis C. DC. Meliaceae	SOL
Cordia alliodora (Ruiz & Pavon) Oken Boraginaceae	SL
Dipteryx panamensis (Pittier) Record & Mell Fabaceae	SO
Hyeronima alchorneoides Allermao Euphorbiaceae	S
Lecythis ampla Miers Lecythidaceae	SO
Minquartia guianensis Aubl. Olacaceae	SOL
Quassia amara L. Simaroubaceae	SOL
Symphonia globulifera L.f. Clusiaceae	SOL
Tetragastris panamensis (Engler) 0. Ktze. Burseraceae	SOL
Vochysia ferruginea Mart. Vochysiaceae	SOL

Moderate

Andira inermis (W. Wright) Kunth Fabaceae	SO
Dussia cuscatlantica Fabaceae	SOL
Dussia macroprophyllata (Donn. Sm.) Harms Fabaceae	SOL
**Laetia procera* (Poepp.) Eichl. Flacourtiaceae	SOL
Licania hypoleuca (C) Benth. Chrysobalanaceae	OL
Talisia nervosa Radlk. Sapindaceae	SOL
Trophis racemosa (L.) Urb. Moraceae	SOL
**Virola koschnyi* Warb. Myristicaceae	SOL
**Virola sebifera* Aubl. Myristicaceae	SOL

Low

Apeiba membranacea Spruce ex Benth. Tiliaceae	SOL
**Aspidosperma spruceanum* Benth. ex Müll. Arg. Apocynaceae	O
**Brosimum guianensis* (Aubl.) J.E. Huber Moraceae	SOL
Cassipourea elliptica Sw. Poir Rhizophoraceae	L
**Ceiba pentandra* (L.) Gaertn. Bombacaceae	S
Couepia polyandra (Kunth) Rose Chrysobalanaceae	O
Dendropanax arboreus (L.) Decne. & Planch. Araliaceae	SOL
**Goethalsia meiantha* (Donn. Sm.) Burret Tiliaceae	SOL
**Guarea rhopalocarpa* Radlk. Meliaceae	SOL
Hernandia didymantha Donn. Sm. Hernandiaceae	SOL
Hernandia stenura Standl. Hernandiaceae	SOL
Jacaranda copaia (Aubl.) D. Don Bignoniaceae	S
Maranthes panamensis (Standl.) Prance & White Chrysobalanaceae	O

Nectandra kunthiana (Nees) Kosterm. Lauraceae	SOL
Ocotea hartshorniana Hammel Lauraceae	SOL
Ocotea mollifolia Mez & Pittier ex Mez Lauraceae	SOL
Ocotea tenera Mez & Donn. Sm. ex Mez Lauraceae	SO
**Otoba novogranatensis* Moldenke Myristicaceae	SO
**Pentaclethra macroloba* (Willd.) 0. Ktze. Fabaceae	SOL
**Pterocarpus hayesii* Hemsl. Fabaceae	SOL
Rollinia pittieri Standl. Annonaceae	SL
**Sacoglottis trichogyna* Cuatr. Humiriaceae	SOL
Sterculia recordiana Standl. var *papyraceae* E. Taylor ined. Sterculiaceae	OL
**Stryphnodendron microstachyum* Poepp. & Endl. Fabaceae	SOL
**Tapirira myriantha* Triana & Planch. Anacardiaceae	SOL
Vismia macrophylla Kunth Clusiaceae	S
**Vitex cooperi* Standl. Verbenaceae	SOL

EFFECTS OF SILVICULTURAL TREATMENTS IN THE TROPICAL RAIN FOREST : A COMPARISON BETWEEN ZF-2 (MANAUS, BRAZIL) AND PARACOU (FRENCH GUIANA)

Favrichon V. & Maître H.F.
CIRAD-Forêt, BP 5035 - 34032 Montpellier Cedex FRANCE
Higuchi N.
INPA-CPST, CP 478 69011 - Manaus -AM BRAZIL

ABSTRACT

The dynamics of two Amazonian forest stands with and without silvicultural treatments are compared on a 10-year basis. The experimental sites at Paracou (French Guiana) and ZF2 (Manaus, Brazil) are located on different substrate but with similar floristic composition. The natural stand at ZF2 is more dynamic than at Paracou, this difference could be due to site conditions but also to a short-term non-equilibrium in the observed dynamics. The stand response during the first three years after logging is characterized by a decrease in stem density and basal area because of high mortality rates. The stand basal area recovered slowly at a comparable rate between sites of about 2%/year; this rate is linked to the intensity of canopy opening. The floristic composition is modified with an increase of light-demanding species. Although the residual stand does not resemble a secondary stand it represents an useful reference vis-à-vis dynamics of logged and secondary forests. This study leads to some proposals for defining silvicultural treatments adapted to this type of ecosystem.

INTRODUCTION

There are very few experiments dealing with tropical rain forest stand management techniques which take into account the spatial scale and the biodiversity of forestry ecosystems. In the Amazon region, the following experiments can be noted : the Tapajos Forest Project, or ZF2 Forest in Brazil, and the Paracou Station in French Guiana. These experiments have assessed the impact of logging and silvicultural treatments on stand dynamics, such as tree growth, mortality and ingrowth. To date, one of the main weaknessess of many management trials has often been the relatively small scale and short duration of the observations. In fact, considering the long-term nature of forest dynamics and the complexity of this ecosystem, studies have to be implemented over a long period and account for many different processes. Another difficulty is how to extrapolate the results to other forest stands. The comparison between different experiments could help to overcome this problem. The rationale lies in the fact that similar stand reactions due to the same causes (e.g., thinning and logging intensities), can be "de facto" taken into account to ensure relevant and worthwhile results. Therefore, the main purpose of this study is to compare the forest dynamics at two research sites in Brazil and French Guiana. The study concerns the regrowth after wood extraction (residual forest dynamics) and not after complete forest removal (secondary forest dynamics). However, the data we present on stand resilience and regeneration can serve as a reference point for other studies (see for example Chazdon and Coe, this volume) and to compare our results with woody regrowth during secondary forest succession.

Therefore, the aim of this paper is to evaluate the ability of stands to maintain (or not) the structure of dense forests in spite of more and more intensive treatments, and therefore, to present an useful reference for the other studies directly concerning secondary forests. Of course, in both sites, similar methodologies have been selected to be able to compare the impact of the silvicultural treatments.

METHODS

Description of the sites

Location

The "terra firme" forest, in Central Amazon, which represents more than 95% of the 250 million hectares forest land, is been increasingly logged. In 1980, the Department of Silviculture at INPA, Brazil, established a research station, called ZF2 for Zona Franca about 3 Km North of Manaus. French Guiana is also part of the Amazonian forest but it is located on the Plateau des Guyanes. The Office National des Forêts (ONF) control logging in the lowland rain forest in the North, near the coast and the main roads. The Paracou Station, located 50 Km West of Kourou, belongs to the French agency CIRAD-Forêt. Table 1 presents a geographical and ecological overview of both stations. There are no records indicating that the ZF2 forest has been harvested during this century and despite its location near the main coastal road, the Paracou forest has not been commercially exploited in the past. The climate is similar in each case, on the other hand the geomorphology is obviously different. ZF2 is located in the center of the Amazonian basin on the Alter do Chao formation, which is composed of red and unconsolidated tertiary sediments among the poorest and most acid soils in this region. On the border of the Plateau des Guyanes, Paracou is located on very old Precambrian geology (Bonidoro schists), with a morphology of small hills. The soils are also ferrallitic, but the main limiting factor is water drainage and the water supply may be scarce during dry season.

Table 1. Geographical and ecological conditions of ZF2 and Paracou experimental stations.

	Brazil - Amazonas	**French Guiana**
geographical coordinates	20 37' - 20 38' S. lat. 600 09' - 600 11' W. long.	50_15' N. lat. 520_55' W. long.
total size of experimental station	23 000 ha	3 000 ha
access	90 km North of Manaus, by road (Manaus - Boa Vista)	50 km West of Kourou, by road
climate	Am type (Köppen classification) (warm and moist all year long)	tropical wet
annual rainfall	2 478 mm	3 159 mm
mean annual temperature	27.6 0C (23.2 - 31.2)	26 0C (24 - 30)
humidity	66 to 94 %	60 to 90%
relief	plateau (500 to 1000 m width), smoothly undulated	small hills
geology	Alter do Chao formation (Cretaceous sup.)	Bonidoro schist (Precambrian)
soil	"yellow latosol" ferrallitic soil	ferrallitic soil
natural ecosystem	probably undisturbed	probably undisturbed

Initial stand structure

Table 2 presents characteristics of the initial stand structure on both sites. The densities are comparable : the mean density of trees more than 10 cm dbh is 613 trees/ha (min=567; max=692) in ZF2 and 626 (min=579; max=682) in Paracou. The dominant stratum is 30 to 40 meters high . The trees in Paracou appear slightly bigger than in ZF2 with a higher total basal area. The ZF2 stand presents more small trees (10 to 20 cm dbh) while the forest in Paracou is richer in medium and big trees (more than 50 cm dbh). Despite the importance of floristic composition, an exhaustive botanical description of the stands was not implemented so any comparison must be made with caution. The dominant families are respectively Lecythidaceae, Chrysobalanaceae and Caesalpinaceae in Paracou and Lecythidaceae, Sapotaceae and Burseraceae in ZF2. The amount of taxa (excluding palm trees) was: 324 species from 57 botanical families in ZF2 and 229 species from 45 families in Paracou. In both cases, the understorey is dominated by species of Burseraceae, Annonaceae, Rubiaceae and Violaceae. The commercial species are obviously not the same in both cases. There are a total of 47 species in ZF2 and 58 in Paracou.

Experimental design

The silvicultural treatments were based on the underlying assumption that natural regeneration

Table 2. Initial forest structure and composition at ZF2 and Paracou.

	ZF2	Paracou
dominant height	40 m	30-40 m
mean diameter (trees >10 cm)	23.9 cm	25 cm
density (N/ha)	613 (s.e. = 9.2)	626 (s.e. = 11.5)
Basal Area (m_/ha)	28.8 (s.e. = 0.5)	30.9 (s.e. = 0.6)
volume (m^3/ha)	302	366
dominant botanical families (% of trees)	Lecythidaceae (19.4) Sapotaceae (9.6) Burseraceae (8.0) Caesalpiniaceae (6.7) Chrysobalanaceae (4.3)	Lecythidaceae (18.4) Chrysobalanaceae (14.3) Caesalpiniaceae (13.2) Sapotaceae (6.9) Burseraceae (2.3)
species richness	324 (on 12 ha)	229 (on 18.75 ha)
N/ha commercial species	190	183
BA/ha commercial species	9.64	13.75

is maintained at a sufficient level (in quantity as well as in species composition) to allow the sustainability of management . Thus, in both cases, interventions are conducted only on the higher-stand and are based on forest logging of the commercial trees and/or thinning of non-commercial species to reduce competition.

Both experiments aimed to evaluate the different logging intensities and the development of the residual stands. The specific objective of the ZF2 station was to study stand dynamics, to evaluate logging impact on the ecosystem, and to identify felling cycles and silvicultural post-logging activities in order to build a sustainable forest management system. In Paracou, following the same approach, the CIRAD-Forêt established the experimental plots to deal whit two issues: What are the stand regeneration possibilities after logging and what are the cheapest and most efficient silvicultural techniques for sustainable timber production ?

