Impacts of Plantations with Native Trees on Soils at La Selva Biological Station, Costa Rica

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Report

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Impacts of Native Trees on Tropical Soils: A Study in the Atlantic Lowlands of Costa Rica

The influence of trees on soil properties should be a determining factor in the choice of species for tree-crop combinations or for tree plantations in the humid tropics. However, information of this kind is scarce, particularly for native species. Soil fertility parameters were compared under six tree species in a 2.5-year-old experimental plantation, under grass, and in a 20-year-old secondary forest. The site is located at the La Selva Biological Station of the Organization for Tropical Studies, in the Atlantic humid lowlands of Costa Rica, Central America. Soil extractable Ca, Mg, K, P, Fe, Mn, Cu and Zn, the pH, exchangeable acidity, organic matter and total N were measured under *Stryphnodendron excelsum, Dalbergia tucurensis, Dipteryx panamensis, Vochysia hondurensis, Vochysia ferruginea* and *Tabebuia rosea*. All species are native and of economic value for the timber industry. Higher soil N and levels of organic matter were found in the tree plantation than under grass, with values close to those in the secondary forest. Within the tree plantation, the highest values for soil organic matter, total N, Ca, and P were found under *V. ferruginea*. There was an apparent trend of higher soil nitrate content under *S. excelsum* and *D. tucurensis*, both leguminous nitrogen-fixing species. The results will be used to make recommendations on species for plantations or for agrogorestry, emphasizing the potential positive effects on soil propertles for recovery of degraded pastures in the region.

INTRODUCTION

There is an increasing need in the lowland humid tropics for promoting land-use systems which can contribute to supplying the demands for timber, fuelwood, and other tree products without continuing the well-documented patterns of deforestation and land-resource degradation (1). Agroforestry systems and tree plantations can contribute to these goals when properly implemented (2). More information is needed on the performance of native tree species grown in plantations or in agroforestry systems; additionally, information on the impacts of trees on soil fertility should be a determining factor on species choice for these systems (2).

The most important beneficial effects of trees on soils can include improvement of soil structure and increases in nutrient availability (3–5). For example, higher pH, Ca, Mg, and N have been reported under plantations of *Gmelina arborea* than under pine or pastures in Brazil and in Nigeria (5). Two to threefold increases in Ca, Mg and K have been found in plantations of *Cordia trichotoma* and *Caesalpina equinata*, compared to levels in native forest, in southern Bahia (Brazil) (6). Symbiotic N fixation by trees can result in increased soil N availability (7–10).

In the Atlantic lowlands of Costa Rica, Central America, the Costa Rican Forest Service, Dirección General Forestal (DGF) is conducting experiments on the growth performance of tree species for plantation. Among the species presently recommended by DGF to farmers (*Gmelina arborea, Pinus caribaea, Eucalyptus deglupta*, and *Cordia alliodora*), only one (*C. alliodora*) is native. In 1985, DGF established a plantation of 13 native tree species at the La Selva Biological Station of the Organization for Tropical Studies (OTS). Measurements after three years showed that, among these species, at least four: *Stryphnodendron excelsum, Vochysia hondurensis, Vochysia ferruginea*, and *Hieronyma oblonga*, exhibited growth rates similar to or above those reported for the species which are recommended for the region after three years (11). This suggests the potential of many native trees for commercial purposes.

In 1988, we initiated an independent study on the impacts of six species on soil fertility and mechanisms of nutrient recycling (12). Two of the species, *Dalbergia tucurensis* Donn. Smith ("granadillo") and *Stryphnodendron excelsum* Harms. ("vainillo") were leguminous, nitrogen-fixing trees. The presence of root nodules was verified before choosing the species for comparison (no inoculation was done). Among the other four, *Vochysia ferruginea* Mart ("botarrama") and *V. hondurensis* Sprague ("mayo") (Vochysiaceae) have been reported to be aluminum accumulators (over 10 000 mg · kg^{-1} in foliar tissue) (13). This characteristic has been associated with better growth compared to other species for which acid soils cause aluminum toxicity problems (14). *Tabebuia rosea* (Vertol.) DC ("roble sabana", Bignoniaceae) and *Dipteryx panamensis* (Pittier) Record and Mell, ("almendro") (Leguminosae, but not an N fixer) were chosen because of their wide distribution in the Latin American tropics (15).

Here we report results of a comparison of soil fertility under the species of the plantation (when it was 2.5 years old), under grass, and in an adjacent 20-year-old secondary forest, emphasizing the effects of the species on soil nutrient conservation, and the possible mechanisms involved in the observed responses. The results will aid understanding of the environmental impacts of native tree species of economic value for forestry and agroforestry. Results may also be applicable to other humid tropical areas where soils are similar.

STUDY SITE

The plantation was established in December 1985 on an abandoned pasture at the OTS La Selva Biological Station (10°26'N, 86°59'W, 50 meters mean elevation, 24°C mean annual temperature, 4000 mm mean annual rainfall, with maximum in July and minimum in March). The soils are Fluventic Dystropepts, derived from alluvially deposited volcanic materials; they are deep, well drained, stone-free, with low or medium organic-matter content, moderately heavy texture, and generally acid and unfertile (16). The area had been cut in the 1950s and grazed until 1984. The dominant species in the pastures were grasses (*Olyra latifolia, Melinis minitiflora*), ferns (*Pteridium* sp.), and brushes (*Psidium guajava* and *Piper culebranum*). The dominant species in the 20-year-old adjacent forest were *Pentachlethra macroloba*, a mimosoid, N-fixing leguminous tree dominant in the primary forest at La Selva; *Piper culebranum*, and species of the Melastomataceae family; with ferns (*Pteridium* spp.) and tree seedlings in the understory. The site was cleaned manually before planting. The trees were planted in a randomized block design with five replicates. Each plot (14 m · 14 m) had seven trees each, with two meters distance between trees. Five 14 m · 14 m plots were also established in an adjacent open area with grass and in an adjacent secondary forest. During the first year of plantation establishment, weeds were cut manually four times. Thereafter, weeding was done mechanically until canopy closure made it no longer necessary. The grass areas were weeded simultaneously to keep them free of trees and were treated in a comparable manner.

Table 1. Ca, Mg and K content, pH, exchangeable acidity, sum of bases, effective cation exchange capacity (CEC), base and acidity saturation, in soils under the six native tree species in plantation, grass and secondary forest; April 1988[1].

Site	Depth (cm)	Ca (cmol · kg^{-1})	Mg	K	pH	Acidity (cmol · kg^{-1})	Sum of bases	CEC	Saturation (%) bases	acidity
S. excelsum	0–15	0.45a	0.63ab	0.27a	5.4ab	1.66ab	1.34a	3.00a	45.5a	54.5bc
	15–30	0.33a	0.35a	0.19a	5.4a	1.54a	0.87a	2.41a	37.2a	62.7b
	30–60	0.26a	0.22a	0.17a	5.6a	1.88a	0.65a	2.53a	34.2a	65.7a
D. tucurensis	0–15	0.44a	0.41ab	0.22a	5.4ab	1.46ab	1.07a	2.53a	41.6a	58.4bc
	15–30	0.32a	0.24a	0.15a	5.4a	1.54a	0.71a	2.25a	31.6a	68.4bc
	30–60	0.24a	0.15a	0.11a	5.6a	1.42a	0.49a	1.91a	26.8a	73.2a
V. ferruginea	0–15	0.73a	0.61ab	0.22a	5.4ab	1.20ab	1.56a	2.76a	52.8a	47.2bc
	15–30	0.66a	0.39a	0.21a	5.6a	1.12a	1.26a	2.38a	47.3a	52.7bc
	30–60	0.42a	0.28a	0.17a	5.6a	1.06a	0.86a	1.92a	42.5a	57.5a
V. hondurensis	0–15	0.25a	0.37ab	0.11a	5.3b	1.86a	0.73a	2.59a	28.2bc	71.8a
	15–30	0.19a	0.18a	0.09a	5.4a	1.58a	0.46a	2.04a	22.5bc	77.5a
	30–60	0.17a	0.32a	0.08a	5.5a	1.32a	0.57a	1.89a	27.5a	72.5a
T. rosea	0–15	0.42a	0.50ab	0.15a	5.5a	1.28b	1.06a	2.35a	44.1a	55.9b
	15–30	0.28a	0.26a	0.12a	5.6a	1.12a	0.66a	1.78a	35.5a	64.5b
	30–60	0.28a	0.24a	0.13a	5.7a	0.98a	0.65a	1.63a	38.8a	61.2a
D. panamensis	0–15	0.52a	0.74ab	0.38a	5.5a	1.18b	1.64a	2.82a	53.4a	46.5bc
	15–30	0.36a	0.45a	0.29a	5.5a	1.06a	1.09a	2.19a	46.2a	53.8bc
	30–60	0.28a	0.28a	0.19a	5.6a	1.08a	0.75a	1.83a	38.9a	60.1a
Grass	0–15	0.32a	0.27b	0.19a	5.3b	1.40ab	0.77a	2.17a	34.8ab	65.2ab
	15–30	0.31a	0.28a	0.17a	5.4a	1.32a	0.76a	2.08a	35.7ab	64.2ab
	30–60	0.23a	0.15a	0.10a	5.5a	1.26a	0.48a	1.74a	27.1a	72.9a
Secon. forest	0–15	0.68a	0.55b	0.17a	5.3b	1.54ab	1.39a	2.93a	46.9a	53.1bc
	15–30	0.60a	0.42a	0.13a	5.4a	1.60a	1.15a	2.75a	42.2a	57.7bc
	30–60	0.42a	0.28a	0.18a	5.5a	1.34a	0.87a	2.21a	39.5a	60.5a

[1] In the present and following tables differences between sites for a given depth and parameter are statistically significant when means are followed by different letters.

Figure 1. Effects of native tree species in plantation, grass and secondary forest on soil organic matter content.

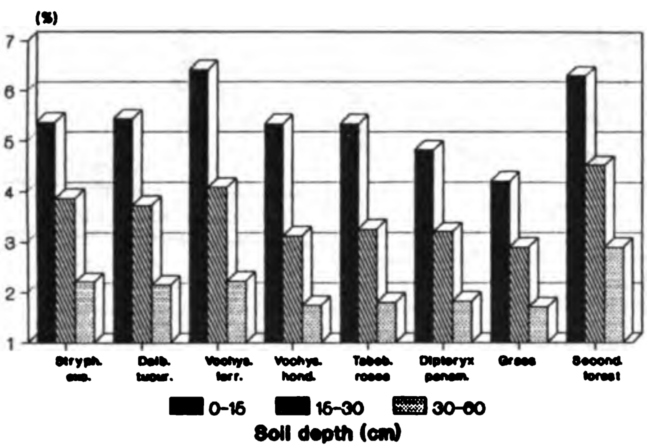
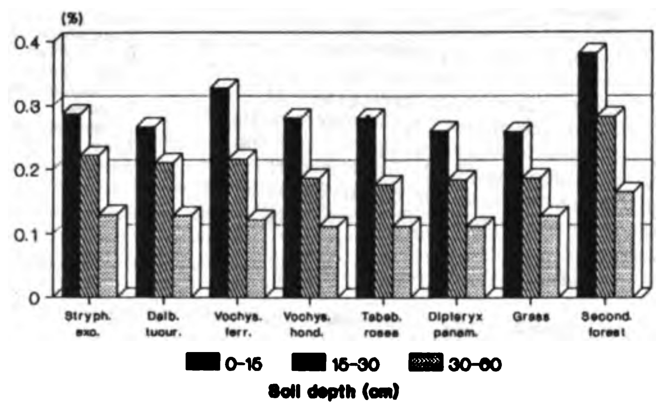


Figure 2. Effects of native tree species in plantation, grass and secondary forest on soil total nitrogen content.



MATERIALS AND METHODS

For the general chemical characteristics of soils, sampling was done with a "Dutch type" ("Edelman") auger, at 0–15, 15–30, and 30–60 cm depth, in April (dry season) and in August (rainy season) of 1988. Chemical analyses were done at the Soils Laboratory of the College at Agriculture, University of Costa Rica, following standard methods currently used by soil testing laboratories in the country (17). The pH was measured in a 1:2.5 mixture of soil: deionized water using a Corning 7 pH meter. Ca and Mg were extracted with a 1 N KCl solution, while P, K and micronutrients were extracted with a modified Olsen solution (17). Cations were measured using a Perkin Elmer 2380 Atomic Absorption Spectrophotometer. Effective cation-exchange capacity was calculated as the sum of Ca, Mg and K, plus the exchange acidity as measured by titration of 1 N KCl soil extracts with 0.01 N NaOH. P was measured colorimetrically after reaction with acid $(NH_4)_2MoO_4$ and $SnCl_2$, using a Perkin Elmer-Coleman 295 Spectrophotometer. Organic matter was measured with the Walkley-Black technique (18) and total N was measured using a semi-micro-Kjeldahl technique (19). For N mineralization and nitrification studies soils were sampled at 0–15 cm with a 2.5 cm diameter soil corer using the same plots as for soil general chemistry, starting in May 1989. NO_3-N and NH_4-N were extracted on field moist soils with 2 N KCl, and measured using a Lachat Flow Injection Analyzer (10500 N Port Wash Rd, Mequon, WI, USA). One subset of samples was extracted immediately after sampling while another subset was incubated in plastic cups in the laboratory (20) for seven days.

The difference between final (after incubation) and initial NO_3-N+NH_4-N concentrations gave the net nitrification or net N mineralization potential rates, which are a measurement of soil N availability (20).

RESULTS AND DISCUSSION

Soil organic matter and total N content were the highest in the secondary forest, followed by the tree plantation, while the grass had the lowest values (Table 1, Figs 1 and 2). Apparently, in just 2.5 years there had been an increase in soil organic matter from a mean of 4.83% in grass to 5.31–6.60% in the plantation, in the upper 15 cm of the soil. The highest mean value in the plantation, found under *Vochysia ferruginea*, was close to the mean in the secondary forest (7.58%). A similar trend was found at 15–30 and at 30–60 cm (Fig. 1). Total N in the tree plantation was 0.26–0.32% (Table 1, Fig. 2), again values higher than in grass (0.22%), with the highest content under *V. ferruginea*, close to the mean found in the forest (0.33%).

Soil NO_3-N concentrations at 0–15 cm depth (Table 2) were higher in grass, possibly due to the presence of leguminous herbs which were invading the area. Within the plantation, NO_3-N was higher under *S. excelsum*, with values similar to those under forest, and there was a trend of higher concentration under *D. tucurensis*. There were no statistically significant differences in NH_4-N or in total N mineralization potential rates (Table 2). The highest net nitrification was under *S. excelsum* followed by grass, forest and *D. tucurensis*, in that order. Apparently, there was a trend of higher NO_3-N production under N fixing species in the plantation, although possibly rates of N fixation in the young plantation were still too low to result in significant changes in soil N availability and total N content.

P concentrations were higher in the plantation than in grass, but they were lower in the forest (Table 1). This is probably due to immobilization of P in plant biomass and in soil organic matter in the forest. Cu concentrations exhibited a similar trend (higher in the tree plantation, lower in grass and forest) (Table 1). The pattern for Zn, Mn and Fe was similar to that of Ca and Mg (Tables 1 and 3).

Soil Ca and Mg content were higher in the plantation than in grass, with values close to those in the forest (Table 3). Within the tree plantation, there were no significant differences among species in soil cation content (Table 3). However, there was a tendency for higher Ca under *D. panamensis* and *V. ferruginea*, higher Mg under *S. excelsum* and *D. tucurensis*, *D. panamensis* and *V. ferruginea*. Based on the cation levels determined by the Ministry of Agriculture of Costa Rica for soil fertility assessments (21) these higher values were close to those acceptable for agricultural crops; under the species mentioned above, soil Mg and K were at or above the critical levels for agriculture, representing an improvement over the grass in only 2.5 years. The base saturation was equal or higher in the plantation (6.1–9.9%) than in the forest, and higher than in the grass, while the reverse was true for pH and the acidity saturation (Table 3).

Results of the measurements done in August 1988 showed similar trends of differences among sites (12), but the soil base content was lower. This was accompanied by higher soil exchangeable acidity (Fig. 3), possibly resulting from leaching of bases during the time of peak precipitation (457 mm in August, in comparison with only 43.6 mm in April 1988, data from La Selva weather station).

A close relation was found between organic matter content and the sum of bases (Fig. 4), showing that organic matter was responsible for much of the cation retention capacity. Hence, poor management practices, such as repeated burning, lack of good soil cover, overgrazing and compaction, which all tend to decrease organic matter content (22), could lower significantly the fertility of these soils, even possibly reaching a point of very difficult recovery. In contrast, practices such as tree planting with species that tend to increase organic-matter content, such as the species in this project, would tend to increase and maintain soil fertility. For example, as shown in Figure 4, a 1–2% increase in soil organic matter in the range of 4–6% would result in a more than double increase in base content, reaching values in the range recommended for agriculture (21).

The results shown above suggest a potential ameliorating effect of these native tree species on soil fertility, especially with respect to organic matter and base content. Results of similar measurements done in 1989 showed trends similar to those found in 1988 (23). It is important to empasize that these effects were apparently occurring at an early stage, during the first years of plantation establishment.

Table 2. Soil nitrate and ammonium concentrations at the time of sampling, net nitrification and net N-mineralization potential rates (0–15 cm depth, May 1989).

Site	NO_3-N ($mg \cdot kg^{-1}$)	NH_4-N ($mg \cdot kg^{-1}$)	Nitrification (mg NO_3-N $kg^{-1} \cdot d^{-1}$)	N mineralization (mg NO_3-N + NH_4-N $kg^{-1} \cdot d^{-1}$)
S. excelsum	2.52^{bc}	7.30^{a}	4.75^{a}	5.01^{a}
D. tucurensis	1.99^{c}	6.83^{a}	2.96^{bc}	2.96^{a}
V. ferruginea	0.81^{c}	7.05^{a}	0.88^{d}	0.49^{a}
V. hondurensis	0.76^{c}	4.36^{a}	1.24^{d}	0.60^{a}
T. rosea	0.34^{d}	6.34^{a}	1.46^{cd}	1.96^{a}
D. panamensis	0.53^{d}	5.84^{a}	1.26^{d}	0.53^{a}
Grass	5.62^{a}	7.77^{a}	3.80^{ab}	4.00^{a}
Forest	2.82^{b}	6.73^{a}	3.49^{ab}	2.79^{a}

Table 3. Organic matter, total N, C/N, P and micronutrients in soils sampled in April 1988.

Site	Depth (cm)	OM (%)	N (%)	C/N	P ($mg \cdot kg^{-1}$)	Cu ($mg \cdot kg^{-1}$)	Zn ($mg \cdot kg^{-1}$)	Mn ($mg \cdot kg^{-1}$)	Fe ($mg \cdot kg^{-1}$)
S. excelsum	0–15	6.04ab	0.288b	12.2a	5.58a	18.6a	1.90a	85.8a	344b
	15–30	4.52b	0.234b	11.2a	5.70a	16.6a	1.64a	97.2a	256b
	30–60	2.54a	0.142a	10.4a	5.54a	9.2a	2.06a	67.8a	126b
D. tucurensis	0–15	5.47ab	0.292ab	10.9a	5.48a	20.0a	1.92a	104a	315b
	15–30	4.06b	0.214b	11.1a	4.60a	36.0a	1.50a	88.4a	218b
	30–60	2.70a	0.132a	11.9a	4.24a	15.4a	1.72a	77.6a	182b
V. ferruginea	0–15	6.60ab	0.318b	12.1a	7.10a	22.2a	2.76a	105a	331b
	15–30	4.60b	0.218b	11.9a	5.30a	20.4a	3.14a	96.4a	218b
	30–60	3.34a	0.156a	12.6a	4.66a	20.6a	2.42a	91.0a	152b
V. hondurensis	0–15	5.46ab	0.288ab	11.0a	5.16a	18.2a	2.36a	115a	323b
	15–30	3.87b	0.204b	11.0a	4.60a	17.6a	1.90a	93.2a	218b
	30–60	2.70a	0.142a	11.0a	4.48a	13.2a	1.78a	79.4a	177b
T. rosea	0–15	5.63ab	0.288ab	11.4a	5.10a	19.8a	1.60a	89.0a	277b
	15–30	3.92b	0.194b	11.6a	4.64a	18.2a	1.44a	81.2a	165b
	30–60	3.00a	0.164a	10.7a	4.66a	18.0a	1.56a	78.2a	138b
D. panamensis	0–15	5.31ab	0.260ab	11.8a	5.34a	20.0a	1.80a	114a	333b
	15–30	4.42b	0.208b	12.4a	5.14a	18.0a	1.60a	96.0a	200b
	30–60	2.96a	0.146a	11.6a	5.58a	20.8a	2.18a	89.4a	158b
Grass	0–15	4.83bc	0.224b	12.8a	4.90a	15.6a	1.40a	96.8a	297b
	15–30	4.03b	0.176b	14.0a	4.44a	14.2a	1.48a	110a	226b
	30–60	2.73a	0.138b	11.8a	4.24a	15.0a	2.04a	82.4a	138b
Secon. forest	0–15	7.58a	0.328a	13.6a	3.64b	16.2a	2.26a	113a	664a
	15–30	6.40a	0.278a	13.4a	3.34b	15.2a	2.24a	101a	461a
	30–60	3.29a	0.170a	11.2a	3.60a	11.2a	2.32a	91.8a	300a

Figure 3. Changes in the sum of bases and extractable acidity with time of sampling (April and August 1988).

