Mixed and Pure Tree Plantations with Native Species at La Selva Biological Station, Costa Rica: Growth, Productivity, Nutrient Cycling and Recovery of Ecosystem Biodiversity

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Sección Forestal

Ensayos forestales con especies nativas: Impacto sobre la fertilidad del suelo en la llanura del Atlántico de Costa Rica

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Uno de los ecosistemas más importantes y que ofrece múltiples beneficios a la humanidad, es el bosque tropical. No obstante, está siendo destruido a un ritmo alarmante, como resultado del proceso de un mal llamado desarrollo. El futuro de nuestro país depende, en gran parte, de la utilización racional de la cobertura forestal. Por ello, en esta sección, BIOCENOSIS *presenta diferentes aspectos referidos a los bosques y a su protección y manejo.*

INTRODUCCIÓN

Tanto para la reforestación como para los sistemas agroforestales (combinaciones de árboles con cultivos), es conveniente utilizar especies de árboles de uso múltiple, los cuales provean beneficios económicos, y que, al mismo tiempo, produzcan impactos favorables sobre los suelos.

Los efectos beneficiosos de los árboles sobre las características de los suelos pueden incluir: el mejoramiento de la estructura, la protección contra la erosión, la conservación de nutrientes y el aumento en la disponibilidad de los mismos. Los impactos de las especies de árboles sobre los suelos dependen de: los requerimientos individuales de nutrientes y agua de las especies, las características de las raíces, la capacidad de fijación de nitrógeno atmosférico y la calidad y la cantidad de hojarasca producida por el árbol. También, pueden ocurrir efectos perjudiciales, tales como aumento de la acidez y disminución del contenido y disponibilidad de nutrientes del suelo; aunque este es un tema de controversia (5, 15, 17).

La información sobre la influencia de los árboles en relación con las propiedades de los suelos, se concentra en unas pocas especies de amplio uso (15, 17). Muy pocas veces se tienen en cuenta estos factores en la elección de especies arbóreas para plantaciones o para combinaciones con cultivos (12, 14).

En la Región Atlántica de Costa Rica la Dirección General Forestal (DGF) lleva a cabo ensayos para la prueba de especies de árboles en plantaciones de campo abierto. Entre las especies recomendadas actualmente para la región (*Gmelina arborea, Pinus caribaea, Eucalyptus deglupta* y *Cordia alliodora*), solamente una, *Cordia alliodora* (laurel) es nativa. En 1985 la DGF estableció un ensayo para la prueba de árboles nativos, en la Estación Biológica La Selva de la Organización para Estudios Tropicales (OET), cerca de Puerto Viejo de Sarapiquí (Provincia de Heredia). De las 13 especies probadas durante los primeros tres años, al menos cuatro: *Stryphnodendron excelsum* ("vainillo"), *Vochysia hondurensis* ("mayo"), *Vochysia ferruginea* ("botarrama") y *Hyeronima oblonga* ("pilón"), mostraron un crecimiento equivalente o superior al de las especies recomendadas para la región (4). Esto muestra el gran potencial de muchas especies nativas las cuales permiten su aprovechamiento con fines económicos.

En 1988 se inició un proyecto independiente para el estudio de la influencia de seis especies de este mismo ensayo, sobre la fertilidad de los suelos y los mecanismos de reciclaje de los nutrientes. Los resultados de estas investigaciones se están utilizando con el fin de planificar el establecimiento de plantaciones forestales con especies mixtas para la recuperación de los suelos, y su uso en sistemas agroforestales.

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EL SITIO EXPERIMENTAL

La plantación experimental de árboles nativos fue establecida en noviembre de 1985 en el anexo "La Guaria" (cercano a la población de este mismo nombre), y pertenece a la Estación Biológica La Selva de la OET. La vegetación natural era de bosque lluvioso tropical de bajura (7). El bosque primario en el área experimental fue cortado en la década de 1950. El área sostuvo ganadería hasta 1983; en la actualidad aún se encuentran áreas con pastos, helechos y algunos arbustos. En partes que no fueron pastoreadas creció un bosque secundario, el cual tiene aproximadamente 20 años. Los suelos han sido clasificados como *Fluventic Dystropept*, originados sobre aluviones volcánicos (16). Son suelos profundos, bien drenados, sin pedregosidad o rocosidad. Los contenidos de materia orgánica son de medios a bajos, con textura moderadamente pesada a pesada; ácidos y poco fértiles.

La plantación se estableció sobre un terreno plano. El sitio fue limpiado con machete. Las ramas pequeñas fueron dejadas en el sitio, mientras que las más grandes se apartaron. Se plantó con plántulas en bolsa y se desmalezó cuatro veces por año. Las 13 especies estaban dispuestas en bloques al azar, con cinco repeticiones, en parcelas de 14 m x 14 m, con 49 árboles cada una, a 2 m de distancia entre árboles. Se delimitaron parcelas de un área con pastos y en otras con bosque, con el fin de realizar comparaciones de las propiedades de los suelos.

ELECCIÓN DE LAS ESPECIES ARBÓREAS

Los criterios para la elección de las especies fueron:

1. Crecimiento: cuando la plantación tenía dos años se eligieron las que presentaban mejor crecimiento a comienzos de 1988;
2. Valor económico: todas las especies del ensayo tienen madera valiosa, comercializable;
3. Capacidad fijadora de nitrógeno atmosférico: se examinaron las raíces de las especies leguminosas del ensayo y se observó la presencia de nódulos, que indican la actividad fijadora.

Stryphnodendron excelsum ("vainillo"; Leguminosae, Mimosoideae) y *Dalbergia tucurensis* ("granadillo"; Leguminosae, Papilionoideae) tienen madera de valor comercial (8); además de fijar nitrógeno, estas especies dan sombra moderada, lo cual podría ser una característica adecuada para su asociación con cultivos en sistemas agroforestales, o en plantaciones mixtas. *Dipteryx panamensis* ("almendro"; Leguminosae, Papilionoideae) se encuentra ampliamente distribuida en América Tropical, y su madera dura es muy apreciada (8). *Vochysia ferruginea* ("botarrama"; Vochysiaceae) y *Vochysia hondurensis* ("mayo"); Vochysiaceae) son apreciadas por su madera; ambas proveen sombra bastante densa. Además, *Vochysia ferruginea* es una especie pionera en la sucesión secundaria (1), se autopoda y produce abundante ramificación baja y hojarasca. *Tabebuia rosea* ("roble de sabana", Bignoniaceae) su madera es muy apreciada tanto industrial como ornamentalmente y se encuentra en abundancia en América tropical (8).

ESTUDIO DE LAS CARACTERÍSTICAS QUÍMICAS DE LOS SUELOS

Los suelos se muestrearon bajo las seis especies de la plantación.

En abril y agosto de 1988, se efectuó este muestreo en las parcelas de pastos y el bosque secundario, a 0-15, 15-30 y 30-60 cm de profundidad; es decir, cuando la plantación tenía alrededor de dos años y medio a casi tres años. Las muestras se procesaron en el Laboratorio de Suelos de la Facultad de Agronomía de la Universidad de Costa Rica, siguiendo los métodos corrientes para determinación de fertilidad de suelos empleados en el país.

INFLUENCIA DE LA PLANTACIÓN EXPERIMENTAL, EL PASTO Y EL BOSQUE SOBRE LA FERTILIDAD DEL SUELO

El promedio de materia orgánica en el horizonte superior del suelo fue mayor en la plantación (5,31 a 6,60%) que en el pasto (4,83%); el valor en la plantación, tomando todas las especies en conjunto, era cercano al del bosque (7,58%). Los datos anteriores son del mes de abril de 1988 (12); en agosto los resultados fueron similares. El nitrógeno total reveló una situación parecida, con valores de 0,26-0,32% en la plantación, mayores que en el

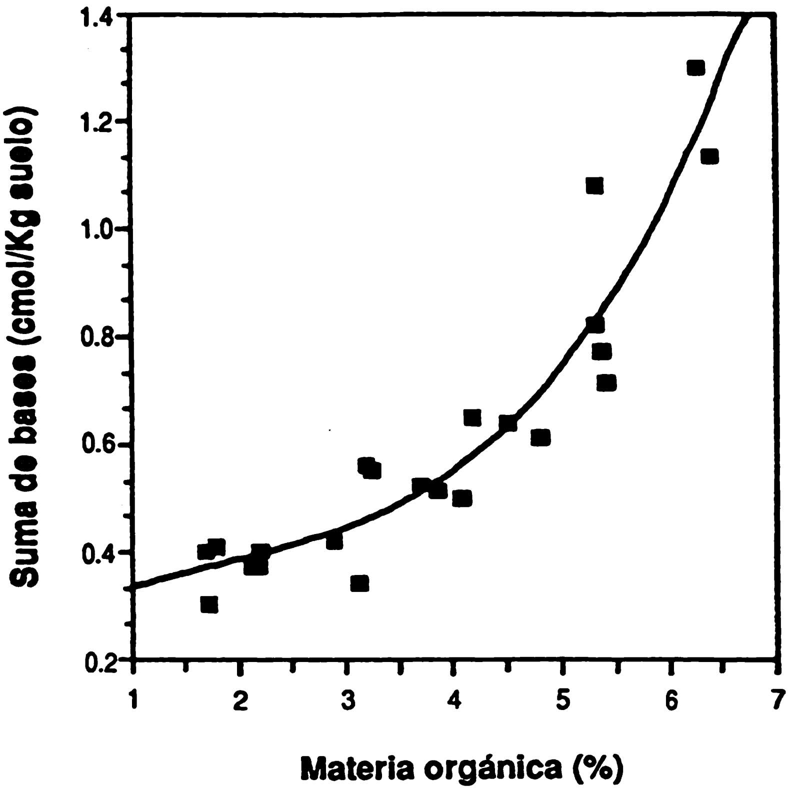

Figura 1. Relación entre la materia orgánica del suelo y el contenido de bases.

pasto (0,22) y cercanos a los del bosque (0,33) (datos de abril; con resultados similares en agosto. Como el contenido de materia orgánica es clave para la recuperación y el mantenimiento de la fertilidad, se puede considerar que en menos de tres años la presencia de la plantación experimental aumentó la fertilidad del sitio. Un incremento entre 0,5 y casi 2 unidades porcentuales de materia orgánica contribuye a la retención de los nutrientes: en la figura 1 se puede observar la estrecha relación entre el contenido de materia orgánica y las bases del suelo (calcio, magnesio y potasio). Asimismo, tomados en conjunto, los valores de calcio y magnesio en el suelo de la plantación fueron mayores que en el pasto, con valores cercanos a los que se encontraron en el bosque (12).

Comparando las seis especies de árboles de la plantación, en el horizonte superficial, se encontró una mayor suma de bases bajo *Vochysia ferruginea* (12). Estos valores fueron cercanos a aquéllos considerados adecuados para cultivos agrícolas, según tablas de valores críticos de nutrientes para los principales cultivos y que fueron desarrolladas por el Ministerio de Agricultura (2). La acumulación de calcio y magnesio se debe posiblemente a la movilización de los nutrientes de las capas profundas y su deposición posterior en la capa superficial a partir de la hojarasca. También bajo esta especie se observó un mayor contenido de materia orgánica y nitrógeno total (*Figura 2*), lo cual de nuevo sugiere la importancia de la materia orgánica en la retención de los nutrientes en estos suelos. Se observa una gran acumulación de hojarasca de hojas y ramas bajo esta especie, mucho mayor que en las otras especies del ensayo.

Por otro lado, tanto bajo *Stryphnodendron excelsum* (*Figura 3*) como bajo *Dalbergia tucurensis*, las dos especies leguminosas fijadoras de nitrógeno del suelo (13) se notó una mayor concentración de nitrógeno en las hojas y en la hojarasca, en comparación con las otras especies del ensayo. Esto sugiere que bajo estas especies existe un mayor reciclaje y disponibilidad de nitrógeno, lo cual las hace interesantes para su uso en combinación con

Figura 2. Muestreo de suelos con *Vochysia ferruginea* (botarrama) de cuatro años, bajo esta especie se encontró mayor materia orgánica y nitrógeno en el suelo que bajo otras especies. Parcela experimental en la Estación Biológica La Selva. (Sarapiquí, C.R.)

Fotografía de Florencia Montagnini

Figura 3. *Stryphnodendron excelsum* (vainillo), especie leguminosa fijadora de nitrógeno, de cuatro años y de buen crecimiento. Estación Biológica La Selva. (Sarapiquí, C.R.)

Fotografía de Florencia Montagnini

cultivos. Como *Stryphnodendron excelsum* y *Vochysia ferruginea* son algunas de las especies de mejor crecimiento del ensayo, y además tienen una aparente influencia positiva sobre la fertilidad del suelo, ambas especies tienen un gran potencial ya que pueden ser utilizadas para la reforestación y la implantación de sistemas agroforestales.

En la segunda fase del presente proyecto se mide la caída de hojarasca y su contenido de nutrientes bajo las seis especies de árboles. También, periódicamente se mide la hojarasca acumulada en el piso bajo los árboles, y su contenido de nutrientes. Asimismo, se ha calculado la cantidad de raíces en los mismos espesores de suelo que han sido considerados para los análisis químicos (11). Estas investigaciones contribuirán a explicar los mecanismos involucrados en estas diferencias y tendencias.

PLANTACIONES MIXTAS CON ESPECIES DE ÁRBOLES NATIVOS

Los resultados mencionados anteriormente indican que aún en los estadios tempranos de establecimiento de plantaciones forestales con especies nativas, es posible lograr una mejoría en la fertilidad del sitio. Actualmente se continúa con la investigación sobre estas especies, con muestreos anuales de los suelos, a fin de detectar otros posibles efectos a más largo plazo.

Además, con la utilización de los datos de la presente investigación, se podrá planificar el establecimiento de plantaciones mixtas, combinando las especies arbóreas según sus requerimientos nutricionales y su efecto potencial sobre los suelos. Estos ensayos se realizan en coordinación con el proyecto forestal para la prueba de especies que mantiene la OET en La Selva desde 1987. En relación con las plantaciones forestales mixtas, además de las especies mencionadas en el presente trabajo, se utilizarán otras especies de buen crecimiento de acuerdo con los resultados del proyecto forestal de la OET en mención(3). Otro criterio para la elección de especies es la disponibilidad de la semilla y el conocimiento de las características de la germinación (6), pues estos factores determinan, en gran medida, la posibilidad de establecer plantaciones a mayor escala.

Son conocidas las ventajas que pueden lograrse con el uso de sistemas diversificados, tales como las plantaciones forestales mixtas que aquí se plantean. Con base en los datos sobre el impacto de las especies en los suelos, se espera lograr combinaciones de especies arbóreas que se complementen en sus requerimientos nutricionales y en sus efectos sobre los suelos. Esto llevaría al logro de una plantación más productiva y al mismo tiempo mejoraría la fertilidad del sitio. Además, en sistemas más diversos se reparte mejor el riesgo de fallas y se pueden acomodar los aprovechamientos según varíen las necesidades o los precios de los productos. Los sistemas más diversos, en comparación con plantaciones puras, están más acordes con el ambiente natural, y se espera su mantención por mayor tiempo en mejor equilibrio con el ambiente que los rodea. Finalmente, el aprovechamiento de especies nativas con usos productivos y sostenibles llevará a una mejor preservación de los recursos genéticos de la región.

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To facilitate these and future programs, the Tropical Resources Institute serves as an "umbrella" organization to promote more international collaboration. Over the years many memoranda of understanding have been signed with international collaborators, the most recent being in Costa Rica, Argentina, and Brazil.

In conclusion, I wish to make clear that our student body is what makes all of this possible. Without this very enthusiastic and creative group coming in every year from around the U.S. and the world, none of these programs would be possible.

TRI UPDATE

COLLABORATION IN COSTA RICA AND ARGENTINA: FOREST AND SOIL RESTORATION EXPERIMENTS

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INTRODUCTION

The Tropical Resources Institute (TRI) of the Yale School of Forestry and Environmental Studies maintains collaborative agreements with a number of institutions worldwide dedicated to the study and promotion of sustainable land use systems and ecological restoration. As part of these efforts, and with funding from the A. W. Mellon Foundation, we are working in humid forest regions of Costa Rica and Argentina to promote the use of native tree species of economic value for reforestation and agroforestry, focusing on species with positive effects on the restoration of soil fertility in degraded areas.

EXPERIMENTS IN COSTA RICA

In the Atlantic humid lowlands of Costa Rica many indigenous tree species are much appreciated for their timber and other uses and can be grown in open plantation. Out of 13 native species in an experimental plantation at La Selva Biological Station of the Organization for Tropical Studies (OTS), at least five had growth rates and economic values similar or greater than the exotic species currently recommended (Espinoza and Butterfield 1989). These indigenous species contributed to soil fertility restoration by increasing organic matter, nitrogen and soil cation levels to values close to those considered adequate for agricultural crops (Montagnini and Sancho 1990a, 1990b).

However, more experience is needed on how to grow native trees for economic yields and soil restoration. The main hypothesis is that mixed species plantations are more productive and have greater positive effects on soils than monospecific stands. These mixed species plantations are also hypothesized to be economically advantageous alternatives for the recovery of degraded lands in the region. To test these hypotheses, experimental plantations are being established in collaboration with OTS and the Center for Agricultural Research of the University of Costa Rica (UCR), on abandoned pasture sites at OTS La Selva Biological Station. Growth rates in pure and mixed stands are being compared, and the impacts of these systems on soil fertility restoration are also being examined. Trees that were chosen are native to the Atlantic region of Costa Rica, have relatively rapid growth rates (data from OTS

TABLE 1.

List of species and their combinations, experiments in Costa Rica.

GROUPS	COMMON NAME	FAMILY
Group 1:		
1- *Stryphnodendron excelsum*	vainillo	Leguminosae (Mimosoid)
2- *Vochysia hondurensis*	mayo	Vochysiaceae
3- *Jacaranda copaia*	jacarand	Bignoniaceae
4- *Lacmellea panamensis*	leche de vaca	Apocynaceae
Group 2:		
5- *Albizia guachapele*	guaitil	Leguminosae (Mimosoid)
6- *Vochysia ferruginea*	botarrama	Vochysiaceae
7- *Terminalia amazonia*	roble coral	Combretaceae
8- *Virola koschny*	fruta dorada	Myristicaceae
Group 3:		
9- *Pentaclethra macroloba*	gaviln	Leguminosae (Mimosoid)
10- *Hyeronima oblonga*	piln	Euphorbiaceae
11- *Laetia procera*	manga larga	Flacourtiaceae
12- *Zanthoxilum mayanum*	lagartillo	Rutaceae

forestry projects, e.g. Espinoza and Butterfield 1989) and have relatively high economic value. Other criteria for choice of these species included consideration of nutrient requirements, effects on soil and nutrient cycling (e.g., Montagnini and Sancho 1990a, 1990b) as well as seed and seedling availability. In addition, field observations of tree architecture, growth habit, presence of insect damage and presence of root nodules in the leguminous trees was also considered.

In each mixture there is at least one leguminous, nitrogen fixing tree and another species with large production of leaf litter (Table 1). The structural architecture of each species was also taken into account to minimize competition for light.

The plantations are in randomized blocks, with four replicates and six treatments: four pure-species plots of each species: a mixed-species plot (mixing the four species): and natural regrowth. Initial plantation distance is 2mx2m to speed up canopy closure and obtain early impacts on soils. Thinning, pruning and other silvicultural treatments will be applied when needed to avoid excessive competition. There are 24 plots in each of the two 24,576m² (approximately 2.5 ha) plantations. The plots are 32mx32m, with a total of 256 trees in each plot.
The existing vegetation in the abandoned pasture sites is inventoried and mapped prior to site clearing in order to detect potential differences in tree growth due to the effects of previous soil cover. The soils are sampled by vegetation types before site cleaning and annually thereafter.

Site cleaning is done manually. Seeds are collected from trees in the La Selva reserve or from other areas in the Atlantic region, and seedlings are produced at the OTS nursery. The first plantation was established in June, 1991, a second one is scheduled for November, 1991, and a third one for June, 1992.

TABLE 2.

List of species and their combinations, experiments in Argentina.

SELECTED SPECIES	COMMON NAME	FAMILY
Plantation in San Antonio:		
Cordia trichotoma	loro negro, peteribo	Boraginaceae
Ocotea puberula	laurel guaia	Lauraceae
Peltophorum dubium *(Caesalpinoid)*	caafstola	Leguminosae
Parapiptadenia rigida	anchico colorado	Leguminosae (Mimosoid)
Plantation in Eldorado:		
Bastardiopsis densiflora	loro blanco	Malvaceae
Enterolobium contortisiliquum	timb colorado	Leguminosae (Mimosoid)
Lonchocarpus muehlbergianum	rabo molle	Leguminosae (Papilionoid)
Balfourodendron riedelianum	guatamb	Rutaceae

Figure 1 - Cassava (manioc) (Manihot esculenta) interplanted in a young stand of Hyeronima oblonga (pilon), in a 10 ha farm in La Flaminea, near La Selva. The seedlings were given to the farmer as part of an on-farm plantation study. Eugenio Gonzalez and Beatriz Eibl in the photograph.

EXPERIMENTS IN ARGENTINA

In Misiones, NE Argentina, about 20 miles east of the Brazilian border and 15 miles south of the Iguaz National Park, experimental mixed plantations with native trees have been started in a subtropical humid forest region. This work was initiated and continues in collaboration with the Subtropical Institute of Forestry Research (ISIF) of the School of Forestry, National University of Misiones (UNAM). In this region, the clearing of large areas of natural forest began in the 1960s, mostly as a result of government incentives for commercial plantations for pulpwood (principally *Pinus elliotii*) and cash crops of high market value such as soybeans, yerba mate (*Ilex paraguariensis*), and tea (Kozarik 1986). Native trees are still extracted from the remaining forests as they provide much of the good quality timber, but this resource is becoming scarce. There is virtually no experience with the silviculture of native trees, many of which extend in their natural range from southeastern Amazonia (Reitz et al. 1979).

The plantations, located in San Antonio and Eldorado, Misiones, were established in November, 1989, and August, 1990. The design of each mixture, as well as site treatment and management, are done using similar criteria as for La Selva experiments (Table 2). We are also evaluating the economic feasibility of these land use systems by comparing them with other alternatives common in each region and by assessing the economic value of the recovery of the degraded lands to a more fertile and productive stage. In Costa Rica, we are studying the potential of the most promising species for combination with agricultural crops (Fig. 1). In Argentina, we are also using some of the native tree species in agroforestry combinations with commercial crops and in forest enrichment practices (Fig. 2). Our interactions with local institutions operating in both regions are expected to ensure the dissemination of the results and contribute to the implementation and management of these systems among the local farmers.

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Figure 2 - Bastardiopsis densiflora (loro blanco) in a three year old enrichment plantation experiment in San Pedro, Misiones. The tree is approximately 7 meters high. Management of light availability in the lines is key to obtaining fast growth rates. Other individuals of the same species in more shaded areas on the same line were shorter

Mixed tree plantations

Experiments with native trees in Costa Rica and Argentina

by
Florencia Montagnini

The Tropical Resources Institute of Yale School of Forestry and Environmental Studies maintains collaborative agreements with a number of institutions for the study and promotion of sustainable land-use systems and ecological restoration. As part of these efforts, we are working in humid forest regions of Costa Rica and Argentina, with funding from the A.W. Mellon Foundation.

Common problems in these two regions are rapid deforestation, loss of biodiversity, and land degradation. Our objective is to promote the use of native tree species of economic value for reforestation and agroforestry, focusing on species that exert a positive effect on the restoration of soil fertility in degraded areas.

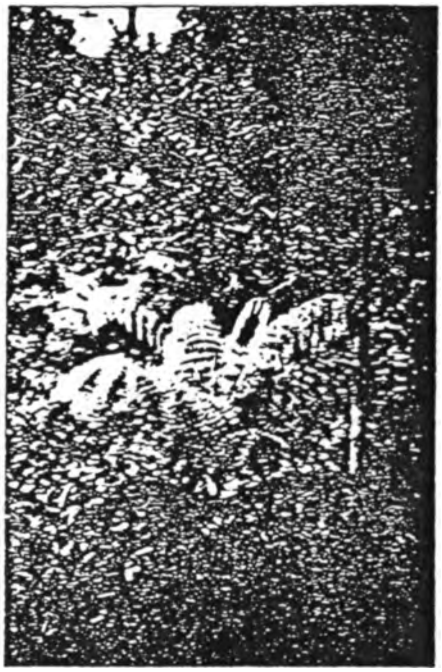
Trials in Costa Rica

In the Atlantic humid lowlands of Costa Rica, the Forest Service recommends three exotic tree species to farmers, *Gmelina arborea, Pinus caribaea* and *Eucalyptus deglupta*, and only one native species, *Cordia alliodora*. Yet, the farmers themselves appreciate many local trees for timber and other uses.

Out of 13 local species planted experimentally at the Organization for Tropical Studies' La Selva Biological Station, the Forest Service recently identified at least five with growth rates and economic value similar to or greater than those of the species currently recommended (Espinoza and Butterfield, 1989). Our own investigations in the same plantation reveal that these species contribute to the restoration of soil fertility, with soil organic matter, nitrogen and cations attaining values close to those which are considered adequate for agricultural crops in the region (Montagnini and Sancho, 1990a; 1990b; Montagnini et al., 1991).

We are now working in collaboration with the Organization for Tropical Studies and the University of Costa Rica's Agricultural Research Centre to establish experimental tree plantations with native species. These have been planted in mixed and pure stands on abandoned pasture sites with poor soils at the La Selva Station. We will compare growth rates under pure and mixed conditions, perform silvicultural treatments and examine the impact of these systems on soil-fertility restoration.

Several criteria were used to choose tree species and combinations. They had to be native to the Atlantic region of Costa Rica and show good growth and good economic value, especially for timber. Finally, seed and seedlings had to be available.



Mixed tree plantation at La Selva, Costa Rica, including 10-month-old Stryphnodendron excelsum *(centre) and* Jacaranda copaia *(right).*

Species selection was also based on information available on nutrient requirements and on the effects of trees on soils and nutrient recycling. Finally, field observations were taken into account, including tree architecture, growth habits, susceptibility to insect damage, and presence of root nodules in leguminous species. Table 1 lists the species and combinations selected.

We are establishing three tree plantations, each with a combination of four native species. In each mixture there is at least one leguminous nitrogen-fixing tree and another species known for its large production of leaf litter.

The architecture of each species has also been taken into account in order to minimize competition for light. Ideally, we will identify mixtures in which trees complement each other in terms of light and nutrient requirements and exert positive effects on soil fertility.

The species are grown in mixtures and also in pure stand. Initial spacing is 2 x 2 metres to speed up canopy closure and thus obtain a positive impact on soil fertility at an early stage. Thinning, pruning and other silvicultural treatments will be applied when needed to avoid excessive competition.

Seed is collected from trees in the La Selva reserve or from other areas of the Atlantic region. Germination trials are conducted and seedlings produced at the station's nursery. Seedlings are planted out in June and November, months when farmers in the region normally plant—immediately after the end of the dry season (June) and after a second dry period (November).

Before clearing the abandoned pasture sites, we are inventorying and mapping the existing vegetation to detect potential differences in tree growth due to the effects of previous soil cover. The soils are also sampled by vegetation types before site clearing. In addition to monitoring tree growth, we plan to sample soils annually to detect possible changes due to the presence of the trees.

Trials in Argentina

We have also started experimental mixed plantations with native trees in an area of subtropical humid forest at Misiones, northeastern Argentina, about 20 miles east of the Brazilian border and 15 miles south of the Iguazú National Park. This work is in collaboration with the Subtropical Forestry Research Institute of the National University of Misiones. In this region, large areas of natural forest have been cleared, beginning in the 1960s,

Montagnini, F. 1992. Mixed-tree plantations with native trees: land use systems for economic returns and soil

mostly as a result of government incentives to commercial plantations for pulpwood (principally *Pinus elliottii*) and for cash crops of high market value such as soybean, yerba mate (*Ilex paraguariensis*) and tea (Kozarik, 1986).

Native trees felled from the remaining forests still provide good-quality timber, but this resource is becoming scarce. There is virtually no experience with the silviculture of native species, many of which extend in their natural range from southeastern Amazonia (Renz et al., 1979).

The plantations are located in San Antonio on land belonging to the local Forest Service and in Eldorado on land provided by the local Forestry Technological Institute. They were established in November 1989 and August 1990. Each plantation includes four native tree species of economic value in pure and mixed designs, similar to those used in Costa Rica, at a spacing of 3 x 3 metres. Seeds and seedlings come from the nursery at the School of Forestry or local commercial nurseries. The species are listed in Table 2.

Here, we are trying to maintain maximum soil cover with regrowth vegetation to protect the young seedlings from excessive insolation in the summer and from frost damage in the winter. This 'minimum-tillage' approach also appears to have reduced pest damage. We are recording seedling height and survival as well as meteorological data for each site and sampling soils to provide a baseline for testing the effects of trees on soil chemical and physical properties.

Long-term objectives

Besides our own silvicultural and soil-restoration research objectives, we hope that these experiments will serve to stimulate other studies on species and site interactions. These might include research on light availability and growth response, on insect and pathogen abundance and diversity, and on tree genetic variability. We are also evaluating the economic feasibility of these land-use systems by comparing them with other alternatives common in each region and by assessing the economic value of restoring degraded land to a more fertile and productive state.

We expect that our experiments will have other practical applications apart from timber production and site restoration. In Costa Rica, we are studying the use of some species for mulching agricultural crops. Local farmers are already interplanting some of the indigenous trees with agricultural species such as cassava (*Manihot esculenta*) in a type of *taungya* system. We are starting work on the productivity of crops and trees under such systems, as well as economic analyses and surveys to determine how much land farmers are willing to allocate to trees.

In Argentina, we are using native trees in other experiments to test agroforestry combinations with commercial crops. For example, we are growing yerba mate, a tea-like crop that is widely planted in the region in monoculture, in combination with *Enterolobium contortisiliquum*, a nitrogen-fixing tree, and *Balfourodendron riedelianum*, a highly appreciated timber species. These combinations are expected to enhance the overall productivity of the land-use system and decrease economic risk. The participation of local institutions in both regions should help to ensure the dissemination of research results and the introduction of successful systems to farmers.

Scientific Name	Common Name	Family
First plantation		
1. [illegible]	[illegible]	[illegible]
2. [illegible]	[illegible]	[illegible]
3. *Jacaranda copaia*	jacaranda	[illegible]
4. *Calophyllum brasiliense*	cedro María	Gutiferae
Second plantation		
5. [illegible]	[illegible]	[illegible]
6. [illegible]	[illegible]	[illegible]
7. [illegible]	[illegible]	[illegible]
8. *Virola koschnyi*	[illegible]	[illegible]
Third plantation		
9. *Pithecellobium elegans*	ajillo	Leguminosae
10. *Hyeronima alchorneoides*	pilón	Euphorbiaceae
11. *Laetia procera*	manga larga	Flacourtiaceae
12. *Nectandra membranacea*	aguacatillo	Lauraceae

Table 1. Indigenous tree species selected for study at La Selva Biological Station, Costa Rica.

Further reading

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Table 2. Indigenous tree species selected for study at San Antonio and Eldorado, Misiones, Argentina.

Scientific Name	Common Name	Family
Plantation in San Antonio		
1. *Cordia trichotoma*	loro negro, peteribí	Boraginaceae
2. *Ocotea puberula*	laurel guaicá	Lauraceae
3. *Peltophorum dubium*	cañafístola	Leguminosae
4. *Parapiptadenia rigida*	anchico colorado	Leguminosae
Plantation in Eldorado		
5. *Bastardiopsis densiflora*	loro blanco	Malvaceae
6. *Enterolobium contortisiliquum*	timbó colorado	Leguminosae
7. *Lonchocarpus muehlbergianum*	rabo molle	Leguminosae
8. *Balfourodendron riedelianum*	guatambú	Rutaceae

restauración de los bosques y los suelos con especies forestales nativas

-experimentos en Costa Rica y Argentina-

Dra. Florencia Montagnini (*)

El Instituto de Recursos Tropicales (TRI) de la Universidad de Yale, Escuela Forestal y de Ciencias Ambientales, mantiene acuerdos de estudio con varias instituciones a nivel mundial que se dedican a [illegible] y promoción de [illegible] de uso sustentable [illegible] Como parte de esos esfuerzos, y con financiamiento de la Fundación A. W. Mellon (EE.UU.), estamos trabajando en regiones de bosques húmedos en Costa Rica y Argentina para promover el uso de especies forestales nativas de valor económico para programas de reforestación y uso de sistemas agroforestales. Se pretende poner énfasis en la utilización de aquellas especies que poseen potencial para favorecer la recuperación de los suelos en áreas degradadas por el manejo inadecuado y la deforestación.

EXPERIMENTOS EN COSTA RICA

En las tierras bajas húmedas del Atlántico en Costa Rica, existen muchas especies de árboles nativos de valor maderable que pueden cultivarse en plantación abierta. Por ejemplo, en una plantación experimental en la Estación Biológica "La Selva", de la OET, se comprobó que de un total de 13 especies nativas maderables, por lo menos 5 exhibieron tasas de crecimiento similares o aún mayores que las especies exóticas que se recomiendan actualmente para la zona (Espinoza y Butterfild, 1989). Además, también se comprobó, por medio de otras investigaciones realizadas en el mismo sitio experimental, que estas especies nativas aumentan la fertilidad del suelo por medio de su contribución en materia orgánica, nitrógeno y cationes, alcanzando el suelo valores cercanos a los que se consideran adecuados para la acti-

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tividad agrícola en la zona (Montagnini y Sancho, 1990a, 1990b, Montagnini et al. 1991).

Sin embargo, se necesita más experiencia sobre la silvicultura de especies nativas, si se pretende utilizarlos con el doble propósito de obtener ganancias económicas y ayudar a recuperar los suelos. Nuestra hipótesis principal es que las plantaciones forestales mixtas son productivas, influyen de manera positiva sobre los suelos y proveen un uso alternativo económicamente rentable en regiones con suelos degradados.

A partir de 1990, comenzamos a establecer plantaciones experimentales con árboles de especies nativas en rodales puros y mixtos, en sitios de pastizales abandonados con suelos poco fértiles en la Estación Biológica de "La Selva", en colaboración con la OTS y el Centro de Investigaciones Agronómicas de la Universidad de Costa Rica (UCR). Se comparan las tasas de crecimiento de los árboles en los sistemas mixtos y puros, así como su impacto sobre la fertilidad del suelo.

Los criterios empleados para escoger las especies y sus combinaciones fueron los siguientes:

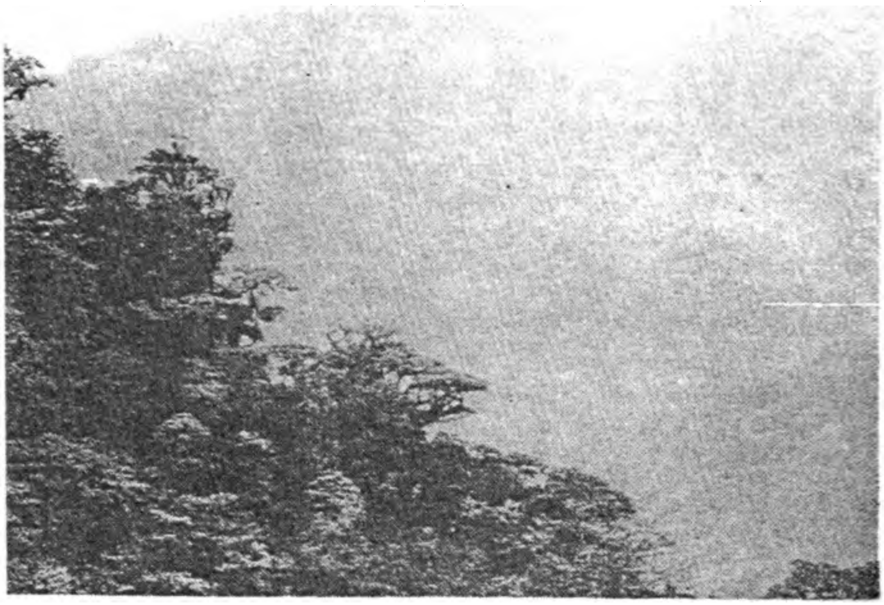
1. Nativas de la región Atlántica de Costa Rica.

2. De crecimiento relativamente rápido (según datos de proyectos forestales de la OTS, Espinoza and Butterfild 1989, Butterfild 1990).

3. Su valor económico, especialmente por la madera.

4. Datos sobre requerimientos de nutrientes, impacto sobre los suelos y reciclaje de nutrientes (Montagnini y Sancho 1990a, 1990b, Montagnini et al. 1991).

5. Disponibilidad de semillas y plántulas (basado en experiencias de proyectos forestales de la OTS).



6. Observaciones sobre la arquitectura de los árboles, hábito de crecimiento, daños causados por insectos, presencia de nódulos indicadores del potencial para fijar nitrógeno en las raíces de los árboles leguminosos.

En cada mezcla de 4 especies arbóreas se tiene por lo menos una leguminosa con capacidad fijadora de nitrógeno, y otra especie con alta producción de hojarasca (ver tabla). La arquitectura de cada especie también se toma en cuenta para minimizar la competencia por la luz entre las especies.

Las plantaciones son en bosques al azar, cada una con cuatro réplicas y seis tratamientos: para cada especie, hay cuatro parcelas puras (mono-específicas), una parcela mixta (mezclando las cuatro especies), y una parcela de regeneración natural. La distancia inicial de plantación es de 2m x 2m para acelerar el cierre del dosel y así obtener impactos en los suelos en una etapa temprana. Las podas, raleos y otros tratamientos silviculturales serán aplicados cuando sean necesarios para evitar competencia excesiva. Cada parcela tiene 32m x 32m, con un total de 256 árboles cada una; cada plantación es de un total de 24.576 m^2, o aproximadamente 2,5 Has.

Los sitios escogidos para los experimentos, son campos abandonados luego del uso para la ganadería en la década de 1960-70. Actualmente, luego de 15 a 20 años sin uso se encuentran en estado temprano de sucesión, con grupos de árboles, arbustos, pastos y helechos. Antes de la tala rasa, se realiza un inventario y mapeo de la vegetación existente en el sitio y se muestrean los suelos en cada tipo de vegetación, para determinar la posible influencia de la cobertura anterior sobre el crecimiento de árboles en la plantación. Se continúa el muestreo de suelos anualmente para detectar diferencias provocadas por las especies de árboles en la plantación experimental.

La limpieza del terreno se hace manualmente. Las semillas son colectadas de árboles de "La Selva" o de otras áreas de la región del Atlántico. Las plántulas se cultivan en el vivero de la OTS. En algunos casos, cuando no estaba disponible en "La Selva", la semilla se consiguió de fuentes comerciales. La primera plantación se estableció en junio de 1991; la segunda plantación se realiza en noviembre de 1991; y la tercera en junio de 1992.

EXPERIMENTOS FORESTALES EN COLABORACION EN ARGENTINA

También hemos comenzado experimentos de plantaciones mixtas con árboles nativos en Misiones, nordeste de Argentina, en una región de bosque húmedo subtropical, en colaboración con el Instituto Subtropical de Investigaciones Forestales (ISIF) de la facultad de Ciencias Forestales, Universidad Nacional de Misiones (UNaM). En esta región, la deforestación da lugar a plantaciones para celulosa (principalmente con *Pinus elliotii*), así como a cultivos tales como la soya, la yerba mate (*Ilex paraguariensis*), y el té (Kozarik, 1986). Los árboles de especies nativas se siguen extrayendo del bosque remanente porque proveen madera de alta calidad, pero este recurso se está volviendo cada vez más escaso. Prácticamente no existe experiencia silvicultural con las especies nativas, muchas de las cuales se extienden en su rango natural hasta en sureste de la Amazonia (Reitz et al, 1979).

Las plantaciones experimentales mixtas se comenzaron en noviembre de 1989, y agosto de 1990, cerca de las localidades de San Antonio y Eldorado, respectivamente. El diseño de cada plantación, el tratamiento y manejo del sitio son similares a los descritos para los experimentos en "La Selva". Las especies se escogieron entre las posibilidades locales, siguiendo también criterios similares.

Estamos también evaluando la viabilidad económica de estos sistemas de uso de la tierra, comparándolos con otras alternativas frecuentes en cada región. En Costa Rica, estamos estudiando el potencial de las especies más prometedoras para combinarlas con cultivos agrícolas. En Argentina, estamos usando algunas de las especies de árboles nativos en combinaciones agroforestales con cultivos comerciales, así como en prácticas de enriquecimiento de montes degradados. Nuestras interacciones con instituciones locales en ambas regiones suponen garantizar la difusión de los resultados y así contribuir a la implementación y manejo de estos sistemas para el beneficio de agricultores locales.

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TABLA

Lista de especies y sus combinaciones en grupos de cuatro. Experimentos en CostaRica

NOMBRE CIENTIFICO	*NOMBRE COMUN*	*FAMILIA*
primer grupo		
1. Stryphodendron excelsum	vainillo	Leguminosa (Mimosoidea)
2. Vochysia hondurensis	mayo	Vochysiácea
3. Jacaranda copaia	jacarandá	Bignoniácea
4. Lacmellea panamensis	leche de vaca	Apocynácea
segundo grupo		
5. Albizia guachapele	guaitil	Leguminosa (Mimosoidea)
6. Vochysia ferruginea	botarrama	Vochysiácea
7. Terminalia amazonia	roble coral	Combretácea
8. Virola koschny	fruta dorada	Myristicácea
tercer grupo		
9. Phitecellobium elegans	ajillo	Leguminosa (Mimosoidea)
10. Hyeronima alchornoides	pilón	Euforbiácea
11. Laetia procera	manga larga	Flacourtiaceae
12. Zanthoxilum mayanum	lagartillo	Rutaceae

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MIXED-TREE PLANTATIONS WITH INDIGNOUS TREES IN THE ATLANTIC LOWLANDS OF COSTA RICA

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ABSTRACT

Since 1989, we are working in humid forest regions of Costa Rica and Argentina to promote the use of native tree species of economic value for reforestation and agroforestry, focusing on species with positive effects on soil fertility. Here we report on preliminary results from mixed-tree experiments in the Atlantic humid lowlands of Costa Rica. We established three experimental plantations with native trees in mixed and pure stands on poor soils, on abandoned pasture sites at La Selva Biological Station, in collaboration with the organization for Tropical Studies (OTS) and the Center for Agricultural Research of the University of Costa Rica (UCR). We are comparing growth rates under pure and mixed conditions, and examining the impacts of these systems on soil fertility and nutrient recycling. In the first experimental plantation, at 18 months, the tallest trees were in *Jacaranda copia* plots, followed by *Vochysia hondurensis, Stryphnodendron excelsum* and *Callaphylum brasiliense.* The average height of *J. copaia* trees was larger in pure than in mixed plots, while diameters were higher in mixed than in pure plots of this species. The average height of S. excelsum was significantly higher in mixed than in pure plots, but there were no statistically significant differences in diameter between pure and mixed plots. For *V. hondurensis* and C. *brasiliense* there were no statistically significant differences in height, diameter or survival between mixed and pure plots. We are also evaluating the socio-economic feasibility of these systems, comparing them with other activities practiced by small farmers in the region.

INTRODUCTION

The Tropical Resources Institute (TRI) of Yale School of Forestry and Environmental Studies maintains collaborative agreements with a number of institutions worldwide dedicated to the study and promotion of sustainable land use systems and ecological restoration. As part of these efforts we are working in humid forest regions of Costa Rica and Argentina to promote the use of native tree species of economic value for reforestation and agroforestry, focusing an species with positive effects on soil fertility in degraded areas. Here we are reporting preliminary results from mixed-tree experiments in the Atlantic humid lowlands of Costa Rica. Earlier investigations indicated that several indigenous tree species in this region had growth rates and economic value similar or greater than exotics (Espinoza Camacho and Butterfield 1989). Increased levels of soil organic matter, nitrogen and cations were found under some of these species grown in pure plantation (Montagnini and Sancho 1990a, 1990b, Montagnini *et al.* 1991). However, more experience is needed on haw to grow native trees for economic yields and soil rehabilitation. The hypothesis was that mixed plantations can be more productive and excert more positive effects on soils than tree monocultures. We established three experimental plantations with native trees in mixed and pure stands on poor soils, on abandoned pasture sites, in collaboration with the organization for Tropical Studies (OTS) and the Center for Agricultural Research of the university of Costa Rica (UCR). We are comparing growth rates under pure and mixed conditions, and examining the impacts of these systems on soil fertility and nutrient recycling.

STUDY SITE AND EXPERIMENTAL DESIGN

The experiments were established on abandoned pasture at the OTS La Selva Biological Station (10°26'N, 86°59'W, 50 meters mean altitude,

TABLE 1. Ecological characteristics of 12 native tree species grown in three experimental mixed- and pure tree plantations at La Selva Biological Station (Gonzalez *et al.* 1990, Holdridge and Poveda 1975).

Scientific name	Common name	Family	Native range	Natural habitat
1st. plantation:				
Stryphnodendron excelsum Harms	vainillo	Leguminosae (Mimosoid)	Costa Rica, Nicaragua and Panama	Upper canopy, low altitude, up to 700m, very humid climate. Alluvial soils with poor drainage, also on hills and slopes. Also on secondary forest. Adapts to poor soils.
Vochysia hondurensis Sprague	mayo, chancho	Vochysiaceae	Mexico to Panama	Upper canopy, lowlands, up to 900m, humid climate, at edge of mountains. Rich alluvial or poor, acidic soils, stands flooding.
Jacaranda copaia (Aubl.) D. Don.	jacaranda	Bignoniaceae	Guatemala to Brazil	Low elevations, humid to very humid climate. Well drained slopes, does not stand poor drainage. Secondary forest, low hills, red clayey soils of low fertility.
Calophyllum brasiliense Cambess.	cedro Maria	Guttiferae (Clusiaceae)	Mexico to N. South America	Found on many types of habitats from wet to dry. Can stand floodling.
2nd. plantation:				
Albizia guachapele (H.B.K.) Little	cenizaro macho,	Leguminosae	Guatemala to Ecuador	Low elevations with humid to dry climate. in low bush, secondary forest, along sandy river beds, savannas. Can grow on old, acid alluvial or sandy soils.
Terminalia amazonia (J.F. Gmel.) Exell.	roble coral	Combretaceae	S. Mexico to N. South America	Found on alluvial, ocassionally flooded areas, or on hills with old, acid, infertile clayey soils.
Virola koschnyi Warb	fruta dorada	Myristicaceae	Central America	Upper canopy, low elevations, up to 1,200m, very humid climate. Lower parts of hills, riparian zones. Alluvial, poorly drained, or sandy soils. Also on clayey, acid, infertile soils high in Al.

TABLE 1. Continued.

Scientific name	Common name	Family	Native range	Natural habitat
Dipteryx panamensis (Pittier) Record & Mell	almendro	Leguminosae	Nicaragua to Colombia	Upper canopy, low elevations, up to 1300 m, very humid climate. Lowland and premontane forest. Alluvial or sandy soils, sometimes acid, clayey soils.
3rd. plantation:				
Pithecellobium elegans D.C. Benth	ajillo	Leguminosae (Mimosoid)	Tropical America	Wet and dry forest, tidal forests, stream banks, limestone cliffs. Alluvial, clayey or sandy loam soils.
Genipa americana L.	genipa	Rubiaceae	Tropical America	Lowland forest, slopes. Adopts to sandy, poor soils.
Vochysia ferruginea Mart	botarrama	Vochysiaceae	Nicaragua to Brazil	Lowland forests. Well-drained, acidic, infertile soils.
Hyeronima alchorneoides Fr. Allema	pilon	Euphorbiaceae	S. Mexico to S. Brazil	Hills, abandoned pas tures. Alluvial aswell as poor soils.

24°C mean annual temperature, 4000 mm mean annual rainfall, with maximum in July and minimum in March) (La Selva Biological Station weather reports). Soils in the experimental area are Fluventic Dystropepts derived from volcanic alluvium; they are deep, well drained, stone-free, with low or medium organic matter content, moderately heavy texture, and are generally acid and infertile (Sancho and Mata 1987). The area had been cleared in the mid-1950s and grazed until 1981 (Pierce 1991). The experimental area was on flat, uniform terrain.

The tree species

The twelve indigenous tree species of this study (Table l) were selected out of approximately 90 species of an OTS Forestry Project at La Selva and in farmers' fields in the La Selva region. The criteria for species selection for this study were: growth rate during the first 3-4 years of the plantation (Espinoza Camacho and Butterfield, 1989; Gonzalez *et al.* 1990); presence of root nodules in the leguminous species (field observations); impacts on soil fertility (Montagnini and Sancho 1990a, 1990b, Montagnini *et al.* 1991, Montagnini and Sancho 1993) and economic value (Chudnoff 1984; Gonzalez *et al.* 1990).

Plantation design

In each mixture of four tree species there was at least one leguminous, nitrogen-fixing tree, and fast- and relatively slower- growing species (Table 1). The plantations were set in randomized blocks, with four replicates and six treatments: four pure-species plots of each species, a mixed-species plot (with the four species), and natural regrowth (Figure 1). Initial plantation distance was 2 m x 2 m to speed up canopy closure and obtain early impacts on soils. Each plot was 32 m x 32 m, with a total of 256 trees each. Each block was 64 m x 96 m; each plantation was 96 m x 256 m, *i.e.* 24,576 m^2, or approximately 2.5 ha. In the individual plots, a systematic layout was used to maximize species interactions. Within each plot, trees of the four species were planted alternating two species per raw. The sequential order of the species within rows was systematically reversed every other row. In that manner, each line contained the four species of the mixture in a sequence.

Soil fertility

Composite samples were taken in each of the four replicate plots per treatment, at 0-5, 5-15, 15-30 and 30-60 cm depth, just after plot layout (before site clearing) (Table 2). After the area was cleared, soils were sampled again; sampling continues at yearly intervals to detect differences in soil fertility due to the presence of the mixed or pure plots in comparison with the regrowth controls.

Site preparation and planting

Site cleaning was done manually, approximately one month before each plantation. The underbrush was first cleared with machetes, and the trees and bushes were felled with a chainsaw and cut into smaller pieces so that they could be spreaded around, as much as their weight allowed. No burning was done. The slash was left on the floor, to protect against soil erosion and to delay the growth of weeds. Because of the high rainfall in the area, it would have been difficult to allow for the slash to dry for burning.

Seeds were collected from trees at the La Selva forest or from other areas in the Atlantic region. Seedlings were produced at the OTS nursery. Plantations were started when at least two of a group of four species were ready. Therefore the planting periods lasted approximately six months. The three plantations were fenced to avoid deer browsing.

FIGURE 1. Experimental mixed and pure-species plantations.

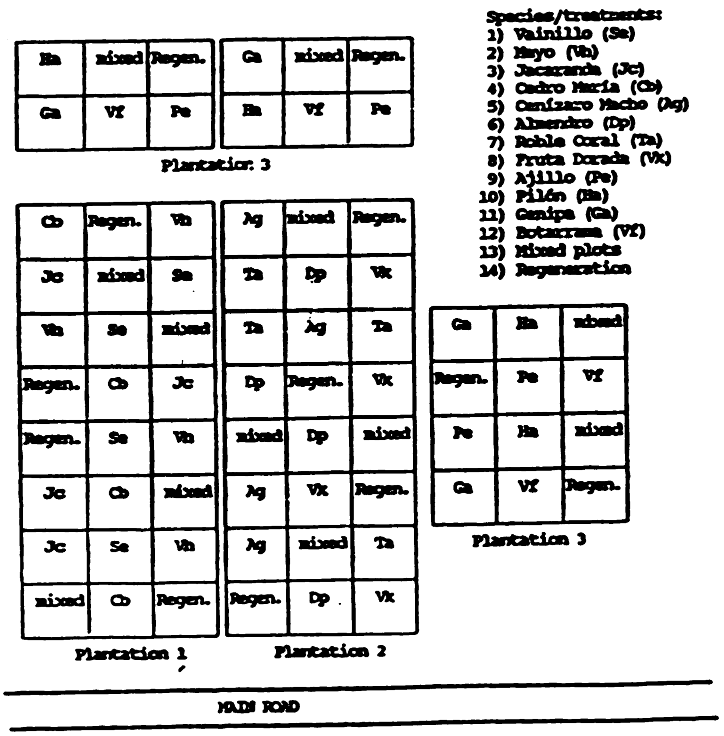


TABLE 2. Soil chemical characteristics in Plantation 1: Ca, Mg, K, exchangeable acidity, pH, organic matter, total N, extractable P and micronutrients in soils sampled in May 1991.

Block	Dept (cm)	Ca	Mg	K	Acidity	pH
				(cmol.kg^{-1})		
1	0-15	1.20a	0.45a	0.22a	1.55a	4.85ab
1	15-30	1.05a	0.40a	0.19a	1.40a	4.90b
1	30-60	1.10a	0.15b	0.11a	1.40a	5.10a
2	0-15	1.10a	0.20b	0.18ab	1.50ab	5.20a
2	15-30	1.00a	0.20ab	0.15ab	1.60a	5.30a
2	30-60	1.10a	0.10b	0.12a	1.40a	4.90a
3	0-15	1.60a	0.50a	0.12b	0.60c	4.90ab
3	15-30	1.30a	0.40ab	0.10bc	0.80b	4.90ab
3	30-60	1.20a	0.30a	0.07a	0.70b	5.10a
4	0-15	1.28a	0.30b	0.12b	0.93cb	4.83b
4	15-30	1.15a	0.20b	0.08c	0.78b	4.98ab
4	30-60	1.10a	0.13b	0.08a	0.55b	5.00a

Block	Dept (cm)	Om (%)	N (%)	P	Cu	Fe	Mn	Zn
						(mg.kg^{-1})		
1	0-15	4.06a	0.285a	10.10a	43.5a	1753.5a	47.5a	4.30a
1	15-30	3.58a	0.185a	9.45b	43.0a	1267.0a	29.5bc	2.70b
1	30-60	2.72a	0.195a	7.70a	37.0a	627.5a	20.0b	2.50b
2	0-15	5.83a	0.220a	12.40a	41.0a	1742.0a	27.0a	4.20a
2	15-30	1.74b	0.150a	12.60a	40.0a	1118.0a	29.0bc	4.00a
2	30-60	3.01a	0.110a	8.50a	32.0a	600.0	26.0ab	4.10a
3	0-15	5.83a	0.190a	7.30a	36.0a	1805.0a	57.0a	3.70a
3	15-30	4.40a	0.150a	5.90c	36.0a	1566.0a	52.0abc	2.40bc
3	30-60	3.22a	0.090a	6.50a	27.0a	626.0ab	41.0ab	2.20b
4	0-15	5.14a	0.250a	6.18a	35.8a	1698.3a	59.8a	3.02
4	15-30	3.65a	0.178a	2.75d	35.8a	1091.3a	55.0ac	1.97c
4	30-60	1.81a	0.108a	1.63b	34.3a	488.8b	53.3a	2.02b

Note* For each parameter and depth, means followed by the same letter are not significantly different ($P>0.05$).

Weeding was done manually and whenever the growth of weeds made it necessary. No herbicides were used.

The total height and the diameter at breast height (dbh) where measured on all 256 trees of each plot. Notes on general tree health, early branching and insect damage were also taken at the time of measurement. Percent survival and basal area were calculated from the measurements. The data on height, dbh, basal area and survival were averaged for each plot. Analysis of variance and tests far means (confidence limits, $P<0.05$) were run using the means of each parameter from the four replicate plots. All parameters were compared among the four species, and also among each species in pure and mixed plot conditions.

TREE GROWTH: PRELIMINARY RESULTS, FIRST PLANTATION

Results of measurements taken 18 months after planting showed that *J. copaia* were the tallest trees, followed by *V. hondurensis*, *S. excelsum* and *C. brasiliense*, in that order (Figure 2). These preliminary results confirm Farlier observations for these species at La Selva and other sites in the region (OTS Forestry Project). Diameter measurements started 12 months following planting for *J. copaia*, *S. excelsum* and *V. hondurensis*. Canopy closure also occurred approximately 12 months after planting in the pure plots of these three species. The average height of *J. copaia* trees was larger in pure than in mixed plots, in measurements taken at 12 and 18 months (Figure 3). Conversely, diameters were higher in mixed than in pure plots of *J. copaia*; these differences were evident at 18 months (Figure 4). Apparently, *J. copia*, a species of monopodial growth, suffered more competition by individuals of the same species resulting in taller, thinner trees in the pure than in the mixed plots.

The average height of *S. excelsum* was significantly higher in mixed than in pure plots (Figure 5). There were no statistically significant differences in diameter between pure and mixed plots of this species at any age (Figure 6). *S. excelsum* showed the lowest survival, with values less than 90% at 6 months; these are high because dead seedlings were replaced, up to 12 months after planting. This was in part related to deer browsing during the first months of the plantation before the fence was built; however, other factors might have also affected survival of this species, since the seedlings brought for replacements often died or lagged way behind. As a result, this species showed the highest heterogeneity in height and diameter.

FIGURE 2. Tree growth in pure and mixed plots. Height at 18 months.

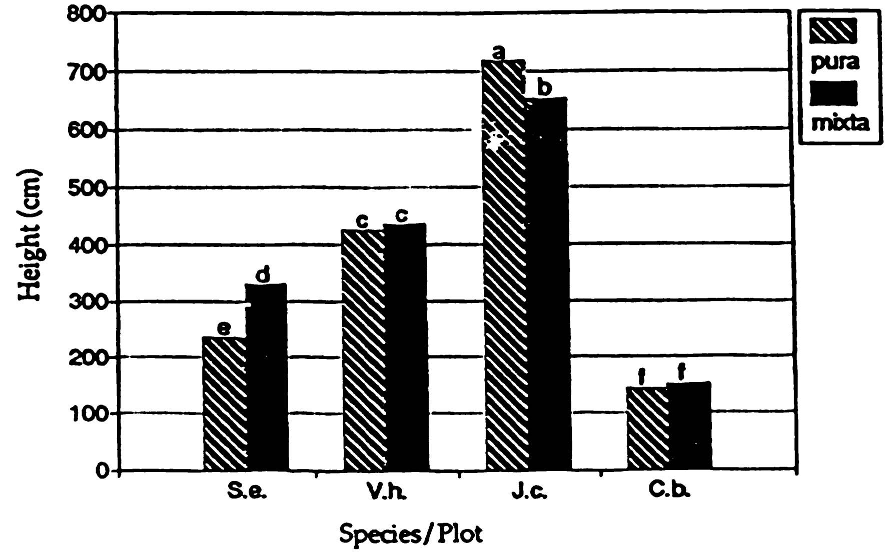


FIGURE 3. Total height of *Jacaranda copaia* in pure and mixed plots.

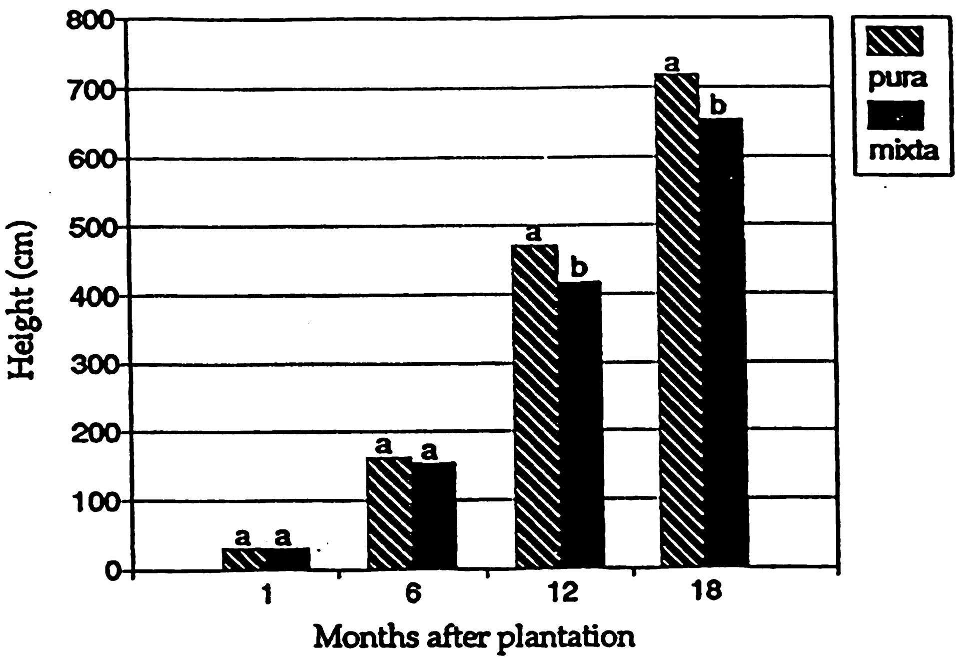


FIGURE 4. Diameter (dbh) growth of *Jacaranda copaia* in pure and mixed plots.

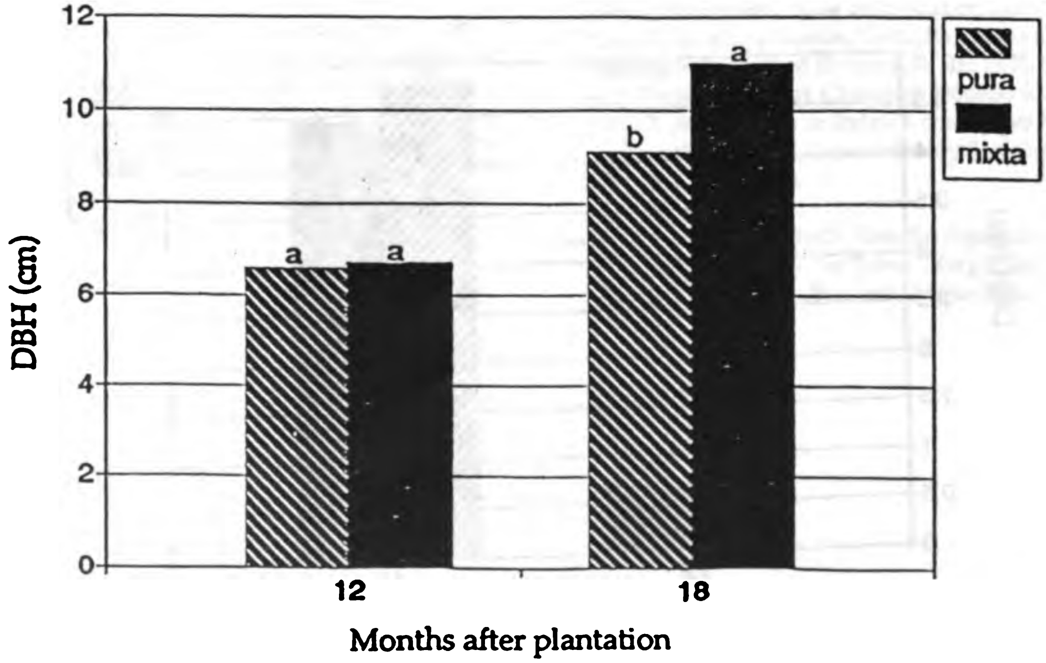


FIGURE 5. Total height of *S. excelsum* in pure and mixed plots.