The measurements were made on permanent sample plots and silvicultural treatments were applied according to a randomized block design. To ensure a reliable interpretation, the following techniques were used: specified shape and size of the plots (square of 1 ha each or more) and existence of a buffer zone around the measured plots. Collection, control and storage of data were conducted using the same rules and techniques. Table 3 presents the description of the layouts and treatments in both stations. In ZF2, only logging was applied as a real silvicultural treatment, because of two factors : the increased opposition of ecological groups against any kind of poison girdling and the assumption that a refining intervention after logging would not be possible due to Brazilian socio-economic conditions. The intensity of disturbance was calculated as a percentage of basal area removed: 0% (control, T0), 25% (low treatment T1), 50% (medium T2) and 67% (high T3).

Table 3. Description of the experimental stations at ZF2 and Paracou, and nature and date of interventions (c : commercial species; nc : non-commercial species)

	ZF2	Paracou
total size of study area	72 ha	108 ha
type of experimentation	randomised complete block	randomised complete block
number of plots	3 blocks, 6 treatments, 18 plots (4 ha each)	3 blocs, 4 treatments, 12 plots (9 ha each)
size and shape of one plot (+buffer zone)	square : 100 * 100 (+50 m)	square : 250 * 250 (+25 m)
first year of measurement	1980	1984
periodicity of measurement	1980, 1986, then each year or two years	yearly
minimum diameter for enumeration	25 cm (until 1985) then 10 cm dbh	10 cm dbh
position of trees	yes (since 1986)	yes
botanical identification	vernacular name (all species)	vernacular name (commercial species, other species since 1991)
assessment of regeneration	yes	yes

Nature of treatment	ZF2	Paracou
T0	no intervention	no intervention
T1	logging in 1987 / com. sp. / d ≥ 55	logging in 1987 / com. sp. / d ≥ 50*
T2	logging in 1987 / com. sp. / d ≥ 50	logging in 1987 / com. sp. / d ≥ 50* thinning in 1988 / non com. sp. / d ≥ 40
T3	logging in 1988 / com. sp. / d ≥ 40	logging in 1987 / com. sp. / d ≥ 50* logging in 1987 / non com. sp. / d ≥ 40 and ≤ 50 thinning in 1988 / non com. sp. / d ≥ 50

* depending on the species considered

In Paracou, logging of valuable tree species was based on a minimum cutting diameter limit system (50 or 60 cm dbh depending on the species considered). This logging was complemented by a further thinning of the largest non-commercial trees. Public opinion is not (yet) against poison-girdling in French Guiana. The thinning was based on a minimum diameter limit (40 cm dbh). The treatments were: control (T0), felling (T1), low-felling and thinning (T2), and intensive felling (T3). In both cases the felling was conducted with chainsaw and the transportation was done by skidder. Damages are proportionally higher in ZF2 because equipment was to small and not well used by field workers.

In terms of the total basal area removed (Table 4), the treatments T1 and T2 at ZF2, and T1 in Paracou are comparable (about 20% of the basal area), treatment T3 at ZF2 was more intensive (30%), and T2 and T3 in Paracou were very heavy (about 45% of the basal area removed). The changes in the stands were compared through the measurement of all trees more than 10 cm dbh. These trees were mapped and measured at the same reference height (on painted rings). The ingrowth or recruitment (new trees entering the stand each year), were carefully recorded, as well as the dead trees. More than 45 000 and 10 000 trees were measured respectively in Paracou and ZF2. The silvicultural experiments were conducted under the same type of experimental design to allow comparisons between the two sites in terms of growth, mortality and ingrowth

RESULTS

Dynamics of the unlogged stands

Short-term differences among sites can be seen in terms of annual rates of mortality, ingrowth and individual growth (Table 5). Paracou had a lower ingrowth rate and a higher mortality rate over the study period. Depending on the plot and the time period, the annual ingrowth and mortality fluctuated widely. In Paracou, annual ingrowth is more or less 15 trees/ha and annual natural mortality about 11 trees/ha. This variation is difficult to evaluate in ZF2 because of diverse time gaps between the two measurements. The difference between the two stands is quite significant, but it could be due either to the different species composition or to the natural environment. To compare this growth accurately, some common species have been selected in the two stations in order to compared their diameter increments (Table 5). Where a difference exists, growth is always equal or higher in ZF2.

The resulting stand dynamics is the change in density and basal area over time. The difference between the two forests is clear : the Paracou stand is in a phase of declining density with a stable basal area, whereas the stand at ZF2 increased in density (N), as well as in basal area(BA):

-Paracou (10 years): N = -1.8 tree/ha/year and BA= +0.00 m²/ha/year;
- ZF2 (9 years): N = +1.3 tree/ha/year and BA= + 0.13 m²/ha/year.

Table 4. Intensity of treatment (density /ha or basal area in m²/ha)

site	**ZF2**					**Paracou**			
treatment	T0	T1	T2	T3		T0	T1	T2	T3
N initial	623	621	607	602		625	603	622	627
N logged	-	6.3	8	18.6		-	10	11	29
N thinned	-	-	-	-		-	-	29	15
N dead = damaged	-	102	104	123		-	69	75	133
N dead / logged		16.1	13	6.6			6.9	6.8	4.6
BA initial	28	29.8	28.3	29.1		30.6	30.3	31.5	31.8
BA logged	-	3.5	2.5	5.2		-	3.2	3.8	6.3
total BA removed (log.+dam.)	-	6.4	5.9	8.8		-	5.2	13.4	14.9
% total BA removed min-MAX	-	21 18-24	20 19-21	30 26-35		-	17 12-22	42 27-45	47 43-57

The dynamics of logged stand

Natural mortality, ingrowth and growth

Mortality was high during the first year after treatment and the proportion of the types of mortality (Paracou, treatments T2+T3: 35% dead standing and 65% by treefall) was a strong indication of high stand perturbation (i.e., large gaps). Table 5 presents rates of mortality, ingrowth and growth, 3 to 6 years after treatment. This length of time after logging was chosen because it ws documented for both sites and all treatments. The ingrowth is similar for control plots, about 1%, in both sites. It increases to a value of 2.3% to 2.9% in ZF2, and 2.8% to 6% in Paracou, depending on the logging and thinning intensities. The mortality is still about 2% of the standing trees, about twice the rate observed in control plots.

Table 5. Natural mortality (number and percentage/ha/year), ingrowth (number and percentage/ha/year) and individual diameter growth (cm/year) for the whole period (T0) and between 3 and 6 years after treatment for treated plots, all species together.

	Treatments (plots)	monitored period to - tn (years)	**mortality**	**ingrowth**	**growth**
	T0 (control)	0 - 9th year	5.7 (0.9%)	7.0 (1.1%)	0.17 cm/y
ZF2	T1 (felling)	3th - 9th year	11.3 (2.1)	12.2 (2.3)	0.26
	T2 (felling)	3 - 9	9 (1.8)	12.5 (2.5)	0.27
	T3 (felling)	3 - 9	9.5 (2.0)	13.8 (2.9)	0.32
	T0 (control)	0 - 10	7.4 (1.1)	5.5 (0.9)	0.13
Paracou	T1 (felling)	4 - 10	6.6 (1.3)	14.8 (2.8)	0.22
	T2 (felling + thinning)	4 - 10	10 (2.0)	22.1 (4.3)	0.35
	T3 (felling)	4 - 10	8.7 (1.9)	27.5 (6.0)	0.33

Ti : plot and ti : year

Mean individual diameter growth in control plots on a 9-year (ZF2) or 10-year (Paracou) basis; all species together and for some species growing at both Paracou and ZF2 stations

	ZF2			**Paracou**		
individual growth (cm/year)	N	**mean**	conf.	N	**mean**	conf.
whole stand	1905	**0.17**	0.0001	9044	**0.13**	0.00003
Minquartia guianensis	16	**0.16**	0.02	7	**0.12**	0.03
Pouteria guianensis	18	**0.08**	0.008	169	**0.08**	0.0009
Hevea guianensis	20	**0.19**	0.02	47	**0.09**	0.004
Gustavia angusta	16	**0.09**	0.01	136	**0.05**	0.0007
Iryanthera spp.	9	**0.12**	0.02	112	**0.10**	0.001

conf. : 95% confidence interval for the mean

The mean individual diameter growth increased by 50 to 90% at ZF2 and 70 to 160% for the more intensive treatment in Paracou. It is difficult to find any difference between the three treatments at ZF2, but the response of treated stands compared to control plot is clear, especially for small trees (less than 30 cm dbh). In Paracou, the difference is significant between T0 and T1 and between T1 and [T2 + T3] grouped. For larger trees the differences in growth behavior are not significant. The growth rate of smaller trees seems to be a good indicator of the intensity of treatment in Paracou: 0.1cm /year (for T0), 0.25 cm (T1) and 0.35 cm (T3). In ZF2: 0.35 cm /year for T1, T2 and T3 (equal). Thus, at Paracou growth seems to be constant during the seven years after treatment. According to Silva *et al.*(1995), a similar conclusion can be made at the Tapajos forest: 8 to 13 years, the net diameter growth is reaching 0.4 cm/year, which is the rate in permanent plots in this region.

Stand density and basal area

A stagnation (or a small decline) in density is the response of the stands over the first three years after treatement. This low balance is due mainly to high mortality rates and the time lag before the response of existing small trees (for ingrowth). Density and basal area increase after this phase. In Paracou, one to six years after logging, the increasing rates of basal area are: 0.9% by year for T1, 1.3% for T2 and 2.0 % for T3. In ZF2, this rates are: 1.2% for T1 and 2.3% for T3 and lower after six years.

CONCLUSIONS

The initial conditions in Paracou and ZF2 are different mainly regarding the morpho-pedological aspect and the floristic composition. This difference is also clear for stand evolution in the permanent plots: the forest in ZF2 seems to be dynamic than in Paracou over the studied period of time. Considering these differences, it is possible to compare the global reaction of the stands after silvicultural treatments in both sites due to the common methodology. Standarized methodology is our main recommendation for further research programmes, as well as the use of large size experimental plots and good replication. Stand response (trends in density and basal area taking into account: growth, mortality and ingrowth) after treatment is quite concording in both sites with three phases. Phase one, one to three years after logging, corresponds to a higher level of distubance of the stand with a little ingrowth and a high mortality rate induced by harvesting operations. Furthermore, the high growth rates are unable to balance the mortality rates. Phase two, three to six years after logging, is characterized by a drop in tree mortality, high growth rates and ingrowth with a large proportion of light demanding tree species entering the stand. However after phase two, the results observed in Paracou and ZF2 seems to imply slow recovery of the total density and basal area. The rotation period required to recover the same density and basal area is at least 20 years. These rates constitute useful references for the compatibility with dynamics of secondary forests. The similarity of the results of these two stands helps to define the best silviculture which can be currently implemented. Finally, these results show that logging is a silvicultural treatment whose impact lasts about six to eight years. The Paracou experiment also indicates that thinning enhances stand growth, without dramatiaclly disturbing the site. Thus, silviculture should be based on a reduced impact logging scheme followed by a first thinning after six or eight years.