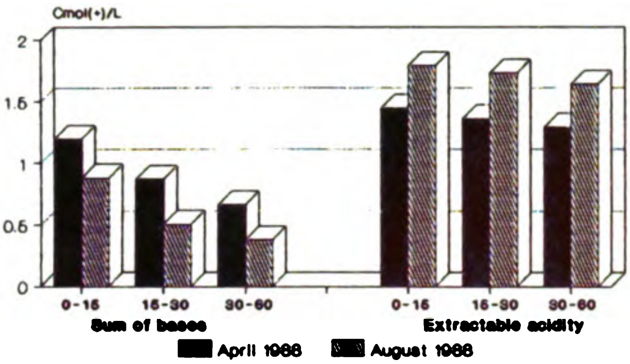
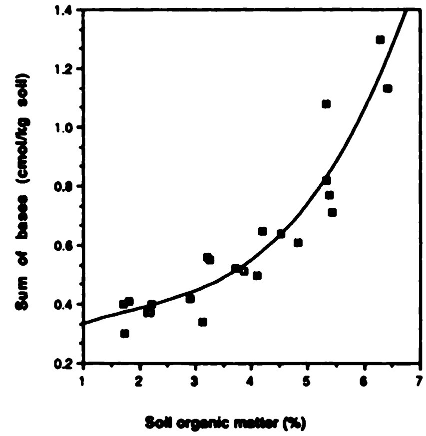


Figure 4. Relation between soil organic matter and base content, soils sampled in August 1988.



Vochysia hondurensis Sprague ("mayo") (Vochysiaceae), after 3.5 years. Photo: F. Montagnini.

Forest floor under *Vochysia ferruginea* Mart.; note abundance of litter and lack of understory growth. Photo: F. Montagnini.

These early effects are certainly a great advantage when there is pressure to produce timber or fuelwood in the short term and to improve soil fertility in degraded areas. This relatively early positive impact on soil fertility will greatly facilitate the demonstration of the potential benefits of plantations or tree-crop combinations using these species.

To help in making this kind of recommendation to farmers, it is necessary to understand the potential mechanisms responsible for such responses. For example, preliminary results of measurements of rates of litter fall suggest that higher organic-matter content in soils under *V. ferruginea* could be related to high amounts of leaf litter fall under this species. *V. ferruginea* is a pioneer species in abandoned fields, forming uniform, even-aged stands (23); it is self-pruning and its wood is used for plywood and construction. Apparently, this species has numerous advantages as a fast-growing tree with additional positive effects on soil nutrients.

We expect that the results of our studies will be disseminated to farmers of the region through the action of the local institutions; for example, through collaboration with DGF, which maintains its interest in the project and is already promoting the plantation of native trees among local farmers. We are continuing long-term measurements of soil fertility to assess the true impacts of the tree species on soil amelioration. To gain a better understanding of processes responsible for differences among species we are presently measuring root density, whole tree biomass and tissue chemistry, leaf litter fall and litter decomposition, and soil N availability. Understanding these mechanisms may help us to anticipate the results of using these species in other areas with similar soils.

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Ecological Restoration of Degraded Tropical Pastures

Experiences with Native Trees in the Humid Lowlands of Costa Rica

AGROFORESTRY SYSTEMS and tree plantations can contribute to the restoration of tropical soils that have been abandoned after extensive use for agriculture or cattle grazing.[2] In designing productive, tree-based land-use systems, exotic species are often preferred because their silviculture and site requirements are better known. However, native species of economic value can be more appropriate than exotics because: indigenous species are more adapted to local environmental conditions; seeds and other propagules are locally available; and farmers are familiar with the species and their uses.

Additionally, native species can be more productive, especially on nutrient-poor soils of abandoned pastures. For example, in an experimental plantation at La Selva Biological Station of the Organization for Tropical Studies (OTS), in the Atlantic lowlands of Costa Rica, Central America, four native species — *Stryphnodendron excelsum (vainillo), Vochysia hondurensis (mayo), Vochysia ferruginea (botarrama),* and *Hyeronima oblonga (pilón)* — exhibited similar or greater growth than the exotic species commonly recommended for the region — *Gmelina arborea, Pinus caribaea,* and *Eucalyptus deglupta.*[1]

Some of these native species can contribute to restore soil fertility by building up organic matter and increasing the soil's capacity to retain nutrients. Results of our studies of soil fertility and nutrient cycling at the same site showed that soil organic matter and nitrogen were higher in the native tree plantation than in grass, with values close to those of secondary forest.[3,4] Apparently, in just 2.5 years soil organic matter in the upper 15 cm had increased from a mean of 4.83% in grass to as much as 5.31 to 6.60% in the plantation. The highest mean value in the plantation (found under *Vochysia ferruginea*), was close to the mean in the secondary forest (7.58%); a similar trend was found at 15 to 30 and at 30 to 60 cm. Soil total nitrogen in the tree plantation was 0.26 to 0.32%; again, values higher than in grass (0.22%), with the highest under *Vochysia ferruginea*, close to the mean in the forest (0.33%). There was a strong, positive correlation between soil organic matter and bases (calcium, magnesium, and potassium). We also found an apparent trend of higher soil nitrate and increased soil nitrogen mineralization under two leguminous trees—*Stryphnodendron excelsum* and *Dalbergia tucurensis (granadillo)*—indicating that the availability of soil nitrogen may be enhanced, with

Figure 3. Stryphnodendron excelsum *Harms*. (vainillo) (*Leguminosae*), *3.5 years old, experimental plantation at La Selva Biological Station.* FLORENCIA MONTAGNINI

potential benefits to associated trees or crops.

These effects were occurring at an early stage, during the first two to four years of plantation establishment. The early effects are certainly a great advantage when timber or fuelwood must be produced in the short term and soil fertility in degraded areas must be improved. These relatively early positive effects on soil fertility will greatly facilitate the demonstration of potential benefits of plantations or tree–crop combinations using these species.

We also examined mechanisms involved in soil changes. Litter-fall was higher under *Vochysia ferruginea*, *Vochysia hondurensis*, and *Stryphnodendron excelsum*, the species that most affected soils. In a leaf-litter decomposition study, *Vochysia ferruginea* showed the slowest rate of weight loss. When leaves of *Vochysia ferruginea*, *Vochysia hondurensis*, *Stryphnodendron excelsum*, and *Hyeronima oblonga* were mixed with soil as mulches for corn as a test crop, the initial growth of corn was better with *S. excelsum* and *H. oblonga*.[5] These results give clues to the best uses of each species: for example, *V. ferruginea*, with its high litter production and slow decomposition, may serve best to protect soils against erosion and build up organic matter, while *S. excelsum* and *H. oblonga* may be better for combinations with annual crops.

We are continuing to measure soil fertility to assess the long-term effects of tree species on soil amelioration. We are also starting more detailed studies with the most promising species of this project and with more native species in the region, designing productive tree-based land-use systems such as combinations of mixed tree plantations and agroforestry. Our first mixed tree plantation, combining four species with different ecological requirements and capacities to restore soil fertility, was on the ground in July 1991. We plan two more mixed plantations with four species each.

We expect the results of our studies to be disseminated to farmers of the region through the local institutions; for example, through collaboration with the local Forest Service, Dirección General Forestal, which maintains interest in the project and is already promoting the plantation of native trees among local farmers.

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Weaverbirds

Egg-color Variability and Conspecific Nest Parasitism

WEAVERBIRDS (sub-family Ploceinae) differ from most birds. Within a species, their egg color varies dramatically from nest to nest. Whereas most birds' eggs look very much like every other egg of that species, in many weaverbird species, some nests contain heavily speckled blue eggs, others contain lightly speckled tan eggs, still others contain immaculate dark brown eggs. For three seasons, beginning in 1986, I traveled to Lake Baringo, Kenya, to study one of these weavers, the northern masked weaver (*Ploceus taeniopterus*), to determine the causes and consequences of this variability.

The observation that eggs within a weaverbird nest typically look alike suggests that each female produces

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

Florencia Montagnini / Freddy Sancho***

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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desde el punto de vista económico, es decir, que provean productos útiles a los agricultores, o tengan buen valor comercial, y que, al mismo tiempo, produzcan impactos favorables sobre los suelos.

Los efectos beneficiosos de los árboles sobre las características físicas y químicas de los suelos pueden incluír: 1) mejoramiento de la estructura del suelo; 2) protección contra la erosión; 3) aumento de la conservación de nutrientes del suelo; y 4) aumento en la disponibilidad de nutrientes (Fassbender 1984, Nair 1984). Los impactos de las especies de árboles sobre los suelos varían dependiendo de : 1) los requerimientos individuales de nutrientes y agua de las especies; 2) características del sistema radicular; 3) capacidad de fijación de N; 4) calidad y cantidad de hojarasca producida por el árbol. También pueden ocurrir efectos perjudiciales, tales como disminución del pH y del contenido y disponibilidad de nutrientes del suelo; este es un tema de controversia (Cozzo 1976, de las Salas y Fassbender 1984, Fernández 1987, Lundgren 1978, Montagnini 1988, Sánchez et al. 1985).

Los efectos de las especies arbóreas sobre los suelos son muy variables. Por ejemplo, se ha observado que los suelos bajo Gmelina arbórea, especie ampliamente difundida en los trópicos húmedos, presentaban mayor contenido de Ca y P, y mayor p H que los suelos bajo bosque o bajo pino, en tres localidades diferentes (Sanchez et al. 1985, Chijicke 1980, Ojeniyi y Agbede 1980); en dos de los sitios, los suelos bajo Gmelina también tenían mayor contenido de Mg y K. Efectos semejantes sobre los cationes y el pH del suelo en regiones tropicales han sido observados en Terminalia ivorensis (Bolfoni et. al. sin publicar), Cordia trichotoma y Caesalpina equinata (Silva 1983). El impacto potencial de estas especies sobre el aumento del pH y del contenido de cationes y P del suelo podría ser importante en áreas del tropico donde el pH bajo, la baja disponibilidad de P y la toxicidad del aluminio tienen influencia negativa sobre el crecimiento de las plantas. En contraste, también han sido documentados los efectos de Pinus spp. sobre la disminución del pH y del contenido de nutrientes del suelo (Bolfoni et al., sin publicar, de Barros y Brandi 1975); asimismo, existen evidencias de los efectos perjudiciales de la palma africana (Elaesis guineensis) (Ollagnier et al. 1978. Kowal y Tinker 1959). Existen numerosos informes sobre el efecto beneficioso de especies de árboles fijadores de nitrógeno en regiones tropicales, con respecto a la conservación de este elemento, y sobre otros nutrientes del suelo (por ejemplo, Alpízar et al. 1986, Cadima Zeballos y Alvim 1967, Carlson y Dawson 1985, Roskowski 1982, Santana y Cabala-Rosand 1982).

La información sobre la influencia de los árboles sobre las propiedades de los suelos se concentra en unas pocas especies de amplio uso. Muy pocas veces se tienen en cuenta estos factores como determinantes en la elección de especies arbóreas para plantaciones o para combinaciones con cultivos (OTS/CATIE 1986).

En la región atlántica de Costa Rica (América Central) la Dirección General Forestal (DGF) lleva a cabo ensayos para la prueba de especies de árboles para plantaciones a campo abierto. Entre las especies recomendadas actualmente para la región (Gmelina arborea, Pinus caribaea, Eucalyptus deglupta y Cordia alliodora), solamente una (C. alliodora) es nativa. En 1985 la DGF estableció un ensayo para la prueba de 13 especies nativas, en la Estación Biológica La Selva de la Organización para Estudios Tropicales (OET) Entre las 13 especies, al menos cuatro: Stryphnodendron excelsum, Vochysia hondurensis, V. ferruginea y Hieronyma oblonga, mostraron a los tres años crecimiento equivalente o superior al de las especies recomendadas para la región (Espinoza y Butterfield 1989). Esto muestra el gran potencial de muchas especies nativas para 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 mecanismos de reciclaje de nutrientes. Entre las seis especies escogidas para este estudio, dos de ellas (Dalbergia tucurensis y Stryphnodendron excelsum) se eligieron por ser leguminosas, para examinar su efecto sobre la disponibilidad de nitrógeno, y sobre otros elementos, en comparación con especies no fijadoras. Entre las otras especies, Vochysia hondurensis y V. ferruginea han sido mencionadas como acumuladoras de aluminio (más de 10,000 ppm en el tejido foliar, P.W. Rundel, datos sin publicar) Esta característica ha sido encontrade en otras especies de la misma familia, asociándose con un mejor crecimiento en comparación con otras especies, en suelos ácidos y con problemas de toxicidad de aluminio en los trópicos (Goodland 1971) Sobre las dos restantes, Tabebuia rosea y Dipteryx panamensis, no existían datos preliminares que dieran indicios sobre su posible efecto sobre los suelos, pero fueron incluídas en el estudio por su valor económico y su amplia distribución en América tropical. En este trabajo presentamos los resultados de las mediciones de fertilidad del suelo, poniendo énfasis en el efecto de la plantación en conjunto sobre la conservación de nutrientes, en el potencial de cada especie desde el punto de vista de su efecto mejorador sobre los suelos, y en los posibles mecanismos involucrados en estos efectos.

Descripción del sitio experimental.

La plantación forestal de 13 especies nativas fue establecida en diciembre de 1985 en el anexo "La Guaria" (cercano a la población de este mismo nombre), perteneciente a la Estación Biológica La Selva de la OET (10° 26' lat. N, 86° 59' long. O, elevación promedio 50 m sobre el nivel del mar). El clima es típicamente tropical, con 24° C de temperatura media anual y 3.800 mm de precipitación anual, con máximas en junio-agosto, y octubre-diciembre (300-400 mm), y mínimas de enero a mayo (150-200 mm) (datos de la Estación Meteorológica de La Selva, promedios de 1957 a 1988) La vegetación natural es de bosque lluvioso tropical de bajura (Hartshorn 1983). El bosque primario en el área experimental había sido cortado en la décad de

1950. El área fue pastoreada con ganado de carne hasta 1984 y luego fue abandonada. En las áreas con pastos se encuentran gramíneas: Olyra latifolia, Melinis minutiflora, helechos (Pteridium spp.), y algunos arbustos (Psidium guajava, Piper culebranum). En partes que no fueron pastoreadas se desarrolló un bosque secundario, actualmente de aproximadamente 20 años. En este bosque las especies dominantes son Pentaclethra macroloba, especie leguminosa mimosoidea, fijadora de nitrógeno, dominante en el monte primario de La Selva; también se encuentran abundantes piperáceas (Piper culebranum y otras) y melastomatáceas, con helechos (Pteridium spp.) y plántulas de las especies arbóreas en el sotobosque.

La plantación experimental se estableció sobre terreno plano, aproximadamente 60 m sobre el nivel del mar. El sitio fue limpiado con machete y se cortaron algunos arbustos pequeños de guayaba. Las ramas pequeñas se dejaron en el sitio, mientras que las más grandes se apartaron. Se quemó parcialmente los restos de ramas que se habían dejado y se plantó con plántulas de bolsa. Durante el primer año se desmalezó a mano cuatro veces, a partir del segundo año, se demalezó con una cultivadora mecánica, también con una frecuencia aproximada de cuatro veces por año. A mediados de 1987, antes de comenzar el presente trabajo, se cortaron los arbustos pequeños de una franja adyacente a la plantación, para tener un terreno libre de árboles para comparación. En esta área de pastos sin árboles, se desmalezó cada vez que se desmalezaba la plantación, para mantener al área sin árboles, y con un tratamiento similar a la plantación en lo referente a las limpiezas. A partir de mediados de 1988 no fue necesario desmalezar las parcelas donde ya se había cerrado el dosel (las dos especies de Vochysia y Hieronyma oblonga).

Los suelos han sido clasificados como Fluventic Dystropepts, originados sobre aluviones volcánicos (Sancho y Mata 1987). Son suelos profundos, bien drenados, sin pedregosidad o rocosidad, de colores pardo oscuro en la superficie a pardo amarillento oscuro en el subsuelo. Los contenidos de materia orgánica son de medios a bajos, con textura moderadamente pesada a pesada; en general la unidad se puede considerar de suelos ácidos y poco fértiles. En la Tabla 1 se resumen las características químicas de un perfil típico de este tipo de suelos (Sancho y Mata 1987).

Métodos

a— Delimitación del área experimental

Las 13 especies se encontraban dispuestas en bloques completos al azar, con cinco repeticiones, en parcelas de 14 m x 14 m, con 49 árboles cada una, a 2 m de distancia entre árboles. Para el presente trabajo se utilizaron las cinco repeticiones de las seis especies mencionadas anteriormente. En el área adyacente con pastos, sin árboles, se delimitaron cinco parcelas de 14 m x 14 m, ubicadas a lo largo de una franja bordeando el lado este de la plantación. En el bosque secundario, que bordea el lado sur, se delimitaron también cinco parcelas de 14 m x 14 m; El área experimental incluyendo la plantación, los pastos y el bosque secundario, era de 19,159 m2, con caminos de 7 m de ancho entre la plantación y las áreas de pastos y de bosque.

b— Elección de las especies arbóreas.

Los criterios para la eleción de especies para este estudio fueron: 1) crecimiento: se eligieron las que presentaban mejor crecimiento a comienzos de 1988, cuando la plantación tenía dos años; 2) valor económico: todas las especies del ensayo tienen madera valiosa, comercializable; 3) capacidad fijadora de nitrógeno: se examinaron las raíces de todos los árboles en una diagonal en las cinco repeticiones de cada especie leguminosa del ensayo, en junio de 1987 y en marzo de 1988. Se encontraron nódulos en las raíces de todos los árboles examinados de S. excelsum y de D. tucurensis; no se encontraron nódulos en D. panamensis ni tampoco esta especie ha sido incluída en listas de especies tropicales fijadoras de N (Halliday 1984); 4) otros posibles efectos sobre los suelos: posible efecto mejorador del suelo bajo las especies acumuladoras de aluminio (V. ferruginea y V. hondurensis)

Aunque no existen experiencias silviculturales con ninguna de estas especies, se han realizado descripciones botánicas y estudios de su biología o fenología; por ejemplo, los estudios forestales de Holdridge et al. 1971; Bethel, 1976, Hartshorn, 1972, 1978; Lieberman et al., 1985; de biología y fenología de Bawa et al., 1985; efectos de los suelos sobre el crecimiento de especies arbóreas, de Huston 1980, 1982; y efectos del régimen de luz y microclima sobre el crecimiento (Budowski, 1961; Denslow 1980; Fetcher et al., 1983; Chazdon y Fetcher, 1984).

Stryphnodendron excelsum ("vainillo"; leguminosa, mimosoidea) y Dalbergia tucurensis ("granadillo"; leguminosa, papilionoidea) tienen madera de valor comercial (Holdridge y Poveda 1975); ambas especies dan sombra moderada, lo cual podría ser una característica adecuada para su asociación con cultivos en sistemas agroforestales, o en plantaciones mixtas. Dipteryx panamensis ("almendro"; leguminosa, papilionoidea) se encuentra ampliamente distribuída en América tropical, y su madera dura es muy apreciada (Holdridge y Poveda 1975) Vochysia ferruginea ("botarrama"; vochysiácea) y Vochysia hondurensis ("mayo"; vochisiácea) son ambas muy apreciadas por su madera; ambas proveen sombra bastante densa; V. ferruginea es una especie pionera en la sucesión secundaria (Berner y Finegan 1988), se autó-poda y produce abundante ramificación baja y hojarasca. Tabebuia rosea ("roble sabana"; bignoniácea) es muy apreciada por su madera y como ornamental, y también se encuentra ampliamente distribuída en América tropical (Holdridge y Poveda 1975).

c– Estudio de las características químicas de los suelos.

Los suelos se muestrearon bajo las seis especies de la plantación, las parcelas de pastos y el bosque secundario, en abril (época menos húmeda, promedio de alrededor de 200 mm en el mes) y en agosto (época más lluviosa, promedio de alrededor de 400 mm) de 1988 (datos pluviométricos de la Estación La Selva). Se utilizaron barrenos de tipo holándes, de 8 cm de diámetro. Se muestró a 0-15, 15-30 y 30-60 cm de profundidad.

Las muestras se procesaron en el Laboratorio de Suelos de la Facultad de Agronomía de la Universidad de Costa Rica, siguiendo los métodos corrientes para determinación de fertilidad de suelos empleados en el país. Se midieron los siguientes parámetros: Ca, Mg, K, capacidad de intercambio catiónico, pH en agua, acidez extraíble, materia orgánica, nitrógeno total, fósforo extraíble y elementos menores (Cu, Fe, Mn, Zn).

El pH se determinó en una relación suelo : agua de 1:2.5, utilizando un potenciómetro Corning 7. Para las muestras de abril, el Ca, Mg., K y la capacidad de intercambio catiónico (CIC) se determinaron por medio de extracción con una solución 1 N de acetato de amonio a pH 7. Además, en abril el Ca y el Mg se extrajeron también con una solución de KCl 1N. En este caso, la capacidad de intercambio catiónico efectiva (CICE) se calculó como la suma de bases más la acidez extraída con la solución de KCll 1N. Para las muestras de agosto, el Ca y el Mg. se extrajeron con KCl solamente.

El P, K y elementos menores se extrajeron con solución de Olsen modificada, la cual consiste en una mezcla de $NaHCO_3$ 0.5 N, EDTA di-sódico 0.01 N y Superfloc 127 (Díaz Romeu y Hunter 1978). Los cationes se midieron utilizando un Espectrofotómetro de Absorción Atómica Perkin Elmer 2380. El P se midió colorimétricamente, luego de reacción con $(NH_4)_2 MoO_4$ ácido y $SnCl_2$ como reductor, utilizando un Espectrofotómetro Perkin Elmer-Coleman 295.

La materia orgánica se midió utilizando la técnica de Walkley-Black (Allison 1975). El nitrógeno total se midió por un método semi-micro Kjeldahl (Bremer y Mulvaney 1982).