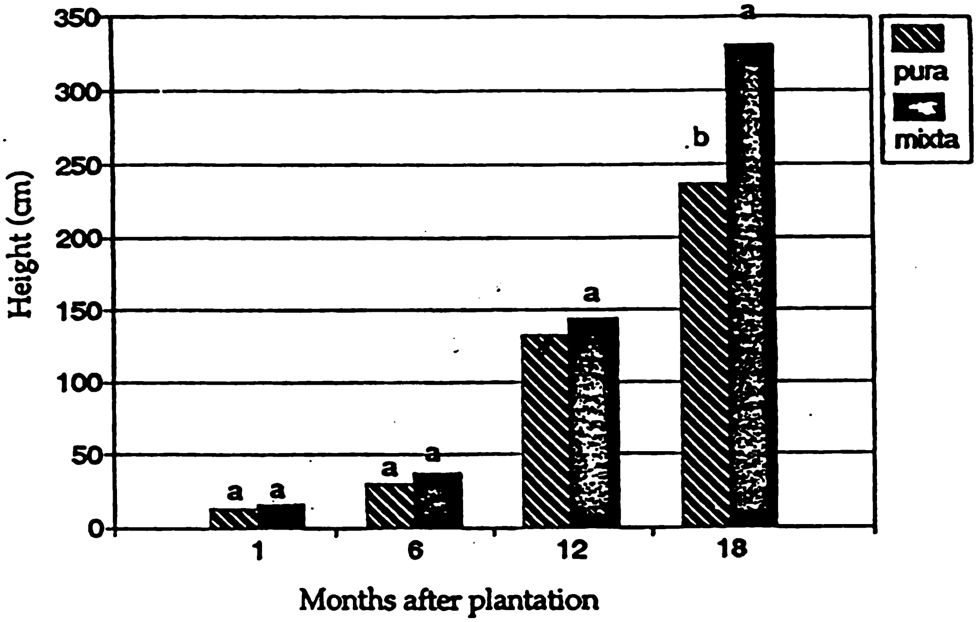
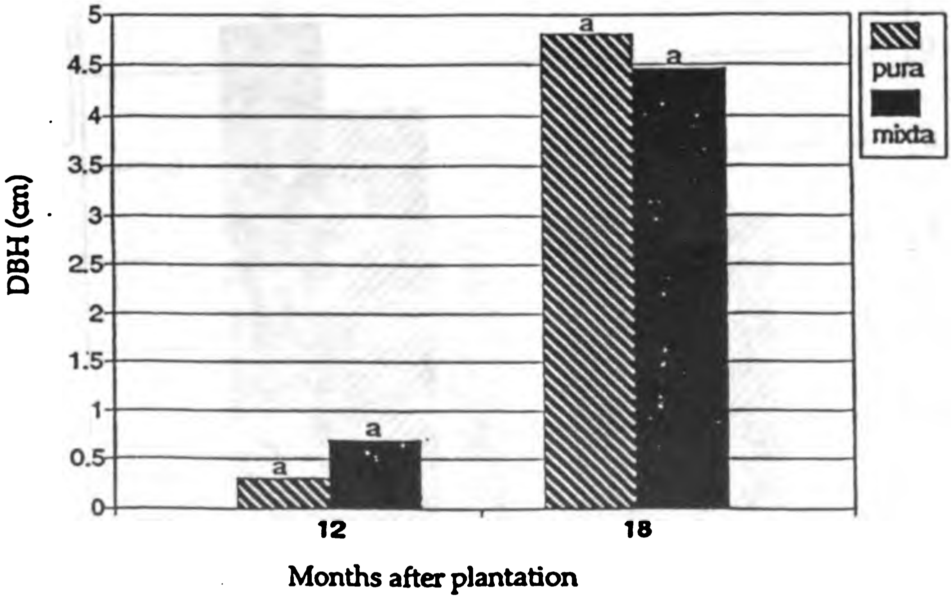


FIGURE 6. Diameter (dbh) growth of *S. excelsum* in pure and mixed plots.



For *V. hondurensis* and *C. brasiliense* there were no statistically significant differences in height, diameter or survival between mixed and pure plots in any of the measurements taken. *C. brasiliense* was six months younger than the other three species; however, even when comparing plots of the same age (12 months) still *C. brasiliense* was the shortest, and diameters were still too small for mensurements at that age.

SOCIO-ECONOMIC FACTORS AND DISSEMINATION OF RESULTS

The cost associated with labor was evaluated by recording the time and number of workers associated with each task. Other costs are also recorded. We are evaluating the economic feasibility of these land use systems, by comparing them with other alternatives common in the region among the small farmers. Our interactions with local institutions operating in the region (OTS, UCR-CIA, Instituto Tecnologico de Costa Rica), as well as with local farmer's groups (Centro Agrícola, other private organizations) are expected to ensure the dissemination of the results and contribute to the promotion of these systems among the local farmers.

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El uso de especies maderables nativas en plantaciones mixtas para la reforestación de terrenos degradados: resultados preliminares de experiencias en la llanura del Atlántico de Costa Rica.

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RESUMEN

Desde 1989 estamos trabajando en regiones de bosque húmedo de Costa Rica y Argentina para promover el uso de especies arbóreas nativas de valor económico para la reforestación y los sistemas agroforestales, con énfasis en especies con impactos positivos sobre la fertilidad de los suelos. En la zona Atlántica de Costa Rica hemos establecido tres plantaciones experimentales con árboles nativos en parcelas mixtas y puras, en un área de pastos abandonados, con suelos pobres. Se comparan las tasas de crecimiento bajo condiciones de parcelas mixtas y puras, y se examinan los impactos de estos sistemas sobre la fertilidad del suelo y el reciclaje de nutrientes. En la primera plantación experimental, a los 18 meses, los árboles más altos se encontraron en parcelas de *Jacaranda copia*, seguidos por *Vochysia hondurensis*, *Stryphnodendron excelsum*, y *Callophylum brasiliense*. La altura media de los árboles *J. copaia* era mayor en las parcelas puras que en las mixtas, mientras que los diámetros eran mayores en parcelas mixtas que en puras. La altura media de *S. excelsum* era mayor en parcelas mixtas que en puras, pero no hubo diferencias estadísticamente significativas en los diámetros. Para *V. hondurensis* y *C. brasiliense* no hubo diferencias estadísticamente significativas en la altura, diámetro o sobrevivencia entre las parcelas puras y mixtas. Los resultados del análisis de suelo a los doce meses de edad, revelaron un mayor contenido de materia orgánica en las parcelas puras de *J. copaia*, que en cualquiera de las otras especies. También se presentan resultados de crecimiento inicial para la segunda plantación. Estos resultados preliminares sugieren que debido a su alta tasa de crecimiento y aparente influencia positiva sobre la

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fertilidad del suelo, las especies de la Plantación 1 pueden ser recomendadas para sistemas de uso de la tierra en esta región, en plantaciones puras o combinadas según sea el objetivo que se pretenda. También se está evaluando la factibilidad socio-económica de estos sistemas, comparándolos con otras actividades practicadas en fincas pequeñas a medianas en la región.

INTRODUCCION

El Instituto de Recursos Tropicales (TRI) de la Escuela Forestal y de Estudios de Medio Ambiente de la Universidad de Yale mantiene proyectos a nivel internacional en colaboración con instituciones dedicadas al estudio y la promoción de usos sustentables de la tierra y la rehabilitación ecológica de áreas degradadas. Como parte de estos esfuerzos, se están llevando a cabo proyectos en las regiones de bosques húmedos de Costa Rica y Argentina para promover el uso de especies arbóreas nativas de valor económico para la reforestación y los sistemas agroforestales, poniendo énfasis en el uso de especies que favorezcan la recuperación de la fertilidad del suelo. En este trabajo se presentan resultados preliminares de experimentos en plantaciones de especies puras y mixtas en la llanura del Atlántico de Costa Rica. Resultados de investigaciones previas habían indicado que algunas especies arbóreas indígenas en esta región tenían tasas de crecimiento y valor económico similar o mayor que las especies exóticas (Espinoza Camacho y Butterfield 1989). Además, en los suelos de plantaciones con estas especies, se encontraron incrementos en los niveles de materia orgánica, nitrógeno y cationes (Montagnini y Sancho 1990a, 1990b, Montagnini et al. 1991). Sin embargo, se necesitan más experiencias sobre la plantación de especies nativas para la producción económica y rehabilitación de suelos. La hipótesis principal de este estudio es que las plantaciones mixtas pueden ser más productivas y ejercer mayores efectos positivos sobre los suelos a largo plazo, que las plantaciones de especies puras. Experiencias anteriores mostraron que algunas especies de este estudio tenían un potencial para el reciclaje de nitrógeno (p.ej, *S. excelsum*), mientras que otras tendían a acumular y reciclar Ca, Mg (*V. hondurensis*) o K (*H. alchorneoides*) (Montagnini et al. 1993a). Asimismo, las especies varían en la tasa de caída y descomposición de hojarasca: por ejemplo, en otros experimentos en La Selva, la hojarasca de *S. excelsum* y *H. alchorneoides* tuvo una tasa de descomposición relativamente rápida, mientras que la de *V. ferruginea* y *V. hondurensis* tendía a acumularse sobre el suelo (Montagnini et al 1993b). Se espera que en parcelas mixtas exista una complementación en los requerimientos lumínicos y nutritivos, y en la influencia de las especies sobre el reciclaje de nutrientes, resultando en sistemas mejor balanceados y que tenderán a un menor deterioro, o aún al mejoramiento de las condiciones del sitio a largo plazo. A su vez, económicamente las plantaciones mixtas tendrían la ventaja de diversificar la producción. Basado en esas experiencias y en otra información previa sobre un total de doce especies nativas de la región (Tabla 1), se establecieron tres plantaciones experimentales con parcelas puras y mixtas sobre pastos abandonados en suelos pobres, en colaboración con la Organización de Estudios Tropicales (OTS) y el Centro de Investigaciones Agronómicas de la Universidad de Costa Rica (UCR). Se están comparando tasas de crecimiento bajo condiciones de parcelas puras y mixtas, y examinando los impactos de estos sistemas sobre la fertilidad del suelo y el reciclaje de nutrientes.

DESCRIPCION DEL SITIO Y DISEÑO EXPERIMENTAL

Los experimentos fueron establecidos en un área de pastos abandonados en la Estación Biológica La Selva de la OTS ($10^{\circ}26'$N, $86^{\circ}59'$W, altitud media de 50m, temperatura media anual de 24°C, precipitación anual media de 4000 mm, con máximos en julio y mínimos en marzo) (Reportes climatológicos de la Estación Biológica La Selva). Los suelos del sitio experimental son Fluventic Dystropepts derivados de aluviones volcánicos; son profundos, bien drenados, sin rocosidad, con contenido de materia orgánica media a baja, textura moderadamente pesada, y generalmente ácidos e infértiles (Sancho y Mata, 1987). El sitio fue limpiado a mediados de la década de los 50 y usado para el pastoreo de ganado hasta 1981 (Pierce, 1991). El sitio experimental era un terreno llano y uniforme.

Las especies arbóreas

Las doce especies arbóreas nativas de este estudio (Tabla 1) fueron seleccionadas de parcelas experimentales de 3-4 años de edad, que formaban parte de un total de aproximadamente 90 especies presentes en un proyecto forestal de OTS en La Selva. Los criterios utilizados en la selección de especies arbóreas de este estudio fueron: la tasa de crecimiento durante los primeros 3-4 años de plantación (Espinoza Camacho y Butterfield, 1989; González et al., 1990); la presencia de nódulos en las raíces de especies leguminosas (observaciones de campo); los impactos sobre la fertilidad del suelo (Montagnini y Sancho 1990a, 1990b, Montagnini et al. 1991, Montagnini y Sancho 1993) y el valor económico (Chudnoff, 1984; González et al., 1990).

Diseño de la plantación

En cada combinación de cuatro especies arbóreas al menos una era leguminosa, fijadora de nitrógeno. También se combinaron especies de crecimiento rápido y especies de crecimiento relativamente más lento (Tabla 1). Las plantaciones fueron montadas en bloques al azar, con cuatro réplicas y seis tratamientos: cuatro parcelas de especies puras para cada especie, una parcela de especies mixtas (con las cuatro especies), y una parcela de regeneración natural. La distancia de plantación inicial fue 2 m X 2 m para acelerar el cierre del dosel y obtener impactos tempranos sobre los suelos. Cada parcela era 32 m X 32 m, con un total de 256 árboles cada uno. Cada bloque era 64 m X 96 m; cada plantación tenia 96 m X 256 m, ó 24,576 m^2, aproximadamente 2.5 hectáreas. En las parcelas individuales, se utilizó un diseño sistemático para maximizar las interacciones entre las especies. Dentro de cada parcela, los árboles de las cuatro especies fueron plantadas alternando dos especies por fila. El orden secuencial de las especies dentro de las filas fue revertido sistemáticamente en fila alternadas. De esta manera, cada fila contenía las cuatro especies combinadas en una secuencia.

Fertilidad del suelo

Se tomaron muestras compuestas en cada una de las cuatro parcelas de cada tratamiento, a 0-15, 15-30, y 30-60 cm de profundidad, inmediatamente después de trazar las parcelas (antes de la limpieza del sitio). Después de la limpieza del terreno, los suelos se muestrearon nuevamente, esta vez la camada superficial se muestreó en dos capas de 0-5 y 5-15 cm, para detectar posibles diferencias en las capas más superficiales. Los muestreos continúan a intervalos anuales para detectar diferencias en la fertilidad del suelo causadas por la presencia de parcelas puras o mixtas en comparación con los controles de regeneración natural.

Preparación del sitio y plantación

La limpieza del sitio se hizo manualmente, aproximadamente un mes antes de cada plantación. El sotobosque se limpió primero con machetes, y los árboles y arbustos fueron talados con motosierra y cortados en partes menores para ser esparcidos, tanto como su peso lo permitiera. No se realizaron quemas. El producto de la limpieza se dejó sobre el suelo, para protegerlo contra la erosión y retrasar el crecimiento de las malezas. A causa de la gran precipitación en el área, hubiera sido difícil programar una quema de los restos de vegetación cortados. Ademas, se estimó que la liberación relativamente lenta de los nutrientes de los restos dejados sobre el terreno sería aprovechada mejor por los árboles, que una liberación súbita provocada por la quema.

Las semillas se recolectaron de árboles del bosque de La Selva o de otras áreas de la región Atlántica. Los plantines fueron producidos en el vivero de la OTS. Las plantaciones se comenzaron cuando por lo menos dos de un grupo de cuatro especies estaban listas. En consecuencia, los períodos de plantación duraron aproximadamente seis meses. Las tres plantaciones fueron cercadas para evitar el daño producido por venados. El desmalezado se hizo manualmente cada vez que el crecimiento de la maleza lo hiciera necesario, en promedio general cada dos o tres meses. No se utilizaron herbicidas.

La altura total y el diámetro a la altura del pecho (dap) fueron medidos en los 256 árboles de cada parcela, sin descartar bordes. Los promedios de altura, dap, área basal y sobrevivencia fueron calculados para cada parcela. El análisis de la varianza y pruebas de significancia estadística (Intervalos de Confianza, P<0.05) fueron realizados usando los promedios de cada parcela para cada parámetro. Todos los parámetros fueron comparados entre las cuatro especies, y también para cada especie en condición pura y mixta.

CRECIMIENTO ARBOREO: RESULTADOS PRELIMINARES

Plantacion 1

Los resultados de las mediciones tomadas a los 18 meses después de la plantación mostraron que los árboles más altos se encontraron en las parcelas de *J. copia*, seguidos por *V. hondurensis*, *S. excelsum* y *C. brasiliense*, en ese orden (Fig. 1). Estos resultados preliminares coinciden con datos anteriores para estas especies en La Selva y sus alrededores (Proyecto Forestal de la OTS). Las mediciones de diámetro empezaron a los 12 meses después de la plantación para *J.*

copia, *S. excelsum* y *V. hondurensis*. El cierre del dosel también ocurrió aproximadamente a los 12 meses después de la plantación en las parcelas puras de estas tres especies. La altura promedio de árboles *J. copia* fue mayor en las parcelas puras que en las mixtas, de acuerdo con las mediciones tomadas a los 12 y 18 meses después de la plantación (Fig. 2). Por otro lado, los diámetros fueron mayores en las parcelas mixtas que en las puras de *J. copia*; estas diferencias eran evidentes a los 18 meses después de la plantación (Fig. 3). Aparentemente, en *J. copia*, especie de crecimiento monopódico, la competencia intra-específica fue mayor que la inter-específica, tendiendo a árboles de mayor altura y menor diámetro en las parcelas puras que en las mixtas. La altura promedio de *S. excelsum* fue significativamente mayor en las parcelas mixtas que en las puras, y no hubo diferencias estadísticamente significativas en los diámetros entre parcelas puras y mixtas de esta especie a ninguna edad, aunque se vio una tendencia a menores diametros en las parcelas mixtas (Figs. 4 y 5). *S. excelsum* presentó la menor sobrevivencia, con valores menores que el 90% a los 6 meses; éstos aún son altos porque los arbolitos muertos fueron reemplazados, hasta los 12 meses después de la plantación original. Esto fue en parte relacionado al daño producido por los venados durante los primeros meses de la plantación antes de que se construyera la cerca; sin embargo, otros factores pueden haber afectado la sobrevivencia de esta especie, ya que los plantines traídos como reemplazo frecuentemente morían o se retrasaban en su crecimiento. Como resultado, esta especie mostró la mayor heterogeneidad en altura y diámetro.

Para *V. hondurensis* y *C. brasiliense* no hubieron diferencias estadísticamente significativas en altura, diámetro o sobrevivencia entre parcelas mixtas y puras en ninguna de las mediciones realizadas. *C. brasiliense* era seis meses menor que las otras tres especies; sin embargo, incluyendo las comparaciones de parcelas de la misma edad (12 meses) todavía *C. brasiliense* era la más baja, y los diámetros eran todavía muy pequeños para ser medidos a esa edad.

Plantación 2.

Como la Plantación 2 fue establecida 6-9 meses después de la Plantación 1, solamente se tenían mediciones de los 3, 9 y 15 meses de edad. A los 15 meses, aún no se tomaban mediciones de diámetro, ni había cierre de dosel en ninguna de las cuatro especies. Como las condiciones del sitio, distancia y procedimientos de plantacion y manejo fueron las mismas para ambas plantaciones, se concluye que al menos en su etapa inicial, en general las cuatro especies de la Plantación 2 (Fig. 6) eran más lentas que las dos especies de mayor crecimiento de la Plantación 1 (*J. copaia* y *V. hondurensis*): la especie con árboles más altos de la Plantación 2: *A. guachapele*, tenía en promedio de 2-2.5 m de altura a los 15 meses, mientras que a los 12 meses *J. copaia* ya tenía más de 4 m de altura en promedio, y *V. hondurensis* tenía 2.5 m. El crecimiento de *A. guachapele*, que era la especie fijadora de N de la Plantación 2, era probablemente más similar al crecimiento de *S. excelsum*, la especie fijadora de N de la Plantación 1.

En la Plantación 2, se vio una tendencia hacia una mayor altura de los árboles en parcelas puras que en mixtas a los 15 meses (Fig. 6), pero las diferencias no fueron estadísticamente significativas ($P<0.05$). A esta fecha, sólo se disponía de resultados de una primera medición para la Plantación 3, los cuales no se presentan en este trabajo.

FERTILIDAD DEL SUELO

En el área de terreno dedicada a la Plantación 1, los suelos en los cuatro bloques presentaron características químicas similares (Tabla 2). Excepto por el pH y al Ca que eran ligeramente mayores en el suelo de la Plantación 1, las tres plantaciones tenían suelos de composición química semejante, y a su vez comparable a otros suelos de áreas experimentales en La Selva. Esto es importante porque permite la comparación con otras experiencias.

En la Plantación 1, los resultados del análisis de suelo a los doce meses de edad, revelaron un mayor contenido de materia orgánica en las parcelas puras de *J. copaia*, que en cualquiera de las otras especies (Fig. 7). Estas diferencias fueron estadísticamente significativas a un nivel de $P<0.12$ a 0-5 cm, y $P<0.07$ a los 5-15 y a los 15-30 cm de profundidad. No hubo diferencias estadísticamente significativas en los otros parámetros medidos. No se esperaba encontrar diferencias entre las parcelas en una etapa tan temprana; sin embargo, es interesante notar que estas tendencias se vieron en la especie de mayor crecimiento, la cual también, según resultados preliminares, presenta una tasa elevada de caída de hojarasca y de acumulación de hojarasca (mantillo) en el suelo. Al igual que las mediciones de crecimiento, la fertilidad de suelos y mecanismos de reciclaje de nutrientes se miden a largo plazo, y servirán para corroborar estos resultados.

FACTORES SOCIO-ECONOMICOS Y DISEMINACION DE RESULTADOS

El costo asociado con las labores de plantación y mantenimiento fue evaluado registrando el tiempo y el número de trabajadores asociados con cada tarea. Otros costos también fueron registrados. Actualmente se está evaluando la factibilidad económica de estos sistemas de uso de la tierra, comparándolos con otras alternativas comunes practicadas por pequeños agricultores en la región. Nuestras interacciones con las instituciones locales operando en la región (OTS, UCR-CIA, Instituto Tecnológico de Costa Rica), así como también con grupos de agricultores locales (Centro Agrícola, otras organizaciones privadas) se espera que contribuyan a la diseminación de los resultados y la promoción de estos sistemas entre los agricultores locales.

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Tabla 1.
Características ecológicas de 12 especies arbóreas nativas cultivadas en plantaciones arbóreas experimentales mixtas- y puras en la Estación Biológica La Selva (Gonzalez et al. 1990, Holdridge & Povada 1975).

Nombre Científico	Nombre común	Familia	Area geográfica nativa	Habitat natural
PLANTACION 1:				
Stryphnodendron excelsum Harms	vainillo	Leguminosa (Mimosoidea)	Costa Rica, Nicaragua y Panamá	Dosel superior, baja altitud, hasta 700m, clima muy húmedo. Suelos aluviales de drenaje pobre, también en colinas y pendientes. También en bosques secundarios. Se adapta a suelos pobres.
Vochysia hondurensis Sprague	mayo, chancho	Vochysiácea	Méjico a Panamá	Dosel superior, tierras bajas, hasta 900m, clima húmedo, en los bordes de montañas. Suelos aluviales ricos o pobres, acídicos, puede crecer en áreas inundadas.
Jacaranda copaia (Aubl.)D.Don.	jacaranda	Bignoniácea	Guatemala a Brasil	Elevaciones bajas, clima húmedo a muy húmedo. Pendientes bien drenadas, no aguanta drenaje pobre. Bosque secundario, colinas bajas, suelos rojos arcillosos poco fértiles.
Calophyllum brasiliense Cambess.	cedro María	Guttífera (Clusiácea)	Méjico al norte de Sur América	Encontrado en varios tipos de habitats de húmedo a seco. Puede aguantar inundación.
PLANTACION 2:				
Albizia guachapele (H.B.K.)Little	cenízaro macho, guayaquil	Leguminosa (Mimosoidea)	Guatemala a Ecuador	Elevaciones bajas con clima húmedo a seco. Común en bosques bajos, bosques secundarios, a lo largo de lechos arenosos de ríos, sabanas. Puede crecer sobre suelos aluviales o arenosos viejos y ácidos.
Terminalia amazonia (J.F.Gmel.)Exell.	roble coral	Combretácea	Sur de Méjico al norte de Sur América	Encontrado en áreas aluviales, ocasionalmente inundadas, o en colinas con suelos arcillosos viejos, ácidos, e infértiles.
Virola koschnyi Warb	fruta dorada	Myristicácea	América Central	Dosel superior, elevaciones bajas, hasta 1,200m, clima muy húmedo. Partes inferiores de colinas, zonas ribereñas. Suelos aluviales, mal drenados, o arenosos. También sobre suelos arcillosos, ácidos, infértiles con alta concentración de Al.
Dipteryx panamensis (Pittier) Record & Mell	almendro	Leguminosa (Papilionoidea)	Nicaragua a Colombia	Dosel superior, elevaciones bajas, hasta 1300m, clima muy húmedo. Tierras bajas y bosques premontanos. Suelos aluviales o arenosos, a veces ácidos, arcillosos.
PLANTACION 3:				
Pithecellobium elegans D.C.Benth	ajillo	Leguminosa (Mimosoidea)	América tropical	Bosque húmedo y seco, bosques inundables, zonas riparias, riscos de caliza. Suelos aluviales, arcillosos o franco-arenosos.
Genipa americana L.	genipa	Rubiácea	América tropical	Bosques de tierras bajas, pendientes. Se adapta a suelos arenosos y pobres.
Vochysia ferruginea Mart	botarrama	Vochysiácea	Nicaragua a Brasil	Bosques de tierras bajas. Suelos bien drenados, ácidos, infértiles.
Hyeronima alchorneoides Fr. Allemao	pilón	Euphorbiácea	Sur de Méjico al sur de Brasil	Colinas, pastos abandonados. Suelos aluviales y pobres.

Tabla 2.
Características químicas del suelo de la plantación 1: Ca, Mg, K, acidez intercambiable, pH, materia orgánica, N total, P extractable y micronutrientes en los suelos muestreados en mayo de 1991.

Bloque	Prof.	Ca	Mg	K	Acidez	pH
	(cm)		$(cmol^+ . l^{-1})$			
1	0-15	1.20a	0.45a	0.22a	1.55a	4.8ab
1	15-30	1.05a	0.40a	0.19a	1.40a	4.9b
1	30-60	1.10a	0.15b	0.11a	1.40a	5.1a
2	0-15	1.10a	0.20b	0.18ab	1.50ab	5.2a
2	15-30	1.00a	0.20ab	0.15ab	1.60a	5.3a
2	30-60	1.10a	0.10b	0.12a	1.40a	4.9a
3	0-15	1.60a	0.50a	0.12b	0.60c	4.9ab
3	15-30	1.30a	0.40ab	0.10bc	0.80b	4.9ab
3	30-60	1.20a	0.30a	0.07a	0.70b	5.1a
4	0-15	1.28a	0.30b	0.12b	0.93bc	4.8b
4	15-30	1.15a	0.20b	0.08c	0.78b	5.0ab
4	30-60	1.10a	0.13b	0.08a	0.55b	5.0a

Bloque	Prof.	MO	N	P	Cu	Fe	Mn	Zn
	(cm)	(%)	(%)			$(mg . kg^{-1})$		
1	0-15	4.06a	0.285a	10.10a	43.5a	1753.5a	47.5a	4.30a
1	15-30	3.58a	0.185a	9.45b	43.0a	1267.0a	29.5bc	2.70b
1	30-60	2.72a	0.195a	7.70a	37.0a	627.5a	20.0b	2.50b
2	0-15	5.83a	0.220a	12.40a	41.0a	1742.0a	27.0a	4.20a
2	15-30	1.74b	0.150a	12.60a	40.0a	1118.0a	29.0bc	4.00a
2	30-60	3.01a	0.110a	8.50a	32.0a	600.0	26.0ab	4.10a
3	0-15	5.83a	0.190a	7.30a	36.0a	1805.0a	57.0a	3.70a
3	15-30	4.49a	0.150a	5.90c	36.0a	1566.0a	52.0abc	2.40bc
3	30-60	3.22a	0.090a	6.50a	27.0a	626.0ab	41.0ab	2.20b
4	0-15	5.14a	0.250a	6.18a	35.8a	1698.3a	59.8a	3.02a
4	15-30	3.65a	0.178a	2.75d	35.8a	1091.3a	55.0ac	1.97c
4	30-60	1.81a	0.108a	1.63b	34.3a	488.8b	53.3a	2.02b

Nota* Para cada parámetro y profundidad, los promedios seguidos por la misma letra no son estadísticamente diferentes $(P>0.05)$.

Leyenda de las figuras:

Jc: *Jacaranda copia*
Vh: *Vochysia hondurensis*
Se: *Stryphnodendron excelsum*
Cb: *Callophylum brasiliense*

Ag: *Albizia guachapele*
Dp: *Dipteyrx panamensis*
Ta: *Terminalia amazonia*
Vk: *Virola koschnyi*

Nota: En todos los gráficos, los promedios en las barras con la misma letra no son estadísticamente diferentes.

g. 1 Crecimiento arboreo en parcelas puras y mixtas (altura a los 18 meses)

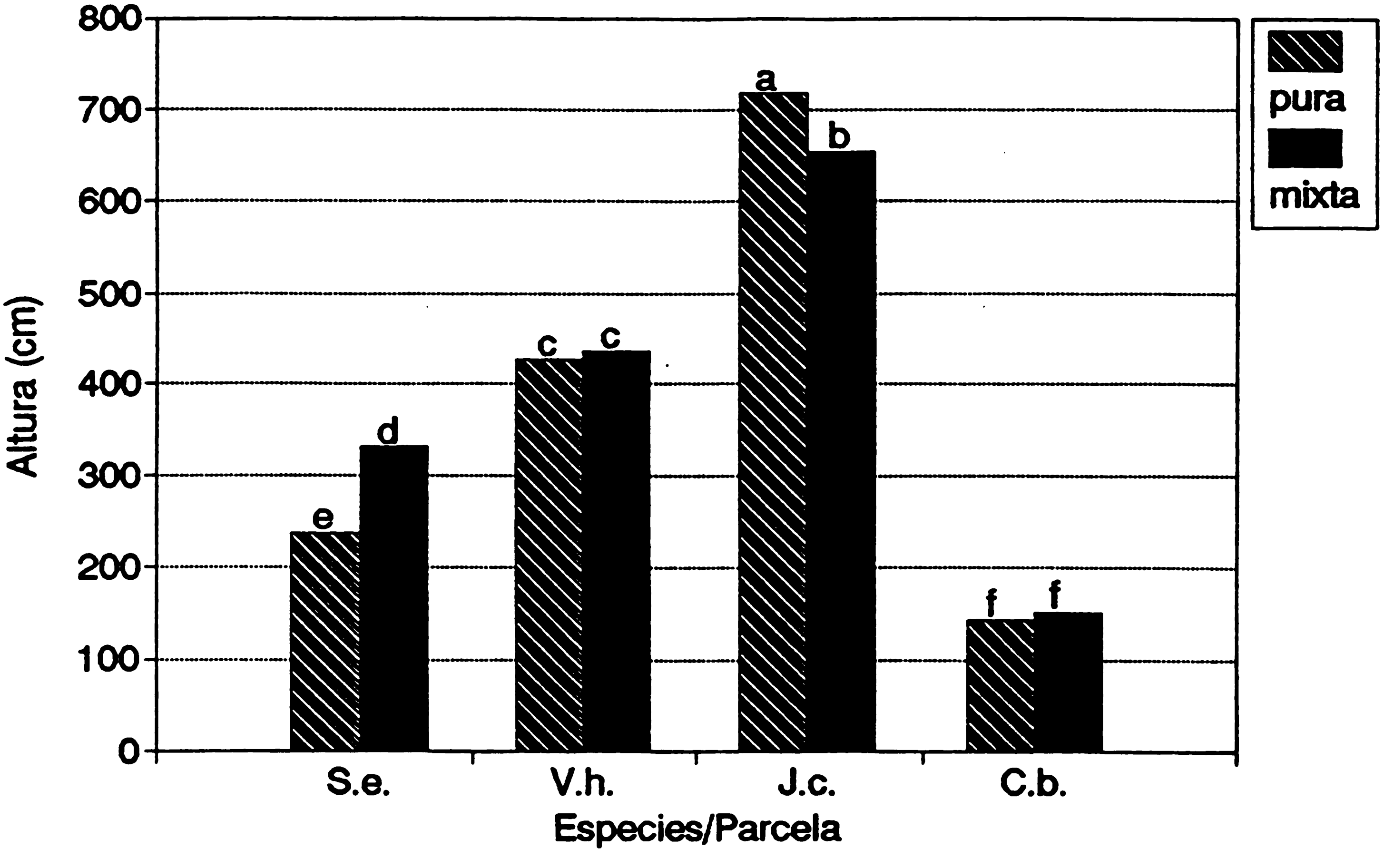
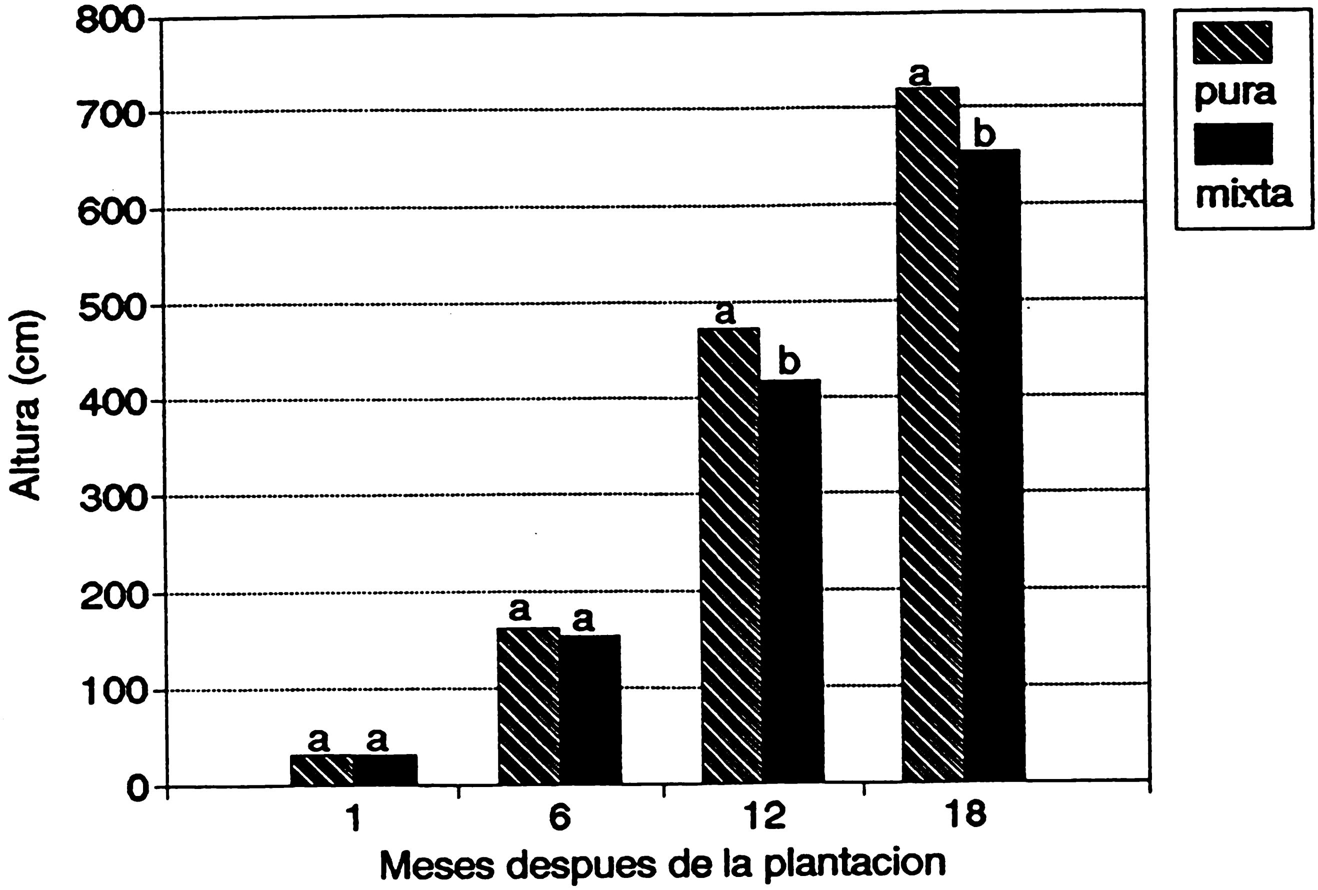


Fig. 2



Altura total de Jacaranda copaia en parcelas puras y mixtas ig. 3

Crecimiento en diametro (dap) de J. copaia en parcelas mixtas y puras

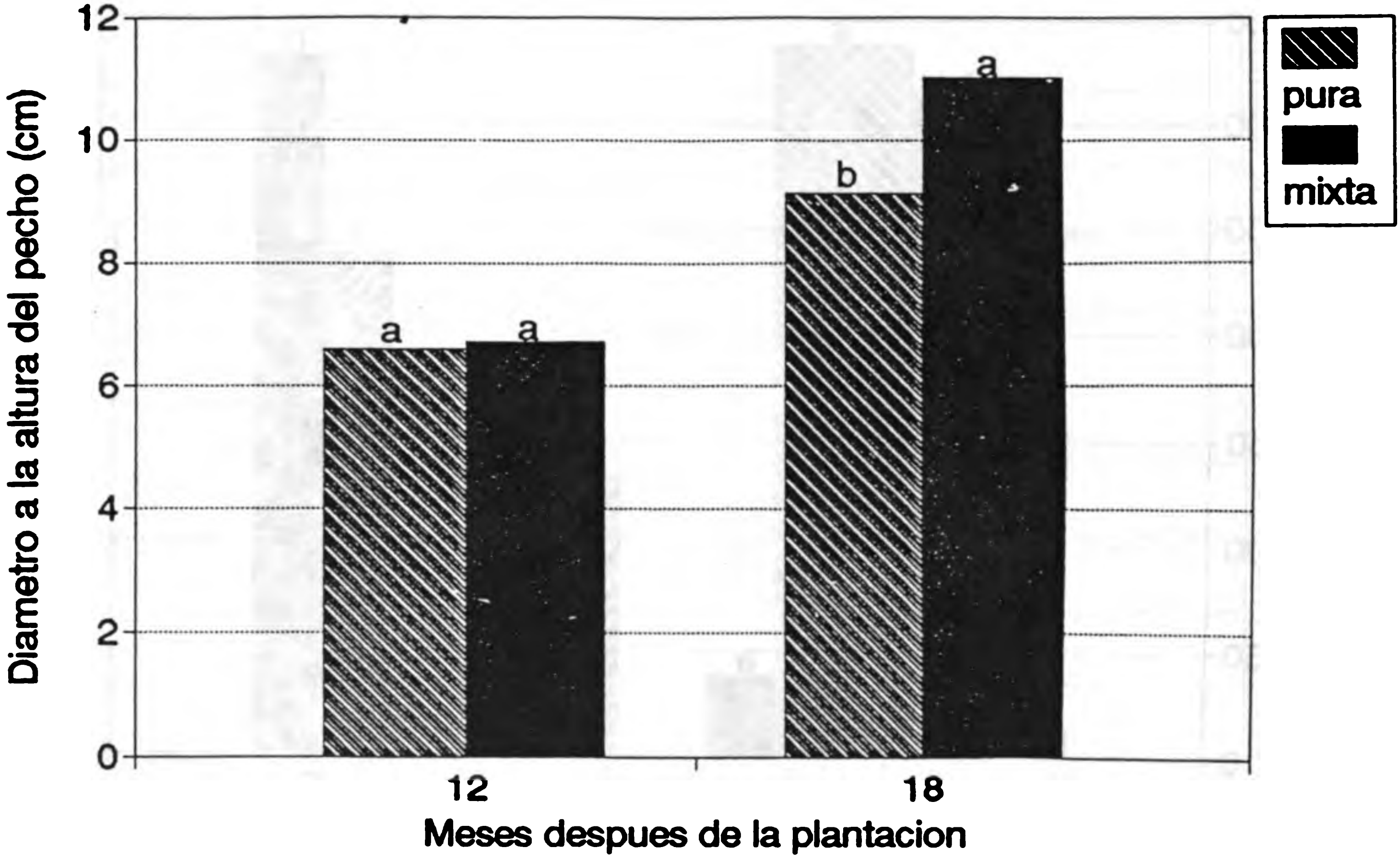
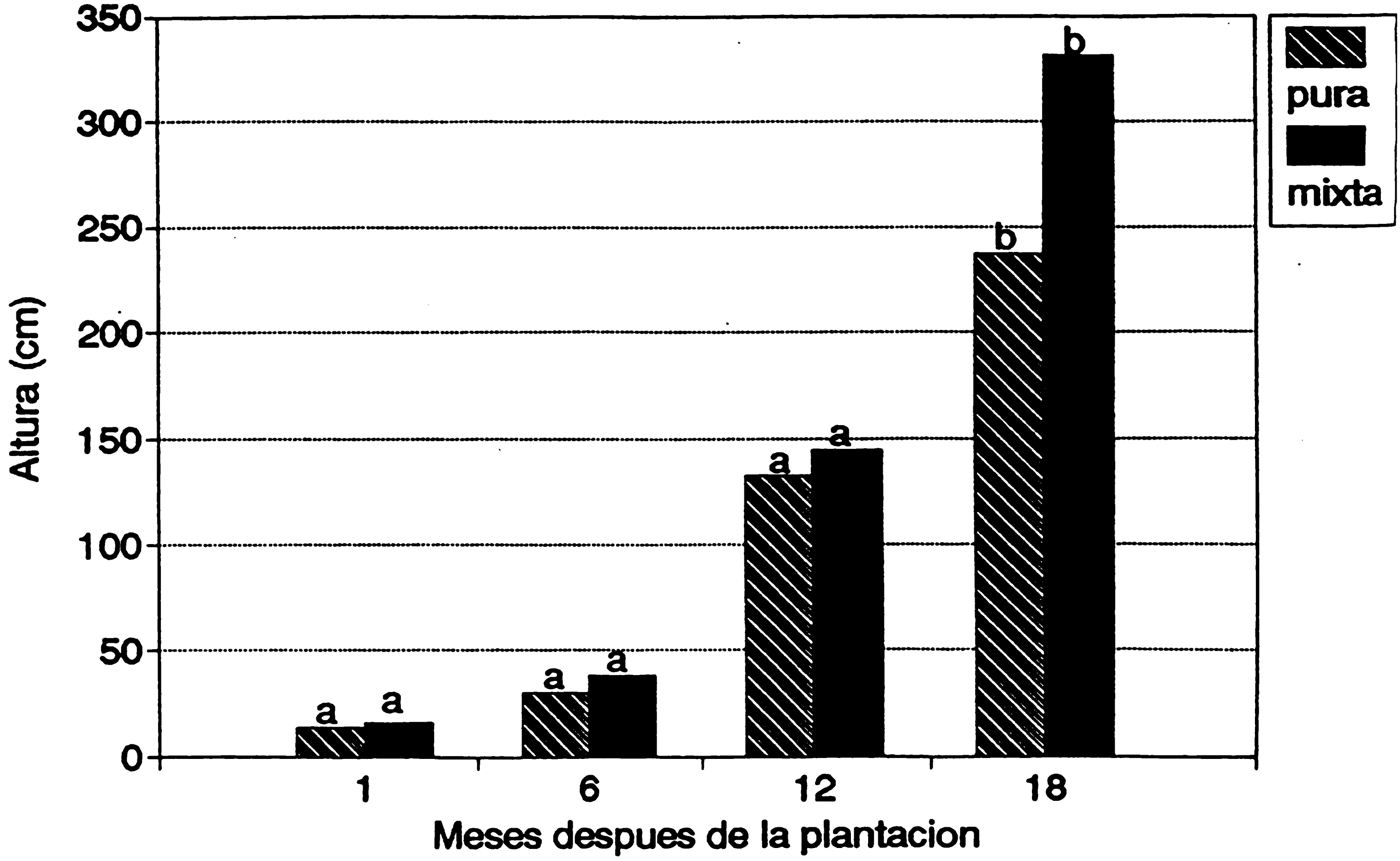
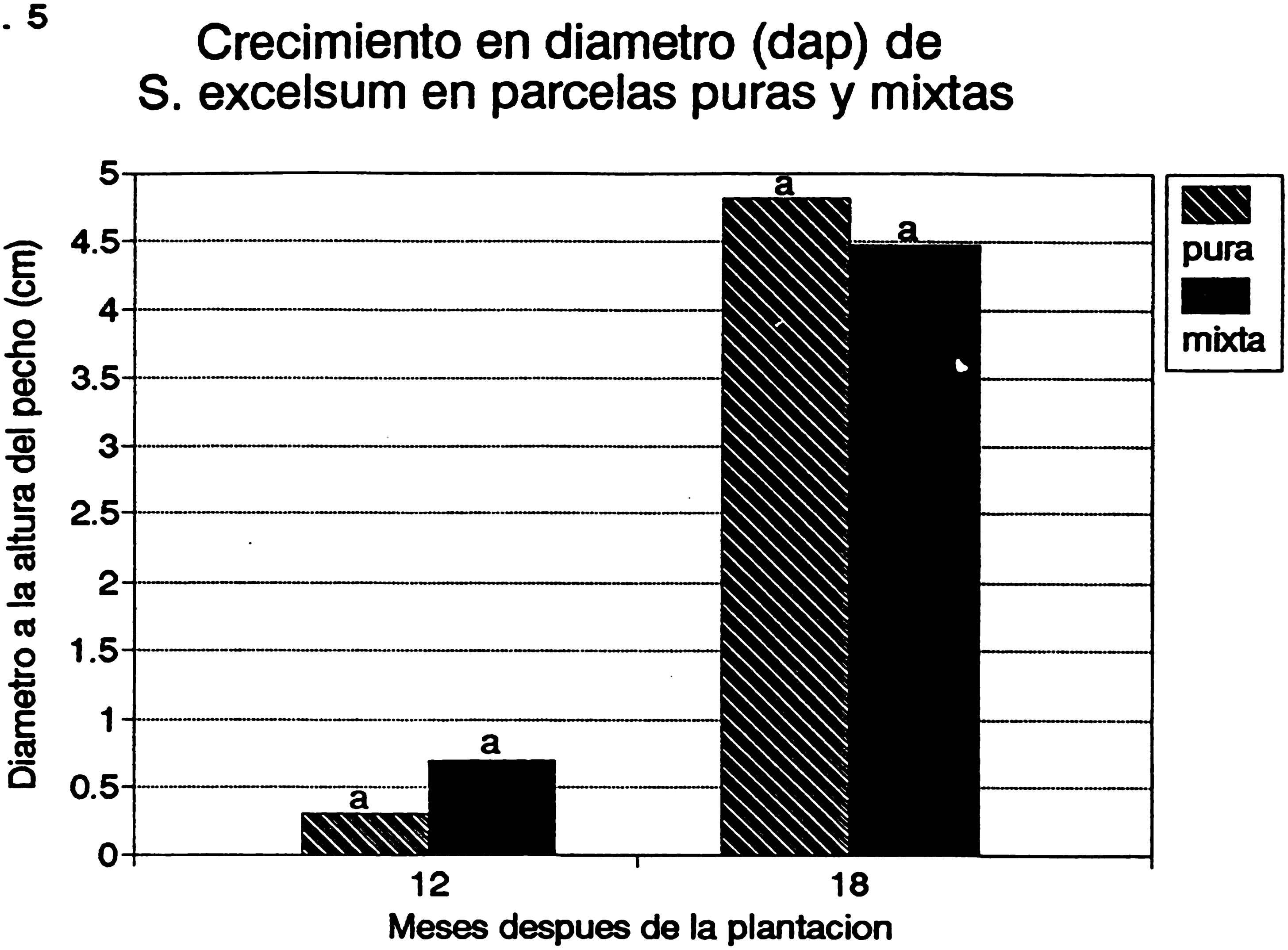


Fig. 4

Altura total de S. excelsum en parcelas puras y mixtas



g. 5



Crecimiento en diametro (dap) de S. excelsum en parcelas puras y mixtas

Fig. 6

Crecimiento arboreo en parcelas puras y mixtas (altura a los 15 meses)

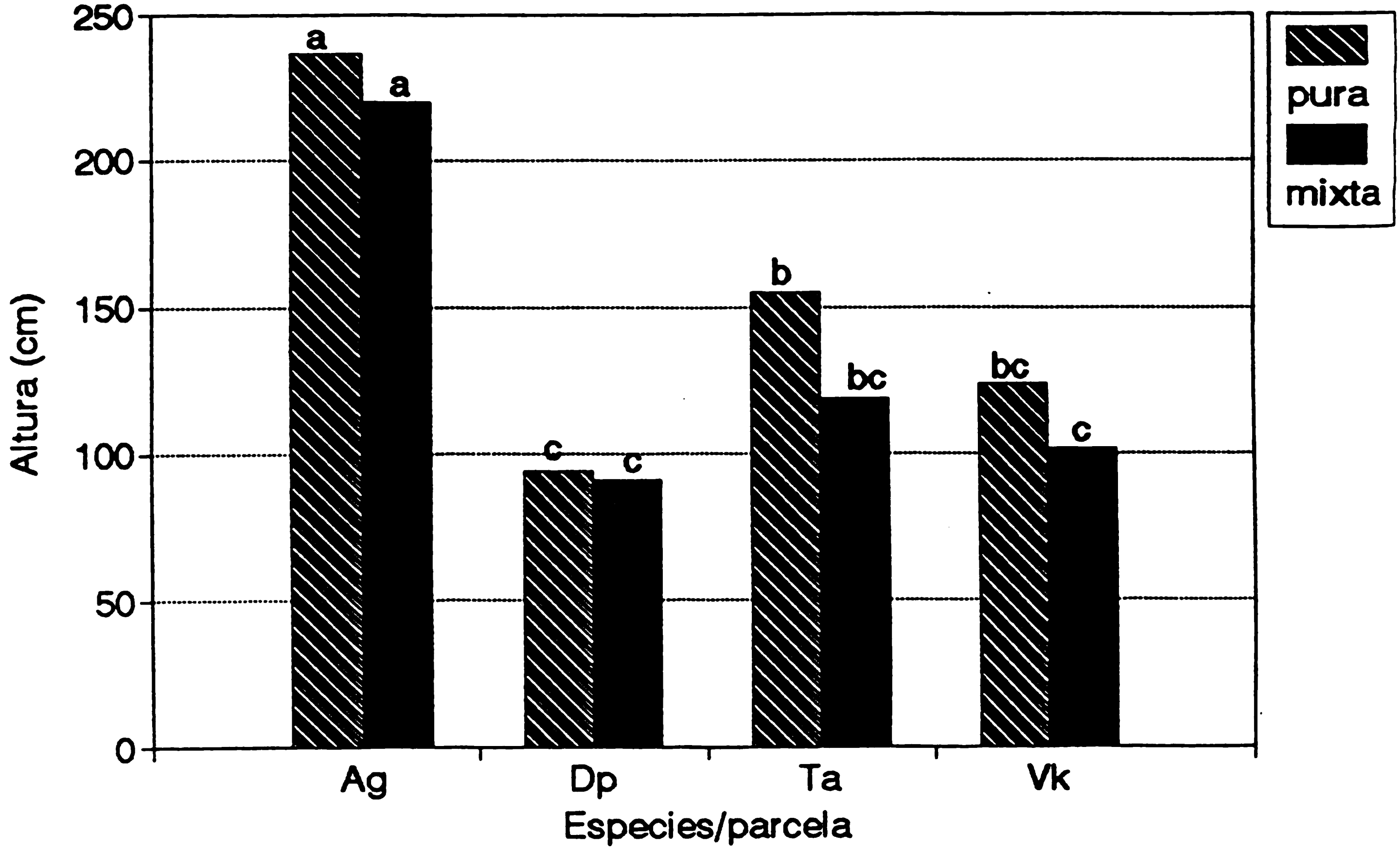
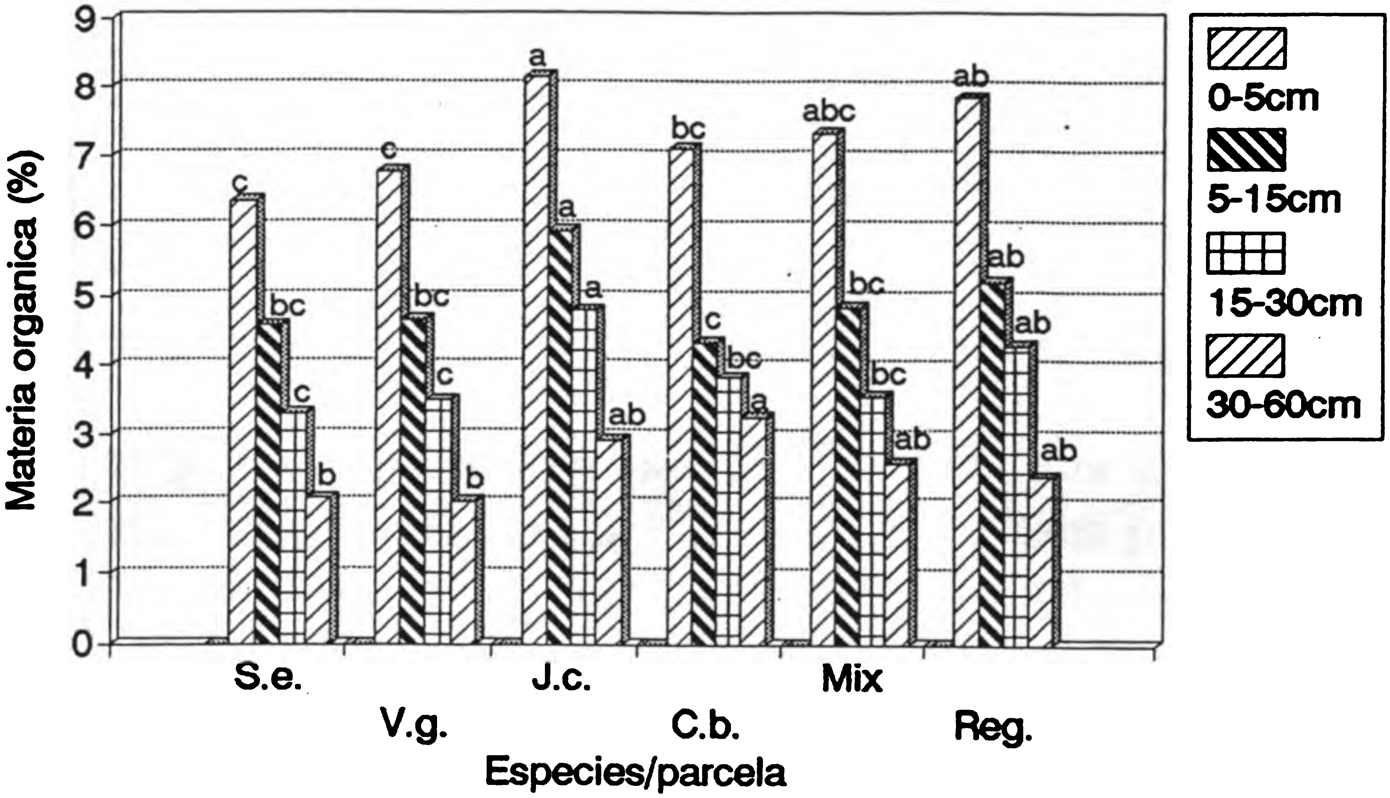


Fig. 7



Materia organica del suelo
Plantacion 1, 12 meses

Vetas 134 . 1993

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CICLAJE DE NUTRIENTES EN PLANTACIONES PURAS Y MIXTAS CON ESPECIES NATIVAS

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Proyecto presentado en la "Segunda Jornada de Trabajo sobre Ecología de Especies Nativas de la Selva Subtropical Misionera"-Eldorado-Misiones- (julio 1992)

I- OBJETIVOS Y RESULTADOS PRELIMINARES DE SOBREVIVIENCIAS Y CRECIMIENTOS.

El objetivo de estos ensayos es de probar el crecimiento de especies forestales de la selva misionera, en plantación a cielo abierto y a la vez, aprovechar el posible efecto beneficioso de la recuperación de áreas degradadas (capueras).

En las plantaciones mixtas se trata de aprovechar los mismos principios que rigen en el ambiente natural, es decir, al combinar diferentes especies, se espera que éstas se beneficien mutuamente, que se complementen desde el punto de vista de sus requerimientos nutricionales, de luz, etc.

Además las mezclas tendrían las ventajas de los sistemas diversos, en oposición a los monocultivos; se espera que a largo plazo, sus efectos sobre los suelos sean mejores que en los monocultivos.

También representarían ventajas desde el punto de vista del ataque de plagas y finalmente, desde el económico se obtendrían productos diversificados que se pueden aprovechar en diferentes momentos según necesidades y precios de mercado.

En Misiones, contamos con dos ensayos de cuatro especies cada uno: el primero en la Estación Manuel Belgrano (San Antonio), a partir de una capuera alta, con situación original de suelos moderadamente degradados y el segundo en terrenos de la Escuela Agrotécnica de Eldorado, sobre un suelo de agricultura de más de 40 años, en una situación original muy degradada y difícil de manejar.

Las especies del primer ensayo son:

Parapiptadenia rigida (Anchico colorado), especie leguminosa que se espera que contribuya a largo plazo con un aporte de nitrógeno al suelo; *Cordia Trichotoma* (Loro negro o peteribí), datos de la literatura indican que ésta puede aportar en el reciclaje del calcio y magnesio; *Ocotea puberula* (Laurel Guaicá) y *Peltophorum dubium* (Cañafistola), de las cuales no existen datos sobre su posible aporte o exigencias nutricionales.

El segundo ensayo lo componen las siguientes especies: *Enterolobium contortisiliquum* (Timbó) y *Lonchocarpus muehlbergianus* (Rabo molle), como dos especies que podrían aportar nitrógeno al sistema; *Balfourodendron riedelianum* (Guatambú blanco) y *Bastardiopsis densiflora* (Loro blanco).

En esta condición de situación original muy degradada la especie que mejor se ha comportado ha sido el Timbó, que a pesar de mostrar gran variabilidad entre individuos, presenta ya árboles de dos a tres metros de altura que pronto requerirán poda de corrección.

Las otras tres especies y más que nada el Loro blanco y Guatambú, exigieron algunos tratamientos especiales. Recientemente se abrieron pozos (60-70 cm de profundidad x 30-40 cm de ancho), colocando en el fondo material degradado de hojas de té como materia orgánica mezclado con tierra a los fines de mejorar la estructura del suelo.

Con este tratamiento se ha observado una mejoría en el aspecto de los plantines.

II- ESTUDIOS PARALELOS SOBRE EL RECICLAJE DE NUTRIENTES PARA LAS ESPECIES INVOLUCRADAS.

Complementando este proyecto se realizó el examen de la influencia de árboles de las especies de este proyecto, sobre los suelos, tomándose para ese fin, rodales puros o casi puros de regeneración, con árboles adultos.(Tuvo a su cargo este proyecto: Healy Hamilton, estudiante de maestría de la Escuela Forestal y de Ciencias Ambientales de la Univ. de Yale).

Se trabajó en tres sitios:

9 de Julio, con Guatambú solamente.

Montecarlo, con Laurel Guaicá.

Victoria, con Guatambú, Loro Negro, Loro Blanco y Timbó.

En todos los casos se muestreó en suelo con barreno a cuatro profundidades: 0-5, 5-15, 15-30, y 30-45 cm.

Las muestras se secaron y pasaron por tamiz de 2 mm y se llevaron a Yale, para análisis de pH, carbono, nitrógeno, calcio, magnesio, potasio, fósforo y aluminio.

Como proyecto aparte, se tomaron muestras de hojas y ramas con una podadora y también de raíces con un barreno especial para raíces; esto se realizó para las ocho especies de este proyecto. Esta muestras también se analizaron en Yale para determinar la composición química para los mismos nutrientes a los fines de tener una indicación preliminar de requerimientos nutritivos y posiblemente al ciclaje de nutrientes de cada especie.

Finalmente se realizó un ensayo de invernadero con plantines de 5 de estas especies, a las que se aplicaron dos dosis de nitrógeno y dos de fósforo, en dos tratamientos separados; se midió la altura y número de hojas en los tratamientos y los controles.

Los resultados de las mediciones de suelo (yerbal con árboles de regeneración natural), muestran que, tomados en conjunto, tiende a haber un mayor contenido de elementos nutritivos que bajo las cuatro especies que se encontraron en rodales puros de árboles adultos, en comparación con áreas tomadas como control, fuera del rodal, sin árboles.

Se observaron diferencias estadísticamente significativas entre las especies y entre éstas y el área de control, para los parámetros estudiados: la especie que más se destacó fué Loro Blanco, con los mayores valores en todos los parámetros y las de menores diferencias fué el Guatambú que presentó valores mayores que el control solo para el calcio, potasio y nitrógeno.

Las otras especies presentaron mayores valores que el control en todos los casos; el Loro Negro en orden en cuanto a cantidadd e nutrientes, excepto en el magnesio, en el cual fué superado por el Timbó. A pesar de ser una especie fijadora de nitrógeno, el Timbó presentó valores similares a Guatambú y Loro Negro, siendo superado en este parámetro por el Loro Blanco.

En 9 de Julio, donde solo se encontró Guatambú en rodal puro, se repitieron algunas de las tendencias encontradas para esta especie en Victoria, es decir diferencias no muy bien marcadas con respecto a los controles, con el mayor impacto aparentemente con respecto a nitrógeno total.

Finalmente en Montecarlo, bajo Laurel Guaicá no se encuentran mayores contenidos de nutrientes con respecto al control, con excepción quizás del nitrógeno y fósforo; aunque estas diferencias no fueron estadísticamente significativas.

El análisis foliar de las especies de estos ensayos mostraron un mayor contenido de nitrógeno en Guatambú, Rabo Molle, y Laurel Guaicá; el menor contenido fué el de Cañafístola y valores intermedios para los demás.

El calcio fué el mayor en Anchico Colorado, Loro Negro, Rabo Molle, Loro Blanco y Guatambú, y menor en Timbó, Laurel Guaicá y Cañafístola.

El potasio fué mayor en Loro Blanco y los menores valores se encontraron en Anchico Colorado y Cañafístola, los valores intermedios en las otras especies.

El magnesio fué mayor en Guatambú, Loro Negro, Loro Blanco y Timbó.

El fósforo fué mayor en Laurel Guaicá, Rabo Molle y Anchico Colorado.

Estos datos necesitan ser complementados con información sobre la velocidad de descomposición de las hojas de estas especies, para comprobar si un alto contenido en un determinado nutriente, resultará en un efecto similar sobre el contenido de un mismo nutriente en el suelo.

Estos trabajos será encarados según un proyecto organizado por Lidia López Cristóbal y Juan D. Perie.

Mycorrhiza (1994) 5:45–51

ORIGINAL PAPER

Heidi Asbjornsen · Florencia Montagnini

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

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

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

Introduction

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

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

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

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

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

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

Materials and methods

Site description

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

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

Soil analysis

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

Mycorrhizal analysis

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

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

Inoculum potential

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

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

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

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

Growth analysis

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

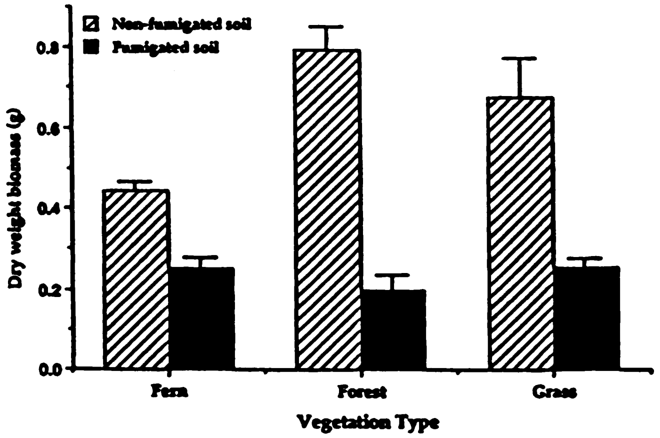

Fig. 1 Total biomass (above and below ground) of *S. microstachyum* seedlings grown in nonfumigated and fumigated soil inoculum collected from beneath fern, forest, and grass vegetation, 160 days after transplanting. The sample size for each treatment group was 6–10 seedlings. Significant differences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

Root colonization

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

Statistics

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

Results

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

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

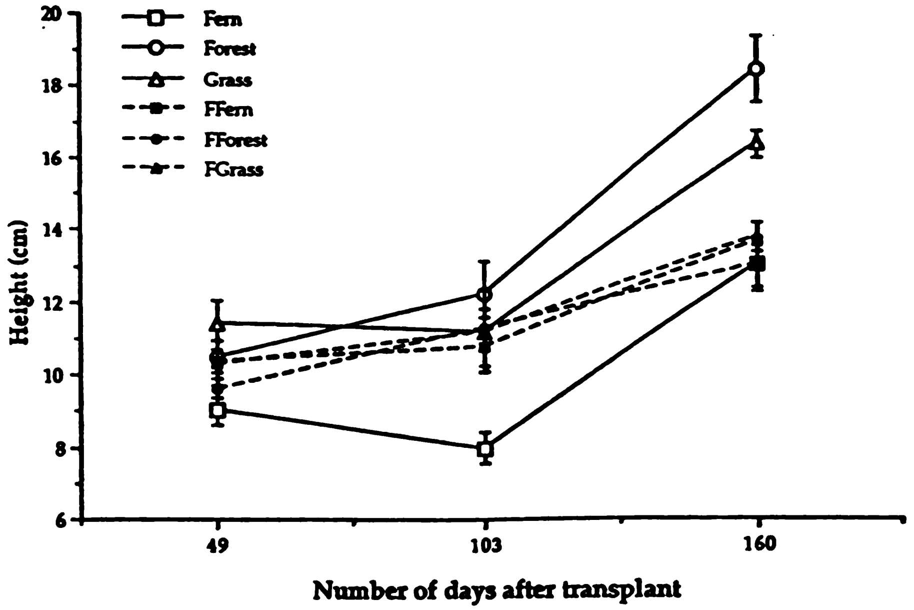

Fig. 2 Height of *S. microstachyum* seedlings grown in nonfumigated and fumigated soils collected from beneath fern, forest, and grass vegetation 49, 103, and 160 days after transplanting. The sample size for each treatment group was 6–10 seedlings. Significant differences between treatment groups are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

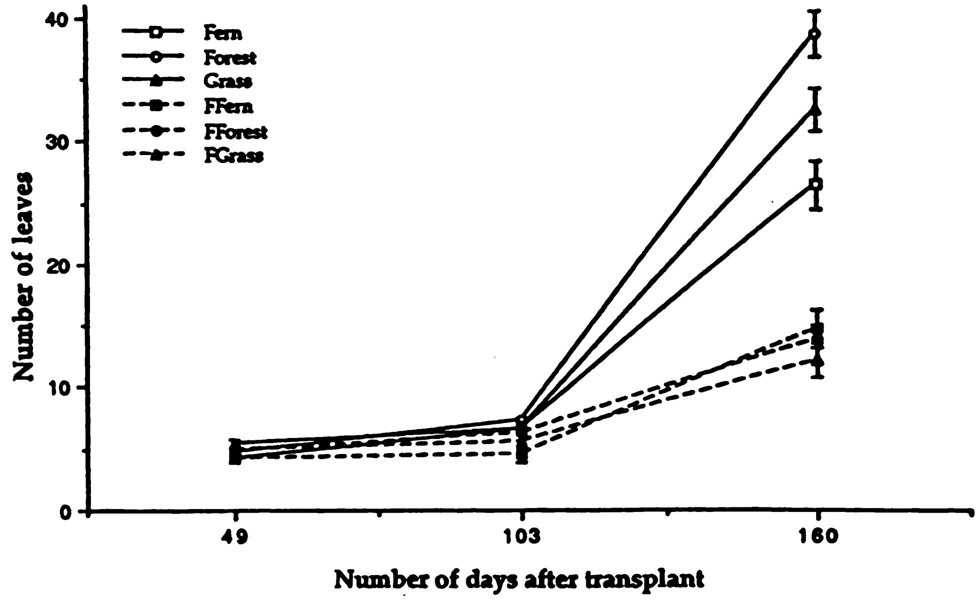

Fig. 3 Number of leaves of *S. microstachyum* seedlings grown in nonfumigated and fumigated soil inoculum collected from beneath fern, forest, and grass vegetation 49, 103, and 160 days after transplanting. The sample size for each treatment group was 6–10 seedlings. Significant differences between treatment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

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

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

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

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

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

Discussion

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

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

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

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

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

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

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

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

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

Introduction

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

Materials and methods

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

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

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

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

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

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

Results

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

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

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

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

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

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

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MIXED-TREE PLANTATIONS IN THE HUMID TROPICS: GROWTH, LITTERFALL AND ECONOMICS OF EXPERIMENTAL SYSTEMS IN LATIN AMERICA

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SUMMARY

Mixed-tree plantations can be more productive, financially attractive and more sustainable in the long term than monospecific systems. Three experiments with four indigenous species each in pure and mixed designs were established on abandoned pastures in the humid lowlands of Costa Rica. In the oldest of the three combinations, at 3 years of age, the highest trees were those of *Jacaranda copaia* (12.7m), followed by *Vochysia guatemalensis* (8.8m) and *Callophylum brasiliense* (3.3m). The DBH of *J. copaia* and *V. guatemalensis* was significantly larger in mixed than in pure plots. Above-ground biomass was also larger in mixed plots. *V. guatemalensis* and *J. copaia* had the highest annual litterfall, while the mixed plots had intermediate values and less pronounced peaks. There was a trend of higher incidence but lower severity of pest damage in mixed than in pure plots. In spite of relatively high establishment costs, with the estimated rotation times and timber prices these systems are financially attractive to the farmers.