REFERENCES

Silva, J. N. M., Carvalho, J. O. P. de, Lopes, J. do C. A., Almeida, B. F. de, Costa, D. H. M., Oliveira, L. C. de, Vanclay, J. K. and Skovsgaard, J. P. 1995. Growth and yield of a tropical rain forest in the Brazilian Amazon 13 years after logging. Forest Ecology and Management 71: 267-274.

BIBLIOTECA
Centro Interamericano de Documentación
e Información Agrícola
IICA - CIDIA

THE ROLE OF SUCCESSIONAL VEGETATION AS FOREST FALLOW: A CASE STUDY IN THE ATLANTIC LOWLANDS OF COSTA RICA

Florencia Montagnini
Management and Conservation of Forests and Biodiversity Area
Tropical Agricultural Research and Higher Education Center (CATIE)
7170 Turrialba, Costa Rica

Eugenio González
Organización para Estudios Tropicales 2050 San Pedro, San José, Costa Rica

Freddy Sancho
Centro de Investigaciones Agronómicas Universidad de Costa Rica
Ciudad Universitaria, San José, Costa Rica

ABSTRACT

In sites abandoned from agriculture or cattle, secondary vegetation can serve as "fallow" as it may contribute to restore organic matter and nutrients to the impoverished soils. The type of secondary vegetation has a strong influence on the rate of recovery of soil fertility and on the specific nutrients that can be incorporated to the soil. The vegetation was inventoried 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 m^2*/ha in a site with extensive grass cover and with* Alchornea costaricensis *as the most abundant tree, to 24.7* m^2*/ha in more dense areas dominated by* Pentaclethra macroloba. *Other species that 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, and extractable P 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 sub-samples 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. These findings are useful for designing strategies for the management of abandoned sites, depending on their future use.*

INTRODUCTION

Following the clearing and conversion of tropical forests prevalent today, about nine million hectares of secondary forests are generated every year (Brown and Lugo 1990, Weaver 1993). The structure and composition of these secondary forests vary according to site fertility, previous land use and distance from seed sources (Finegan 1992, Nepstad *et al.* 1991). When a secondary forest replaces a crop or pasture, the production of biomass by the vegetation and the cooler soil temperatures under the forest canopy contribute to the addition of organic matter to the soil and its decomposition. Typically, fallow periods of 5 to 15 years are required for soils to recover organic matter levels similar to those of the original forests in most tropical humid areas (Van Wambeke 1992).

The type of secondary vegetation and the predominant species present influence the rate of recovery of soil fertility and the specific nutrient inputs to the soil. The influence of trees on soil fertility in bush fallows has been documented in a number of tropical environments (Grubb 1989). The positive effects of plantation trees on soil fertility, in comparison with nearby forest and grass areas, have been reported by several authors (e.g., Lugo 1988, Montagnini and Sancho 1990 a, b, Montagnini *et al.* 1994, Sánchez *et al.* 1985, Young 1989). Better understanding of the role different vegetation types have on soil chemistry can be a useful tool for soil rehabilitation and forest management projects.

Since 1990 we have been investigating alternatives for forest and soil rehabilitation at La Selva Biological Station of the Organization for Tropical Studies (OTS) in the Atlantic humid lowlands of Costa Rica. As part of this project a 10 ha secondary forest which had developed on abandoned pastures was chosen for a study of the relationships between vegetation cover and soil chemistry. Three sites were chosen: one site with fewer trees and extensive herbaceous cover and two sites with a more developed forest structure and relatively less grass. The existing secondary forest was described, and soils under forest and herbaceous vegetation were sampled and analyzed for pH, organic matter, total N, cations and extractable P. The hypothesis was that due to increased nutrient cycling and improved microenvironmental conditions, soils under patches of trees would have higher nutrient concentrations than those under grass or other herbaceous vegetation. Although cause and effect relationships between vegetation cover and soil chemistry cannot be conclusively established under the experimental conditions of this study, the findings can contribute to the understanding of the present status and future development of soils and forests in the area.

STUDY SITE

The experimental area was located in the northern portion of the La Guaria Annex at OTS La Selva Biological Station (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). The studied area had been logged in the early 1950s for its valuable hardwoods. The area was then cleared and rice was grown for two or three years before it was lightly burned and seeded to pastures with the native *Cynodom nlenfuensis* (Pasto estrella), and the exotic *Pennisetum maximum* (Guinea grass), *Pennisetum purpureum, Brachiaria* spp. and *Melinis minutiflora* (calinguero or San Juan). The land was used for raising cattle for about 20 years until the farm was sold to OTS (Pierce 1992). This pattern of land use was typical for the region at the time (Montagnini 1994).

No management or other interventions occurred at the study area after abandonment from pasture use. At the time this research took place, the study site had areas of grass interspersed with ferns and patches of secondary forest. Three sites were studied, according to vegetation cover. Site 1 had a large proportion of land covered with a variety of grass and fern species as well as patches of secondary forest. Site 3 had the most dense forest cover, and it was the closest to old housing. Site 2 was located between Site 1 and Site 3, and it was expected that its vegetation composition was intermediate between Sites 1 and 3.

The experimental area was on flat, uniform terrain. Soils were Fluventic Dystropepts derived from volcanic alluvium; they were deep, well drained, stone-free, with low or medium organic matter content (2.5-4.5%), moderately heavy texture, and generally acid (pH in H_2O <5.0) with low concentrations of basic cations and extractable P (Sancho and Mata 1987).

METHODS

Vegetation survey

The size of each site was determined by the area available for sampling, with limits demarcated by streams, a road or old housing, as mentioned before. Additionally, the size and placement of the study sites was influenced by the needs of subsequent research: following vegetation and soil surveys, the sites would be cleared for the establishment of experimental plantations with indigenous trees. After a first site was chosen with a size of 96 m x 256 m, the other two were delineated with the same size for consistency in sampling. Each site was subdivided in four blocks with six plots 32 m x 32 m each (same plots where the future native trees plots would be established). All trees and shrubs in each plot were identified and counted, and the diameter at breast height (dbh) was measured for all stems greater than 2 cm dbh. The sites were characterized according to tree diameter distribution, basal area and abundance of trees and shrubs.

Soil chemistry

Composite soil samples were taken during the rainy season of 1991 in the six plots of each block and site. Soil samples were taken with an Edelman auger at 0-15, 15-30 and 30-60 cm depth. The pH was measured in a 1:2.5 mixture of soil:deionized water. Exchangeable acidity was measured by titration of *1 N* KCl soil extracts with *0.01 N* NaOH. Exchangeable Ca and Mg were extracted with a *1N* KCl solution using a 1:10 proportion of soil:extracting solution. The 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), using a 1:20 proportion of soil:extracting solution (Diaz-Romeu and Hunter 1978). The Ca, Mg and K 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). The means for each variable and soil depth ($n=4$) were compared among sites in an analysis of variance (Confidence Limits, $P<0.05$).

RESULTS

Original vegetation cover

Site 1 had fewer trees than either Site 2 or 3 for any diameter class considered; overall, Site 3 had the highest numbers of trees (Table 1). In Sites 2 and 3, the highest numbers of trees were in the smaller size classes (< 15 cm and 15.1-20 cm dbh) (Fig. 1). Total basal area for trees > 15 cm dbh was 4.34, 16.4 and 24.7 m^2/ha, and number of individuals > 15 cm dbh totaled 22, 149 and 139 per ha in Sites 1, 2 and 3, respectively (Table 1).

Table 1.
Arboreal vegetation in three 10 year old secondary forest sites at La Selva, Costa Rica

Site	No. Individuals/ha	Basal area m^2/ha
1	22	4.3
2	149	16.3
3	139	24.7

In Site 1, *Alchornea costaricensis* (fosforillo) was the most abundant tree, comprising 52.8% of total basal area and 37.0% of individuals. The majority of individuals were less than 15 m high. *Pentaclethra macroloba* followed with 32.9% of basal area and 31.7% of individuals. Only four trees of commercial size were identified: *Cordia alliodora* (Site 1), *Cedrela odorata* (Site 2), and

Cedrela odorata and *Carapa guianensis* (Site 3). The grasses were a mixture of native species which typically grow in cleared forest, as well as the introduced species which had been seeded to improve the quality of the native pasture (Pierce 1992). Among the native species were *Cynodon* spp. and *Paspalum fasciculatum* (gamalote). Also in patches and mixed with the grass were two species of fern: *Nephrolepis viscerata* (Polypodiaceae) (helecho serrucho or Boston) and *Hylepis repens*. In Sites 2 and 3, *P. macroloba* ranked first, with the greatest proportion of basal area and number of individuals. However other species considered emergent or canopy trees of the natural forest (e.g., *Dipteryx panamensis* and *Hyeronima alchorneoides*) were also present. Other timber species were less abundant, such as *Cedrela odorata, Dipteryx panamensis* and *Zanthoxyllum panamensis*.

Site 3 had the greatest basal area, but it had fewer individuals > 15 cm dbh than Site 2 (Table 1, Fig. 1). The species composition was similar to that of Site 2 with the addition of other, emergent species, such as *Stryphnodendron microstachyum* and *Carapa guianensis*. A full list of tree species found in the three sites of this study is reported in Montagnini *et al.* (1996).

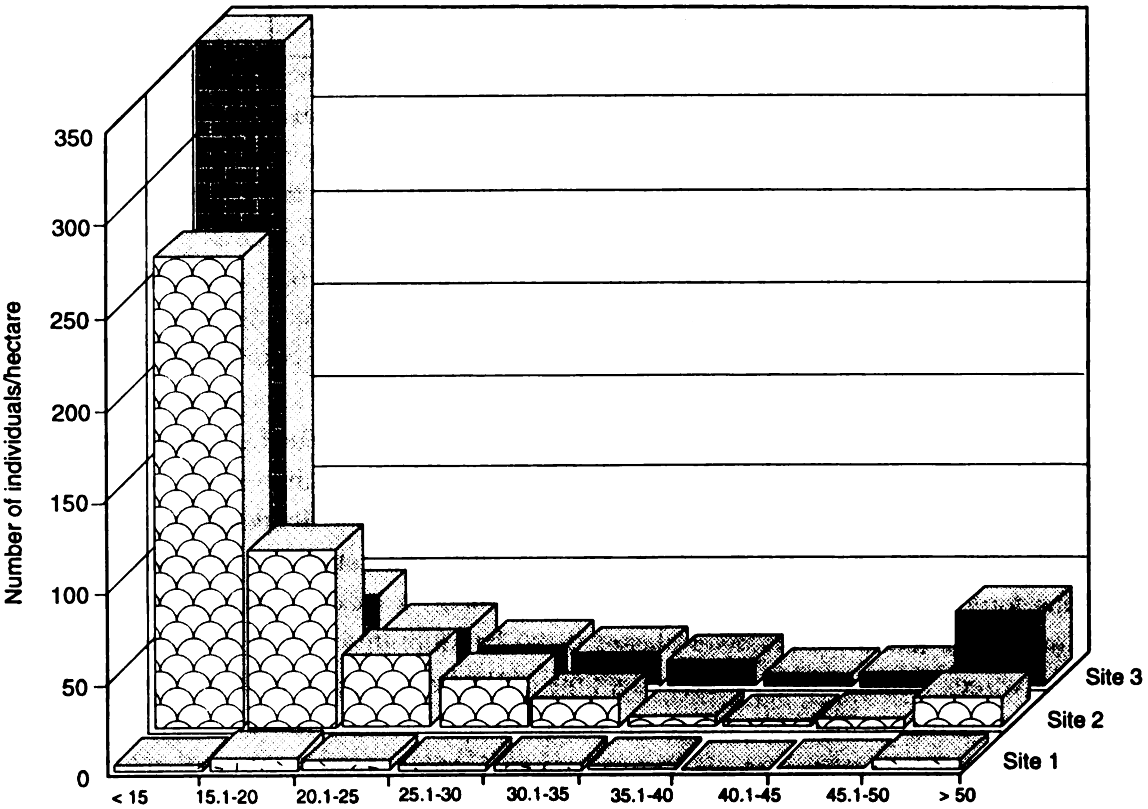


Figure 1. Number of trees per hectare in each diameter size class for the three sites of this study.