Resultados

Los resultados de las mediciones de la composición química de los suelos realizados en abril se presentan en las Tablas 2 a 4 y Figs. 1 a 5. Los valores de Ca y Mg obtenidos mediante extracción con acetato de amonio fueron mayores a los obtenidos en la extracción con KCl (Tablas 2 y 3). Esta diferencia era más acentuada para el Ca que para el Mg: por ejemplo, en el horizonte superficial (0-15 cm de profundidad), para S. excelsum el Ca era casi 1.5 veces mayor en acetato de amonio que en KCl, mientras que para esta misma especie, el Mg extraído con acetato de amonio era 1.2 veces mayor que el extraído con KCl (Tablas 2 y 3). Además, bajo esta misma especie para el Ca esta diferencia se acentuaba con la profundidad: el Ca a 15-30 y 30-60 cm era el doble en acetato de amonio que en KCl, mientras que para el Mg la diferencia se mantenía en niveles semejantes para las tres profundidades. Tendencias similares a aquéllas ejemplificadas con S. excelsum se manifestaban para los otros sitios.

El análisis de la varianza no reveló diferencias significativas entre los sitios para Ca, tanto para los resultados de la extracción en acetato de amonio como para los de KCl. Sin embargo, en las extracciones con acetato de amonio, a 0-15 cm de profundidad se notó una tendencia a una mayor concentración de Ca en el suelo bajo V. ferruginea (1.02 cmol/1, en bosque secundario (0.96 cmol/1) y en D. panamensis (0.93 cmol/1), en comparación con otras especies como por ejemplo S. excelsum (0.67 cmol/1), o bajo el pasto (0.47 cmol/1). La misma tendencia se observó en las extracciones en KCl para este mismo horizonte superficial del suelo; bajo V. ferruginea la concentración de Ca era 0.73 cmol/1, bajo bosque 0.68 y bajo D. panamensis 0.52, mientras que bajo S. excelsum era 0.45 cmol/1 y bajo pasto 0.32 cmol/1. Estas tendencias a diferencias entre sitios eran menos marcadas con la profundidad (Tablas 2 y 3).

Con respecto al Mg., en las extracciones con acetato de amonio existían diferencias significativas entre los sitios, para las tres profundidades en el horizonte superficial, la concentración de Mg era mayor bajo todas las especies del ensayo (entre 0.48 y 0.84 cmol/1) y bajo el bosque (0.72 cmol/1). que bajo el pasto (0.32 cmol/1) (probabilidad menor del 5 o/o). En el subsuelo, la concentración de Mg era mayor en el bosque que en el pasto y que en las seis especies del ensayo (probabilidad menor del 10 o/o) (Tabla 3).En las extracciones con KCl, las diferencias eran menos pronunciadas, pero se observó una mayor concentración de Mg en el horizonte superficial en el bosque, que en las especies del ensayo, y en éstas a su vez se observó una mayor concentración de Mg que bajo pasto, para una probabilidad menor del 10 o/o en ambos casos. No había diferencias significativas entre sitios en la concentración de Mg en el subsuelo (Tabla 2).

Con respecto al K, no se observaron diferencias significativas entre sitios, aunque se observo una tendencia de mayor contenido de K bajo D. panamensis, S. excelsum, D. tucurensis y V. ferruginea (Tabla 2). Los tres cationes considerados disminuían con la profundidad (Tabla 2).

El pH en el horizonte superficial era mayor bajo T. rosea y D. panamensis (pH 5.5, probabilidad menor de 5 o/o) , que bajo bosque y pasto (pH 5.3), con valores intermedios bajo las otras especies (Tabla 2 y Fig. 1) A 15-30 cm el pH era menor bajo bosque que bajo las especies o bajo pasto (pH 5.4) ; no había diferencias significativas entre los sitios a mayor profundidad. Se observó una tendencia a un aumento de pH con la profundidad, aunque este aumento era de 0.1-0.2 unidades solamente, es decir de igual magnitud que las diferencias de pH entre los sitios (Tabla 2 y Fig. 1).

La acidez extraíble fue menor en el horizonte superficial bajo T. rosea (1.28 cmol/1) y D. panamensis (1.18) que bajo V. hondurensis (1.86) (probabilidad menor que 5 o/o); con valores intermedios en los otros sitios (Tabla 2 y Fig. 2) No hubo diferencias significativas entre sitios a mayores profundidades; la acidez extraíble disminuyó con la profundidad, excepto en S. excelsum, D. tucurensis y bosque secundario (Fig. 2).

No se observaron diferencias significativas entre los sitios en la suma de bases extraídas con KC1, a ninguna profundidad (Tabla 2), aunque se observó una tendencia de menor cantidad de bases bajo V. hondurensis (0.73 cmol/1) y bajo pasto (0.77) en el horizonte superficial, en comparación con los otros sitios (Tabla 2 y Fig. 3), con valores entre 1.06 y 1.64 cmol/1.

La capacidad de intercambio catiónico (CIC) medida en acetato de amonio fue mayor (entre 7 y 10 veces) en todos los casos, que la capacidad de intercambio catiónico efectiva (CICE) (Tablas 2 y 3). No hubo diferencias significativas en los valores de CIC o de CICE, para ninguna de las tres profundidades consideradas (Tablas 2 y 3). La saturación de bases en el horizonte superficial fue menor bajo V. hondurensis (28.2 o/o probabilidad menor que 5 o/o) que en los otros sitios; bajo pasto, también fue menor (34.8 o/o, probabilidad menor de 10 o/o) (valores calculados según extracción con KC1); la saturación de bases tendió a disminuír con la profundidad (Tabla 2 y Fig. 4) La saturación de acidez fue mayor bajo V. hondurensis (71.8 o/o probabilidad menor de 5 o/o) y bajo pasto (65.2 o/o. probabilidad menor de 5 o/o) , en los 0-15 y en los 15-30 cm de profundidad, con valores intermedios en los otros sitios (Tabla 2). No hubo diferencias significativas entre sitios a 30-60 cm de profundidad. La saturación de acidez tendió a aumentar con la profundidad.

La materia orgánica en el horizonte superficial fue mayor en el bosque (7.58 o/o, probabilidad menor del 1 o/o) que en los otros sitios (Tabla 4). A su vez, la materia orgánica en el horizonte superficial fue mayor bajo las seis especies del ensayo (5.31 a 6.60 o/o) que bajo pasto (4.83 o/o) (probabilidad menor de 5 o/o) Aunque no hubo diferencias significativas entre las seis especies, se notó una tendencia a mayor contenido de materia orgánica en el suelo superficial bajo V. ferruginea (6.60 o/o). A 15-30 cm, la materia orgánica fue mayor en el bosque que en los otros sitios (probabilidad menor de 10 o/o) No hubo diferencias significativas entre sitios a 30-60 cm. La materia orgánica disminuyó con la profundidad.

El nitrógeno total a 0-15 cm fue mayor bajo bosque (0.328 o/o) que bajo pasto (0.224 o/o), con valores intermedios en las especies del ensayo (0.260 a 0.318 o/o) (probabilidades menores de 5 o/o) (Tabla 4) El mayor valor de nitrógeno total (0.318 o/o) se encontró bajo V. ferruginea, aunque la diferencia no fue significativa (probabilidad menor del 10 o/o). A 15-30 cm, el nitrógeno total fue mayor en el bosque (probabilidad menor del 5 o/o), no habiendo diferencias significativas entre los otros sitios. A 30-60 cm el nitrógeno total fue mayor en el bosque que en el pasto (probabilidad menor de 5 o/o) , sin diferencias entre los otros sitios. El nitrógeno total disminuyó con la profundidad. No hubo diferencias significativas entre sitios en la relación C/N a ninguna de las tres profundidades (Tabla 4).

El fósforo extraíble fue menor a 0-15 cm de profundidad bajo el bosque (3.64 mg/kg, probabilidad menor de 5 o/o) que en los otros sitios (4.90 a 7.10 mg/kg, con el menor valor en el pasto y el mayor en V. ferruginea, aunque las diferencias no fueron estadísticamente significativas) (Tabla 4 y Fig. 5.) No existieron diferencias significativas en P extraíble entre sitios a 15-30 o 30-60 cm, aunque los valores tendieron a ser mayores en V. ferruginea y menores en pasto y en bosque. El P también disminuyó con la profundidad (Fig. 5).

En cuanto a los elementos menores, no hubo diferencias significativas entre sitios a ninguna profundidad para Cu, Zn o Mn. Sin embargo, a 0-15 cm se observó mayor cantidad de Cu bajo V. ferruginea, D. tucurensis y D. panamensis, que bajo pasto y bajo bosque, con valores intermedios en los otros sitios (Tabla 4). El Zn tendió a ser mayor bajo V. ferruginea, V. hondurensis y bosque, mientras que el Mn tendió a ser menor en T. rosea y en pastos que en los otros sitios. El Zn tendió a aumentar o mantener sus valores con la profundidad, mientras que el Cu y el Mn disminuyeron a mayor profundidad. El Fe fue significativamente mayor en el suelo bajo bosque, para las tres profundidades consideradas, que en los otros sitios (probabilidad menor de 1 o/o) y tendió a disminuír con la profundidad.

Los resultados de las mediciones realizadas en agosto se presentan en Tablas 5 y 6 y Figs. 6 y 7. No se observaron diferencias significativas en Ca, Mg o K, para ninguna de las tres profundidades consideradas (Tabla 5). Sin embargo, se observó una tendencia a mayor contenido de Ca en el horizonte superficial en V. ferruginea, T. rosea y bosque, mayor Mg bajo V. ferruginea, V. hondurensis, T. rosea y bosque, y mayor K bajo V. ferruginea, T. rosea y bosque.

No hubo diferencias significativas en el pH entre los sitios, excepto a 15-30 cm, donde el pH fue menor en el bosque (5.1) que en los otros sitios (5.2-5.3— (probabilidad menor del 10 o/o) A 0-15 cm el pH variaba de 4.9 (bosque y pasto) a 5.2 (T. rosea) (Tabla 6) Se observó al igual que en abril, una tendencia a un aumento del pH a mayor profundidad. La acidez extraíble fue menor en T. rosea y D. panamensis que en los otros sitios, para las tres profundidades (probabilidad menor de 5 o/o).

La capacidad de intercambio catiónico efectiva (CICE), fue mayor en el bosque, para las tres profundidades, que en los demás sitios (probabilidad menor del 5 o/o). No hubo diferencias significativas en el porcentaje de saturación de bases entre los sitios para 0-15 y 15-30 cm; solamente a 30-60 cm la saturación de bases fue mayor en T. rosea que en los demás sitios (probabilidad menor de 15 o/o) De igual manera, no se observaron diferencias significativas en la saturación de acidez entre los sitios a 0-15 y 15-30, pero se encontraron diferencias significativas a 30-60 cm, con los menores valores bajo T. rosea y D. panamensis (probabilidad menor del 15 o/o) (Tabla 5). La saturación de acidez aumentó con la profundidad.

La materia orgánica fue significativamente mayor en el bosque (probabilidad menor de 5 o/o) y en V. ferruginea (probabilidad menor de 15 o/o) a 0-15 y a 15-30 cm (Tabla 6 y Fig. 6) Los menores valores correspondieron al pasto. A 30-60 cm, la materia orgánica fue mayor bajo bosque que bajo las especies del ensayo y que bajo el pasto, en ese orden (Tabla 6 y Fig 6). El nitrógeno siguió una tendencia similar al de la materia orgánica, con mayores valores en V. ferruginea y bosque (Tabla 6 y Fig. 7) No hubo diferencias significativas en la relación C/N entre los sitios (Tabla 6) No se observaron diferencias significativas en el contenido de P, aunque se observó una tendencia a mayor P bajo V. ferruginea y menor contenido bajo bosque.

El Cu fue mayor bajo bosque a 0-15 cm (probabilidad menor del 10 o/o) El Zn fue mayor bajo bosque a las tres profundidades. No hubo diferencias significativas en el contenido de Mn, excepto a 30-60 cm, donde el contenido fue menor en el pasto. Existió una tendencia a mayor contenido de hierro bajo bosque, que era significativa a 15-30 y 30-60 (Tabla 6).

Comparando los valores de abril con los de agosto, se manifestó una menor concentración de Ca, Mg y K (menor suma de bases) en agosto, una mayor acidez extraíble (Fig. 8) , menor pH, y mayor saturación de acidez. En algunos casos también se notaron menores valores de materia orgánica y nitrógeno total, aunque no ocurrió esto en las parcelas que tenían mayores contenidos, como en V. ferruginea y bosque. El P, Mn y Fe fueron menores en agosto, mientras que el Zn fue mayor en agosto que en abril, y el Cu fue mayor o menor según los sitios.

Discusión

Características químicas de los suelos en el área experimental.

Al comparar los datos de las características químicas de los suelos de la consociación La Guaria (Sancho y Mata 1987, Tabla 1) con los resultados de la presente investigación, se observa que en el horizonte superficial del bosque se encontró un contenido similar de Ca y Mg (extracciones en acetato de amonio en ambos casos), mayor contenido de materia orgánica, menor contenido de K y de P, un mayor pH, y contenidos similares de elementos menores. Los niveles generales son lo suficientemente parecidos como para considerar que los suelos en el ensayo podrían ser parte de la consociación mencionada, con diferencias debidas a la vegetación que se encontrara en el sitio muestreado por Sancho y Mata (1987).

En concordancia con lo expresado por Sancho y Mata (1987) en referencia a los suelos de la consociación La Guaria, en general se puede observar que el contenido de Ca y Mg en la plantación experimental, en el pasto y en el bosque fue relativamente bajo, tanto en abril como en agosto, con valores menores de los considerados críticos para los cultivos agrícolas, según niveles utilizados por el Ministerio de Agricultura de Costa Rica (Tabla 7 , Berstch 1986). Estos niveles críticos fueron determinados para los mismos extractantes utilizados en el presente estudio, y son utilizados para la mayoría de los cultivos en el país.

El contenido de potasio en el horizonte superficial de este ensayo fue menor o mayor que el nivel crítico, según el sitio considerado, en el muestreo de abril; mientras que los datos de agosto muestran en todos los casos valores menores que los críticos. El menor contenido de bases en agosto en todos los sitios (Fig. 8) se atribuye al mayor lavado durante la época de mayores precipitaciones: el total de lluvia para el mes de agosto de 1988 fue de 457 mm, mientras que en abril fue 43.8 mm (datos de la estación meteorológica de La Selva) Los contenidos de Cu, Mn y Fe fueron superiores al nivel crítico, y existió una aparente deficiencia de Zn; esto para todos los sitios en ambos muestreos. Los valores de pH fueron bajos en los dos muestreos, pero mostraron una tendencia a bajar en el muestreo de agosto, con un aumento en la acidez extraíble en todos los sitios en conjunto (Fig. 8), coincidiendo esto también con la época más lluviosa en la cual existe un mayor lavado de bases.

Los valores de materia orgánica y N en general parecen relativamente altos en este ensayo. Esto podría deberse a la presencia anterior de un bosque maduro en el sitio, y a la dominancia de especies fijadoras de N como Pentacrethra macroloba, en el bosque de bajura de la región, que ocupaba el sitio antes de su corta en los años 1950. Excepto por estos dos últimos parámetros, los suelos del área muestreada eran muy poco fértiles. Como la materia orgánica es responsable en gran parte de la capacidad de retención de nutrientes del suelo, las prácticas de manejo que tiendan a disminuir el tenor de materia orgánica, tales como quemas repetidas, sobrepastoreo, falta de cobertura vegetal, tenderán a disminuir aún más su fertilidad, hasta hacer muy difícil su recuperación para niveles productivos. La disminución de la materia orgánica con la profundidad que se observó en todos los sitios del ensayo puede ser la causa del aumento relativo del pH en el subsuelo; puesto que la materia orgánica es una fuente de acidez. El aumento de pH con la profundidad no podría atribuirse a un aumento en el contenido de bases, pues todas estas disminuyeron en el subsuelo.

Influencias de la plantación experimental, pasto y bosque sobre la fertilidad.

Siendo el contenido de materia orgánica un factor clave en la recuperación y mantenimiento de la fertilidad, se puede considerar que en menos de tres años la presencia de la plantación experimental en conjunto había aumentado la fertilidad del sitio, pues si se compara el promedio de materia orgánica en el horizonte superior del suelo en el pasto en abril (4.83 o/o) con los valores en la plantación, que variaron entre 5.31 y 6.6 o/o se nota un incremento sustancial en este parámetro, con un valor cercano al del bosque (7.58 o/o) Se observó una tendencia similar en el subsuelo en ambos muestreos; asimismo, en agosto los resultados fueron similares (Fig. 6). El nitrógeno total reveló una situación parecida, con valores de 0.260-0.318 o/o en la plantación, mayores que en el pasto (0.224) y cercanos a los del bosque (0.328) (datos de abril; con resultados similares en agosto; Fig. 7). Un incremento entre 0.5 y casi 2.0 unidades porcentuales en lo que respecta a materia orgánica en el suelo superficial es sustantivo, por su contribución a la retención de nutrientes. El coeficiente de correlación entre el contenido de materia orgánica y la suma de bases, considerando los datos de las tres profundidades muestreadas, fue de 0.40 en abril y de 0.60 en agosto, mostrando la estrecha relación entre ambos parámetros importantes para la fertilidad.

Asimismo, tomados en conjunto, los valores de Ca y Mg en el suelo de la plantación fueron mayores que en el pasto, con los valores cercanos a los que se encontraron en el bosque (Fig. 3); la saturación de bases fue similar o mayor en la plantación que en el bosque, y también mayor que en el pasto (Fig. 4), mientras que se dió la situación inversa con referencia a la saturación de acidez. Con el potasio la situación fue diferente, con valores bajos en general y sin una clara tendencia con respecto a diferencias entre sitios. Una tendencia también diferente se encontró para el P extraíble, cuyos valores fueron en general bastante bajos (menores que el nivel crítico) y aún más en el bosque (Fig. 5) La tendencia con respecto a los elementos menores fue similar a la encontrada con los cationes básicos, con valores en la plantación mayores que en el pasto y menores que en el bosque. Sin embargo serían necesarias mediciones a más largo plazo para confirmar estas tendencias, y para dilucidar los mecanismos involucrados. Además, debe recalcarse que el área de pastos en este ensayo no representa un pasto abandonado típico de la región, pues como se aclaró antes, esta área ha sido mantenida bajo pasto con el fin de tener un sitio de comparación, con todos los tratamientos que se le daban a ésta, incluídos los desmalezados. El área de pastos representa entonces una porción de terreno sobre los mismos suelos, donde se dan condiciones idénticas excepto la presencia de especies arbóreas, y debe tomarse como tal en la interpretación de estos resultados. Asimismo el bosque representa un terreno sobre los mismos suelos, con árboles que han estado en el sitio por un período más prolongado, de aproximadamente 20 años, y podría considerarse representativo de otros bosques secundarios de la región.

Comparando las seis especies dentro de la plantación, en las extracciones en acetato de amonio se notaron tendencias más claras que en las realizadas con KC1; si bien el KC1 sería mas apropiado por realizarse la extracción en condiciones de pH más parecidas a las de campo, por otro lado con valores tan bajos se oscurecen algunas diferencias potenciales, por lo cual es posible que otro tipo de solución extractora sea una alternativa más adecuada.

Aún en las extracciones con KC1, en el horizonte superficial se revelaron tendencias a una mayor concentración de Ca y Mg, con una mayor suma de bases bajo V. ferruginea (Fig. 3) . La acumulación se debe posiblemente a la movilización de cationes de capas profundas al árbol y su deposición en la capa superficial a partir de la hojarasca. También bajo esta especie se observó mayor contenido de materia orgánica y nitrógeno total (Figs. 6 y 7), lo cual sugiere la importancia de la materia orgánica en la retención de nutrientes en estos suelos. Se observa una gran acumulación de hojarasca de hojas y ramas bajo esta especie, mucho mayor que en las otras especies del ensayo. Como V. ferruginea es una de las especies de mejor crecimiento del ensayo, su influencia positiva sobre la fertilidad del suelo aumenta su importancia como especie para la reforestación y para la recuperación de áreas degradadas. En la segunda fase del presente proyecto, se está muestreando la caída de hojarasca y su contenido de nutrientes bajo las seis especies de árboles. También se muestrea el piso de hojarasca, para examinar la distribución de sus diferentes partes (material reciente, material en estado de descomposición) y su contenido de nutrientes. Asimismo, se han muestreado las raíces en los mismos espesores de suelo que han sido considerados para los análisis químicos. Estas investigaciones contribuirán a explicar los mecanismos involucrados en estas diferencias y tendencias.

Otras diferencias entre especies incluyen el mayor pH y la menor acidez intercambiable bajo T. rosea y D. panamensis y la tendencia inversa (menor pH y mayor acidez) bajo V. hondurensis (Figs. 1 y 2). Entre las especies en estudio, tanto D. panamensis como T. rosea son las de menor crecimiento hasta la fecha, en contraste con V. hondurensis, que es una de las de mayor crecimiento. Posiblemente debido al menor crecimiento de las dos primeras, exitè una menor absorción de bases, en comparación con V. hondurensis, que por su rápido crecimiento tendría una mayor demanda. No sería muy probable que estas diferencias se debieran al reciclaje de bases en T. rosea y D. panamensis, pues en estas parcelas el dosel no había cerrado completamente en el momento de los muestreos, y es poco probable que los mecanismos de reciclaje se hubieran establecido. Al igual que en el caso anterior, las mediciones que se están realizando en la segunda fase del proyecto contribuirán a explicar estos mecanismos. Posiblemente estas pequeñas diferencias en el pH y acidez entre especies, al igual que otros parámetros, cambien a más largo plazo.

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Tabla 1. Composición química de un perfil típico de la Consociación La Guaria (tomado de Sancho y Mata 1987).