Key words: mixed plantations, native trees, rehabilitation, pest damage, economics

INTRODUCTION

Despite the benefits of tree plantations, such monospecific systems and especially monocultures, i.e. the succession of one pure stand by another of the same species --particularly when they contain low genetic variation-- are likely to result in soil degradation, yield decline, and losses from pests, diseases and adverse weather conditions. Mixed-species plantations can help offset some of these disadvantages. Mixed plantations can provide heterogeneity of leaf

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

litter which may promote its decomposition and prevent its accumulation on the forest floor, thus helping to maintain soil organic matter. They can also supply a more permanent ground cover and reduce risks of soil erosion (Wormald 1992). Mixtures including nitrogen-fixing species are likely to be beneficial on N-deficient sites. Additionally, higher species diversity in mixed plantations in comparison with monospecific systems of low genetic variation, may be an important defense mechanism against pests and diseases, although it cannot be assumed that species diversity will provide stability in all artificial stands (Perry and Maghembe 1989). Experiences comparing monospecific and mixed species plantations are still few and evidence of their advantages and disadvantages appear to be site specific (Wormald 1992). Mixed systems should be carefully planned and managed taking into consideration both ecological interactions and economic aspects.

In this article we report results from two experimental plantations with native trees in mixed and pure stands on abandoned pasture sites in the Atlantic humid lowlands of Costa Rica. Some of the species have had high performance in monospecific plantations on degraded pastures (Butterfield and Espinoza 1994; González and Fisher in press), but they have not been tested in mixed plantations, neither have their effects on soils in mixed designs been studied. The hypothesis was that mixed plantations are more productive and financially attractive, and exert more positive effects on soils than tree monocultures. The experiments involved examining a set of tree productivity, nutrient recycling and economic parameters, which are suggested as key factors for the evaluation of the sustainability of the proposed systems.

STUDY SITE AND METHODS

Plantation Establishment and Management

The experiments were established on abandoned pasture at the La Selva Biological Station in the Atlantic humid lowlands of Costa Rica (10°26'N, 86°59'W, 50 meters mean altitude, 24°C mean annual temperature, 4000 mm mean annual rainfall). Soils are Fluventic Dystropepts derived from volcanic alluvium; they are deep, well drained, stone-free, with low or medium organic matter content, moderately heavy texture, and are generally acid and infertile (Sancho and Mata 1987). The area had been cleared in the mid-1950s and grazed until 1981, in a land use pattern common in the region (Montagnini 1994). The area was on flat, uniform terrain. By the time of clearing for the plantations, the area was covered with shrubs and early successional trees, interspersed with patches of grass and ferns.

In each mixture of four tree species there was at least one leguminous, nitrogen-fixing tree, and fast- and relatively slower- growing species. The criteria for species selection were: growth rate and economic value (Chudnoff 1984; González et al. 1990), potential impacts on soil fertility (Montagnini and Sancho 1990a, 1990b; Montagnini et al. 1991, 1993a, 1993b; Montagnini and Sancho 1994a, 1994b, 1994c), and seedling availability. The plantations were set in randomized blocks, with four replicates and six treatments: four pure-species plots of each species, a mixed-species plot (with the four species), and natural regrowth. Initial plantation distance was 2m x 2m to speed up canopy closure and obtain early impacts on soils. Thinning was planned after canopy closure to leave a 2m x 4m distance. Each plantation was 96m x 256m (24,576 m^2) subdivided in four 64m x96 m blocks, each with six 32m x 32m plots. Within each plot, trees of the four species were planted alternating two species per row. The sequential order of the species within rows was systematically reversed every other row. In that manner, each line contained the four species of the mixture in a sequence.

Site clearing was done manually and no burning was done. The slash was left on the floor, to protect against soil erosion and to delay the growth of weeds. Seeds were collected from trees at the La Selva forest or from other areas in the region. Seedling replacement was done one month after planting and again as needed during the first year. The plantations were fenced to avoid deer browsing. Weeding was done manually as needed (including the natural regrowth plots for consistency) and no herbicides were used. The total height and the diameter at breast height (DBH) where measured on all 256 trees of each plot. Measurements were taken every six months for the first two years and annually thereafter. Analysis of variance and tests for means (confidence limits, $P<0.05$) were run using the means of each parameter from each of the four replicate plots. All parameters were compared among the four species, and also among each species in pure and mixed plots.

Litterfall and Soil Sampling

Procedures for litterfall collections and analysis are described in Montagnini et al. (1993b). Soils were sampled annually. Methods for soil sampling and analysis are found in Montagnini and Sancho (1990a, 1990b) and Montagnini et al. (1993a).

Pest Damage

Evaluations of pest damage were done during plantation establishment up to two years of age. Each plantation was examined at least twice at two different times of the year. The methodology followed Moulaert and Arguedas Gamboa (1993). Damage incidence (%) was calculated as the number of affected individuals, divided by the total number of individuals in each plot. Damage severity was calculated as the number of damaged parts (leaves, branches) present, divided by the maximum number of damaged parts possible (independently of the number of individuals affected).

Financial Analysis

Establishment and maintenance costs were calculated from field observations on activities carried on by workers during the first three years, and estimates were projected to five years. The data were adjusted for experimental costs: i.e. the costs of those tasks that were exclusively research oriented were subtracted from the final calculations.

RESULTS AND DISCUSSION

Tree Growth

In Plantation 1, three years after planting, *Jacaranda copia* had the tallest trees with more than 12 meters, followed by *Vochysia guatemalensis* with almost 9 meters. *Callophylum brasiliense*, six months younger than the others, was less than 4 meters (Table 1). *Stryphnodendron microstachyum* showed the lowest survival, in part related to deer browsing before the fence was built; however, other factors might have also affected early survival of this species, since the seedlings brought for replacements often died or lagged far behind. A fungal disease resulted in significant mortality of *S. microstachyum* after 2 years, and at 3 years only trees in the mixed plots had survived. *J. copaia* and *V. guatemalensis* had greater diameters in mixed than in pure plots just after canopy closure (Fig. 1), and their total above-ground biomass (stems, branches and leaves) was also larger in mixed plots (Fig. 2).

In Plantation 2, 27 months after planting the tallest trees were those of *Terminalia amazonia* and *Albizia guachapele* (Table 1). *Dipteryx panamensis* was 6 to 8 months younger than the others. The four species had closed canopies at 27 months. *T. amazonia* showed the lowest survival (60-65%), related with attacks by leaf-cutting ants (*Atta cephalotes)*, and with no differences between pure and mixed plots. *D. panamensis* and *Virola koschnyi* followed with 73-75% and 76-88% respectively, in both cases probably related to a delay in the time of planting due to unavailability of seedlings, which led to planting in April-May, when the weather was drier. At 27 months diameters at breast height were greater in the mixed plots of *A. guachapele, T. amazonia* and *D. panamensis*, and they were smaller in the mixed plots of *V. koschnyi* (Table 1). Plantation 3 was 18 months old and results are not presented here.

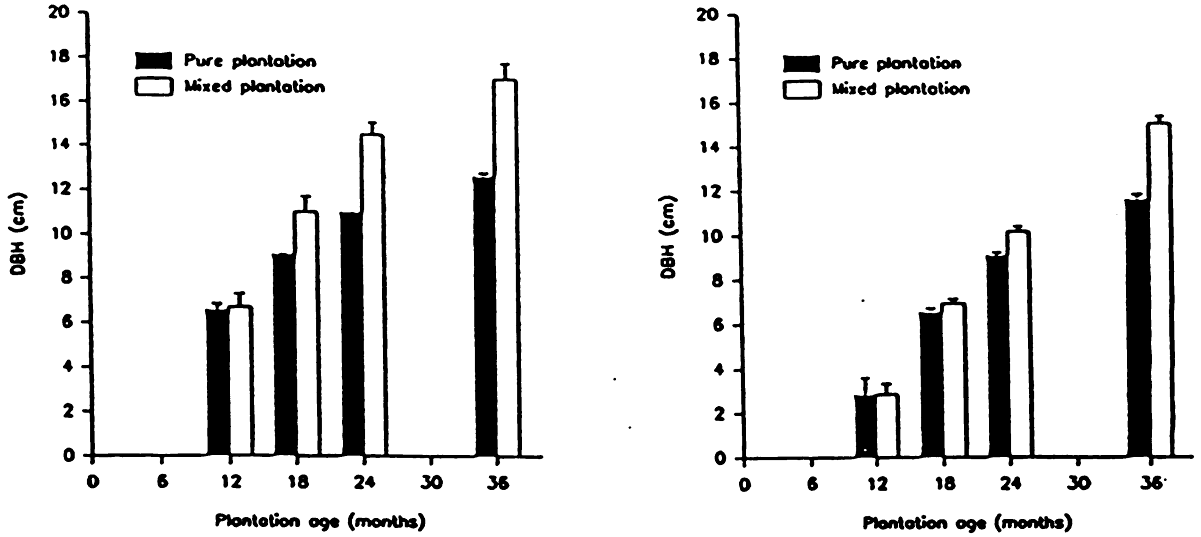
The growth rates shown here agree with those reported earlier for these species at La Selva and elsewhere in Costa Rica (González et al. 1990; Butterfield and Espinoza 1994; González and Fisher in press; Nichols 1994), all in pure plantations. The larger DBH in mixed plots found just after canopy closure for the species of this research is problably the result of less competition in mixed conditions in comparison with more intense, intra-specific competition in the pure treatments. Conversely, with their relatively slower growth, *C. brasiliense* and

V. koschnyi had not closed canopies by the time of these measurements and they were probably subject to competition by the other, faster growing or (for *C. brasiliense*) older species. However, management practices (e.g. thinning, pruning) could favor the future growth of the more suppressed species.

Table 1. Growth and survival of the species of plantations 1 and 2: within each plantation, all parameters are compared among 4 species and also among pure and mixed conditions. Means are significantly different when the standard errors are followed by different letters (n=4, P<0.05).

Species/ Plots	Total height (m)	DBH (cm)	Survival (%)
Plantation 1: 3 years of age.			
S. microstachyum			
pure	ND	ND	ND
mixed	4.59(0.30)c	4.91(0.12)e	46.1(5.61)d
V. guatemalensis			
pure	8.86(0.25)b	11.6(0.25)d	98.4(0.32)a
mixed	8.81(0.13)b	15.1(0.33)b	97.6(1.50)a
J. copaia			
pure	12.6(0.29)a	12.6(0.15)c	95.7(1.51)a
mixed	12.7(0.69)a	17.0(0.70)a	97.6(1.50)a
*C. brasiliense**			
pure	3.77(0.21)d	4.26(0.15)f	82.2(2.71)b
mixed	3.31(0.14)d	3.30(0.09)g	76.9(2.15)c
Plantation 2: 27 months of age.			
A. guachapele			
pure	4.38(0.08)bc	4.73(0.09)de	87.5(3.93)a
mixed	4.64(0.16)b	5.52(0.30)b	92.6(3.01)a
*D. panamensis**			
pure	4.19(0.30)bc	4.06(0.13)f	75.8(2.45)b
mixed	4.44(0.20)bc	4.23(0.14)ef	73.4(3.38)bc
V. koschnyi			
pure	3.94(0.42)c	5.28(0.50)bc	88.5(3.16)a
mixed	4.05(0.13)bc	5.02(0.24)cd	76.2(2.50)b
T. amazonia			
pure	5.57(0.48)a	5.69(0.12)b	66.3(6.79)cd
mixed	5.52(0.23)a	6.45(0.10)a	58.9(3.01)d

Note* Six to eight months younger than the others.
ND: no data for *S. microstachyum* in pure plots (see text).



J. copaia

V. guatemalensis

Fig. 1. Diameter growth (DBH) of J. copaia and V. guatemalensis in pure and mixed conditions. Bars are standard errors.

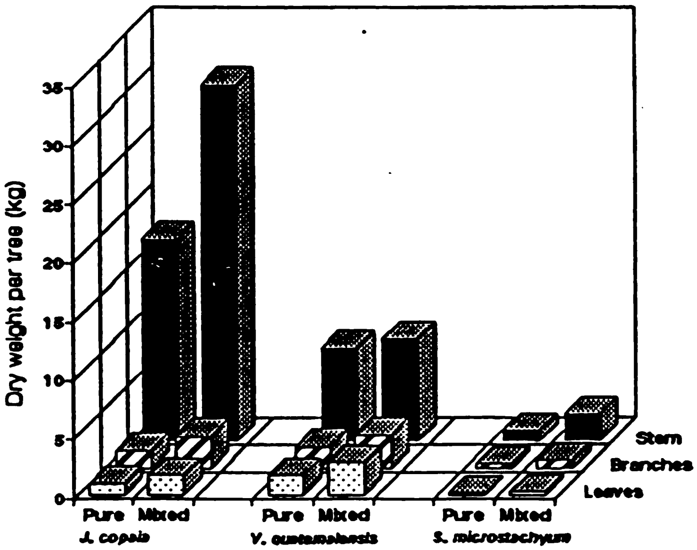


Fig. 2. Biomass of three species of Plantation 1 at 26 months of age.

Litterfall and Soil Chemistry: Plantation 1

The total annual litterfall was higher in *V. guatemalensis*, followed by *J. copaia* and the mixed plots (Fig. 3). The mixtures had intermediate values and less pronounced peaks and low points, resulting in a more even soil cover year round. The organic matter was higher in the topsoil under *J. copaia* and *V. guatemalensis*, the lowest values were found under *C. brasiliense*, with the mixed and the regrowth in an intermediate position (Fig. 4). Apart from the effects of the trees, organic matter inputs to the soils in all treatments (including the regrowth) was probably increased by weeding, until canopy closure when weeding was no longer needed.

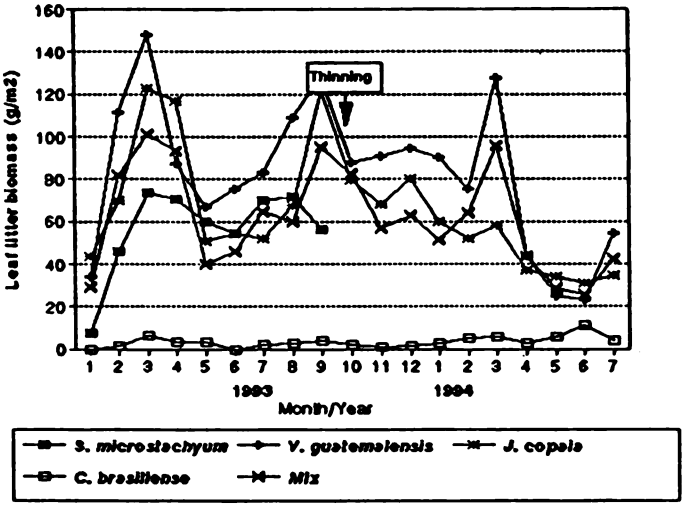


Fig. 3. Leaf litter monthly totals, Plantation 1, 1993-1994.

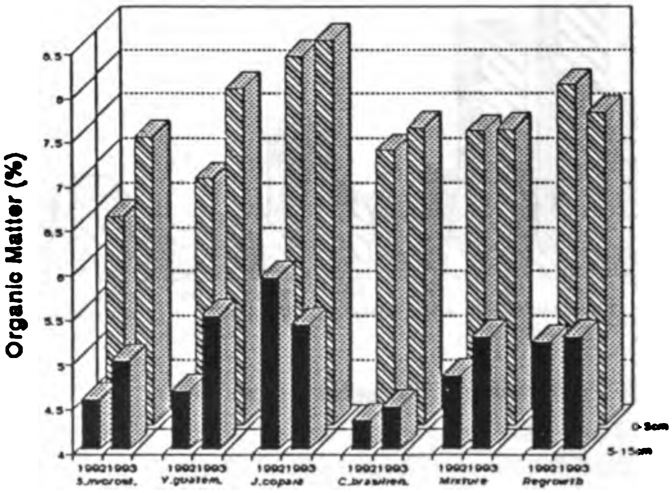


Fig. 4. Soil organic matter in Plantation 1, 1992-1993, 1 and 2 years old.

Pest Damage: Plantation 1

In Plantation 1, at 28 months of age (Fig. 5), *V. guatemalensis* and *C. brasiliense* had higher damage incidence (i.e., a higher number of affected individuals) in the mixed than in the pure plots. Probably in the mixed plots, higher tree diversity favored a more diverse arthropod population which attacked more trees. In contrast, damage severity was lower in the mixed than in the pure plots of *S. microstachyum*, reaching levels of approximately 40% and 90%, respectively (Fig. 5). Although it is not shown in the herbivory data because it started later, the disease that affected *S. microstachyum* (antracnosis, caused by the fungus *Glomerella spp.*), resulted in complete mortality in pure plots (as it can be seen in Table 1) while many trees still survived in mixed plots at 3 years. Damage severity (i.e., the intensity of damage, independent on the number of damaged individuals) was expected to be higher in pure than in mixed plots, because the pure plots with more uniform conditions could favor the spread of individual pests. However, although true for *S. microstachyum*, this was not the case for either *V. guatemalensis* or *C. brasiliense*: there were no significant differences in severity between pure and mixed plots, although severity was relatively low in both cases (<20%). Probably differences in severity between pure and mixed plots only become evident at relatively high levels of damage.

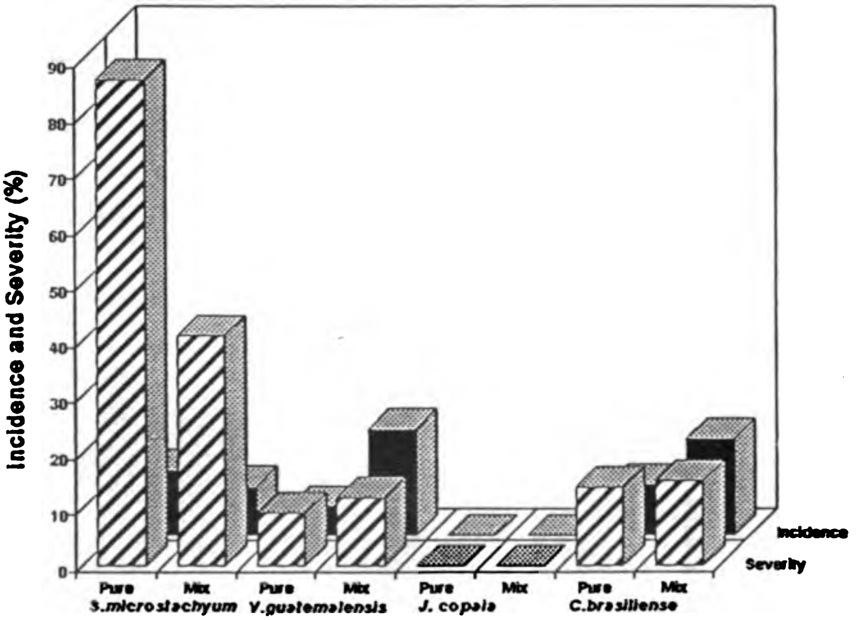


Fig. 5. Pest damage, Plantation 1, Nov. 1993

Financial Analysis

The majority (68%) of the labor costs for the first 5 years of the plantations occurred in the first year (Table 2). These estimates were high in comparison with national estimates by the Costa Rican Forest Service, due to the initial dominance of aggressive grasses and the relatively short dry season. However, these costs are in the range of other estimates for the region, and they lie within the limits that the Costa Rican Forest Service fixes for reforestation projects. The use of mixed designs could help reduce establishment costs for the slower growing species, which take longer to close canopies in pure than in mixed conditions resulting in higher weeding costs. Although at the moment little price differentiation exists among the twelve species, prices are expected to rise as availability in natural forests decreases. At present, local mill prices can be found for logs with a minimum small end diameter of 40 cm, however logs of as little as 15 cm are also purchased, although at 1/3 the price. With estimated rotation times of 15-25 years, with expected volumes at harvest of 250-300 m^3/ha, planting these species is attractive for the small farmers in the region. In fact, several farmers are already using the species, and interest has developed recently on mixed designs including the fastest growing trees (*J. copaia, V. guatemalensis*).

Table 2. Establishment cost estimates, Years 1-5.

Year 1	**Work-days/ha**	**$/ha**
Clearing	30.5	338.4
Prep and planting	32.0	354.9
Weeding	36.6	406.3
Sub-total	99.1	1,099.6
Seedlings		122.6
Annual total	99.1	1,222.2
Year 2		
Weeding	23.4	260.0
Year 3		
Weeding	5.5	60.9
Pruning[a]	8.8	97.8
Annual total	14.3	158.7
Year 5		
Pruning[a]	8.8	97.8
TOTAL, Years 1-5	145.6	$1,738.8

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[a] Source: Morales Soto, O., 1992: Análisis de costos e incentivos CAF-FDF, San José, Costa Rica. Ministerio de Recursos Naturales, Energía y Minas, Dirección General Forestal, San José, Costa Rica.

CONCLUSIONS

Although it is still early to assess the performance of some of the slower growing species of these experiments, some of the advantages of mixed-species systems were evident, especially those concerning growth in diameter, above-ground biomass, litterfall and severity of pest and disease damage. The diameter at breast height was larger in mixed than in pure plots. For Plantation 1, above-ground biomass was larger in mixed than in pure plots. Except when a species was suppressed by the others in the mixture, as in *C. brasiliense*, apparently the mixed designs favored growth in diameter, starting just after canopy closure. Management practices (thinning, pruning) could be directed to favor the future growth of the most suppressed species. In Plantation 1, where data were available, the mixed treatments had intermediate values and less pronounced peaks in litterfall, resulting in a more even forest-floor cover. Increased levels of soil organic matter were recorded under the fastest growing species. Severity of pest damage was higher in pure than in mixed plots, although it varied with the level of damage and the species involved.

In spite of relatively high establishment costs, with the estimated rotation times and timber prices these systems are financially attractive to the farmers. Savings in establishment costs could be gained in mixed designs when slower-growing species are considered. Mixed-species systems could also be more flexible by offering a variety of products in an unstable market.

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

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SUMMARY

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

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

INTRODUCTION

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

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

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

STUDY SITE

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

METHODS

Plantation establishment and management

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

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

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

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

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

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

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

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

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

Pest damage

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

Costs

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

RESULTS

Tree growth

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

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

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

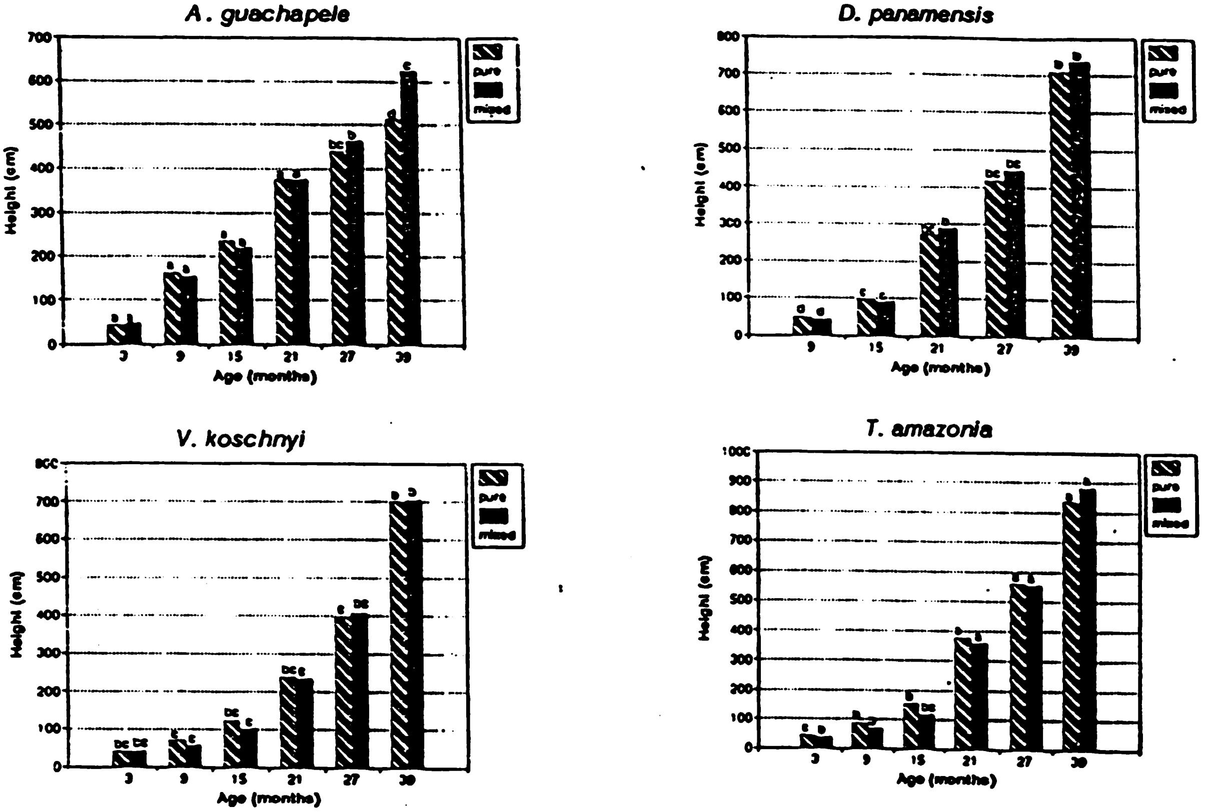

FIGURE 1. *Total height of the four species of Plantation 2 in pure and mixed plots. For each date, differences in total height among species and between pure and mixed plots are statistically significant when the bars are marked with different letters. (Notice that the scales in the vertical axes differ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

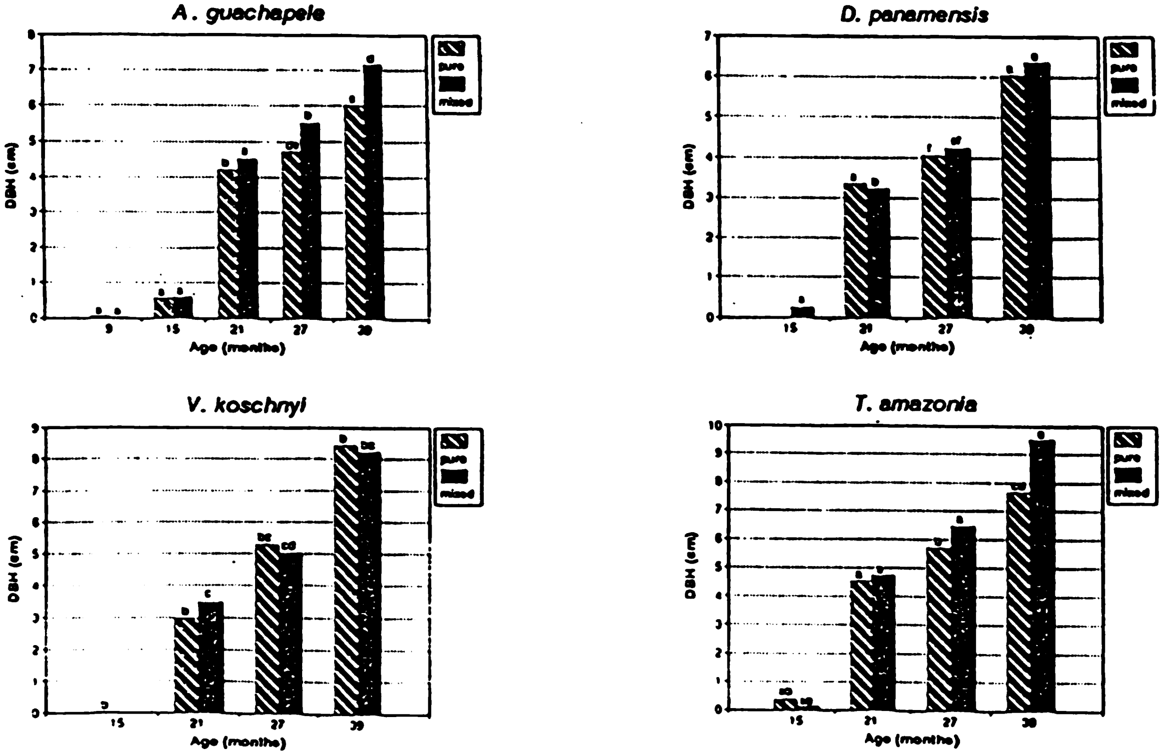

FIGURE 2. *DBH of the four species of Plantation 2 in pure and mixed plots. For each date, differences in DBH among species and between pure and mixed plots are statistically significant when the bars are marked with different letters. (Notice that the scales in the vertical axes differ among the species).*

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

TABLE 2. *Growth and survival.*

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

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

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

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

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

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

Pest damage

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

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

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

Costs

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

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

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

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

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

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

DISCUSSION

Tree growth and yield in pure and mixed stands

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

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

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

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

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

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

Pest damage incidence and severity in pure and mixed plots

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

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

Economic advantages and disadvantages of pure and mixed plantation designs

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

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

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

CONCLUSIONS

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

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

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ESTIMACION DE LA FIJACION DE NITROGENO POR EL ARBOL TROPICAL *Stryphnodendron microstachyum* Poepp. et Endl.

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(1995)

RESUMEN

Se llevó a cabo un estudio de campo para estimar la magnitud de la fijación de N por *Stryphynodendron microstachyum* Poepp. et Endl., especie leguminosa arbórea mimmosoidea nativa de Costa Rica. Se empleó una metodología de isótopo diluído en N (^{15}N), utilizando *Vochysia guatemalensis* Donn. Sm. como especie de referencia no fijadora de nitrógeno.

Plantines de 3 a 6 meses de edad de ambas especies fueron transplantadas a parcelas de 6 m x 6 m en un diseño mixto sobre terrenos de pastos abandonados en la Estación Biológica La Selva de la Organización de Estudios Tropicales (Costa Rica). La aplicación de fertilizantes enriquecido con ^{15}N se realizó en sub-parcelas de 2 m x 2 m, aisladas hasta 60 cm de profundidad por capas de polietileno grueso. Se realizaron aplicaciones de ^{15}N cada sies meses a una tasa de 0.092 g m^{-2}, con un total de N aplicado de 1.0 g m^{-2}. Los valores de pNda (proporción de nitrógeno derivado de la atmósfera) para *S. microstachyum* a los 18 y 22 meses de edad fueron de 61.2 y 51.9%, respectivamente. Otros estudios conducidos en plantaciones monoespecíficas en La Selva demostraron que *S. mirostachyum* tenía crecimiento rápido y una capacidad relativamente alta de reciclar N en sus tejidos. Con los resultados del presente estudio se comprobó que la mayoría de este N es proporcionado por la fijación simbiótica de N y una cantidad menor del N asimilado proviene del N disponible en el suelo.

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PALABRAS CLAVES: *Stryphnodendron microstachyum*, fijación simbiótica, isótopo diluído ^{15}N, estimación.

ABSTRACT

A field study was conduced to estimate the magnitude of N fixation by *Stryphno-dendron microstachyum* Poepp. et Endl., a leguminous, mimosoid tree species native to Costa Rica, using a ^{15}N dilution methodology and with *Vochysia guatemalensis* Donn.Sm. serving as a reference, non-N fixing especies. Three to six-month old seedlings of both species were transplanted to 6 m x 6 m plots in a mixed design on abandoned pastures at La Selva Biological Station of the Organization for Tropiucal Studies (Costa Rica). The applications of fertilizer enriched with ^{15}N were done on 2 m x 2 m sub-plots, which were isolated to 60 cm depth with several layers of thick polyethylene. The ^{15}N was applied every six months at a rate of 0,092 g m^{-2}, with a total N application of 1,0 g m^{-2}. The values of pNdfa (proportion of nitrogen derived from the atmosphere) for *S. micros-tachyum* at 18 and 22 months of age were 61,2 and 51,9%, respectively. Other studies on monospecific plots at La Selva showed that *S. microstachyum* had fast growth and a relatively high N recycling capacity. The results of the present study demonstrate that the majority of this N is provided by symbiotic N fixation and a lesser amount from N uptake from the soil N pool.

Key words: *Stryphnodendron microstachyum*, symbiotic nitrogen fixation, isotope dilution, ^{15}N, estimation.

INTRODUCCION

Stryphodendron microstachyum Poepp. et Endl.(sinon: *S.excelsum* Harms) es una especie arbórea leguminosa nativa de los trópicos húmedos de Costa Rica. Esta especie está siendo experimentada en su uso forestal y en combinaciones agroforestales en la región de la llanura del Atlántico de Costa Rica (González et al. 1990, Montagnini 1992). Como muchos otros árboles leguminosos, obtiene nitrógeno (N) a través de una simbiosis en nódulos radiculares con bacterias azotróficas de la familia Rhizobiácea. La cantidad de N fijado no está bien documentada bajo condiciones de campo. Se llevó a cabo un estudio de campo para estimar la magnitud de la fijación de N por *Stryphnodendron* usando una metodología de isótopo diluído de N (^{15}N).

MATERIALES Y METODOS

La estimación de N fue realizada en el campo usando la metodología de ^{15}N-diluído descrita por Parrotta et al. (1994). Semillas de *Stryphnodendron microstachyum* (la especie leguminosa fijadora de nitrógeno) y *Vochysia guatemalensis* Donn. Sm. (sinon: *V.hondurensis* Sprague; la especie de referencia no fijadora de nitrógeno) fueron recolectadas de árboles nativos de Costa Rica y plantadas en bolsas de polietileno. Los plantines de *V.guatemalensis* tenían 7 meses y los de *S.microstachyum* tenían 3 meses en el momento de la plantación.

Establecimiento del Experimento. En julio de 1991, las dos especies arbóreas fueron transplantadas a parcelas 6 m x 6 m en plantación mixta sobre terreno de pastos abandonados en la Estación Biológica La Selva de la Organización de Estudios Tropicales (Costa Rica). El sitio se encuentra a 10° 26' N, 86° 59' W, a 50 m de altura media y es caracterizado por una temperatura media anual de 24°C y una precipitación media anual de 4000 mm, con precipitación máxima en julio y mínima en marzo. Los suelos son Fluventic Dystropepst derivados de depósitos aluviales de material volcánico; son profundos, bien drenados, libres de rocas, de contenido orgánico bajo o medio, de textura moderadamente pesada, y generalmente ácidos e infértiles (Sancho y Mata, 1987). El área fue deforestada a mediados de la década de los 50 y pastoreada hasta 1981. Las dos especies arbóreas fueron alternadas en cada fila con un espaciamiento de 1 m x 1 m. Cuatro réplicas de cada parcela fueron establecidas originalmente, pero a causa de la mortalidad de plantines debido al ramoneo del venado en dos de la cuatro parcelas, sólo dos réplicas fueron estudiadas.

Dentro de cada parcela 6 m x 6 m, se determinó una sub-parcela 2 m x 2 m, la cual fue aislada hasta una profundidad de 60 cm colocando múltiple capas de polietileno grueso (de construcción). Esta sub-parcela se convirtió en el área de aplicación de fertilizante enriquecido con ^{15}N para propósitos de estimación de estimación de la dilución de N atmosférico. Empezando en agosto 1992 y continuando cada seis meses después de esa fecha, se realizaron las aplicaciones de fertilizante enriquecido con ^{15}N a una tasa de 0.092 g m^{-2}, con un total de N aplicado de 1.0 g m^{-2}.

Muestreo. Los muestreos de tejido foliar fueron llevados a cabo justo antes de cada aplicación de fertilizante enriquecido. Las muestras de hojas escogidas al azar (Parrotta et al. 1994) fueron tomadas de los cuatro árboles dentro de las sub-parcelas y reunidas por especie. Las hojas fueron secadas a 70° C hasta peso constante y molidas hasta lograr un polvo fino en una procesadora doméstica marca "Tecator". Los análisis de %N y %^{15}N fueron realizados en el Laboratorio de Análisis de Suelos de la Universidad de Saskatchewa usando un espectrómetro de masas marca ANCA-MS.

Estimación de la fijación de nitrógeno. La proporción de N derivado de la atmósfera (pNda) fue estimada usando la fórmula de Fried y Middelboe (1977).

Resultados

En mayo de 1993, en el momento de la cosecha final, los árboles de *S. microstachyum* tenía de 2 a 7 cm de diámetro a la altura del pecho (dap) y de 1 a 5.4 m de altura; y los de *V. guatemalensis* tenían de 4.3 a 6.6 cm dap y 4.4 a 5.6 m de altura. El crecimiento de *Stryphnodendron* fue más variable que de *Vochysia*, un patrón similar al encontrado en una plantación experimental cercana sobre el mismo tipo de suelo.

Los valores de pNda para *Stryphnodendron* a los 6 y 12 meses de crecimiento en esta plantación se presentan en la Tabla 1. Se ovbservaron diferencias en pNda entre los árboles de las dos parcelas, sugiriendo diferencias en el N disponible en los suelos de las dos parcelas. La parcela 1 tuvo valores mayores de pNda que los de la parcela 1. Los valores obtenidos para pNda en éste estudio son similares en magnitud a los reportados por Parrotta et al. (1994) para *Leucaena* y *Casuarina*; por Sanginga et al. (1989) para *Leucaena*; o por Baker et al. (1992) para *Paraserianthes, Leucaena* y *Enterolobium*. Debido a que *Stryphnodendron* es una especie arbórea de crecimiento rápido, la contribución de esta especie al N del suelo con la descomposición de la hojarasca o las raices finas puede ser considerable.

Resultados de otros estudios conducidos en parcelas de plantaciones monoespecíficas de cuatro años sobre pastos abandonados en La Selva, demostraron que *S. microstachyum* tenía crecimiento rápido (más de 3.0 cm dap por año), alta concentración de N en los tejidos foliares (2,25%) y en ramas (0,93%), alta tasa de caída de hojarasca, y relativamente rápida tasa de descomposición de hojarasca (Montagnini et al. 1993). En otro estudio llevado a cabo en la misma plantación, los suelos bajo *S. microstachyum* tenían mayores tasas de potencial de nitri-ficación neta (1.1 - 1.9 mg de nitrato . kg-1día-1) que los suelos bajo especies no fijadoras N en el mismo experimento (Montagnini y Sancho 1994b, 1994c). Además, las plántulas de maíz cultivadas en suelos abonados con hojas de *S. microstachyum* crecieron mejor y extrajeron más N del suelo que los abonados con especies arbóreas no fijadoras de N, o que los controles no abonados (Montagnini et al. 1991, 1993). Hemos demostrado que la mayoría de este N es proporcionado por la fijación simbiótica de N y una cantidad menor del N asimilado proviene del N disponible en el suelo.

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Tabla 1.- Valores de pNda (proporción de nitrógeno derivado de la atmosféra).

Edad*	Parcela	pNda	Promedio
18 meses	1	69.2	61.2
	2	54.1	
22 meses	1	76.7	51.9
	2	32.5	

* después de la plantación

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

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Abstract

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

Introduction

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

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

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

Study Site and Methods

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

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soil rehabilitation (Montagnini & Sancho 1990; Montagnini 1992). Seedlings of four tree species – *Calophyllum brasiliense* (Guttiferae), *Jacaranda copaia* (Bignoniaceae), *Stryphnodendron microstachyum* (Mimosoideae), and *Vochysia guatemalensis* (Vochysiaceae) – were planted during June 1991 in an abandoned pasture at La Selva Biological Station (10° 26'N, 84° 00'W), operated by the Organization for Tropical Studies (OTS), Heredia Province, Costa Rica. Annual rainfall and temperature average 4000 mm and 26°C, respectively (Sanford et al. 1994).

The study site was logged in the early 1950s and subsequently cleared for rice cultivation for three years. The rice fields were burned lightly and seeded to pasture for beef and dairy cattle with the grasses *Cynodon nlemfuensis*, *Pennisetum maximum*, *P. purpureum*, *Brachiaria* spp., and *Melinis minutiflora*. Cattle raising lasted for about 20 years until the property was sold to OTS in 1981 with no further human intervention (Pierce 1992). Ten years before plantation establishment, secondary vegetation was dominated by shrubs and ferns, and tree regeneration was patchy. The terrain is flat, and soils are derived from volcanic alluvium; they are well drained, acidic ($pH < 5.0$), and infertile (Sancho & Mata 1987). Currently, the forested surroundings are dominated by secondary vegetation (10–15 meters tall) in early and mid-successional stage, and by pasture with scattered remnant trees.

Prior to tree planting, all existing vegetation was cleared manually, and the debris was left in place; the site was not burned. The plantations were set in randomized blocks, with four replicates and six treatments: four pure-species plots of each species, a mixed-species plot (with the four species), and a control plot (natural regrowth). Inter-tree distance was 2 meters by 2 meters to speed up canopy closure. Within each block, plot size was 32 meters by 32 meters (256 trees total). In the mixed-species plot, trees of the four species were planted, alternating two species per row, and the sequential order of the species was systematically reversed every other row.

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

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

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

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

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

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

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

Results

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

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

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

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

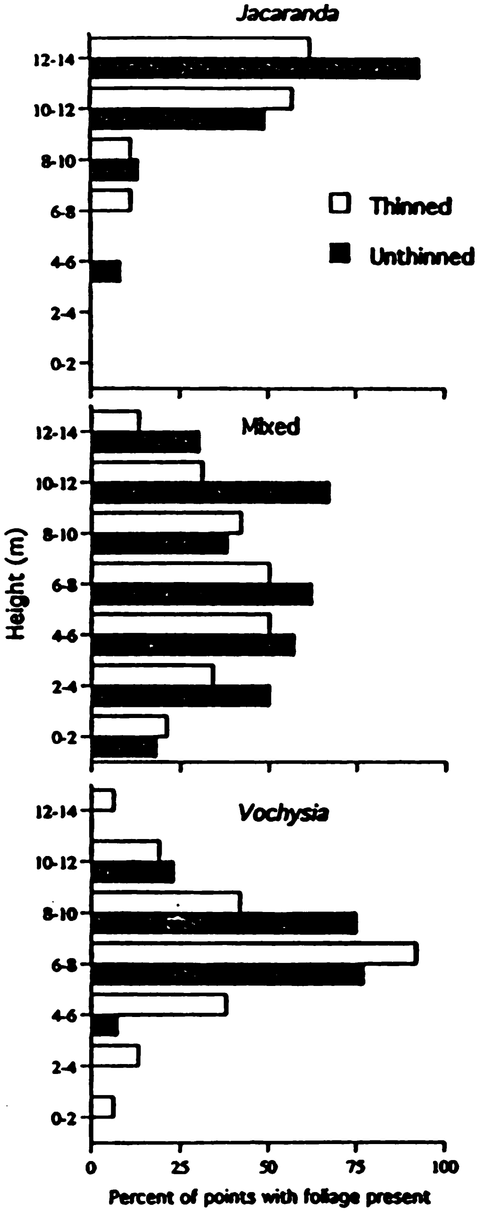

Figure 1. Vertical profiles of foliage in the three plantation treatments taken simultaneously from the unthinned sections (solid bars) and thinned sections (open bars), 10 months after thinning.

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

	Individuals/m^2						*1-Year Height Growth (m)*		
	Unthined Section			*Thinned Section*					
Treatment	*1993*	*1994*	p	*Pre-thinning*	*Post-thinning*	p	*Unthinned*	*Thinned*	p
Jacaranda	2.4 (0.0–6.5)	2.6 (0.0–7.0)	0.34	0.8 (0.0–3.0)	1.5 (0.5–2.5)	0.04	1.2 (0.4–2.2)	1.1 (0.3–1.2)	0.92
Mixed	0.9 (0.0–4.5)	1.4 (0.0–6.5)	0.11	0.6 (0.0–1.5)	2.3 (1.0–6.0)	0.01	0.8 (0.3–1.8)	0.98 (0.5–1.6)	0.09
Vochysia	0.0 (0.0–0.0)	0.1 (0.0–0.5)	0.31	0.0 (0.0–0.0	0.9 (0.0–3.0)	0.05	—	0.5 (0.2–1.8)	—

woody species were present in the understory of the *Jacaranda* and mixed-species treatments. One year later, this pattern was still consistent across treatments. Thinning promoted woody plant invasion in all three plantation treatments (Table 2). No woody seedlings were recorded in the control treatment, which was dominated by dense, grassy stands of *Penisetum* spp. and *Melinis minutiflora*.

There were differences in the number of one-year recruits among plantation treatments ($\chi^2 = 14.5$, 2 d.f., $p < 0.001$). More recruits were recorded in the mixed-species plantation (39), than in *Jacaranda* (17), and *Vochysia* (15) treatments. Overall, woody vegetation was taller in *Jacaranda* (Tukey, $p < 0.01$; mean height: 1.1 m; range: 0.4–1.2) than in mixed species (mean height: 0.8 m; range: 0.5–1.5) and *Vochysia* (which did not differ from each other; Tukey, $p = 0.3$; mean height: 0.5 m; range: 0.2–1.8). There were no statistical differences in absolute height growth in thinned versus unthinned sections of established woody vegetation in both *Jacaranda* and mixed-species treatments (Table 2). There was no block effect in the height of woody vegetation for the plantation treatments (ANOVA, $p > 0.2$ in all cases).

In both *Jacaranda* and mixed-species treatments, shrubs (*Conostegia*, *Leandra*: Melastomataceae; *Piper*, Piperaceae; *Psychotria*, Rubiaceae) comprised more than 75% of all stems recorded either during the initial vegetation sampling or as recruits one year later (Fig. 2). Shrub species also dominated the seed bank (Table 3); for example, seeds of *Conostegia subcrustulata* accounted for 40% of all seedlings emerged from seed bank samples taken from all four treatments. This shrub species is abundant in active and abandoned pastures across the area, and it is likely that a constant propagule input into the soil since pasture creation may have kept soil seed numbers of this species at high levels. It is interesting to note that the grasses that dominate the unplanted control treatment appear to inhibit buried seed germination because we found comparable densities and species composition of the germinable seed bank in the control and the plantations (Table 3). Although we did not measure the light microenvironment in the control, low light levels at the soil

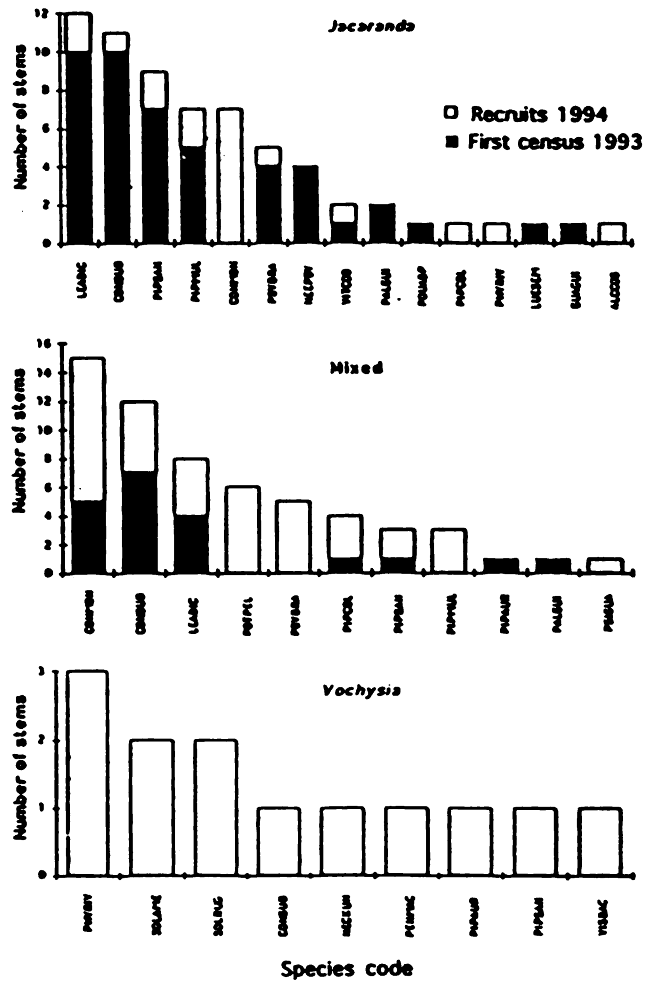

Figure 2. Total number of woody stems (except *Phytolacca rivinoides* and *Potomorphe peltata*, which are giant herbs; > 1 m tall as adults) recorded initially in 1-meter-by-2 meter regeneration plots in 1993 (solid bars). The open bars are the 1994 recruits (individuals > 0.2 m tall) that were distributed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

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

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

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

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

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

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

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

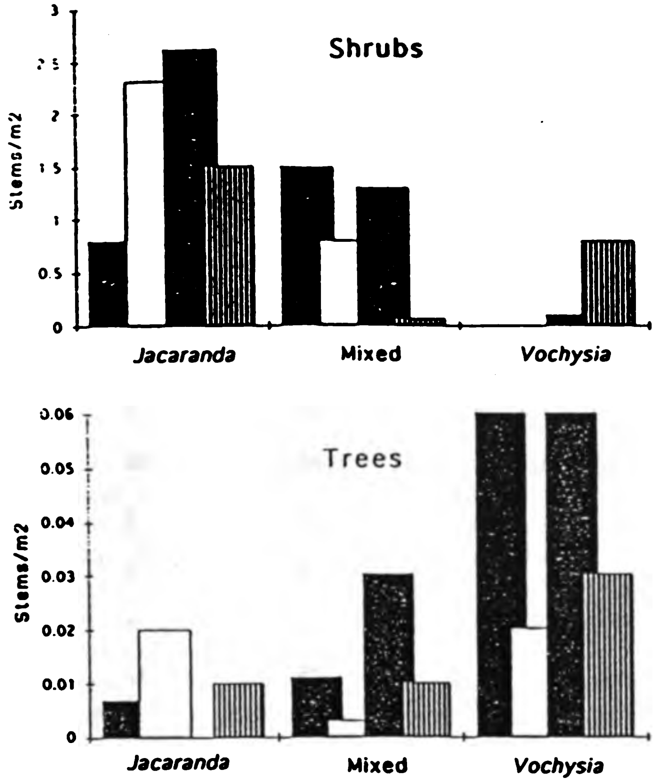

Figure 3. Density of shrub and tree seedlings (individuals $\geq$ 0.2 m but $\leq$ 1 m tall) in the three plantation treatments. Within treatments, different bars represent density estimates for each block. Shrub and tree density was statistically different across treatments (ANOVA, $p < 0.03$ in both cases). Note that the y axis is on different scales.

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

Discussion

We found contrasting patterns in the quantity and quality of early woody regeneration in the understory of three different plantation treatments. The understory of *Vochysia* plantations had a higher density of tree seedlings than both *Jacaranda* and mixed-species treatments. In contrast, shrub species were dominant under *Jacaranda* and mixed-species treatments. It is interesting to note that seedlings of *Cecropia obtusifolia*, a small-seeded (< 0.1 g), light-demanding pioneer tree, appeared more abundant under *Vochysia* than under *Jacaranda* and mixed species, even though *Vochysia* showed the darkest understory of all plantations. Although we cannot separate the combined effects of differential seed deposition of *Cecropia* under *Vochysia* from understory effects (low herb cover may facilitate seedling establishment), our results suggest that small-seeded pioneers like *Cecropia* could encounter more-suitable sites for early establishment under *Vochysia* than in the other two plantation treatments. Once weeds have been suppressed, a careful opening of the canopy in *Vochysia* could release *Cecropia* seedlings that may serve as additional attracting points to vertebrate frugivores later in time. *Cecropia* trees are visited by a wide variety of birds and bats; they grow rapidly in height and reproduce precociously (Estrada et al. 1984; Alvarez-Buylla & Martinez-Ramos 1992).

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

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

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

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

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

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

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

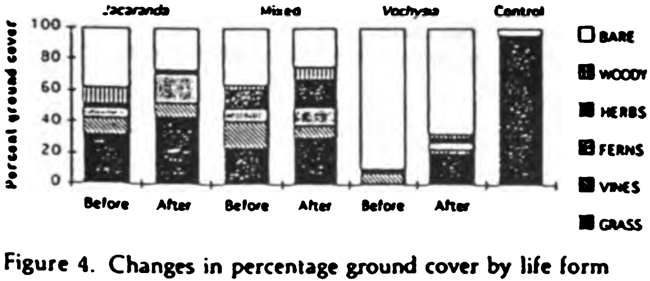

Figure 4. Changes in percentage ground cover by life form before and 10 months after thinning in the plantation treatments. The control treatment is included as a comparison.

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

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

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Appendix. Plant species codes.

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

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

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

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Abstract

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

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

1. Introduction

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

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

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

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

2. Study site

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

3. Tree species

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

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

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

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

4. Methods and materials

4.1. Litter decomposition: litter bag experiment

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

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

4.2. Soil and air temperature

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

4.3. Mulch experiment

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

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

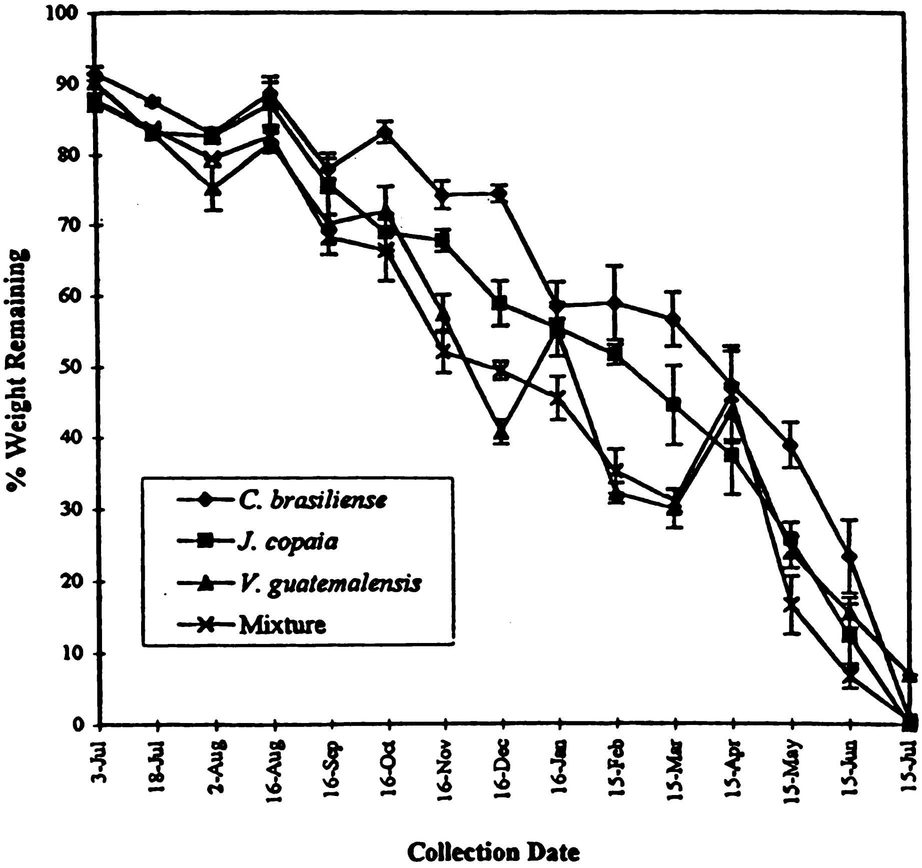

Fig. 1. Leaf litter decomposition from July 1993 to July 1994: percent weight remaining at each collection (means and standard error bars).

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

5. Results

5.1. *Litter decomposition*

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

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

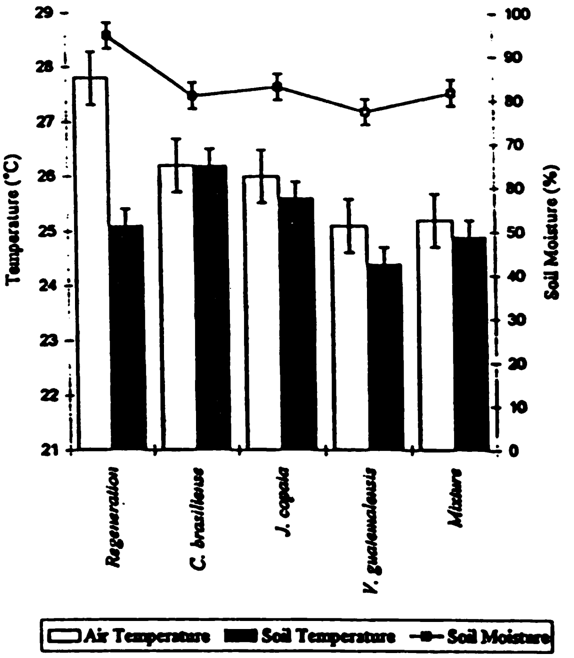

Fig. 2. Air temperature, soil temperature, and soil moisture in pure and mixed tree stands, and regeneration control (means and standard error bars).

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

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

5.2. *Maize seedling growth under mulch treatments*

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

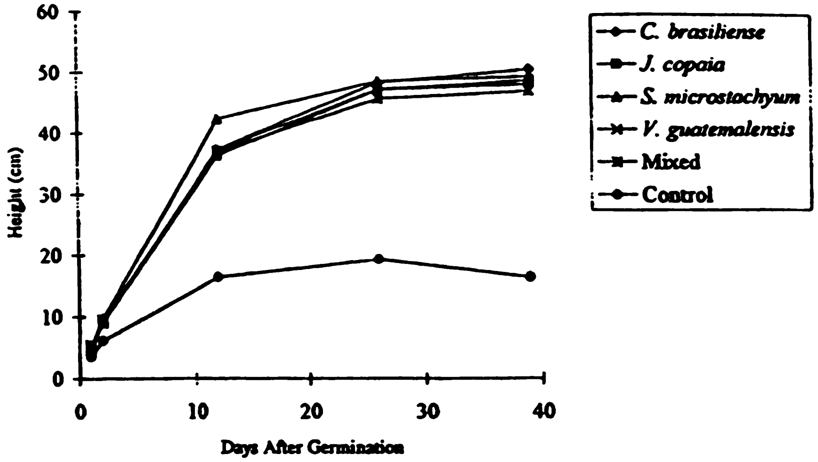

Fig. 3. Height of maize seedlings in soils mulched with leaves from a single tree species, a mixture and an untreated (no mulch) control.

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

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

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

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

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

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

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

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

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

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

6. Discussion

6.1. Leaf litter decomposition

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

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

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

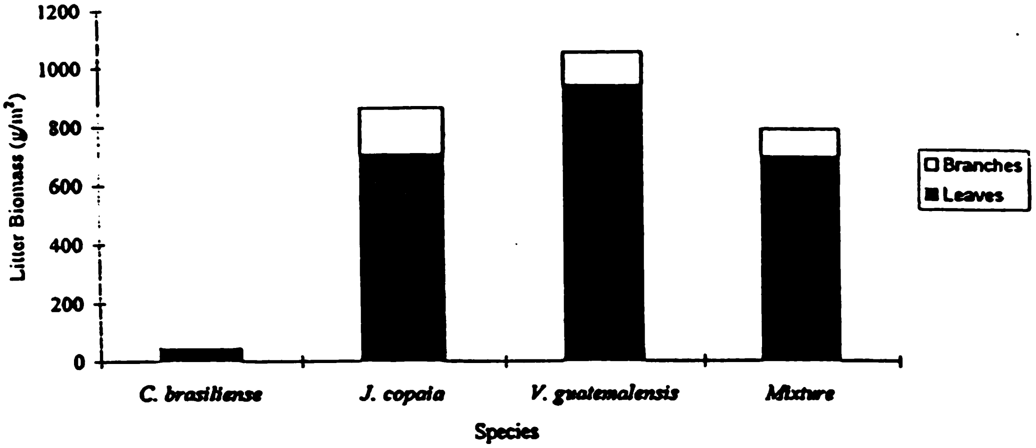

Fig. 4. Total annual litter fall from August 1993 to July 1994 (means and standard error bars). Source: Montagnini et al. (1994).