Soil chemistry

Only results for the top soil (0-15 cm) are presented here; a complete soils description can be found in Montagnini *et al* (1996). Soil exchangeable Ca, soil extractable P (Table 2) and pH were higher in Site 1 than in Sites 2 and 3, while soil organic matter was higher in Sites 2 and 3 ($P<0.05\%$). There were no statistically significant differences in soil exchangeable Mg, K and acidity among sites. Although differences were not statisticaly significant, total N tended to be higher in Sites 2 and 3 than in Site 1.

Table 2.
Chemical characteristics of soils in Sites 1, 2 and 3: Ca, Mg, K, pH, organic matter (OM), total N and extractable P.

Site	Depth (cm)	Ca	Mg	K	pH	OM (%)	N (%)	P (mg/kg)
		(cmol/L)						
1	0-15	1.29a	0.36a	0.16a	4.9a	5.21b	0.23b	8.9a
2	0-15	0.81b	0.47a	0.18a	4.5b	5.66ab	0.26ab	5.9b
3	0-15	1.03ab	0.47a	0.15a	4.4b	6.30a	0.28a	3.3c

DISCUSSION

Forest development in the secondary growth sites

This discussion is based on the survey results for adult trees, since no information was available on the smaller size classes (seedlings and saplings) which determine the future regeneration potential of a site. Sites 2 and 3 apparently offered more alternatives than Site 1 with respect to their future development into forest. In Sites 2 and 3, the shape of the diameter distribution figure (Fig. 1) with higher number of individuals in the smaller size categories, is typical of young regenerating forests, while the flatter shape in Site 1 reflects a lack of vigorous regrowth. The presence of trees of the larger diameter classes (> 30 cm dbh) in the three sites was due to the fact that many trees were left untouched at the time of land clearing, since these diameters could not be attained by regrowing trees in just ten years.

The most abundant species, *Pentaclethra macroloba*, is common in the natural forest at La Selva, and it is found in primary and secondary forests throughout the Atlantic region of Costa Rica (Finegan and Sabogal 1988, González and Chaves 1994, Hartshorn 1983, Peralta et al. 1987). The majority of *P. macroloba* stems were less than 15 cm in diameter and were found in dense patches around an older parent tree that had not been cut at the time of original selective cutting or clearing.

The higher number of trees found in Sites 2 and 3 in comparison with Site 1 is probably the result of their proximity to a nearby stream. According to aerial maps of 1981 (La Selva files) Site 1 was covered with grass and sparse trees, while Site 2 had a fence sided with trees, many of which could have survived and served as sources of propagules after pasture abandonment. In general, Sites 2 and 3 had a high abundance of shrubs and short-lived, shade-intolerant (pioneer) trees (e.g., *Apeiba* spp., *Cecropia* spp., *Hampea* spp., *Miconia* spp.), which are characteristic of the early phases of forest succession in the neotropics (Budowski 1965, Denslow 1980, Swaine and Whitmore 1988). At this early stage, alternatives to aid the regeneration process could include artificial regeneration techniques, e.g., enrichment with tree seedlings of native species, either in lines or in natural openings of the secondary forest canopy (Ramos and del Amo 1992, Weaver 1987, Montagnini *et al* 1997).

Site 1 apparently showed less potential for rapid forest development as a result of longer distance to sources of seeds, its extensive cover with grass and ferns and a lower number of tree species of all size categories. The most abundant tree in Site 1, *Alchornea costaricensis*, is a pioneer species which invades open fields, has low stature and open branches, and is not considered a commercial timber species (Hartshorn 1983). To aid in forest and soil rehabilitation processes, a potential alternative involves planting fast-growing tree species adapted to full sunlight and relatively infertile soils, which may accelerate site recovery by hastening the natural regeneration of local species (Nepstad *et al.* 1991, Parrotta 1992). Other research at La Selva has shown that regeneration of native tree species was more abundant below the canopy of the trees of a young experimental plantation than in areas left unplanted as a control: woody regeneration was hampered by competition with aggressive grasses (Guariguata *et al.* 1995).

Vegetation cover and soil chemical properties

The range of values of soil variables found for the three sites of this study were comparable to those found in another site with similar land use history at the La Guaria Annex of La Selva (Montagnini and Sancho 1990a, b). According to standards set by the Costa Rican Ministry of Agriculture (Bertsch 1986), fertility levels in these sites were not adequate for conventional agriculture even after 10 years of secondary succession.

Site 1, with the lowest tree basal area (Table 1), also had less soil organic matter than Sites 2 and 3. In Sites 2 and 3, dominance by *Pentaclethra macroloba,* a leguminous nitrogen-fixing tree (Nichols and Rodríguez 1990), could contribute to higher soil organic matter and higher N found in these sites. However, the anticipated relationship between tree cover and improved soil conditions did not hold for all nutrients: Site 1 had higher P than Sites 2 and 3. This trend is similar to that found by Montagnini and Sancho (1990a,b): in another young secondary forest at La Selva, lower P was found under trees than under grass. To help clarify these trends, subset samples corresponding to grass and forest areas from Site 1 were treated independently in an analysis of variance. In Site 1, soil total N was higher under patches of trees, soil extractable P was higher in areas covered with grass and fern, and there were no statistically significant differences in cations, pH or organic matter (Table 3). High demand for P for N-fixation by the trees, coupled with P accumulation in tree biomass, could account for lower extractable P in soil found under patches of trees.

Table 3.
Chemical characteristics of soils in areas with trees or grasses in Site 1: Ca, Mg, K, pH, organic matter (OM), total N and extractable P.

Vegetation	Depth	Ca	Mg	K	PH	OM	N	P
Type	(cm)		(cmol/L)			(%)	(%)	(mg/kg)
Trees	0-15	1.35a	0.35a	0.14a	4.8a	5.58a	0.278a	5.87b
Grass	0-15	1.20a	0.35a	0.16a	4.9a	4.50a	0.218b	10.27^{a}

The influence of secondary forest trees on soil properties varies according to the nutrient demands of tree species on soils and their nutrient cycling characteristics. In situations such as that of Site 1 of this study, an area with poor regeneration and covered with grasses and ferns, tree plantations can accelerate forest rehabilitation by shading off herbaceous vegetation and by increasing organic matter and nutrient imputs to the soil. The choice of adequate tree species is a key aspect influencing the speed of recovery and the specific nutrients that are recycled. Mixtures of tree species, if chosen with consideration of their influence on soils, can be more appropriate than monospecific systems, because the demands and inputs of nutrients to the soil of the different component species can be more balanced. In our research at La Selva, soils under tree species mixtures had intermediate levels of nutrients in comparison with monospecific plots of the same species (Montagnini and Porras 1997). Tree plantations can be used for soil rehabilitation purposes, if species choices and designs are such that they can function as fallows or analogs of secondary forests.

Recommendations and future lines of research

In projects that aim at secondary forest management for production, it is important to evaluate the status of vegetation cover and its associated soil characteristics. This information can help in assessing the potential of the site for forest management. In sites with poor forest development it may be necessary to aid the regeneration process, planting tree species that can help restore soil organic matter and nutrients (Montagnini *et al.* 1995). Tree plantations can also help accelerating forest regeneration (Guariguata *et al.* 1995). In sites with intermediate forest development, enrichment with native species can be a good alternative to increase the biologic and economic value of the forest, and thus avoid its clearing and replacement by other land uses (Montagnini *et al.* 1997).

Future lines of research should use an ecosystem approach to the study of secondary forest development, including soil and vegetation characterization. Research on alternatives for management of secondary forests should aim at designing a specific system for each situation, based on both the degree of forest development and the associated soil characteristics. Research should focus on systems that mimic secondary forests while yielding attractive products, so as to avoid forest replacement with other land uses. Therefore, the ecological and economic aspects of management alternatives should be taken into account.

In designing forest enrichment or tree plantation systems, research should focus on the choice of indigenous species of economic value and positive effects on soil properties. Mixed species designs can function as better analogs to the forest than monospecific plantations. For mixed-plantation systems, species should be chosen so as to complement nutrient cycling and growth characteristics.

Acknowledgements

This study was performed under a grant for Ecological Research from the A. W. Mellon Foundation (USA).

REFERENCES

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, 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 p.

Bremner J M and Mulvaney C 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. Amer. Soc. Agron., Inc., Madison, Wisconsin.

Brown, S. And 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.

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. pp 9-11 and 15-27.

Finegan B 1992. The management potential of neotropical secondary lowland rain forest. For. Ecol. Manage. 47, 295-321.

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.

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

Grubb P J 1989. The role of mineral nutrients in the tropics: a plant ecologist view. In Mineral Nutrients in Tropical Forest and Savanna Ecosystems. Ed. J Proctor. pp 417-440. Blackwell Scientific Publications. Boston.

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

Hartshorn G S 1983. Plants. *In* Costa Rican Natural History. Ed. D. Janzen. pp. 158-183. Univ. of Chicago Press. Chicago.

Lugo, A.E. 1992. Comparison of tropical tree plantation with secundary forests of similar age. Ecological Monographs 62:1-41.

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, 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, 386-390.

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, Chicago.

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., 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., González, E. y 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) 7:47-56.

Montagnini, F., Eibl, B., Grance, L., Maiocco, D. and Nozzi, D. 1997. Enrichment planting in overexploited forests of the Paranaense region of Misiones, Argentina. Forest Ecology and Management 99: 237-246.

Montagnini, F. and Porras, C. 1997. Evaluating the role of plantations as Carbon sinks: an example of an integrative approach fron the humid tropics. Environmental Management 00: 1-13

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

Nichols D and 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 and Lieberman M 1987. Reseña de estudios a largo plazo sobre composición florística y dinámica del bosque tropical en La Selva, Costa Rica. *In* Ecología y Ecofisiología de Plantas en los Bosques Mesoamericanos. Eds. D A Clark, R Dirzo and N Fetcher. 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.

Ramos J M and 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 and Russell E C 1985. Tree crops as soil improvers in the humid tropics? In Attributes of Trees as Crop Plants. Eds. M G R Cannell and J E Jackson. pp. 327-350. Inst. of Terr. Ecol., Nat. Environ. Res. Council, Abbots Ripton, Huntingdon, England.

Sancho F and Mata R 1987. Estudio Detallado de Suelos. Estación Biológica La Selva. Organización para Estudios Tropicales, San José, Costa Rica. 162 p.