HORIZONTE		A	AB	Bw1	Bw2	IIA
Profundidad (cm)		0-15	15-38	38-79	79-106	106+
pH	H_2O	4.6	5.0	5.0	4.9	5.0
	KCl	4.2	4.7	4.4	4.7	4.8
	NaF	9.4	9.7	9.8	9.6	9.7
MAT.ORG. (%)		2.80	2.14	T	T	0.34
Cmol/l						
	Ca	0.80	0.73	0.73	0.75	0.75
	Mg	0.46	0.33	0.29	0.25	0.25
	K	0.77	0.66	0.87	0.41	0.41
	Acidez	1.4	0.9	0.8	0.5	0.5
	CIC	13.5	15.9	14.0	14.4	13.8
SAT. BASES (%)		15.0	10.8	13.5	9.8	10.2
SAT.ACIDEZ (%)		10.3	5.6	5.7	3.5	3.6
mg/kg						
	P	12.6	3.2	13.1	12.2	10.7
	Cu	20.0	9.5	7.4	10.5	9.2
	Zn	1.7	0.6	1.9	1.7	3.9
	Mn	68.0	28.9	27.5	29.0	43.0
	Fe	663	98	186	166	163
ARENA (%)		51	53	52	50	60
LIMO (%)		8	11	2	11	17
ARCILLA (%)		41	36	46	39	23
NOMBRE TEXTURAL		Aa	Aa	Aa	Aa	FAa

Tabla 2. Contenido de Ca, Mg y K, pH, acidez, suma de bases, capacidad de intercambio catiónico efectivo, saturación de acidez y de bases, en suelos bajo las seis especies del ensayo, pasto y bosque; abril 1988 (Ca y Mg extraídos con KCl, K extraído con acetato de NH_4)[a].

SITIO	PROFUNDIDAD (cm)	Ca (cmol/kg)	Mg (cmol/kg)	K (cmol/kg)	pH	Acidez (cmol/kg)	Suma de bases (cmol/kg)	CICE (cmol/kg)	% SATURACION BASES	% SATURACION ACIDEZ
Str. exc.	0-15	0.45a	0.63ab	0.27a	5.4ab	1.66ab	1.34a	3.00a	45.5a	54.5bc
	15-30	0.33a	0.35a	0.19a	5.4a	1.54a	0.87a	2.41a	37,2a	62.7b
	30-60	0.26a	0.22a	0.17a	5.6a	1.88a	0.65a	2.53a	34,2a	65.7a
Dal. tuc.	0-15	0.44a	0.41ab	0.22a	5.4ab	1.46ab	1.07a	2.53a	41.6a	58.4bc
	15-30	0.32a	0.24a	0.15a	5.4a	1.54a	0.71a	2.25a	31,6a	68.4bc
	30-60	0.24a	0.15a	0.11a	5.6a	1.42a	0.49a	1.91a	26,8a	73.2a
Voch. ferr.	0-15	0.73a	0.61ab	0.22a	5.4ab	1.20ab	1.56a	2.76a	52,8a	47.2bc
	15-30	0.66a	0.39a	0.21a	5.6a	1.12a	1.26a	2.38a	47,3a	52.7bc
	30-60	0.42a	0.28a	0.17a	5.6a	1.06a	0.86a	1.92a	42,5a	57.5a
Voch. hond.	0-15	0.25a	0.37ab	0.11a	5.3b	1.86a	0.73a	2.59a	28.2bc	71.8a
	15-30	0.19a	0.18a	0.09a	5.4a	1.58a	0.46a	2.04a	22.5bc	77.5a
	30-60	0.17a	0.32a	0.08a	5.5a	1.32a	0.57a	1.89a	27.5a	72.5a
Tab. rosea	0-15	0.42a	0.50ab	0.15a	5.5a	1.28b	1.06a	2.35a	44.1a	55.9b
	15-30	0.28a	0.26a	0.12a	5.6a	1.12a	0.66a	1.78a	35.5a	64.5b
	30-60	0.28a	0.24a	0.13a	5.7a	0.98a	0.65a	1.63a	38.8a	61.2a
Dip. pan.	0-15	0.52a	0.74ab	0.38a	5.5a	1.18b	1.64a	2.82a	53.4a	46.5bc
	15-30	0.36a	0.45a	0.29a	5.5a	1.06a	1.09a	2.19a	46.2a	53.8bc
	30-60	0.28a	0.28a	0.19a	5.6a	1.08a	0.75a	1.83a	38.9a	60.1a
PASTO	0-15	0.32a	0.27b	0.19a	5.3b	1.40ab	0.77a	2.17a	34.8ab	65.2ab
	15-30	0.31a	0.28a	0.17a	5.4a	1.32a	0.76a	2.08a	35.7ab	64.2ab
	30-60	0.23a	0.15a	0.10a	5.5a	1.26a	0.48a	1.74a	27.1a	72.9a
BOSQ. SECUN.	0-15	0.68a	0.55b	0.17a	5.3b	1.54ab	1.39a	2.93a	46.9a	53.1bc
	15-30	0.60a	0.42a	0.13a	5.4a	1.60a	1.15a	2.75a	42.2a	57.7bc
	30-60	0.42a	0.28a	0.18a	5.5a	1.34a	0.87a	2.21a	39.5a	60.5a

[a]En ésta y en las tablas siguientes, los valores de cada parámetro, para una misma profundidad y para los diferentes sitios, presentan diferencias estadísticamente significativas cuando están seguidos de letras diferentes.

Tabla 3. Ca, Mg y capacidad de intercambio catiónico (CIC) determinados por extracción en acetato de amonio, en abril de 1988.

SITIO	PROFUNDIDAD (cm)	Ca	Mg	CIC
		(cmol / kg)		
Stryphnodendron excelsum	0-15	0.67a	0.80a	21.5a
	15-30	0.67a	0.51b	19.9a
	30-60	0.54a	0.28b	18.2a
Dalbergia tucurensis	0-15	0.68a	0.48ab	21.4a
	15-30	0.68a	0.39b	19.3a
	30-60	0.63a	0.26a	18.2a
Vochysia ferruginea	0-15	1.02a	0.69a	22.3a
	15-30	0.98a	0.47b	19.5a
	30-60	0.74a	0.39b	18.5a
Vochysia hondurensis	0-15	0.65a	0.56a	22.1a
	15-30	0.54a	0.32b	19.1a
	30-60	0.57a	0.26b	18.2a
Tabebuia rosea	0-15	0.69a	0.58a	25.9a
	15-30	0.57a	0.37b	19.0a
	30-60	0.52a	0.40b	17.9a
Dipteryx panamensis	0-15	0.93a	0.84a	21.5a
	15-30	0.76a	0.59b	19.8a
	30-60	0.66a	0.41b	18.7a
PASTOS	0-15	0.47a	0.32b	20.6a
	15-30	0.50a	0.30b	18.7a
	30-60	0.54a	0.22b	24.6a
BOSQUE SECUNDARIO	0-15	0.96a	0.72a	23.3a
	15-30	0.89a	0.58a	21.5a
	30-60	0.62a	0.36a	19.0a

Tabla 4. Materia orgánica, N total, C/N, P y elementos menores en los suelos muestreados en abril 1988.

SITIO	PROFUNDIDAD	M.O.	N	C/N	P	Cu	Zn	Mn	Fe
	(cm)	(%)	(%)		(mg/kg)				
Str.	0-15	6.04ab	0.288b	12.2a	5.38a	18.6a	1.90a	85.8a	344b
exc.	15-30	4.52b	0.234b	11.2a	5.70a	16.6a	1.64a	97.2a	258b
	30-60	2.54a	0.142a	10.4a	5.34a	9.2a	2.08a	67.8a	126b
Dal.	0-15	5.47ab	0.292ab	10.9a	5.48a	20.0a	1.92a	104a	315b
tuc.	15-30	4.06b	0.214b	11.1a	4.60a	38.0a	1.50a	88.4a	218b
	30-60	2.70a	0.132a	11.9a	4.24a	15.4a	1.72a	77.6a	182b
Voch.	0-15	6.60ab	0.318b	12.1a	7.10a	22.2a	2.76a	105a	331b
ferr.	15-30	4.60b	0.218b	11.9a	5.30a	20.4a	3.14a	96.4a	219b
	30-60	3.34a	0.156a	12.6a	4.66a	20.6a	2.42a	91.0a	152b
Voch.	0-15	5.46ab	0.288ab	11.0a	5.16a	18.2a	2.36a	115a	323b
hond.	15-30	3.87b	0.204b	11.0a	4.60a	17.6 a	1.90a	93.2a	218b
	30-60	2.70a	0.142a	11.0a	4.46a	13.2a	1.78a	79.4a	177b
Tab.	0-15	5.63ab	0.288ab	11.4a	5.10a	19.8a	1.60a	89.0a	277b
rosea	15-30	3.92b	0.194b	11.6a	4.64a	18.2a	1.44a	81.2a	165b
	30-60	3.00a	0.164a	10.7a	4.66a	18.0a	1.56a	78.2a	138b
Dip.	0-15	5.31ab	0.260ab	11.8a	5.34a	20.0a	1.80a	114a	333b
pan.	15-30	4.42b	0.208b	12.4a	5.14a	18.0a	1.60a	96.0a	200b
	30-60	2.96a	0.146a	11.6a	5.58a	20.8a	2.18a	89.4a	158b
PASTOS	0-15	4.83bc	0.224b	12.8a	4.90a	15.8a	1.40a	96.8a	297b
	15-30	4.03b	0.176b	14.0a	4.44a	14.2a	1.46a	110a	226b
	30-60	2.73a	0.138b	11.8a	4.24a	15.0a	2.04a	82.4a	138b
BOSQ.	0-15	7.58a	0.328a	13.6a	3.64b	16.2a	2.26a	113a	664a
SECUN.	15-30	6.40a	0.278a	13.4a	3.34b	15.2a	2.24a	101a	461a
	30-60	3.29a	0.170a	11.2a	3.60a	11.2a	2.32a	91.8a	300a

Tabla 5. Contenido de Ca, Mg y K, pH, acidez, suma de bases, capacidad de intercambio catiónico efectiva (CICE), y saturación de bases y acidez, en suelos muestreados en agosto 1988.

SITIO	PROFUNDIDAD (cm)	Ca	Mg	K	pH	Acidez	Suma de bases	CICE	SATURACION (%) BASES	SATURACION (%) ACIDEZ
		(cmol/kg)				(cmol/kg)				
Str. exc.	0-15	0.28a	0.38a	0.11a	5.0a	1.70a	0.77a	2.48b	30.5a	69.5a
	15-30	0.20a	0.22a	0.10a	5.2a	1.64a	0.51a	2.16b	23.5a	76.5a
	30-60	0.20a	0.11a	0.07a	5.4a	1.46a	0.37a	1.84b	20.5b	79.5a
Dal. tuc.	0-15	0.27a	0.29a	0.14a	5.0a	1.70a	0.71a	2.40b	29.1a	70.9a
	15-30	0.21a	0.19a	0.13a	5.1a	1.58a	0.52a	2.08b	25.1a	74.9a
	30-60	0.17a	0.11a	0.09a	5.3a	1.52a	0.37a	1.90b	19.6ab	80.4a
Voch. ferr.	0-15	0.55a	0.43a	0.16a	5.0a	1.72a	1.13a	2.86b	35.2a	64.8a
	15-30	0.22a	0.17a	0.11a	5.3a	1.52a	0.50a	2.02b	24.6a	75.4a
	30-60	0.19a	0.11a	0.10a	5.4a	1.38a	0.40a	1.80b	22.2b	77.8a
Voch. hond.	0-15	0.27a	0.43a	0.12a	5.1a	1.70a	0.82a	2.52b	31.5a	68.5a
	15-30	0.14a	0.13a	0.08a	5.2a	1.70a	0.34a	2.06b	17.4a	82.6a
	30-60	0.13a	0.10a	0.07a	5.3a	1.56a	0.30a	1.84b	16.1b	83.9a
Tab. rosea	0-15	0.39a	0.50a	0.18a	5.2a	1.46b	1.08a	2.54b	41.4a	58.6a
	15-30	0.22a	0.22a	0.12a	5.3a	1.46b	0.55a	2.02b	27.1a	72.9a
	30-60	0.18a	0.14a	0.09a	5.5a	1.24b	0.41a	1.66b	25.8a	74.2b
Dip. pan.	0-15	0.21a	0.25a	0.15a	5.1a	1.64b	0.61a	2.24b	27.6a	72.4a
	15-30	0.21a	0.22a	0.12a	5.2a	1.56b	0.56a	2.12b	25.2a	74.8a
	30-60	0.17a	0.15a	0.10a	5.4a	1.54b	0.41a	1.94b	21.5b	78.5b
PASTO	0-15	0.22a	0.28a	0.15a	4.9a	7.06a	0.65a	2.70b	23.5a	76.5a
	15-30	0.17a	0.15a	0.11a	5.2a	2.10a	0.42a	2.54b	16.2a	83.8a
	30-60	0.17a	0.14a	0.09a	5.3a	1.88a	0.40a	2.28b	17.4b	82.6b
BOSQ. SECUN.	0-15	0.60a	0.51a	0.19a	4.9a	2.34a	1.30a	3.62a	31.0a	69.0a
	15-30	0.28a	0.25a	0.11a	5.1a	2.34a	0.64a	2.96a	20.9a	79.1a
	30-60	0.20a	0.14a	0.08a	5.2a	2.60a	0.42a	3.02a	13.6b	86.4a

Tabla 6. Materia orgánica, N total, C/N, P y elementos menores, muestras recolectadas en agosto 1988.

SITIO	PROFUNDIDAD (cm)	MO (%)	N (%)	C/N	P (mg/kg)	Cu (mg/kg)	Zn (mg/kg)	Mn (mg/kg)	Fe (mg/kg)
Str.	0-15	5.38ab	0.286b	10.9a	4.10a	17.4b	2.22b	57.4a	235a
exc.	15-30	3.86ab	0.222b	10.2a	4.16a	17.6a	1.74b	42.2a	199b
	30-60	2.20ab	0.130b	10.0a	3.98a	18.1a	1.52b	32.6a	132b
Dal.	0-15	5.44ab	0.266b	11.9a	4.96a	18.6b	2.64b	54.8a	281a
tuc.	15-30	3.72ab	0.218b	10.2a	3.76a	21.5a	1.92b	52.2a	235b
	30-60	2.14ab	0.128b	9.8a	3.14a	21.7a	2.14b	43.2a	145b
Voch.	0-15	6.42a	0.326a	11.4a	5.10a	23.4b	3.24b	61.4a	336a
ferr.	15-30	4.08a	0.216a	10.9a	4.42a	22.6a	2.22b	55.2a	203b
	30-60	2.22ab	0.122b	10.6a	3.24a	20.7a	1.96b	63.2a	166b
Voch.	0-15	5.34ab	0.28ab	11.0a	4.72a	22.9b	2.78b	78.0a	294a
hond.	15-30	3.12ab	0.186ab	9.8a	4.02a	26.6a	2.30b	52.6a	228b
	30-60	1.74ab	0.112b	9.0a	5.44a	30.8a	2.74b	39.6a	146b
Tab.	0-15	5.34ab	0.280a	11.0a	4.74a	20.8b	2.48b	78.0a	272a
rosea	15-30	3.26ab	0.176a	11.2a	3.36a	19.2a	1.74b	64.2a	184b
	30-60	1.80ab	0.112b	9.3a	2.26a	19.8a	2.78b	41.4a	101b
Dip.	0-15	4.82ab	0.260b	10.7a	4.00a	22.6b	2.34b	55.4a	267a
pan.	15-30	3.20ab	0.184b	10.1a	3.50a	21.4a	2.04b	53.6a	184b
	30-60	1.82ab	0.112b	9.3a	3.20a	24.2a	2.42b	42.0a	109b
PASTO	0-15	4.20b	0.250b	9.4b	4.56a	19.2b	2.56b	48.8a	293a
	15-30	2.90b	0.186b	8.9a	3.60a	23.8a	2.34b	35.0a	213b
	30-60	1.70b	0.128b	7.7b	2.84a	27.5a	3.34b	27.8b	86.8b
BOSQ.	0-15	6.30a	0.380a	9.6b	4.04a	25.4a	4.32a	61.6a	389a
SEC.	15-30	4.52a	0.282a	9.4a	2.94a	26.4a	4.20a	57.8a	356a
	30-60	2.90a	0.164a	10.6b	3.54a	27.5a	5.10a	40.4a	220a

Tabla 7. Niveles de parámetros del suelo utilizados para interpretar análisis de fertilidad, basados en procedimientos utilizados por el Ministerio de Agricultura de Costa Rica (Bertsch 1986).

Parámetro	Nivel		
	Bajo	Optimo	Alto
pH	5.0	5.5-6.5	7.0
cmol/l:			
Al		0.3	1.5
Ca	4.0	4-20	20
Mg	1.0	1-10	10
K	0.2	0.2-1.5	1.5
mg/l:			
P	10	10-40	40
Mn	5.0	5-50	50
Zn	3.0	3-15	15
Cu	1.0	1-20	20
Fe	10	10-50	50

Fig 1.

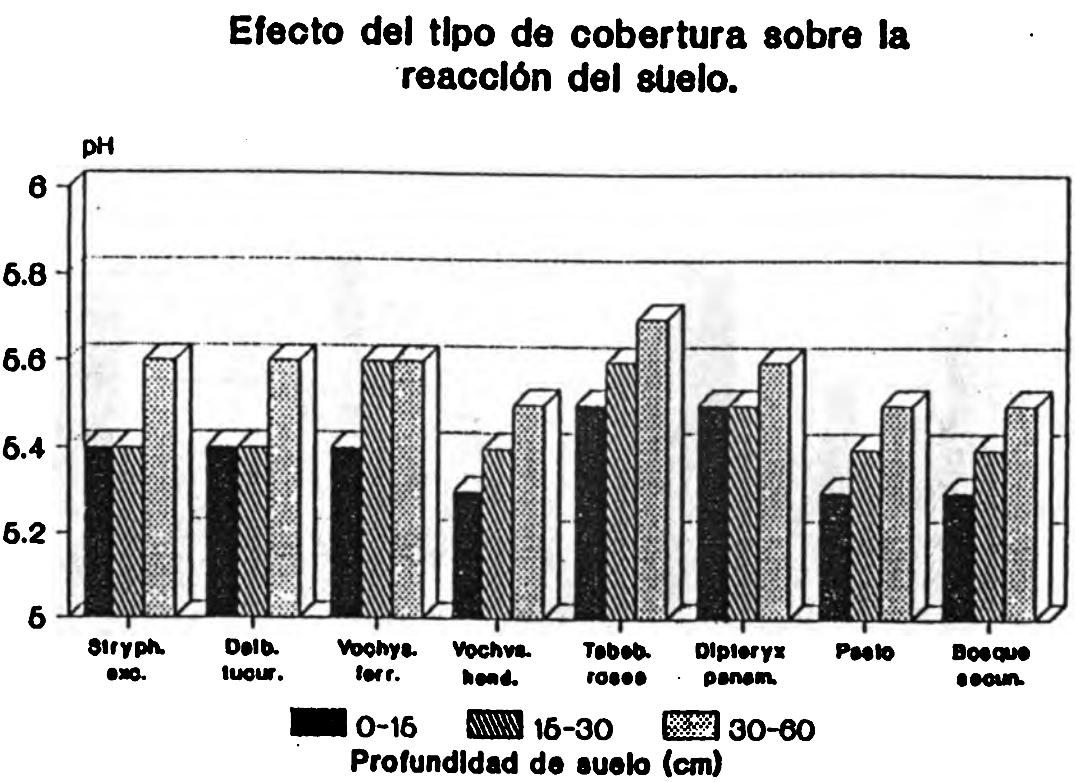

Efecto del tipo de cobertura sobre la
reacción del suelo.
pH
6
5.8
5.6
5.4
5.2
5
Stryph. exc.
Dalb. lucur.
Vochys. ferr.
Vochys. hond.
Tabeb. rosea
Dipteryx panam.
Pasto
Bosque secun.
0-15
15-30
30-60
Profundidad de suelo (cm)

Fig 2.

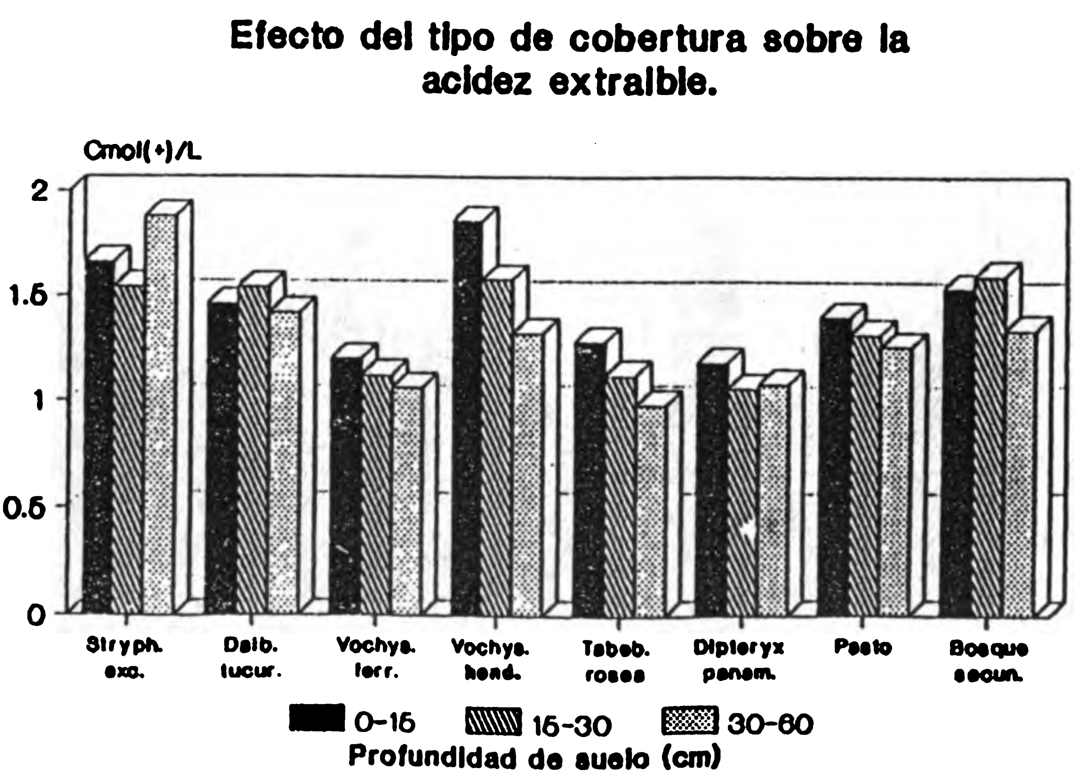

Efecto del tipo de cobertura sobre la
acidez extraible.
Cmol(+)/L
2
1.5
1
0.5
0
Stryph. exc.
Dalb. lucur.
Vochys. ferr.
Vochys. hond.
Tabeb. rosea
Dipteryx panam.
Pasto
Bosque secun.
0-15
15-30
30-60
Profundidad de suelo (cm)

Fig 3.