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

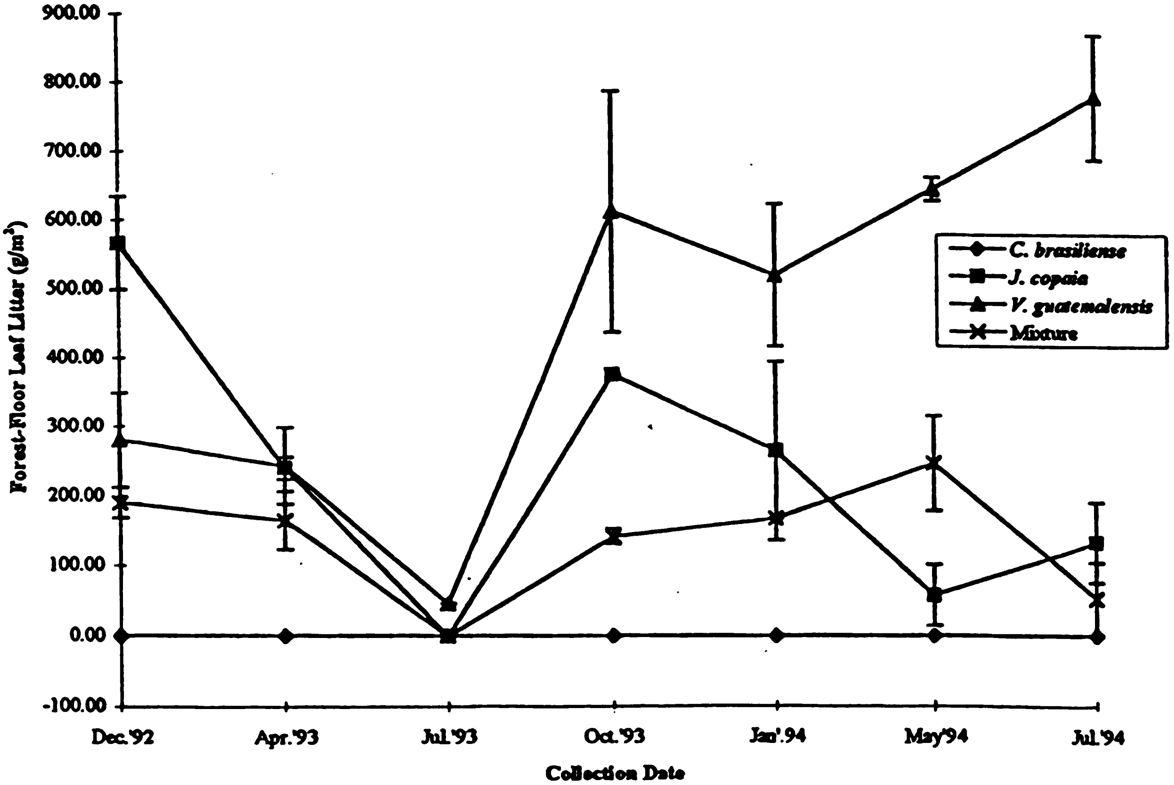

Fig. 5. Forest-floor leaf litter. Data are from collections made every 3 months from January 1992 to August 1994 (means and standard error bars). Source: F. Montagnini, unpublished data. Note: Except for a small amount under *V. guatemalensis*, there was no leaf litter on the forest floor in July 1993,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

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

6.2. Litter fall and forest-floor litter

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

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

6.3. Mulch experiment

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

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

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

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

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

6.4. Application to species choice for site rehabilitation

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

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

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

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

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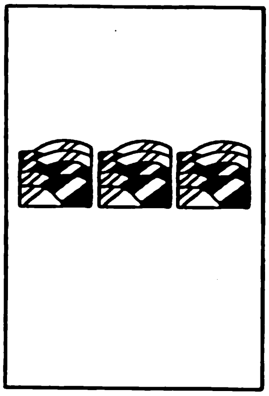

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Article

Florencia Montagnini and Robert O. Mendelsohn

Managing Forest Fallows: Improving the Economics of Swidden Agriculture

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

INTRODUCTION

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

Improved fallows have been proposed as a management alternative to shifting cultivation in the tropics (3, 4). Traditionally, shifting cultivators have encouraged the presence of certain tree or herb species in fallows to restore site fertility, suppress weeds and increase economic yields. Several types of traditional "enriched" fallows have been described, including those techniques involving planting or tending selective species for fruit, fuelwood or timber in fallow fields or secondary forests which are maintained by local populations over long periods of time, for local consumption, for markets or both (4–11). Some of these systems produce crops for local consumption and for a regional market, providing substantial cash income for many farmers (6).

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

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

ECONOMIC MODEL OF SHIFTING AGRICULTURE

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

Because this process takes a long time, in order to make it comparable with other land uses with different timing, we discount all future costs and revenues to the present using an interest rate, r. Using the same interest rate for each land use, we then can compare their present values. The present value, V_S, of shifting agriculture is:

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

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

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

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

OIL IMPACTS OF MANAGED FOREST FALLOWS

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

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

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

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

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

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

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

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

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

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

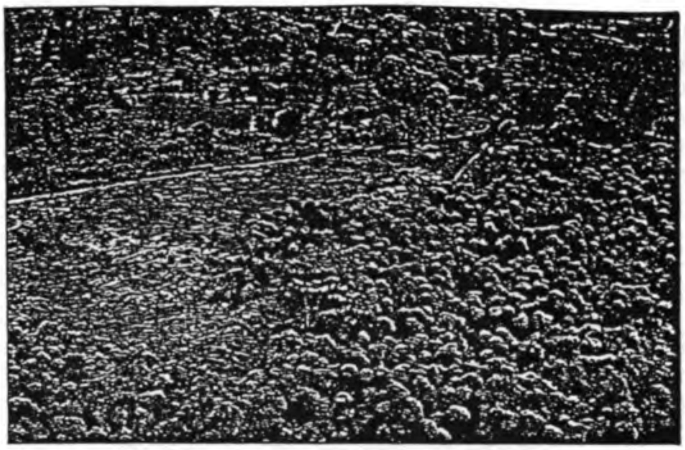
Nitrogen fertilizers are heavily used in the La Selva region, especially for the most demanding commercial crops such as bananas, in which case capital is available for fertilizer in a more extensive land-use system (22, 23). From the results shown in Table 1, *S. microstachyum*, a N-fixing tree, did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

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

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

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

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



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

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

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

ECONOMIC ANALYSIS

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

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

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

Table 2. The economics of managing forest fallows.

Forest fallow costs[a] (per ha)

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

Timber revenue (per hectare)

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

[a] Source: (30)

[b] Source: (31)

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

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

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

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

DISCUSSION

Traditional shifting agriculture may be sustainable but its land-intensive nature makes it unprofitable when there is a scarcity of land. By enriching forest fallows with timber species of economic value and positive impacts on soils, the economics of shifting agriculture can be substantially improved. After cutting and extracting timber from the tree plantation, leaving slash on the ground to protect soils, farmers can plant subsistence crops on the improved soils. By growing trees on one portion of the farm while growing crops on others, the farmer can maintain a nsistent flow of food while following the rotational scheme ng recommended in this article. Further, by carefully select- the tree species, the traditional role of a fallow period can be preserved ensuring the sustainability of the entire process. Even with careful management, and depending on the nutrient-supplying capacity of the soils, the application of low levels of lime or fertilizers may be needed to restore nutrients extracted at harvest in the long run. However, the surplus generated from the timber sales is expected to allow farmers to purchase fertilizers to accommodate these needs.

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

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

Many existing managed fallow systems are quite site-specific and have limited distribution, while others occur over large geographical areas and could be adapted to other regions (4, 6, 11). Our model applies to the particular experimental site in Costa Rica, and we expect the conditions will vary according to economic access and ecological characteristics. However the species used here have broad natural ranges throughout tropical America (32, 38) and thus we expect that this system could be applied in other regions with comparable ecological and socioeconomic characteristics. The soils at our site have low bulk den-

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

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

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

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

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

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

sities, indicating their volcanic origin, while in other parts of Latin America different soils occur (Ultisols and Oxisols) which have different constraints. The particular characteristics of the site will dictate what species, rotation length and management strategies are adequate. For example, experiments are now underway in Misiones, NE Argentina and Bahia, Brazil (39, 40) to explore whether this system can be adapted to other humid tropical and subtropical forest regions. Initial feedback on soil recovery rates suggest that managed forest fallows will generally be sustainable (40, 41). Economic analyses of these sites will test whether enriched fallows-shifting agriculture will be broadly competitive.

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

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RELACIÓN ENTRE ÁREA BASAL ARBÓREA Y PROPIEDADES QUÍMICAS DEL SUELO EN UN BOSQUE TROPICAL SECUNDARIO DE 10 AÑOS DE EDAD

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RESUMEN

El área basal arbórea y las propiedades químicas del suelo fueron medidas en tres sitios de bosque tropical secundario de 10 años de edad en las tierras bajas húmedas de la zona Atlántica de Costa Rica. El total del área basal arbórea varió entre 4.34 m^2/ha en un sitio con extensa cubierta de pasto y con *Alchornea costaricensis* como el árbol más abundante, y 24.7 m^2/ha en áreas más densamente pobladas de árboles, dominadas por *Pentaclethra macroloba*. Otras especies consideradas como árboles emergentes de los bosques de la región, tales como *Stryphnodendron microstachyum* y *Hyeronima alchorneoides*, también estuvieron presentes en los sitios con mayor área basal. El Ca intercambiable del suelo, el pH, y el P y el Cu extraible fueron mayores en el sitio con menor área basal, mientras que la materia orgánica del suelo y el N total fueron mayores en los sitios con más árboles. Cuando submuestras del suelo bajo pasto y bajo árboles fueron comparadas, el N total del suelo resultó mayor en lugares poblados con árboles, y el P extraible mayor en áreas cubiertas por pasto, sin diferencias estadísticamente significativas en otros parámetros. Hubieron correlaciones positivas y estadísticamente significativas entre el área basal total y la materia orgánica del suelo, el N total, y la acidez intercambiable, con coeficientes de correlación entre 0.33 y 0.52, mientras que hubo una correlación significativa pero negativa entre área basal y P y K. Estos resultados son útiles para la comprensión del desarrollo futuro del bosque o para tomar decisiones sobre el manejo de tales áreas.

Palabras clave: bosque secundario, trópicos húmedos, materia orgánica del suelo, Costa Rica, Pentaclethra macroloba, Stryphnodendron microstachyum.

ABSTRACT

Tree basal area and soil chemical properties were measured in three sites of 10-year-old tropical secondary forest in the Atlantic humid lowlands of Costa Rica. Total tree basal area ranged from 4.34 m2/ha in a site with extensive grass cover and with Alchornea costaricensis as the most abundant tree, to 24.7 m2/ha in more dense areas dominated by Pentaclethra macroloba. Other species which are considered emergent trees of the forests of the region such as Stryphnodendron microstachyum and Hyeronima alchorneoides were also present in the sites of highest basal area. Soil exchangeable Ca, pH, extractable P and Cu were higher in the site with lower basal area, while soil organic matter and total N were higher in the sites with more trees. When subsamples from under grass and under trees were compared, soil total N was higher under patches of trees, and soil extractable P was higher in areas covered with grass, with no statistically significant differences among the other parameters. There were positive and statistically significant correlations between total tree basal area, and soil organic matter, total N, and acidity, with correlation coefficients ranging from 0.33 to 0.52, while there was a significant but negative correlation between basal area and P and K. These findings are useful as a tool in assessing future forest development or management of such areas.

Key words: secondary forest, humid tropics, soil organic matter, Costa Rica, Pentaclethra macroloba, Stryphnodendron microstachyum

INTRODUCCIÓN

Simultáneamente con la actual deforestación y conversión mundial de los bosques tropicales, aproximadamente 5 millones de hectáres de bosques secundarios son generados cada año (Lugo 1988). Aproximadamente el 60% del área de bosques secundarios en América Latina se origina de la conversión de bosques vírgenes, mientras que en

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Asia y Africa, un 72-76% proviene de la tala de bosques (Brown & Lugo 1990). La estructura, diversidad y funciones de los bosques secundarios son variables, dependiendo de la fertilidad del sitio, el uso previo de la tierra y la distancia a las fuentes de semillas (Nepstad et al. 1990; Finegan 1992). Los bosques secundarios pueden representar refugios para la fauna y flora nativa, y constituyen una manera de restaurar la productividad de tierras abandonadas (Wadsworth 1987). Se necesita más información sobre las relaciones entre los usos previos de la tierra y la diversidad y productividad de bosques secundarios, y su potencial de manejo en sitios degradados (Finegan 1992; del Amo & Ramos 1993).

Generalmente es aceptado que la productividad de bosques es limitada por la disponibilidad de nutrientes del suelo, aunque hasta ahora se ha encontrado poca correlación entre la composición química del suelo y la estatura del bosque natural (Proctor 1992). Sin embargo, la mayoría de los estudios relacionando la biomasa forestal y los nutrientes del suelo, se refieren a bosques tropicales maduros y no a la vegetación joven secundaria con tasas de crecimiento relativamente mayores. Cuando un bosque secundario reemplaza a un cultivo o pasto, la rápida tasa de producción de biomasa vegetal y las menores temperaturas del suelo bajo el dosel del bosque aumentan las contribuciones de materia orgánica al suelo. El tiempo necesario para la restauración de la materia orgánica del suelo después del abandono de la agricultura o el pastoreo depende de la velocidad con la que se establezca el barbecho del bosque secundario. Esta velocidad, a su vez, depende de la precipitación, las condiciones físicas y químicas del suelo, la topografía y la erosión. Típicamente, la mayoría de las áreas tropicales húmedas requieren períodos de barbecho de 5 a 15 años para que los suelos recuperen niveles de materia orgánica similares a los del bosque original (Van Wambeke 1992). Debido a que la recuperación de la materia orgánica del suelo depende del desarrollo de la vegetación en el sitio abandonado, la evaluación de la cobertura arbórea, tal como la medición del área basal, podría dar una indicación de las condiciones de los nutrientes del suelo en el área en un período dado en el desarrollo de la sucesión.

Desde 1990 hemos conducido estudios sobre alternativas para la rehabilitación de bosques y suelos en la Estación Biológica La Selva de la Organización para Estudios Tropicales (OET) en la zona Atlántica de tierras bajas húmedas en Costa Rica. Como parte de un estudio sobre el uso de árboles nativos para la rehabilitación de bosques y suelos en pastos abandonados, en 1991-92 un sitio de aproximadamente 10 ha fue escogido para plantaciones experimentales futuras en el Anexo La Guaria de La Selva (Montagnini 1992; Montagnini et al. 1993). Antes de limpiar el área para las plantaciones, la vegetación existente fue inventoriada para evaluar las condiciones del bosque secundario, y el suelo fue muestreado como parte de la caracterización del sitio. En este manuscrito reportamos la relación entre el área basal arbórea y los macronutrientes del suelo para la nueva vegetación secundaria, 10 años después del abandono del pastoreo intensivo, y sin ninguna otra intervención humana. Los resultados deberían ser útiles en la caracterización de bosques secundarios en situaciones ecológicas similares, para ayudar en la evaluación del desarrollo futuro del bosque o en el manejo de tales áreas.

Sitio Experimental

El sitio experimental está localizado en la porción norte del Anexo La Guaria, Estación Biológica La Selva de la OET (10°26'N, 86°59'O, altitud media 50 metros, temperatura media anual 24°C, precipitación anual 4000 mm, con máxima en julio y mínima en marzo) (Reportes climatológicos de la Estación Biológica La Selva). El Anexo La Guaria, de 120 ha, fue comprado por OET en 1981 para servir de zona de amortiguamiento para la reserva forestal y para conducir estudios experimentales sobre suelos y plantaciones arbóreas. El área donde se realizó este estudio fue talado a principios de los años 50 para la extracción de maderas comerciales (*Cedrela, Cordia, Hyeronima, Hymenolobium, Lecythis, Zanthoxylum*, fueron los géneros principales escogidos para la extracción). Después de la extracción de madera, el área fue despejada y se cultivó arroz por dos o tres años, pero esta actividad altamente mecanizada fue abandonada por razones financieras. Los campos de arroz fueron levemente quemados y sembrados con pasto: *Cynodom nlenfuensis* (Pasto estrella, una especie nativa), y las exóticas *Pennisetum maximum* (pasto de Guinea), *Pennisetum purpureum*, *Brachiaria* spp. y *Melinis minutiflora* (calinguero, San Juan) fueron los pastos principales usados para el ganado de carne y de leche. La cría de ganado duró aproximadamente 20 años, hasta que la hacienda fue vendida a la OET (Pierce 1992). Este patrón de uso de la tierra era típico en la región en ese entonces: el corte selectivo dirigido a las maderas más valiosas, seguido por la tala rasa para un período breve (2-3 años) de agricultura intensiva, cría de ganado, y abandono del pastoreo a causa de una producción deficiente y bajos precios de la carne (Montagnini 1994).

Al momento de realizarse el presente estudio, el sitio experimental tenía áreas de pasto así como áreas con helechos y pasto, y porciones de bosque secundario. No se llevó a cabo ningún tipo de manejo u otra intervención en el sitio después del abandono del pastoreo. El área experimental se encuentra en un terreno plano y uniforme. Los suelos son Fluventic Dystropepts derivados de aluviones volcánicos; son profundos, bien drenados, libres de piedras, con contenido de materia orgánica baja o media (2.5-4.5%), textura moderadamente pesada, y generalmente ácidos (pH in H_2O <5.0) e infértiles (Sancho & Mata 1987).

MÉTODOS

a- Inventario de la vegetación

Un inventario de la vegetación fue llevado a cabo en los tres sitios escogidos para plantaciones experimentales futuras. Cada sitio de plantación era 96 m x 256 m (24,576m^2) subdividó en cuatro bloques, y con seis parcelas de 32 m x 32 m cada una. Para el muestreo de la vegetación y el suelo, cada una de las 24 parcelas marcadas para cada plantación fue usada como una unidad de muestra. Todos los árboles y arbustos en cada parcela fueron identificados y contados, y el diámetro a la altura del pecho (dap) fue medido en todos los troncos mayores de 2 cm dap. Aunque se tienen los datos para cada parcela y bloque, por brevedad sólo se presentan el número total de individuos y el área basal por especie en m^2/ha en cada uno de los tres sitios experimentales.

b- Fertilidad del suelo

Las muestras compuestas fueron tomadas en cada una de las seis parcelas en cada bloque de cada sitio. Las muestras fueron tomadas con un barreno tipo holandés a 0-15, 15-30 y 30-60 cm de profundidad. Los suelos fueron muestreados durante la estación lluviosa de 1991. Los promedios de los resultados de las seis parcelas en cada bloque fueron calculados para obtener promedios por bloque para cada factor de suelo analizado. Seguidamente, los datos de los cuatro bloques de cada sitio fueron usados para comparar los tres sitios en un análisis de la variancia, usando Intervalos de Confianza para pruebas de promedios ($p<0.05$).

El Sitio 1 tenía una gran proporción cubierta con varias especies de pastos y helechos, así como también partes de bosque secundario, mayormente con *Pentaclethra macroloba*. Los datos correspondientes a las áreas de pasto y bosque del Sitio 1 fueron tratados independendientemente en un análisis de variancia para una comparación de los parámetros de la fertilidad del suelo entre los dos tipos de vegetación.

El análisis químico fue realizado en el Laboratorio de Suelos de la Facultad de Agronomía, Universidad de Costa Rica, siguiendo métodos estándar actualmente utilizados por laboratorios de suelos en el país. El pH fue medido en una mezcla 1:2.5 de suelo:agua deionizada. El Ca y Mg fueron extraídos con una solución 1N KCl, mientras que el P, K y los micronutrientes fueron extraídos con un solución Olsen modificada (Díaz-Romeu & Hunter 1978). Los cationes fueron medidos usando un Espectrofotómetro de Absorción Atómica. El P fue medido colorimétricamente después de reacción con ácido $(NH_4)_2MoO_4$ y $SnCl_2$, usando un espectrofotómetro. La materia orgánica fue medida por la técnica de Walkley-Black (Allison 1975) y el N total fue medido usando una técnica semi-Micro-Kjeldahl (Bremner & Mulvaney 1982). El análisis de la variancia y las pruebas de Intervalos de Confianza fueron llevados a cabo para comparar los promedios de cada parámetro y la profundidad de suelo (n=4) entre sitios.

Un análisis de regresión simple fue usado para correlacionar el área basal total con cada parámetro del suelo, usando los datos de suelos de las parcelas individuales y el área basal de todas las parcelas de los tres sitios. Los parámetros de suelo utilizados en este análisis incluyeron materia orgánica, el N total, P, Ca, Mg, y K extraibles, la acidez intercambiable y el pH. Los micronutrientes Cu, Fe, Mn y Zn fueron excluídos porque no se esperaba que mostraran correlaciones significativas con la cubierta vegetativa. Para las correlaciones, los valores de pH fueron transformados a concentraciones de iones de H^+. Ambas regresiones, linear y exponencial, fueron calculadas. El análisis fue hecho usando los datos originales y las transformaciones logarítmicas. Los datos de la profundidad de suelo de 0-15 cm fueron usadas porque las diferencias más signi-ficativas en los parámetros de suelo entre sitios fueron encontradas a esa profundidad del suelo.

RESULTADOS

a- Vegetación original

El Sitio 1 tenía menos árboles que los Sitios 2 y 3 (Tablas 1, 2, 3). El total del área basal fue 4.34, 16.4 y 24.7 m^2/ha, y el número de individuos arbóreos totalizó 22, 149 y 139/ha en los Sitios 1, 2 y 3, respectivamente. Los pastos eran una mezcla de especies nativas, que generalmente crecen en bosques despejados, y algunas especies introducidas, las cuales habían sido sembradas para mejorar la calidad del pasto nativo (Pierce 1992). Entre las especies nativas estaban *Cynodon* spp. (pasto estrella) y *Paspalum fasciculatum* (gamalote); el gamalote no es preferido por el ganado. Entre los pastos exóticos, estaban *Brachiaria* spp., *Melinis minutiflora* (calinguero, San Juan), y *Panicum maximum* (pasto Guinea). También en manchones y mezclados con los pastos, habían dos especies de helechos: *Nephrolepis viscerata* (Polypodiaceae) (helecho serrucho o Boston), e *Hylepis repens*. Aunque menos abundante, las mismas mezclas de hierbas y helechos estuvieron presentes en las áreas despejadas de los Sitios 2 y 3.

En el Sitio 1, *Alchornea costaricensis* (fosforillo) fue el árbol más abundante con 52.8% del total del área basal y 37.0% de los individuos (Tabla 1). La mayoría de los individuos eran de estatura baja (<15 m), con doseles redondos y copas abiertas. *Pentaclethra macroloba* siguió con 32.9% del total del área basal y 31.7% del número de individuos.

En contraste, en los Sitios 2 y 3 *P. macroloba* fue más prevalente, con la mayor proporción del área basal y número de individuos, y *A. costaricensis* mucho menos abundante, con <2% del total del área basal (Tablas 2 y 3). En el Sitio 2, entre los más abundantes estaba también *Ficus* spp. (Tabla 2). Sin embargo, otras especies consideradas como emergentes o árboles de dosel del bosque natural (i.e. *Hyeronima alchorneoides*) también estuvieron presentes con valores >2% del total del área basal (Tabla 2). Otras especies maderables fueron menos abundantes, cada una con <2% del total del área basal: *Cedrela odorata*, *Dipteryx panamensis* y *Zanthoxyllum panamensis* (Tabla 2). La presencia de especies como *Bactris gasipaes* (pejibaye), *Psidium guajava* (guava) y *Elaeis guianensis* (palma de aceite) (Tabla 2) evidenció la ocupación humana relativamente reciente en el área. En particular, *Gliricidia sepium*, aunque en proporciones bajas (3.3% del área basal y 4.9% del total del número de individuos medidos), es frecuentemente usado en cercas vivas en la región.

El Sitio 3 tuvo la mayor área basal, pero menor número de individuos que el Sitio 2 (Tabla 3). La composición de especies era similar a la del Sitio 2, con otras especies emergentes en los bosques de la región, tales como *Stryphnodendron microstachyum* y *Dipteryx panamensis*. Sólo cuatro árboles de tamaño comercial fueron extraídos en el momento de la limpieza del sitio para el establecimiento de las plantaciones experimentales: un *Cordia alliodora* del Sitio 1, un *Cedrela odorata* del Sitio 2, y un *Cedrela odorata* y un *Carapa guianensis* del Sitio 3.

b- Fertilidad del suelo

El Ca intercambiable del suelo y el pH fueron más altos en el Sitio 1 que en los Sitios 2 y 3 en las profundidades examinadas, mientras que la materia orgánica fue mayor en los Sitios 2 y 3 ($p<0.05\%$). El P y Cu extraible fueron mayores en el Sitio 1 que en los Sitios 2 y 3 a 0-15 y 15-30 cm de profundidad (Tabla 4). No hubo diferencias estadísticamente significativas en el Mg, K, acidez, Fe y Mn intercambiable. El Zn fue mayor en el Sitio 3 a 30-60 cm de profundidad solamente. Aunque las diferencias no fueron estadísticamente significativas ($p<0.05$), el N total tendió a ser mayor en los Sitios 2 y 3 que en el Sitio 1.

En el Sitio 1, el N total en el suelo fue mayor en áreas bajo árboles, y el P extraible del suelo fue mayor en las áreas cubiertas con pasto y/o helechos a 0-15 cm de profundidad (Tabla 5). No hubieron diferencias estadísticamente significativas en cationes, pH, materia orgánica, Cu, Fe, Mn y Zn entre los suelos bajo pasto y/o helechos y árboles a ninguna de las profundidades estudiadas.

El análisis de regresión de parámetros para el total del área basal arbóreo y la fertilidad del suelo para los tres sitios demostró que había correlaciones positivas y estadísticamente significativas entre el total del área basal arbóreo y la materia orgánica del suelo, el N total, y la acidez, con coeficientes de correlación entre 0.33 y 0.52 (Tabla 6). Estos resultados fueron obtenidos calculando regresiones lineares, usando valores no-transformados de los parámetros utilizados: los coeficientes de correlación disminuyeron cuando las regresiones exponenciales o las transformaciones logarítmicas de los datos fueron usados para el análisis. Hubo una relación negativa, pero estadísticamente significativa entre el área basal y el P y K extraible. No hubieron correlaciones estadísticamente significativas entre el área basal y el Ca, Mg o las concentraciones de iones de H^+ del suelo (Tabla 6).

DISCUSIÓN

Desarrollo futuro del bosque en sitios de crecimiento secundario

Esta discusión está basada en los resultados del muestreo de árboles maduros, ya que no se tomó información sobre las clases de tamaño menores (plantones y árboles jóvenes) que determinan el potencial de regeneración futura de un sitio. Los Sitios 2 y 3, con mayor área basal, mayor número de árboles, y mayor materia orgánica y N en el suelo, aparentemente ofrecían más alternativas que el Sitio 1 con respecto al desarrollo futuro de los árboles, ya sea natural o manejado. La especie más abundante, *Pentaclethra macroloba*, es dominante en el bosque natural de La Selva, y es comúnmente encontrada tanto en bosques primarios como en secundarios en la región Atlántica de Costa Rica (Hartshorn 1983; Peralta et al. 1987; Finegan & Sabogal 1988). Esta especie también fue la más abundante en un bosque talado en regeneración de 5 años cerca de La Selva (González & Chaves 1993). La mayoría de los árboles de *P. macroloba* en los Sitios 2 y 3 eran muy delgados, encontrándose en alta densidad alrededor de árboles adultos padres que no habían sido talados durante el corte selectivo del bosque. El número mayor de árboles encontrado en los Sitios 2 y 3 en comparación con el Sitio 1 es probablemente el resultado de la proximidad de una quebrada relativamente profunda. De acuerdo con mapas aéreos de 1981, justo cuando la OET compró La Guaria (archivos de La Selva), el Sitio 1 estaba cubierto con pasto y árboles esparcidos, mientras que el Sitio 2 tenía una cerca de árboles, muchos de los cuales podrían haber sobrevivido o servido como fuentes de semillas después del abandono del pastoreo. En general, los Sitios 2 y 3 tenían una alta abundancia de arbustos y árboles de corta vida e intolerantes a la sombra (especies pioneras, como por ejemplo,*Apeiba* spp., *Cecropia* spp., *Hampea* spp., *Miconia* spp.), lo cual es característico en las etapas tempranas de la sucesión vegetal de bosques neotropicales (Budowski 1965; Denslow 1980; Swaine & Whitmore 1988). La intervención silvicultural para facilitar a los individuos preferidos en esta fase de la sucesión no es recomendable, porque los tratamientos podrían revertir el proceso de sucesión al incrementar el nivel de luz que favorece al crecimiento del pasto (Finegan 1992). En esta temprana etapa, las alternativas para ayudar el proceso de regeneración podría incluir técnicas de regeneración artificial, es decir, enriquecimiento con plantones arbóreos de especies nativas, ya sea en líneas o en áreas de claros del bosque secundario (Weaver 1987; Ramos & del Amo 1992).

En contraste, el Sitio 1 con su distancia relativamente mayor a fuentes de semillas, su cubierta de pasto y helechos extensa, el bajo número de especies arbóreas y la menor área basal demostró menos potencial para el desarrollo rápido del bosque secundario.En este tipo de situación, para ayudar a los procesos de rehabilitación de bosques y suelos, una alternativa potencial involucra la reforestación con especies arbóreas nativas, de crecimiento rápido, adaptadas a la alta luminosidad y a suelos relativamente infértiles. Los árboles de crecimiento rápido con alta capacidad para el reciclaje de nutrientes pueden mejorar la fertilidad del suelo en muchas regiones húmedas tropicales (Sánchez et al. 1985; Lugo 1988; Montagnini & Sancho 1990a, b). Aparte del rol potencial en la restauración de la productividad del sitio, las plantaciones arbóreas pueden acelerar el proceso de regeneración en ciertos sitios: por ejemplo, los árboles pueden servir como hábitat para aves y estimular la regeneración natural de las especies locales (Parrotta 1992).

Correlación entre las propiedades químicas del suelo y el área basal arbórea

El rango de valores de los parámetros del suelo para los tres sitios de este estudio fue comparable a los encontrados en otro sitio en el Anexo La Guaria de La Selva con un patrón del uso de la tierra similar (Montagnini & Sancho 1990a, b), excepto que el pH tendía a ser más bajo en este estudio (4.1-5.2) que en el otro sitio (5.3-5.5) a profundidades del suelo de 0-15 cm. Además, las diferencias en los parámetros del suelo entre las áreas de pasto y árboles del Sitio 1 (Tabla 5) fueron comparables a los hallados en las áreas de pasto abandonado y bosque en regeneración del otro sitio en La Guaria (Montagnini & Sancho 1990a, b). En otra comparación de suelos bajo bosques y pastos en el mismo sitio (Asbjornsen & Montagnini 1994), el pH fue menor bajo árboles que bajo pasto o helecho, pero no hubo diferencias significativas entre tipos de vegetación en los otros parámetros estudiados.

El Sitio 1, con la menor área basal (Tablas 1, 2 y 3) también tenía menos materia orgánica que los Sitios 2 y 3 (Tabla 4). En los Sitios 2 y 3, la dominancia por *Pentaclethra macroloba*, un árbol leguminoso fijador de nitrógeno (Nichols & Rodríguez 1990), puede que contribuya, aunque sea parcialmente, a una mayor materia orgánica y a la tendencia a mayor N encontrado en estos sitios. El Sitio 1 tenía más P que los Sitios 2 y 3. Esta tendencia es similar a la encontrada por Montagnini & Sancho (1990a,b): menos P bajo árboles que bajo pastos. La alta demanda por P por árboles leguminosos (*Pentaclethra macroloba*) para la fijación de nitrógeno podría explicar el bajo nivel de P extraible del suelo.

Los resultados del análisis de regresión demostraron correlaciones estadísticamente significativas entre el área basal arbórea y la materia orgánica del suelo, el N total, la acidez intercambiable y el P extraible. Aunque los coeficientes de correlación fueron relativamente bajos (0.3-0.5), dado que las cantidades de nutrientes en el suelo en un sitio particular son el resultado de muchos factores interactivos (tales como el clima, el material parental, la topografía, la vegetación), es llamativo que hasta un 30-50% de un efecto en particular pueda ser atribuído a un factor individual, la vegetación (área basal). Se reconoce que las correlaciones no demuestran relaciones de causa y efecto; es decir que una mayor área basal puede ser encontrada en suelos más ricos porque la mayor fertilidad del suelo probablemente favoreció el crecimiento arbóreo, o, de manera contraria, que las condiciones mejoradas del suelo pueden ser encontradas en áreas de mayor cubierta arbórea a causa de los efectos beneficiosos de los árboles sobre los suelos. El patrón de distribución espacial de árboles encontrado aquí aparenta estar muy relacionado con la proximidad de otros árboles que fueron dejados en pie al momento del corte del sitio y que aparentemente sirvieron como fuentes de semillas, como explicamos anteriormente. Probablemente una imagen más clara de los efectos de los árboles en regeneración sobre los factores del suelo puede ser obtenida en una situación donde un corte o limpieza completa (tala rasa) es seguido por la regeneración natural arbórea. En tales situaciones, las medidas de área basal arbóreo podrían ser una herramienta útil para la evaluación de las alternativas de desarrollo del bosque.

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■

Tabla 1. Inventario de vegetación en un bosque secundario de 10 años en La Selva, Costa Rica: Sitio 1, Mayo 1991.

Especies	Area Basal		Número de individuos	
arbóreas	m²/ha	Relativa(%)	Totales/ha	Relativa(%)
≥2% del área basal total:				
Alchornea costaricensis	2.28	52.84	8.14	36.90
Cecropia obtusifolia	0.21	4.75	0.41	1.85
Nectandra membranacea	0.16	3.65	0.82	3.69
Pentaclethra macroloba	1.43	32.99	7.00	31.71
≤2% del área basal total:				
Apeiba membranacea	0.01	0.29	0.41	1.85
Cordia bicolor	0.05	1.16	0.41	1.85
Dipteryx panamensis	0.01	0.29	0.41	1.85
Gliricidia sepium	0.04	0.81	0.82	3.69
Hampea appendiculata	0.01	0.17	0.41	1.85
Psidium guajava	0.04	0.98	2.04	9.24
Pterocarpus spp.	0.04	0.81	0.41	1.85
Vitex cooperi	0.06	1.33	0.82	3.69
Totales	4.34	100.00	22.1	100.00

Tabla 2. Inventario de vegetación en un bosque secundario de 10 años en la La Selva, Costa Rica: Sitio 2, Julio 1991.

Especies	Area Basal		Número de individuos	
arbóreas	m²/ha	Relativa(%)	Totales/ha	Relativa(%)
>2% del área basal total:				
Cordia alliodora	0.65	3.94	12.21	8.19
Ficus spp.	0.96	5.83	4.07	2.73
Guarea spp.	0.33	2.00	0.41	0.28
Gliricidia sepium	0.55	3.34	7.32	4.91
Hyeronima alchorneoides	0.46	2.79	0.41	0.28
Nectandra membranacea	0.50	3.03	7.33	4.92
Pentaclethra macroloba	9.43	58.29	65.10	43.70
<2% del área basal total:				
Alchornea costaricensis	0.11	0.67	2.85	1.91
Andira inermis	0.05	0.30	0.82	0.55
Apeiba membranacea	0.42	2.55	2.44	1.64
Bactris gasipaes	0.05	0.34	2.04	1.37
Brosimum alicastrum	0.02	0.09	0.82	0.56
Casearea arborea	0.05	0.30	0.82	0.55
Cassia fruticosa	0.03	0.18	1.22	0.82
Cecropia obtusifolia	0.07	0.42	3.26	2.19
Cedrela odorata	0.36	2.19	2.85	1.91
Clusia spp.	0.13	0.79	1.22	0.82
Cordia bicolor	0.02	0.12	0.41	0.28
Dendropanax arboreus	0.15	0.91	0.41	0.28
Dipteryx panamensis	0.23	1.39	0.82	0.55
Genipa americana	0.03	0.18	0.41	0.28
Hampea appendiculata	0.02	0.12	0.41	0.28
Inga spp	0.01	0.06	0.41	0.28
Laetia procera	0.09	0.55	0.41	0.28
Luehea semannii	0.16	0.97	1.63	1.09
Miconia affinis	0.14	0.85	5.70	3.82
Neea psychotroides	0.02	0.12	0.41	0.28
Piper spp.	0.01	0.06	0.41	0.28
Pithecellobium macrademium	0.03	0.18	0.41	0.28
Protium glabrum	0.01	0.06	0.41	0.28
Psidium guajava	0.08	0.49	3.66	2.46
Pterocarpus spp.	0.17	1.03	2.44	1.64
Rollinia microsepala	0.16	0.97	1.22	0.82
Simarouba amara	0.19	1.15	2.44	1.64
Socratea durissima	0.01	0.06	0.41	0.28
Tabebuia guayacan	0.09	0.59	0.41	0.28
Trema spp.	0.02	0.12	0.82	0.55
Especie desconocida 1	0.16	0.97	0.82	0.55
Especie desconocida 2	0.01	0.06	0.41	0.28
Virola sebifera	0.02	0.12	0.25	0.28
Vismia panamensis	0.31	1.90	6.92	4.64
Vitex cooperi	0.09	0.55	1.22	0.82
Zanthoxylum panamensis	0.07	0.42	0.82	0.55
Totales	16.45	100.00	149.03	100.00

Tabla 3. Inventario de vegetación en un bosque secundario de 10 años en La Selva, Costa Rica: Sitio 3, Julio 1991.

Especies arbóreas	Area Basal m^2/ha	Area Basal Relativa (%)	Número de individuos Totales/ha	Número de individuos Relativa(%)
<u>>2% del área basal total:</u>				
Andira inermis	0.54	2.17	3.26	2.25
Casearea arborea	1.90	7.69	4.07	2.82
Ficus spp.	0.90	3.62	2.44	1.69
Miconia affinis	0.66	2.65	9.77	6.76
Nectandra membranacea	0.98	3.95	8.14	5.64
Pentaclethra macroloba	12.93	52.29	48.42	33.53
Pithecellobium macrademium	0.65	2.63	0.82	0.56
Stryphnodendron microstachyum	0.88	3.56	0.41	0.28
<u><2% del área basal total:</u>				
Alchornea costaricensis	0.48	1.95	2.79	1.93
Apeiba membranacea	0.32	1.27	5.29	3.66
Bactris gasipaes	0.30	1.22	0.41	0.28
Cassia fruticosa	0.01	0.03	0.41	0.28
Cecropia obtusifolia	0.09	0.36	2.04	1.41
Cedrela odorata	0.18	0.74	0.41	0.28
Clusia spp.	0.10	0.41	2.44	1.69
Cordia alliodora	0.42	1.69	7.33	5.07
Cupania spp.	0.33	1.33	2.44	1.69
Dendropanax arboreus	0.33	1.31	0.41	0.28
Dipteryx panamensis	0.01	0.05	1.63	1.13
Elaeis guianensis	0.08	0.32	0.41	0.28
Genipa americana	0.01	0.05	0.41	0.28
Gliricidia sepium	0.02	0.06	0.41	0.28
Guatteria invicta (diospirioides)	0.08	0.31	0.41	0.28
Guarea spp.	0.13	0.51	0.41	0.28
Hampea appendiculata	0.02	0.06	0.41	0.28
Hyeronima alchorneoides	0.49	1.97	0.41	0.28
Hura crepitans	0.02	0.08	0.82	0.56
Hymenollobium mesoamericana	0.10	0.40	0.41	0.28
Inga spp.	0.27	1.07	0.82	0.56
Laetia procera	0.09	0.34	1.63	0.13
Lonchocarpus spp.	0.19	0.77	0.82	0.56
Luehea semanii	0.16	0.63	8.14	5.64
Neea psychotroides	0.04	0.14	1.22	0.84
Pachira aquatica	0.04	0.17	0.41	0.28
Protium glabrum	0.01	0.05	0.41	0.28
Psidium guajava	0.31	1.26	6.51	4.51
Pterocarpus spp.	0.15	0.62	3.26	2.26
Rollinia microsepala	0.05	0.18	2.04	1.41
Simarouba amara	0.21	0.84	3.26	2.26
Spondias radlkoferi	0.06	0.22	1.22	0.85
Especie desconocida 1 (Ficus)	0.07	0.29	0.82	0.56
Especie desconocida 2 (Solanaceae)	0.01	0.04	0.41	0.28
Especie desc. 3 (arborescent fern)	0.01	0.01	0.41	0.28
Virola sebifera	0.01	0.05	0.41	0.28
Vismia panamensis	0.07	0.26	4.48	3.10
Vitex cooperi	0.03	0.10	0.82	0.56
Totales	24.73	100.00	138.82	100.00

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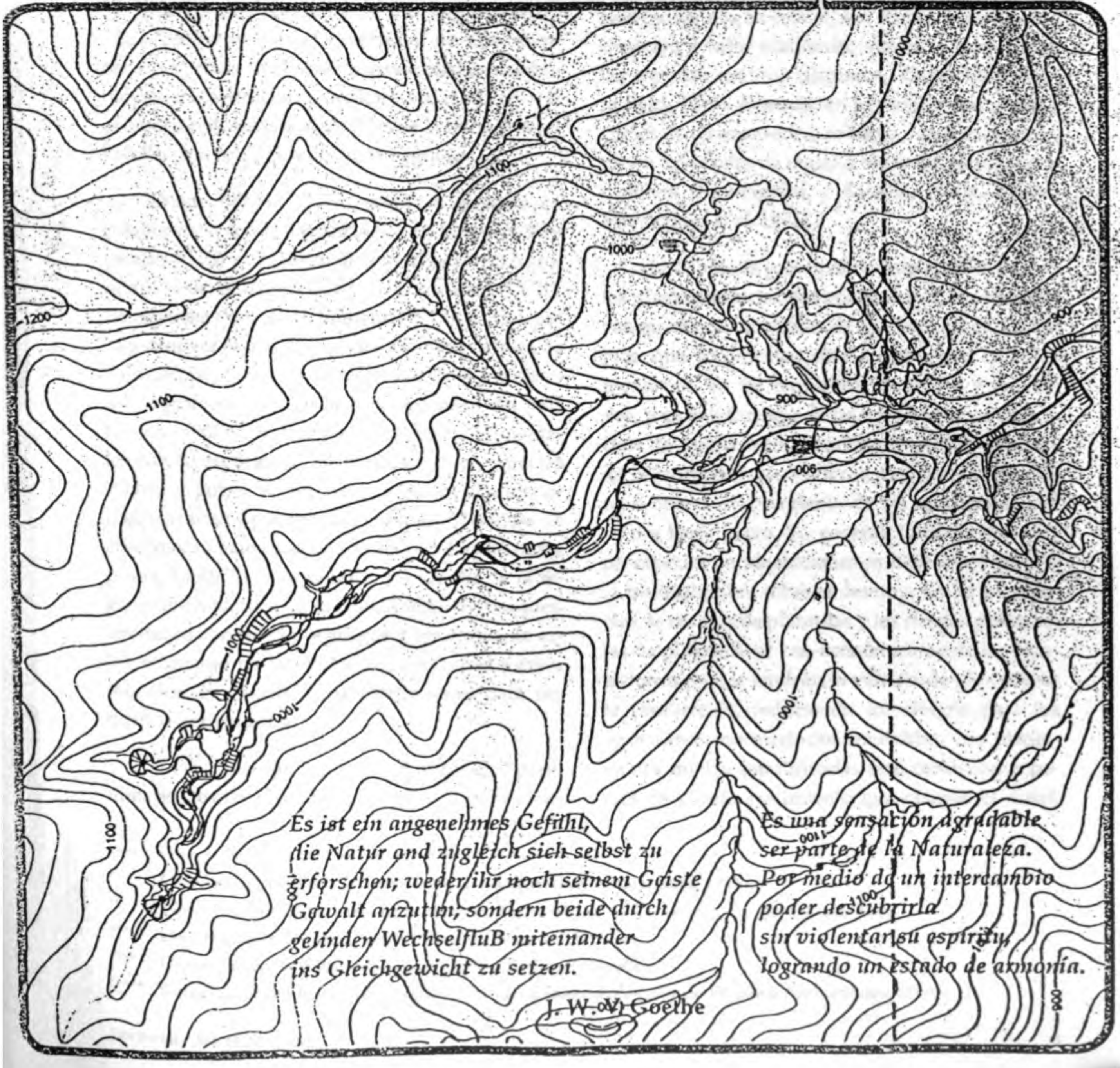

*Es ist ein angenehmes Gefühl,
die Natur and zugleich sich selbst zu
erforschen; weder ihr noch seinem Geiste
Gewalt anzutun, sondern beide durch
gelinden WechselfluB miteinander
ins Gleichgewicht zu setzen.*

J. W. v. Goethe

*Es una sensación agradable
ser parte de la Naturaleza.
Por medio de un intercambio
poder descubrirla
sin violentar su espíritu,
logrando un estado de armonía.*

PLANTACIONES FORESTALES PURAS Y MIXTAS CON ESPECIES NATIVAS PARA LA REFORESTACIÓN DE TERRENOS DEGRADADOS EN COSTA RICA: ESTUDIO COMPARATIVO DEL CRECIMIENTO, DAÑO POR PLAGAS, REGENERACIÓN NATURAL Y COSTOS DE ESTABLECIMIENTO

Florencia Montagnini[*], Freddy Sancho[**], Eugenio González[***],
Carlos Porras[****], Azur Moulaert[****], Antonio del Mónaco[*****]

Introducción

El Instituto de Recursos Tropicales (TRI) de la Escuela Forestal y de Estudios de Medio Ambiente de la Universidad de Yale, mantiene proyectos en el nivel internacional en colaboración con instituciones dedicadas al estudio y a la promoción de usos sustentables de la tierra y la rehabilitación ecológica de áreas degradadas.

Desde 1989 el TRI ha estado trabajando en colaboración con la Organización de Estudios Tropicales (OTS) y el Centro de Investigaciones Agronómicas de la Universidad de Costa Rica (UCR), en regiones de bosque húmedo de Costa Rica para promover el uso de especies arbóreas nativas de valor económico para la reforestación y los sistemas agroforestales. En la zona Atlántica del país hemos establecido tres plantaciones experimentales con 12 especies de árboles nativos en parcelas mixtas y puras, en un área de pastos abandonados, con suelos pobres para comparar las tasas de crecimiento bajo condiciones de parcelas mixtas y puras. También se estudiaron los efectos de la regeneración natural en la restauración de bosques, los daños causados por plagas y los costos de establecimiento de la plantación, con miras a crear modelos de desarrollo de plantaciones para pequeños agricultores.

En este trabajo se presentan resultados preliminares de experimentos en plantaciones de especies puras y mixtas en la llanura del Atlántico de Costa Rica. Resultados de investigacio-nes previas habían indicado que algunas especies arbóreas indíge-nas en esta región tenían tasas de crecimiento y valor económico similar o mayor que las especies exóticas (Espinoza, Camacho y Butterfield, 1989). Además, en los suelos con plantaciones de estas especies, se encontraron incrementos en los niveles de materia orgánica, nitrógeno y cationes (Montagnini y Sancho 1990a, 1990b, Montagnini *et al.* 1991).

La hipótesis principal de este estudio es que las plantacio-nes mixtas pueden ser más productivas que las plantaciones de especies puras. Se espera que en parcelas mixtas exista una complementación en los requisitos lumínicos y nutritivos, y en la influencia de las especies sobre el reciclaje de nutrimentos, resultando en sistemas mejor balanceados que tenderán a un menor deterioro, o aun al mejoramiento de las condiciones del sitio a largo plazo. En general, la diversificación de especies en plantaciones es deseable debido a la incertidumbre sobre el desempeño de las especies, la escasez de plántulas y los riesgos potenciales de plagas. A su vez, económicamente las plantaciones mixtas tendrán la ventaja de diversificar la producción, reduciendo los riesgos para los agricultores en mercados inestables. Las plantaciones mixtas estratificadas que combinan especies de rápido crecimiento que ocupan el dosel,

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con especies de crecimiento más lento tienden a ser más productivas que plantaciones puras de especies intolerantes a la sombra, debido a la reducción de la competencia interespecífica (Smith, 1986 and Kelty, 1992). Las plantaciones mixtas también contribuyen a una más alta diversidad del paisaje. La severidad de los daños por plagas también disminuye en las plantaciones mixtas debido a que las plantaciones monoespecíficas favorecen la formación y diseminación de poblaciones de plagas individuales. Sin embargo, existen casos en los cuales las plantaciones puras son más resistentes a ciertas plagas que plantaciones de la misma especie combinada con otra especie más susceptible (Smith, 1986; Perry and Maghembe, 1989; Watt, 1992).

La colonización de plantas bajo las plantaciones de árboles depende de una serie de mecanismos. Para estudiarlos se documen-taron los patrones de regeneración natural, la composición y la dinámica de la capa de hierbas bajo el dosel de las plantaciones forestales a los tres años. Esto se hizo con la finalidad de establecer los efectos mutuos entre árboles plantados y especies invasoras, y determinar lineamientos para la restauración de ecosistemas terrestres tropicales degradados. También se documentaron los roles de los bancos de semillas y los efectos del aclareo en la dinámica de las plantas bajo el dosel.

Descripción del sitio y diseño experimental

Los experimentos fueron establecidos en un área de pastos abandonados en la Estación Biológica La Selva de la OTS, altitud media 50 m; temperatura media anual 24 °C, y precipitación anual media 4000 mm. Los suelos del sitio experimental son Fluventic Dystropepts derivados de aluviones volcánicos, profundos, bien drenados, sin rocosidad, con contenido de materia orgánica media a baja, textura moderadamente pesada y, generalmente, ácidos e infértiles (Sancho y Mata, 1987). El sitio se deforestó a mediados de la década de los 50 y fue usado para el pastoreo de ganado hasta 1981 (Pierce, 1991). El terreno experimental era llano y uniforme.

Diseño de la plantación

En cada combinación de cuatro especies arbóreas al menos una era fijadora de nitrógeno. También se combinaron especies de crecimiento rápido y especies de crecimiento relativamente más lento (Tabla 1). Además, las especies fueron combinadas para obtener diferentes patrones de ramificación, tamaño y forma de la corona. Los criterios utilizados en la selección de especies arbóreas de este estudio fueron: la tasa de crecimiento, el valor económico y la preferencia de los agricultores (Chudnoff, 1984; González *et al.*, 1990), la presencia de nódulos en las raíces de especies leguminosas, los impactos sobre la fertilidad del suelo y el reciclaje de nutrimentos (Montagnini y Sancho, 1990a, 1990b; Montagnini *et al.*, 1991; Montagnini y Sancho, 1993) y la disponibilidad de plántulas. Las plantaciones fueron montadas en bloques al azar, con cuatro réplicas y seis tratamientos: cuatro parcelas de especies puras para cada especie, una parcela de especies mixtas (con las cuatro especies), y una parcela de regeneración natural. La distancia de plantación inicial fue 2m X 2m para acelerar el cierre del dosel y obtener impactos tempranos sobre los suelos. Ca-

Ilustración: Bernal Murillo

da parcela era 32m X 32m, con un total de 256 árboles cada una. Cada bloque era 64m X 96m; cada plantación tenía 96m X 256m, ó 24,576m^2, aproximadamente 2.5 hectáreas. En las parcelas individuales mixtas, se utilizó un diseño sistemático para maximizar las interacciones entre las especies. Dentro de cada parcela, los árboles de las cuatro especies fueron plantadas alternando dos especies por fila. El orden secuencial de las especies dentro de las filas fue revertido sistemáticamente en filas alternas. De esta manera, cada fila contenía las cuatro especies combinadas en una secuencia.

Tabla 1

Características ecológicas de 12 especies arbóreas nativas cultivadas en plantaciones arbóreas experimentales mixtas y puras en la Estación Biológica LaSelva.

Nombre científico	Nombre común	Familia	Area geográfica nativa	Habitat natural
Plantación 1				
Stryphnodendron microstachyum Poepp. et Endel (*S. excelsum* Harms)	vainillo	Leguminosae (Mimosoidea)	Costa Rica Nicaragua y Panamá	Dosel superior, baja altitud, hasta 700m, clima muy húmedo. Suelos aluviales de drenaje pobre, también en colinas y pendientes. También en bosques secundarios. Se adapta a suelos pobres.
Vochysia guatemalensis Donn. Smith (*V. hondurensis* Sprague)	mayo, chancho	Vochysiaceae	Méjico a Panamá	Dosel superior, tierras bajas, hasta 900m, clima húmedo, en los bordes de montañas. Suelos aluviales ricos o pobres, ácidos, puede crecer en áreas inundadas.
Jacaranda copaia (Aubl.)D.Don	jacaranda	Bignoniaceae	Guatemala a Brasil	Elevaciones bajas, clima húmedo a muy húmedo. Pendientes bien drenadas.no aguanta drenaje pobre. Bosque secundario, colinas baja, suelos rojos arcillosos poco fértiles.
Calophyllum brasiliense Cambess	cedro María	Guttiferae (Clusiaceae)	Méjico a norte de Sur América América	Encontrado en varios tipos de hábitats de húmedo a seco. Puede aguantar inundación.
Plantación 2				
Albizia guachapele (H. B. K.)Little	cenízaro macho guayaquil	Leguminosae (Mimosoidea)	Guatemala a Ecuador	Elevaciones bajas con clima húmedo a seco. Común en bosques bajos, bosques secundarios, a lo largo de lechos arenosos de ríos, sabanas. Puede crecer sobre suelos aluviales o arenosos viejos y ácidos.

Continua...

Continuando...

Nombre científico	Nombre común	Familia	Área geográfica nativa	Hábitat natural
Terminalia amazonia (J. F. Gemel.)Exell.	roble coral	Combretaceae	Sur de Méjico al norte de Sur América	Encontrado en áreas aluviales, ocasionalmente inundadas, o en colinas con suelos arcillosos, viejos, ácidos e infértiles.
Virola koschnyi Warb	fruta dorada	Myristicaceae	América Central	Dosel superior, elevaciones bajas, hasta 1 200m, clima muy húmedo. Partes inferiores de colinas, zonas ribereñas. Suelos aluviales, mal drenados, o arenosos. También sobre suelos arcillosos, ácidos, infértiles con alta con concentración de Al.
Dipteryx panamensis (Pittier) Record & Mell	almendro	Leguminosae (Papilionoidea)	Nicaragua a Colombia	Dosel superior, elevaciones bajas, hasta 1 300m, clima muy húmedo. Tierras bajas y bosques premontanos. Suelos aluviales o arenosos,a veces ácidos, arcillosos.
Plantación 3				
Pithecellobium elegans D. C. Benth	ajillo	Leguminosae (Mimosoidea)	América tropical	Bosque húmedo y seco, bosques inundables, zonas riparias, riscos de caliza. Suelos aluviales, arcillosos o franco arenosos.
Genipa americana L.	genipa	Rubiaceae	América tropical	Bosques de tierras bajas, pendientes. adapta a suelos arenosos y pobres.
Vochysia ferruginea Mart	botarrama	Vochysiaceae	Nicaragua a Brasil	Bosques de tierras bajas. Suelos bien drenados, ácidos, infértiles.
Hyeronima alchorneoides Fr.	pilón	Euphorbiaceae	Sur de Méjico al sur de Brasil	Colinas, pastos abandonados. Suelos aluviales y pobres. Crece cerca de áreas permanentemente inundadas.

Fuente: González *et al.* 1990, Holdridge & Poveda, 1975.

Preparación del sitio y plantación

La limpieza del sitio se hizo en forma manual, aproximadamente un mes antes de cada plantación. El sotobosque se limpió primero con machetes; los árboles y arbustos fueron talados con motosierra y cortados en partes menores para ser esparcidos, tanto como su peso lo permitiera. No se realizaron quemas. El producto de la limpieza se dejó sobre el suelo, para protegerlo contra la erosión y retrasar el crecimiento de las malezas.

Las semillas se recolectaron de árboles del bosque de La Selva o de otras áreas de la región Atlántica. Los plantines fueron producidos en el vivero de la OTS. El desmalezado se hizo manualmente en promedio general cada dos o tres meses. No se utilizaron herbicidas.

La altura total y el diámetro a la altura del pecho (DAP: diámetro del árbol medido a 1 m. de altura) fueron medidos en los 256 árboles de cada parcela, sin descartar bordes. Los promedios de altura, dap, área basal y sobrevivencia fueron calculados para cada parcela. El análisis de la varianza y las pruebas de significancia estadística (Intervalos de Confianza, $P<0.05$) fueron realizados usando los promedios de cada parcela para cada parámetro. Todos los parámetros fueron comparados entre las cuatro especies, y también para cada especie en condición pura y mixta.

Crecimiento arbóreo

Plantación 1

Los resultados de las mediciones tomadas a los 48 meses después de la plantación mostraron que los árboles más altos se encontraron en las parcelas de *J. copaia*, seguidos por *V. guatemalensis*, y C. *brasiliense*, sin diferencias significativas entre las plantaciones puras y las mixtas. Estos resultados preliminares coinciden con datos anteriores para estas especies en La Selva y sus alrededores (Espinoza y Butterfield, 1989). *S. microstachyum* mostró la tasa más baja de sobrevivencia, calculada luego del reemplazo de las plántulas. Esto se debió en parte a la depredación de venados y al ataque de un hongo en las plantaciones puras. Las plantaciones mixtas de *J. copaia* y de *V. guatemalensis* presentaron un mayor DAP que en las plantaciones puras. Esta diferencia se hizo más evidente después del cierre del dosel. Por el contrario, *C. brasiliense* fue suprimido por las especies del dosel por lo que presentó un DAP mayor en las plantaciones puras (Tabla 1a,b).

Plantación 2

Los árboles más altos en la plantación 2 después de 39 meses, fueron *Terminalia amazonia* seguida por *Dipteryx panamensis* y *Virola koschnyi*. Los árboles de *Albizia guachapele* eran más altos en las plantaciones mixtas, lo que fue detectado luego del cierre del dosel. No se observaron diferencias estadísticamente significativas entre plantaciones mixtas y puras para ninguna de las otras especies. La especie con más baja tasa de supervivencia fue *T. amazonia* debido a los ataques de hormigas. Esta especie presentó el mayor DAP a los 39 meses en las plantaciones mixtas. El DAP de esta especie y de *A. guachapele* fue significativamente mayor en las plantaciones mixtas que en las puras (Tabla 1a,b).

Plantación 3

Los árboles de mayor altura y diámetro a los 24 meses en la plantación 3 fueron *Hyeronima alchorneoides*, seguido por *Pithecellobium elegans*, *Genipa americana* y *Vochysia ferruginea*. *G. americana* presentó la tasa de supervivencia más baja, debido a su crecimiento lento y susceptibilidad a condiciones climáticas calientes y frías. Sin embargo, su supervivencia fue mayor en las parcelas mixtas que en las puras. El DAP del *H. alchorneoides* fue mayor en las plantaciones mixtas. No se encontraron diferencias estadísticamente significativas en la altura entre parcelas mixtas y puras para ninguna especie (Tabla 1a,b).

Tabla 1a.

CRECIMIENTO Y DIÁMETRO A LA ALTURA DEL PECHO (DAP) PARA LAS PARCELAS MIXTAS Y PURAS DE LAS PLANTACIONES 1, 2 Y 3.

Especies/ Parcelas	Altura total(mt)	DAP (cm)
Plantación 1: 48 meses		
S. microstachyum		
Plantación Pura	0	0
Plantación Mixta	5,73	6,38

Continua...

Continuando...

Especies/Parcelas	Altura total(mt)	DAP (cm)
V. guatemalensis		
Plantación Pura	11,6	11,8
Plantación Mixta	11,4	18,0
J. copaia		
Plantación Pura	14,4	12,7
Plantación Mixta	15,4	18,8
C. brasiliense		
Plantación Pura	5,38	6,09
Plantación Mixta	4,58	3,80
Plantación 2: 39 meses		
A. guachapele		
Plantación Pura	5,15	6,02
Plantación Mixta	6,25	7,15
D. panamensis		
Plantación Pura	7,10	6,04
Plantación Mixta	7,36	6,35
V. koschnyi		
Plantación Pura	7,01	8,44
Plantación Mixta	7,06	8,24
T. amazonia		
Plantación Pura	8,35	7,64
Plantación Mixta	8,82	9,51
Plantación 3: 24 meses		
G. americana		
Plantación Pura	3,36	4,51
Plantación Mixta	3,77	4,79
H. alchorneoides		
Plantación Pura	5,96	6,96
Plantación Mixta	5,47	7,76
V. ferruginea		
Plantación Pura	2,59	4,05
Plantación Mixta	2,99	3,78
P. elegans		
Plantación Pura	4,98	6,58
Plantación Mixta	5,14	6,33

Tabla 1b.

ÁREA BASAL E ÍNDICE DE VOLUMEN PARA LAS PARCELAS MIXTAS Y PURAS DE LAS PLANTACIONES 1,2 Y 3.

Especies/Parcelas	Área basal (m²/ha)	Índice de volumen (m³/ha)
Plantación 1: 48 meses		
S. microstachyum	0	0
V. guatemalensis	28,4	172
J. copaia	34,1	272
C. brasiliense	5,53	16,1
Comb. de 4 especies	34,8	231
Plantación 2: 39 meses		
A. guachapele	6,12	17,7
D. panamensis	5,38	21,1
V. koschnyi	12,0	45,1
T. amazonia	8,08	37,2
Comb. de 4 especies	9,24	36,5
Plantación 3: 24 meses		
G. americana	2,66	4,78
H. alchorneoides	9,26	27,7
V. ferruginea	2,84	3,70
P. elegans	8,18	20,9
Comb. de 4 especies	6,43	15,9

Daños por plagas

En la plantación 1, *V. guatemalensis* y *C. brasiliense* presentaron mayor incidencia de ataques de insectos comedores de hojas en las plantaciones mixtas que en las plantaciones puras, sin embargo, la frecuencia general fue baja por lo que ni el crecimiento ni la supervivencia se vieron reducidos. Por el contrario, la severidad de los daños fue menor en las parcelas mixtas que en las puras.

La antracnosis, causada por el hongo *Glomerella spp.* que afectó a *S. microstachyum* causó la muerte de todos los individuos de las plantaciones puras, mientras que en las mixtas sobrevivió 42.2% (en el año 4). La severidad de los daños para *V. guatemalensis* y *C. brasiliense* fue menor a 20% sin diferencias entre plantaciones mixtas y puras. No se registraron daños en *J. copaia*.

En la plantación 2, la frecuencia de los daños fue mayor en las plantaciones puras de *V. koschnyi* y *A. guachapele*. Sin embargo, la severidad de los daños producidos por las hormigas comedoras de hojas fue casi el doble en las plantaciones puras comparadas con las mixtas, y no se observaron diferencias en la severidad entre plantaciones puras y mixtas de *A. guachapele*.

En la plantación 3 se observó mayor frecuencia y menor severidad de daños por plagas en las parcelas mixtas que en las parcelas puras de *G. americana*. *V. ferruginea*, *H. alchorneoides* y *P. elegans* no presentaron daños por plagas ni en plantaciones mixtas ni en las puras (Tabla 2).

Tabla 2.

INCIDENCIA, SEVERIDAD, TIPO DE DAÑO Y PORCENTAJE DE SUPERVIVENCIA PARA LAS DOCE ESPECIES ESTUDIADAS AL MOMENTO DEL ESTABLECIMIENTO.

Especies/ Parcelas	% de incidencia	% de severidad	Tipo de daño	% de supervivencia
Plantación 1: 48 meses				
S. microstachyum			Antacnosis	
Plantación Pura	11,6	86,4		0
Plantación Mixta	8,56	41,2		42,2
V. guatemalensis			Daños en las hojas, huecos circulares	
Plantación Pura	11,6	11,8		97,6
Plantación Mixta	11,4	18,0		97,7
J. copaia			No visibles	
Plantación Pura	0,0	0,0		97,0
Plantación Mixta	0,0	0,0		97,7
C. brasiliense			Daños en las hojas, puntas amarillas	
Plantación Pura	8,94	14,1		74,4
Plantación Mixta	17,1	15,3		77,3
Plantación 2: 39 meses				
A. guachapele			Clorosis asociada a daños causados por topos en las raíces.	
Plantación Pura	25,4	70,0		83,8
Plantación Mixta	31,2	70,6		90,2
D. panamensis			Daños en las hojas, huecos circulares	
Plantación Pura	20,3	11,7		75,5
Plantación Mixta	21,9	10,4		72,7

Continua...

Continuando...

Especies/ Parcelas	% de incidencia	% de severidad	Tipo de daño	% de supervivencia
V. kochnyi			Daños en las hojas, huecos circulares	
Plantación Pura	13,2	24,7		87,9
Plantación Mixta	17,3	13,7		76,6
T. amazonia			No visibles	
Plantación Pura	0,0	0,0		66,3
Plantación Mixta	0,0	0,0		58,9
Plantación 3: 24 meses				
G. americana			Puntas quemadas, hojas dobladas. Daños en las venas de las hojas	
Plantación Pura	3,32	8,83		64,2
Plantación Mixta	5,08	6,67		79,3
H. alchorneoides			No visibles	
Plantación Pura	0,0	0,0		97,3
Plantación Mixta	0,0	0,0		99,2
Y. ferruginea			Daños en las hojas, por hormigas cortadoras	
Plantación Pura	2,54	6,25		88,2
Plantación Mixta	3,13	5,50		91,4
P. elegans			No visibles	
Plantación Pura	0,0	0,0		95,7
Plantación Mixta	0,0	0,0		97,7

Tabla 3.

CAMBIOS EN LA DENSIDAD DE ESPECIES MADERABLES (INDIVIDUOS CON ALTURAS MAYORES A 0.2 M. Y MENORES A 1 M.) PRESENTES EN 1993 EN SECCIONES CON ACLAREO Y SIN ACLAREO DE TRES PLANTACIONES.

	Individuos/m²				Altura al año (m)	
	Sección sin aclareo		Sección aclareada			
Especie/ tratamiento	1993	1994	Pre-aclareo	Post-aclareo	Con aclareo	Sin aclareo
Jacaranda	2,4	2,6	0,8	1,5	1,2	1,1
Mixta	0,9	1,4	0,6	2,3	0,8	0,98
Vochysia	0,0	0,1	0,0	0,9	–	0,5

Regeneración natural de especies maderables

Cuando se tomó la primera medición de regeneración natural (antes del aclareo en agosto de 1993), la densidad de las plántulas maderables bajo el dosel eran diferentes para los tres tratamientos mostrados en la tabla 3.