Swaine M D and Whitmore T C 1988. On the definition of ecological species groups in tropical rain forests. Vegetatio 75, 81-86.

Van Wambeke A 1992. Vegetation, soil organic matter, and crops. In Soils of the Tropics. Properties and Appraisal. Ed. A Van Wambeke. pp. 69-95. McGraw-Hill. New York.

Weaver P L 1987. Enrichment planting in tropical America. In Management of the Forests of Tropical America: Prospects and Technologies. Eds. J C Figueroa, F Wadsworth and S Branham. pp. 259-278. Inst. of Trop. For., USDA Forest Service, San Juan, Puerto Rico.

Weaver, P.L. 1993. Secundary forest management. In: J.A. Parrota and M. Kanashiro (editors). Management and rehabilitation of degraded lands and Secundary Forests in amazona. IITF, USDA Forest Service and UNESCO Man and the Biosphen Program. Rio Piedras, Puerto Rico. Pp 117-128.

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.

Co$_2$ MITIGATION SERVICE OF COSTA RICAN SECONDARY FORESTS AS ECONOMIC ALTERNATIVE FOR JOINT IMPLEMENTATION INITIATIVES

Rosalba Ortiz, Octavio Ramírez, Bryan Finegan
CATIE 7170, Turrialba,
Costa Rica

SUMMARY

This paper summarizes work in progress by the Silviculture and Natural Forests Management Project (PROSIBONA) CATIE-COSUDE[1] on quantification and valuation of carbon sink service in humid tropical forests. The study deals specifically with secondary forests and the possibility for this ecosystem to be an option for Costa Rican joint implementation initiatives.

The results demonstrated the economic potential of secondary forests for its carbon sink service, basically for carbon storage. According to our calculations, if all of Costa Rican secondary forests were included in joint implementation accounting at the current negotiated price of US$10 tC stored, they could generate an estimated US$77.3 million during a period of 20 years that the current "carbon parking" schemes are promoted.

If international negotiations determines that Joint Implementation Initiatives should use current best knowledge on marginal costs of global warming, preliminary valuation results suggest, that carbon storage by Costa Rican secondary forests could generate US$127.4 millions product of one time discounted economic benefits and carbon sequestration reach a value of US$308 per hectare per year. According with this study, promoting the preservation of secondary forest ecosystem Costa Rica could mitigate current and avoid future CO$_2$ emissions.

---

[1] Swiss Cooperation for Development.

[2] One of the ecological functions or services that has been recognized at the international level is carbon sequestration capacity, for both natural forests and plantations. Through photosynthesis, plants capture CO$_2$ from the atmosphere, fixing carbon (C) in their biomass and releasing oxygen (O$_2$) back into the atmosphere. It is estimated that forest ecosystems contain 20 to 100 times more carbon per unit area than agricultural ecosystems (Andrasko 1990; Schoeder et al. 1993).

INTRODUCTION

Traditionally, forests have been perceived as a source of timber, wood and other extractive products such as medicinal and ornamental plants. The importance of the ecological services provided by the forests had been neglected. However, this perspective has recently undergone a considerable change, due to international as well as local initiatives to visualize them as ecosystems rendering a multitude of productive and service functions[2].

The use of forests to mitigate the atmospheric concentration of toxic gases was introduced on the political agenda by the Intergovernmental Panel on Climate Change (IPCC). The United Nations Convention on Climate Change was a result of the Río Conference process, and was signed by 162 countries and ratified by more than 20 already. Nearly all these countries have agreed to reduce their carbon dioxide (CO_2) emissions to 1990 levels by the year 2000 (Andersen 1996).

In order to comply with their commitments in the Convention, a meeting of the parties in Berlin in 1995 agreed to establish a pilot phase program of "joint implementation". Joint implementation refers to cooperative initiatives between two or more governments with the aim of reducing future CO_2 emissions or sequestering CO_2 currently in the atmosphere.

Parties to the convention have the option to achieve mitigation credits via joint action along two routes; by reducing their domestic emissions through the introduction of improved technologies or by financing forest regeneration and preventing future land use changes through conservation measures[3]. Therefore, joint implementation might be an important instrument for increasing forest area and sequestering the CO_2 currently in the atmosphere, or for slowing the process of deforestation and land use change thus avoiding future emissions.

This study aims to determine the magnitude of the global service of carbon dioxide sequestration and storage that is being rendered by Costa Rica's humid tropical secondary forests. It explores how the rapid increase in secondary forest areas of recent years could be considered in the international joint implementation negotiations between the Costa Rican Government and foreign countries wanting to reduce overall CO_2 emissions outside their own borders. A specific objective is to determine the potential economic value of these forests' carbon sink service within the context of Costa Rica's Joint Implementation agreements.

---

[3] According to the IPCC (1990) deforestation has been the cause of releasing up to 1.6 billion tons of carbon (1 tC = 3.67 tCO_2) into the atmosphere. The Panel estimates that one would need to plant 450 million hectares of forest (i.e., an area about the size of Australia) in order to sequester the estimated 2.9 billion tons of carbon accumulated in the atmosphere as a result of all past emissions.

BENEFITS FROM JOINT IMPLEMENTATION INITIATIVES

Joint implementation (JI) efforts render different benefits at the national and global levels (OCIC, 1995). At the global level these include:

- Mitigation of global warming through sequestration of atmospheric CO_2 and the reduction of potential future CO_2 emissions.
- Support environmentally sound, sustainable development initiatives in developing countries through the transfer of funds from industrialized countries.

For the country investing in carbon certificates:[4]

- Cost-effectiveness through access to cheaper mitigation alternatives per ton of carbon sequestered/not emitted.
- Compliance with commitments to greenhouse gas emissions reduction when available domestic mitigation measures are not sufficient.

For the host country:

- A source of funds for investment in productive activities that prevent undesirable land-use changes and biodiversity conservation, fundamental pillars of local sustainable development policies.
- The transfer of cleaner technologies for reducing national CO_2 emissions at a lower cost.
- Employment generation in urban areas and for forest owners in rural areas.

The Costa Rican Office for Joint Implementation (OCIC) was created in 1995 in order to direct and facilitate the international negotiations on JI initiatives. At the local level, Costa Rica established the National Investment Found for Forest Financing (FONAFIFO) to handle the payment for environmental services to farmers and forest owners (PSA)[5]. (Figure 1).

---

[4] Carbon certificates vouch the contribution of polluting countries to solve the global warming problem through international initiatives that reduce CO_2 emissions at a specified amount.

[5] Environmental Services Payment

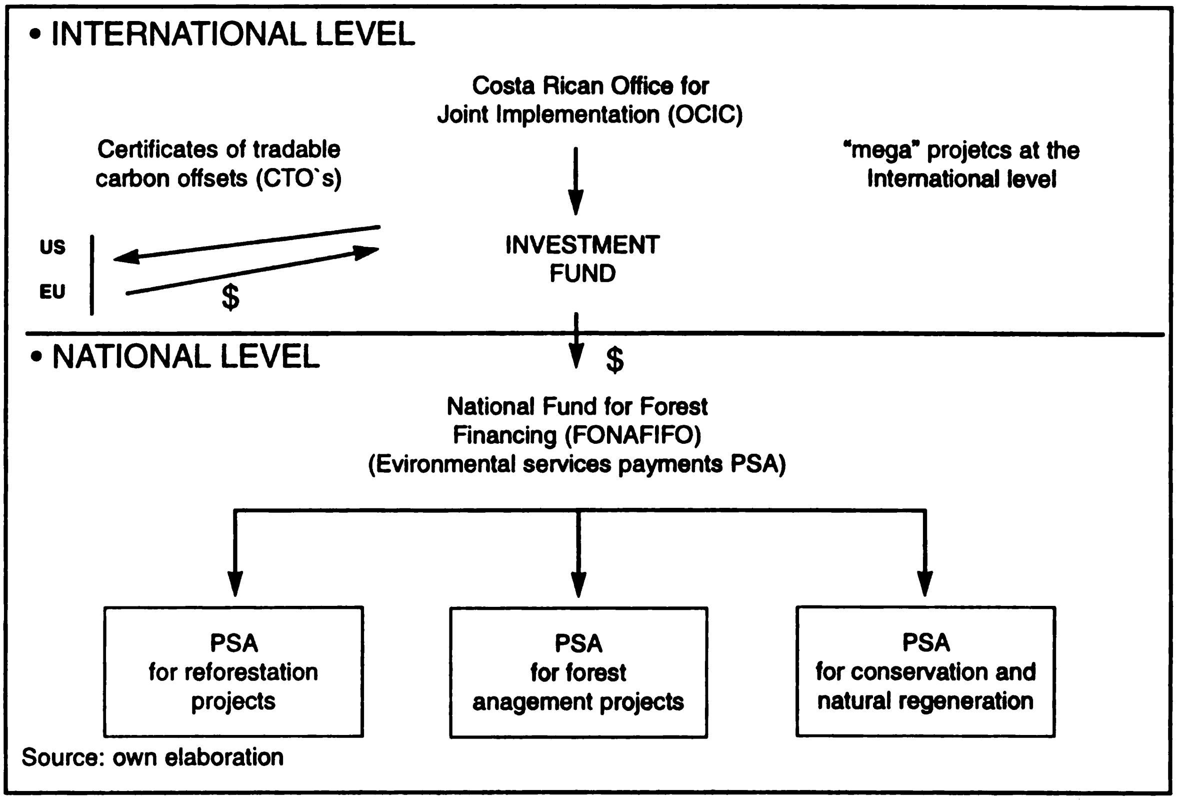


Figure 1. Costa Rican structure for Joint Implementation initiatives

The OCIC is promoting Costa Rican projects that undertake a commitment to preserve natural forests, to promote/aid their regeneration, or to plant artificial forests (plantations) in return for a per hectare compensation by industrialized countries who receive equivalent carbon credits. For example, an agreement with Norway worth U.S.$2 million was signed for the parking[6] of 200 thousand tons of carbon through watershed conservation and hydropower development in the Virilla basin in the Central Valley. Joint implementation projects promoted by the OCIC also include alternative energy generation and transportation solutions.

The Costa Rican government is currently promoting various other initiatives to the international community, that involve monetary compensation for the global carbon sink services provided by its forests. In this regard, there is considerable interest in a more accurate estimation of the magnitude of the services being provided through plantation forestry and natural forest regeneration/conservation. As well, it is necessary to determine the level of compensation that should be transferred to forest growers/owners, since the value of the current "forest conservation certificates" (U.S.$200 per hectare of primary or secondary forest, regardless of its initial stage) was established on an ad-hoc basis.

---

[6] The price of U.S.$10 per ton of carbon, lower that the average marginal damage costs figures mentioned above could be attributed to the fact that this specific agreement was for carbon parking. Net sequestration was not required.

Costa Rican secondary forests as a joint implementation alternative

Secondary forest cover in Costa Rica has increased during the last 15 years mainly due to the abandoning of large areas previously used for cattle ranching. In 1984, 2,3 million hectares of pasture land were being used for beef production, by 1995 this had been reduced to around 2 million hectares. During the same period, it is estimated that areas under secondary forest increased from 229 to 425 thousand hectares (Kaimowitz, 1995; CORFOGA, 1995). In contrast, according to the Ministry of Environment, there were 705 thousand hectares of secondary forest in Costa Rica during the early 1990's (MINAE, 1993); while Toumasjukka (1996) estimates that there are now more that 1.1 million hectares. In any event, it would appear that a large share of the abandoned pasture land has been left to regenerate into secondary forest.