Efecto del tipo de cobertura sobre la suma de bases.

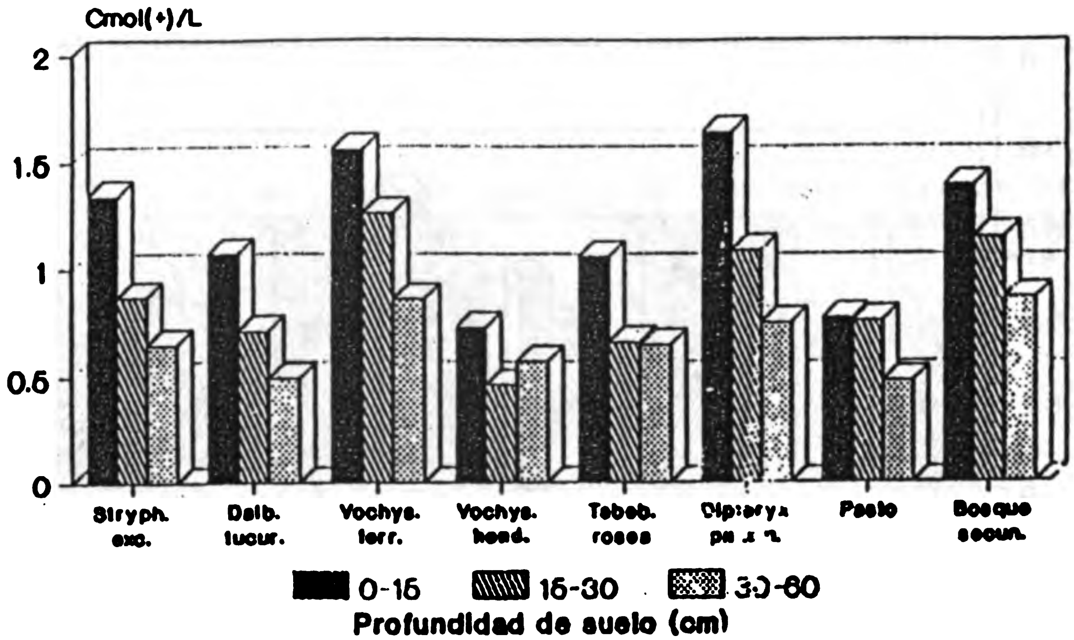


Fig 4.

Efecto del tipo de cobertura sobre la saturación de bases.

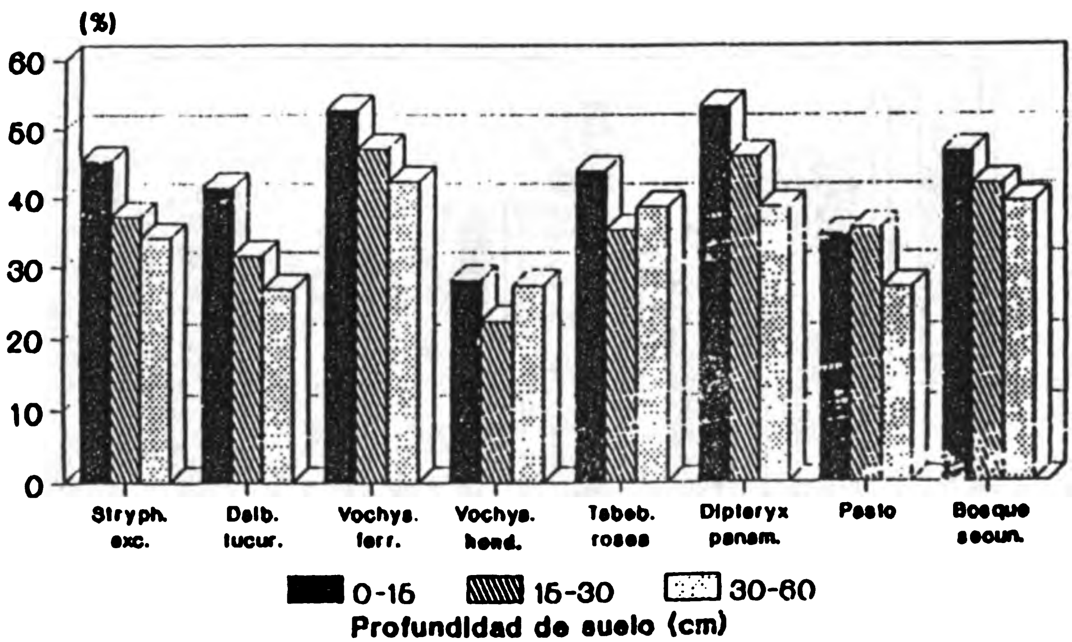


Fig 5.

Efecto del tipo de cobertura sobre el contenido de fósforo en el suelo.

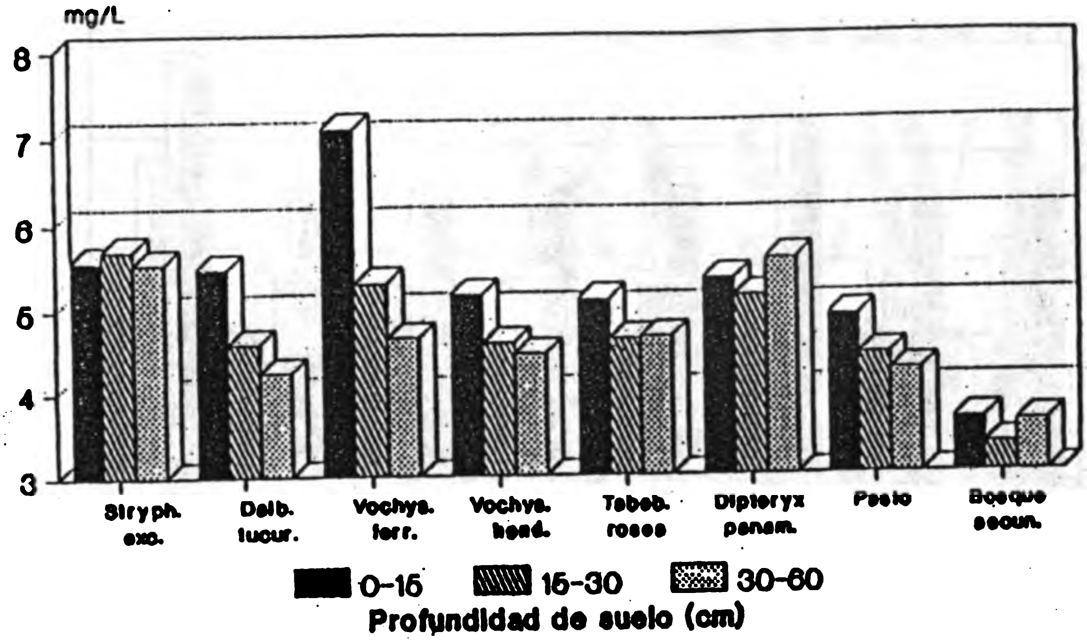


Fig 6.

Efecto del tipo de cobertura sobre el contenido de materia orgánica.

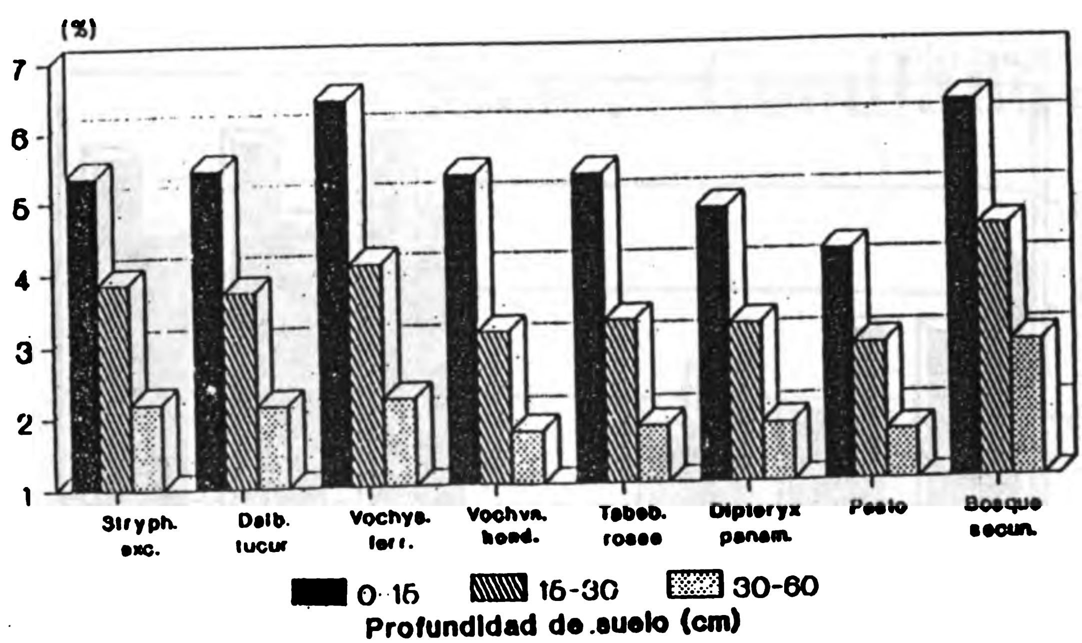


Fig 7.

Efecto del tipo de cobertura sobre el contenido de nitrogeno.

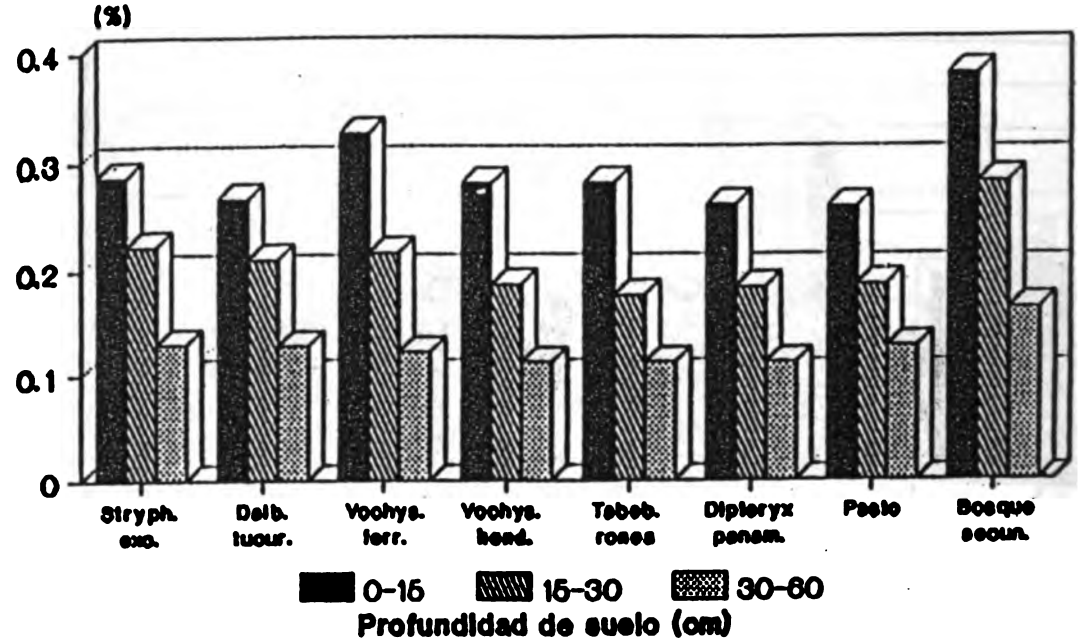
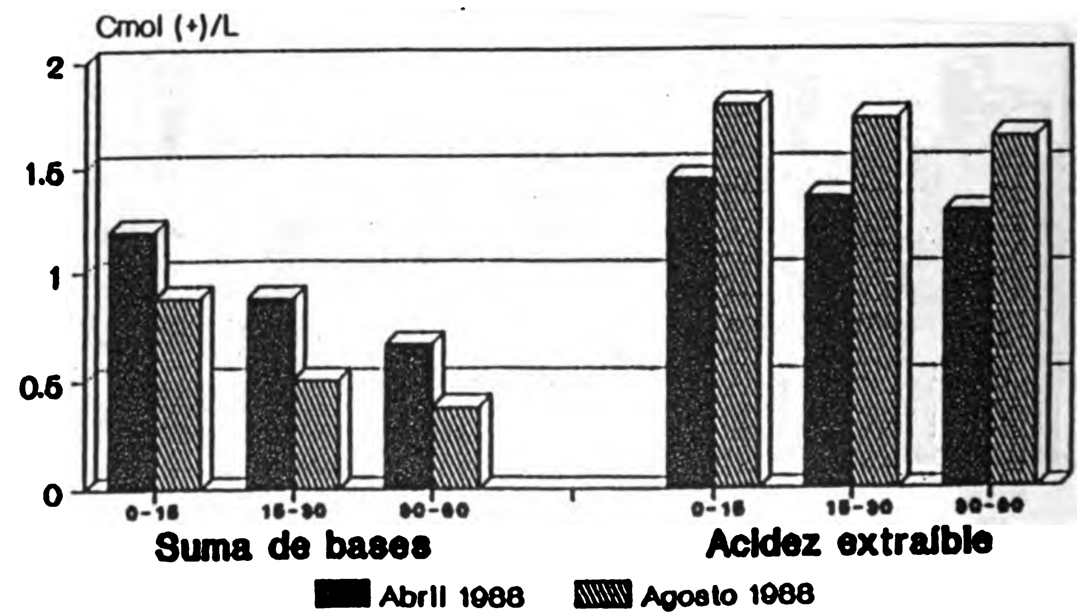


Fig 8.

Variación en la suma de bases y acidez extraible en dos muestreos.



RACE TO SAVE THE TROPICS

Ecology and Economics for a Sustainable Future

Edited by Robert Goodland

(1990)

ISLAND PRESS

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Race to Save the Tropics. Ecology and Economics for a Sustainable Future. Island Press. Washington, D.C.

Chapter 2

ECOLOGY APPLIED TO AGROFORESTRY IN THE HUMID TROPICS

FLORENCIA MONTAGNINI

In the lowland humid tropics, more and more often, we see the need to develop alternative land-use systems that contribute to supply timber, fuel wood, and other tree products without continuing the well-documented patterns of extensive agriculture, deforestation, and land resources degradation. Alternative land-use systems should be productive while at the same time help preserve natural resources. Agroforestry systems can contribute to these goals when properly implemented.

Agroforestry systems, which combine trees with crops or pastures, are one of the alternatives for sustainable land use in the tropics. The incorporation of trees in the production system can shade animals and crops; improve the nutrient status of the soil, especially when nitrogen-fixing species are used; control soil erosion; provide tree products such as timber, fuelwood, fruits, and forage; make better use of the land through the association of species; and diversify the system, thus decreasing economic risks of crop failure and dependence on markets.

Proper choice of tree species for agroforestry systems can decrease the need for fertilizers and pesticides. For example, nitrogen-fixing species can help maintain soil fertility. In agroforestry systems, the appropriate association of trees with crops can reduce the need for herbicides, and insecticides. Costa Ricans, for example, grow coffee under open sun in extensive, high-input plantations owned by large companies. Small farmers cannot afford to buy the agrochemicals required. But they can grow coffee in association with nitrogen-fixing trees and other species valuable for lumber, fruit, and other tree products. The coffee plantations are productive for many more years and provide benefits beyond their cash-crop function. At the same time the risk of crop failure and market dependence decreases when the crop is diversified.

CHOICE OF TREE SPECIES

In agroforestry systems soil-improving tree species help increase productivity of low-resource agriculture. The improved supply of forest and agricultural products decreases the pressure over natural forests and virgin lands. Using fewer agrochemicals diminishes soil and water pollution. Better protection of headwaters decreases soil erosion and helps maintain water supply for agricultural, industrial, and domestic use.

Since the 1950s more people have become interested in experimenting with agroforestry practices. Some of these practices have existed for centuries, but are not well understood from a scientific point of view. In the neotropics several agroforestry systems are integrated into current practices and others are being developed. But, in most cases, studies that can help us understand mechanisms that influence their performance are missing.

In the Latin American tropics, studies are being conducted to test the performance of trees for reforestation or for agroforestry (Cozzo, 1976; CATIE, 1986; and others). Exotic species such as *Leucaena leucocephala, Acacia mangium, Gmelina arborea, Eucalyptus* spp., and *Pinus* spp. are widely used in agroforestry, although these represent only a small fraction of the trees that might prove useful in the tropics (NAS, 1983). Researchers concentrate on a small number of exotic species because of the experience generated in years of trials, genetic improvement, and silvicultural experiments.

However, the incorporation of native tree species offers several advantages. Native trees are well adapted to the local environment and are thus less likely to be affected by pests, diseases, and adverse weather conditions. Because they are adapted to local soils and vegetation, the design of mixed systems (as in agroforestry) is more feasible. Native species are in better balance with the natural ecosystem and allow better preservation of habitats for wildlife. Hence they help preserve biological diversity. The spread of the use of native species in profitable systems will increase the appreciation for these resources and help preserve the native flora of potential economic value.

In Costa Rica, tree trials for forestry and agroforestry have included exotic and a few native, generally fast-growing species. These trials are being conducted by institutions such as the Forest Service (Dirección General Forestal, DGF), Centro Agronómico Tropical de Investigación y Enseñanza (CATIE) (see, for example, Alpízar et al., 1986, CATIE, 1986; Glover and Beer, 1986), and private enterprises. In most of the regions where these projects are being conducted, we need strategies to help restore soil fertility, to decrease soil erosion and compaction, and to protect headwaters. However, very few projects devote resources to studies of potential effects of these tree species on soil properties (Montagnini, in press).

Research projects are needed to help fill this gap. In some cases there are not even enough data on general soil properties in the established systems. Thus, very often we cannot interpret differences in performance between systems. As a general consequence, it is often risky to extrapolate the results to other areas. Failure or success remains related to local conditions, and years and resources spent in the trials are not as profitable as they could be.

The Organization for Tropical Studies (OTS) and the Costa Rican Forest Service (Dirección General Forestal, DGF) have been studying the performance of 14 native tree species since 1985 at the OTS La Selva Biological Station (at Puerto Viejo de Sarapiquí, in the Atlantic Lowlands of Costa Rica) with funding from the Canadian Embassy (Table 1). The original objectives of the project were to provide local farmers with information on the potential of native trees for plantation forestry and agroforestry by establishing demonstration plots for use in a community-based environmental education program. Currently, funding is being requested from the U.S. Agency for International Development (AID) for an independent project to use the native tree-species plots to measure effects of these species on soil properties. The results of this project will provide more information on the native trees and increase the value of the demonstration plots.

TABLE 1

SPECIES USED IN THE OTS-DGF NATIVE TREES TRIALS

Tree Species	Family	Common Name
Hieronyma oblonga	Euphorbiaceae	Pilón
Calophyllum brasiliensis	Guttiferae	Cedro María
Cordia alliodora	Boraginaceae	Laurel
**Dipteryx panamensis*	Papilionaceae	Almendro
Lonchocarphus velutinus	Papilionaceae	Chaperno
Vitex cooperi	Verbenaceae	Cacho de venado
Dalbergia tucurensis	Papilionaceae	Granadillo
Pterocarpus officianalis	Papilionaceae	Sangrillo
**Schizolobium parahyloum*	Caesalpiniaceae	Gallinazo
**Stryphnodendron excelsum*	Mimosaceae	Vainillo
**Tabebuia rosea*	Bignoniaceae	Roble de sabana
Terminalia spp.	Combretaceae	Surá
**Vochysia ferruginea*	Vochysiaceae	Botarrama
**Vochysia hondurensis*	Vochysiaceae	Chancho

* Species of better growth after one year.

In January 1987, OTS began a major project funded by the MacArthur Foundation to study the performance of exotic and native trees at La Selva, Costa Rica. It emphasizes growth performance of a large number of species; separate blocks were established for future use in studying the effects of 10 to 12 species on soil properties. Independent investigators can use the plots to study soil parameters and specific processes in far more detail than is planned in the MacArthur-funded project. Soil studies emphasize native tree species with the specific goal of putting existing regional resources into use for tree plantation and agroforestry.

A major contribution of OTS and CATIE to this area of applied ecology has been the production of the first agroforestry textbook in Spanish (OTS and CATIE, 1986), with funding from AID's Forestry Support Program. The book compiles information on the functioning of agroforestry systems, along with several case studies, bibliographies, inventories, and sources of information, covering most technical aspects. Besides its wide use as a university textbook and by extensionists, it represents a first step in gathering essential information useful as a starting point for a research program.

Soil-improving tree species are the key to the success of agroforestry systems. The performance of promising tree species and their effects on soil properties should be investigated in detail. This basic knowledge is needed before recommending the concept to farmers.