No se observaron plántulas de regeneración natural en la plantación de *Vochysia*. Por el contrario, la regeneración de especies maderables bajo Jacaranda y las plantaciones mixtas fue abundante. Un año después este patrón se mantuvo igual. El aclareo estimuló la regeneración natural en los tres tratamientos. No se observaron plántulas maderables en la parcela control, la cual estaba dominada por poblaciones densas de *Penisetum spp.* y *Melinis minutiflora.*

Costos

Los estimados de los costos de establecimiento y mantenimiento (Día de trabajo/ha y US-$/ha), calculados de observaciones en campo de las actividades realizadas por los trabajadores han sido publicados en Montagnini *et al.* (1994).

En el presente trabajo se presenta una comparación entre parcelas puras y mixtas de la plantación 1. Los costos ajustados estimados para las parcelas mixtas y tres de las parcelas puras de la plantación 1 se muestran en la tabla 3.

Discusión

La disminución de la competencia intraespecífica en las plantaciones mixtas probablemente sea una de las causas de mayores DAP en las especies de más rápido crecimiento. También se cree que esto es atribuible a los micro habitats de luz asociados a la estructura del follaje de los árboles (Guariguata *et al.*, 1995). No se encontraron diferencias en la altura de los árboles, ya que esta depende del lugar. Sin embargo, *A. guachapele* presentó mayor tamaño y troncos más derechos en las plantaciones mixtas debido a la competencia interespecífica. Se cree que *C. brasiliense* tuvo un DAP menor debido a que fue suprimido por otras especies ubicadas en el dosel. A pesar de que no se tomaron medidas para el control de plagas, estas cesaron luego de tres meses con la llegada de las lluvias. Los resultados sugieren que el uso de diseños mixtos puede reducir los costos de establecimiento de las especies de más lento crecimiento debido a que estas tardan más en cerrar el dosel, lo cual aumenta el costo de remoción de las hierbas de regeneración natural. La disminución de los costos se hizo más marcada con el paso del tiempo debido al cierre del dosel. Estos costos incluyen los beneficios sociales estipulados por la Ley (35-40% de los salarios brutos). Los resultados sugieren también que la competencia con la vegetación herbácea es un factor determinante en la regeneración natural temprana en pastos abandonados. Comparados con *Vochysia* se encontró una cobertura herbácea mayor bajo las plantaciones mixtas y las puras de Jacaranda debido probablemente a los altos requerimientos lumínicos de las hierbas y a la presencia de semillas en el banco.

Conclusiones

Las plantaciones mixtas aparentemente favorecieron el crecimiento del diámetro de las es-

Tabla 4.

COMPARACIÓN ENTRE COSTOS DE ESTABLECIMIENTO Y DE MANTENIMIENTO POR HECTÁREA PARA LAS ESPECIES EN LAS PARCELAS MIXTAS Y PURAS DE LA PLANTACIÓN 1.

	V. guatemalensis		*J. copaia*		*C. brasiliensis*		Combinación	
Año	Día trab	US$	Día trab	US$	Día trab	US$	Día trab	US$
1	108,7	1329.2	108,7	1329,2	108,7	1329,2	108,7	1329,2
2	14,6	162.1	0	0	29,3	352,2	14,6	162,1
3	0	0	0	0	14,6	162,1	7,3	81,0
Totales	123,3	1491.3	108,7	1329,2	152,6	1816,5	130,6	1572,3

pecies de crecimiento rápido. Los tratamientos mixtos más exitosos son los estratificados, compuestos por especies de rápido crecimiento que no toleran la sombra y especies de crecimiento más lento y que pueden vivir bajo la sombra. Comparando las plantaciones puras y las mixtas de las especies estudiadas, las últimas presentaron un rendimiento más alto con la ventaja adicional de incluir especies de alto valor económico. Las operaciones de aclareo y poda pueden favorecer el crecimiento de las especies suprimidas. Las plantaciones mixtas pueden resultar ventajosas para la reducción de daños por plagas, como es el caso de antracnosis y ataques de hormigas cortadoras de hojas.

Los tiempos estimados de rotación de la plantación y los precios de la madera sugieren que estos cultivos son financieramente atractivos. Los costos de establecimiento se pueden reducir si se combinan especies de crecimiento lento en las plantaciones mixtas. Además, las plantaciones mixtas ofrecen una más amplia variedad de productos en un mercado incierto.

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excessive removal of living biomass, particularly if nutrients in tree crowns are lost through harvest or site preparation (Jorgensen and Wells 1986, Perry and Maghembe 1989). This can be particularly serious when plantations are established on soils that are inherently poor. Therefore, examination of the role of tropical plantations as C sinks necessitates integrative approaches to evaluate not only the rates of C sequestration by different tree species, but also their design and management to minimize potential deleterious effects on ecosystem nutrients and to make plantations economically, socially, and environmentally sound land use options.

Mixed plantations yield more diverse forest products than monospecific stands, helping to diminish farmers' risks in unstable markets. If planned with consideration for each species' response to mixed conditions, mixed designs can be more productive than monospecific systems (Smith 1986, Burkhart and Tham 1992, Kelty 1992, Wormald 1992). In this article we report results of biomass accumulation and soil nutrients from three young experimental plantations with native trees in mixed and pure stands in the Atlantic humid lowlands of Costa Rica. In previous reports we have shown that the growth of dominant species was faster in mixed than in pure conditions and that total volume per hectare in mixed plantations ranked first or second in comparison with pure stands of the fastest growing species (Montagnini and others 1994, 1995). We expected that total aboveground biomass production, stem biomass increments, and C sequestration rates were higher in mixed than in pure plantations. In addition, we hypothesized that soil nutrient depletion had occurred in the pure plantations, while soils in the the mixed plantations maintained more consistent nutrient levels. Although the young age of the plantations precludes proper extrapolation over a whole rotation, the results do suggest design and management options that can enhance the value of tropical plantations as C sinks, diminish their potential negative influences on ecosystem nutrients, and make them economically attractive to the local farmers.

Study Site

The experiments were established on abandoned pasture at the Guaira Annex of La Selva Biological Station in the Atlantic humid lowlands of Costa Rica (10°26'N, 86°59'W, 50 m mean altitude, 24°C mean annual temperature, 4000 mm mean annual rainfall). Soils are Fluventic Dystropepts derived from volcanic alluvium; they are deep, well drained, stone-free, acid, with low or medium organic matter, low nutrient content, and moderately heavy texture (Sancho and Mata 1987). The area had been cleared in the mid-1950s and grazed until 1981, a sequence of land uses common in the region at the time (Montagnini 1994). The area is on flat, uniform terrain. By the time of clearing for the plantations, the area was covered with shrubs and early successional trees, interspersed with patches of grass and ferns. Soil conditions at the time of clearing were too poor for cultivation of bananas or other commercial crops commonly grown in the region (Berstch 1986, Sancho and Mata 1987). The site was cleared manually, and no burning was done. The slash was left on the ground, to protect against soil erosion and to delay the growth of weeds.

Experimental Setting

A total of 12 native tree species of economic value were tested in three plantations, each with four species: plantation 1: *Jacaranda copaia* (Aubl.)D.Don, *Vochysia guatemalensis* D.Sm., *Calophyllum brasiliense* Cambess, and *Stryphnodendrom microstachyum* Poepp. et Endl.; plantation 2: *Terminalia amazonia* (Gmell.)Exell., *Dipteryx panamensis* (Pittier) Record & Mell, *Virola koschnyi* Warb, and *Albizia guachapele* (H.B.K.) Little; and plantation 3: *Hyeronima alchorneoides* Fr. Allemao, *Pithecellobium elegans* D.C. Benth., *Genipa americana* L., and *Vochysia ferruginea* Mart. In each plantation of four tree species there was at least one nitrogen-fixing tree, a relatively fast growing species, and a slower growing species. The criteria for species selection were: growth rate and economic value, potential impacts on soils and nutrient cycling, and seedling availability (Montagnini and others 1995). The plantations were in randomized blocks, with four replicates and six treatments: four pure plantation plots of each species, a mixed-species plot (with the four species), and a fallow (natural regrowth) plot. Each plot was 32 m × 32 m. Initial planting distance was 2 m × 2 m to speed canopy closure and obtain early impacts on soils, with 50% thinning planned after canopy closure. Within each mixed-tree plot, trees of the four species were planted alternating two species per row. The sequential order of the species within rows was systematically reversed every other row. In that manner, each column contained the four species of the mixture in a sequence.

Methods

Aboveground Tree Biomass and Carbon Accumulation

The plantations were thinned after canopy closure, which occurred approximately 2.5–3 years after plant-

Evaluating the Role of Plantations as Carbon Sinks: An Example of an Integrative Approach from the Humid Tropics

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ABSTRACT / Despite their fast growth, tropical plantations are a small sink of atmospheric carbon because they occupy only a small area in relation to other land uses worldwide. Proper design and management of plantations can increase biomass accumulation rates, making them more effective C sinks. However, fast-growing plantations can extract large amounts of nutrients from the soil, and site fertility declines may limit sustained plantation forestry after a few rotations. We measured aboveground biomass accumulation, carbon sequestration, and soil chemistry in three young plantations of 12 indigenous tree species in pure and mixed designs in the humid lowlands of Costa Rica. Annual biomass increments for the three mixed plantations ranged from 10–13 Mg/ha. The mixtures of four species gave higher biomass per hectare than that obtained by the sum of one fourth hectare of each species in pure plots. At this early age of the plantations, estimated annual C sequestration values were comparable to other reports from young plantations of exotic species commonly grown in the tropics. Four years after planting, decreases in soil nutrients were apparent in pure plots of some of the fastest growing species, while beneficial effects on soils were noted under other species. The mixed plots showed intermediate values for the nutrients examined and, sometimes, improved soil conditions. A mixture of fast and slower growing species yields products at different times, with the slower growing species constituting a longer term sink for fixed carbon. Examination of the role of tropical plantations as C sinks necessitates integrative approaches that consider rates of C sequestration, potential deleterious effects on ecosystem nutrients, and economic, social, and environmental constraints.

It is generally accepted that forests can play a critical role in capturing and storing large amounts of carbon from the atmosphere and can thus contribute to reducing the buildup of atmospheric carbon dioxide. Despite their relatively fast growth, it has been suggested that tropical plantations are a small sink of atmospheric carbon because they occupy a relatively small area in relation to other vegetation types and land uses worldwide (Brown and others 1986). The area of plantations annually planted in the tropics is currently <10% of the simultaneously deforested area, and tree planting currently compensates for 0.3% (at most) of the carbon released by deforestation (Bruenig 1996). To have a significant impact as a global C sink, plantations would need to be established on an unprecedented scale (Sedjo 1989, Myers and Goreau 1991, Houghton 1996). However, rates of reforestation and afforestation worldwide are likely to grow over the next decades as many countries seek to compensate for the loss of natural forests, and thus the role of plantations in sequestering C may also increase (Gladstone and Ledig 1990, Rotmans and Swart 1991, Houghton 1996). Several exotic and indigenous tree species growing in a variety of tropical environments should be tested with respect to their rates of growth and biomass accumulation, especially those that produce good quality timber, which results in longer-term storage of the fixed carbon.

Afforestation and other forest management options to sequester C in tropical latitudes may fail unless they address local economic, social, environmental, and political needs of people in the developing world (Cairns and Meganck 1994, Houghton 1996). Tree plantations are a source of cash, savings, and insurance for the individual farmers (Chambers and Leach 1990). On the other hand, fast growing tropical tree plantations incorporate considerable amounts of nutrients in their biomass over a relatively short period of time. Site fertility declines can limit sustained plantation forestry in tropical regions: soil fertility can be decreased through

KEY WORDS: Native trees; Aboveground biomass; Stem increments; Rotation length; Soil nutrients; Economics

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ing, although some species such as *Jacaranda copaia* closed canopies within a year. For consistency, the three plantations were thinned three years after planting. With thinning, the initial 2 m × 2 m planting distance was widened to 2 m × 4 m (1250 trees/ha). This plantation density is similar to the prevalent 3 m × 3 m (1111 trees/ha), and thus it would allow for comparison with other experiences in the region. Thinning was performed in one half of each plot, leaving the other unthinned half for comparison. For thinning, all trees were cut in alternate rows. From every thinned row, two trees were randomly selected for biomass determinations, giving a total of 16 sampled trees per plot. The material from each tree was separated into its parts (stem, branches, and leaves) and weighed fresh at the site using a field scale. Subsamples of all materials, including stems (lower, middle, and top parts) were taken to the laboratory and dried at 70°C to constant weight. Dry-wet weight ratios from felled trees were used to correct the field weight determinations and obtain biomass on a per tree basis. Data from the 16 sampled trees were averaged to obtain values per plot. The average biomass per tree was multiplied by the number of trees per plot, corrected for tree mortality, and extrapolated to a hectare. Analysis of variance and LSD tests were run to compare mean biomass ($N = 4$) of tree parts among species. Comparisons were made among species in pure and mixed conditions on a per tree basis and also among pure and mixed plots on a per hectare basis.

For calculation of carbon accumulation by each plantation species, only stem biomass values were used, because most leaves and a great portion of the branches are expected to turnover every year, i.e., they represent only a short-term carbon storage. In addition, C sequestration by harvestable timber can be compared with other values from the literature. Stem biomass was divided by plantation age (3 years) to calculate average annual increments. Average stem biomass increments were converted to total carbon content by assuming that biomass is approximately 50% carbon (Brown and Lugo 1982).

Soil Chemistry

Soils were sampled before clearing the land and annually thereafter. Soil conditions before clearing (1991) have been reported elsewhere (Montagnini and others 1993, 1994), and only results of sampling from 1992 to 1995 are reported here. Composite samples were taken in each of the four replicate plots per treatment, at 0–5, 5–15, 15–30, and 30–60 cm depth. The pH was measured in a 1:2.5 mixture of soil–deionized water. The exchangeable Ca and Mg were extracted with a 1 N KCl solution, while the exchangeable P and K were extracted with a modified Olsen solution, which is a mixture of 0.5 N $NaHCO_3$, 0.01 N bisodium EDTA, and Superfloc 127 (a commercial flocculant) (Diaz-Romeu and Hunter 1978). A 1:5 proportion of soil–extractant was used in all cases. Cations were measured using an Atomic Absorption Spectrophotometer. Extractable P was measured colorimetrically after reaction with $(NH_4)_2MoO_4$ and $SnCl_2$, using a spectrophotometer. Organic matter was measured with the Walkley-Black technique (Allison 1975) and total N was measured using a semi-micro-Kjeldahl technique (Bremner and Mulvaney 1982). Analysis of variance and LSD tests were run to compare the means for each variable and soil depth ($N = 4$, $P < 0.05$) among sites.

Results

Aboveground Tree Biomass

Comparisons among species in pure and mixed conditions on a per tree basis. In plantation 1, *Jacaranda copaia* and *Vochysia guatemalensis* had the highest total aboveground biomass per tree when grown in mixture (Figure 1a). These differences were statistically significant ($P < 0.05$). In contrast, for *C. brasiliense*, biomass of each plant part and the total were higher in pure than in mixed plots. For *S. microstachyum* there were no statistically significant differences in biomass between pure and mixed plots.

In plantation 2, the highest total biomass per tree was found in *Terminalia amazonia* and *Dipteryx panamensis* growing in mixed conditions (Figure 1b). In *T. amazonia*, total biomass in mixed plots was more than twice that in pure plots. In the other three species of this plantation, biomass of tree parts was always higher in mixed than in pure plots, although the differences were not as pronounced as for *T. amazonia*.

In plantation 3, total biomass was similar for *Hyeronima alchorneoides*, *Pithecellobium elegans*, and *Vochysia ferruginea* (Figure 1c), while the total biomass in *Genipa americana* plots was about half that of the other three species. Biomass of plant parts was higher in mixed than in pure stands of *H. alchorneoides* and *P. elegans*, while the opposite was true for the other two species.

Biomass per hectare in pure plots of 12 species and in mixtures of four species. Annual biomass increments for the three mixtures were 10.8 Mg/ha for plantation 1, 13.0 Mg/ha for plantation 2, and 10.3 Mg/ha for plantation 3. In the three plantations, the biomass of 1 ha of the mixture was higher than the sum of one fourth of a hectare of each of the four species in pure stands (Table 1). In plantation 1 the total biomass was higher

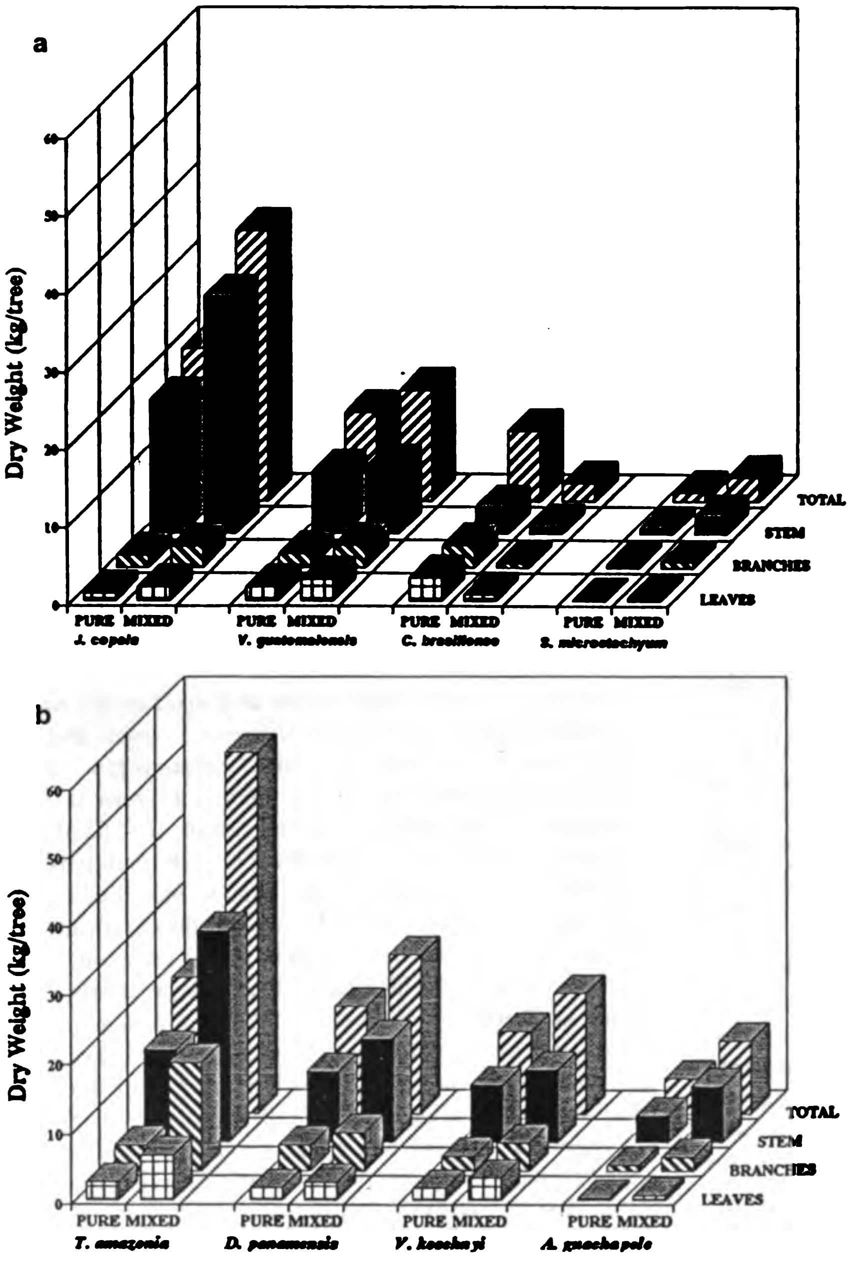

Figure 1. (a) Aboveground tree biomass (leaves, branches, stem, and total) of *Jacaranda copaia*, *Vochysia guatemalensis*, *Calophyllum brasiliense*, and *Stryphnodendron microstachyum* in pure and mixed plots. (b) Aboveground tree biomass (leaves, branches, stem, and total) of *Terminalia amazonia*, *Dipteryx panamensis*, *Virola koschnyi*, and *Albizia guachapele* in pure and mixed plots. (c) Aboveground tree biomass (leaves, branches, stem, and total) of *Hyeronima alchorneoides*, *Pithecellobium elegans*, *Vochysia ferruginea*, and *Genipa americana* in pure and mixed plots.

in *J. copaia* pure plots, followed by the mixture; in plantation 2, the highest total biomass per hectare was found in the mixed plots, followed by *T. amazonia;* and in plantation 3, the three leading species in pure plots shared similar amounts of total biomass per hectare (Table 1).

Carbon Sequestration in Pure and Mixed Plantations

As for biomass, in plantation 1 the mixture of four species ranked second after *J. copaia* in average annual carbon sequestration (Table 2). In plantation 2 the mixture of four species had the highest value, close to that of the mixture in plantation 1. In plantation 3, the two leading species were *P. elegans* and *H. alchorneoides*, and the mixture ranked third, again with a value close to those of the mixtures in the other two plantations.

Soil Chemistry

In plantation 1, statistically significant differences in soil nutrients between treatments were found only for K and P four years after planting (Table 3). The natural regrowth plots had the highest and the *V. guatemalensis* plots had the lowest concentrations of soil K at all

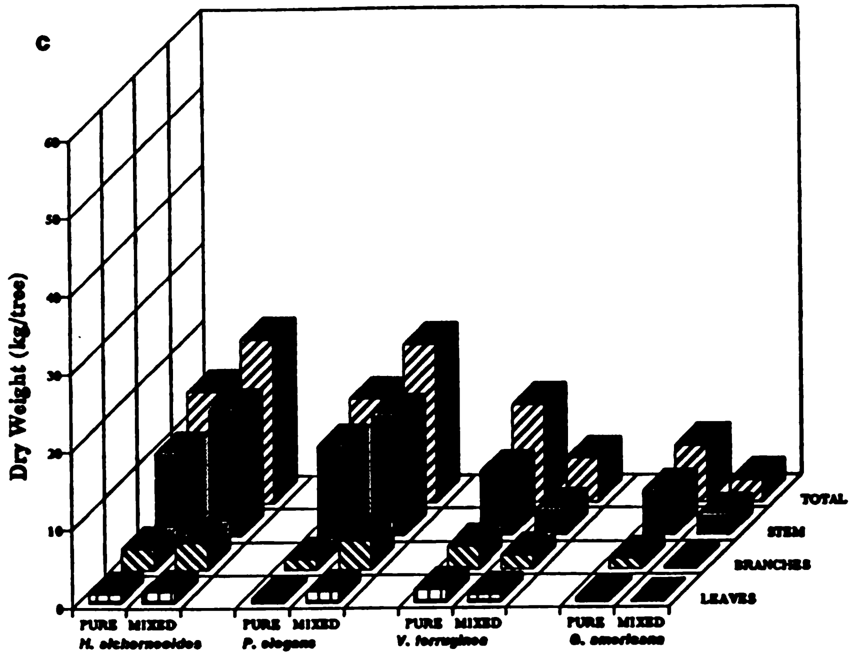

Figure 1. (Continued)

Table 1. Aboveground biomass per hectare of tree species in pure plots and in mixtures of four species each (means, standard errors, and statistical significance)

Treatment	Aboveground biomass (Mg/ha)							
	Stems		Branches		Foliage		Total	
Plantation 1								
Jacaranda copaia	40.9	0.84 a[a]	3.48	0.13 b	2.23	0.13 c	46.6	0.94 a
Vochysia guatemalensis	19.0	0.89 c	4.25	0.22 b	4.03	0.38 b	27.3	1.38 b
Calophyllum brasiliense	7.2	1.46 d	5.71	0.71 a	5.89	0.52 a	18.8	2.67 c
Stryphnodendron microstachyum	1.7	1.26 e	0.56	0.42 c	0.20	0.14 d	2.5	1.82 d
Mixture of 4 species	25.3	1.38 b	3.86	0.24 b	3.13	0.23 bc	32.3	1.53 b
Plantation 2								
Terminalia amazonia	22.4	3.46 a	5.96	0.47 b	4.19	0.38 a	32.5	4.23 ab
Dypterix panamensis	19.1	2.21 a	6.84	0.83 ab	3.22	0.49 a	29.1	3.05 ab
Virola koschnyi	17.8	2.39 a	4.28	1.00 bc	3.61	0.75 a	25.7	3.54 b
Albizia guachapele	7.9	0.85 b	1.92	0.24 c	0.54	0.14 b	10.3	1.10 c
Mixture of 4 species	24.8	2.58 a	9.66	1.72 a	4.68	0.63 a	39.1	4.41 a
Plantation 3								
Pithecellobium elegans	28.8	3.83 a	3.17	0.77 b	1.21	0.23 c	33.2	4.20 a
Hyeronima alchorneoides	26.3	4.99 a	6.74	0.97 a	2.87	0.27 ab	35.9	6.09 a
Vochysia ferruginea	20.3	1.07 a	7.25	1.11 a	3.62	0.44 a	31.1	2.36 a
Genipa americana	13.9	2.85 b	3.06	0.74 b	1.26	0.23 c	18.2	3.70 b
Mixture of 4 species	23.1	2.58 ab	5.55	0.36 ab	2.32	0.18 b	31.0	3.06 ab

[a] For each plantation and tree parts, differences among means are statistically significant when standard errors are followed by different letters ($N = 4$, $P < 0.05$).

depths. Similarly, the natural regrowth had the highest and *V. guatemalensis* the lowest concentration of soil P, although significant differences for P only occurred in the topsoil (0–5 cm depth). A general trend of slightly decreasing amounts of K over time was seen in all treatments, with the largest declines occurring in the *J. copaia*, mixed, and *V. guatemalensis* treatments (Figure 2). Soil P increased only slightly from 1992 to 1995, especially in the mixed and natural regrowth plots (Figure 3).

In plantation 2, four years after planting, the highest values of soil K were found in *D. panamensis* and *A.*

Table 2. Stem biomass and carbon sequestration by 12 tree species in pure plots and in mixtures of four species each

Treatment	Mean annual stem increment (Mg/ha)	Mean annual C sequestr. (Mg/ha)	Estimated rotation length (yr)
Plantation 1			
Jacaranda copaia	13.6	6.82	12
Vochysia guatemalensis	6.3	3.17	15
Calophyllum brasiliense	2.4	1.20	25
Stryphnodendron microstachyum	0.6	0.28	20
Mixture of 4 species	8.4	4.21	18
Plantation 2			
Terminalia amazonia	7.5	3.73	20
Dypterix panamensis	6.4	3.18	20
Virola koschnyi	5.9	2.96	15
Albizia guachapele	2.6	1.31	20
Mixture of 4 species	8.3	4.13	18.75
Plantation 3			
Pithecellobium elegans	9.6	4.80	20
Hyeronima alchorneoides	8.8	4.39	20
Vochysia ferruginea	6.8	3.38	15
Genipa americana	4.6	2.32	20
Mixture of 4 species	7.7	3.85	18.75

guachapele, and the lowest in *T. amazonia* and *V. koschnyi*, with intermediate values in the natural regrowth and mixed plots (Table 4). A similar trend was found for Ca and Mg, although statistically significant differences were only found for Mg at 5–15 cm depth. There were no statistically significant differences in P among treatments in the top soil. Increases in cation content under *D. panamensis* and *A. guachapele* had only occurred in the current year, following a decline in cations from 1992 to 1994 (data not shown).

In plantation 3, three years after planting, the highest values of soil K, Ca, and Mg were found in the regrowth plots and the lowest in the *H. alchorneoides* plots (Table 5). *P. elegans* plots had the second highest values of soil K. The reverse was true for P: *H. alchorneoides* plots had the highest soil P values at 0–5 cm depth, significantly different from those in the mixed and natural regrowth plots (Table 5). *G. americana* plots followed with the second highest values. There was a small trend of an increase in most nutrients at all depths over time, especially for the natural regrowth and mixed plots (data not shown).

Discussion

Aboveground Tree Biomass in Pure and Mixed Plantations

The most successful mixed plantings are stratified mixtures composed of faster growing, shade-intolerant species above slower starting tolerants (Smith 1986). If the trees in the upper canopy are not too dense, they grow more rapidly in diameter than if crowded into the single canopy of a pure plantation; lower-stratum species can influence stem form and self-pruning of upper-stratum species in ways similar to that of a pure stand (Burkhart and Tham 1992). In the present research, the dominant species of each plantation grew larger when grown with other species compared to single-species plantations. Apparently in the mixtures, the dominant species, with less intraspecific competition, can attain larger diameters, as reported in earlier research (Montagnini and others 1995). Only two of the 12 species tested were seemingly suppressed by the dominant species and thus grew better in pure plots: *C. brasiliense* (plantation 1) and *G. americana* (plantation 3). Except in the two cases noted, the other species associated with the faster growing dominants apparently shared resources with the dominant species and had higher biomass of plant parts in mixed than in pure plots.

Farmers may prefer species diversification for financial reasons or because of uncertainties about species' performance, scarcity of seedlings, or risks from potential pest damage. Species diversification could be achieved by planting species mixtures or planting a set of monospecific plots. In the three plantations tested, the mixtures always had greater biomass accumulation rates than the sum of each of the component species in pure plots. These results suggest that mixed designs, if planned with consideration for each species' response to mixed conditions, may result in greater production than using the same area of land for pure species stands.

The inclusion of faster and relatively slower growing species in a mixture has the additional advantage of providing harvestable products at different rotation times, with the slower growing species (e.g., *C. brasiliense*, *V. ferruginea*) producing relatively more valuable wood. This product constitutes a longer-term sink for fixed carbon (e.g., construction timber, furniture, wood crafts), than timber of less value, whose uses may be relatively shorter-lived (e.g., boxes, poles, fuelwood). Additionally, because the different species of the mixture have different rotation lengths, the land is in use for a longer period than if planted with just one fast-growing, short-rotation species (such as *J. copaia*). This diminishes incentives for changing to other land uses, keeps a vegetative cover that protects the soil, and serves other environmental purposes as well.

The values of mean annual aboveground biomass production and stem biomass increments for the three mixtures lie within the ranges reported elsewhere for fast-growing, monospecific plantations of commonly used exotics in the humid tropics (Table 6). The values

Table 3. Soil chemical characteristics in plantation 1, four years after planting[a]

Treatment and depth (cm)	pH			Extractable cations (cmol/kg) Ca			Extractable cations (cmol/kg) Mg			Extractable cations (cmol/kg) K			Extractable P (mg/kg)			Organic matter (%)			Total N (%)		
	Mean	SE	Sig.	Mean	SE	Sig.	Mean	SE	Sig.	Mean	SE	Sig.	Mean	SE	Sig.	Mean	SE	Sig.	Mean	SE	Sig.
Jacaranda copaia																					
0–5	4.43	0.09	ab	1.60	1.13	a	0.48	0.09	a	0.12	0.02	c	9.55	3.07	ab	6.04	2.19	a	0.39	0.05	a
5–15	4.45	0.10	a	1.00	0.73	a	0.33	0.07	a	0.12	0.03	b	8.30	2.26	a	6.22	1.11	a	0.30	0.05	a
15–30	4.43	0.08	a	0.67	0.50	ab	0.26	0.06	a	0.13	0.03	ab	7.08	2.17	a	4.52	1.04	a	0.24	0.03	a
30–60	4.53	0.11	a	0.41	0.32	a	0.17	0.04	a	0.11	0.03	abc	5.38	1.85	a	3.32	0.61	a	0.18	0.02	a
Calophyllum brasiliense																					
0–5	4.30	0.04	b	0.75	0.47	a	0.46	0.07	a	0.19	0.05	bc	15.08	4.85	ab	7.23	0.47	a	0.38	0.03	a
5–15	4.45	0.05	a	0.47	0.33	a	0.31	0.04	a	0.17	0.06	b	10.33	2.61	a	4.54	0.74	a	0.26	0.02	a
15–30	4.43	0.03	a	0.23	0.14	b	0.44	0.15	a	0.19	0.06	ab	11.58	3.75	a	3.48	0.50	a	0.22	0.01	a
30–60	4.53	0.05	a	0.15	0.05	a	0.21	0.04	a	0.20	0.06	ab	10.00	1.73	a	2.60	0.46	a	0.15	0.01	ab
Stryphnodendron microstachyum																					
0–5	4.45	0.03	ab	0.75	0.11	a	0.86	0.14	a	0.24	0.05	b	9.83	2.41	ab	8.17	0.50	a	0.37	0.02	a
5–15	4.50	0.00	a	0.39	0.13	a	0.40	0.07	a	0.13	0.02	b	6.43	1.73	a	5.41	0.56	a	0.25	0.01	a
15–30	4.48	0.05	a	0.22	0.10	b	0.28	0.04	a	0.11	0.04	ab	6.63	2.21	a	3.34	0.69	a	0.19	0.02	a
30–60	4.55	0.10	a	0.46	0.26	a	0.17	0.03	a	0.11	0.04	abc	5.58	1.93	a	2.34	0.45	a	0.12	0.01	b
Vochysia guatemalensis																					
0–5	4.55	0.09	a	1.50	1.03	a	0.88	0.36	a	0.11	0.01	c	6.70	0.76	b	7.98	1.13	a	0.41	0.04	a
5–15	4.43	0.05	a	0.69	0.62	a	0.30	0.09	a	0.09	0.02	b	5.80	0.88	a	5.64	1.28	a	0.29	0.05	a
15–30	4.45	0.06	a	2.16	1.17	a	0.70	0.25	a	0.09	0.03	b	7.58	1.21	a	4.36	1.24	a	0.23	0.05	a
30–60	4.50	0.04	a	1.06	0.70	a	0.29	0.07	a	0.08	0.03	bc	5.25	1.96	a	1.90	0.25	a	0.14	0.01	b
Mixed																					
0–5	4.45	0.09	ab	1.07	0.24	a	0.57	0.17	a	0.14	0.01	bc	10.18	3.88	ab	6.99	0.37	a	0.37	0.20	a
5–15	4.38	0.10	a	0.44	0.14	a	0.30	0.06	a	0.10	0.01	b	8.43	4.14	a	4.68	0.37	a	0.26	0.02	a
15–30	4.50	0.00	a	0.40	0.08	b	0.32	0.08	a	0.11	0.02	ab	9.23	2.69	a	3.68	0.42	a	0.22	0.02	a
30–60	4.55	0.05	a	0.12	0.03	a	0.15	0.03	a	0.07	0.01	c	5.83	1.39	a	2.61	0.27	a	0.14	0.01	b
Regeneration																					
0–5	4.60	0.12	a	1.02	0.46	a	0.88	0.23	a	0.36	0.05	a	17.70	3.87	a	6.61	0.68	a	0.36	0.03	a
5–15	4.53	0.08	a	0.52	0.20	a	0.37	0.03	a	0.31	0.06	a	11.35	2.88	a	5.32	0.74	a	0.28	0.02	a
15–30	4.50	0.12	a	0.49	0.22	b	0.71	0.42	a	0.22	0.07	a	11.50	2.90	a	3.76	0.63	a	0.23	0.02	a
30–60	4.53	0.08	a	0.17	0.04	a	0.29	0.07	a	0.21	0.07	a	7.60	1.71	a	3.40	0.82	a	0.15	0.01	ab

[a] Means, standard errors (SE), and statistical significance (Sig.). In this and in Tables 4 and 5 differences between sites for a given depth and soil variable are statistically significant when standard errors are followed by different letters ($N = 4$, $P < 0.05$).

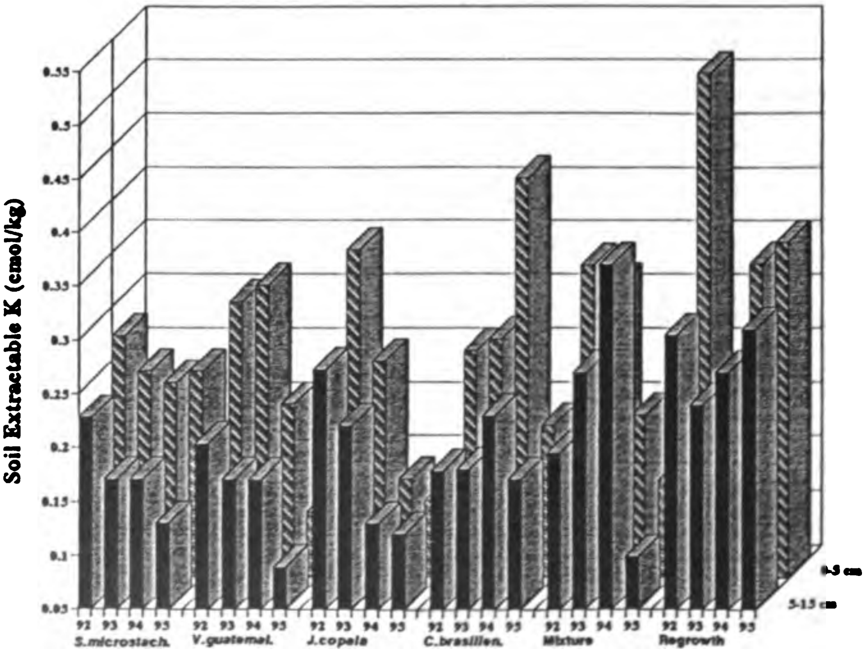

Figure 2. Soil potassium in plantation 1 at 0–5 cm and 5–15 cm depths, in sampling done from 1992 to 1995 (one to four years after planting), under *Stryphnodendron microstachyum*, *Vochysia guatemalensis*, *Jacaranda copia*, *Calophyllum brasiliense*, mixture of four species, and regeneration plots (natural regrowth). See text for statistical significances.

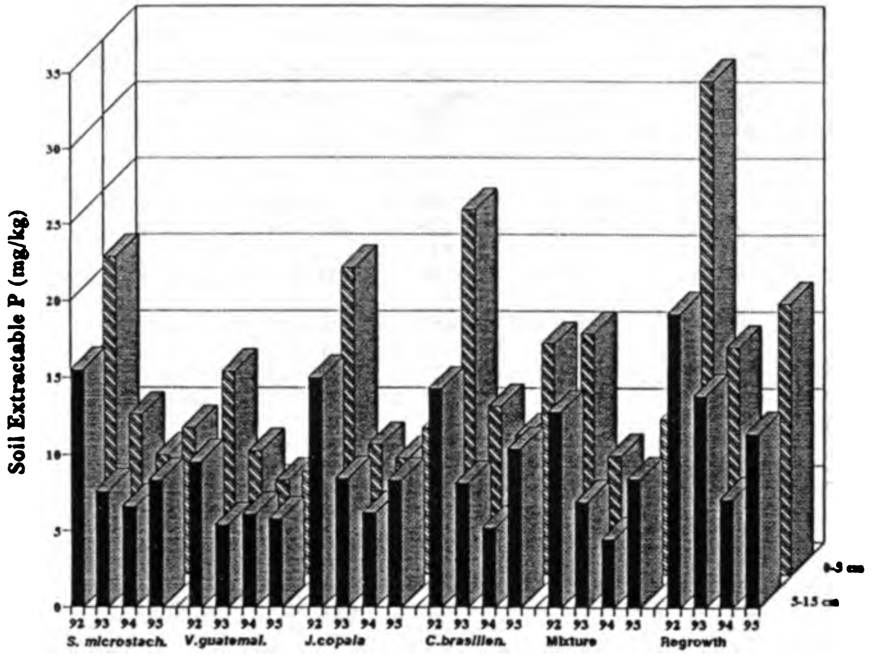

Figure 3. Soil phosphorus in plantation 1 at 0–5 cm and 5–15 cm depths, in sampling done from 1992 to 1995 (one to four years after planting), under *Stryphnodendron microstachyum, Vochysia guatemalensis, Jacaranda copia, Calophyllum brasiliense*, mixture of four species, and regeneration plots (natural regrowth). See text for statistical significances.

Table 4. Soil chemical characteristics in plantation 2, four years after planting[a]

Treatment and depth (cm)	pH			Extractable cations (cmol/kg)									Extractable P (mg/kg)			Organic matter (%)			Total N (%)		
				Ca			Mg			K											
	Mean	SE	Sig.	Mean	SE	Sig.	Mean	SE	Sig.	Mean	SE	Sig.	Mean	SE	Sig.	Mean	SE	Sig.	Mean	SE	Sig.
Albizia guachapele																					
0–5	4.38	0.10	a	1.03	0.34	a	0.88	0.24	a	0.43	0.10	a	13.45	2.17	a	6.86	0.97	a	0.41	0.01	a
5–15	4.50	0.00	a	0.68	0.14	a	0.50	0.07	ab	0.26	0.06	ab	8.35	0.74	a	4.66	0.54	a	0.27	0.02	ab
15–30	4.60	0.00	ab	0.55	0.12	a	0.40	0.07	a	0.22	0.06	a	7.03	0.75	a	3.66	0.28	b	0.20	0.02	b
30–60	4.73	0.05	a	0.38	0.05	a	0.23	0.03	a	0.20	0.04	ab	5.60	1.26	b	2.69	0.23	ab	0.14	0.02	ab
Dipteryx panamensis																					
0–5	4.48	0.13	a	1.13	0.23	a	0.75	0.28	a	0.42	0.06	a	9.93	0.16	a	7.06	0.67	a	0.40	0.02	a
5–15	4.58	0.16	a	0.63	0.07	a	0.78	0.29	a	0.33	0.06	a	7.98	1.27	a	4.48	0.16	a	0.26	0.01	ab
15–30	4.65	0.60	a	0.43	0.05	a	0.38	0.09	a	0.28	0.07	a	5.93	0.89	a	3.29	0.24	b	0.19	0.01	b
30–60	4.58	0.06	ab	0.28	0.05	a	0.23	0.03	a	0.24	0.03	a	4.40	0.23	b	2.68	0.21	ab	0.16	0.01	ab
Terminalia amazonia																					
0–5	4.28	0.05	a	0.75	0.05	a	0.55	0.09	a	0.23	0.04	b	13.26	0.64	a	7.18	0.62	a	0.38	0.03	a
5–15	4.43	0.09	a	0.45	0.07	a	0.33	0.05	b	0.13	0.02	c	8.45	1.00	a	4.94	0.59	a	0.25	0.02	b
15–30	4.58	0.09	ab	0.38	0.03	a	0.28	0.03	a	0.15	0.04	a	7.70	1.48	a	3.37	0.12	b	0.20	0.01	b
30–60	4.60	0.07	ab	0.25	0.03	a	0.18	0.03	a	0.10	0.02	c	5.78	1.00	ab	2.23	0.51	b	0.15	0.01	ab
Virola koschnyi																					
0–5	4.28	0.05	a	1.00	0.26	a	0.55	0.16	a	0.21	0.02	b	13.05	1.72	a	6.70	1.39	a	0.41	0.03	a
5–15	4.35	0.03	a	0.53	0.09	a	0.30	0.04	b	0.16	0.01	bc	10.60	1.68	a	4.33	0.44	a	0.28	0.02	ab
15–30	4.45	0.06	b	0.43	0.11	a	0.28	0.05	a	0.16	0.02	a	9.60	1.85	a	3.61	0.28	b	0.22	0.00	ab
30–60	4.58	0.08	ab	0.35	0.10	a	0.23	0.05	a	0.13	0.02	bc	7.53	1.47	ab	2.52	0.39	ab	0.14	0.01	b
Mixed																					
0–5	4.33	0.05	a	0.68	0.21	a	0.43	0.06	a	0.27	0.05	ab	10.78	2.16	a	6.61	0.38	a	0.38	0.02	a
5–15	4.45	0.03	a	0.50	0.12	a	0.38	0.09	b	0.22	0.05	abc	8.40	2.08	a	4.72	0.26	a	0.27	0.02	ab
15–30	4.55	0.05	ab	0.43	0.11	a	0.30	0.06	a	0.16	0.03	a	6.98	1.44	a	3.54	0.15	b	0.23	0.02	ab
30–60	4.60	0.04	ab	0.30	0.04	a	0.20	0.00	a	0.12	0.02	bc	5.50	1.12	b	2.57	0.09	ab	0.14	0.00	ab
Regeneration																					
0–5	4.33	0.05	a	1.00	0.12	a	0.58	0.03	a	0.34	0.05	ab	11.80	2.50	a	8.29	0.74	a	0.43	0.02	a
5–15	4.38	0.06	a	0.58	0.11	a	0.43	0.03	ab	0.22	0.04	abc	8.43	1.96	a	5.76	0.76	a	0.32	0.04	a
15–30	4.48	0.06	ab	0.45	0.06	a	0.35	0.05	a	0.23	0.04	a	8.13	1.45	a	4.85	0.70	a	0.27	0.04	a
30–60	4.53	0.08	b	0.35	0.07	a	0.25	0.05	a	0.21	0.05	ab	10.55	3.14	a	3.42	0.30	a	0.18	0.01	a

[a] Means, standard errors (SE), and statistical significance (Sig.).

Table 5. Soil chemical characteristics in plantation 3, four years after planting[a]

Treatment and depth (cm)				Extractable cations (cmol/kg)																	
	pH			Ca			Mg			K			Extractable P (mg/kg)			Organic matter (%)			Total N (%)		
	Mean	SE	Sig.	Mean	SE	Sig.	Mean	SE	Sig.	Mean	SE	Sig.	Mean	SE	Sig.	Mean	SE	Sig.	Mean	SE	Sig.
Genipa americana																					
0–5	4.50	0.06	b	0.57	0.21	b	0.64	0.35	b	0.34	0.10	bc	6.28	1.31	ab	6.77	0.33	ab	0.33	0.02	a
5–15	4.60	0.08	a	0.27	0.08	b	0.31	0.17	ab	0.24	0.10	bc	4.30	0.65	a	4.30	0.63	a	0.23	0.02	a
15–30	4.63	0.09	a	0.26	0.11	b	0.27	0.13	ab	0.22	0.09	bc	4.30	0.62	a	3.23	0.42	a	0.20	0.02	a
30–60	4.53	0.05	a	0.10	0.04	b	0.13	0.07	a	0.12	0.07	a	3.50	0.82	a	1.67	0.38	a	0.13	0.01	a
Hieronyma alchorneoides																					
0–5	4.33	0.05	b	0.44	0.06	b	0.39	0.04	b	0.14	0.02	c	8.30	1.30	a	5.90	0.59	b	0.34	0.01	a
5–15	4.43	0.09	a	0.17	0.05	b	0.21	0.02	b	0.10	0.01	c	4.43	0.99	a	4.49	0.85	a	0.24	0.01	a
15–30	4.43	0.05	a	0.19	0.06	b	0.19	0.04	b	0.10	0.02	c	4.38	1.12	a	3.68	0.29	a	0.22	0.02	a
30–60	4.50	0.06	a	0.06	0.02	b	0.10	0.02	a	0.09	0.02	a	3.83	0.78	a	1.85	0.30	a	0.13	0.01	a
Pithecellobium elegans																					
0–5	4.50	0.13	b	1.19	0.44	b	0.67	0.28	ab	0.32	0.03	bc	4.75	1.03	ab	8.15	0.15	a	0.32	0.06	a
5–15	4.48	0.14	a	0.88	0.35	a	0.52	0.15	ab	0.25	0.06	bc	3.73	0.24	a	5.10	0.29	a	0.26	0.02	a
15–30	4.50	0.09	a	0.52	0.11	ab	0.29	0.06	ab	0.19	0.04	bc	3.33	0.60	a	3.69	0.87	a	0.16	0.03	a
30–60	4.50	0.06	a	0.80	0.53	a	0.43	0.30	a	0.17	0.07	a	3.13	1.00	a	3.32	0.87	a	0.20	0.07	a
Vochysia ferruginea																					
0–5	4.55	0.10	b	1.06	0.46	b	0.97	0.27	ab	0.52	0.19	b	4.90	0.53	ab	6.64	0.62	ab	0.38	0.01	a
5–15	4.58	0.09	a	0.49	0.19	ab	0.49	0.08	ab	0.39	0.12	ab	2.85	0.40	a	4.81	0.63	a	0.27	0.01	a
15–30	4.63	0.09	a	0.36	0.19	ab	0.33	0.10	ab	0.30	0.09	ab	2.25	0.44	a	3.69	0.46	a	0.19	0.01	a
30–60	4.55	0.10	a	0.19	0.05	ab	0.16	0.03	a	0.19	0.05	a	2.35	1.01	a	1.85	0.15	a	0.12	0.00	a
Mixed																					
0–5	4.38	0.06	b	0.65	0.13	b	0.63	0.13	b	0.22	0.03	bc	3.88	1.00	b	7.05	0.18	ab	0.38	0.01	a
5–15	4.48	0.08	a	0.34	0.13	b	0.37	0.07	ab	0.17	0.03	bc	2.45	0.78	a	5.00	0.43	a	0.27	0.03	a
15–30	4.60	0.17	a	0.30	0.11	b	0.26	0.07	ab	0.12	0.02	bc	2.38	0.71	a	3.75	0.31	a	0.20	0.01	a
30–60	4.55	0.10	a	0.27	0.12	ab	0.17	0.06	a	0.11	0.02	a	1.90	0.66	a	1.89	0.43	a	0.13	0.00	a
Regeneration																					
0–5	4.90	0.18	a	2.49	0.59	a	1.38	0.28	a	0.96	0.21	a	3.93	1.83	b	8.30	1.21	a	0.38	0.02	a
5–15	4.68	0.16	a	0.90	0.12	a	0.57	0.09	a	0.58	0.12	a	3.20	0.75	a	5.09	0.34	a	0.25	0.01	a
15–30	4.65	0.12	a	0.70	0.13	a	0.43	0.07	a	0.41	0.07	a	3.80	0.93	a	2.91	0.20	a	0.20	0.01	a
30–60	4.55	0.06	a	0.30	0.10	ab	0.17	0.02	a	0.18	0.03	a	2.00	0.65	a	2.83	1.42	a	0.13	0.01	a

[a] Means, standard errors (SE), and statistical significance (Sig.).

Table 6. Above ground biomass and stemwood production in tropical plantations

Species	Age (yr)	Aboveground biomass production (Mg/ha/yr)	Stemwood biomass production (Mg/ha/yr)	Country	Source
Eucalyptus citridiora	9	11.8	7.2	Brazil	Lugo *et al.* (1988)
Eucalyptus deglupta	8	13.1	11.9	Costa Rica	Lugo *et al.* (1988)
Gmelina arborea	5	12.9	11.8	Costa Rica	Lugo *et al.* (1988)
Gmelina arborea	6.6	13.9	10	Sarawak	Halenda (1993)
Albizia lebbek	3	9.8	8.4	Puerto Rico	Wang *et al.* (1991)
Leucaena leucocephala	5.5	11	9	Puerto Rico	Wang *et al.* (1991)
Swietenia spp.	9–13	NA	1–4	Nicaragua	Wadsworth (1983)
Tectona grandis	14	NA	7–11	Cuba	Wadsworth (1983)

NA: not available.

in Table 6 were for plantations of relatively young age; values will also vary with climate and site fertility (Lugo and others 1988). Values for the two slower growing trees in pure plots, *C. brasiliense* and *G. americana*, are similar to ranges reported for relatively slower growing species (Table 6). Thus, the species of the present research had acceptable growth rates in pure and mixed conditions and were adequate for their incorporation as timber species in forestry/agroforestry systems in the region.

Carbon Sequestration in Pure and Mixed Plantations

Values of mean carbon storage over a whole rotation have been recently reported for several tree species commonly grown in tropical regions (Schroeder 1992).

The plantations of the present research were too young for proper extrapolation of initial growth data over a whole rotation. Calculations based on data obtained at an early age of the plantations can overestimate C sequestration, since most of the carbon uptake occurs in the youngest age classes (0–10 yr) (Brown and others 1986).

Rotation length is a key factor in the ability of plantations to remove carbon from the atmosphere over the long term (Schroeder 1992). Rotation times of 12–15 years are expected for the fastest growing species and 20 years for the slower growing species of these experiments (Table 2) (Montagnini and others 1995, Montagnini and Mendelsohn 1996). The longer the rotation time, the larger the error associated with extrapolating annual C sequestration calculated at an early age.

Several assumptions are commonly used when calculating C storage by tree plantations: for example, stem biomass is calculated using data on volume yield and wood density, because stem biomass is not generally measured at the time of harvest. We expect to obtain additional biomass measurements at intermediate and mature ages of each species of these experiments to obtain accurate estimations of C storage over a full rotation.

Live trees generally comprise the greatest portion of the aboveground biomass of a plantation. For example, in a 6.6-year-old *Gmelina arborea* plantation in Sarawak, total aboveground biomass (92.1 Mg/ha) was comprised of 92% overstory, 3.5% undergrowth, and 4.2% litter (Halenda 1993). The undergrowth is expected to be a small component of aboveground biomass in managed plantations, although this may vary with the weeding intensity, site characteristics, and planting distance. In another plantation at La Selva that included some of the species of the present research, with the same planting distance, and on similar soils, the undergrowth was <2% of the total aboveground biomass (Montagnini and Sancho 1994).

Our current estimates of C sequestration only include aboveground tree parts. Roots of tropical trees appear to decay at slower rates than leaf tissue (Bloomfield and others 1993), which means that they may function as a longer-term C storage mechanism. However, tropical plantations have a smaller fraction of total tree biomass in roots than natural forests (Vogt and others 1997). To date, estimates of root biomass density have been made only in the topsoil (0–15 cm) of these plantations, data far too incomplete to consider here. Accurate measurements of root biomass, especially coarse roots with longer residence time, could aid in a more precise evaluation of C sequestration by plantation ecosystems.

Soil Chemical Characteristics in Pure and Mixed Plantations

K and P, the two nutrients most likely to be depleted from plantation soils (Wadsworth 1983, Bowen and Nambiar 1984), were most depleted in the soils under faster growing species, such as *V. guatemalensis*, while depletion of these nutrients was less pronounced in the plots of the slower growing species of this plantation (*C. brasiliense*). This suggests that rapid uptake and accumulation of nutrients in tree biomass served as the main mechanism responsible for this decrease. In contrast, the natural regrowth plots seemingly functioned as "fallows" and contributed to the recovery of soil nutrients from initial preplantation levels, presumably through biomass turnover and nutrient release.

In other cases, beneficial effects on some of the same soil nutrients were noted: increases in cations, especially K, were found under *D. panamensis* and *A. guachapele*. These increases had occurred only recently, following initial declines, thereby pointing to a recovery presumably caused by nutrient cycling mechanisms. Plantation 3 exhibited both types of results, with P enrichment in two treatments (*H. alchorneoides* and *G. americana*), in comparison with natural regeneration plots; the reverse pattern was found for K. On the other hand, the mixed plots showed intermediate values for the nutrients examined, and even improved soil conditions, as in plantation 3. This suggests that in mixed conditions it may take longer to deplete soil nutrients than in monospecific stands of fast-growing species.

Ameliorating effects of plantation forests on soils generally occur during the period immediately following canopy closure (the fallow enrichment phase), while during the maximum production phase a deterioration of site quality may occur, as mineral nutrients are taken up by the trees and litter accumulates on the floor due to unfavorable conditions for organic matter decomposition (Sánchez and others 1985). Results of continued sampling will be needed to assess the long-term effects of plantation treatments on soil chemistry. Additionally, the examination of whole-stand nutrient budgets, including soil and biomass nutrients, and litter decomposition studies, may help sort out the relative roles of nutrient uptake by trees and nutrient inputs from weeding and from litterfall for the five treatments.

Potential of Tropical Tree Plantations as Carbon Sinks

Tropical forests harbor more carbon than most other ecosystems and roughly 44 times more than agricultural lands; therefore, although young plantation forests sequester C at a higher rate than mature forests, primary forests conserve much more C per hectare (Cairns and Meganck 1994, Bruenig 1996). Carbon loss associated with deforestation occurs more rapidly than reforestation can sequester C; thus it may be less effective to focus on plantations, except as an alternative to cutting more primary forest (Brown and Adger 1994, Cairns and Meganck 1994).

Fearnside (1995) assessed the monetary carbon costs and benefits for the Brazilian Amazon and showed that reduction of deforestation has a potential C benefit about four times that of plantation establishment for pulp and sawlogs. In a survey from 94 nations in tropical and temperate regions, the mean initial cost of soil rehabilitation and revegetation has been estimated at US $500–3000/ha (Dixon and others 1994). These authors estimated that natural regeneration of woody vegetation or agroafforestation establishment costs were less than US $1000/ha in temperature and tropical regions. These values are similar to our own estimates of establishment costs for tree plantations in the humid lowlands of Costa Rica (Montagnini and others 1995, Montagnini and Mendelsohn 1996). Establishment costs were lower for the slower growing species in mixtures than alone. In comparison with pure stands of the fastest growing species, mixtures had the advantage of including other species of high economic value.

Tropical plantations can serve diverse productive, economic, social, political, and ecological functions. With their relatively high yields, tropical and subtropical plantations can make substantial contributions to world timber and pulp production (Wadsworth 1983, Evans 1992). Plantations may help stabilize rural populations in regions where shifting agriculture is the predominant land use. In combination with subsistence and commercial crops (agroforestry) or cattle (agrosilvopastoral systems), plantations have been used as tools in rural development projects worldwide. In Indonesia, policy efforts aimed at reducing deforestation and biomass burning include the development of plantation forests, the integration of transmigration policies with these new forest plantations, and the reduction of shifting cultivation (Murdiyarso 1993). Industrial plantations can make developing countries producers of wood-based commodities and at the same time bring about net reductions of atmospheric carbon (Dabas and Bhatia 1996). If put in context with their other economic, social, and environmental functions, well-designed and managed tropical plantations can provide viable alternatives to help reduce levels of atmospheric carbon.

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THE ROLE OF SUCCESSIONAL VEGETATION AS FOREST FALLOW: A CASE STUDY IN THE ATLANTIC LOWLANDS OF COSTA RICA

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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.*

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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).

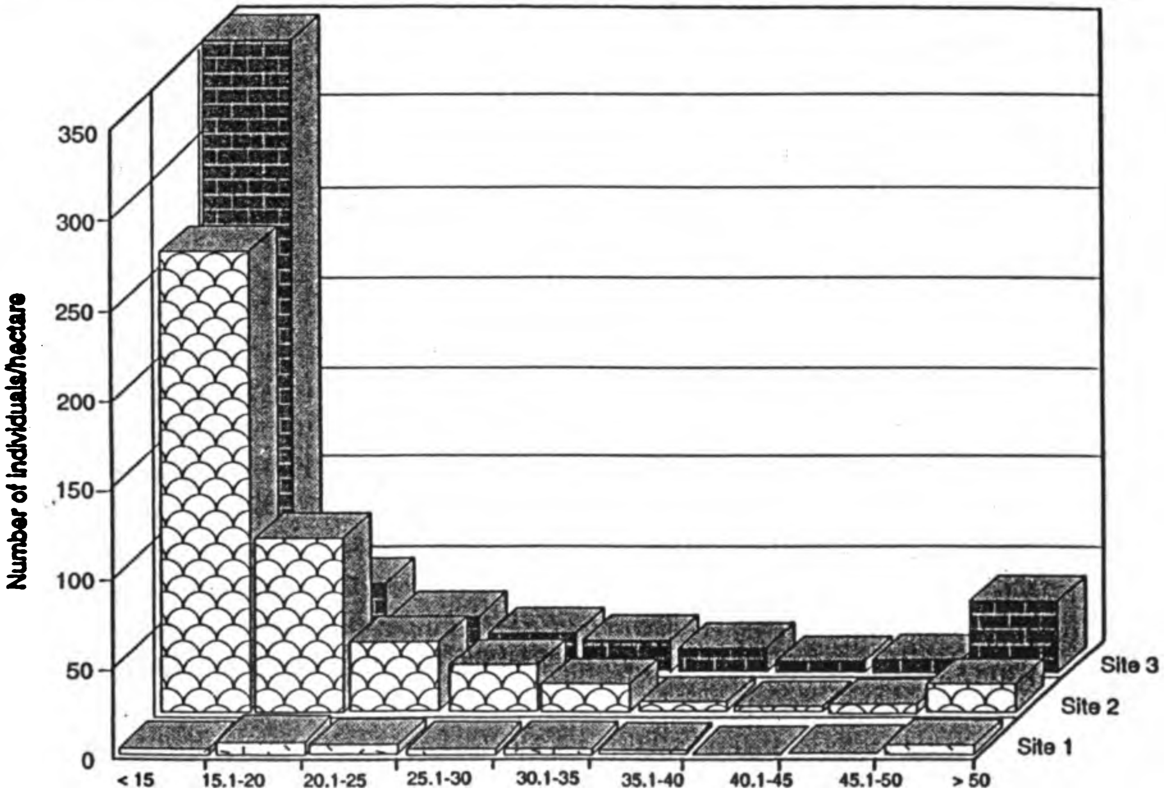

Figure 1. Number of trees per hectare in each diameter size class for the three sites of this study.

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 Type	Depth (cm)	Ca	Mg (cmol/L)	K	PH	OM (%)	N (%)	P (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.

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Leaf Litter Decomposition, Litterfall, and Effects of Leaf Mulches from Mixed and Monospecific Plantations in Costa Rica

Rebecca Kershnar
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ABSTRACT. Rates of litter decomposition and nutrient release from litter provide valuable information on the capacity of different tree species to replenish soil nutrients in degraded tropical areas. Leaf litter decomposition, leaf litterfall, plantation floor leaf litter, and mulch performance were studied for four indigenous timber species, *Virola koschnyi* Warb, *Dipteryx panamensis* (Pittier) Record and Mell, *Terminalia amazonia* (J.F. Gmel.) Exell., and *Albizia guachapele* (H.B.K.) Little, grown in mixed and monospecific plantations in the Atlantic humid lowlands of Costa Rica. *Terminalia amazonia* litter decomposed the fastest: no litter remained after 6 months. After 12 months, *D. panamensis*, *A. guachapele*, and the mixed litter decomposed completely, while 15% of the original weight of *V. koschnyi* litter remained. Differences in decomposition rates were closely related to leaf nutrient content.

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Total annual leaf litterfall was highest in *T. amazonia* (872.9 g/m^2), followed by *D. panamensis*, *V. koschnyi*, and the mixed plots. *A. guachapele* had the lowest leaf litterfall (236.0 g/m^2). The highest plantation-floor leaf litter was found in *V. koschnyi* and *D. panamensis*. Both litterfall and plantation-floor litter accumulation fluctuated least in the mixed plots. *A. guachapele* and *D. panamensis* mulch most positively affected maize seedling growth, followed by the mixed mulch. Recommendations are drawn from the results to suggest species choice for sustainable land management in the region.
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INTRODUCTION

The degradation of fertile land and the high cost of chemical inputs have intensified the search for sustainable agriculture and farming methods in many humid tropical regions. Several types of agroforestry systems have provided low-cost, sustainable alternatives for land rehabilitation and, in some instances, have increased productivity. Many recent studies examine single factors that pertain to the use of tree species in agroforestry systems or plantations (e.g., Beer 1988; Budelman 1988, 1989; Cuevas and Medina 1988; Glover and Beer 1986; Montagnini and Sancho 1994a, 1994b; Nair 1990; Young 1989). Holistic approaches that study tree, soil, and crop interactions are also needed so that managers may make informed decisions regarding tree species choice and management options.

Decomposition rates and the release of nutrients from decomposing litter provide valuable information on the capacity of different species to replenish nutrient concentrations in the soil over time (Ghuman and Lal 1990; Glover and Beer 1986; Szott et al. 1991). Precise knowledge of the rate of litter decomposition combined with measurements of litterfall and forest-floor litter allow for better manipulation of the litter for mulch to meet specific requirements of a crop or system. If a high rate of litterfall along with fast litter decomposition and nutrient release are timed to suit a crop's nutrient requirements, crop growth may be favored. On the other hand, consistent litterfall with slower decomposition can protect soils against erosion (Palm 1995; Sanchez 1995). For example, in a previous study comparing four indigenous trees in pure and mixed plantations in the Atlantic lowlands of Costa Rica, *Vochysia guatemalensis* J.D. Smith had the greatest amount of annual leaf litter fall and accumulation, making it best suited for soil protection, while *Jacaranda copaia* (Aubl.) D. Don. showed high litterfall but also had a fast decomposition rate, suggesting that it could be used with advantage in combination with annual crops (Byard et al. 1996).

Mulch derived from tree litter can provide a low-input alternative to fertilizer. In the research mentioned above, the mulch of the four species tested significantly surpassed the unmulched control soils in terms of effects on survival and growth of maize, confirming results from earlier research including some of the same species (Montagnini et al. 1993). In particular, the mulch of *Stryphnodendron microstachyum* Poepp. et Endl., a nitrogen fixing tree (Baker and Montagnini 1994) had the most beneficial effect on initial maize seedling growth and N uptake (Byard et al. 1996). Mulch can have several effects on soil properties, both physical and chemical (Stigter 1984; Van der Werf 1985). In addition to affecting soil nutrient content and acidity, mulch can influence weed growth and microbial activities (Jama et al. 1991). Soil temperature, soil moisture, and soil erosion can also be mediated by mulch (Wade and Sanchez 1983).