The Costa Rican government has recognized the importance of natural forests because of the environmental services that they provide. In law No. 7575 it has established legal measures to compensate owners for the services provided by forests in reducing greenhouse gases[7]. Ecosystem studies conclude that the dry biomass contained in tropical forests varies between 150 and 382 tons per hectare. Assuming a carbon to dry biomass ratio of 45% (Houghton, Skole and Lefkowitz, 1991; Brown, *et al*, 1993), their maximum carbon storage capacity would be between 67.5 and 171 tons per hectare. On the other hand, Fearnside et al. (1996) measured biomass levels of 52.8 tons/ha in 5 year old stands of Brazilian secondary forest, that reached 196.6 tons/ha after 20 years, which implies an increase in carbon storage capacity of 88.5 tons in 20 years.

In contrast, carbon storage in pasture land has been estimated at approximately 10 tons/ha; at 140 tons/ha in mature primary forests; an at 55 tons/ha in partially intervened forests (Andersen, 1996). By comparison calculations for primary forests in Costa Rica have yielded biomass levels of between 167 and 283 tons/ha, and of between 152 and 237 tons/ha for secondary forests (Carranza, *et al*, 1996). This is equivalent to 75.15-127.3 and 68.4-106.6 tons of carbon per hectare, respectively. On the basis of these initial figures it is easy to appreciate the carbon storage potential of secondary forests. However, compared to primary tropical forests, these ecosystems have been minimally studied, and this lack of information and interest contributes to their being very vulnerable to land use change.

Methodology

Eight years of data from the monitoring of silvicultural management practices in the demonstration areas of the PROSIBONA Project are used for the biomass analysis. The data

---

[7] Law 7575, Art. 3, paragraph k states "Environmental Services are those provided by forests and plantations which directly protect and improve the environment, and include the following: mitigation of greenhouse gases (fixing, reduction, sequestration, storage, and absorption), protection of urban, rural and hydropower sources of water, protection of biodiversity through its conservation and sustainable use for scientific, pharmaceutical, research and genetic improvement purposes, protection of ecosystems, life-forms and natural scenic beauty for tourism and scientific purposes (Alcance No.21 a la Gaceta No.72 del 16 abril de 1996).

comes from of 4 different demonstration areas and 9 experimental plots in secondary humid tropical forests with stands between 2 and 44 years old, which allowed for an analysis of biomass accumulation across stands of different ages.

1. Description of Experimental Areas

Data from four different experimental sites was used for the biomass accumulation analysis: the "Florencia" experimental area, the "Tirimbina" forest, the Ian Hutchinson experimental farm and the "Espaveles" experimental farm.

The Ian D. Hutchinson demonstrative site is in a 44 year-old secondary forest. The original primary forest was selective exploited and, thereafter, cut down and used for cattle ranching. However, this activity did not render acceptable economic results and the site was later abandoned (RENARM, 1994). This forest covers a total area of 180 ha's distributed in two blocks, "La Sandía" and "Laguna" with an extension of 90 ha's each. It is a humid tropical forest (bh-T), according to the life zone classification of Holdridge (1982). PROSIBONA started experimental studies in this site in 1987. In 1988, plots were established and a first measurement was taken when the forest was 34 years old; follow up measurements were obtained in 1989, 1990, 1991, 1993, 1994 and 1995.

The "Tirimbina" demonstrative site is located in Sarapiqui, in the Atlantic zone of Costa Rica. It is in a life zone classified as very humid premontane forest transition to basal (bmh-P) and very humid tropical forest (bmh-T), according to Holdridge (1982). This secondary forest has an extension of 29.16 ha's and contains 5 permanent plots that are 2, 5, 15 and 25 years of age. Its origins are traced to the abandonment of rice crops after only one year of farming. The minimum diameter for the first measurement was 5 cm at breast height for the 2 to 15 year old forests; and 10 cm for the 25 year old forest. The PROSIBONA project started the studies in this area in 1986. The first measurement was taken in 1987, and follow ups were made from 1988 through 1992 and in 1995.

The "Espaveles" has an extension of 20 ha's, which combine primary and secondary forests. The secondary forest represents 33% of the total area (6.6 ha.). It is located in Turrialba, Costa Rica, and classified as a humid premontane forest (bh-P) according to Holdridge (1982). The original vegetation was cut down in 1937 and the area was dedicated to rubber (Hevea brasiliensis) plantations in 1944. Additionally, other crops such as plantain and pineapple were grown, and experimental studies with rice production conducted. The area was abandoned in 1954. (Salcedo, 1986). The PROSIBONA studies started in 1986, and a first measurement was taken in 1988 when the secondary forest was 35 years old; follow up measurements were made annually during the 1989-1992 period and then in 1997.

"Florencia" is in Florencia de San Carlos, in the Northeast of Costa Rica. It contains 32 ha's of secondary forest located in a very humid tropical forest (Bmh-T) life zone according to Holdrige (1982). The soils have a low productivity (Guillén, 1997). The PROSIBONA Project started measurements in 1993 when the forest was 27 years old. Follow up measurements were made in 1994, 1995 and finally in 1998.

2. Biomass Storage Estimation

Biomass accumulation was estimated using an equation for humid tropical forests by Brown et al (1989), which rendered a coefficient of multiple determination (R^2) of 90%[8]:

$$(1) \qquad Y = 13.675 - 6.1181 (D) + 0.8391 (D^2) + e$$

where Y is total biomass storage in kg of dry weight, D is the diameter at breast height (DAP) for any given tree and e is an error term. Biomass accumulation per-unit-area is estimated by adding up the results for all trees. Simple averages of the four experimental sites were used to infer levels of biomass accumulation through time as well as maximum biomass storage.

Besides, we used the equations estimated specifically for secondary forests by Saldarriaga, et al (1988). We tasted the following equations:

$$Y = -0.29 + 0.39(D^2) + 0.087(H); \quad (r^2 = 0.93)$$
$$\ln Y = -1.981 + 1.047 \ln(D) + 0.572 \ln(H) + 0.931 \ln(d); \quad (r^2 = 0.92)$$
$$\ln Y = -1.086 + 0.876 \ln(D) + 0.604 \ln(H) + 0.871 \ln(d); \quad (r^2 = 0.93).$$

Where Y is biomass storage in kg of dry weight, D is the diameter at breast height (dbh); H is the height and d is wood density. We assume a wood density according with the dominant tree population in the different farms.

3. Valuation of carbon sink service

In valuing the carbon sink services it is important to make the distinction between three different accounting philosophies, partially reflected in current joint implementation programs: Carbon storage, carbon parking and carbon sequestration. Carbon storage is related to the forest capacity to maintain a certain quantity of biomass per ha, which means carbon that is not being released

---

[8] This equation was obtained with data from humid tropical primary forests, however, it is not unreasonable to assume that wood density would be similar in primary and secondary forests of the same type.

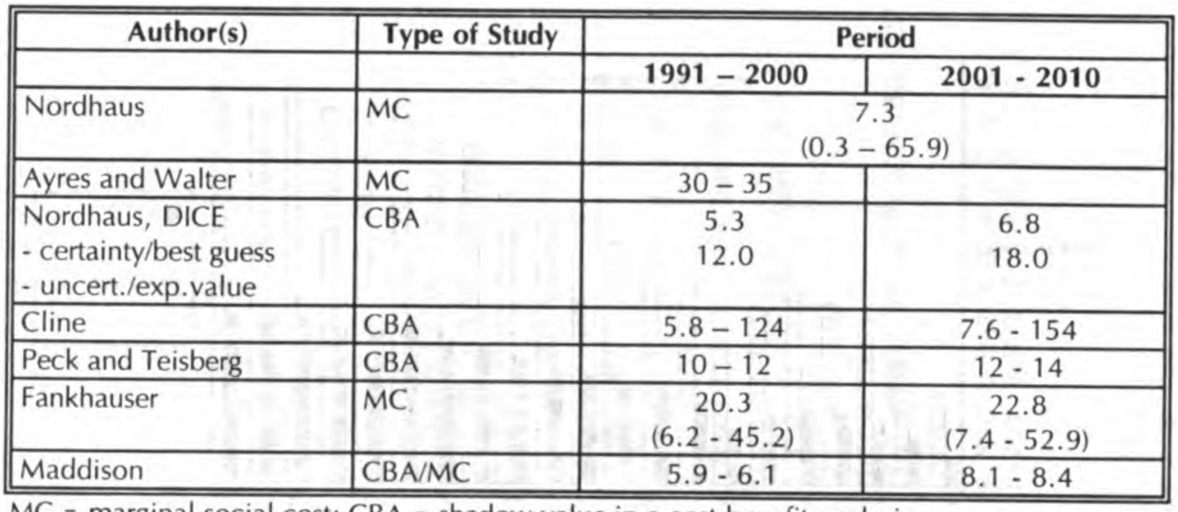
into the atmosphere. In this case, pricing refers to a one-time payment for forest conservation in which land-use change is permanently voided (i.e. through the establishing of a national park). The value of this permanent carbon storage service lies in avoiding potential future CO_2 emissions forever.

Carbon parking is less restrictive than carbon storage, since pricing refers to the principle currently adopted in the agreements with land owners in Costa Rica. This sanctions land-use changes during a limited period of time (20 years), in return for an economic compensation of U.S.$200 per hectare per year during the first five years of the agreement. In mature forests, little net carbon sequestration takes place, but deforestation and potential land-use change is forestalled avoiding potential carbon emissions into the atmosphere while the agreement is in force.

Carbon sequestration refers to the removal of CO_2 currently in the atmosphere, i.e. the mitigation of past emissions. Payments are made for net sequestration (which is function of biomass growth rates), i.e. the increase in the global carbon stock on an annual basis as long as the forest is a net absorber of CO_2. Assuming that the marginal damage of past and future greenhouse gas emissions is about the same, marginal economic or damage cost avoidance values can be used for pricing in this case. Valuing the amount of CO_2 sequestered at social damage costs is the more conceptually correct approach.

However, the government of Costa Rica uses a value of U.S.$10 per ton for all three types of carbon sink services provided by forests; independently of whether it is storage, parking or sequestration. This is the market price agreed in the Costa Rican joint implementation initiatives negotiated with the Norwegian government, but it does not necessarily reflect the marginal economic value of reducing atmospheric CO_2, or of avoiding that it increases.

Table 1. Estimates of Marginal Social Costs of CO_2 Emissions (1990 U.S.$)



Author(s)	Type of Study	Period	
		1991 – 2000	2001 - 2010
Nordhaus	MC	7.3 (0.3 – 65.9)	
Ayres and Walter	MC	30 – 35	
Nordhaus, DICE - certainty/best guess - uncert./exp.value	CBA	5.3 12.0	6.8 18.0
Cline	CBA	5.8 – 124	7.6 - 154
Peck and Teisberg	CBA	10 – 12	12 - 14
Fankhauser	MC	20.3 (6.2 - 45.2)	22.8 (7.4 - 52.9)
Maddison	CBA/MC	5.9 - 6.1	8.1 - 8.4

MC = marginal social cost; CBA = shadow value in a cost-benefit analysis

Source: Fankhauser and Tol, 1995.