EFFECTS OF TREES ON SOIL PROPERTIES

The most important beneficial effects of trees on soil properties include improvement of soil structure and increase of soil nutrient availability. Deleterious effects such as decreases in soil acidity (pH) and soil nutrient content can also occur. Note, however, that this is a highly controversial issue (Cozzo, 1976; de las Salas and Fassbender, 1984; Lundgren, 1978; c.f. Sánchez et al., 1985) and that most of the reports of soil differences for different tree species do not indicate the processes involved (Lundgren, 1978).

Sánchez et al. (1985) concluded that the overall effect of mature fast-growing trees on nutrient availability is positive, but major differences exist among species. We also need to compare well-characterized soils, and to experiment with various tree/crop combinations compared with annual crops, pastures, or fallows to demonstrate to what degree trees improve or maintain soil properties in the humid tropics.

Tree species can influence soil pH, cations (calcium, magnesium, potassium), organic matter, and total nitrogen and phosphorus content and availability. For example, in a plantation of *Gmelina arborea* on an Ultisol soil in Brazil the soil pH was 5.2, while under *Pinus* (pine) the soil pH was 3.9—about the same as under native rain forest. The soil under *Gmelina* also had more exchangeable calcium (860 kilograms per hectare) than under pine (100) or native forest (40). Exchangeable manganese, exchangeable potassium, and total nitrogen under *Gmelina* were similar to rain forest, while the soil under pine had much lower potassium, magnesium, and total nitrogen content. Thirteen-year-old *Gmelina* plantations on Alfisol soil in Nigeria showed similar effects: an increase in soil pH from 4 to 5.5, a decrease in aluminum saturation from 58 percent to 6 percent, a two to three times increase in exchangeable calcium, and an increase in exchangeable manganese. Ten-year-old plantations of *Cordia trichotoma* and *Caesalpina equinata* showed a two to three times increase in exchangeable calcium, magnesium, and potassium, in comparison with the native forest; in contrast, no changes in soil properties were observed under *Dalbergia nigra*. These examples show how the effects of trees on soils differ among species.

Three species of eucalyptus exert the deleterious effect of extracting three to eight times more calcium and potassium from the soil than other forestry species, depending on silvicultural management. On the other hand, organic matter content was four times higher, and calcium, magnesium, and potassium content two times higher than in an adjacent pasture. Eucalyptus can absorb nutrients from deep layers of the soil with its 2- to 4-meter-deep root system, and contribute to increased soil nutrient content through litter-fall.

Controversial effects have also been reported for pine. Soils under an eight-year-old pine forest in Brazil had lower pH (4.2) and higher organic matter (5.3 percent) than an adjacent pasture of *Melinis minutiflora* 4.4 pH and 4.3 percent organic matter content. Soils under pine also had less calcium and much less potassium but higher magnesium content; there were no differences in phosphorus.

Apparently significant improvement of soil physical conditions—mainly increased porosity and decreased bulk density—occur only after tree canopy closure. Positive effects on soil physical properties are relevant in degraded lands where cattle have compacted soils, a common case in abandoned pastures in the humid tropics.

Obviously an understanding of the mechanisms whereby a tree species affects soil structure and nutrient availability is important to assess a species' true effects and to predict the outcome of its use. We must then use this understanding when designing agroforestry systems. In particular, knowledge of the effects of certain trees on soil properties can be used to achieve any management goals and to associate complementary tree/tree or tree/crop species.

THE ROLE OF APPLIED ECOLOGY: CASE STUDIES

Applied ecological projects can play a significant role by providing information needed for the design of successful systems. Studies of nutrient-cycling processes can be useful in the design and management of agroforestry systems, as the following examples illustrate.

Litter-fall (along with root decomposition) is frequently a main pathway of nutrient transfer (or recycling) from trees to soils. A thick layer of litter on the floor can also help maintain soil humidity and protect against soil erosion. These are also significant benefits from trees used for shade in agroforestry systems. For example, the net harvest output of nitrogen in a cacao plantation in Venezuela equaled the input of nitrogen to the soil in shade-tree leaf litter.

In Costa Rica, when organic matter and nutrients in the components of a system of cacao under shade trees were inventoried, leaf litter under the nitrogen-fixing leguminous tree *Erythrina poeppigiana* (commonly used in agroforestry systems in Costa Rica) was found to have more nitrogen than under *Cordia alliodora*, but less potassium, calcium, magnesium, and phosphorus. In another project in Costa Rica, the amount of nutrients recycled via litter-fall by associated trees (*Cordia alliodora* and *Erythrina poeppigiana*) was found to reach the recommended levels of fertilizer for coffee production.

Nitrogen-fixing trees are a prominent component of several agroforestry systems worldwide, because they can improve the performance of the associated crops or pastures. For example, nitrogen fixation by the leguminous tree *Inga jinicuil* was 53 percent of the average amount of fertilizer nitrogen applied annually on coffee plantations in Veracruz, Mexico. In Turrialba, Costa Rica, *Erythrina poeppigiana*, a widely used tree in agroforestry systems, was found to have a high potential for nitrogen fixation.

The influence of nitrogen-fixing tree species on soil nutrients other than nitrogen has also been reported, although the tendency has been to focus studies on effects on soil nitrogen and organic matter content. Soil properties in areas close and distant from *Erythrina glauca* trees in an old association with cacao in Brazil were compared: in three of five cases the pH was .2 to .3 units lower—closer to *Erythrina* than away from *Erythrina*. Phosphorus content was 50 percent lower under *Erythrina*, while calcium, magnesium, and potassium were twice as high under *Erythrina* than away from *Erythrina*. Soil bulk density was 1.55 under *Erythrina* and 1.61 away from this tree. It is interesting to notice the potential impacts of this nitrogen-fixing tree on phosphorus and soil pH.

Researchers in Costa Rica compared soils of cacao plantations associated with *Cordia alliodora* and with *Erythrina poeppigiana* trees. Soils under cacao plus *Erythrina* had 6 percent less phosphorus, 15 percent more organic matter, 22 percent more calcium, 15 percent more magnesium, and 19 percent more potassium than under *Cordia*. The effects of nitrogen-fixing species on soil nitrogen and cations can be positive, but questions arise as to their effects on soil pH and phosphorus content. We need comparisons of soil cations, phosphorus, nitrogen, organic matter, and pH between soils under nitrogen-fixing and other tree species to assess more realistically the role of nitrogen fixing and other tree species on these soil parameters.

Other projects stress the need of applied ecology to contribute to the design of agroforestry systems. In a hypothetical model of nitrogen, phosphorus, and potassium for a cacao/coconut association in Brazil, leaching of potassium was approximately 50 percent less than in a coconut monoculture. The appropriate choice of species for an association can thus contribute to nutrient conservation.

In southeast Bahia, Brazil, failure to expand promising agroforestry practices to a desirable extent was ascribed to the lack of scientific knowledge on the subject. As part of a crop diversification program in the traditional cacao-growing area, farmers combined clove trees with coffee or coconuts, cloves with passion fruit, papaya and coffee, cloves and vanilla, cardamom and coffee, and rubber trees, cacao, and other groups. This was successful, but the practitioners of these systems would not easily divulge the information on the management and production particulars in their farms. We need much more research and development if we are to realize the full potential of these systems.

PROMOTION OF APPLIED ECOLOGICAL PROJECTS

Applied ecological projects of the kind listed above may not always appeal to scientists who are interested in asking very specific questions and doing more sophisticated hypothesis testing. Since so much basic information is missing, many of these applied studies must start with preliminary inventories and comparisons. However, so many mechanisms of these systems need elucidation that it is hard to believe that scientists would not be stimulated to examine them. The implementation of applied ecology projects can be encouraged by science administrators who promote the funding of projects that would not be considered under their regular programs; by university professors and researchers from other academic institutions who encourage graduate students and fellow scientists to do theses and projects in the tropics; and by the scientific community as a whole, which can bridge the gap between basic and applied ecology and thus contribute to stimulating the kind of projects that are needed for this purpose.

Agroforestry systems—the combination of trees with crops or pastures—can be a productive and environmentally sound alternative land-use in the humid tropics. The choice of appropriate tree species is key to the success of these systems. Tree species differ widely in their effects on soils and in their nutrient requirements. The effects of tree species (including nitrogen-fixing trees) on soil properties remains controversial. We very much need projects that examine the performance of native tree species in agroforestry combinations, the effects of different tree species on soil properties, and tree/crop combinations that contribute to efficient nutrient usage and soil nutrient conservation. Applied ecology projects can contribute basic information on the systems to support the recommendations given to farmers.

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Multipurpose Trees for Soil Restoration in the Humid Lowlands of Costa Rica

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Summary

This paper describes impacts of seven native species of economic value (*Stryphnodendron excelsum, Dalbergia tucurensis, Dipteryx panamensis, Vochysia ferruginea, Vochysia hondurensis, Tabebuia rosea* and *Hyeronima oblonga*) on soil fertility and nutrient cycling in the humid lowlands of Costa Rica. Results of a three-year study of pure plantation stands revealed that soil conditions were improved: in the top 15 cm, soil nitrogen and organic matter were higher under the trees than under grass, with values close to those found in an adjacent 20-year-old forest. Highest values for soil organic matter, total N, Ca and P were found under *V. ferruginea*. Soil nitrate and increased soil N mineralization were higher under the two leguminous species, *S. excelsum* and *D. tucurensis*.

Litterfall was higher under *V. ferruginea, V. hondurensis* and *S. excelsum*. *D. tucurensis* had the highest concentrations of N, P, Ca, Mg and K in living leaf and in litter tissue, but there was greater accumulation of forest floor litter under *V. ferruginea* and *V. hondurensis*. Greatest understory biomass was found under *T. rosea, S. excelsum* and *D. tucurensis*. The highest nutrient concentrations in understory biomass were found under *S. excelsum* and *D. tucurensis*.

Other investigations used the four best-growing species of this experiment: *S. excelsum, V. ferruginea, V. hondurensis* and *H. oblonga*. *H. oblonga* and *V. ferruginea* had the highest biomass of fine roots (< 1 mm) in the 0-15 cm soil depth, while *S. excelsum* and *V. hondurensis* had a more even root distribution in the soil profile. In a study of leaf litter decomposition, *V. ferruginea* showed the slowest rate of weight loss. When leaves of these four species were mixed with soil as mulches for a maize crop, initial maize growth was better with *S. excelsum* and *H. oblonga*.

Introduction

Agroforestry systems and tree plantations can help restore soil fertility of locations that have been abandoned after extensive use for agriculture or cattle raising. Information on native species that can be used for soil restoration in the tropics is scarce. Native trees can be more appropriate than exotics because (1) they are better adapted to local environmental conditions, (2) seeds and other propagules are locally available, and (3) farmers are familiar with them and their uses.

In the Atlantic lowlands of Costa Rica, the Costa Rican Forest Service, Direccion General Forestal (DGF) is conducting experiments on the growth performance of tree species for plantation. Among the species currently recommended by DGF to farmers (*Gmelina arborea, Pinus caribaea, Eucalyptus deglupta* and *Cordia alliodora*), only *C. alliodora* is native to the region. In 1985, DGF established a plantation of 13 native tree species at the La Selva Biological Station of the Organization for Tropical Studies (OTS). After three years, four of these species (*Stryphnodendron excelsum, Vochysia hondurensis, Vochysia ferruginea* and *Hyeronima oblonga*) exhibited growth rates equal to or greater than those reported for

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the officially recommended species (Espinoza and Butterfield 1989). In 1988, we initiated an independent study on the impacts of seven species in this experiment on soil fertility and mechanisms of nutrient recycling (Montagnini and Sancho 1990a, 1990b). Here we report on the impacts of trees on soil fertility, rates of litterfall and litter decomposition, root biomass, and nutrient recycling. The results are being used to design tree-based productive systems such as agroforestry combinations and mixed tree plantations. The results may also apply to other humid tropical areas with similar soils.

Study site

The experimental plantation was established in December 1985 on abandoned pasture at the OTS La Selva Biological Station. Soils are Fluventic Dystropepts derived from alluvially deposited volcanic materials; they are deep, well drained, stone-free, with low or medium organic matter content, moderately heavy texture, and generally acid and unfertile (Sancho and Mata 1987). The area had been cleared in the 1950s and grazed until 1984. The dominant species in the pastures were grasses (*Olyra latifolia, Melinis minutiflora*), ferns (*Pteridium* sp.), and bushes (*Psidium guajava* and *Piper culebranum*). In the pastures there were patches of approximately 20-year-old forest with: *Pentachlethra macroloba*, a mimosoid, N-fixing legume dominant in the primary forest at La Selva; *Piper culebranum*, and species of the Melastomataceae family; and ferns (*Pteridium* spp.) and tree seedlings in the understory. The site was cleaned manually before planting. The tree species were planted in a randomized block design with five replicates, each plot containing seven rows of seven trees (14 m x 14 m each), with two meters between trees. Five 14 m x 14 m plots were also established in an adjacent open area with grass, and in a nearby patch of secondary forest. During the first year, weeds were manually cut four times; weeding was done mechanically thereafter until canopy closure made it no longer necessary. The grass was weeded simultaneously to keep it free of trees and with comparable treatments

The seven species used for our comparis of soil fertility and nutrient recycling are presented in Table 1. The criteria for specie selection were: (1) good growth, (2) presence of root nodules in the leguminous species, and (3) other potentially important effects o soils. Although it does not fix nitrogen, the leguminous *D. panamensis* was included because it has wide distribution in tropical Latin America (Holdridge and Poveda 1975 *V. ferruginea* is a self-pruning pioneer specie that forms uniform, even-aged stands in abandoned fields; its wood is used for plywood and construction. Botanical characteristics and general uses of all the species are described by Holdridge and Poveda (1975), Hartshorn (1983), Standley (1937-38), and Hartshorn and Hammel (unpublished). All the species have econon uses (timber of medium to high quality) anc seeds are available from natural forests at

Table 1. Species studied for their effects on soils and nutrient cycling.

Scientific name	Common name	Family
Stryphnodendron excelsum	vainillo	Leguminosae (mimosoid)
Vochysia ferruginea	botarrama	Vochysiaceae
Vochysia hondurensis	mayo	Vochysiaceae
Hyeronima oblonga	pilon	Euphorbiaceae
Dalbergia tucurensis	granadillo	Leguminosae (papilionoi
Dipteryx panamensis	almendro	Leguminosae (papiliono:
Tabebuia rosea	roble sabana	Bignoniaceae

*Does not fix nitrogen.

La Selva and elsewhere in the region. Detailed studies on seed and germination characteristics are presented by Gonzalez (in press).

Initial selection of species for studies of impacts on soils was made in 1987, when the plantation was 2.5 years old. In 1988, *H. oblonga* was added due to its better growth that year; *T. rosea* was dropped due to stunted growth. In 1989 and 1990, detailed studies on root biomass and litter decomposition concentrated on the four most promising species (i.e., best growth): *S. excelsum*, *V. ferruginea*, *V. hondurensis* and *H. oblonga*.

Materials and Methods

Soil fertility

For general chemical characteristics of the soil, samples were taken with a "Dutch type" corer at 0-15, 15-30, and 30-60 cm depth. During the first year, soils were sampled in April (dry season) and August (rainy season); in 1989 and 1990, soils were sampled in May only (end of dry season). Chemical analyses were performed at the Soils Laboratory of the College of Agriculture, University of Costa Rica, following standard methods currently used by soil testing laboratories in the country. The pH was measured in a 1:2.5 mixture of soil: de-ionized water using a Corning 7 pH meter. Ca and Mg were extracted with a 1 N KCl solution, while P, K, and micronutrients were extracted with a modified Olsen solution (Diaz Romeu and Hunter 1978). Cations were measured using a Perkin Elmer 2380 Atomic Absorption Spectrophotometer. P was measured colorimetrically after reaction with acid $(NH_4)_2MoO_4$ and $SnCl_2$, using a Perkin Elmer-Coleman 295 Spectrophotometer. Organic matter was measured with the Walkley-Black technique (Allison 1975) and total N was measured using a semi-Micro-Kjeldahl technique (Bremmer and Mulvaney 1982).

Soil nitrogen mineralization

For N mineralization and nitrification studies, soils were sampled at 0-15 cm with a 2.5 cm diameter soil corer, using the same plots as for soil general chemistry. These measurements were taken quarterly, starting in May 1989. NO_3-N and NH_4-N were extracted on field moist soils with 2 NKCl, and measured using a Lachat Flow Injection Analyzer. One subset of samples was extracted immediately after sampling; another subset was incubated in plastic cups in the laboratory (Keeney 1982) for seven days. The difference between final (after incubation) and initial NO_3-N concentration or NO_3-N + NH_4-N concentration gave the net nitrification or net N mineralization potential rates, respectively. These measure soil N availability (Keeney 1982).

Nutrient concentration in living biomass

To obtain an indication of nutrient requirements and potential effects on nutrient cycling, living tree tissue was sampled in August 1989. Using a pole pruner, leaves and branches were harvested from one tree per plot for the seven species. At least two whole branches of opposite orientation on the upper portion of the canopy were sampled. Leaves from the tip, medium, and lower portions of each branch were pooled to obtain one sample per tree. Portions of tip, medium, and bottom parts of branches were cut and pooled in the same manner. Taking advantage of plot thinning performed in August 1989, we were able to obtain stem samples (lower, medium, and bottom parts) of *S. excelsum*, *V. ferruginea* and *V. hondurensis* for chemical analysis. *H. oblonga* plots were thinned in July 1990, at which time we also obtained stem samples for chemical analysis. Roots were sampled as described below; subsamples were also analyzed for their nutrient content. The material was oven-dried at 70°C and ground for chemical analysis. The total N, P, Ca, K, Mg, Cu, Fe, Zn, and Mn were measured on nitro-perchloric digests: N and P were measured using a Lachat Flow Injection Analyzer, while cations were measured using an Atomic Absorption Spectrophotometer.

Biomass and nutrient concentration of understory vegetation

Biomass and nutrient concentration of herbaceous vegetation growing under the seven species were measured in August 1989 to assess the contribution of the trees to nutrient redistribution. Grass and other herbaceous vegetation were cut at ground level by hand using 50 x 50 cm iron frames to define the sample area. The material was oven-dried and analyzed in the same manner as tree tissue.

Root biomass and chemistry

Roots were sampled in May-June 1989 in *S. excelsum*, *V. ferruginea*, *V. hondurensis*, *H. oblonga*, grass, and secondary forest using an 80 mm diameter x 150 mm length root auger (Stijfhoorn 1989). Sampling sites within each plot were chosen randomly in areas within 1 m from the trees. Two root cores from 0-15, 15-30, and 30-60 cm depth were obtained per plot. The roots were separated from the soil by manual wet sieving, and divided into four size classes: fine (< 1mm), medium fine (1-2mm), medium coarse (2-5mm), and coarse roots (> 5mm). Roots in all categories were oven-dried and weighed. For chemical analysis, roots from 1-5 mm were pooled together, thus having three categories: < 1, 1-5, and > 5mm. Chemical analysis was performed as described above.

Litter fall

Litter was collected from 90 x 55.5 cm litterfall traps made of a wooden frame with fiberglass screen bottoms (1 mm mesh size), set at 50 cm above the ground. There was one trap per plot for the seven species of the study, 35 traps total. The traps were emptied every two weeks, their contents oven-dried (70°C), sorted (leaves and branches), and weighed. Collections began in April 1988 and continued through 1989-90. Chemical analyses, as described above, were performed on samples of leaf and branch litter collected in April, July, and October 1989.

The amount of litter accumulating on the ground under the seven species was measured in August 1989, December 1989, and in March, May, and August 1990. A 50 x 50 cm iron frame (one per plot) was used to demarcate an area in which all material to the top of the mineral soil was collected. The material was oven-dried, sorted (whole leaves, fragments, branches, and dry grass of understory vegetation), and weighed. Chemical analysis was performed on the material collected in August 1989.

Litter decomposition

Litter bags were weighed and sampled every two weeks for seven weeks. Approximately 2,500 g of whole leaves were collected from each species plot for *V. ferruginea*, *V. hondurensis*, and *H. oblonga*. Only leaves with complete or almost complete margins were chosen. Leaves from *S. excelsum*, leaflets and rachis of which are difficult to collect from the ground, were collected fresh. All leaves were dried at 70°C prior to filling litter bags.

Litter bags (50cm x 50cm) were constructed out of plastic mesh (average mesh size 2mm x 2mm). Each bag was filled with 100 g of dried leaves, weighed to 0.1 g.

The subplots were designated randomly in each of the four species plots, which were replicated five times. An area slightly larger than the litter bags was cleared of leaf litter; once the bags were in place they were covered with most of the displaced litter. The soil under the bags was exposed but not entirely bare of decomposing leaves. Within each plot, each subplot represented a different treatment of its corresponding litter bag. These treatments were: (1) Undisturbed throughout the duration of the experiment; (2) Weighed, but not subsampled; (3) Subsampled and weighed at two-week intervals.

Subsampling consisted of removing 30-60 of the field weight of the leaves, which were then dried at 70°C to determine a field weight:dry weight ratio. After subsampling, the bags were returned to the field. The experiment ran from 6 June to 25 July, 1990. On the final pick-up, the bags were destructively sampled and residual mud was cleaned off the leaves before drying and weighing.

For the sampled bags, weight loss due to decomposition was calculated by comparing the expected weight loss (loss due to sample removed) with the actual weight loss. The actual weight loss was determined by the wet:dry ratio of the sample from each bag. For each species, the weight loss due to decomposition was calculated from its 100 g initial weight (for the sampled bags) and from the final dry weight of the leaves when the bags were destructively sampled at the end of the experiment (for all treatments).