This paper presents results of litter decomposition, litterfall, forest-floor litter, and mulch experiments from four tree species in pure and mixed plantations in Costa Rica. Leaf chemical composition and structure, as well as physical micro-environmental conditions, were explored as factors affecting differences in decomposition among litter types. The total amount of litterfall, its seasonality and its rate of decomposition were also examined as factors influencing nutrient release from litter. Finally, a mulch experiment was used as a bioassay to measure the effects of nutrient release from decomposing leaf litter on initial growth of maize seedlings. The potential use of each tree species for land management is also discussed, including the implications of using mixed species designs in agroforestry and forest plantation systems.

STUDY SITE

The plantation for this research was established in June 1991 on a cattle pasture which had been abandoned in 1981. The site is located at La Selva Biological Station in the Atlantic humid lowlands of Costa Rica (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 soils are Fluventic Dystropepts derived from volcanic alluvium. They are deep, well-drained, stone-free, with low or medium soil organic matter, moderately heavy texture, and are generally acid and infertile (Montagnini and Sancho 1994a).

Each plantation consists of a different set of four indigenous, fast growing species, including at least one nitrogen fixing legume in each set. Indigenous species were selected for their ability to grow well on poor and degraded soils. Other criteria for species selection included seedling availability, tree growth, economic value, and potential impacts on soil fertility (Montagnini et al. 1995a, 1995b).

The plantation used in this experiment contains the following tree species: *Virola koschnyi* Warb, *Dipteryx panamensis* (Pittier) Record and Mell, *Terminalia amazonia* (J.F. Gmel.) Exell., and *Albizia guachapele* (H.B.K.) Little. All four species are indigenous timber trees, commonly used by local farmers. *A. guachapele* is also a N-fixing legume. *D. panamensis* is also a legume (Papilionoid sub-family), but no evidence of nodulation was found in this or in earlier research involving this species, and no reports exist of its nodulation in other environments (Montagnini and Sancho 1994b). However, symbiotic N fixation has been shown for other non-nodulating legumes, and recent evidence of its occurrence in *D. panamensis* has been found (Bryan et al. 1996). The plantation covers an area of 24,576 m^2 (96 m × 256 m) and is divided into four 64 m × 96 m blocks which, in turn, are divided into six 32 m × 32 m plots set at random. The treatments were: four pure plantation plots of each species, a mixed-species plot (with the four species), and a fallow (natural forest regrowth) plot. Planting distance was 2 m × 2 m to speed canopy closure and obtain early impacts on soils. Within each mixed-tree plot, trees of the four species were planted alternating two species per row. The sequential order of the species within rows was systematically reversed every other row. In that manner, each column contained the four species of the mixture in a sequence. By the time the present experiments were started (mid 1994), trees of the four plantation species were 3 years of age and had already closed canopies. The elemental composition of the leaves of each species is presented in Table 1.

The natural regrowth treatment was only included in the study for a comparison of physical micro-environmental variables with the plantation treatments. At the time of this research, the regrowth areas were covered with grasses, ferns and small shrubs, therefore they were taken as an open, treeless control environment. The plantation was weeded manually as needed, generally 2-3 times per year (including the natural regrowth plots for consistency) with no herbicides.

METHODS

Leaf Litter Bag Decomposition Experiment

The procedures for this experiment followed those from a previous litter decomposition study conducted using a different set of species in another area of the same experiment (Byard et al. 1996). Litter was expected to decompose within 12 months, as suggested by results of previous research and climatic conditions at La Selva. For the first 2 months, one litter bag from each site was collected every two weeks because initial litter weight loss was expected to be relatively fast. For the remaining 10 months or until all the litter

TABLE 1. Elemental composition of leaves of tree species used for studies of litter decomposition and mulch effectiveness (Montagnini, unpublished data).

Species	P (%)	Ca (%)	Mg (%)	K (%)	N (%)	Zn (mg/kg)	Al (mg/kg)	Fe (mg/kg)	Mn (mg/kg)
A. guachapele	0.23	0.18	0.27	0.85	3.93	14.9	80.6	122	744
D. panamensis	0.19	0.66	0.30	0.72	1.56	30.4	0.00	123	426
T. amazonia	0.34	0.64	0.35	1.12	1.45	28.6	0.00	103	850
V. koschnyi	0.15	0.70	0.32	0.70	1.25	20.0	0.00	87.2	1190

decomposed, one litter bag was collected from each treatment once a month. Accordingly, 14 litter bags were prepared for each treatment. Two sub-plots were established in each pure plot of the four species, and 3 sub-plots were established in each mixed-species plot. An extra replicate was included in the mixed plots to account for increased variation. This required a total of 616 litter bags for the duration of the study: 14 collections × 4 pure plots × 2 sub-plots × 4 species + 14 collections × 3 sub-plots × 4 mixed-species plots.

Fresh leaves were harvested from live trees in each of the four replicate plots for the four species. Collecting dry leaves would have probably given a more realistic measure of decomposition, especially because leaf nutrient content decreases with leaf age; however, it would have been very difficult to gather enough material for the experiment in a relatively short period of time, and using fresh leaves ensured having material of uniform age. Additionally, it was desirable to use similar procedures as in previous decomposition studies (e.g., Montagnini et al. 1993; Byard et al. 1996). Leaves were collected from differently-aged branches of each tree and from trees located on all four sides of each plot. The leaves were air-dried for 2 days and then oven-dried at 70°C for 48 hours. Eight grams of dried leaves were placed in 20 cm × 20 cm litter bags, which had been sewn from 1 mm fiberglass mesh (window screen) using nylon thread. For the pure plots, 8.0 g of leaf material of a single species was put in one litter bag. For the mixed plots, 2.0 g from each species, or 8.0 g total litter, was placed in a litter bag. Whenever possible, whole dried leaves were used; however, the larger leaves of *V. koschnyi* and *D. panamensis* were broken in half. *A. guachapele* has compound leaves, and individual leaflets, excluding the rachis, were used for the decomposition study.

Each group of 14 bags was placed in the middle of four non-border trees in a space of approximately 3 m × 5 m. The top litter layer was scraped aside before laying the bags down, and the removed litter was then sprinkled on top. The bags were placed in the field on June 29-30, 1994. General plot observations of shade conditions and amount of ground litter were recorded at that time.

After collection, the bags were lightly sprayed with water to remove mud and then were oven dried at 70°C for 72 hours. The percent of original weight remaining at each collection time was then calculated. Values for each sub-plot were averaged to give one value per plot for each monospecific and mixed plot. To compare weight loss of the mixed and monospecific treatments, ANOVAs were used ($n = 4$, $P < 0.05$) for each collection date, using LSD tests for means.

Soil Moisture, Soil Temperature, and Air Temperature

On six different dates, evenly distributed through the first two months, soil moisture and air and soil temperatures were recorded for each sub-plot, including 2 sub-plots in each regeneration plot. Temperature measurements and soil collections were taken during peak heat hours, from 10 a.m. to 2 p.m. Air temperatures were taken at approximately 10 cm height above each sub-plot with standard ambient thermometers. Soil temperatures and collections were taken at a depth of 5 cm, at the same location of air temperature measurement, using Weskler soil thermometers. This depth was used because the soil thermometers had to be dug into the soil for the readings, and because it was expected that influences on decomposition rates would be manifest at this shallow depth, while the air temperatures were expected to be an indication of surface temperatures as well. Soil collections (0-5 cm depth) were made with a 2.5 cm diameter soil corer. Approximately 20 grams wet weight of each soil sample was dried at 105°C for 72 hours and a dry weight taken. Percent moisture was calculated according to the formula: (wet weight − dry weight)/dry weight × 100. ANOVAs were used to compare differences in soil moisture and soil and air temperature among treatments.

Litterfall and Plantation-Floor Litter Accumulation

Litterfall traps were set in the field in July 1994, when the species had closed canopies. Two traps per plot were placed in each of the pure and mixed-species plots. The location of each trap in the plots was randomly selected inside border rows. Each trap was placed in the center of four trees in a square. In the mixed-species plots, each was placed in the center of a square containing one individual of each of the four species in each corner. The traps were 90 cm × 60 cm × 50 cm tall with fiberglass screen bottoms. Litter was collected every two weeks and the amounts collected were added together to calculate monthly litterfall. The material was sorted into leaves and branches. For the mixed plots, it was also sorted into species. The litter was dried at 70°C and weighed. Analysis of variance and range tests (LSD, $P < 0.05$) were run for each individual collection to compare mean biomass of branches and leaves among species. Comparisons of litterfall amounts were made among pure and mixed-species plots on an area basis (g/m^2), as well as among species in pure and mixed plantations on a per tree basis.

Plantation-floor litter was measured for all treatments every three months. Three 30 cm × 30 cm PVC frames were placed one meter from randomly selected tree stems in each plot. All litter was collected from the frames to the top of the mineral soil. The material was oven-dried, sorted (whole leaves, fragments, and branches), and weighed. Analysis of variance and LSD tests for means were used to compare the amounts of plantation-floor litter among treatments for each collection ($n = 4$, $P < 0.05$).

Mulch Experiment

Maize seedlings were grown using the following treatments: pure mulches of *V. koschnyi*, *D. panamensis*, *T. amazonia*, and *A. guachapele*, mixed mulch, and a control with no mulch. Leaf material was harvested and dried in the same manner as the decomposition experiment. Dried material was then ground using a domestic grinder with a 1 mm sieve. Before grinding, observations of the structure and color of the dried leaves were recorded.

Ten cups of soil and mulch were prepared for each treatment. The cups were 10 cm high with an upper diameter of 9 cm and held about 300 g of soil. The soil was collected from a depth of 10-30 cm from land adjacent to the plantation and with similar soil characteristics because it was expected that a more distinct response to the addition of mulch would be detected from soil from this depth than if the more nutrient-rich topsoil was used. Soils were homogenized with a trowel and sifter before filling in the cups. Eight grams of mulch were used per cup. Mixed mulch consisted of 2.0 g of ground leaf material from each of the four species. Four grams of mulch were mixed with the top third of the soil two days before sowing the maize seeds. The cups were saturated with deionized water to begin litter decomposition and retain soil moisture. Control cups were also mixed and watered but no mulch was added. The remaining 4.0 g of mulch were placed on top of the soil after the maize seeds were embedded. This second application was expected to prolong the effects of mulching and obtain a longer term nutrient release. The proportions of mulch corresponded approximately to 8000 kg ha^{-1}, an amount similar to the quantity of litterfall which might be collected under the tree plots.

A non-hybrid variety of maize, locally available in agricultural supply stores was used to test the different mulches. One hundred maize seeds were placed in petri dishes with wet towels to estimate germination rate. Before planting, maize seeds were soaked in deionized water for 2 days, and then 2 seeds were placed in each cup, approximately 2 cm deep. The shoots first appeared four days after sowing, at which time the smaller of the two shoots was removed. The cups were placed in a shadehouse which let in 75% of sunlight. Every day each cup was watered with deionized water to saturation.

Maize seedling height was measured from the base of each plant to the tip of the longest leaf when fully extended. Initially, height was measured every day. About three weeks after sowing, growth slowed down, and measurements were taken every other day for one week, and then every three days until harvest. Thirty days after germination, the maize plants were harvested and final height measurements were taken. Heights for every date were analyzed using a one-way ANOVA ($n = 10, P < 0.05$) and LSD tests for means.

Stems and roots of the maize seedlings were separated and dried at 70°C for 72 hours, at which time a dry weight was taken. Stem, root, and total seedling biomass were compared using ANOVAs ($n = 10, P < 0.05$) and LSD tests for means.

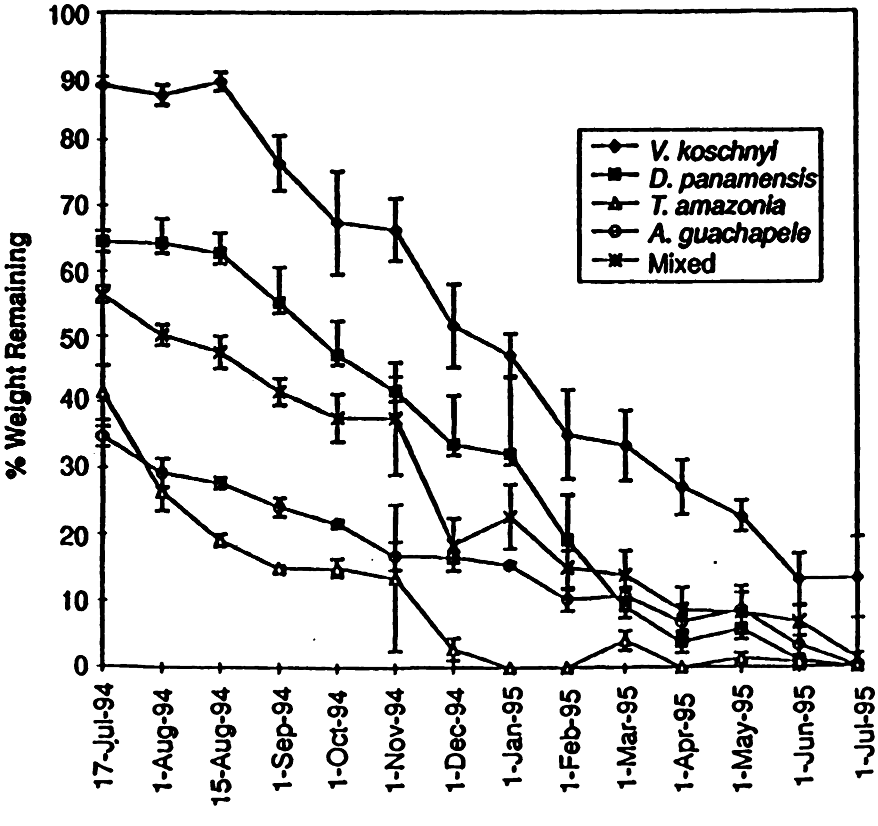
RESULTS

Leaf Litter Decomposition

During the first two weeks, litter decomposed in the following order, from fastest to slowest: *A. guachapele*, *T. amazonia*, mixed litter, *D. panamensis*, and *V. koschnyi* (Figure 1). The different litter types lost half of their biomass at different time intervals. *A. guachapele* and *T. amazonia* had half-lives of less than 2 weeks; the mixed litter had a half-life of about 1 month; *D. panamensis* had a half-life of 2.5 months; and *V. koschnyi* had a half-life of 5.5 months. After 6 months, *T. amazonia* litter had decomposed completely and *V. koschnyi* litter retained 50% of its original weight.

General plot observations were noted concerning shade and litter covering in each of the plots. *V. koschnyi* plots were highly shaded and had a thick litter cover; *D. panamensis* plots had moderate to slight shade and moderate litter cover; *T. amazonia* plots were extremely shaded and had thick litter cover; and *A. guachapele* plots had very slight to no shade and little litter cover.

FIGURE 1. Initial weight remaining (%) in leaf litter bags at each collection time from 17 July 1994 to 1 July 1995 (means and standard error bars).



Soil Moisture, Soil Temperature, and Air Temperature

Soil moisture ranged between 70 and 75% in the treatments with no statistically significant differences among them (Table 2). Soil moisture was about 10% higher in the regeneration plots than in the tree plots, and this difference was statistically significant.

The lowest soil temperatures were found in the plots with the densest canopy covers, *V. koschnyi* and *T. amazonia*, while the highest soil temperatures were found in *A. guachapele* plots, which were the least shaded (Table 2). These differences were statistically significant ($P < 0.05$) although the differences among plots were not greater than 2.3°C. The highest air temperatures were observed in *A. guachapele* and in the regeneration plots (Table 2).

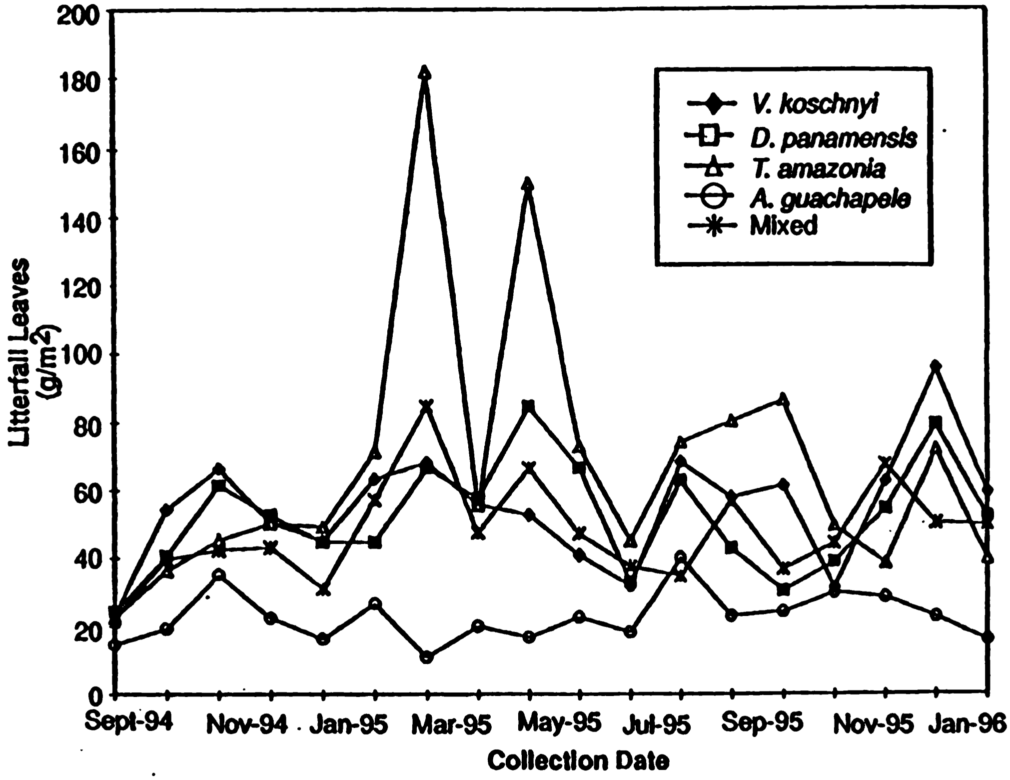
Litterfall and Plantation-Floor Litter

Peaks in leaf litterfall occurred in March, May and August through October (Figure 2), which coincides with months of lower precipitation at La Selva. Total annual leaf litterfall was highest in *T. amazonia* (852.9 g/m^2), followed by *D. panamensis* (639.0 g/m^2), *V. koschnyi* (619.0 g/m^2), and the mixed plots (553.4 g/m^2). *A. guachapele* had the lowest annual litterfall (263.0 g/m^2). The mixed plots had less pronounced peaks and lower points in litterfall during the year than the pure species plots (Figure 2). Total annual

TABLE 2. Soil moisture, soil and air temperature for the different treatments (means and standard errors). For each variable, means are significantly different when the standard errors are followed by different letters ($n = 6$, $P < 0.05$).

Treatment	Soil moisture (%)	Soil temperature (°C)	Air temperature (°C)
Albizia guachapele	75.5(2.22)b	27.5(0.17)a	29.4(0.39)a
Dipteryx panamensis	74.2(1.90)b	25.7(0.08)bc	27.5(0.26)b
Terminalia amazonia	70.1(2.50)b	25.0(0.24)d	27.2(0.27)b
Vochysia koschnyi	73.4(1.01)b	25.2(0.13)d	27.2(0.20)b
Mixed	72.1(1.50)b	25.4 (0.21)cd	26.7(0.55)b
Regeneration	85.5(1.85)a	26.0(0.24)b	28.9(0.29)a

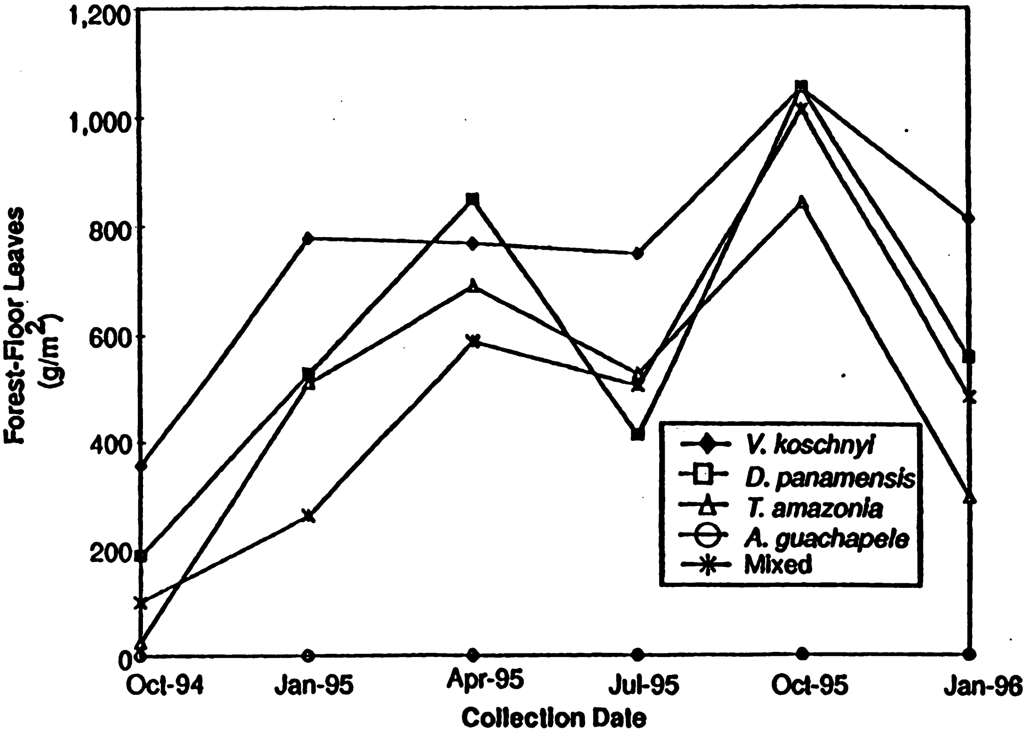
FIGURE 2. Leaf litterfall monthly totals, September 1994 to February 1996. Note: standard error bars are not shown for clarity.



branch litterfall followed similar trends as that of leaf litterfall (data not shown). When the amounts of litterfall per tree were compared among pure and mixed conditions for each individual species, leaf litterfall was similar in mixed and pure plots (data not shown).

The highest amounts of plantation-floor litter occurred in the pure plots of *V. koschnyi* and *D. panamensis*, with peaks in April and October (Figure 3). There were no statistically significant differences among *V. koschnyi* and *D. panamensis*. The highest branch litter was found in the floor under *D. panamensis*, which included branches as well as leaf rachis (data not shown). As in the litterfall, the amounts of plantation-floor material fluctuated less through time in the mixed plots (Figure 3). Very small amounts of leaf litter were found on the floor under *A. guachapele*; however, material

FIGURE 3. Forest-floor litter (leaves), October 1994 to January 1996. Note: standard error bars are not shown for clarity.

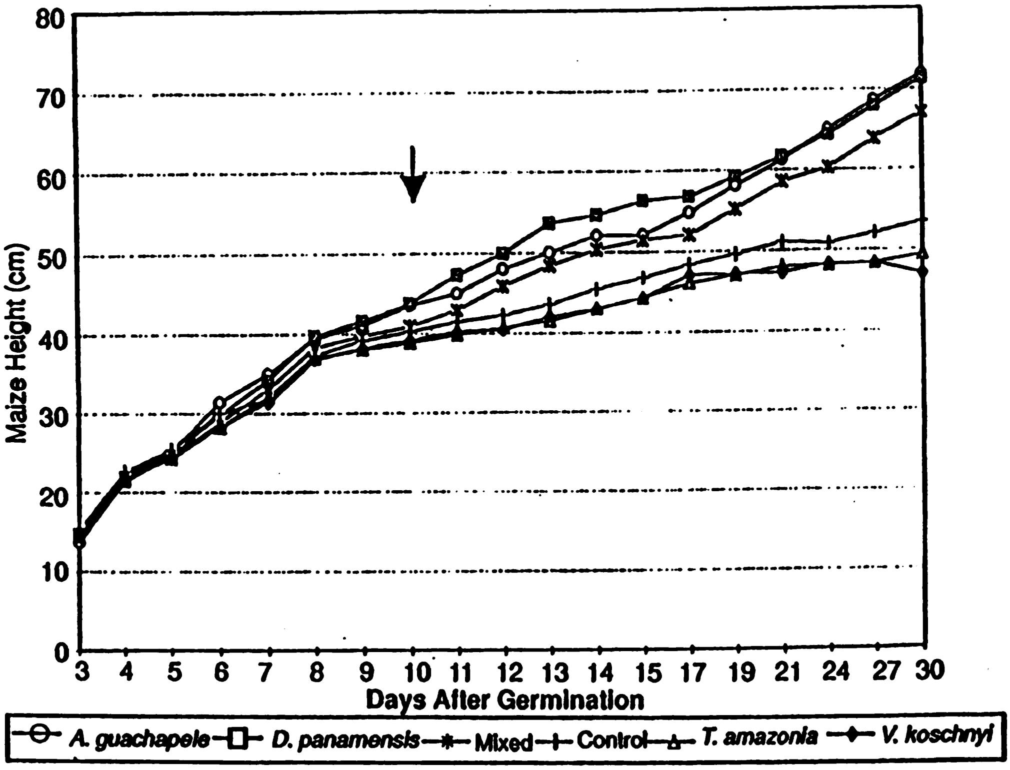


classified as "other" (unidentified leaves and branches, mostly material from weedings) was larger under this species.

Mulch Effects on Maize Seedling Growth

Germination of maize seeds under control conditions was 95%. Germination in the mulch experiment was 91%. Significant differences in plant height were first observed 10 days after germination (Figure 4). These differences increased consistently with time. Overall, the most marked effects on maize height were observed with the *A. guachapele*, *D. panamensis*, and mixed mulch treatments (Figure 4). The most marked effects for stem, root and total biomass were found for maize treated with *D. panamensis* and *A. guachapele* mulch, followed by the mixed mulch (Table 3). These differences among treatments were statistically significant ($P < 0.05$). However, while there was a significant distinction between

FIGURE 4. Maize seedling height in mulched pots and unmulched control. Note: the arrow marks the first date at which heights between treatments differed significantly (n = 10, P < 0.05).



the mixed mulch and *A. guachapele* and *D. panamensis* in terms of biomass, no such differentiation occurred with height. Maize grown under *V. koschnyi* and *T. amazonia* obtained essentially the same biomass but lower height than control treatments (Table 3, Figure 4).

General observation of leaf characteristics were noted as follows: *V. koschnyi* leaves were the darkest and most tough; *T. amazonia* leaves were medium in color and toughness; and *D. panamensis* and *A. guachapele* leaves were the lightest in color and the least tough. *V. koschnyi* and *D. panamensis* had large (>20 cm long) leaves while *T. amazonia* and *A. guachapele* had small leaves (<10 cm long).

TABLE 3. Dry biomass of maize grown in different mulch treatments (means and standard errors). For each variable, means are significantly different between treatments when the standard errors are followed by different letters ($n = 10$, $P < 0.05$).

Mulch type	Stem dry biomass (g)	Root dry biomass (g)	Total biomass (g)
Albizia guachapele	1.10(0.06)a	0.56(0.03)a	1.67(0.08)a
Dipteryx panamensis	1.01(0.06)a	0.50(0.03)a	1.51(0.08)a
Terminalia amazonia	0.41(0.02)c	0.26(0.02)c	0.67(0.04)c
Vochysia koschnyi	0.37(0.02)c	0.23(0.01)c	0.60(0.02)c
Control	0.48(0.03)c	0.29(0.02)c	0.76(0.05)c
Mix	0.76(0.05)b	0.40(0.03)b	1.17(0.08)b

DISCUSSION

Litter Decomposition in Pure and Mixed Plantations

Litter decomposition through time for each of the species followed a similar pattern, with a large initial decrease in weight in the first 2 weeks. Thereafter, decomposition proceeded in a steady and slower manner. This pattern is consistent with other reports of litter decomposition in humid tropical regions: an initial and rapid reduction of litter biomass due to leaching and utilization of easily decomposable compounds by soil fauna is followed by the slower degradation of more complex and recalcitrant compounds (La Caro and Rudd 1985; Byard et al. 1996).

Nitrogen, potassium, and phosphorus content of the different species litter may explain differences in litter decomposition. The species whose litter initially decomposed quickly had the highest N, P, and K content in their leaves. *A. guachapele* leaves contained approximately three times the N of the other species' leaves, and *T. amazonia* and *A. guachapele* leaves contained considerably more P than *D. panamensis* and *V. koschnyi* leaves (Table 1). However, several decomposition studies suggest fiber, lignin, and, in particular, polyphenol content are the main factors determining decomposition rates (La Caro and Rudd 1985; Palm 1995; Palm and Sanchez 1990, 1991; Tian et al. 1992). Tannin content may also be a factor, rendering litter unpalatable to soil fauna (Gutteridge 1990). Thus, while the high N content of *A. guachapele* litter may have caused its initial rapid decomposition, a high lignin or polyphenol content in relation to *T. amazonia* and *D. panamensis* could explain *A. guachapele*'s subsequently slower decomposition. As suggested from observations of leaf texture, *T. amazonia* probably has low fiber, lignin, and polyphenol content while *V. koschnyi* might have a higher concentration of these complex molecules. Future analysis of each species for lignin, fiber, polyphenol, and tannin content would help clarify these trends.

Results of litterfall and plantation-floor litter measurements confirm the relative decomposition rates between the different pure and mixed species litter found with litter bags. For example, litter accumulated on the floor under *V. koschnyi* and *D. panamensis*, the two species with slowest decomposition, while the reverse was true for the other treatments. The absence of *A. guachapele* plantation-floor litter throughout the year most likely resulted from a combination of considerably low litterfall of *A. guachapele*, the unrestrained effects of larger decomposers, and more favorable physical environment for decomposition in the field, as compared with litter enclosed in litter bags.

Decomposition rates did not correlate with differences in air and soil temperature or soil moisture between treatments. Soil moisture did not differ significantly between plots and therefore did not affect differences in decomposition rates between litter types. The two plot types with the most shade and lowest air and soil temperatures were *V. koschnyi* and *T. amazonia*, the species which exhibited the slowest and fastest litter decomposition, respectively. Thus, differences in the physical environmental variables tested did not influence decomposition rates under the present experimental conditions. Rather, leaf chemical composition and structure must be of chief importance in determining differences in decomposition among litter types.

Some restrictions inherent in the experimental design and field research should be taken into consideration when viewing the data. The use of mesh bags to confine litter introduces a certain amount of error. Mesh can lessen the impact of heavy rain and other mechanical processes, thereby affecting decomposition rates. Mesh litter bags may further restrict access of fungal structures (St. John 1980), changing decomposition rates and nutrient release in sites where fungi are important decomposers. Access of decomposition fauna also may be restricted by 1 mm mesh. Tian et al. (1992) found that nutrient release from litter increased with bags of three increasing mesh sizes, 0.5 mm, 2 mm, and 7 mm. However, even though the rate of decomposition and nutrient release differed with mesh size, the overall pattern remained consistent. Montagnini et al. (1993) found similar results when comparing tethered leaf decomposition with decomposition of litter in 1 mm and 2 mm mesh bags. Decomposition patterns remained consistent for each species and between species regardless of mesh-size or tethering. Thus, although the 1 mm bags used in this experiment may have slowed decomposition rates or nutrient release, the overall decomposition patterns observed among species should be fairly accurate.

Inconsistencies among different sites and sub-sites and among bags within the same sub-site are reflected in occasional increases in litter weight through time. Such inconsistencies may be partly due to expected variance in temperature and other physical variables which may result in micro-site differences in decomposition. Air and soil temperature and soil moisture were not significantly different among sub-plots or plots of the same type. The amount of replication and the consistency of plot and sub-plot characteristics should ensure that the overall decomposition pattern observed reflects the average natural decomposition process for each litter type.

Another factor that may affect the recorded data is the difference between wet and dry season decomposition rates. The litter bags were set outside in the middle of the wet season. As a result, initial decomposition rates are likely to be higher than those that would be observed if the litter had initially decomposed during the dry season. Luizao and Schubart (1987) found marked differences between wet and dry season litter decomposition in a terra-firme forest of Central Amazonia. During the wet season, root penetration and termite activity were particularly important for litter decomposition, resulting in a calculated wet season litter half-life of 32 days compared to a dry season litter half-life of 218 days. Such extreme differences in decomposition rates could greatly affect the application of decomposition data in agroforestry or plantation use. However, the length and intensity of the dry season in the Amazonian site studied by Luizao and Schubart is probably much greater than the dry season at La Selva. La Selva has a mean annual rainfall of 4000 mm, almost twice that of Manaus which has a mean annual rainfall of 2186 mm (Anon. 1978). Thus although decomposition may indeed be slower in the dry season, the effects at our study site are not expected to be as marked as in Manaus.

Litterfall and Plantation-Floor Litter

The rates of leaf litterfall of the four species of this study are comparable to others reported for pure stands in tropical humid regions. For example, our values are higher than those reported from Nigeria for 17-year-old *Tectona grandis* L. (teak) and 13-year-old *Terminalia superba* Engl. & Diels. (431 and 404 $g/m^2/yr$, respectively; Ola-Adams and Egunjobi 1992), and from those found in a 7-year-old plantation of four species in southern Brazil (98 to 475 $g/m^2/yr$; Garrido and Poggiani 1981/1982). In these studies, trees were planted at spacings similar to this study. The higher amounts reported from La Selva may be due to a more favorable climate and to the younger age of the plantations: younger trees have a greater proportion of branch and foliage biomass than older trees that have allocated proportionally larger resources to root and stem biomass (Montagnini and Sancho 1994c).

In the mixed treatments, there were intermediate values and less pronounced peaks and low points, with a more even distribution of litterfall and plantation-floor litter year round than in pure plots (Figure 2). Other studies have also reported higher consistency of litterfall in mixed stands, providing improved soil protection and a more even nutrient return to soils over the year (Garrido and Poggiani 1981/1982; Beer 1988).

Effects of Pure and Mixed Species Mulch on Maize Seedling Growth

A. guachapele and *D. panamensis* showed promising results for use as mulch while *T. amazonia* and *V. koschnyi* had no effect or a negative effect on maize seedling growth. One explanation for the different effects of litter lies in their decomposition rates, as discussed previously: the slowest (*V. koschnyi*) and fastest (*T. amazonia*) litter to decompose made the worst mulches. This suggests that a moderate decomposition rate is a desirable characteristic for mulch. *T. amazonia* litter may have decomposed so quickly that litter nutrients were leached or immobilized by soil fauna and thus unavailable to maize seedlings, and *V. koschnyi* mulch may have decomposed too slowly to release nutrients in time to benefit maize growth.

Litter chemical composition probably also affected its performance as a mulch. The positive effect of N inputs on plant growth is well documented. High N content of fertilizer inputs is considered to be so important that most current mulch research is restricted to the examination of N-fixing species (e.g., Rosecrance et al. 1992; Gutterridge 1990). Accordingly, *A. guachapele* litter was expected to have the most positive influence on maize growth of all the litter species. However, *D. panamensis* litter had an equally positive influence on plant growth, while it ranked second to *A. guachapele* in terms of N concentration (with a value half that of *A. guachapele*) (Table 1). *D. panamensis* had a relatively high concentration of Ca and Mg in its leaves, suggesting that nutrients other than high N content are important in determining the influence of mulch on plant growth and provides incentive to examine other species, besides those whose tissues are rich in N, for mulch use.

The presence of chemicals other than essential plant nutrients may also influence mulch performance. For example, high levels of Mn in *V. koschnyi* and *T. amazonia* litter (Table 1) could explain the negative effect of these mulches on plant growth. Yobterik et al. (1994) found high Mn content in mulch suppressed corn growth. Concentrations of Mn are relatively high in the soils of the experimental areas (Montagnini et al. 1993). The addition of mulch rich in Mn could possibly result in toxic effects to maize. Concentrations of 50 mg Mn per kg of soil are considered toxic to most annual crops in the region (Bertsch 1986).

Problems may also exist in extrapolating the results of the mulch experiment to potential effects on field crops. Conditions in a shadehouse are more uniform and favorable for plant growth than typical field situations. The physical protection offered by mulch may be more beneficial under field conditions. Erosion control, moisture retention and temperature control also would be of greater importance. Certain litter types may be better than others in preventing herbivory and weed growth. Moreover, while plant biomass and height are good indications of plant health, high crop yield is the desired goal. Ideally, a mulch experiment should be conducted long enough to obtain crop yield.

Experimental design for a shadehouse experiment could be improved as well. Bigger pots should be used to prevent pot size from restricting root and plant growth. No control was prepared for the physical properties of the mulch. Sawdust or perlite could be used to imitate the physical effects of mulch, providing a clearer indication of the influence of mulch on physical soil conditions such as aeration, water retention, and temperature reduction.

In the absence of a physical control, it is difficult to determine if color or structure of litter affected mulch performance. Also, as mentioned before, the mechanical effects of mulch are likely to be more important in the field where high soil temperatures and water loss from evaporation and run-off would have a greater effect on plant growth. Color differences between mulches are likely to be more important when mulches with similar chemical compositions and decomposition rates are compared. In the case of *V. koschnyi* and *T. amazonia* litter, chemical content and decomposition dynamics probably determined their poor performance as mulches, and leaf physical characteristics did not matter as much. *D. panamensis* and *A. guachapele* litter were very light in color, suggesting that both litter types would be fairly effective at decreasing soil temperatures. The amount of each type of mulch necessary to achieve a desired result and the time interval over which each type of mulch is effective, both in terms of nutrient input and physical effects, are other aspects of mulch management that should be explored for each tree species.

Implications for Management of Agroforestry or Plantation Systems

Detailed information concerning litter composition, litterfall, forest-floor litter, and mulch performance of different tree species provides a solid foundation from which agroforestry or plantation systems can be developed. The combined results of the litter decomposition and mulch experiments suggest that *D. panamensis* and *A. guachapele* would be good candidates for agroforestry use. Both species have relatively persistent litter that performed well as mulch. In addition, both species have relatively open canopies that produce moderate shade: good conditions for light-demanding crop species. On the other hand, *V. koschnyi* and *T. amazonia* might be best suited for plantation forestry. These species have dense canopies that produce dense shade, and their litter had a negative effect on maize growth. If for economic or other reasons the association of these species with agricultural crops is still desirable, tree planting density could be adjusted to allow more light for the associated crops and to decrease potential negative effects of the tree species' litter.

Litterfall and forest-floor litter measurements also provide suggestions for effective management of different tree species. The quantity of litterfall produced and the amount of forest-floor maintained influence the practical application of litter from a given tree species. A consistent forest-floor litter layer must be maintained for the litter to have beneficial mechanical effects on soils. Although *A. guachapele* was a promising mulch in the maize experiment, its litterfall and plantation-floor data suggest that in a field situation, it may not contribute substantially to crop or soil improvement. *D. panamensis* exhibited medium to high litterfall and plantation-floor litter, which reinforces the possibility that *D. panamensis* would be a good source of mulch and a good species for an agroforestry system.

T. amazonia plots exhibited a substantially greater amount of total annual litterfall compared to the other plots. The combination of *T. amazonia*'s rapid litter decomposition rate and heavy litterfall provides a likely explanation for the medium thick plantation-floor litter layer observed in *T. amazonia* plots, comparable to plantation-floor litter observed in mixed and *D. panamensis* plots. If rapid decomposition proved to be the limiting factor of *T. amazonia* mulch performance in the maize experiment, *T. amazonia*'s high litterfall might provide enough litter to make it an effective mulch in a field situation. The medium litterfall and high plantation-floor litter observed in *V. koschnyi* plots, combined with *V. koschnyi* litter's slow decomposition rate and poor mulch performance emphasizes that *V. koschnyi* is a poor candidate for an agroforestry system. However, *V. koschnyi* mulch may provide a good, low-cost weed control in a situation when no crop growth is desired.

The mixed plots exhibited the most consistent litterfall and plantation-floor litter throughout the year. Mixed litter also displayed an average decomposition rate and performed well as a mulch. Mixed plots may provide the most stable and productive environment for an agroforestry system. Those species whose litter takes longer to decompose could provide mechanical benefits as a mulch, while species with faster litter decomposition rates could provide more in the way of nutrient release.

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LITTERFALL, LITTER DECOMPOSITION AND MAIZE BIOASSAY OF MULCHES FROM FOUR INDIGENOUS TREE SPECIES IN MIXED AND MONOSPECIFIC PLANTATIONS IN COSTA RICA

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SUMMARY

Three plantations with native timber species were established in the Atlantic humid lowlands of Costa Rica to compare growth and nutrient cycling in pure and mixed stands. As part of the project, leaf litter decomposition, litterfall and accumulation of leaf litter on the plantation floor were studied in a young plantation of *Pithecellobium elegans* D. C. Benth, *Genipa americana* L., *Vochysia ferruginea* Mart., and *Hyeronima alchorneoides* Fr. Allemao. Of the four species studied, *V. ferruginea* had the highest annual litterfall (867.6 g m^{-2}), *G. americana* had the lowest (386.7 g m^{-2}), and the mixed plots had an intermediate level (660 g m^{-2}). *P. elegans*' leaves decomposed the most rapidly, *V. ferruginea*'s leaves decomposed the slowest, and the mixed litter decomposed at an intermediate rate. Mulch bioassays testing maize seedling growth showed higher survival and growth rates than the unmulched control in every treatment except for the *G. americana* mulch. Overall, *P. elegans* appears to be a good candidate for agroforestry combinations: the sparse canopy allowed light to penetrate, and its mulch showed the most positive effect on growth of maize seedlings. The large amount of litter produced by *H. alchorneoides* and *V. ferruginea* makes them helpful in protecting against soil erosion. A mixed species treatment may combine beneficial effects of the different species' characteristics, with the additional advantage of product diversification, especially important for the subsistence-oriented farmers of the region.

Key words: humid tropics, decomposition, mixed plantation, mulch, native species

INTRODUCTION

The performance and potential role of individual tree species on nutrient cycling affect the suitability of each species for soil rehabilitation and for its combination with agricultural crops. Knowledge of each species' potential, then, is important in influencing tree species choice. Decomposition rates and the release of

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nutrients from decomposing litter provide valuable information on the capacity of different species to replenish nutrient concentrations in the soil over time (Glover and Beer 1986, Szott *et al.* 1991). Precise knowledge of the rate of litter decomposition combined with measurements of litterfall and forest-floor litter allow for better manipulation of the litter to meet specific requirements of a crop or system. For instance, large amounts of litter may decompose and nutrients may be released at a time when plant nutrient uptake is low, resulting in a loss of nutrients to the crop. On the other hand, if a high rate of litterfall along with fast litter decomposition and nutrient release are in synchrony with a crop's nutrient requirements, crop growth may be favored (Swift 1987). Alternatively, constant litterfall along the year coupled with slower decomposition can protect soils against erosion (Palm 1995, Sanchez 1995).

Mulch from leaf litter can protect soils against erosion, decrease weed growth, release nutrients to the soil via decomposition, and moderate soil moisture loss and temperature fluctuations (Budelman 1988, 1989, Montagnini *et al.* 1993). Mulches of a mixture of species can provide more diverse benefits to crop growth and soil protection than mulches of a single species. For example, the mulch of a rapidly decomposing N-fixing species may provide higher N availability, while the mulches of other species may release other nutrients important to plant nutrition such as P or K, or may decompose more slowly and contribute better protection against soil erosion.

In the present research, leaf litterfall, litter decomposition and litter accumulation on the plantation floor were compared among species grown in pure plots and in mixture (a combination of all four species). Additionally, a mulch experiment was used as a bioassay to measure the effects of nutrient release from decomposing leaf litter on initial growth of maize (*Zea mays* L.) seedlings. The plantation was part of a larger project to compare growth, nutrient cycling, effects on soil chemical and physical properties, pest damage, and economics in pure and mixed stands, with the objective of developing suitable plantation models for small farms (Montagnini *et al.* 1995a). In the region of study, farmers grow trees in a portion of their land allocated for tree products and also as an investment (Rheingans 1996). Farmers generally grow crops between the lines of trees if tree spacing and canopy and nutrient cycling characteristics favor intercropping, or they plant crops in the area previously covered by trees in a rotational scheme (Montagnini and Mendelsohn 1997). The results of this study are discussed in context with growth rates of the tree species, and suggestions are offered on land use options which include these species.

Site description

The plantation used in this study was established in 1992 with native species on abandoned pastures. Soils are Fluventic Dystropepts derived from volcanic alluvium. They are deep, well drained, stone-free, acid (pH in water <5.0), with low or medium organic matter prior to planting (2.5–4.5%), cation exchange capacity 10–14 cmols kg^{-1}, 10–15% base saturation, and moderately heavy texture (50–60% sand, 5–15% silt and 25–45% clay) (Sancho and Mata 1987). Prior to plantation establishment, soil conditions were too poor for cultivation of bananas or other commercial crops commonly grown in the region (Montagnini and Porras 1998). The plantation is located at La Selva Biological Station in the Atlantic humid lowlands of Costa Rica (10° 26'N, 86° 59'W; 50 m altitude; 24°C mean annual temperature; and 4000 mm mean annual rainfall, with a maximum in August of 400 mm on the average, and a minimum in April with an average of 50 mm).

Species selection for this research was based upon preference by farmers; good growth (González and Fisher 1994, González *et al.* 1990), economic value, potential impacts on soil and nutrient cycling (Montagnini and Sancho 1990, 1994), and seedling availability. Nutrient cycling characteristics have already been studied for eight of the indigenous species of these same experimental plantations (Byard *et al.* 1996, Kershnar and Montagnini 1998). The four species under investigation here were: *Pithecellobium elegans* D. C. Benth (Leguminosae, subfamily Mimosoideae), *Genipa americana* L. (Rubiaceae), *Vochysia ferruginea* Mart. (Vochysiaceae), and *Hyeronima alchorneoides* Fr. Allemao (Euphorbiaceae). *V. ferruginea* and *H. alchorneoides* are good timber species preferred by farmers in the region, and seeds or seedlings are commercially available. *G. americana* and *P. elegans* are not being planted by farmers in the region at present, but they were used in the experiments because earlier research had identified them as promising species for reforestation. In addition, *P. elegans* was chosen to have a N-fixing species in the experiment. More detail on the characteristics of the four species used in this research can be found in Montagnini *et al.* (1995a).

Plantation plots were set in randomized blocks, with four replicates of each of six treatments: pure plantation plots of each species, one mixed-species plot (with all four species), and one fallow (natural forest regeneration) plot. Each plot was 32 m × 32 m. Initial planting distance was 2 m × 2 m to speed canopy closure and obtain early impacts on soils, with 50% thinning planned after canopy closure. The plantation was 3½ years old at the time of this experiment.

Materials and Methods

Litter decomposition

Methods for litter decomposition studies followed those previously used for other species of the same experiment (Byard et al. 1996, Kershnar and Montagnini 1998). Litter bags measuring 20 cm × 20 cm were made from 1-mm fiberglass mesh (window screen) and sewn with nylon thread. Fresh leaves were collected from several perimeter trees of each species in each of the four replicate blocks. Although using fresh leaves may overestimate nutrient availability, fresh leaves rather than freshly abscised litter was used for the experiments because of the large amounts of material needed for the litter bags. In addition, it was difficult to collect fresh litter from some species such as *G. americana* (low litterfall rates) and *P. elegans* (very small leaflets). Before placement in bags, litter was oven-dried to constant weight at 70°C. In previous research, leaves were air-dried, and air/oven-dried weight ratios were used to correct the leaf weights, but this procedure introduced high variability among leaf samples (Ruvinsky 1995); therefore, and following Byard *et al.* (1996) and Kershnar and Montagnini (1998), oven-drying was used in the present study. It was assumed that even if experimental values of decomposition rates differed from those in natural conditions, the method was still valid for comparisons among treatments, since they were all subject to the same limitation. Dry litter (8 g) of each species was placed in litter bags. For the mixed litter treatments 2 g of each species were mixed and placed in litter bags.

A metal tag identifying each block, species, and site was placed in each bag. The bags for each group were strung loosely together with colored fishing wire to aid in recovery of the individual bags. Each group of bags was placed in the middle of four non-border trees in a space of approximately 3 m × 5 m. The top litter layer was scraped aside before laying the bags down, and the removed litter was then sprinkled on top. The bags were placed in the field on October 1, 1995.

Litter was expected to decompose within 12 mo, as suggested by results of previous research and climatic conditions at La Selva. For the first 2 mo, one litter bag from each site was collected every two weeks because initial litter weight loss was expected to be relatively fast. For the remaining 10 mo, or until all the litter decomposed, one litter bag was collected from each treatment once a month. Accordingly, 14 litter bags were prepared for each treatment. Two sub-plots were established in each pure plot of the four species, and 3 sub-plots were established in each mixed-species plot. An extra replicate was included in the mixed plots to account for possible increased variation. This required a total of 616 litter bags for the duration of the study: 14 collections × 4 pure plots × 2 sub-plots × 4 species + 14 collections × 3 sub-plots × 4 mixed-species plots.

After each collection, litter bags were taken to the laboratory, dried to constant weight at 70°C, and weighed. The percentage of the original weight remaining at each collection time was then calculated. Values for each sub-plot were averaged to give one value per plot for each monospecific and mixed plot.

Litterfall and plantation-floor litter accumulation

As for the decompositions studies, methods were consistent with those used in previous studies with other species of the experiment (Byard *et al.* 1996, Kershnar and Montagnini 1998). Litterfall traps were set in the field in January 1995, when the species had closed canopies. Two traps per 32-m^2 plot were placed in each of the pure and mixed-species plots. The location of each trap in the plots was randomly selected inside border rows. Each trap was placed in the center of a square formed by four trees. In the mixed-species plots, each was placed in the center of a square containing one individual of each of the four species in each corner. The traps were 90 cm × 60 cm × 50 cm tall with fiberglass traps had proven enough to sample the variability found in plantations of similar age and design (Montagnini *et al.* 1993, Byard *et al.* 1996, Kershnar and Montagnini 1998). Litter was collected every two weeks and the amounts collected were added together to calculate monthly litterfall. The material was sorted into leaves and branches. For the mixed plots, litterfall was also sorted into species. The litter was dried at 70°C for 72 h, and weighed. Comparisons of litterfall amounts were made among pure and mixed-species plots on an area basis (g m^{-2}), as well as among species in pure and mixed plantations on a per tree basis.

Plantation floor litter was measured for all treatments every three months. Three 30 × 30 cm PVC frames were placed 1 m from randomly selected tree stems in each plot. All litter was collected from the frames to the top of the mineral soil. The material was oven-dried at 70°C for 72 h, sorted into whole leaves, fragments, and branches, and weighed.

Maize seedling bioassay of mulch

A controlled shade-house environment was created for maize seedlings grown in pots that were mulched with the litter of each of the four species. The methodology for this experiment was based on similar mulch studies on other La Selva plantations (Byard *et al.* 1996, Kershnar and Montagnini 1998). In order to fill the pots for the maize seedlings, soil known to have poor nutrient content was collected from about 10 to 30 cm below the surface to avoid contamination from existing leaf litter. Nutrient concentrations in the 10–30 cm soil layer were about 50–70% lower than those in the surface layer, and were all below levels recommended for conventional agriculture in the region (Montagnini and Porras 1998). The use of low nutrient soil was intended to result in a more marked effect from mulching. To prepare the mulch, leaves were collected from several trees in each plot, oven-dried at 70°C for 48 h and then ground by hand almost to powder. This mulch was added to soil and mixed in a ratio of 1 g mulch per 150 g of soil. This amount of mulch was intended to approximate to 8000 kg ha^{-1}. This is the amount that would realistically be expected to be present in the field, based on studies of litterfall and litter accumulation from tree plots of similar age and spacing to those in the plantation (Montagnini *et al.* 1993). The soil/mulch mixture was watered and allowed to soak for a week undisturbed before planting.

Eighteen large pots were used for the experiment, each 40 cm long × 15 cm wide × 15 cm high. There were six different mulch treatments: mulch from each of the four species, a mixture of the four species, and a control without mulch. Each gram of the mixed species mulch was made from 0.25 g of each species' mulch. There were ten plants per pot, planted at 7 cm × 8 cm spacing, and three pots per treatment, for a total of 30 replicate plants per treatment. At the time of planting, a second application of the same amount of mulch was added to the top of each pot. This second application was to achieve a prolonged nutrient release.

The seedlings were grown in a shade-house with mesh walls and ceiling, and a transparent tarp for protection from the rain. The seedlings were allowed to grow for 34 days after germination. Maize seedling height was measured daily in the first week after germination, and every 4 to 7 days thereafter. The measurements were taken from soil level to the tip of the longest leaf when fully extended.

Leaf chemical composition

Leaves were collected from at least five individual trees per species using a pole pruner. Three whole branches of opposite orientation from the upper portion of the canopy of each tree were sampled. Leaves from the tip, medium and lower portions of each branch were pooled to obtain one sample per tree. The material was oven-dried at 70 °C for 72 h and then ground for chemical analyses. The total N, P, Ca, Mg and K were measured on nitro-perchloric digests (Díaz-Romeu and Hunter 1978); N and P were measured using a Lachat flow injection analyzer (10500 N Port Wash Rd, Mequon, WI, USA), while cations were measured using a Perkin Elmer 2380 atomic absorption spectrophotometer (Perkin Elmer, Norwalk, CT, USA).

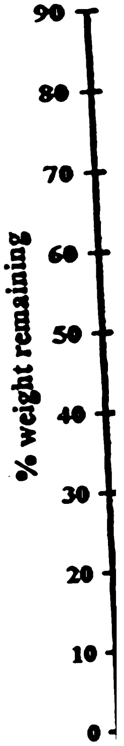
Data Analysis

For the decomposition study, analysis of variance and least significant differences (LSD) tests for means were used to compare weight loss of the mixed and monospecific treatments (n= 4, $P < 0.05$) for each collection date. Analysis of variance and LSD tests for means were also used to compare the amounts of litterfall, as well as the amounts of plantation-floor litter among treatments for each collection (n= 4, $P < 0.05$), and the leaf nutrient composition (n= 5, $P < 0.05$). In the mulch bioassay, the height of the seedlings were compared among treatments for each measurement date using analysis of variance and LSD tests (n= 30, $P' < 0.05$).

Results

Leaf litter decomposition

Trends in the relative rates of weight loss between the treatments were established in the first month (Figure 1). After two months, *V. ferruginea* and *P. elegans*' rates of weight loss were significantly different from all other species. At two months, the order of rates of weight loss (as a proportion of the original weight), from highest to lowest, was *P. elegans*, *G. americana*, mixed species, *H. alchorneoides*, and *V. ferruginea*. The half-lives of the litter (time it takes to lose half its original weight) ranged from 1 mo (*P. elegans*) to 6 mo (*V. ferruginea*). The treatments that were initially slower, such as *V. ferruginea*, *H. alchorneoides* and the mixed species litter, all began to decompose more rapidly at about 3–5 mo. At 12 mo, all the species leaves had lost 97–99% of their initial mass.



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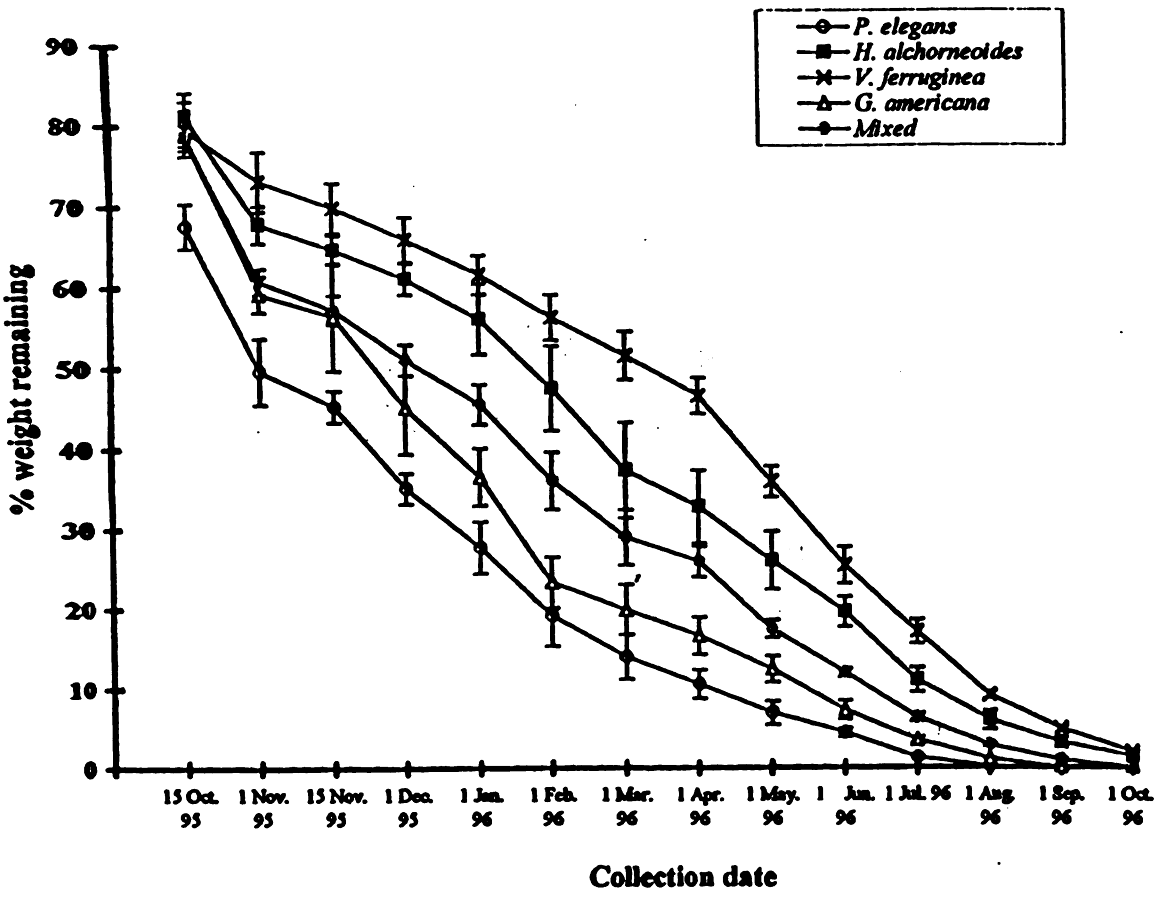

Figure 1. Relative rates of leaf litter decomposition in pure and mixed treatments: percent weight remaining at each collection (means and standard error bars calculated from ANOVAs, n= 4, P <0.05).

Leaf litterfall

P. elegans showed a more uniform shedding of leaves than the other species, with litterfall between 20 and 45 g m^{-2} for all months studied (Figure 2). The other species showed more marked peaks and lows, for example *H. alchorneoides* had a peak in May and low in July of both years studied. In the mixed species treatment the litterfall range was fairly consistent from 30 to 82 g m^{-2} per month.

On an individual tree basis, the amount of leaves collected from each tree species differed depending on the composition of its neighbors. The representatives of *P. elegans*, *V. ferruginea*, and *G. americana* in the mixed plots all shed less leaves than their cohorts in the pure treatments, while *H. alchorneoides* lost more leaves per tree in the mixed treatments than in the pure treatments. The leaf loss for *H. alchorneoides* trees in mixed treatments ranged from 405 to 1225 g m^{-2}, and in pure treatments from 170 to 425 g m^{-2}. The leaf loss for *V. ferruginea* ranged from 115 to 420 g m^{-2} in the pure treatments and from 0 to 50 g m^{-2} in the mixed treatments. *G. americana*'s leaf loss in pure treatments ranged from 5 to 260 g m^{-2}, and in mixed treatments from 0 to 187 g m^{-2}. The leaf loss in P. elegans pure treatments ranged from 75 to 170 g m^{-2}, and in mixed treatments from 0 to 120 g m^{-2}.

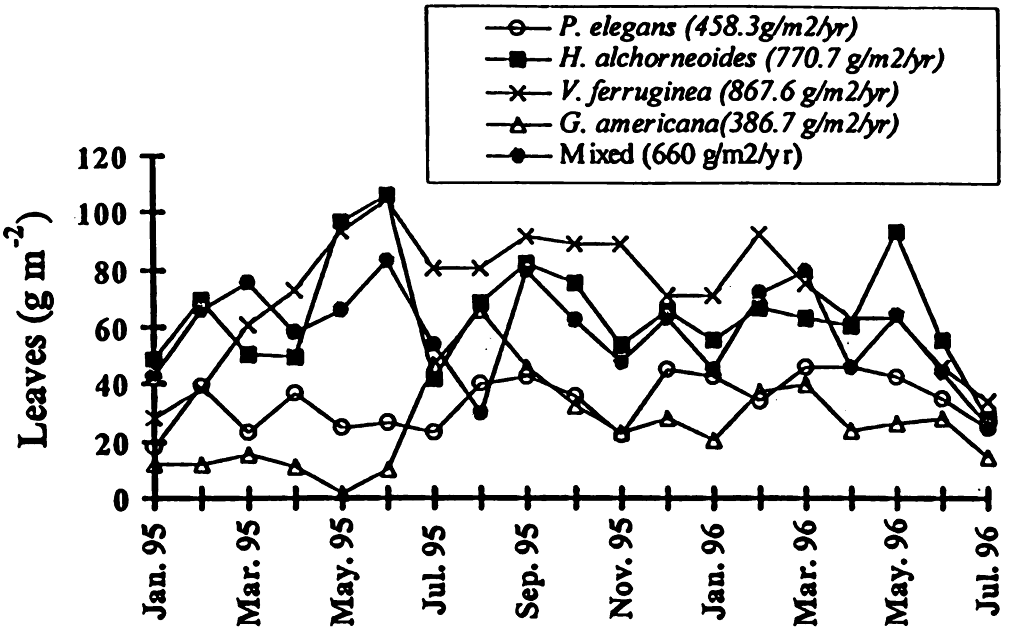

Figure 2. Monthly leaf litterfall in pure and mixed treatments.

Total annual litterfall over the period studied (August 1995 to July 1996) was higher under *V. ferruginea* (867.6 g m^{-2}), *H. alchorneoides* (770.7 g m^{-2}) and the mixed treatment (660.1 g m^{-2}). *P. elegans* and *G. americana* had the lowest annual litterfall, with values about half those under *V. ferruginea.*

Plantation floor leaf litter accumulation

For all months studied, the species showing the most litter accumulation on the plantation floor were consistently *H. alchorneoides* and the mixed treatment, followed by *V. ferruginea* (Figure 3). Other than *P. elegans*, which had no litter accumulation in any month, *G. americana* had the least. The month of highest litter accumulation for all species was January 1996. The months of the least litter accumulation for all species were April, July and October 1995.

Maize seedling bioassay of mulch

P. elegans' mulch showed the most positive effect on the overall height of the maize seedlings. This effect was statistically significant by the 15th day after germination, when seedlings treated with *P. elegans*' mulch were 32.9 cm on average, in comparison with a control height average of 21.3 cm, and a range among the other treatments of 32.0 to 26.5 cm. This trend was maintained throughout the remainder of the experiment (Figure 4). At the end of the experiment at day 34, the *P. elegans*-treated seedlings were almost twice as tall as those in the control treatment. There were no statistically significant differences between the *H. alchorneoides, V. ferruginea* and mixture treatments

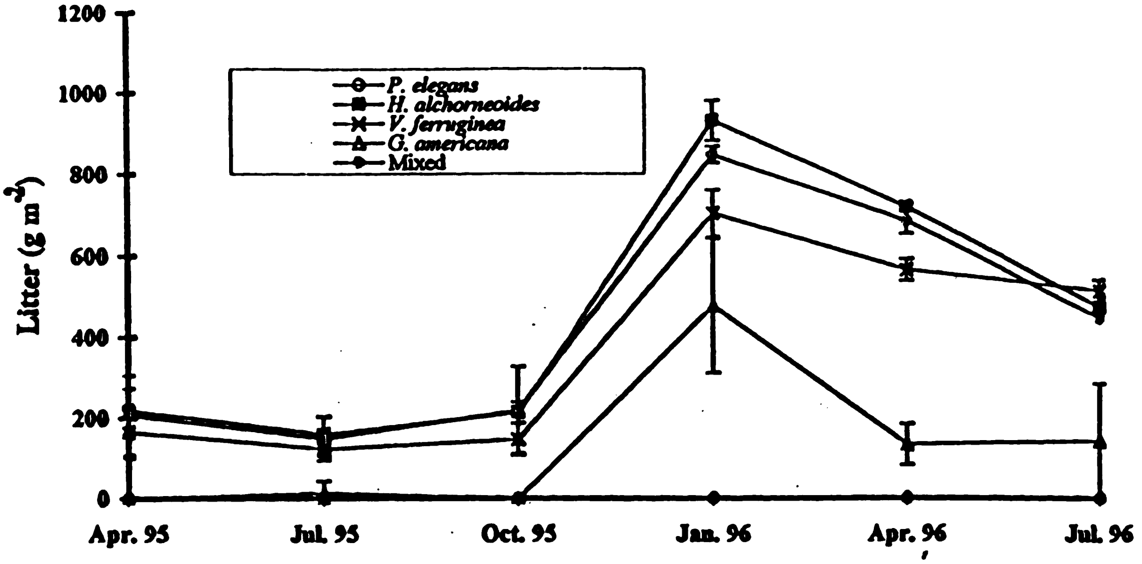

Figure 3. Forest floor litter leaves in pure and mixed treatments. Data are from collections made every three months from April 1995 to July 1996 (means and standard error bars calculated from ANOVAs, n= 4, $P < 0.05$).

during the course of the experiment, with a final range in height of 40.4 to 42.9 cm ($P < 0.05$).