Table 1 illustrates the wide range of marginal social damage costs estimated by various authors. For emissions occurring during the period 1991-2010, for example, the marginal social cost estimated by Nordhaus (1991) is of between U.S.$0.3 and U.S.$65.9 per ton. The average of all available estimates is of approximately U.S.$20 per ton. Since net CO_2 sequestration occurs during the growth stage of a secondary forest (0-25 years), it is appropriate to use the former average for valuation.

V. Quantification and valuation of carbon sink services of total Costa Rica`s humid tropical secondary forest

1. Biomass Accumulation

Figures 2 and 3 provide an overview of biomass sinking capacity per hectare in secondary forest at the four different demonstration areas of the CATIE/PROSIBONA project.

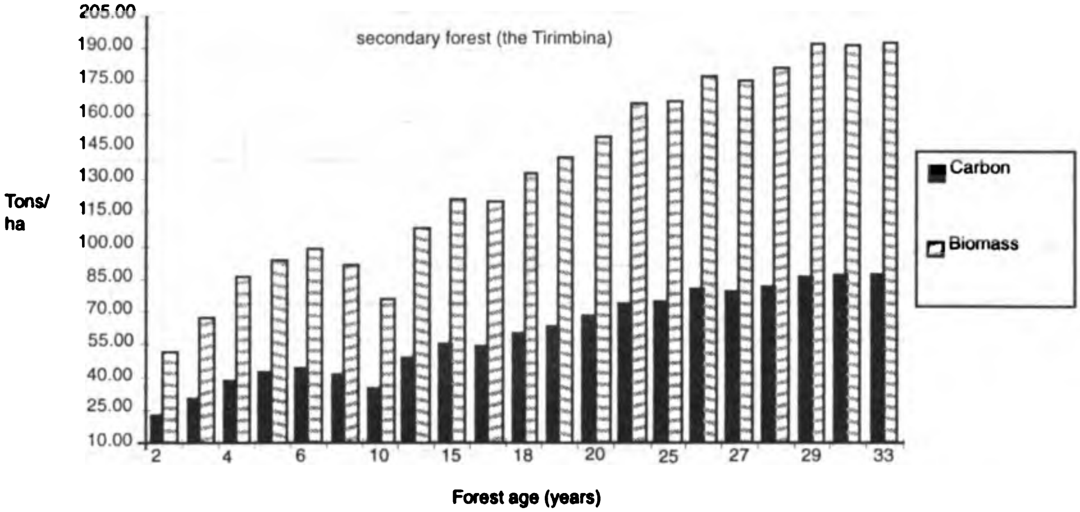


Figure. Biomass and carbon accumulation in a Costa Rica young secondary forest

Close examination of figures 2 and 3 reveals irregularities in biomass accumulation levels through time, while one would expect to observe a relatively smooth parabolic growth and stabilization of biomass content for any given stand over its lifetime. This is due to the relatively small size of the measurement plots (1 ha). In general, it would appear that biomass accumulation can reach anywhere between 100 and 200 tons per hectare in stands of 25 to 40 years of age. It is also apparent that some sites could plateau at different maximum biomass accumulation levels that others, although at about the same time (30-35 years).

Adapting the Saldarriaga's equations to our data we estimated a biomass accumulation of 82.25 t biomass per ha. for the range of trees with dbh less that 5 cm.; 120.7 t biomass per ha. for the range among 5 and 20 dhp cm; and 115.7 for the range dhp superior to 20 cm. Which means and average of biomass accumulation of 106.21 t biomass per ha for first measurement[9] in Tirimbina's secondary forests.

---

[9] It was only for the first measurement because we did not had height measurements for the rest years.

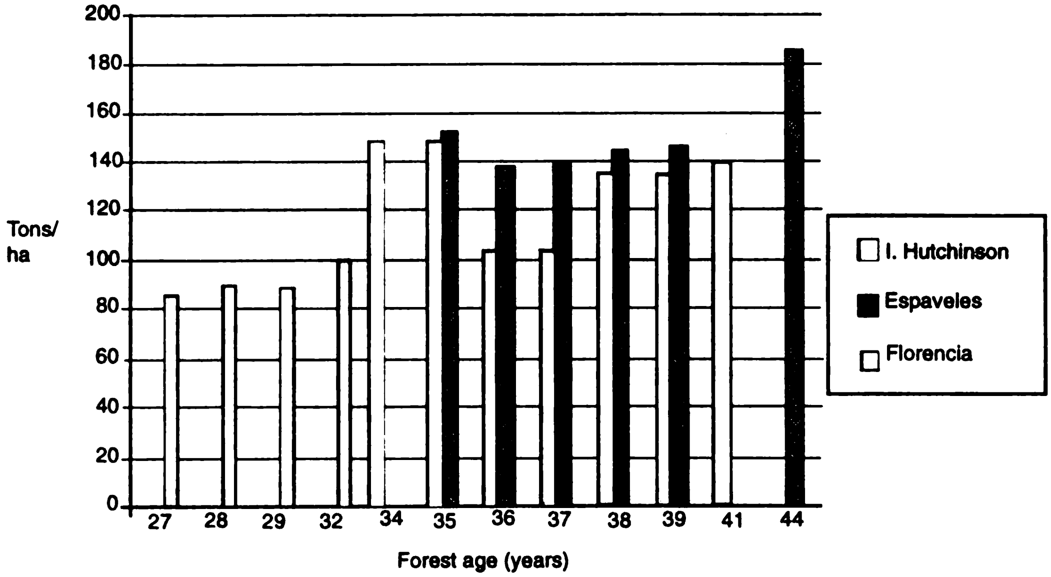


Figure 3. Biomass accumulation in 3 Costa Rica humid secondary forest between 27 and 44 years of age Source: own calculations.

2. Valuation of Carbon Sink Services

The biomass data discussed above suggests that true significant CO_2 mitigation (i.e. sequestration) occurs in tropical secondary forest stands up to about 20 years of age. If sequestration were the prime motive of JI agreements, payment should be made to regenerating forest areas while they experience net biomass growth. The payment is this case should be the full mitigation or marginal social cost of U.S.$20 per ton discussed earlier. In addition, payments could be made for avoiding land-use changes in mature secondary forests (i.e. carbon parking at U.S.$10 per ton per 20-year period), which would not be eligible under a "true" CO_2 sequestration agreement. In order to be able to extrapolate per hectare values to all of Costa Rica's humid secondary forests, several strong assumptions have to be made:

•The best secondary forest cover estimates are reasonably correct: A total of 425 thousand ha's, of which 302 thousand (71%) are humid (Solórzano et al, 1991); of the later, 160 thousand (53%) are less than 15 years old and the rest (142 thousand) are over 15 years old.• Forest age distribution is homogeneous within the two former categories. • Most secondary forests are less that 50 years old.

Then, forest areas are divided into two categories according to age: 1-20 years (during which most of the carbon sequestration occurs), and over 20 years old (after which very little sequestration occurs and, thus, only the lower carbon parking price is paid). Average carbon sequestration and parking levels for each category are estimated from the experimental data, as follows:

- On average for all sites, biomass accumulation levels reach 157 tons/ha after 20 years of forest growth, or 70.65 tons of carbon/ha. However, since it is assumed that at year zero (1998) forest areas are more or less evenly distributed within that category (1-20 years of age), the actual average sequestration rate that can be expected to occur during the next 20 years would be 0.5x70.65= 35.325 tons/ha.

- For experimental forest sites from 21 to 50 years of age, the average biomass storage is of 141 tons/ha, or 63.45 tons of carbon per hectare.

Table 2. Economic value of carbon sink services from Costa Rica's tropical humid secondary forests for the period 1998-2028.

Age Range	1-20	21-50
Forest Area ha.	180,290	121,710
Average Carbon Storage	35.32	0
Average Carbon Parking	0	63.45
Value of Carbon Storage	127,356,856	0
Value of Carbon Parking	0	77,224,995
Total Value of Carbon Sink Services	--	**204,581,851**

Source: own calculations.

Table 2 shows the estimated economic value of the carbon sink services of Costa Rica's humid tropical secondary forests; carbon storage using the previously discussed price of U.S.$20 per ton, and carbon parking paid at U.S.$10 per ton stored in the case of older forests. Under those circumstances, the 302 thousand hectares that are believed to exist to date have an estimated economic value of nearly 204,5 million dollars. This is a very conservative estimate for two reasons:

- It is based on a fixed, terminal period of 20 years of services. A second 20-year period of carbon parking services by those same 302 thousand hectares is estimated to be worth an additional U.S.$191.6 million.

- It does not consider the possibility that the recent trend of increased secondary forest areas will continue: Every additional 10,000 ha's of regenerating secondary forests have an estimated initial 20-year carbon storage value of U.S.$14.1 million, and a future potential carbon parking value of U.S.$6.35 million per 20-year period.

- It ignores the value of the large amounts of carbon sequestered from 1984 to 1997 as a result of the previously discussed extraordinary expansion of secondary forest areas in Costa Rica during that period.

Related with carbon sequestration philosophy this ecosystem could provide an average sequestration level of 2 ton/ha/year.). In the case of carbon sequestration the average is 2 ton per hectare per year, and the possible value is US$308 ha/year. (assuming the highest social value from of US$154 from table 1).

FINAL COMMENTS

Valuing carbon sink services assumes that owners of sinks (mainly developing countries) have an implicit right to emit all their stored carbon and should be compensated for not doing so. This is based on the fact that the large incremental amounts of CO_2 already in the atmosphere are the main historical responsibility of industrialized countries.

On the other hand, valuation carbon sequestration only assumes that "sink countries" have no such right and may only be compensated for reducing CO_2 already in the atmosphere, most of which has been emitted by industrialized countries.

In addition to the uncertainty about compensation rights, the supply of carbon sink services from a country like Costa Rica may be much larger than current international demand through JI agreements. It is unlikely that a significant proportion of the value estimated above will be "captured" by Costa Rica in the near future, given the lack of agreement about relative national responsibilities in alleviating global warning and the limited extent of JI markets.

In any instance, its is important that a distinction between carbon storage and carbon parking or permanent storage services begins to be made in countries like Costa Rica, which are attempting to capture international compensation for such services. It is obvious that carbon sequestration carries a larger economic value per unit, and differential payments have to be made in order to improve economic efficiency.

Secondary forests should receive greater attention than at present due to their superior sequestration rates and the fact that, in their early stages of growth, these ecosystems are highly vulnerable to land-use changes, which means avoiding potential future CO_2 emissions.

REFERENCES

ANDRASKO, KENNETH. 1990. *El recalentamiento del globo terráqueo y los bosques: estado actual de los conocimientos*. FAO, conferencia sobre cambio climático. Roma, Italia.

ANDERSEN, LYKKE E. 1996. *A cost Benefit Analysis of Deforestation in the Brazilian Amazon*. Departament of Economics, Universtity of Aarhus, Denmark.

BROWN, SANDRA; GILLESPI, ANDREW; ARIEL, LUGO. 1989. Biomass Estimation Methods for Tropical Forests with Applications to Forest Inventory Data. Forest Science. Vol. 35. Pp 881-902.