Mulch experiment

In the mulch experiment, maize seedlings were grown for 40 days in small plots mulched with the litter of the four species used in the litter decomposition study mentioned above. In preparation, a small amount of pasture on the north side of the tree trials (7m x 7m) was cleared to soil level. In this clearing, 25 plots measuring 50 x 50 cm each and spaced 30 cm apart were laid out in a square, five plots on each side. Grass was cleared within 1-2 m of the plots, shade and sun patterns were consistent over the plots, and a chicken-wire fence was erected around the entire experiment area. For each treatment, including the control with no mulch, there were five replicates; all were set at random.

For mulch, 100 g of dried leaves of each species were "scrunched" and incorporated into the top 10-15 cm of soil in an appropriate plot with a trowel. After a week, each plot was planted with 25 maize seeds. The maize was a local, non-hybrid variety that had been cleaned and culled beforehand. After cleaning it exhibited a 96% germination rate in the lab. The seed was planted at 3 cm depth, 8-12 cm apart, using a planting dibble. Ten days after planting (approximately one week after germination), 100 g scrunched leaves were again laid on the soil in the maize plots. All but two plots experienced an initial germination rate of at least 92%.

Maize seedlings were measured at 10-day intervals, beginning 10 days after sowing. The height of each seedling was recorded according to the "reach" of the entire plant along a meter stick held parallel to it. Forty days after planting, the maize seedlings were carefully dug up. Shoots and roots from the top 10-15 cm of soil were washed, separated (shoots from roots), oven-dried, and weighed.

Results and Discussion

Soil fertility

Results from April 1988, revealed that organic matter and total N were higher in the tree plantation than in grass, with values close to those of secondary forest (Montagnini and Sancho 1990a, 1990b). In just 2.5 years, there was an increase in soil organic matter in the upper 15cm, from a mean of 4.83% in grass to 5.31-6.60% in the plantation. The highest mean value in the plantation (for *Vochysia ferruginea*), was close to the mean in the secondary forest (7.58%); a similar trend was found at 15-30 and at 30-60 cm. Total N in the tree plantation was 0.26-0.32%; these values are again higher than in grass, with the highest, under *V. ferruginea*, close to the mean in the forest (0.33%).

The soil P concentrations were higher in the plantation than in grass, and lowest in the forest (Montagnini and Sancho 1990a, 1990b). This is probably due to immobilization of P in plant biomass and in soil organic matter in the forest. Cu concentrations exhibited a similar trend (higher in the tree plantation, lower in grass and forest). The pattern for Zn, Mn and Fe was similar to that of Ca and Mg. Soil Ca and Mg content were higher in the plantation than in grass, with values close to those in the forest. Within the tree plantation, there were no significant differences among species in soil cation content. However, there was a trend of higher Ca under *D. panamensis* and *V. ferruginea*, higher Mg under *S. excelsum and D. panamensis*, and higher K under *S. excelsum, D. tucurensis, D. panamensis* and *V. ferruginea*. Based on levels determined by the Ministry of Agriculture of Costa Rica for soil fertility assessments (Bersth 1986), these higher cation values were close to those acceptable for agricultural crops. Under the species mentioned above, soil Mg and K were at or above the critical levels for agriculture, representing an improvement over the grass in only 2.5 years (Montagnini and Sancho 1990a, 1990b).

Results of measurements taken in August 1988 showed similar trends of differences among sites (Montagnini and Sancho 1990a), but the soil base content was lower. This was accompanied by higher soil exchangeable acidity, possibly resulting from leaching of bases during the time of peak precipitation (457 mm in August, in comparison with only 43.6 mm in April 1988, data from La Selva weather station). Results of similar measurements done in May 1989 and May 1990 showed trends similar to those found in 1988 (Montagnini and Sancho, unpublished data).

A close relation between organic matter content and sum of bases was found (Montagnii and Sancho 1990a, 1990b), indicating that organic matter was responsible for much of the cation retention capacity. Thus, poor management practices of repeated burning, lack of good soil cover, over-grazing, and compaction — all of which tend to decrease organic matter content (Sanchez 1976) — could significantly lower soil fertility to a point from which recovery is very difficult. By contrast, tree planting with species that tend to increase organic matter content (like some tested in this project), would tend to increase and maintain soil fertility. For example, a 1-2% increase in soil organic matter in the range of 4-6% would more than double base content (Montagnini and Sancho 1990a, 1990b), reaching values in the range recommended for agriculture (Bertsch 1986).

Soil N mineralization

Measurements taken in May 1989 (Montagnini and Sancho 1990b) showed that soil NO_3-N concentrations at 0-15 cm depth were higher in grass (Table 2), possibly due to the presence of leguminous herbs which were invading the area. Within the plantation, NO_3-N was higher under *S. excelsum*, with values similar to those under forest, and there was a trend of higher concentration under *D. tucurensis*. There were no statistically significant differences in NH_4-N or in total N mineralization potential rates. The highest net nitrification was under *S. excelsum*, followed by grass, forest and *D. tucurensis*. There appeared to be a trend of higher NO_3-N production under N-fixing species in the plantation, although rates of N fixation in the young plantation possibly were still too low to result in significant changes in soil N availability and total N content. Current analysis of data from 1989 and 1990 measurements is revealing trends similar to those found in May 1989 (Montagnini and Sancho, unpublished data).

The results above suggest a potential ameliorating effect of these native tree species on soil fertility, especially with respect to organic matter and base content. It is emphasized that these effects were occurring at an early stage, during the first 2-4 years of plantation establishment. This should be stressed as a great advantage where pressure exists to produce timber or fuelwood quickly and improve soil fertility in degraded areas. This relatively quick, positive impact on soil fertility will greatly facilitate demonstration of the potential benefits of using these species in plantations or tree-crop combinations.

Developing recommendations for farmers requires understanding of the mechanisms potentially responsible for these responses. The following sections suggest several possible causes and help toward an understanding of the role of each species.

Nutrient concentrations in living tree biomass

The N, Ca, K, Mg, P, Fe, Cu, Zn and Mn concentrations in leaves and branches of the seven species of this study are shown in Table 3. There were significant differences in nutrient concentrations in leaf tissue, except for Fe and Cu ($p = 0.05$). The two N-fixing species (*D. tucurensis* and *S. excelsum*) had the highest N concentrations in leaf tissue. *V.*

Table 2. Soil nitrate and ammonium concentrations, net nitrification, and net N-mineralization potential rates (0-15 cm depth, May 1989).

	NO_3-N (mg/kg)	NH_4-N (mg/kg)	Nitrification (mg NO_3-N $kg^{-1}d^{-1}$)	N mineralization (mg NO_3-N + NH_4-N $kg^{-1}d^{-1}$)
S. excelsum	2.52^{bc}	7.30^{a}	4.75^{a}	5.01^{a}
D. ucurensis	1.99^{c}	6.83^{a}	2.96^{bc}	2.96^{a}
V. ferruginea	0.81^{c}	7.05^{a}	0.88^{d}	0.49^{a}
V. hondurensis	0.76^{c}	4.36^{a}	1.24^{d}	0.60^{a}
T. rosea	0.34^{d}	6.34^{a}	1.46^{cd}	1.96^{a}
D. panamensis	0.53^{d}	5.84^{a}	1.26^{d}	0.53^{a}
Grass	5.62^{a}	7.77^{a}	3.80^{ab}	4.00^{a}
Forest	2.82^{b}	6.73^{a}	3.49^{ab}	2.79^{a}

Values followed by the same letter do not differ significantly at $p = 0.05$.

Table 3. Tree tissue composition (August 1989).

	N	Ca	K	Mg	P	Fe	Cu	Zn	Mn
			(%)				(mg/kg)		
Leaves									
S. excelsum	2.25^{b}	0.47^{d}	0.76^{c}	0.22^{c}	0.20^{ab}	91.8^{b}	21.0^{b}	1.8^{bc}	53.0^{ef}
D. tucurensis	2.52^{a}	1.01^{b}	1.20^{ab}	0.49^{a}	0.23^{a}	172^{b}	36.0^{ab}	73.2^{a}	1149^{a}
V. ferruginea	1.58^{d}	1.06^{ab}	0.41^{d}	0.25^{c}	0.18^{ab}	450^{a}	42.5^{a}	15.5^{cd}	321^{bc}
V. hondurensis	1.49^{d}	1.22^{a}	0.29^{d}	0.41^{b}	0.09^{c}	189^{b}	25.0^{b}	11.4^{d}	181^{de}
T. rosea	1.78^{c}	0.71^{c}	1.22^{a}	0.52^{a}	0.19^{ab}	94.2^{b}	27.0^{bc}	17.0^{cd}	40.4^{f}
D. panamensis	1.78^{c}	0.67^{c}	0.99^{b}	0.20^{c}	0.18^{ab}	140^{b}	26.8^{bc}	25.4^{b}	233^{cd}
H. oblonga	1.81^{c}	1.02^{ab}	0.71^{c}	0.41^{b}	0.15^{b}	252^{ab}	31.4^{ab}	29.0^{b}	372^{b}
Branches									
S. excelsum	0.93^{b}	0.44^{bc}	0.70^{cd}	0.15^{c}	0.15^{ab}	76.4^{b}	22.6^{bc}	33.2^{a}	31.4^{c}
D. tucurensis	1.17^{a}	0.70^{a}	0.77^{c}	0.25^{b}	0.22^{a}	155^{a}	49.4^{a}	37.2^{a}	276^{b}
V. ferruginea	0.29^{d}	0.36^{c}	0.56^{de}	0.10^{c}	0.09^{b}	58.4^{b}	22.6^{bc}	15.8b	411^{a}
V. hondurensis	0.29^{d}	0.44^{bc}	0.49^{e}	0.16^{c}	0.12^{b}	54.8^{b}	22.0^{c}	13.2^{b}	490^{a}
T. rosea	0.54^{c}	0.60^{ab}	0.97^{b}	0.35^{a}	0.22^{a}	58.6b	34.0^{b}	37.6^{a}	28.6^{c}
D. panamensis	0.52^{c}	0.56^{ab}	0.59^{de}	0.10^{c}	0.15^{ab}	45.2^{b}	23.4^{bc}	12.8^{b}	81.0^{c}
H. oblonga	0.55^{c}	0.59^{ab}	1.14^{a}	0.15^{c}	0.17^{ab}	66.0^{b}	24.2^{bc}	13.4^{b}	91.0^{c}
Stems									
S. excelsum	0.49^{a}	0.81^{b}	0.20^{b}	0.04^{b}	0.07^{a}	172^{a}	5.8^{a}	15.4^{a}	18.6^{b}
V. ferruginea	0.17^{b}	1.12^{b}	0.23^{b}	0.10^{a}	0.09^{a}	125^{a}	4.0^{a}	11.3^{a}	1040^{a}
V. hondurensis	0.26^{b}	1.46^{a}	0.42^{a}	0.12^{a}	0.09^{a}	249^{a}	4.4^{a}	11.4^{a}	641^{a}

Values followed by the same letter do not differ significantly at $p = 0.05$.

ferruginea and *V. hondurensis* had the lowest N concentrations, but they had relatively high Ca concentrations. *D. tucurensis* also had high Ca concentrations in leaf tissue, as well as high Mg, K, P, Cu, Zn and Mn concentrations. *T. rosea* also had high K and Mg concentrations. *H. oblonga* had relatively lower or intermediate concentrations of most nutrients. *S. excelsum* had relatively low Ca, K and Mg concentrations. Similar trends held for branch tissue, with lower general values than those for leaves.

Data for comparison of stem nutrients was available for only three species. Stems had lower N concentrations than either leaves or branches (10-20% of leaf values), with the highest value found in *S. excelsum* (Table 3). Stems also had relatively low P, but differences among species were not statistically significant. The Ca values in stems were similar or greater than those of leaves, with the highest in *V. hondurensis*, which also had the highest stem K and Mg.

Table 4 shows that fine roots had higher nutrient concentrations than medium and coarse roots. Of the four species compared, *S. excelsum* had the highest N, Ca and Zn concentrations in the fine root fraction. *H. oblonga* had the highest Mg and Mn concentrations, while *V. ferruginea* and *V. hondurensis* had the highest P and Cu.

These data suggest that the two N-fixing species have the greatest potential for recycling N from their tissue as leaf, branch, or root litter, while *V. ferruginea*, *V. hondurensis* and *T. rosea* may recycle more cations or P. However, this should be examined in conjunction with litter production and decomposition rates. Data on stem nutrient concentrations will be useful in calculating total tree biomass and nutrient content for estimates of total nutrient loss from the site at harvest.

Biomass and nutrient concentration of understory vegetation

There was no understory vegetation in either *V. ferruginea* or *V. hondurensis* plots, probably because these two species had completely closed canopies at the time of sampling and light levels underneath were very low. The largest biomass of understory vegetation was found in *T. rosea* plots, which performed most poorly and thus allowed more light and growth of grasses. Abundant understory growth was found also in *S. excelsum* and *D. tucurensis* plots (Table 5).

In understory vegetation, the highest N concentrations were found under *S. excelsum* and *D. tucurensis*, the highest Ca was found under *D. tucurensis* and *H. oblonga*, and the highest K and Mg were found under *D. tucurensis*. Differences among other nutrients were not statistically significant.

When biomass of understory vegetation was multiplied by nutrient concentrations, differences in nutrients on a g/m^2 basis were not statistically significant, but there was a trend of higher nutrient content under *T. rosea* and *D. tucurensis* (Table 5a and b).

The two N-fixing species appear to have indeed recycled N from their tissues, with the increased N being used by the associated vegetation. Consistent with findings of higher Ca and Mg in *D. tucurensis* tissue, recycling of these cations appears greater under this species. Data on litterfall and decomposition should clarify these mechanisms.

Root biomass

Overall, the forest area had the highest total root biomass (all size classes) in the top horizon. Within root-size classes, however, the plantation as a whole had greater fine-root biomass than the grass, with values similar to that of the forest (Figure 1). Among the four species compared, *H. oblonga* and *V. ferruginea* had the highest fine-root biomass in the top soil horizon. *H. oblonga* also had the highest medium-fine and medium-coarse root biomass. The forest had the highest coarse root biomass in the top soil, followed by *S. excelsum*.

In the intermediate and lower horizons, *V. ferruginea* and the forest plots again had more fine (>2mm) and medium-fine (>5mm)

Table 4. Root tissue composition (August 1989).

	N	Ca	K	Mg	P	Fe	Cu	Zn	Mn
			(%)				(mg/kg)		
Root diameter									
<1 mm									
S. excelsum	1.68^{a}	0.42^{b}	0.08^{bc}	0.16^{b}	0.07^{c}	4135^{c}	177^{bc}	440^{a}	318^{d}
V. ferruginea	1.33^{b}	0.34^{b}	0.12^{ab}	0.19^{b}	0.29^{a}	4731^{c}	430^{a}	318^{ab}	585^{bc}
V. hondurensis	1.39^{b}	0.34^{b}	0.04^{d}	0.17^{b}	0.20^{b}	7858^{a}	469^{a}	441^{a}	632^{b}
H. oblonga	1.14^{c}	0.35^{b}	0.06^{cd}	0.52^{a}	0.17^{c}	5920^{b}	216^{b}	266^{bc}	1419^{a}
Grass	1.07^{c}	0.65^{a}	0.14^{a}	0.18^{b}	0.18^{b}	8022^{a}	151^{c}	170^{c}	411^{cd}
Forest	1.82^{a}	0.47^{b}	0.14^{a}	0.17^{b}	0.10^{d}	3870^{c}	128^{c}	140^{c}	252^{d}
1-5mm									
S. excelsum	0.92^{ab}	0.55^{ab}	0.19^{ab}	0.16^{b}	0.27^{ab}	4741^{b}	80.0^{a}	98^{b}	173^{c}
V. ferruginea	0.61^{c}	0.40^{b}	0.22^{a}	0.14^{b}	0.27^{a}	5482^{ab}	42.2^{b}	123^{b}	602^{b}
V. hondurensis	0.67^{c}	0.39^{b}	0.04^{c}	0.09^{b}	0.25^{ab}	5150^{b}	37.2^{bc}	224^{a}	1349^{a}
H. oblonga	0.76^{bc}	0.63^{a}	0.13^{b}	0.49^{a}	0.18^{ab}	6749^{a}	57.6^{ab}	93^{b}	779^{b}
Grass	-	-	-	-	-	-	-	-	-
Forest	1.07^{a}	0.42^{ab}	0.23^{a}	0.14^{b}	0.09^{b}	3042^{c}	17.0^{c}	75^{b}	224^{c}
>5mm									
S. excelsum	0.63	0.39	0.19	0.12	0.11	3615	45.0	37.0	180
V. ferruginea	0.29	1.06	2.09	0.22	0.27	1821	6.0	15.0	275
V. hondurensis	0.32	0.16	0.03	0.06	0.14	1432	13.0	27.0	351
H. oblonga	0.28	1.76	0.32	0.48	0.32	4432	8.0	40.0	256
Grass	0.79	0.80	0.20	0.20	0.16	2388	12.0	72.0	256
Forest	0.60	0.34	0.26	0.12	0.08	1913	8.0	26.0	220

roots than the rest. *S. excelsum* had more roots >2mm and >5mm below 15 cm depth.

Distribution of root biomass among soil horizons is a consideration when choosing species of trees or crops for mixed plantings. Especially in the upper horizons, there would seem to be greater root competition in mixtures that included *V. ferruginea* and *H. oblonga*. These species would serve better where the need is to protect against soil erosion. On the other hand, *S. excelsum*'s more uniform distribution of roots at various depths would present less competition with other trees or crops in the upper soil horizons. Roots of *V. ferruginea* and *H. oblonga* show great potential for nutrient recycling; this could be clarified with root decomposition studies.

Litterfall

Figure 2 shows that total annual leaf litterfall for April 1989 through March 1990 was highest under *V. ferruginea* (1101 g/m^2). This was followed by *V. hondurensis*

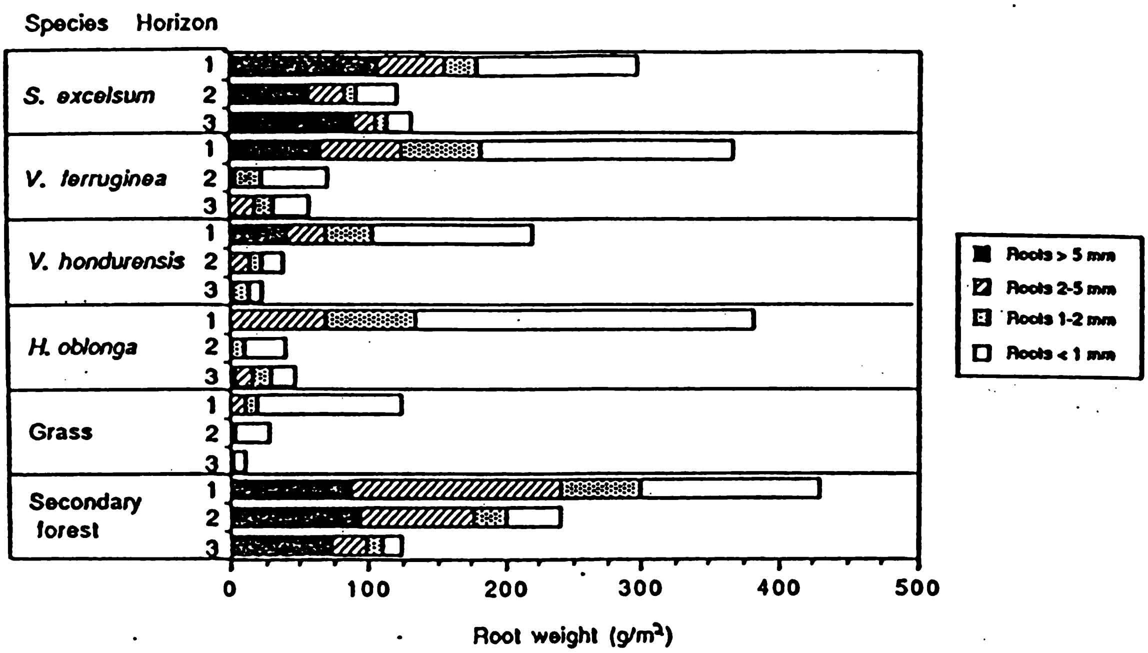

Figure 1. Mean root biomass, by class and horizon.

(885 g/m^2), *S. excelsum* (827 g/m^2) and *H. oblonga* (802 g/m^2). Other species ranged between 125 and 363 g/m^2. Branch litterfall was higher under *S. excelsum* and *V. ferruginea*. Monthly means for leaf litterfall, calculated from biweekly collections, are plotted in Figure 3 to show the seasonal pattern. Annual totals were calculated as the sum of all collections and not as the sum of these means. *V. ferruginea* and *V. hondurensis* exhibited peaks in leaf fall in June and September-October (beginning and end of rainy season, respectively). *S. excelsum* peaked in November; *H. oblonga* showed a more even pattern. Results of current data collection may clarify these trends.

Leaf and branch litter chemistry for October 1989 was chosen for comparison because data were more complete and differences in nutrient concentrations among species were similar to those of April and July 1989. *D. tucurensis* had the highest N concentration, followed by *T. rosea* and *S. excelsum* (Table 6). *H. oblonga*, *V. hondurensis* and *D. tucurensis* had the highest Ca and Mg, while *D. tucurensis* and *H. oblonga* had the highest K and P. There were no significant differences in Fe litter concentrations. *D. tucurensis* had the highest Cu, Zn and Mn concentrations.

Nutrient concentrations of branch litter were lower than those of leaf litter (Table 6). Although differences were not statistically significant, N concentrations were higher in *D. tucurensis*, *S. excelsum* and *T. rosea*, the same pattern found for leaf litter. *V.*

Table 5a. Nutrient concentrations in tissue of understory vegetation (August 1989).