G. americana was the only treatment that showed a negative effect on the growth of the maize seedlings, and was even surpassed by the unsupplemented control group. Within the first two days after germination, *G. americana*-treated seedlings were significantly shorter than the other treatments. The *G. americana* treatment had a higher seedling mortality rate than that of any other treatment, at 50%. The next highest seedling mortality was in the control group, at 10%. *H. alchorneoides* and *V. ferruginea*-treated seedlings showed no mortality. These differences were statistically significant ($P < 0.05$).

Leaf nutrient concentrations

The N and K concentration of live leaves of *P. elegans*, *H. alchorneoides*, and *G. americana* were higher than those of *V. ferruginea* (Table 1). *P. elegans*' leaves had the lowest Ca concentrations of the species studied, and *G. americana* had the highest leaf concentrations of Mg. There were no statistically significant differences in leaf P concentrations among the species studied.

DISCUSSION

Leaf litter: the interactions between decomposition, litterfall, and litter accumulation

Several researchers have shown that chemical composition and leaf structure are important in determining the rate at which the leaves decompose (Weider and

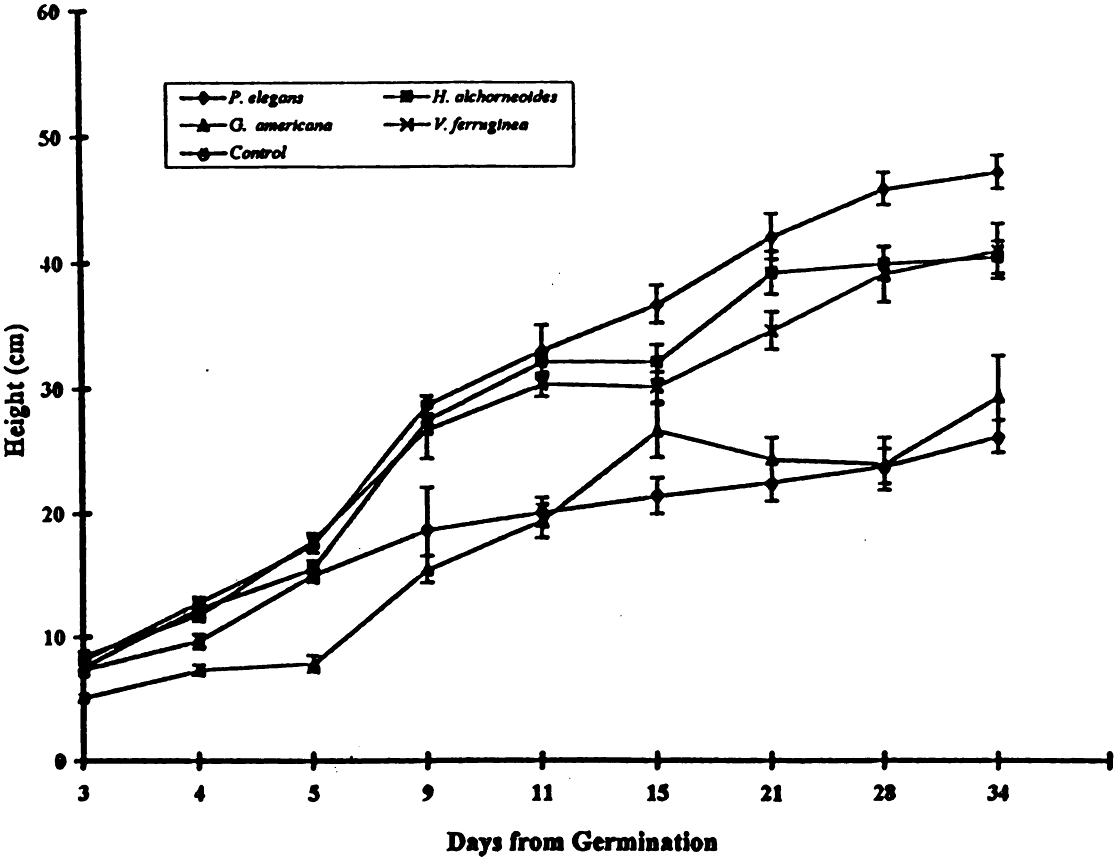

Figure 4. Height of maize seedlings in soils mulched with leaves from single tree species, a mixture of four species and an untreated (no mulch) control (means and standard error bars calculated from ANOVAs, n= 4, P <0.05).

TABLE 1

Nutrient concentrations (% of dry weight) of the leaves of the species under study. For each nutrient, differences among means are statistically significant when standard errors are followed by different letters (P <0.05, n= 5).

Species	N	P	Ca	Mg	K
P. elegans	1.97(0.19)ab	0.16(0.01)bc	0.58(0.04)c	0.45(0.01)b	0.96(0.12)bc
H. alchorneoides	1.81(0.06)bc	0.15(0.01)bc	1.02(0.14)a	0.41(0.02)b	0.71(0.08)cd
G. americana	1.61(0.13)cd	0.22(0.02)ab	0.97(0.13)ab	0.82(0.08)a	1.02(0.26)ab
V. ferruginea	1.39(0.08)e	0.13(0.01)cd	1.14(0.08)a	0.25(0.01)c	0.43(0.11)e

Lang 1982, La Caro and Rudd 1985, Palm and Sanchez 1990, Cornejo *et al.* 1994, Byard *et al.* 1996). *P. elegans*' leaflets decomposed faster than any of the other species throughout the course of the experiment, and they were the smallest, and more tender and thin than leaves of the other species. Decomposition should be faster for leaves of high nutrient content (Edwards 1977, Tanner 1981, Toky and Singh 1993, Constantinides and Fownes 1994). Accordingly, the slowly decomposing *V. ferruginea* leaves had the lowest levels of N and K and P. On the other hand, leaves of *P. elegans* with the fastest decomposition rate had the lowest levels of Ca.

The accumulation of litter during the dry months was pronounced. During this period, trees lose more leaves due to water stress, and decomposition rates are slowed (Tanner 1981, Luizao and Schubart 1987). However, by April, when the rains began again, the amount of litter was again reduced. This effect can yield a strong pulse of nutrients at the beginning of the wet season (Cornejo *et al.* 1994), at just the time when young plants will be ready to grow.

The trees in the mixed treatment (other than *H. alchorneoides*) generally shed fewer leaves than their counterparts in the pure plantations. Apparently this was due to competition by dominant species in the mixture: *G. americana* and *V. ferruginea* were shaded by the faster growing, densely crowned *H. alchorneoides* trees and grew more slowly in mixed than in pure stands (Montagnini and Porras 1998).

Maize seedling bioassays grown in mixed and monospecific treatments

The *P. elegans*-treated seedlings showed greater growth than the other species, which was to be expected from the species with the fastest leaf decomposition. Except for *G. americana*, any mulch-treated seedlings performed better than the unmulched control plants, a result consistent with previous studies at La Selva (Montagnini et al. 1993, Byard *et al.* 1996, Kershnar and Montagnini 1998). In contrast, *G. americana* mulch appeared to inhibit the growth of the seedlings, an effect that was apparent by the second day. At that point in seedling growth, the major source of nutrients is still the endosperm, which indicates that there may be some sort of substance that was released by the mulches that affects the seeds by the time of germination. The small size of *G. americana*-grown seedlings was apparent throughout the experiment. In addition, the *G. americana*-treated seedlings had the highest mortality of all treatments. Other researchers have reported inhibitory effects of mulches on maize seedlings (Yobterik *et al.* 1994). It is possible that an inhibitory substance in *G. americana*'s leaves has an effect at high concentrations. However, under field conditions the inhibitory substances may leach, evaporate or decompose (Yobterik *et al.* 1994).

The intermediate performance of *H. alchorneoides*, *V. ferruginea*, and mixed mulch treatments suggests that they may improve the nutrient concentration of the soil relative to the control, as has been indicated by other studies. For example, in another experiment which investigated *H. alchorneoides* and *V. ferruginea* mulch effects on seedling growth, *H. alchorneoides*- and *V. ferruginea*-treated seedlings grew better than the control. Seedlings treated with *H. alchorneoides* and *V. ferruginea* mulches had mortality rates < 8%, with *H. alchorneoides*-treated seedlings showing more vigorous growth than *V. ferruginea* (Montagnini *et al.* 1993). In other experiments with some of the species of this experiment, better growth in height of maize seedlings corresponded with higher seedling biomass and greater extraction of N and P by maize (Montagnini *et al.* 1993).

Implications for the use of the species in plantations and in agroforestry

Of the species under study, *V. ferruginea* and *H. alchorneoides* have been shown to function well as reforestation species on marginal lands (González and Fisher 1994, Butterfield and Espinoza 1995), and their seeds and seedlings are available in the region. Rates of litterfall, litter accumulation, litter decomposition and nutrient release from litter are also important factors in species choice. For example, *V. ferruginea* provides ground cover that reduces susceptibility to soil erosion, it builds a large store of litter that would act as an important nutrient source in subsequent rotations, and it has a dense canopy which helps to reduce the growth of understory vegetation and decrease costs of weeding.

If nutrients are severely depleted, species with higher decomposition rates, such as *P. elegans*, may be preferred over those that have litter that is more resistant to decomposition. However, when examining data from 1993 to 1996, initial trends indicated that soil K concentrations may be decreasing in the *P. elegans* pure plantations (Montagnini and Porras 1998). In other research including 20 tree species with potential for reforestation in the Atlantic forest region of Bahia, Brazil, *P. elegans* did not show any outstanding positive effects on soil properties (Montagnini *et al.* 1995b). However, *P. elegans* is a N-fixing tree (Montagnini *et al.* 1995b) increasing its appeal if N is a primary concern. It would be worth examining rates of N fixation and N availability in soils under this species. *P. elegans*' sparse canopy allows light to penetrate, making it well suited for tree-crop combination systems where crops are planted during the first few years of plantation establishment. This practice is fairly common among small, subsistence farmers of the region who choose to reforest portions of their land to increase its value and as a form of savings (Rheingans 1996).

G. americana had low rates of litterfall, and its negative effects on seedling growth both pose questions regarding the real beneficial role of this species on accompanying crops. In addition, this species has relatively low market value and ranks low in preference by farmers in the region.

If both protection from runoff and beneficial nutrient recycling abilities were desired, a mixed treatment could provide an appropriate compromise, as it would yield some of the benefits of each. An additional benefit to the mixed treatment approach is the increased economic stability that would be enjoyed by diversification of the tree crops. This could help to protect the farmer from market price fluctuations.

Ultimately, the selection of tree species and system designs are dependent upon preference by farmers. These preferences are in turn determined by numerous factors, such as economic values, the desired commodities or production systems, and specific site characteristics, such as soil fertility and susceptibility to soil erosion. It is important that the type of information presented in this article is supplied to farmers so that they may consider it along with other factors.

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Biomass and nutrient accumulation in pure and mixed plantations of indigenous tree species grown on poor soils in the humid tropics of Costa Rica

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Biomass and nutrient accumulation in pure and mixed plantations of indigenous tree species grown on poor soils in the humid tropics of Costa Rica

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Abstract

Aboveground biomass and nutrients and soil chemical characteristics were examined in young plantations of four indigenous tree species: *Hieronyma alchorneoides*, *Vochysia ferruginea*, *Pithecellobium elegans*, and *Genipa americana*, growing in mixed and pure stands at La Selva Biological Station, Costa Rica. Total tree biomass production rates ranged from about 5.2 Mg ha^{-1} year^{-1} for *G. americana* to 10.3 Mg ha^{-1} year^{-1} for *H. alchorneoides* pure stands, and for the species mixture it was about 8.9 Mg ha^{-1} year^{-1}. Branches and foliage formed 25–35% of total tree biomass but they represented about 50% of total tree nutrients. *H. alchorneoides*, the four species mixture, and *P. elegans* had the greatest accumulations of total aboveground nutrients per hectare. The importance of the plantation floor as a nutrient compartment varied temporally. When forest floor litter biomass was at its peak, plantation floor litter N, Ca, and Mg were roughly equal to, or greater than stem nutrients for all species except for *P. elegans*. For *P. elegans*, the plantation floor consistently represented a very low proportion of total aboveground nutrients. *G. americana* and *V. ferruginea* trees showed 55–60% less biomass accumulation in mixed than in pure stands while *H. alchorneoides* and *P. elegans* trees grew 40–50% more rapidly in mixture. *P. elegans* foliage had 60% lower Ca but higher P concentrations in mixed than in pure stands, and *G. americana* had higher foliar Mg in mixed than in pure stands. *V. ferruginea* stands had the highest concentrations of soil Ca, Mg, and organic matter, particularly in the top layers. Relative to pure plantations, soil nutrient concentrations in mixed plantations were intermediate for N, P, and K, but lower for Ca and Mg. The results of this study can be used in the selection of tree species and harvest designs to favor productivity and nutrient conservation. © 1999 Elsevier Science B.V. All rights reserved.

Keywords: Abandoned pasture; Floor litter; Nutrient conservation; Soil fertility; Tree tissues

1. Introduction

Some researchers have suggested that short-rotation tropical plantations may not be sustainable without fertilization (Jorgensen and Wells, 1986; Fölster and Khanna, 1997; Wadsworth, 1997). Fast-growing plantations often cause declines in soil fertility that may limit harvest to a few rotations (Perry and Maghembe, 1989; Montagnini and Porras, 1997). The harvest of forest products represents a nutrient 'cost' to the site

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(Wang et al., 1991; Montagnini and Sancho, 1994; Nykvist, 1997). Losses of nutrients during harvest may far exceed the rate of their replenishment by weathering of minerals in soils or by input via precipitation, especially when rotations are short (Fölster and Khanna, 1997). However, the amounts of nutrients in various tree tissues (foliage, branches, stems) differ substantially. Adjusting harvest regimes in consideration of the differing nutrient contents of these tissues can be an effective means of managing site nutrients (Wang et al., 1991; Montagnini and Sancho, 1994; Fölster and Khanna, 1997; Nykvist, 1997). In many cases it is best not to remove some tissues, such as small branches and leaves, that can be more valuable as nutrient stores than as forest products. Managers can also conserve site nutrients by preferentially planting tree species that do not place high nutrient demands on the site (Bruijnzeel, 1989; Wang et al., 1991; Montagnini and Sancho, 1994).

Opportunities for managing site nutrition through the planting of mixtures of species deserve consideration (Fölster and Khanna, 1997). Mixed plantations may be composed of fast-growing species with relatively high yields, while also containing slower growing species that have higher economic value (Montagnini et al., 1995), thus providing a diversified source of income. Even though there are instances when pure stands are more resistant, mixtures of species can also help to reduce the risks of total crop loss from species-specific pests and diseases (Watt, 1992; Montagnini et al., 1995). Species forming a plantation mixture may be complementary with regards to conservation, and/or replenishment of some soil nutrients (Smith, 1986; Bruijnzeel, 1989; Matthews, 1989; Binkley et al., 1992; Montagnini et al., 1995).

In this paper we present the results of a study on aboveground tree biomass and nutrient content (N, P, K, Ca, Mg), in young pure and mixed stands of four indigenous tree species: *Hieronyma alchorneoides* Fr. Allemao (Euphorbiaceae), *Vochysia ferruginea* Mart. (Vochysiaceae), *Pithecellobium elegans* D.C. Benth (Leguminosae, subfamily Mimosoideae), and *Genipa americana* L. (Rubiaceae). In addition, soil nutrient concentrations, organic matter, and pH were measured, and values compared to investigate relationships between aboveground nutrient content and soil fertility. The objective was to provide comparisons of biomass and nutrient content between different plantation systems. This information may be used in the selection of species and harvest regimes in order to conserve or replenish plantation soil fertility.

2. Methods

2.1. *Site description*

The experimental plantations were part of a larger project to compare growth and nutrient dynamics in mixed and pure stands with a total of 12 indigenous tree species (Montagnini et al., 1995). There were three plantations with four species each; just one plantation of four species in pure and mixed stands was used in the present research. The plantations were established on land that was cleared in the mid-1950s, grazed until 1981, then abandoned. The plantation used in the present research was established in November 1992. The plantations were at La Selva Biological Station, Costa Rica (10°26′N, 86°59′W, 50 m mean altitude, 24°C means annual temperature, 4000 mm mean annual rainfall). Soils are Fluventic Dystropepts derived from volcanic alluvium. They are deep, well drained, stone-free, acid (pH in water <5.0), with low or medium organic matter prior to planting (2.5–4.5%), cation exchange capacity 10–14 cmols kg^{-1}, 10–15% base saturation, and moderately heavy texture (50–60% sand, 5–15% silt and 25–45% clay) (Sancho and Mata, 1987). Prior to plantation establishment, soil conditions were too poor for cultivation of bananas or other commercial crops commonly grown in the region (Bertsch, 1986; Sancho and Mata, 1987; Montagnini, 1994). The abandoned pasture site was covered with shrubs and early successional trees, interspersed with patches of grass and ferns. For the purposes of this research, the site was cleared manually and the slash was left on the floor to protect against soil erosion and to delay the growth of weeds.

2.2. *Experimental design*

Species selection for this research was based upon preference by farmers; good growth (González et al., 1990; González and Fisher, 1994), economic value, and seedling availability. Additionally, for the specific

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purposes of the research, the potential impacts on soil and nutrient cycling were taken into account in designing the species mixtures (Montagnini and Sancho, 1990, 1994). More detail on the characteristics of the four species used in this research can be found in Montagnini et al. (1993).

Plantation plots were in randomized blocks, with four replicates of six treatments: pure plantation plots of each species, mixed species plots (with all four species), and fallow (natural forest regeneration). Each plot was 32×32 m^2. Initial planting distance was relatively tight (2×2 m^2) to speed canopy closure and obtain early impacts on soils. After canopy closure, about 3 years after planting, the plots were thinned to 50% of their original density. Within each mixed-tree plot, trees of the four species were planted with two species per row. Within each row the different species were planted alternately. The sequential order of the species within rows was systematically reversed every other row (Montagnini et al., 1995). The experimental plots were weeded manually as needed and no herbicides were used. Planting date was November 1992; the plantations were 3.5 years old when this research was completed.

2.3. Aboveground tree biomass and nutrients

Thinning widened the initial 2×2 m^2 planting distance to 2×4 m^2 (1250 trees ha^{-1}). This plantation density is similar to the commercially prevalent 3×3 m^2 (1111 trees per ha), allowing for comparison with other plantations in the region. Thinning was performed in one-half of each plot, leaving the other half for comparison. For thinning, all trees were cut in alternate rows. From every thinned row, two trees were randomly selected for biomass determinations, giving a total of 16 sampled trees per plot. The data from the 16 sampled trees from each plot were averaged to obtain values per tree for biomass and nutrients.

The material from each tree selected for biomass determination was separated into stem, branches and foliage, and weighed fresh at the site using a field scale. Portions of stems (lower, middle and top parts) and tip, medium and bottom parts of branches of the sampled trees were collected. Foliage from the tip, medium, and lower portions of each branch were pooled to obtain one sample of each tissue type and species for laboratory analysis. In mixed plots, foliage samples were collected to compare nutrient concentrations between trees growing in mixed and in pure plantations. These foliar nutrient concentrations were used in subsequent calculations for species in mixed plots. Stem and branch samples were not collected in mixed plots because concentrations of nutrients in those tissues were assumed to be very similar to nutrient concentrations found in pure plots.

All tissue-types were oven-dried at 70°C to constant weight and then ground. Dry:wet weight ratios from felled trees were used to correct the field weight determinations and obtain biomass on a per tree basis. The average biomass per tree was multiplied by the number of trees present in each plot before thinning, and extrapolated to a hectare. Data from the four plots of each treatment were then used for ANOVA (n=4).

Concentrations of total N, P, Ca, Mg and K for the different tissue-types and species were measured on nitro-perchloric digests (Díaz-Romeu and Hunter, 1978); N and P were measured using a Flow Injection Analyzer, while cations were measured using an Atomic Absorption Spectrophotometer. Total nutrient content (nutrient accumulation) for each tissue and for each species in pure and mixed plots were calculated by multiplying the mean biomass of each species' plant part (n=4) by the average nutrient concentration of the respective plant parts. Totals for whole trees were obtained by adding results for stems, branches, and foliage. For mixed species stands, the nutrient content of the four species was calculated separately and then added in order to obtain a total. ANOVA and LSD tests were run to compare mean biomass (n=4), and nutrient content (n=4) of tree parts and whole trees among pure and mixed plots on per tree and per hectare bases.

2.4. Plantation floor litter biomass and nutrients

Plantation floor litter was measured for all treatments every 3 months by using three 30×30 cm^2 PVC frames which were placed 1 m from randomly selected tree stems in each plot. All litter was collected from the frames to the top of the mineral soil. The material was oven-dried, sorted and weighed. Biomass of plantation floor leaf litter from the three collections per plot was used to calculate average amounts per m^2 for each plot. The data from each of the four plots of each treatment were used to run ANOVA and LSD tests to compare mean biomass (n=4) of plantation floor leaf litter among pure and mixed plots.

Chemical analyses of plantation floor litter leaves were conducted in the same manner as for live tree tissue. Mean leaf litter biomass and nutrient concentrations of January 1996 were used to calculate the nutrient content of floor litter leaves because the chemistry data were most complete for that month. Also, January 1996 was the collection closest to when thinning was done and data for total tree calculations obtained. To determine mean nutrient contents of floor leaf litter, biomass values for each treatment (n=4) were multiplied by their average nutrient concentrations. ANOVA and LSD tests were run to compare nutrient concentrations and nutrient content (n=4) of plantation floor leaf litter among treatments.

2.5. Soil fertility

Soils were sampled before clearing the land for plantations, and annually thereafter. Soil conditions before clearing (1991) have been reported elsewhere (Montagnini et al., 1993), and only results of sampling from 1996 are reported here. Composite samples were taken for every treatment in each of the four replicate plots at 0–5, 5–15 and 15–30 cm depths. The pH was measured in a 1:2.5 mixture of soil:deionized water. The exchangeable Ca and Mg were extracted with a 1 N KCl solution, while the exchangeable P and K were extracted with a modified Olsen solution, which is a mixture of 0.5 N $NaHCO_3$, 0.01 N bi-sodium EDTA and Superfloc 127 (a commercial flocculant) (Díaz-Romeu and Hunter, 1978). A 1:5 proportion of soil:extractant was used in all cases. Cations were measured using an Atomic Absorption Spectrophotometer. Extractable P was measured colorimetrically after reaction with $(NH_4)_2MoO_4$ and $SnCl_2$, using a spectrophotometer. Organic matter was measured with the Walkley–Black technique (Allison, 1975) and total N was measured using a semi micro-Kjeldahl technique (Bremner and Mulvaney, 1982). ANOVA and LSD tests were run to compare the means for each variable and soil depth (n=4, p<.05) among sites.

3. Results

3.1. Aboveground tree biomass

On a per hectare basis, *G. americana* stands had significantly lower total tree biomass than any of the other pure stands (Table 1). *V. ferruginea* and *H. alchorneoides* had the greatest branch and foliar biomass. Relative to the pure stands, the four species mixture had intermediate biomass for all tissues.

On a per tree basis, total tree biomass was 50% greater for *P. elegans*, and 44% greater for *H. alchorneoides* in mixed stands over pure plantations (data not shown). Total tree biomass for *V. ferruginea*, however, was 57% less in mixed than in pure stands, while for *G. americana* total tree biomass was 55% less in mixed stands.

3.2. Nutrient concentrations in aboveground tree tissues

Though there were some exceptions, *P. elegans* and *G. americana* generally had higher nutrient concen-

Table 1
Aboveground biomass of tree tissues in pure and mixed plots of four indigenous tree species on a per hectare basis. Means, standard error (SE), and statistical significance (Sig.)[1]

Species	Above ground biomass (Mg ha^{-1})											
	Stems			Branches			Foliage			Total tree		
	Mean	SE	Sig.	Mean	SE	Sig.	Mean	SE	Sig.	Mean	SE	Sig.
P. elegans	28.8	3.83	a	3.17	0.77	b	1.21	0.23	c	33.2	4.20	a
H. alchorneoides	26.3	4.99	a	6.74	0.97	a	2.87	0.27	ab	35.9	6.09	a
V. ferruginea	20.3	1.07	a	7.25	1.11	a	3.62	0.44	a	31.1	2.36	a
G. americana	13.9	2.85	b	3.06	0.74	b	1.26	0.23	c	18.2	3.70	b
Four species mixture	23.1	2.58	ab	5.55	0.36	ab	2.32	0.18	b	31.0	3.06	ab

[1] Differences between species for a given tissue are statistically significant (p<0.05) when means are followed by different letters.

Table 2
Nutrient concentrations in tissues of four indigenous tree species. Means, standard errors (SE), and statistical significance (Sig.)[1]

Tissue/species	Nutrient concentrations (%)														
	N			P			K			Ca			Mg		
	Mean	SE	Sig.	Mean	SE	Sig.	Mean	SE	Sig.	Mean	SE	Sig.	Mean	SE	Sig.
Stems															
P. elegans	0.62	0.03	a	0.14	0.02	a	0.65	0.09	a	0.18	0.02	a	0.10	0.01	a
H. alchorneoides	0.24	0.03	c	0.09	0.01	b	0.24	0.02	b	0.24	0.05	a	0.04	0.01	c
V. ferruginea	0.21	0.01	c	0.11	0.02	ab	0.32	0.02	b	0.16	0.02	a	0.06	0.01	bc
G. americana	0.35	0.03	b	0.10	0.01	ab	0.32	0.12	b	0.21	0.10	a	0.08	0.03	ab
Branches															
P. elegans	0.73	0.05	b	0.20	0.01	a	1.18	0.09	a	0.35	0.04	b	0.16	0.02	ab
H. alchorneoides	0.47	0.04	c	0.12	0.01	b	0.59	0.10	b	0.24	0.04	b	0.08	0.01	b
V. ferruginea	0.32	0.02	c	0.10	0.01	b	0.53	0.04	b	0.22	0.02	b	0.07	0.01	b
G. americana	1.07	0.17	a	0.17	0.02	a	1.36	0.34	a	0.73	0.19	a	0.28	0.10	a
Foliage															
P. elegans															
Pure	3.28	0.14	a	0.20	0.02	bcd	1.02	0.13	bcd	0.46	0.06	c	0.32	0.01	b
Mixed	3.76	0.29	a	0.31	0.05	a	1.22	0.16	bc	0.19	0.03	d	0.29	0.02	bc
H. alchorneoides															
Pure	2.21	0.11	b	0.21	*	bcd	0.77	0.08	cde	0.75	0.05	a	0.27	0.02	bc
Mixed	2.29	2.29	b	0.23	*	bc	0.91	0.19	cde	0.58	0.10	abc	0.23	0.01	cd
V. ferruginea															
Pure	1.79	0.05	b	0.15	0.01	d	0.60	0.02	de	0.72	0.03	a	0.17	0.02	de
Mixed	1.73	1.73	b	0.16	*	cd	0.49	0.03	e	0.65	0.04	ab	0.15	*	e
G. americana															
Pure	1.98	0.21	b	0.27	0.05	ab	1.82	0.32	a	0.50	0.09	bc	0.31	0.07	b
Mixed	2.27	0.30	b	0.26	0.04	ab	1.46	0.23	ab	0.57	0.08	abc	0.42	0.02	a
Floor leaf litter[2]															
H. alchorneoides	1.40	0.05	b	0.14	0.003	b	0.47	0.06	b	0.84	0.04	b	0.34	0.01	b
V. ferruginea	1.43	0.03	b	0.11	0.003	c	0.12	0.02	c	0.85	0.06	b	0.16	0.03	c
G. americana	1.74	0.10	a	0.18	0.02	a	2.71	0.01	a	1.58	0.22	a	0.65	0.10	a

[1] Differences between species for a given tissue are statistically significant ($p<0.05$) when means are followed by different letters.

[2] Data of plantation floor litter of January 1996.

*SE<0.01.

trations than the other two species (Table 2). *P. elegans* had the highest stemwood nutrient concentrations. *P. elegans* had the highest branch P concentrations, and was second to *G. americana* for all other branch nutrients.

P. elegans had the highest foliar N concentrations, followed by *H. alchorneoides* (Table 2). *G. americana* had significantly higher foliar P concentrations than *V. ferruginea*, and significantly higher foliar K than any of the other species. A noteworthy exception to the trend of *P. elegans* and *G. americana* having the highest nutrient concentrations was found for foliar Ca: *H. alchorneoides* and *V. ferruginea* had significantly higher foliar Ca concentrations than either *P. elegans* or *G. americana*.

Comparing foliar nutrient concentrations for each species grown in pure and mixed stands, differences were found for only two species: *P. elegans* had 60% higher Ca concentrations, and lower P concentrations in foliage in pure than in mixed stands; and *G. americana* had lower Mg concentrations in pure than in mixed stands (Table 2).

3.3. Nutrient content of aboveground tree biomass per hectare

On a per hectare basis, *P. elegans* stands had higher total tree N, P, K, and Mg than the other treatments, while *H. alchorneoides* stands had the greatest accumulation of Ca (Fig. 1). The four species mixture had the second highest total tree nutrient content for all nutrients. These results were closely aligned with the differences found for stem nutrients.

Due to relatively high stem biomass, coupled with high nutrient concentrations, *P. elegans* had significantly higher stem N, P, K, and Mg than any of the other pure stands, while *H. alchorneoides* had the highest stem Ca content (Fig. 1). The four species mixture had the second highest stem biomass N, P, K, and Mg, and the third highest stem Ca.

G. americana stands had low branch biomass, but particularly high concentrations of Mg and Ca relative to the other species. As a result, *G. americana* stands had significantly higher branch Ca content than *P. elegans*, and it also had the highest branch Mg content (Fig. 1). The four species mixture had the highest branch K content, and also had high branch N and P content relative to the pure stands. However, there were no statistically significant differences in branch N, P, or K content among treatments.

H. alchorneoides and *V. ferruginea* had greater foliar biomass N, P, Mg, and Ca than the other pure stands (Fig. 1). Accumulations of foliar N, P, and K in the four species mixture were similar to those found for *H. alchorneoides* and *V. ferruginea*.

3.4. Plantation floor litter biomass and nutrients

For all months studied, the species showing the most leaf litter accumulation of the plantation floor were *H. alchorneoides* and the mixed treatment, followed by *V. ferruginea* (Table 3). *G. americana* had very little floor litter biomass, and no litter accumula-

Table 3
Aboveground biomass of plantation floor leaf litter in pure and mixed plots of four indigenous tree species on a per hectare basis. Means, standard errors (SE), and statistical significance (Sig.)[1]

Collection date	Plantation floor leaf litter (Mg ha^{-1})				
	P. elegans	*H. alchorneoides*	*V. ferruginea*	*G. americana*	Mixed
April 1995	0 (0)c	2.17 (1.56)a	1.64 (1.76)b	0 (0)c	2.07 (0.27)ab
July 1995	0 (0)c	1.59 (1.22)a	1.22 (0.05)b	0.14 (0.08)c	1.48 (0.15)a
October 1995	0 (0)c	2.13 (0.70)a	1.46 (0.10)b	0 (0)c	2187 (292)a
January 1996	0 (0)d	9.31 (4.95)a	7.04 (0.58)b	4.77 (1.65)c	8.48 (0.21)ab
April 1996	0 (0)d	7.17 (0.86)a	5.64 (0.26)b	1.34 (0.50)c	6.83 (0.31)a
July 1996	0 (0)b	4.72 (2.57)a	5.14 (0.26)a	1.42 (1.42)b	4.46 (5.9)a

[1] Differences between species for a given tissue are statistically significant ($p<0.05$) when means are followed by different letters.
For each individual oollection time, differences among treatments are statistically significant when standard errors are followed by different letters ($n=4$, $p<0.05$).

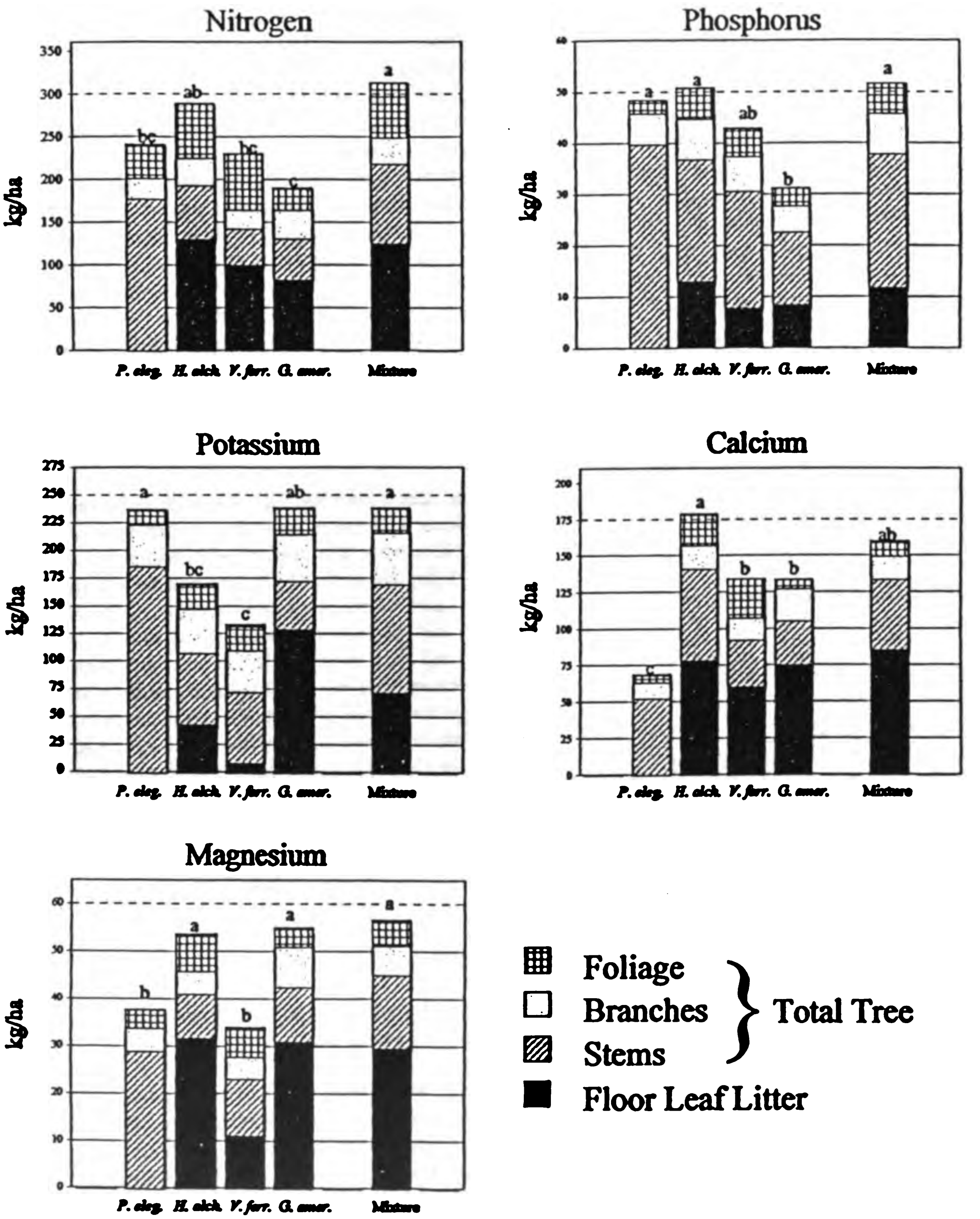

Fig. 1. Total aboveground nutrient content per hectare of four species grown in pure plantation and in mixtures of four species. Total nutrient content differs among treatments when bars are topped by different letters ($p<0.05$).

tion was found under *P. elegans*. The month of highest leaf litter accumulation for all species was January 1996, 3 years after plantation establishment, and the months of the least litter accumulation for all species were April, July and October 1995.

G. americana had significantly higher nutrient concentrations in floor leaf litter than any of the other species, followed by *H. alchorneoides* (Table 2). N and P concentrations for each species were generally lower in the floor leaf litter than in live foliage, while concentrations of Ca and Mg were higher (Table 2). There were no clear trends regarding concentrations between leaf litter and live foliage.

In January 1996, *H. alchorneoides* and the four species mixture had the greatest plantation floor N and P content (Fig. 1). Other than *P. elegans*, which had no litter accumulation in any month, *V. ferruginea* had the least plantation floor leaf litter P, K, Ca, and Mg content. *G. americana* had the highest plantation floor K, primarily due to its high concentrations of K in plantation floor leaf litter (Table 2).

3.5. Total nutrient content of aboveground plantation components

Though concentrations of nutrients in stems were low relative to other five tree tissues, biomass of stems was high, making them the largest compartment of total tree P, K, Ca, and Mg for all plantation-types (Fig. 1). Stems accounted for a particularly large proportion (>60%) of total tree P across all plantation-types. In general, stems were also the largest compartment of total tree N, though foliage was also very important.

Branches were the second largest compartment of total tree P and K (Fig. 1). For *G. americana* a particularly large proportion, over 30%, of total tree N, K, Ca and Mg was found in branches. Overall, branches and foliage were roughly equal in importance as compartments of Ca and Mg.

In general, foliage represented the second largest compartment of total tree N, after stems (Fig. 1). For *V. ferruginea*, high N concentrations in foliage, coupled with relatively high foliar biomass, resulted in foliage being the largest compartment (about 50%) of total tree N. In contrast, foliage was the smallest N compartment for *G. americana*.

In January 1996, except for *P. elegans*, the plantation floor litter generally accounted for greater biomass nutrients than either live branches or foliage, and greater biomass nutrients than stems for all nutrients except for P and K (Fig. 1). At the time of thinning, plantation floor leaf litter represented between 6% and 59% of total aboveground nutrient content for any given nutrient for all species except for *P. elegans*. However, the relative importance of plantation floor litter as a nutrient compartment varied temporally due to fluctuations in floor litter biomass (Table 3). These differences in nutrient content were often dramatic: for example, *G. americana* had 82.9 kg ha^{-1} of floor litter N in January 1996, the month with highest biomass, and virtually no floor litter N only 3 months earlier.

3.6. Soil fertility

Analyses of soil samples collected in 1996 showed few significant differences between concentrations of N, P, or K among the different plantation-types (Table 4). *V. ferruginea* had the highest concentrations of soil Mg, particularly at the 0–5 cm depth. *V. ferruginea* also had the highest concentrations of soil Ca between 0 and 5 cm while *P. elegans* had the highest soil Ca concentrations between 15 and 30 cm. Relative to pure plantations, soil nutrient concentrations in the mixed plantations were intermediate for N, P, and K, but lower for Ca and Mg. Organic matter for the four species mixture and for *V. ferruginea* were relatively high in the top layers. Soil nutrient concentrations, organic matter, and pH in the natural regeneration plots were among the highest (Table 4).

4. Discussion

4.1. Applying knowledge of tissue nutrient content to plantation nutrient management

Our results show that, with few exceptions, the relative tree tissue nutrient concentrations for all species were foliage>branches>stems (Table 2). This is in agreement with the results reported by Wang et al. (1991) for five plantation species of Puerto Rico. In tropical plantations, generally, the nutrients in the tree crowns account for a higher proportion of the total

Table 4
Nutrient concentrations, organic matter, and pH of soil under four indigenour tree species grown in pure stands, mixtures of the four species, and natural regeneration stands. Means, standard errors (SE), and statistical significance (Sig.)[1]

Species	Depth (cm)	Nutrient concentrations																				
		N (%)			P (mg l^{-1})			K (cmol l^{-1})			Ca (cmol l^{-1})			Mg (cmol l^{-1})			Organic matter (%)			pH		
		Mean	SE	Sig.	Mean	SE	Sig.	Mean	SE	Sig.	Mean	SE	Sig.	Mean	SE	Sig.	Mean	SE	Sig.	Mean	SE	Sig.
P. elegans	0–5	0.35	0.03	a	9.53	1.30	a	0.17	0.04	a	0.72	0.14	ab	0.43	0.12	c	7.79	0.67	a	4.05	0.05	abc
	5–15	0.24	0.02	ab	9.78	3.36	a	0.11	0.04	a	1.20	0.57	a	0.35	0.07	ab	5.88	0.38	a	4.43	0.23	a
	15–30	0.19	0.01	ab	6.53	1.76	a	0.12	0.05	ab	0.55	0.03	a	0.30	0.04	ab	4.78	0.52	a	4.23	0.05	a
H. alchorneoides	0–5	0.33	0.02	a	12.65	2.92	a	0.17	0.03	a	0.49	0.36	b	0.30	0.03	c	7.22	0.48	a	3.93	0.05	bc
	5–15	0.21	0.01	b	10.13	2.07	a	0.10	0.02	a	0.28	0.02	b	0.16	0.01	b	4.86	0.52	a	3.93	0.03	b
	15–30	0.17	0.02	b	9.05	3.79	a	0.09	0.01	b	0.32	0.04	a	0.16	0.03	b	4.41	0.31	a	3.95	0.03	b
V. ferruginea	0–5	0.36	0.03	a	8.04	1.15	a	0.23	0.08	a	1.05	0.26	a	1.17	0.33	a	8.43	1.29	a	4.28	0.20	a
	5–15	0.28	0.04	a	9.05	2.40	a	0.15	0.04	a	0.47	0.10	ab	0.41	0.12	ab	5.97	0.61	a	4.08	0.17	ab
	15–30	0.18	0.02	ab	10.20	4.25	a	0.13	0.04	ab	0.37	0.03	a	0.22	0.05	b	5.02	0.27	a	4.13	0.11	a
G. americana	0–5	0.35	0.02	a	11.13	1.79	a	0.30	0.07	a	0.73	0.04	ab	0.50	0.08	bc	8.24	0.99	a	4.03	0.05	abc
	5–15	0.25	0.03	ab	10.20	2.50	a	0.16	0.04	a	0.41	0.04	b	0.29	0.08	ab	5.19	0.77	a	4.08	0.05	ab
	15–30	0.21	0.01	a	9.75	1.66	a	0.14	0.03	ab	0.40	0.03	a	0.27	0.09	ab	4.66	0.52	a	4.15	0.06	ab
Four species mixture	0–15	0.34	0.02	a	10.35	1.71	a	0.16	0.03	a	0.47	0.06	b	0.33	0.04	c	8.64	0.62	a	3.90	0.07	c
	5–15	0.24	0.01	ab	9.83	2.31	a	0.11	0.03	a	0.29	0.05	b	0.18	0.03	b	5.38	0.41	a	3.93	0.06	b
	15–30	0.17	0.01	ab	6.95	3.69	a	0.12	0.03	ab	0.49	0.16	a	0.17	0.03	b	4.17	0.36	a	4.10	0.08	ab
Natural Regen.	0–5	0.36	0.01	a	7.63	2.41	a	0.28	0.04	a	0.82	0.26	ab	0.97	0.24	ab	8.31	0.50	a	4.23	0.11	ab
	5–15	0.23	0.01	ab	8.13	2.94	a	0.22	0.07	a	0.60	0.24	ab	0.56	0.17	a	5.01	0.32	a	4.28	0.13	ab
	15–30	0.19	0.01	ab	7.30	2.94	a	0.24	0.08	a	0.68	0.31	a	0.50	0.18	a	4.61	0.22	a	4.33	0.15	a

[1] Differences between species for a given parameter and depth are statistically significant ($p<0.05$) when means are followed by different letters.

aboveground nutrients in the stand than do those in other compartments (Fölster and Khanna, 1997). For non-conifers, the proportion of nutrients in branches and foliage ranges from 15–25% in *Tectona grandis*, 18–37% in *Gmelina arborea*, and 18–46% in young plantations of *Eucalyptus* spp. (Fölster and Khanna, 1997). Though in our research branches and foliage summed together represented only 25–35% of total tree biomass (Table 1), they generally represented about 50% of total tree nutrients (Fig. 1). To reduce the nutrient cost of harvests, site tree tissue biomass conservation should be prioritized as: (1) foliage, (2) branches, and (3) stems. Leaving branches and leaves on the site at the time of harvest, rather than harvesting the whole tree, would typically reduce the nutrient cost of log harvest by one-half. Additionally, the slash left on the ground would act as a mulch, helping to improve soil conditions and potentially increasing the number of rotations before fertilization or fallow would be necessary.

The amount of nutrients represented by branches or foliage which may be left behind varies between nutrients, species, and sites. For example, if rather than harvesting whole trees, branches and foliage are left as slash, N removal would be reduced by 26% in the case of *P. elegans*, and 60% in the case of *H. alchorneoides*. However, our results are from young plantations; crowns form a high proportion of total biomass in young stands, but their importance decreases as the stand ages (Fölster and Khanna, 1997).

Timber removal from forest ecosystems can result in the loss of significant proportions of total site nutrients. For example, in a tropical rainforest in Sabah, Malaysia, log extraction removed about 19% of total ecosystem Ca, suggesting that in the long term, forest management of this intensity may need fertilization (Nykvist, 1997). In managing short-rotation tropical forest plantations, harvest designs and timber species may be chosen so as to conserve or replenish site nutrients (Jorgensen and Wells, 1986; Bruijnzeel, 1989; Wang et al., 1991; Montagnini and Sancho, 1994). The variable nutrient concentrations between tissues and species which are to be harvested, and total nutrient content, are among the factors that need to be assessed in order to achieve long-term productivity with minimum nutrient 'cost' (Wang et al., 1991; Fölster and Khanna, 1997).

4.2. *The influence of plantation floor litter on plantation management*

The relative importance of the litter layer in plantation nutrient conservation has been shown by Lugo et al. (1990), who reported that the amount of litter in 10 tropical plantations ranged from 5 to 28 Mg ha^{-1}. In the present research on young plantations, plantation floor leaf litter represented up to 59% of the aboveground tree nutrient content (Fig. 1). This figure comes from the month of peak litterfall, emphasizing the importance of floor leaf litter to nutrient cycling. Green mulch from decomposing indigenous leaf litter can be a low-cost and effective soil supplement in the La Selva region, so it is likely that small farmers will remove litter from the plantation floor to use in fields or homegardens or otherwise aid in the growth of subsistence crops (Byard et al., 1996). This could have a significant nutrient cost. For example, during this peak period, floor leaf litter represented between 40% and 45% of the aboveground N found in stands of *H. alchorneoides*, *V. ferruginea*, *G. americana*, and the mixture. Furthermore, in stands of *G. americana* up to 54% of the aboveground K, and 56% of the Mg, were in floor leaf litter (Fig. 1). On the other hand, floor leaf litter never represented more than 28% of aboveground P.

When leaf litter is not removed it decomposes and is reincorporated into the soil or is recycled. However, decomposition and litterfall rates vary along the year; for example, we observed large temporal variations in leaf litter accumulation and nutrient content. Litterfall rates, decomposition rates, and litter accumulation also varied significantly between species.

In experiments conducted within these plantations, rates of annual litterfall from highest to lowest were *V. ferruginea*, *H. alchorneoides*, the four species mixture, *P. elegans*, and *G. americana*. Decomposition rates, from highest to lowest, were *P. elegans*, *G. americana*, the four species mixture, *H. alchorneoides* and *V. ferruginea* (Horn and Montagnini, 1998). Though *P. elegans* produces litter, it decomposes quickly, so there is very little accumulation on the plantation floor.

While quick decomposition may have a positive effect on productivity by making nutrients available for incorporation into the soil where it is available to plants, species that have large amounts of litter that decompose slowly may provide other benefits. For example, thick litter layers, such as those found under *V. ferruginea*, provide ground cover that reduces susceptibility to soil erosion and are an important nutrient source in subsequent rotations. *V. ferruginea* also has a dense canopy, which helps to deter the growth of understory vegetation and decrease costs of weeding (Montagnini and Mendelsohn, 1997; Horn and Montagnini, 1998).

In situations where soil fertility is severely depleted and rotations are short, species characterized by quick nutrient recycling, such as *P. elegans* and *G. americana*, become more desirable. *P. elegans* also fixes N, increasing its appeal if N is a primary concern. Again, if more than one benefit is sought, a mixture of species may offer an attractive option.

4.3. Impacts of aboveground plantation nutrients on soil fertility

While the nutrient cost of harvest is different between species, what is of more concern to long-term sustainability is the influence of these differences upon soil fertility. Sánchez et al. (1985) suggested that plantation forests are most effective at improving soil conditions in the 5–10 year period immediately following canopy closure. The soil samples analyzed for this research were collected within a year of canopy closure. Therefore, any positive effects shown at the time of this study are likely to understate the longer term effects.

Though the plantations were young at the time of sample collection, there were some general differences that suggest patterns which may be attributed to the varying nutrient cycling characteristics of the species. For example, the highest soil Ca and Mg were found under *V. ferruginea*, a species of relatively low total aboveground Ca and Mg content. *V. ferruginea* has a high rate of litterfall and its leaf litter has a slow decomposition rate, therefore large amounts of litter accumulate on the plantation floor (Montagnini et al., 1993; Horn and Montagnini, 1998). Since it contributes large amounts of leaf litter to the floor, and high organic matter inputs to the soil (Montagnini and Sancho, 1990; Montagnini et al., 1993; Horn and Montagnini, 1998), the inclusion of *V. ferruginea* to the mixture should improve cation exchange capacity, helping to conserve K, Ca, and Mg (Montagnini and Sancho, 1990).

Though as stated above longer term research is needed to verify this, it appears that inter-specific differences in nutrient accumulation rates can alter soil fertility. Later in the life of these plantations, if soil trends become more apparent, it may be worth calculating whole ecosystem nutrient budgets, including the soil compartment. This may help clarify the influence of tree species upon soil nutrient declines.

4.4. Using knowledge of species characteristics to conserve nutrients

Due to the differences in soil fertility suggested previously, it is clear that the initial selection of species to be planted is critical in terms of its influence on the nutrient budget. One limitation of this research is that it is based on young plantations, and as trees grow older their nutrient demands diminish as the proportion of nutrient-rich tissues decline in relation to stemwood (Wang et al., 1991). Though the importance of stemwood as a nutrient compartment increases as the plantation ages, we think that relative differences between species are likely to hold.

The selection of species for nutrient conservation or replenishment is enhanced when trends in site fertility, and tissues that are to be harvested, are known in advance. In general, species that have low nutrient concentrations in the tissues which are to be harvested are best suited to the long-term conservation of these nutrients. For example, *V. ferruginea* and *H. alchorneoides* had the lowest tissue nutrient concentrations (except for Ca). Therefore, overall these species may not pose very high demands on site nutrients. On the other hand, *P. elegans* and *G. americana* had relatively low concentrations of Ca. This makes them strong plantation candidates when Ca is a concern.

Mixed plantations may be designed to limit or reverse declining soil fertility. For example, *H. alchorneoides* has relatively low tissue nutrient concentrations, and high contributions of plantation floor litter that decompose fairly quickly (Horn and Montagnini, 1998). Its primary drawback may be its greater accumulation of Ca in stemwood in comparison with the other species of this study, which may result in site Ca depletion at harvest. On the other hand, *V. ferruginea* is not as demanding of Ca as *H. alchorneoides*. The mixture generally offered an intermediate level of total tree biomass nutrients relative to the pure stands.

In our present research, species growth rates were influenced considerably by interspecific competition, a factor that must be considered when developing harvest schedules and assessing nutrient demand. Furthermore, foliage nutrient concentrations were different between mono-specific and mixed stands (Table 2). The greatest difference was the 60% lower Ca concentration found in *P. elegans* foliage grown in the mixed stands On the other hand, for *P. elegans* foliage represented a greater proportional compartment of total tree P in mixed than in pure stands (Fig. 1).

In summary, the mixture represented a compromise in terms of both productivity and nutrient cost. For some nutrients the mixture offered an intermediate level of content (e.g. K and Ca) relative to the pure stands, while for others (e.g. N, P, Mg) it was most similar to the dominant species for the particular nutrient. In this case pure stands of *H. alchorneoides* generally had higher productivity:nutrient cost ratios than the mixture. However, performance of the mixture would have been better if *G. americana*, with its low growth rate and relatively high nutrient concentrations, had not been included.

5. Conclusions

These results may serve as a basis for offering suggestions on the design of small-scale plantation systems that are both economical and sustainable. Ultimately, the selection of tree species and harvest designs is dependent upon preference by farmers. These preferences are in turn determined by numerous factors, such as economic values, the desired products or silvicultural system, soil fertility concerns, desired rotation lengths, and specific site characteristics, such as susceptibility to soil erosion. It is important that the type of information presented in this article is supplied to farmers so that they may consider it along with other factors.

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ACUMULACION DE CARBONO EN PLANTACIONES MIXTAS Y PURAS EN EL TROPICO HUMEDO

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Abstract

Proper design and management of plantations can increase biomass accumulation rates, making them more effective carbon sinks. We compared biomass production and carbon sequestration by three 6-year-old native tree plantations in pure and mixed-species plots in the Atlantic humid lowlands of Costa Rica. In Plantation 1, *Vochysia guatemalensis* had the highest levels of carbon accumulation (40.2 Mg C ha^{-1}) followed by *Jacaranda copaia* (40.1 Mg C ha^{-1}) and the four-species mixed stands (39.0 Mg C ha^{-1}). In Plantation 2, the mixed plantations and *Dipteryx panamensis* (19.9 and 19.57 Mg C ha^{-1}) had the highest carbon accumulation. In Plantation 3, *Hyeronima alchorneoides* had the highest values (15.8 Mg C ha^{-1}) followed by *V. ferruginea* (13.4 Mg C ha^{-1}) and the four-species mixture (11.4 Mg C ha^{-1}). The results suggest that several native tree species in the region have a potential for high carbon accumulation and that changing plantation design can increase the biomass accumulation rates of tree plantations.

Introducción

El uso de plantaciones forestales para la acumulación de carbono de la atmósfera se ha incrementado en la última década (Andrasko 1990, Cairns & Meganck 1994). El uso de plantaciones puede ser múltiple: rehabilitación de suelos, beneficios económicos directos, y absorción de carbono. Sin embargo, deberían probarse diseños alternativos, incluyendo las plantaciones mixtas, para determinar la manera más efectiva y productiva de acumular carbono, especialmente en áreas degradadas. Las plantaciones mixtas bien planificadas proveen productos más diversos que las plantaciones puras, contribuyendo a disminuir los riesgos ante la inseguridad de los mercados, además de disminuir la incidencia y severidad de ataque de ciertas plagas, complementar el uso de recursos del ecosistema, y otros beneficios (Wormald 1992, Montagnini *et al.* 1995).

En este trabajo medimos la producción de biomasa aérea de doce especies nativas en tres plantaciones experimentales en rodales mixtos y puros en la región húmeda del Atlántico de Costa Rica. Resultados anteriores habían indicado la capacidad de las plantaciones mixtas de producir niveles relativamente elevados de biomasa (Montagnini & Porras 1998). En el presente estudio se realizaron mediciones a los seis años de edad. Aunque es difícil extrapolar a una rotación completa, los resultados sugieren opciones para aumentar la acumulación del carbono atmosférico, en alternativas económicamente factibles para los agricultores.

Shepherd, D. y Montagnini, F. 1999. Acumulación de carbono en plantaciones mixtas y puras en el trópico húmedo. IV Semana Científica: "Logros de la Investigación para el Nuevo Milenio". 6-9 de abril de 1999. Programa de Investigación, Centro Agronómico Tropical de Investigación y Enseñanza (CATIE), Turrialba, Costa Rica. Pp. 345-349.

Metodología

El estudio se desarrolló en La Estación Biológica La Selva, cantón Sarapiquí, provincia de Heredia, Costa Rica (10°22'N, 83°59'W, 35-137 msnm). La temperatura promedio es de 24°C y la precipitación anual promedio es de 4000 mm. Las plantaciones se establecieron en 1991 en un área de pastizal abandonado. El área experimental es plana y uniforme. Los suelos son Fluventic Dystropepts, derivados de aluviones volcánicos. Son profundos, bien drenados, libres de rocas, con contenido de materia orgánica bajo o mediano (2.5-4.5%), textura moderadamente pesada, ácidos (pH < 5.0) y poco fértiles (Sancho & Mata 1987).

Las plantaciones consistían de 12 especies nativas: Plantación 1: *Jacaranda copaia*, *Vochysia guatemalensis*, *Calophyllum brasiliense* y *Stryphnodendron microstachyum*; Plantación 2: *Terminalia amazonia*, *Dipteryx panamensis*, *Virola koschnyi* y *Albizia guachapele*; Plantación 3: *Hyeronima alchorneoides*, *Pithecellobium elegans*, *Genipa americana* y *Vochysia ferruginea*. Las parcelas de 32 x 32 m^2 se encuentran en bloques al azar con cuatro repeticiones y seis tratamientos: parcelas puras de cada especie, una parcela mixta con las 4 especies, y una parcela de regeneración natural (Montagnini & Porras 1998).

En el presente estudio, las plantaciones se ralearon por segunda vez, eliminando la mitad de los árboles de las parcelas que habían sido raleadas 3 años, atrás, dejando a las plantaciones a una distancia de 4 m x 4 m (625 árboles/ha). En cada parcela se seleccionaron tres árboles para determinaciones de biomasa. Se separó el material en troncos, ramas y hojas, se pesó en el campo, y se tomaron sub-muestras para llevar a estufa a 70°C.

Se usó la relación peso seco: peso húmedo para corregir los datos de campo. La biomasa promedio por árbol se multiplicó por el número de arboles por hectárea, corrigiendo según la mortalidad, para obtener biomasa por hectárea. El contenido de carbono fue calculado asumiendo que la biomasa es aproximadamente un 50% de carbono (Brown & Lugo 1982).

Resultados y Discusión

En la Plantación 1, *Jacaranda copaia* en rodales mixtos tuvo la mayor biomasa aérea por árbol, más del doble que en plantación pura (Fig. 1). Más del 90% de la biomasa total se encontró en el tronco. En segundo lugar se encontraba *Vochysia guatemalensis*, también con mayor biomasa en plantación mixta que en pura. Por el contrario, los árboles de *Calophyllum brasiliense* tuvieron más del doble de biomasa en plantación pura que en mixta. Al extrapolar a biomasa por hectárea, las plantaciones puras de *V. guatemalensis* tuvieron la mayor biomasa (91.2 Mg ha^{-1}), seguidas por la plantación mixta de 4 especies (90.1 Mg ha^{-1}), *J. copaia* y *C. brasiliensis* (Shepherd & Montagnini 1999). Sin embargo, la biomasa total de la plantación mixta fue mayor que la suma de ¼ de hectárea de cada una de las especies plantada en rodales puros (10.8 + 21.0 + 22.8 + 0 = 54.6 Mg ha^{-1}).

En la Plantación 2, *Terminalia amazonia* en rodales mixtos tuvo la mayor biomasa por árbol (Fig. 2) seguido por *Dipteryx panamensis* en rodales mixtos, mientras que *Albizia guachapele* en plantación mixta tuvo la menor biomasa. La mayor biomasa total por hectárea se encontró en la plantación mixta de 4 especies, seguida por *D. panamensis*, *T. amazonia*, y *V. koschnyi* (Shepherd & Montagnini 1999). Nuevamente, la biomasa de la plantación mixta (57.0 Mg ha^{-1}) fue mayor que la suma de ¼ de hectárea de cada una de las especies plantada en rodales puros (7.06 + 13.7 + 12.8 + 12.4 = 46.0 Mg ha^{-1}).

En la Plantación 3, *Hyeronima alchorneoides* en mixtas tuvo la mayor biomasa, seguida por *Vochysia ferruginea* y *H. alchorneoides* en plantaciones puras (Fig. 3). *H. alchorneoides* tuvo la mayor biomasa por hectárea, seguida por *V. ferruginea* y la plantación mixta. Tal como en las otras dos plantaciones, la suma de la biomasa de ¼ de hectárea de cada especie en plantación pura (2.32 + 11.0 + 5.94 + 10.5 = 29.8 Mg ha^{-1}) fue menor que la biomasa de la plantación mixta (36.0 Mg ha^{-1}).

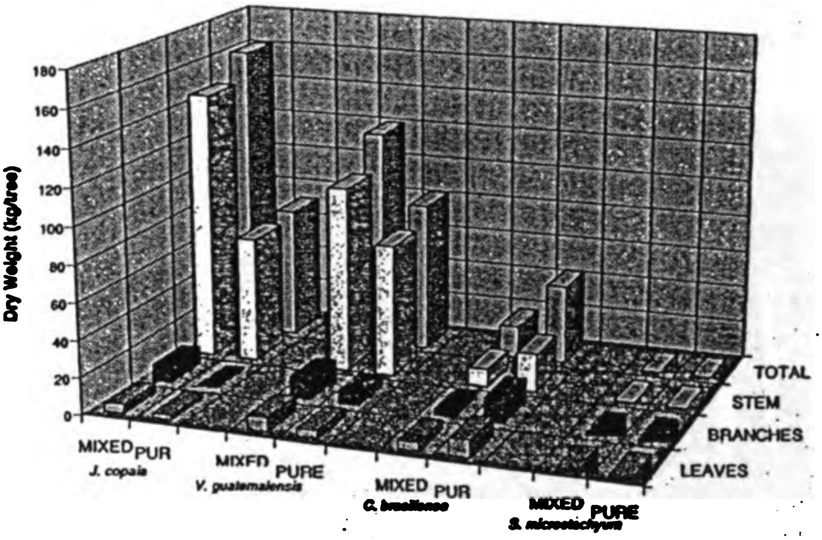


Figure 1. Average dry weight per tree in the four different tree species of Plantation #1

Figure 2. Average dry weight per tree in the four different tree species of Plantation #2

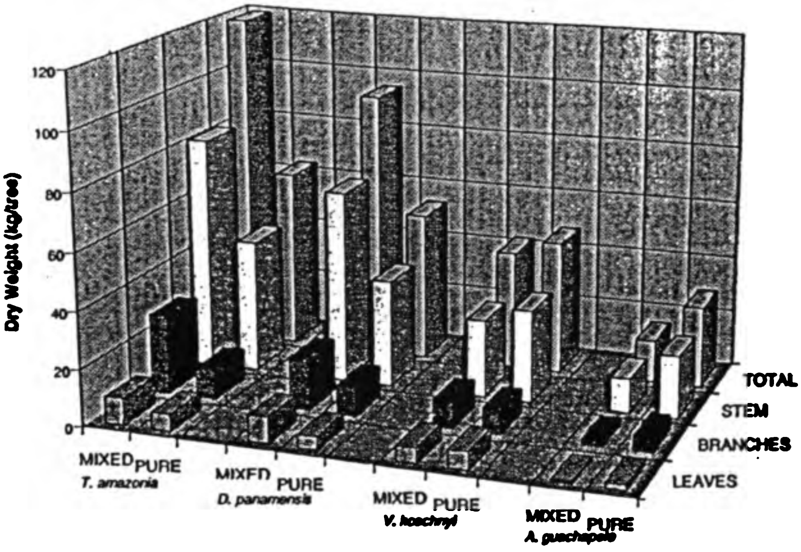
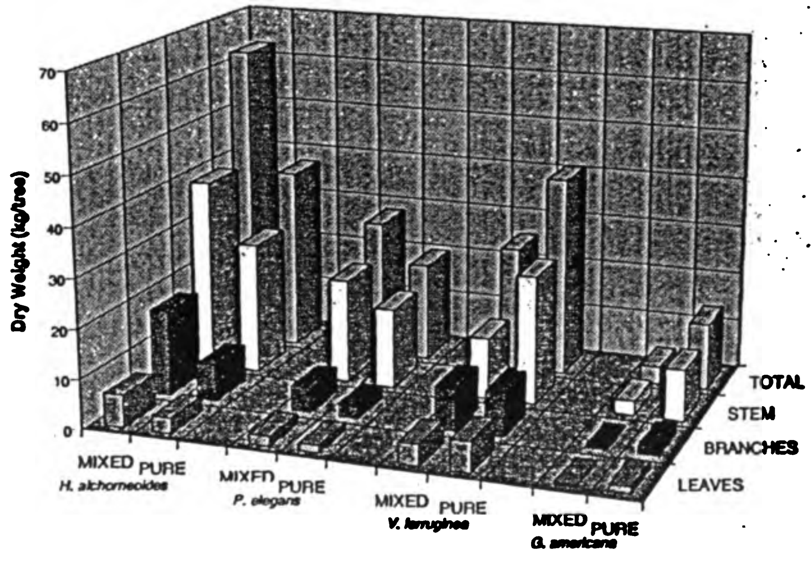


Figure 3. Average dry weight per tree in the four different tree species of Plantation #3



Aparentemente en condiciones mixtas, con menor competencia intra-específica, las especies mencionadas crecen mejor en diámetro, lo cual es consistente con resultados anteriores (Montagnini *et al.* 1995, Montagnini & Porras 1998). Las parcelas mixtas en la Plantación 2 tuvieron mayor biomasa por hectárea, y en las otras dos plantaciones las parcelas mixtas dieron valores intermedios. Sin embargo, en las tres plantaciones, las parcelas mixtas tuvieron mayor biomasa que la suma de ¼ de hectárea de cada una de las especies que la componen en plantación pura. Esto sugiere que las plantaciones mixtas, si son planificadas considerando la respuesta de cada especie, pueden producir mayor biomasa que si en la misma área de terreno se plantara con parcelas puras.