BROWN, SANDRA; ADGER, NEIL. 1993. *Forests for International offsets: aeconomic and political issues of carbon sequestration*. CSERGE, Working Paper gec 93-15. Centre for Social and Economic Researchon the Global Environment, University of East Anglia and University College London.

CARRANZA, CARLOS ET AL. 1996. *Valoración de los servicios ambientales de los bosques costarricenses*. Sistema Nacional de Conservación (SINAC), Centro Científico Tropical (CCT).

CLINE, W.R. 1992. *The economics of Global Warming*. Institute for International Economics. Washington, DC.

COSTANZA, R.; ARGE, R.; GROOT, R.; FARBER, S.; GRASSO, M.; HANNON, B.; LIMBURG, D.; NAEEM, S.; O´NEILL, R.; PARUELO, J.; RASKIN, R.; SUTTON, P.; VAN DEN BELT, M. 1997. The value of the world´s ecosystem services and natural capital. Pricing the Planet: Nature. International weekly journal of science. pp. 253-259.

CORPORACIÓN DE FOMENTO GANADERO (CORFOGA). 1995. *El subsector ganadería de carne en Costa Rica*. Documento para discusión. San José, Costa Rica.

FANKHAUSER, SAMUEL AND TOL, RICHARD. 1995. *Recent Advancements in the economic assesment of climate change costs*. Centre for Social and Economic Research on the Global Environment (CSERGE) and Vrije Universiteit, Amsterdam. CSERGE-Working Papers No.31.

FEARNSIDE, P.; MALHEIROS, W. 1995. *Carbon uptake by secondary forests in Brasilian Amazonia*. Forest Ecology and Management 80 (1996). Elsevier Science. Pp.35-46.

FAETH, PAUL; CORT, CHERIL Y LIVERNASH, ROBERT. 1994. *Evaluating the Carbon Sequestration Benefits of Forestry Projects in Developing countries*. World Resources Institute. USA.

GONZÁLEZ. 1995. *Breve Reseña Histórica de la dirección General Forestal. Ministerio de Ambiente y Energía (MINAE)*. San José, Costa Rica.

HOUGHTON, R.A., SKOLE, D.L. AND LEFKOWITZ, D. S. 1991. *Changes in the landscape of Latin America Between 1850-1985: II Net realease of* CO_2 *to the atmosphere*. Forest and Ecology Management. 38: 173-199.

KAIMOWITZ, DAVID. 1995. *Cattle Ranching expansion and secondary forest in Central America*. IICA. San José, Costa Rica.

LUGO, A.; BROWN, S.. 1992. Tropical forests as sinks of atmospheric carbon. Forest Ecology and Management, 54. 239-255.

MINISTERIO DE AMBIENTE Y ENERGÍA (MINAE). 1996. *Ley Forestal No.7575*. Alcance No. 21 a la Gaceta No.72 del 16 abril de 1996. Compilación Departamento Legal. San José, Costa Rica.

NORDHAUS, W. D. 1991. *To Slow or not Slow*. The economics of the Greenhouse Effect, Economic Journal, Vol 101, No. 47. Pp 920-937.

NORDHAUS, W. D. 1994. *Managing the Global Commons*: The economics of Climate Change. MIT, Press, Cambridge, MA.

OFICINA DE IMPLEMENTACIÓN CONJUNTA DE COSTA RICA (OCIC). 1995. *Notas Técnicas*. San José, Costa Rica.

ORTIZ, R. 1996. Bosque secundario por abandono de pastizales en Costa Rica: algunas implicaciones económicas y ambientales. Universidad Nacional. Costa Rica.

SCHROEDER, PAUL E.; DIXON, R.K.; WINJUM, J.K. 1993. *Ordenación forestal y agrosilvicultura para reducir el dióxido de carbono atmosférico*. Unasylva. 173. Vol. 44.

SEGURA, OLMAN. 1997. *Política Forestal en Costa Rica*. Centro Internacional en Política Económica (CINPE). III Congreso Forestal Costarricense. Agosto, 1997.

SOLÓRZANO,R; DE CAMINO, R; WOODWARD, R.; TOSSI, J.; WATSON, V.; VÁSQUEZ, A.; VILLALOBOS, C., JIMÉNEZ, J. 1991. La depreciación de los recursos naturales en Costa Rica y su relación con el sistema de cuentas nacionales. Centro Científico Tropical (CCT), World Resource Institute (WRI). San José, Costa Rica.

TOUMASJUKKA, TOMI. 1996. Estado del sector forestal en Centroamérica. Comisión Centroamericana de Ambiente y Desarrollo (CCAD); Consejo Centroamericano de Bosques y Areas Protegidas (CCAB-AP). International Union for Nature Conservation (UICN). San José, Costa Rica.

List of Participants

Budowski, Gerardo
Apartado 198
2300 Curridabat, Costa Rica
smiles@so.racsa.co.cr

Campos, José Joaquín
CATIE
Turrialba, Costa Rica
jcampos@catie. ac. cr

Chaverri, Adelaida
Apartado 86-3000
Escuela Ciencias Ambientales
Universidad Nacional Autónoma
Heredia, Costa Rica
achaverr@una.ac.cr

Chazdon, Robin
Department of Ecology and Evolutionary
Biology, University of Connecticut,
Storrs, CT 06269, USA
chazdon@uconnvn.uconn.edu

Cunha de Oliveira, Lia
Facultade de Ciencias Agrarias do Pará
Av.Presidente Tancredo Neves SIN,
CEP.-66077530
Terra Firme, Belén, Pará, Brasil
lcoliva@amazon.com.br

de las Salas, Gonzalo
Universidad Distrital Francisco José de
Caldas
Apartado aéreo 12803
Bogotá, Colombia
gonzalo5@hotmail.com

Dotzauer, Helmut
GTZ
P.O. Box 5180,
65726 Eschbom, Germanny
helmut.dotzauer@gtz.de

Perera, Dhammika
Oxford Forestry Institute
Oxford University
South Parks Road
Oxford OXI 3RB
England
dhammika.perera@plant-
sciences.oxfordac.uk

Falck, Maria Luisa
P.O. Box 44
Siguatepeque, Comayagua
Honduras C.A.

Finegan, Bryan
CATIE 7170
Turrialba, Costa Rica
bfinegan@catie.ac.cr

Gomide, Guilherme
Rua Bom Jesus
650, Curitiba, Parana, Brazil
CEP. 800035-01 0
ggomide@cce. ufpr. br

Grau, Ricardo
Laboratorio de Investigaciones
Ecológicas de las Yungas
Universidad Nacional de Tucumán
Casilla de Correo 34, 4107
Yerba Buena, Tucumán, Argentina
and
Dept. of Geography
University of Colorado at Boulder
Campus Box 260, 80309, Boulder,
Colorado, USA
grau@ucsu.colorado.edu

Guariguata, Manuel
CIFOR, Box 6596 JKPWB
Jakarta 10065, Indonesia
and
CATIE 7170
Turrialba, Costa Rica
mguarigu@catie.ac.cr

Guillen, Lucrecia
Apartado #68
CATIE-7170
Turrialba, Costa Rica
lguillen@catie.ac.cr

Herrera, Bernal
Proyecto CATIE/CIA
Centro de Investigaciones Agronómicas, UCR
Código Postal 2060
San José, Costa Rica
bemalh@cariari.ucr.ac.cr

Kammesheidt, Ludwig
Institut für Waldbau
Universität Göttingen, Büsgenweg 1, D-37077 Göttingen
Federal Republic of Germany
lkammes@ufobi6.uni-forst. gwdg. de

Kanashiro, Milton
Embrapa Amazonia Oriental
P.O. Box 48
66.095-100 Bel6m-PA, Brazil
milton@nautilus.com.br

Kanninen, Markku
CATIE 7170
Turrialba, Costa Rica
kanninen@catie.ac.cr

Maitre, Henri-Félix
CIRAD-FORET,
B. P. 5035, MONTPELLIER 34032,
CEDEX 1 France
maitre@cirad.fr

Mejia, Alejandro
Universidad Centroamericana
Apartado 69
Managua, Nicaragua,
acmc@ns.edu.uca.ni

Montagnini, Florencia
CATIE 7170
Turrialba, Costa Rica
montagni@catie.ac.cr

Morera Albert
Universidad Nacional
Apartado 12973-100
San José, Costa Rica

Müller, Eva
GTZ-COSEFORMA
Apartado 8-4190, 1000 San José,
Costa Rica
coseform@sol.racsa. co. cr

Olvera Vargas, Miguel
Universidad de Guadalajara
Instituto Manantlán de Ecología y
Conservación de la Biodiversidad
Apdo. Postal 108. C.P. 48900.
Autlán, Jalisco, Mexico
molvera@fisher.autlan.udg.mx

Ortiz, Rosalba
CATIE 7170
Turrialba, Costa Rica
rortiz@catie.ac.cr

Sabogal, César
CIFOR, Box 6596 JKPWB
Jakarta 10065, Indonesia
sabogal@interconect.com.br

Sanquetta, Carlos R.
Departamento de Silvicultura e Manejo -
UFPR/SCA
Rva Bom Jesus, 650 - Juvevé, Curitibe-
PR, Brasil CEP 80.510-250
sanqueta@cce.ufpr.br

Siles, Gustavo
Facultad de Ciencias Económicas
Universidad nacional Autónoma de
Nicaragua
Managua, Nicaragua
funda lvs@ibul.com.ni

Sips, Peter
BOS Foundation, Organization for
International Forestry Cooperation
P.O. Box 23
6700 AA Wageningen, The Netherlands
stichting.bos@ibn.dlo.nl

Smith, Joyotee
CIFOR, Box 6596 JKPWB
Jakarta 10065, Indonesia
e.smith@cgnet.com

Torres, Armando
INDEFOR, Facultad de Ciencias
Forestales
Universidad de Los Andes, Mérida
Via los Chorros de Milla, Venezuela
torres@ing.ula.ve

Tucker, Joanna
Department of latin American Studies
Douglas Bldg., University of Arizona
Tucson, Arizona, U.S.A.
jtucker@u.arizona.edu

Veneklaas, Erick
Centro International de Agricultura
Tropical
Apartado aéreo 6713,
Cali, Colombia
e.veneklaas@cgnet.com

Vester, Hans
ECOSUR, A.P. 424, Chetumal, Quintana
Roo, México
hvester@nicte-ha.ecosur-qroo.mx

Vieira, Ima
Museu Paraense Emilio Goeldi,
Departamento de Botánica, C.P. 399
Belém, Pará, Brasil, CEP 66.040-170
ima@museu-goeldi.br

Whitmore, Tim C.
Geography Dept, Downing Place,
Cambridge CB2 3EN England
Tw103@cam.ac.uk

DEVUELTO

[illegible] ENE 2005

DATE DUE

[illegible] 1999

1 0 NOV 2000

DEVUELTO

0 5 [illegible] 2001

1 1 [illegible]

DEVUELTO

1 1 JUN 2002

DEVUELTO

DEVUELTO

[illegible] SEP 2003

DEVUELTO

DEVUELTO

[illegible] JUN 2004

[illegible] ABR 2005

DEVUELTO