El uso de especies de crecimiento rápido y lento en la misma plantación tiene la ventaja adicional de producir madera en diferentes rotaciones, con productos mas rápidos pero de menor precio, y otros más lentos pero de mejor valor de mercado. La madera de las especies más lentas es también un reservorio de carbono a más largo plazo. La tasa de acumulación de carbono en la Plantación 1 fue 1.74-6.86 Mg C ha^{-1} $año^{-1}$, el doble que en Plantación 2 y el triple que en Plantación 3, valores comparables con otras plantaciones tropicales (Schroeder 1992).

Los bosques acumulan más del 90% del carbono terrestre (Andrasko 1990). Aunque las plantaciones forestales acumulan carbono a una tasa más rápida que los bosques naturales, los bosques primarios conservan más carbono por hectárea. Sin embargo, las opciones para acumular carbono atmosférico deben ser integradoras e incluir las plantaciones forestales, ya que éstas pueden contribuir a la toma de carbono, y al mismo tiempo proveer beneficios económicos a los agricultores (Schroeder & Ladd 1991).

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REGENERACION NATURAL EN PLANTACIONES PURAS Y MIXTAS DE ESPECIES NATIVAS

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Abstract

We measured natural regeneration and understory light availability in two plantations in pure and mixed designs in the humid lowlands of Costa Rica. The plantations consisted of 8 native species: Plantation 1: *Jacaranda copaia*, *Vochysia guatemalensis*, *Calophyllum brasiliense* and *Stryphnodendron microstachyum*; Plantation 2: *Terminalia amazonia*, *Dipteryx panamensis*, *Virola koschnyi* and *Albizia guachapele*. In Plantation 1, at 3 and 7 years forest tree invasion was higher under *V. guatemalensis*, while shrubs were more abundant under *J. copaia* and under mixed-species treatments. In Plantation 2, at 5 years the mixed treatment had the highest number of herbaceous understory species, while *D. panamensis* had the highest understory biomass. At 7 years, *V. koschnyi* and *T. amazonia* had the highest number of woody species. Competition for grasses is a major factor influencing woody invasion under these plantations. High accumulation of litter on the plantation floor may contribute to diminish grass growth and thus encourage woody invasion under the species' canopies.

Introducción

Las plantaciones forestales pueden brindar múltiples beneficios tales como producción de madera, protección del suelo, captura de carbono atmosférico, y protección de cuencas hidrográficas. Además el uso de plantaciones con especies nativas monoespecíficas o mixtas puede desempeñar un papel importante en la recuperación de suelos, y la estructura y diversidad florística de ecosistemas tropicales degradados (Lugo 1992, Montagnini and Sancho 1990, Guariguata et al. 1995, Parrotta 1992).

Los principales factores limitantes para la regeneración en pastizales abandonados en regiones de bosque húmedo tropical pueden incluir escasez de nutrientes, niveles altos de compactación del suelo, falta o exceso humedad en el suelo, elevada radiación solar, y competencia intra e interespecífica (Nepstad et al.1991). Además otro elemento limitante crítico es la disponibilidad de semillas, especialmente en sitios cuyo tamaño o distancia de fuentes semilleras pueda limitar la dispersión de propágulos.

Las plantaciones forestales pueden contribuir a la recuperación de condiciones ambientales favorables a los procesos de regeneración natural en su sotobosque (Parrotta 1995, Guariguata et al. 1995). Por ejemplo, en Puerto Rico, bajo el dosel de plantaciones de *Albizia lebbek* de 6 años de edad, se encontraron 22 especies de árboles y arbustos, en comparación con una sola especie en parcelas control sin plantar (Parrotta 1992). La mayoría de las especies encontradas eran dispersadas por aves o murciélagos, por lo cual se concluyó que el dosel de las plantaciones puede cumplir un papel clave en los procesos de regeneración proveyendo perchas y hábitat para los animales dispersores. En La Estación Biológica La Selva, Costa Rica, resultados de estudios de diversidad vegetal bajo la

Montagnini, F., Guariguata, M., Ribeiro, N., y Mariscal, A. 1999. Regeneración natural en plantaciones puras y mixtas de especies nativas. IV Semana Científica: "Logros de la Investigación para el Nuevo Milenio". 6-9 de abril de 1999. Programa de Investigación, Centro Agronómico Tropical de Investigación y Enseñanza (CATIE).

cobertura de ocho especies forestales y un tratamiento de regeneración natural sugieren también que las plantaciones presentan un buen potencial para acelerar los procesos de recuperación de suelos degradados (Powers et al. 1997).

En el presente trabajo se compara la regeneración natural en el sotobosque de plantaciones forestales de ocho especies nativas en parcelas monoespecíficas y mixtas, en La Estación Biológica La Selva. En todos los casos se compara además con parcelas sin plantar, dejadas como parcelas testigo de regeneración natural.

Metodología

Sitio de estudio: El estudio se desarrolló en La Estación Biológica La Selva, cantón Sarapiquí, provincia de Heredia, Costa Rica (10°22'N, 83°59'W, 35-137 msnm). La temperatura promedio es de 24°C y la precipitación anual promedio es de 4000 mm.

Diseño experimental: Los tratamientos se establecieron en 1991 en un área de pastizal abandonado. Las parcelas de 32x32 m^2 se encuentran en bloques al azar con cuatro repeticiones y seis tratamientos; parcelas puras de cada especie, una parcela mixta con las 4 especies, y una parcela de regeneración natural (Montagnini and Porras 1998). El presente trabajo consideró las siguientes especies: Plantación 1: *Jacaranda copaia*, *Vochysia guatemalensis*, *Calophyllum brasiliense* y *Stryphnodendron microstachyum*; Plantación 2: *Terminalia amazonia*, *Dipteryx panamensis*, *Virola koschnyi* y *Albizia guachapele*. La distancia inicial entre árboles fue de 2x2 m, con raleos a los 3 y 6 años hasta un espaciamiento de 4x4 m.

El muestreo de la vegetación se realizó en sub-parcelas establecidas dentro de los tratamientos mencionados. Las sub-parcelas fueron establecidas en el centro de cada parcela, para evitar efectos de borde. Para el muestreo de vegetación arbórea se consideraron los individuos mayores a 15 cm de altura. Se clasificaron las especies inventariadas con ayuda de personal la Estación Biológica La Selva y comparación con ejemplares de herbario.

Resultados y discusión

Abundancia y riqueza de vegetación

En la plantación 1, a los 3 años de edad la colonización por especies arbóreas fue mayor bajo *V. guatemalensis*, mientras que los arbustos fueron más abundantes bajo *J. copaia* y en plantaciones mixtas. Asimismo, en *V. guatemalensis* se encontró una mayor diversidad de hábitos de vegetación (Guariguata et al. 1995). A los 7 años de edad se encontró mayor abundancia de individuos (tanto arbóreos como otras formas de vida) bajo *Vochysia guatemalensis*, plantación mixta, y *Calophyllum brasiliense* (Tabla 1). Estos resultados coinciden con las experiencias de Powers et al. (1997) en La Selva, quienes encontraron que plantaciones de *Vochysia guatemalensis* y *V. ferruginea* contribuyeron con la supresión temprana del pasto y atrayeronn a gran cantidad de dispersores; además, ellos también reportaron que el tratamiento regeneración (control), presentó el promedio más bajo de todos los tratamientos.

Tabla 1. Promedios de abundancia de individuos por tratamiento en Plantación 1, a los 7 años.

Tratamiento	Número de individuos en 0.057ha	Error estándar
Vochysia	90.3 a	5.2
Mixta	87.6 a	8.3
Calophyllum	78.6 a	7.5
Jacaranda	57.1 b	6.9
Regeneración	28.6 ab	7.3

Medias con letras iguales no difieren estadísticamente; Prueba de Tukey, α= 0,05

Concentraciones relativamente altas de C y N fueron encontradas en el suelo bajo *Vochysia guatemalensis* (Montagnini y Porras 1998). La descomposición de hojarasca fue más rápida en parcelas de *Vochysia*, *Jacaranda* y mixta, que en los otros tratamientos. Además, *Vochysia* presentó la mayor caída de hojarasca, seguida por *Jacaranda* (Byard et al.1996).

En la Plantación 2, a los 5 años la plantación mixta presentó el mayor número de especies herbáceas en el sotobosque. A los 7 años, *T. amazonia*; *V. koschnyi* y la plantación mixta tuvieron la mayor cantidad de especies arbóreas en el sotobosque (Tabla 2). La tasa de descomposición de hojarasca fue mayor bajo *Terminalia amazonia*, mientras que el mayor espesor del mantillo de hojarasca fue encontrado bajo *D. panamensis* y *V. koschnyi* (Kershnar y Montagnini 1998).

No se encontraron especies arbóreas bajo *A. guachapele*. Se podría deducir que la mayor disponibilidad de nitrógeno bajo *A. guachapele* favorecería más a las especies herbáceas, las cuales compiten con la regeneración natural arbórea.

A pesar de la temprana edad de estas plantaciones, se encontró que tanto *Terminalia amazonia* como *Dypterix panamensis* se regeneraban a sí mismas, factor favorable para la recuperación de áreas, en casos de que los agentes dispersores de otras especies arbóreas no actúan eficientemente.

Tabla 2. Número de individuos arbóreos bajo los seis tratamientos en Plantación 2.

Tratamiento	Número de individuos/16 m^2	Número de individuos/ha
Virola koschnyi	19	11 875
Dypterix panamensis	9	5 625
Terminalia amazonia	44	27 500
Albizia guachapele	0	0
Plantación mixta	17	10 625
Regeneración natural	7	4 375

Conclusiones

En ambas plantaciones estudiadas, y en las condiciones del sitio experimental, la regeneración arbórea fue más exitosa bajo plantaciones forestales que en potreros

abandonados. Aparentemente es más recomendable la plantación de especies forestales en lugar de esperar los procesos naturales de recuperación natural.
En las condiciones de estos ensayos (especies y ambiente), las especies más exitosas para recuperar potreros abandonados fueron *Vochysia guatemalensis*, *Terminalia amazonia*, *V. koschnyi*, y las plantaciones mixtas. En la Plantación 2, la regeneración arbórea fue mayor bajo *T. amazonia*, especie cuya hojarasca descompone rápidamente; por otro lado, la regeneración arbórea bajo *Albizia guachapele* fue nula, a pesar de ser ésta una especie fijadora de nitrógeno. En ciertos casos es posible que el establecimiento de la regeneración natural arbórea no dependa tanto del mejoramiento del suelo, como de otros factores tales como la dispersión de semillas y la creación de condiciones microclimáticas apropiadas.

La regeneración arbórea fue mayor bajo las especies cuya caída de hojarasca y acumulación de mantillo fueron más abundantes. La producción elevada de hojarasca y acumulación de mantillo contribuyen a inhibir el crecimiento de pastos, favoreciendo así la competencia por especies arbóreas.

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Accumulation in above-ground biomass and soil storage of mineral nutrients in pure and mixed plantations in a humid tropical lowland

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Abstract

As fast-growing, short-rotation plantations are being planted in the tropics on low fertility soils, the problem of sustaining soil fertility becomes an important management issue. Above-ground biomass, nutrient concentration of above-ground tree tissues, and soil nutrients were examined in two young plantations of eight indigenous tree species grown in pure and mixed designs in a low fertility site in the humid lowlands of Costa Rica. The goal was to assess the role of nutrient accumulation in above-ground biomass on potential site nutrient decline, and to draw recommendations to conserve site nutrients in the long term.

In Plantation 1, *Jacaranda copaia* pure stands had higher above-ground tree N, P, and Mg than the other treatments, while *Vochysia guatemalensis* had the greatest accumulation of K and Ca. For *J. copaia*, stem harvest would remove about 54% of total above-ground tree N, but about 80% of P, K, Ca and Mg. For *V. guatemalensis*, stem harvest would remove less than 30% of N but from 50 to 60% of total above-ground tree Ca, K, Mg and P. Branches and foliage summed together were 25 to 35% of total above-ground tree biomass, but they generally represented about 50% of above-ground tree nutrients. In Plantation 2, the mixed stands had the highest above-ground nutrient content for all nutrients, and both the mixture and *Terminalia amazonia* pure stands had the highest stem P and Mg.

Five years after planting, decreases in soil P, K and Ca were apparent in pure plots of the fastest growing species with the largest accumulation of nutrients in above-ground biomass, such as *J. copaia* and *V. guatemalensis*. However, in other cases, beneficial effects on some soil nutrients were noted: for example, increases in soil Ca under *T. amazonia* and *Virola koschnyi*, both species with high Ca content in foliage and high rates of annual litterfall. The mixed plots showed intermediate values for the nutrients examined, and even improved soil conditions, as for P in Plantation 1. This suggests that in mixed conditions it may take longer to deplete soil nutrients than in monospecific stands of fast-growing species.

Results of continued sampling will be needed to assess the long term effects of plantation treatments on soil chemistry, especially near the end of the rotation (estimated at 12–15 years, depending on the species). The calculation of whole-stand nutrient budgets can help in the selection of tree species and plantation management strategies to favor nutrient recycling mechanisms and site nutrient conservation.

Keywords: Above-ground nutrients; Humid tropics; Mixed plantations; Native trees; Soil nutrients

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1. Introduction

Tropical tree plantations incorporate considerable amounts of nutrients in their biomass over a relatively short period of time (Bruijnzeel, 1991; Montagnini and Sancho, 1994; Fölster and Khanna, 1997; Gonçalves et al., 1997). Soil nutrients may be generally abundant early in stand growth as a result of low plant uptake, stimulation of nutrient mineralization, and low immobilization in plant biomass, but as plantations grow, decreased nutrient availability can result from immobilization into woody biomass and detritus pools, and decreased mineralization (Binkley, 1986; Binkley et al., 1997). Site fertility declines can limit sustained plantation forestry in tropical regions, especially on soils that are inherently nutrient-poor: soil fertility can be decreased through excessive removal of living biomass, particularly if nutrients in tree crowns are lost through harvest or site preparation (Jorgensen and Wells, 1986; Fölster and Khanna, 1997; Wadsworth, 1997).

Alternatives to conserve site nutrients may include preferential planting of tree species that do not place high nutrient demands on the site (Bruijnzeel, 1984; Wang et al., 1991; Montagnini and Sancho, 1994). Bruijnzeel (1984) found, for example, a higher production of wood per unit of N or P in the wood in plantations of *Pinus merkusii* compared with nearby plantations of *Agathis damara* in Java. Large differences may exist in nutrient use efficiency among tropical tree species (Wang et al., 1991; Montagnini, 1994a). For example, in Puerto Rico, Wang et al. (1991) found that *Casuarina* spp. was twice as efficient as *Leucaena* spp. for N, 3–4 times as efficient as *Albizia* and *Leucaena* for K, and about twice as efficient as all of the studied species for Mg. To design viable tropical plantations, focusing on efficient use of nutrients on a stand level may be as important as considering production rates (Wang et al., 1991).

Mixed plantations yield more diverse forest products than monospecific stands, helping to diminish farmer's risks in unstable markets. If planned with consideration for each species' response to mixed conditions, mixed designs can be more productive than monospecific systems (Smith, 1986; Binkley et al., 1992; Burkhart and Tham, 1992; Kelty, 1992; Wormald, 1992). In addition, a mixture of species, each with different nutrient requirements and different nutrient recycling properties, may be overall less demanding on site nutrients than pure stands (Binkley et al., 1997; Fölster and Khanna, 1997). In this article, above-ground nutrient accumulation and soil chemistry are compared among eight native species growing in young plantations in mixed and pure stands in the Atlantic humid lowlands of Costa Rica. In previous reports, it was shown that the growth of dominant species was faster in mixed than in pure plantation, and that mixed plantations had high volume and biomass production in comparison with pure stands ~~(Montagnini and Sancho, 1994;~~ Montagnini et al., 1995; Montagnini and Porras, 1998). In other plantations ~~of the same experiment,~~ the mixed plantations had intermediate values of soil N, P and K, but lower soil Ca and Mg relative to pure plantations (Stanley and Montagnini, 1999). Although the young age of these plantations precludes proper extrapolation over a whole rotation, the results can suggest design and management options of tropical plantations to conserve nutrients in the long term.

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2. Methods

2.1. Site description

The experiments were established on abandoned pasture at the Guaria Annex of La Selva Biological Station in the Atlantic humid lowlands of Costa Rica (10°26′N, 86°59′W, 50 m mean altitude, 24°C mean annual temperature, 4000 mm mean annual rainfall). Soils are Fluventic Dystropepts derived from volcanic alluvium. They are deep, well drained, stone-free, acid (pH in water <5.0), with low or medium organic matter prior to planting (2.5–4.5%), cation exchange capacity 10–14 cmols/kg, 10–15% base saturation, and moderately heavy texture (50–60% sand, 5–15% silt and 25–45% clay) (Sancho and Mata, 1987). Soil conditions before clearing were reported by Montagnini et al. (1993): soils were too poor for cultivation of the commercial crops commonly grown in the region (Bertsch, 1986; Sancho and Mata, 1987; Montagnini, 1994b). The area had been cleared in the mid-1950s and grazed until 1981, a sequence of land uses common in the region at the time (Montagnini, 1994b). The area is on flat, uniform terrain. The site was cleared manually and no burning was done. The slash was left on the floor, to protect against soil erosion and to delay the growth of weeds.

2.2. *Experimental design*

A total of eight native tree species of actual or potential economic value were tested in two plantations, each with four species: Plantation 1: *Stryphnodendron microstachyum* Poepp. et Endl.; *Vochysia guatemalensis* D.Sm., *Jacaranda copaia* (Aubl.) D. Don, and *Callophylum brasiliense* Cambess; Plantation 2: *Albizia guachapele* (H.B.K.) Little, *Terminalia amazonia* (Gmell.) Exell., *Virola koschnyi* Warb., and *Dipteryx panamensis* (Pittier) Record and Mell. Ecological characteristics of the eight species of this study are given in Table 1. The criteria for species selection were: growth rate and economic value, potential impacts on soils and nutrient cycling, and seedling availability (Montagnini et al., 1995). In each plantation of four tree species there was at least one nitrogen-fixing tree, one relatively fast-growing species, and a slower-growing species. Both plantations were established in 1991. The plantations were in randomized blocks, with four replicates and six treatments: four pure plantation plots of each species, a mixed-species plot (with the four species), and a fallow (natural regrowth) plot. Each plot was 32 m × 32 m. Initial planting distance was 2 m × 2 m to speed canopy closure and obtain early impacts on soils, with 50% thinning planned after canopy closure. Within each mixed-tree plot, trees of the four species were planted alternating two species per row. The sequential order of the species within rows was systematically reversed every other row. In that manner, each column contained the four species of the mixture in a sequence.

2.3. *Above-ground tree biomass and nutrients*

Biomass values were calculated from data obtained at the time of thinning. The plantations were thinned after canopy closure, which occurred approximately 3 years after planting. With thinning, the initial 2 m × 2 m planting distance was widened to 2 m × 4 m (1250 trees per hectare). Thinning was performed in one half of each plot, leaving the other non-thinned half for comparison. For thinning, all trees were cut in alternate rows. From every thinned

Table 1
Characteristics of tree species grown in mixed and pure plantations at La Selva Biological Station (Montagnini et al., 1995)

Scientific name	Common name	Family	Native range	Growth, habitat
Plantation 1				
S. microstachyum Poepp. et Endl.	vainillo	Leguminosae (Mimosoid)	Costa Rica, Nicaragua, Panama	Upper canopy of mature forest. Also on secondary forest. Fast growth
V. guatemalensis Donn. Sm.	mayo, chancho	Vochysiaceae	Mexico to Panama	Upper canopy, early-mid successional. Fast growth < Space
J. copaia(Aubl.) D. Don.	jacaranda	Bignoniaceae	Guatemala to Brazil	Pioneer, early successional. Secondary forest. Very fast growth
C. brasiliense Cambess.	cedro Maria	Guttiferae (Clusiaceae)	Mexico to N. South America	Mature forest. Slower growth
Plantation 2				
A. guachapele (H.B.K.) Little	cenizaro, guayaquil	Leguminosae (Mimosoid)	Guatemala to Ecuador	Pioneer. Common in low secondary forest. Fast growth [illegible]
T. amazonia (J.F.Gmel.) Exell.	roble coral	Combretaceae	S. Mexico to N.South America	Upper canopy, mid-successional. Relatively slow growth
V. koschnyi Warb	fruta dorada	Myristicaceae	Central America	Upper canopy, mid-successional. Moderate growth
D. panamensis (Pittier) Record & Mell	almendro	Leguminosae (Papilionoid)	Nicaragua to Colombia	Upper canopy, mid-to late successional. Slower growth

row, two trees were randomly selected for biomass determinations, giving a total of 16 sampled trees per plot. Data from the 16 sampled trees were averaged to obtain values per plot. Biomass data from these plantations were also used for a separate study of the role of the plantations on carbon accumulation (Montagnini and Porras, 1998).

Portions of stems (lower, middle and top parts) and tip, medium and bottom parts of branches of the sampled trees were collected. Foliage from the tip, medium, and lower portions of each branch were pooled to obtain one sample of each tissue type and species for laboratory analysis. In mixed plots, foliage samples were collected to compare nutrient concentrations between trees growing in mixed and in pure plantations. These foliar nutrient concentrations were used in subsequent calculations for species in mixed plots. Due to limitations in the number of chemical analyses that could be performed with the available resources, stem and branch samples were not collected in mixed plots. Although there was no background information to substantiate this assumption, concentrations of nutrients in those tissues were assumed to be very similar to nutrient concentrations found in pure plots.

All tissue types were oven-dried at 70°C to constant weight and then ground. Dry : wet weight ratios from felled trees were used to correct the field weight determinations and obtain biomass on a per tree basis. The average biomass per tree was multiplied by the number of trees present in each plot before thinning, and extrapolated to a hectare. The data from the four plots of each treatment were then used for analysis of variance and LSD tests for means ($n = 4$, $P < 0.05$).

Concentrations of total N, P, Ca, Mg and K for the different tissue types and species were measured on nitro-perchloric digests (Díaz-Romeu and Hunter, 1978); N and P were measured using a Flow Injection Analyzer, while cations were measured using an Atomic Absorption Spectrophotometer. Total nutrient content (nutrient accumulation) for each tissue and for each species in pure plots and in mixed plots were calculated by multiplying the mean biomass of each species' plant part ($n = 4$) by the average nutrient concentration of the respective plant parts. Totals for whole trees were obtained by weighted means of tree parts (stems, branches, and foliage). For mixed species stands, the nutrient content of the four species were calculated separately and then added in order to obtain a total. Analysis of variance and LSD tests were run to compare mean biomass ($n = 4$), nutrient concentration ($n = 4$), and nutrient content ($n = 4$) of tree parts and whole trees among pure and mixed plots.

2.4. Soil chemistry

Soils were sampled before clearing the land, and annually thereafter. Soil conditions up to 4 years after planting had been reported by Montagnini and Porras (1998). Results of sampling from 1996, 5 years after planting, are reported here, and compared with those of previous years. Composite samples were taken in each of the four replicate plots per treatment, at 0–5, 5–15, 15–30 and 30–60 cm depth. The pH was measured in a 1 : 2.5 mixture of soil : deionized water. The exchangeable Ca and Mg were extracted with a 1N KCl solution, while the exchangeable P and K were extracted with a modified Olsen solution, which is a mixture of 0.5N $NaHCO_3$, 0.01N bi-sodium EDTA and Superfloc 127 (a commercial flocculant) (Díaz-Romeu and Hunter, 1978). A 1 : 5 proportion of soil : extractant was used in all cases. Cations were measured using an Atomic Absorption Spectrophotometer. Extractable P was measured colorimetrically after reaction with $(NH_4)_2MoO_4$ and $SnCl_2$, using a spectrophotometer. Organic matter was measured with the Walkley-Black technique (Allison, 1975) and total N was measured using a semi-Micro-Kjeldahl technique (Bremner and Mulvaney, 1982). Analysis of variance and LSD tests were run to compare the means for each variable and soil depth ($n = 4$, $P < 0.05$) among sites.

3. Results

3.1. Above-ground tree biomass and nutrient concentrations

In Plantation 1 the total above-ground biomass was higher in *J. copaia* pure plots, followed by the mixture of four species and *V. guatemalensis*. About 87% of total biomass of *J. copaia* and 70% of total biomass of *V. guatemalensis* was found in stems, while 78% of total biomass of the mixture was in stems. In Plantation 2, the highest total above-ground biomass per

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Table 2
Above-ground biomass of tree tissues in pure plots and in mixture of eight species on a per hectare basis. Means, standard errors (SE), and statistical significance (Sig.)[a]

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Species	Above-ground biomass (mg/ha)											
	Stems			Branches			Foliage			Total tree		
	Mean	SE	Sig.	Mean	SE	Sig.	Mean	SE	Sig.	Mean	SE	Sig.
Plantation 1												
J. copaia	40.9	0.84	a	3.48	0.13	b	2.23	0.13	c	46.6	0.94	a
V. guatemalensis	19.0	0.89	c	4.25	0.22	b	4.03	0.38	b	27.3	1.38	b
C. brasiliense	7.2	1.46	d	5.71	0.71	a	5.89	0.52	a	18.8	2.67	c
S. microstachyum	1.7	1.26	e	0.56	0.42	c	0.20	0.14	d	2.5	1.82	d
Four sps. mixture	25.3	1.38	b	3.86	0.24	b	3.13	0.23	bc	32.3	1.53	b
Plantation 2												
T. amazonia	22.4	3.46	a	5.96	0.47	b	4.19	0.38	a	32.5	4.23	ab
D. panamensis	19.1	2.21	a	6.84	0.83	ab	3.22	0.49	a	29.1	3.05	ab
V. koschnyi	17.8	2.39	a	4.28	1.00	bc	3.61	0.75	a	25.7	3.54	b
A. guachapele	7.9	0.85	b	1.92	0.24	c	0.54	0.14	b	10.3	1.10	c
Four sps. mixture	24.8	2.58	a	9.66	1.72	a	4.68	0.63	a	39.1	4.41	a

[a] Differences between species for a given parameter and depth are statistically significant ($P < 0.05$) when means are followed by different letters.

hectare was found in the mixed plots, *T. amazonia*, *Dipteryx panamensis* and *V. koschnyi*, with values 2.5–3 times those found in *A. guachapele* (Table 2). For *T. amazonia* and *D. panamensis*, almost 70% of total biomass was in the stems, while for the mixture of four species, 63% of total biomass was in the stems.

In Plantation 1, *J. copaia* and *S. microstachyum* had the highest foliar N concentrations, *S. microstachyum* had the highest foliar P concentrations, and *V. guatemalensis* had significantly higher foliar Ca, Mg and K concentrations than any of the other three species (Table 3). *S. microstachyum* had the highest stemwood N concentrations, and *J. copaia* and *V. guatemalensis* had the highest stemwood Mg and K concentrations. Similar trends as for stemwood were found for branch nutrient concentrations (Table 3).

species

In Plantation 2, *A. guachapele* and *D. panamensis* had the highest foliar N, P and K concentrations, *V. koschnyi* and *T. amazonia* had the highest foliar Ca, and *A. guachapele* had higher foliar Mg concentrations than any of the other three species (Table 4). Comparing foliar nutrient concentrations for each species grown in pure and mixed stands, differences were found for only one species: *T. amazonia* had higher N concentration in foliage in mixed (1.96%), than in pure stands (1.65%). *A. guachapele* had the highest stemwood N concentrations, *A. guachapele* and *V. koschnyi* had significantly higher stemwood Mg concentrations, and there were no statistically significant differences in stemwood P, Ca or K concentrations among the four species. Again, similar trends as for stemwood were found for branch nutrient concentrations (Table 4).

3.2. Nutrient content of above-ground tree biomass

In Plantation 1, on a per hectare basis, *J. copaia* stands had higher total tree N, P, and Mg than the other treatments, while *V. guatemalensis* stands had the greatest accumulation of K and Ca (Fig. 1). The four species mixture had the second greatest total tree nutrient content for all nutrients. Due to lower tree biomass, *S. microstachyum* stands had the lowest nutrient content per hectare. Due to relatively high stem biomass, coupled with high nutrient concentrations, *J. copaia* had significantly higher stem N, P, K, Ca and Mg than any of the other pure stands, followed by the mixture of four species, and by *V. guatemalensis* pure stands, in that order (Fig. 1). Similar trends to those of stemwood were found for branch nutrient content (Fig. 1). *V. guatemalensis* had greater foliar biomass N, P, Mg, and K than the other pure stands, and *V. guatemalensis* and *C. brasiliense* had the greatest foliar biomass Ca (Fig. 1).

In Plantation 2, on a per hectare basis, the mixed stands had the highest nutrient content for all nutri-

Table 3
Nutrient concentrations in tissues of four indigenous tree species of Plantation 1. Means, standard errors (SE), and statistical significance (Sig.)[a]

Tissue/Species	Nutrient concentrations (%)														
	N			P			K			Ca			Mg		
	Mean	SE	Sig.	Mean	SE	Sig.	Mean	SE	Sig.	Mean	SE	Sig.	Mean	SE	Sig.
Leaves															
J. copaia	2.68	0.09	a	0.18	0.01	b	0.58	0.03	c	0.40	0.02	c	0.21	0.01	b
V. guatemalensis	1.73	0.17	b	0.14	0.01	b	1.01	0.05	a	1.01	0.10	a	0.40	0.02	a
S. microstachyum	2.35	0.11	a	0.23	0.23	a	0.87	0.04	b	0.37	0.01	c	0.18	0.01	b
C. brasiliense	0.99	0.03	c	0.75	0.03	c	0.35	0.03	c	0.68	0.03	b	0.09	0.01	c
Branches															
J. copaia	0.66	0.04	b	0.16	0.02	b	0.64	0.05	c	0.54	0.04	a	0.13	0.01	b
V. guatemalensis	0.77	0.10	b	0.18	0.02	b	3.06	0.41	a	0.59	0.03	a	0.16	0.01	ab
S. microstachyum	1.10	0.10	a	0.26	0.02	a	1.51	0.09	b	0.36	0.01	b	0.17	0.02	a
C. brasiliense	0.38	0.04	c	0.07	0.00	c	0.38	0.03	c	0.65	0.07	a	0.08	0.00	c
Stems															
J. copaia	0.25	0.01	b	0.09	0.01	ab	0.52	0.07	b	0.2	0.04	a	0.09	0.00	a
V. guatemalensis	0.24	0.02	bc	0.1	0.02	a	0.87	0.09	a	0.26	0.01	a	0.08	0.00	a
S. microstachyum	0.49	0.08	a	0.12	0.02	a	0.55	0.02	b	0.21	0.02	a	0.06	0.01	b
C. brasiliense	0.12	0.01	c	0.05	0.01	b	0.12	0.01	c	0.3	0.05	a	0.04	0.00	c

[a] Differences between species for a given tissue are statistically significant ($P < 0.05$) when means are followed by different letters. SE < 0.01.

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ents, while the reverse was true for *A. guachapele* stands (Fig. 2). Due to relatively high stem biomass, coupled with high nutrient concentrations, the mixed stands had significantly higher stem N and Ca than any of the other pure stands, and both the mixture and *T. amazonia* pure stands had the highest stem P and Mg (Fig. 2). The mixture, *T. amazonia* and *V. koschnyi* pure stands had the highest stem K. The mixed stands and *D. panamensis* had significantly greater branch N, P, K and Ca content, while the mixture, *A. guachapele* and *T. amazonia* had the greatest branch Mg (Fig. 2). The mixed stands had significantly higher foliar N and K than any of the other pure stands, and the mixture, *T. amazonia* and *V. koschnyi* had the highest foliar P, Ca and Mg (Fig. 2).

3.3. Soil chemistry

In Plantation 1, 5 years after planting, statistically significant differences in soil nutrients between treatments were found only for P (Table 5). The mixture and the *C. brasiliense* plots had the highest while the *V. guatemalensis* and the *J. copaia* plots had the lowest concentrations of soil P at all depths ($P < 0.05$). In Plantation 2, 5 years after planting there were no statistically significant differences among treatments for any depth or nutrient (Table 6).

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Mg

4. Discussion

4.1. Above-ground tree biomass in pure and mixed plantations

Converting the above-ground biomass accumulation for 3 years to an annual basis for the fastest growing species of these experiments: *V. guatemalensis*, *J. copaia*, *T. amazonia*, *D. panamensis* and *V. koschnyi*, yields a range from 6.2 to 15.5 mg/ha per year. These values are within the range found for several tree species in young plantations in humid tropical regions. For example, for sites in Brazil and Costa Rica, Lugo et al. (1988) reported tropical species above-ground biomass accumulation rates of 1.6–29.8, with most in the range from 6–15 mg/ha per year. For *Gmelina arborea*, Halenda (1993) reported total above-ground biomass accumulation rate of 13 mg/ha per year in a 7 year-old plantation in Sarawak. However, all these values were for plantations of relatively

Mg

Table 4
Nutrient concentrations in tissues of four indigenous tree species of Plantation 2. Means, standard errors (SE), and statistical significance (Sig.)[a]. For leaves, an additional comparison is presented among pure and mixed stands (Ag: *A. guachapele*, Vk: *V. koschnyi*, Ta: *T. amazonia*, Dp: *D. panamensis*)

Tissue/Species	Nutrient concentrations (%)														
	N			P			K			Ca			Mg		
	Mean	SE	Sig.	Mean	SE	Sig.	Mean	SE	Sig.	Mean	SE	Sig.	Mean	SE	Sig.
Leaves															
A. guachapele	4.09	0.13	a	0.23	0.01	a	1.34	0.11	a	0.39	0.04	b	0.29	0.01	a
V. koschnyi	1.57	0.13	c	0.12	0.01	d	0.63	0.06	c	0.86	0.09	a	0.23	0.02	b
T. Amazonia	1.65	0.03	c	0.16	0.01	c	0.72	0.09	c	0.74	0.11	a	0.27	0.02	ab
D. panamensis	2.48	0.1	b	0.2	0.00	b	1.09	0.02	b	0.46	0.04	b	0.14	0.00	c
Mixed versus pure leaves:															
Ag	4.1	0.13	a	0.23	0.00	a	1.35	0.11	a	0.39	0.04	a	0.29	0.01	a
Ag mix	4.43	0.13	a	0.25	0.01	a	1.46	0.12	a	0.49	0.03	a	0.34	0.02	a
V k	1.57	0.13	a	0.12	0.01	a	0.63	0.06	a	0.86	0.09	a	0.23	0.02	a
V k mix	1.64	0.1	a	0.12	0.01	a	0.71	0.06	a	0.9	0.11	a	0.18	0.02	a
Ta	1.65	0.03	b	0.16	0.01	a	0.72	0.09	a	0.74	0.11	a	0.27	0.02	a
Ta mix	1.96	0.08	a	0.16	0.01	a	0.87	0.1	a	0.82	0.15	a	0.29	0.02	a
Dp	2.48	0.1	a	0.2	0.00	a	1.09	0.02	a	0.46	0.04	a	0.14	0.00	a
Dp mix	2.21	0.1	a	0.2	0.01	a	0.96	0.06	a	0.44	0.06	a	0.16	0.01	a
Branches															
A. guachapele	1.21	0.23	a	0.18	0.02	a	1.11	0.29	a	0.41	0.06	a	0.14	0.02	b
V. koschnyi	0.71	0.25	ab	0.09	0.02	b	1.05	0.34	a	0.49	0.06	a	0.18	0.02	a
T. amazonia	0.31	0.05	b	0.1	0.01	b	0.44	0.15	a	0.23	0.04	b	0.06	0.01	c
D. panamensis	0.67	0.08	ab	0.12	0.02	b	0.73	0.18	a	0.38	0.04	ab	0.05	0.00	c
Stems															
A. guachapele	0.64	0.08	a	0.1	0.01	a	0.4	0.07	a	0.29	0.04	ab	0.08	0.01	a
V. koschnyi	0.23	0.03	b	0.07	0.01	a	0.42	0.07	a	0.2	0.02	bc	0.08	0.01	a
T. amazonia	0.24	0.01	b	0.08	0.01	a	0.34	0.05	ab	0.17	0.03	c	0.03	0	b
D. panamensis	0.27	0.04	b	0.08	0.01	a	0.22	0.03	b	0.32	0.04	a	0.04	0.00	b

[a] Differences between species for a given tissue are statistically significant ($P < 0.05$) when means are followed by different letters. SE < 0.01.

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young age; values will also vary with climate and site fertility (Lugo et al., 1988).

The value for *C. brasiliense* in the present research is similar to ranges reported for relatively slower-growing species in the humid tropics, such as *Swietenia macrophylla* and *Tectona grandis* (Wadsworth, 1983). On the other hand, in the present research the nitrogen-fixing species of each plantation (*S. microstachyum*, Plantation 1, and *A. guachapele*, Plantation 2) gave the lowest biomass values, a finding that contrasts with the more general good performance of N-fixing species found in a variety of tropical environments. For example, Wang et al. (1991) reported biomass production rates of 9.8 mg/ha per year for *Albizia lebbek*and 11 mg/ha per year for *Leucaena leucocephala* in Puerto Rico. In the present research, the poor performance of *S. microstachyum* was due to a fungal disease, anthracnosis, caused by *Glomerella* spp. (Montagnini et al., 1995). This disease resulted in complete mortality of *S. microstachyum* in pure plots, while 42% of the trees survived in mixed plots at 4 years. The poor performance of *A. guachapele* was due to attacks by root gophers (*Orthogeomys* spp.) (Montagnini et al., 1995). Initially the trees apparently recovered from the damage, but after 4 years their poor performance became apparent. In another plantation in the same experimental setting, the nitrogen-fixing species, *Pithecellobium elegans*, was among the most productive of the species tested, both in pure and in mixed designs (Stanley and Montagnini, 1999).

Mn Mg

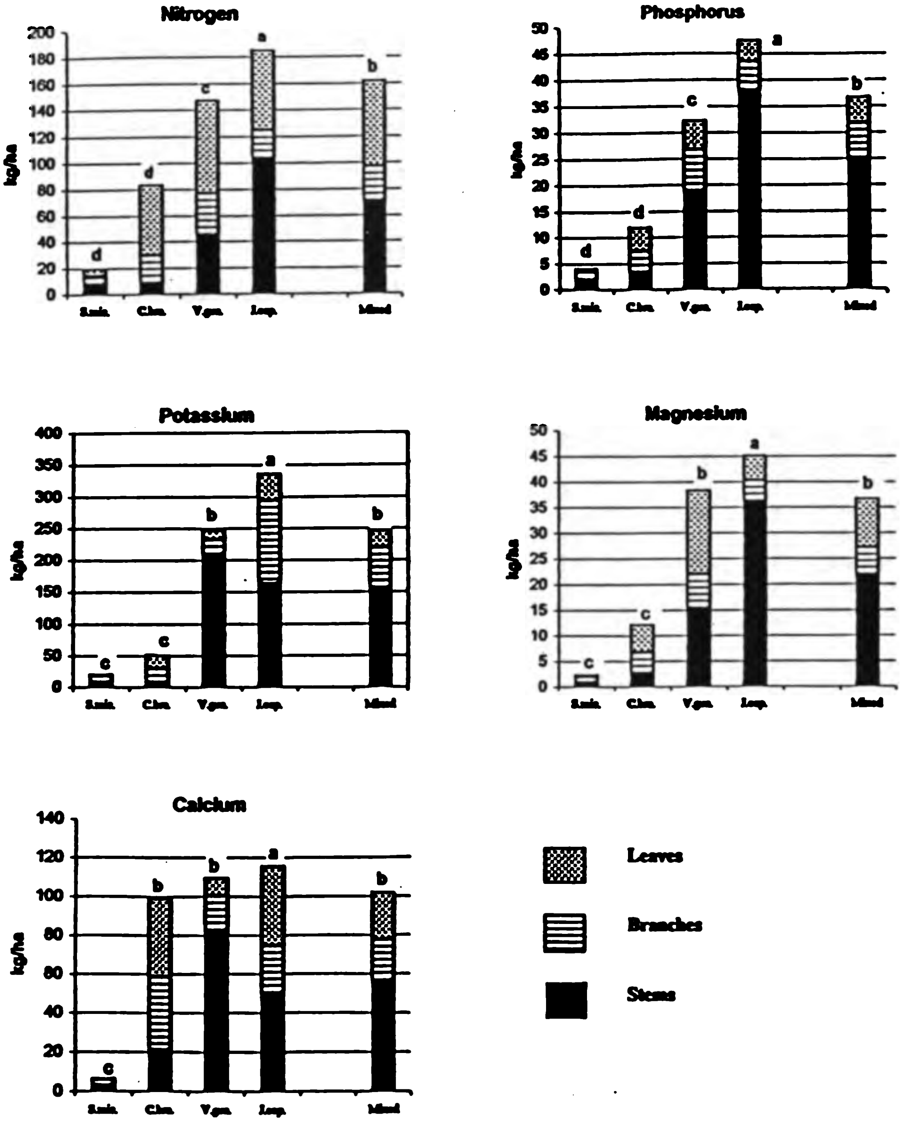

Fig. 1. Total above-ground nutrient content per hectare of *J. copaia*, *V. guatemalensis*, *C. brasiliense*, and *S. microstachyum* grown in pure plantation, and a mixture of the four species. Total nutrient content differs among treatments when bars are topped by different letters ($P < 0.05$).

The values of total above-ground biomass and stem biomass for the two mixed plantations of the present research are within the ranges reported elsewhere for fast-growing, monospecific plantations of commonly used species in the humid tropics. The most successful mixed plantings are stratified mixtures composed of faster-growing, shade-intolerant species above slower-starting tolerants (Smith, 1986). If the trees in the upper canopy are not too dense, they grow more rapidly in diameter than if crowded into the single canopy of a pure plantation (Burkhart and Tham, 1992). In the present research, the dominant species of each plantation grew larger when grown with other species compared to single species plantation. Apparently in the mixtures the dominant species, with less intra-specific competition, can attain larger diameters,

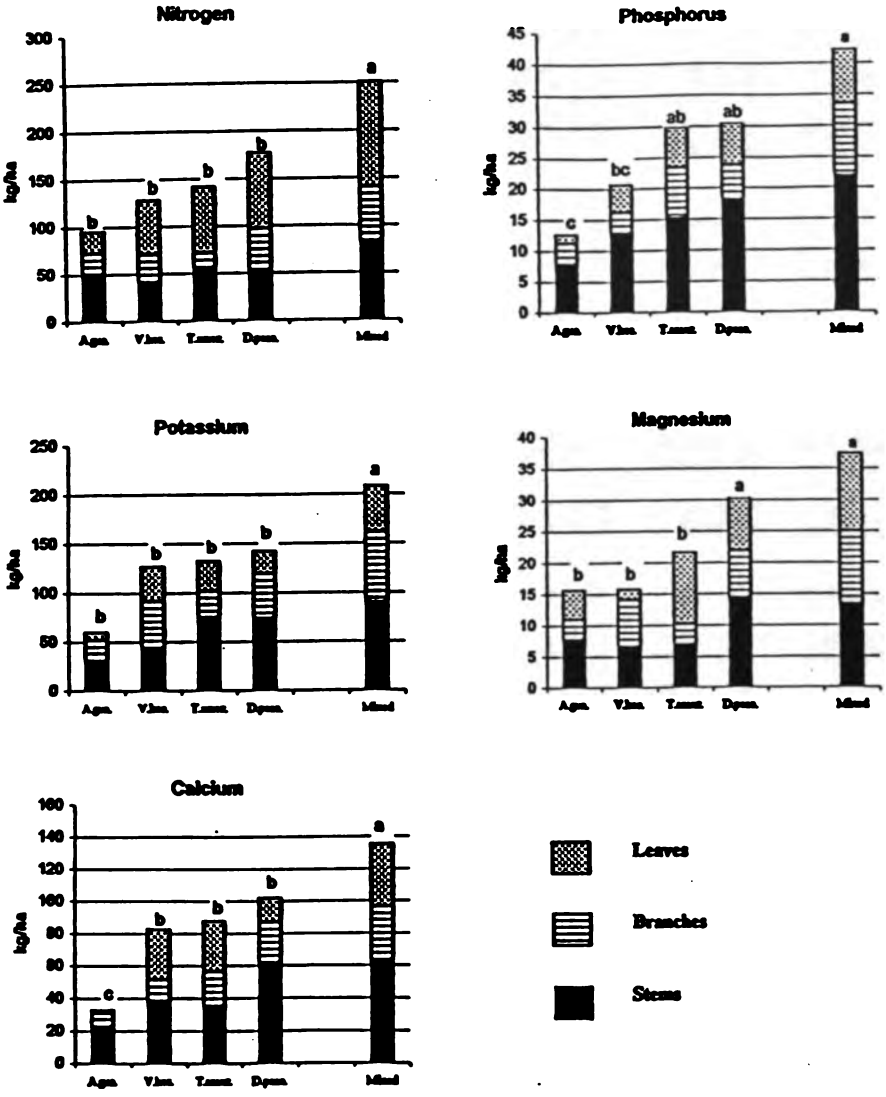

Fig. 2. Total above-ground nutrient content per hectare of *T. amazonia*, *D. panamensis*, *V. koschnyi* and *A. guachapele* grown in pure plantation, and a mixture of the four species. Total nutrient content differs among treatments when bars are topped by different letters ($P < 0.05$).

as reported in earlier research (Montagnini et al., 1995; Montagnini and Porras, 1998; Stanley and Montagnini, 1999). Only one of the eight species tested here was seemingly suppressed by the dominant species and thus grew better in pure plots: *C. brasiliense* (Plantation 1). Except in the case noted, the other species associated with the faster growing dominants apparently shared resources with the dominant species and had higher biomass of plant parts in mixed than in pure plots.

The inclusion of faster and relatively slower growing species in a mixture has the advantage of providing harvestable products at different rotation times, with the relatively slower growing species (e.g., *C. brasiliense, D. panamensis*) producing more valuable wood. For the slower growing species, establishment costs are less in mixed than in pure plots, because the trim/x6

Table 5
Nutrient concentrations, organic matter, and soil pH under indigenous tree species grown in pure stands, mixture of the four species, and natural regeneration stands in Plantation 1. Means, standard errors (SE), and statistical significance[a]. Soils were sampled in June 1996.

Treatment	Depth (cm)	pH			Ca (cmol/l)			Mg (cmol/l)			K (cmol/l)			P (mg/l)			OM (%)			N (%)		
		Mean	SE	Sig.	Mean	SE	Sig.	Mean	SE	Sig.	Mean	SE	Sig.	Mean	SE	Sig.	Mean	SE	Sig.	Mean	SE	Sig.
J. copaia																						
	1–5	4.05	0.10	a	0.94	0.19	a	0.40	0.06	abc	0.16	0.01	a	11.2	1.3	ab	9.73	0.93	a	0.37	0.06	a
	5–15	4.08	0.10	a	0.88	0.06	a	0.32	0.04	a	0.19	0.09	a	8.75	1.61	c	7.27	0.97	a	0.28	0.02	a
	15–30	4.13	0.11	a	0.77	0.06	a	0.30	0.02	a	0.11	0.01	ab	7.98	1.6	c	6.69	1.28	a	0.30	0.03	a
	30–60	4.1	0.15	a	0.80	0.02	a	0.31	0.05	a	0.10	0.02	ab	7.98	1.89	b	6.77	1.35	a	0.24	0.03	a
C. brasiliense																						
	1–5	4.1	0.11	a	0.52	0.10	ab	0.24	0.05	c	0.14	0.02	a	14.4	2.23	a	7.63	0.69	b	0.35	0.01	a
	5–15	3.98	0.08	a	0.44	0.07	b	0.22	0.06	a	0.14	0.02	a	13	1.19	ab	6.05	0.65	a	0.29	0.02	a
	15–30	4.08	0.08	a	0.51	0.11	a	0.23	0.07	a	0.16	0.02	ab	13.9	1.63	ab	5.29	0.94	a	0.29	0.04	a
	30–60	4.05	0.10	a	0.47	0.13	a	0.21	0.08	a	0.14	0.01	ab	13.5	0.86	a	4.76	1.32	a	0.25	0.05	a
S. microstachyum																						
	1–5	4.1	0.11	a	0.69	0.10	ab	0.39	0.04	abc	0.16	0.02	a	13.3	0.35	ab	8.17	0.81	ab	0.35	0.02	a
	5–15	4.08	0.14	a	0.61	0.13	ab	0.32	0.06	a	0.15	0.03	a	11.9	0.66	abc	6.83	1.01	a	0.3	0.02	a
	15–30	4.1	0.15	a	0.60	0.13	a	0.25	0.05	a	0.21	0.05	a	10.6	0.62	bc	5.82	1.37	a	0.26	0.04	a
	30–60	4.1	0.18	a	0.52	0.11	a	0.23	0.06	a	0.20	0.05	a	11.1	1.33	ab	5.32	1.67	a	0.25	0.06	a
V. guatemalensis																						
	1–5	4.18	0.15	a	0.89	0.17	ab	0.65	0.20	a	0.13	0.01	a	9.35	1.74	b	6.65	0.18	b	0.31	0.01	a
	5–15	4.08	0.13	a	0.58	0.09	b	0.35	0.02	a	0.10	0.02	a	8.5	1.09	c	5.85	0.91	a	0.27	0.03	a
	15–30	4.08	0.10	a	0.52	0.10	a	0.26	0.04	a	0.09	0.01	b	8.8	0.77	c	5.15	1.08	a	0.26	0.05	a
	30–60	4.13	1.38	a	0.54	0.14	a	0.23	0.08	a	0.09	0.02	b	7.45	1.46	b	4.28	1.25	a	0.22	0.06	a
Mixture																						
	1–5	4.03	0.08	a	0.61	0.08	b	0.29	0.01	bc	0.15	0.02	a	15.1	1.46	a	7.77	0.33	b	0.32	0.05	a
	5–15	4.03	0.05	a	0.61	0.11	ab	0.26	0.06	a	0.13	0.02	a	14.2	1.38	a	6.81	0.70	a	0.32	0.02	a
	15–30	4.08	0.10	a	0.52	0.06	a	0.23	0.05	a	0.13	0.01	ab	14.3	1.44	a	6.43	1.08	a	0.28	0.03	a
	30–60	4.13	0.13	a	0.58	0.13	a	0.22	0.07	a	0.12	0.02	ab	14	1.36	a	5.64	1.58	a	0.24	0.05	a
Regeneration																						
	1–5	4.18	0.13	a	0.68	0.12	ab	0.61	0.18	ab	0.32	0.17	a	11.9	1.82	ab	7.69	0.58	b	0.36	0.03	a
	5–15	4.13	0.10	a	0.62	0.12	ab	0.34	0.02	a	0.23	0.11	a	10.1	1.28	bc	6.78	0.47	a	0.29	0.01	a
	15–30	4.18	0.16	a	0.53	0.06	a	0.26	0.04	a	0.19	0.08	ab	9.95	0.88	c	5.87	1.06	a	0.25	0.04	a
	30–60	4.13	0.20	a	0.55	0.13	a	0.24	0.08	a	0.15	0.05	ab	10.4	2.35	ab	4.56	1.3	a	0.23	0.06	a

[a] Differences between species for a given parameter and depth are statistically significant ($P < 0.05$) when means are followed by different letters.

trim/x6

Table 6
Nutrient concentrations, organic matter, and pH of soil under four indigenous tree species grown in pure stands, mixture of the four species, and natural regeneration stands in Plantation 2. Mean,standard errors (SE), and statistical significance[a]. Soils were sampled in June 1996

Treatment	Depth (cm)	pH			Ca (cmol/l)			Mg (cmol/l)			K (cmol/l)			P (mg/l)			OM (%)			N (%)		
		Mean	SE	Sig.	Mean	SE	Sig.	Mean	SE	Sig.	Mean	SE	Sig.	Mean	SE	Sig.	Mean	SE	Sig.	Mean	SE	Sig.
A. guachapele																						
	0–5	4.43	0.06	a	1.02	0.51	a	0.33	0.16	a	0.16	0.04	a	12	1.00	a	6	1.33	a	0.33	0.08	a
	5–15	4.43	0.05	a	1.01	0.53	a	0.34	0.17	a	0.17	0.04	a	11.4	0.68	b	6.11	0.92	a	0.29	0.05	a
	15–30	4.40	0.04	a	0.99	0.48	a	0.30	0.15	a	0.16	0.05	a	11.7	0.56	a	5.51	1.32	a	0.30	0.06	a
	30–60	4.35	0.05	a	1.05	0.42	a	0.33	0.14	a	0.17	0.06	a	11.7	0.91	a	5.86	1.2	a	0.32	0.06	a
D. panamensis																						
	0–5	4.40	0.00	a	1.01	0.42	a	0.35	0.14	a	0.19	0.06	a	12.2	1.59	a	5.93	0.36	a	0.32	0.03	a
	5–15	4.35	0.03	a	1.02	0.41	a	0.34	0.13	a	0.18	0.06	a	11.9	0.99	b	5.83	0.17	a	0.32	0.03	a
	15–30	4.30	0.04	a	1.27	0.28	a	0.45	0.07	a	0.18	0.06	a	12.2	1.54	a	6.31	0.84	a	0.36	0.05	a
	30–60	4.30	0.04	a	1.22	0.27	a	0.44	0.07	a	0.18	0.07	a	15	3.66	a	5.81	1.36	a	0.34	0.04	a
T. amazonia																						
	0–5	4.30	0.04	a	1.13	0.31	a	0.36	0.08	a	0.17	0.04	a	11.1	0.52	a	7.41	1.00	a	0.38	0.05	a
	5–15	4.35	0.03	a	1.15	0.30	a	0.38	0.09	a	0.17	0.04	a	11.1	0.73	b	6.9	1.23	a	0.38	0.05	a
	15–30	4.40	0.04	a	1.13	0.37	a	0.37	0.10	a	0.17	0.04	a	11.9	0.38	a	7.11	1.35	a	0.36	0.05	a
	30–60	4.33	0.03	a	1.13	0.33	a	0.38	0.10	a	0.18	0.04	a	12.8	1.26	a	7.15	1.44	a	0.38	0.06	a
V. koschnyi																						
	0–5	4.40	0.07	a	1.55	0.45	a	0.52	0.12	a	0.18	0.05	a	12.8	0.97	a	6.56	1.48	a	0.36	0.08	a
	5–15	4.38	0.09	a	1.54	0.44	a	0.52	0.12	a	0.18	0.05	a	13.5	1.26	ab	7.11	2.02	a	0.35	0.08	a
	15–30	4.30	0.04	a	1.54	0.44	a	0.51	0.12	a	0.18	0.04	a	13.9	1.36	a	7.7	1.42	a	0.38	0.06	a
	30–60	4.30	0.04	a	1.47	0.38	a	0.49	0.10	a	0.18	0.05	a	14.3	2.05	a	7.43	1.11	a	0.38	0.05	a
Mixed																						
	0–5	4.40	0.12	a	0.63	0.14	a	0.24	0.07	a	0.16	0.06	a	13.4	1.29	a	5.26	1.33	a	0.24	0.05	a
	5–15	4.43	0.09	a	0.66	0.13	a	0.23	0.07	a	0.17	0.06	a	15.6	1.32	a	5.52	1.47	a	0.26	0.04	a
	15–30	4.38	0.11	a	1.12	0.44	a	0.52	0.24	a	0.17	0.06	a	13.6	0.56	a	5.08	1.5	a	0.28	0.05	a
	30–60	4.40	0.09	a	1.19	0.50	a	0.41	0.15	a	0.17	0.06	a	14.6	0.93	a	4.62	1.18	a	0.27	0.05	a
Regeneration																						
	0–5	4.35	0.05	a	1.31	0.27	a	0.44	0.07	a	0.18	0.04	a	13.8	1.43	a	6.21	1.14	a	0.33	0.05	a
	5–15	4.40	0.08	a	1.16	0.32	a	0.39	0.10	a	0.15	0.04	a	12.9	1.8	ab	5.4	1.03	a	0.30	0.04	a
	15–30	4.40	0.09	a	0.99	0.32	a	0.34	0.10	a	0.17	0.06	a	10.3	3.48	a	6.15	1.15	a	0.30	0.05	a
	30–60	4.30	0.08	a	1.15	0.45	A	0.38	0.13	a	0.18	0.05	a	11.2	0.91	a	6.11	1.66	a	0.33	0.06	a

[a] Differences between species for a given parameter and depth are statistically significance ($P < 0.05$) when means are followed by different letters.

need for weeding is substantially less in mixed plots (Montagnini et al., 1995). Additionally, because the different species of the mixture have different rotation lengths, the land is in use for a longer period than if planted with just one fast-growing, short-rotation species (such as *J. copaia*). This diminishes incentives for changing to other land uses, keeps a vegetative cover that protects the soil, and serves other environmental purposes as well (Montagnini and Mendelsohn, 1996).

4.2. *Nutrient accumulation in above-ground tree biomass in pure and mixed plantations*

In Plantation 1, high foliar N found in *S. microstachyum*, the N-fixing species of the plantation, coincides with results of previous studies in other plantations at La Selva (Montagnini and Sancho, 1994). The high N concentration in foliage found in *J. copaia*, a tree of the Bignoniaceae family, is a result consistent with earlier studies of leaf litter decomposition and nutrient release from litter at La Selva by Byard et al. (1996). Likewise, high cation concentrations in foliage and stemwood of *V. guatemalensis* coincide with earlier findings by Montagnini and Sancho (1994). In Plantation 2, the highest foliar N was found in the N-fixing component of the plantation, *A. guachapele*, and the second highest was found in another leguminous species, *D. panamensis*. No evidence of nodulation was found in this or in earlier research involving *D. panamensis* (Montagnini and Sancho, 1994; Kershnar and Montagnini, 1998), and no reports exist of its nodulation in other environments. However, symbiotic N fixation has been shown for other non-nodulating legumes, and recent evidence of its occurrence in *D. panamensis* has been found (Bryan et al., 1996).

The higher N concentration of leaves of *T. amazonia* when grown in mixed plantation, in comparison with leaves of trees of this species in the pure plots, could be attributed to additional uptake of N released by its N-fixing neighbors (*A. guachapele, D. panamensis*) (Kershnar and Montagnini, 1998). A similar trend was found in *V. koschnyi*, but the smaller difference in N concentration between leaves of mixed and pure stands was not statistically significant.

At the time of plantation harvest, the amount of nutrients represented by foliage or branches which may be left behind varies between nutrients, species, and sites. The results of the present research are from young plantations; crowns form a high proportion of total biomass in young stands, but their importance decreases as the stand ages (Fölster and Khanna, 1997). However, these early results can point out to potential effects of stem harvest on site nutrients by each species. For example, stems of *J. copaia* and *V. guatemalensis* represented 88 and 70% of total above-ground tree biomass, respectively. For *J. copaia*, stem harvest would remove about 54% of total above-ground tree N, but about 80% of P, K, Ca and Mg. For *V. guatemalensis*, stem harvest would remove less than 30% of N but from 50 to 60% of total above-ground tree Ca, K, Mg and P. On the other hand, branches and foliage summed together represented about 25–35% of total tree biomass (Table 2), but they generally represented about 50% of total tree nutrients (Figs. 1 and 2). For broad leaved species, the proportion of nutrients in branches and foliage may range from 15 to 46% of total tree nutrients (Fölster and Khanna, 1997). Leaving branches and leaves on the site, rather than harvesting the whole tree, can generally reduce nutrient losses by one-half, a result consistent with earlier findings on other species at La Selva (Stanley and Montagnini, 1999).

4.3. *Influence of nutrient accumulation in above-ground tree biomass on soil nutrients*

five (Spell out 5)

In Plantation 1, 5 years after planting, the pure plots of the two fastest growing species, *V. guatemalensis* and *J. copaia*, had the lowest values of soil P concentration. This result could be attributed to high accumulation of P in above-ground biomass of these two species. This trend is consistent with results from the previous years (Montagnini and Porras, 1998). In addition, this result was more marked in the present research: in 1995, significant differences for P had only occurred in the top soil (0–5 cm depth) (Montagnini and Porras, 1998), while in 1996 the differences were detected at all depths studied (Table 5).

(delete comma)

Although, there were no statistically significant differences in other soil nutrients among treatments, some differences were found with respect to results of the previous years. For example, under *V. guatemalensis* values of soil K and Ca in 1996 were about half those found in 1995 (Montagnini and Porras, 1998).

These results are again consistent with findings on nutrient accumulation in above-ground biomass by the tree species: *V. guatemalensis* had the greatest accumulation of K and Ca of the four species of this plantation.

In Plantation 2, there had been changes with respect to the levels measured the previous years as well (Montagnini and Porras, 1998). For example, in 1996 soil K concentrations had decreased in all treatments with respect to 1995, while soil Mg had decreased in all treatments except for *V. koschnyi*. However, in other cases, beneficial effects on some soil nutrients were noted: for example, about 30% increases in soil Ca were found under *T. amazonia* and *V. koschnyi* with respect to the previous year (Montagnini and Porras, 1998).

Knowledge of the nutrient cycling characteristics of the species can also help in choosing management strategies to conserve site nutrients. For example, *J. copaia* and *V. guatemalensis* had the highest annual litterfall of the four species of Plantation 1, and they also had the highest accumulation of litter on the ground, therefore these two species can provide good soil protection (Byard et al., 1996). The mixed designs provided intermediate to fast decomposition rates, releasing nutrients to the soil and allowing a litter layer to protect the soil (Byard et al., 1996).

Likewise, in Plantation 2, both *T. amazonia* and *V. koschnyi* had the highest Ca content in foliage, and they also had high rates of annual litterfall (*T. amazonia*: 853 g/m^2, *V. koschnyi*: 620 g/m^2) (Kershnar and Montagnini, 1998). *T. amazonia* had the fastest litter decomposition of the species studied, while *V. koschnyi* decomposed the slowest (Kershnar and Montagnini, 1998). *T. amazonia* can have beneficial effects on soil nutrients, as suggested by results of the present research; while *V. koschnyi* can contribute to better soil protection. Again, the mixed plots exhibited the most consistent litterfall and plantation-floor litter throughout the year, and mixed litter had an average decomposition rate and performed well as a mulch (Kershnar and Montagnini, 1998).

Apparently some decreases in soil nutrients with time were detected for K and P, the two nutrients more likely to be depleted from plantation soils (Wadsworth, 1983; Bowen and Nambiar, 1984). These decreases were most apparent under the fastest growing species with the highest nutrient accumulation in above-ground biomass, such as *V. guatemalensis* and *J. copaia*. This suggests that rapid uptake and accumulation of nutrients in tree biomass served as the main mechanism responsible for this decrease. Results of continued sampling will be needed to assess the long term effects of plantation treatments on soil chemistry, especially near the end of the rotation (estimated at 12–15 years, depending on the species).

On the other hand, beneficial effects on soil nutrients were noted under pure stands of some of the studied species, therefore nutrient cycling characteristics must also be taken into account when assessing the potential impacts of plantation species on site nutrients. The mixed plots showed intermediate values for the nutrients examined, and even improved soil conditions, as for P in Plantation 1. This suggests that in mixed conditions it may take longer to deplete soil nutrients than in monospecific stands of fast-growing species.

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