	N	Ca	K	Mg	P	Fe	Cu	Zn	Mn
			(%)				(mg/kg)		
S. excelsum	1.70^{a}	0.33^{ab}	1.01^{b}	0.41^{bc}	0.13^{a}	3458^{a}	43.2^{a}	62.7^{b}	540^{a}
D. tucurensis	1.53^{ab}	0.69^{a}	1.48^{a}	0.48^{a}	0.71^{a}	8054^{a}	93.8a	82.8^{b}	704^{a}
T. rosea	1.26^{c}	0.30^{b}	1.09^{b}	0.37^{c}	0.18^{a}	3382^{a}	46.0^{a}	82.2^{b}	596^{a}
D. panamensis	1.27^{c}	0.42^{ab}	0.96^{b}	0.35^{c}	0.18^{a}	3510^{a}	48.5^{a}	120^{a}	738^{a}
H. oblonga	1.35^{bc}	0.77^{a}	0.79^{b}	0.45^{ab}	0.73^{a}	2773^{a}	74.3^{a}	83.7^{b}	747^{a}

Values followed by the same letter do not differ significantly at $p = 0.05$.

Table 5b. Understory biomass and nutrient content per unit area (August 1989).

	Biomass	N	Ca	K	Mg	P	Fe	Cu	Zn	Mn
	(g/m^2)					(g/m^2)				
S. excelsum	87.4^{b}	1.49^{ab}	0.29^{ab}	0.88^{bc}	0.36^{ab}	0.11^{ab}	0.31^{ab}	0.004^{ab}	0.005^{b}	0.05^{b}
D. tucurensis	83.3^{b}	1.25^{ab}	0.46^{a}	1.24^{ab}	0.39^{ab}	0.39^{a}	0.49^{a}	0.006^{a}	0.007^{b}	0.06^{b}
T. rosea	148.4^{a}	1.96^{a}	0.42^{a}	1.73^{a}	0.56^{a}	0.26^{ab}	0.50^{a}	0.007^{a}	0.011^{a}	0.09^{a}
D. panamensis	41.8^{b}	0.51^{ab}	0.18^{b}	0.38^{c}	0.15^{c}	0.07^{b}	0.15^{b}	0.00	0.006^{b}	0.03^{b}
H. oblonga	42.5^{b}	7.23^{bc}	0.29^{ab}	0.71^{bc}	0.23^{bc}	0.13^{ab}	0.18^{b}	0.002^{b}	0.003^{b}	0.02^{b}

Values followed by the same letter do not differ significantly at $p = 0.05$.

Table 6. Litter nutrient concentrations (October 1990).

	N	Ca	K	Mg	P	Fe	Cu	Zn	Mn
			(%)				(mg/kg)		
Leaves									
S. excelsum	1.27^{b}	1.72^{d}	0.16^{de}	0.29^{c}	0.19^{cd}	140^{c}	8.4^{e}	527^{b}	1.2^{e}
D. tucurensis	2.00^{a}	2.12^{bc}	0.43^{a}	0.49^{ab}	0.18^{a}	233^{ab}	27.8^{a}	860^{a}	1472^{a}
V. ferruginea	0.71^{d}	1.97^{c}	0.15^{e}	0.22^{c}	0.10^{d}	263^{a}	12.4^{d}	75^{c}	288^{d}
V. hondurensis	0.74^{cd}	2.28^{ab}	0.14^{e}	0.41^{b}	0.11^{d}	190^{ab}	11.8^{d}	46.4^{c}	343^{d}
T. rosea	1.30^{b}	1.89^{cd}	0.33^{bc}	0.50^{ab}	0.15^{bc}	186^{ab}	15.5^{c}	290^{bc}	4.2^{e}
D. panamensis	0.90^{c}	2.00^{c}	0.24^{cd}	0.25^{c}	0.10^{d}	237^{ab}	19.4^{b}	140^{c}	494^{c}
H. oblonga	0.88^{cd}	2.39^{a}	0.37^{ab}	0.54^{a}	0.18^{ab}	173^{bc}	17.2^{bc}	146^{c}	682^{b}
Branches									
S. excelsum	0.65^{a}	1.36^{b}	0.26^{c}	0.16^{bc}	0.10^{b}	100^{cd}	10.4^{bc}	187^{a}	148^{c}
D. tucurensis	0.71^{a}	2.14^{a}	0.67^{b}	0.35^{ab}	0.13^{b}	117^{cd}	29^{a}	119^{ab}	883^{b}
V. ferruginea	0.32^{b}	1.80^{ab}	0.13^{c}	0.46^{a}	0.16^{b}	179^{bd}	11^{bc}	43.5^{b}	1030^{ab}
V. hondurensis	0.50^{ab}	2.18^{a}	0.21^{c}	0.30^{ab}	0.27^{a}	248^{a}	14.0^{b}	96^{ab}	1290^{a}
T. rosea	0.68^{a}	1.59^{ab}	0.11^{c}	0.16^{bc}	0.11^{b}	66^{e}	3.00^{c}	105^{ab}	51^{c}
D. panamensis	0.62^{ab}	1.92^{ab}	0.54^{bc}	0.14^{d}	0.15^{b}	99^{cd}	12^{bc}	40^{b}	168^{c}
H. oblonga	0.59^{ab}	1.47^{ab}	1.13^{a}	0.21^{ab}	0.11^{b}	118^{bc}	30^{a}	50^{ab}	145^{c}

Values followed by the same letter do not differ significantly at $p = 0.05$.

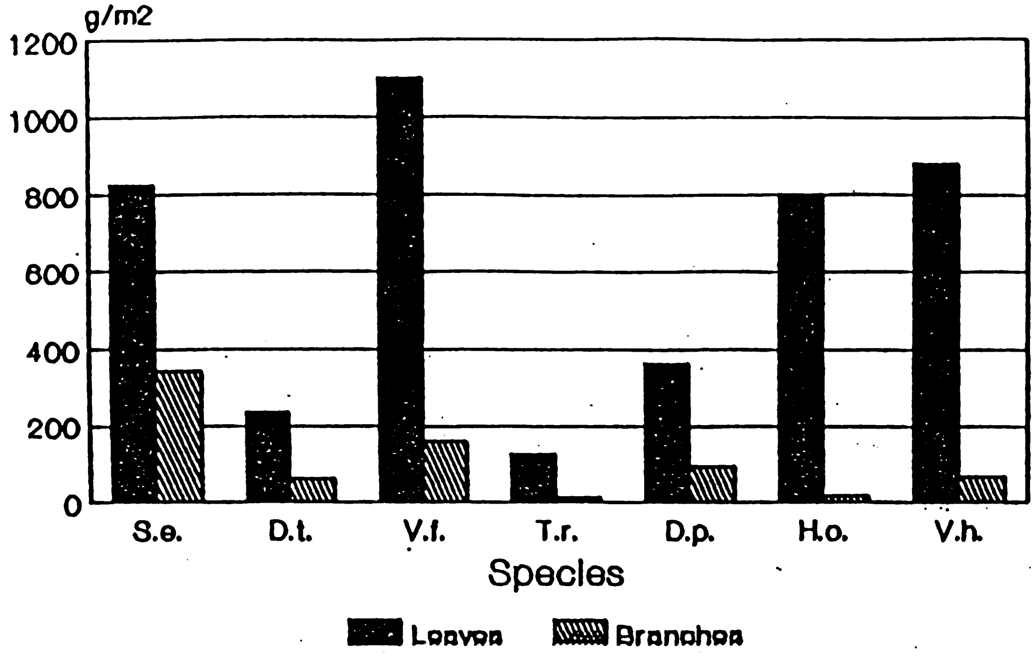

Figure 2. Litterfall for April 1989 - March 1990, leaf and branch annual totals. S.e. = *Stryphnodendron excelsum*; D.t. = *Dalbergia tucurensis*; D.p. = *Dipteryx panamensis*, V.f. = *Vochysia ferruginea*; V.h. = *V. hondurensis*; T.r. = *Tabebuia rosea*; H.o. = *Hyeronima oblonga*.

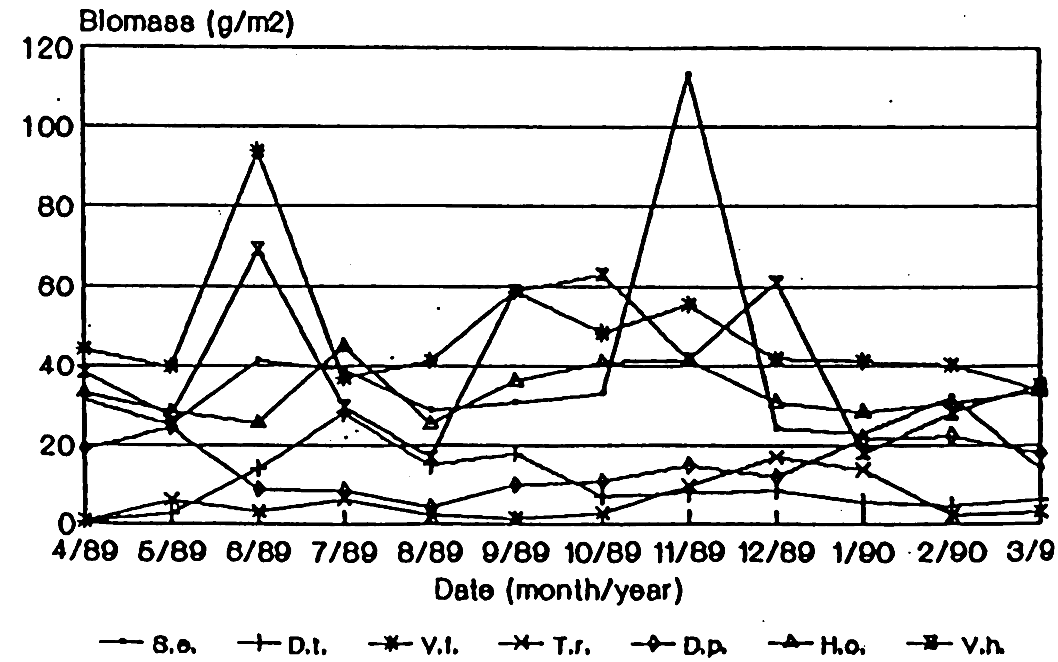

Figure 3. Litterfall for April 1989 - March 1990, monthly means for leaf biomass.

hondurensis and *D. tucurensis* had the highest Ca in branch litter. *H. oblonga* had the highest K; *V. ferruginea* had the highest Mg; *V. hondurensis* had the highest P and Fe. *D. tucurensis* had the highest Cu; *S. excelsum* the highest Zn and *V. hondurensis* the highest Mn in branch litter.

The high organic matter accumulation under *V. ferruginea* may be related to this species' high rates of litterfall; high Mg recycling could also be expected. Recycling of Ca and Mg should be high under *V. hondurensis*; K and P recycling could be high under *H. oblonga*. *S. excelsum*'s high rates of litterfall and litter N concentration suggest high N recycling under these species. Although *D. tucurensis* litter showed high concentrations of most nutrients, its capacity for recycling maybe limited by low rates of litterfall.

Comparison of forest floor litter accumulation at five dates between August 1989 and August 1990 (Figure 4) reveals that overall leaf litter accumulation tends to be greatest under *V. ferruginea*, followed by *S. excelsum*. This ranking is reversed starting in May 1990, with higher accumulation under *S. excelsum*. Leaf litter under *V. hondurensis* increased thoroughout the sampling period, the largest accumulation occurring in August 1990. A similar pattern was found for *H. oblonga*; accumulation under this species, though, was less than under *V. ferruginea*. For leaf fragments, *V. ferruginea* and *V. hondurensis* showed the highest values in August and May 1989 and in August 1990 (Figure 5).

Nutrient concentrations in forest floor material revealed a pattern similar to that of litterfall: N was higher in *S. excelsum; D. tucurensis* and *T. rosea*; Ca was higher in *D. tucurensis* and *V. hondurensis;* K was higher in *D. tucurensis*; Mg was higher in *D. tucurensis, V. hondurensis*, *H. oblonga* and *T. rosea* (Montagnini and Sancho, unpublished data).

The high litter accumulation recorded under *V. ferruginea* makes it well suited for protecting soil against erosion. On the other hand, an approximate indication of litter decomposition rates (given by the proportion of litter accummulation with respect to total litterfall) indicates that *V. ferruginea* litter would decompose slower than that of the other species. More detailed decomposition studies shed some light on these interactions.

Litter decomposition

Although the difference among decomposition rates (weight loss) was not significant (Table 7), the trends between them stayed fairly consistent throughout the experiment, based on initial and final leaf weights. The variance within the treatments was larger than expected; this was attributed to the unanticipated accumulation of mud in the litter bags and problems removing it completely from leaf fragments. Overall, however, the data suggest that *V. ferruginea* litter decomposes more slowly than the litter of other species, and that the fresh-dried, N-rich litter of *S. excelsum* does not decompose significantly faster than the other species, as we had expected.

Mulch experiment

Differences in seedling heights between treatments were significant at $p = 0.05$ and consistent throughout the experiment (Table 8). Within treatments there was very little variance. Initially, maize growing in plots with *H. oblonga* and *S. excelsum* showed greatest growth, while seedlings in the unmulched control plots showed significantly inferior growth. After 20 days, maize growth in the *H. oblonga* plots began to slow relative to *S. excelsum* plots, but plants in those plots remained larger and stronger than the maize seedlings in either of the *Vochysia* treatments. The control plots were slow-growing throughout the experiment and the seedlings in these plots were noticeably weaker and yellower than the plants in the other plots.

Differences in dry shoot weights were significant at $p = 0.05$ as well. The primary difference was between the shoots of the maize grown in *S. excelsum* mulch and all the others (Table 8a and b). Shoot weight of the maize grown in *S. excelsum* plots averaged

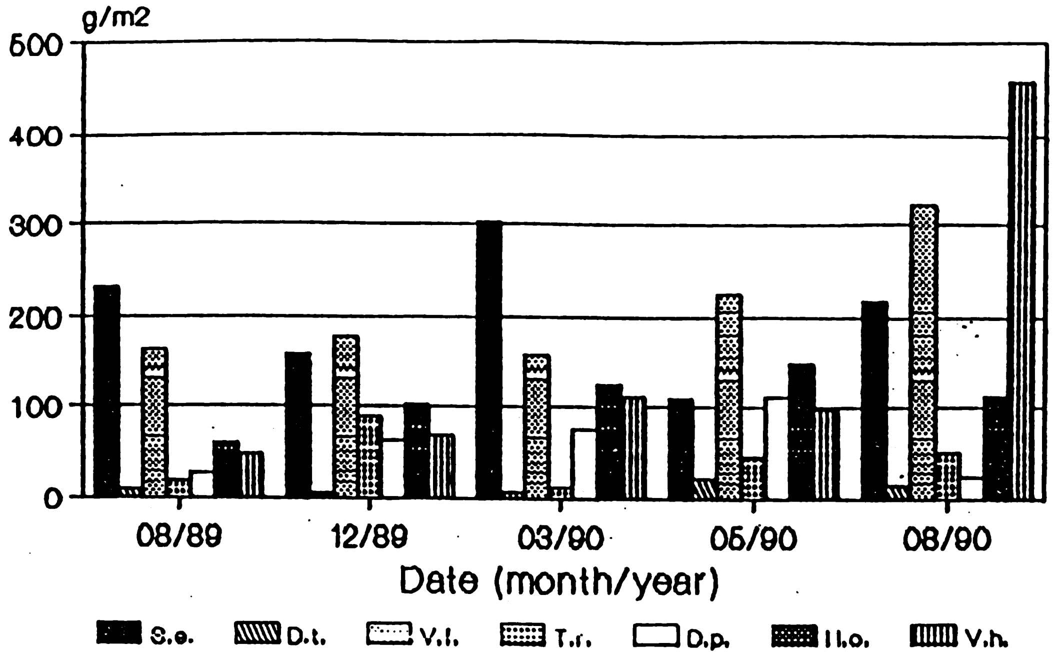

Figure 4. Overall forest-floor accumulation of leaf litter, August 1989 - August 1990. S.e. = *Stryphnodendron excelsum*; D.t. = *Dalbergia tucurensis*; D.p. = *Dipteryx panamensis*, V.f. = *Vochysia ferruginea*; V.h. = *V. hondurensis*; T.r. = *Tabebuia rosea*; H.o. = *Hyeronima oblonga*.

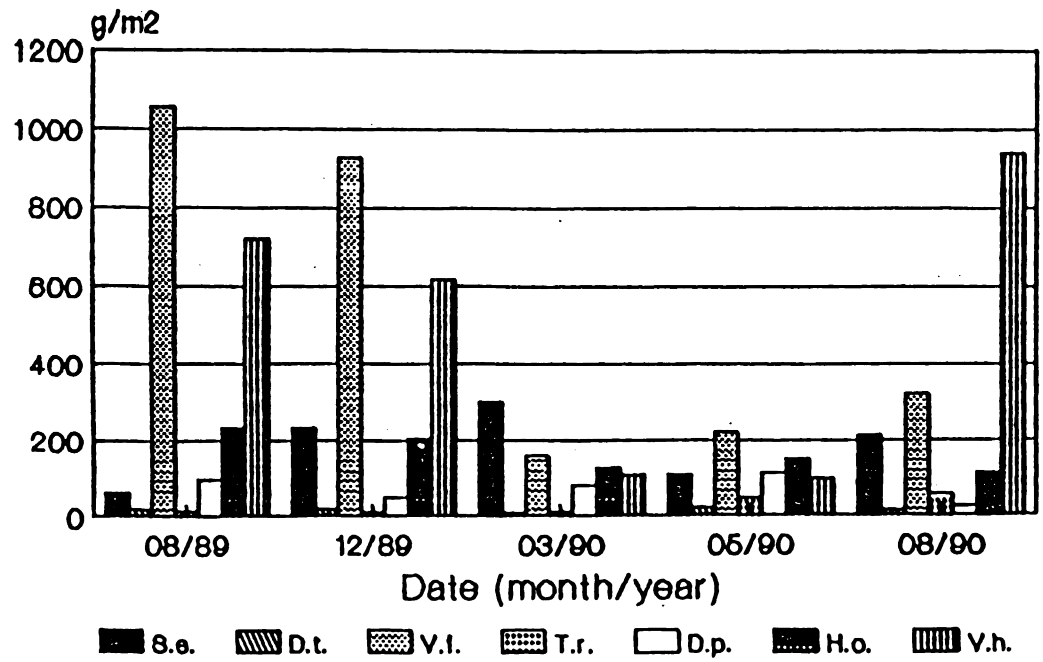

Figure 5. Leaf fragment accumulation on the forest floor, August 1989 - August 1990.

Table 7a. Leaf litter decomposition: percentage of initial weight (June-July 1990).

	Date of collection			
	6/18	6/28	7/10	7/25
S excelsum	96.94[a]	78.92[a]	77.13[a]	74.98[a]
V. ferruginea	96.25[a]	87.64[a]	81.67[a]	83.59[a]
V. hondurensis	92.31[ab]	81.82[a]	76.06[a]	77.63[a]
H. oblonga	86.61[b]	81.05[a]	78.91[a]	77.80[a]
p =	.2669	.5874	.8157	.5206

Table 7b. Leaf litter decomposition percentage of initial weight (means pooled from all treatments, sampled, undisturbed, and weighed).

	7/25
S excelsum	95.42[a]
V. ferruginea	96.93[a]
V. hondurensis	85.27[a]
H. oblonga	84.43[a]

Values followed by the same letter do not differ significantly at p = 0.0455.

Table 8a. Growth of maize seedlings in plots with mulch of four tree species (cm).

	Date			
	6/28	7/7	7/17	7/28
S. excelsum	17.9[a]	36.8[a]	48.9[a]	53.7[a]
V. ferruginea	15.2[b]	24.2[c]	29.6[c]	35.7[c]
V. hondurensis	15.1[b]	25.2[b]	30.8[c]	39.5[bc]
H. oblonga	17.9[a]	30.9[b]	38.1[c]	44.6[b]
Control	12.7[c]	19.8[d]	23.8[b]	25.2[d]
p =	.0002	.0000	.0006	.0021

Table 8b. Shoot and root biomass growth of maize in mulch plots.

	Shoots	Roots
S. excelsum	16.5	5.1
V. ferruginea	5.1	2.3
V. hondurensis	5.7	2.7
H. oblonga	8.2	3.3
Control	2.8	1.6
p =	.0465	.0004

two to eight times greater than that grown in other plots. Root biomass of maize grown in *S. excelsum* mulch also had the greatest biomass.

These results suggest that (1) tree leaf mulches played a significant role in maize seedling growth, and (2) some species had more important effects on initial maize growth. In particular, maize seedlings grown with the *Stryphnodendron* mulch were taller and visibly healthier looking than the other seedlings. This may be due in part to the fact that these leaves were dried fresh, instead of as litter; it also may be due to the higher levels of N they contain. The lackluster growth of the seedlings grown in both *Vochysia* treatments may be due to a variety of factors, including the prevalence of Al + ions released from the litter in the upper strata of soil, or the immobilization of N in the process of breaking down the fibrous litter. Although it was not reflected in the decomposition experiment, stands of *H. oblonga* showed low accumulation of leaf litter on the floor. This suggests that litter from this species decomposes relatively quickly; and perhaps explains the strong initial growth of maize in plots mulched with *Hyeronima* leaves.

Conclusions

S. excelsum, V. ferruginea, V. hondurensis and *H. oblonga* were the most promising species studied, for both growth and nutrient recycling capabilities.

V. ferruginea performed best for organic matter accumulation in soil, protection against erosion, and recycling of certain nutrients such as Ca. However, it may not be the best species for N recycling. Its effects on Al in soils should be further investigated. Strong competition with roots of nearby crops or trees should also be considered when planning species mixtures.

S. excelsum and *D. tucurensis* showed greater potential for N recycling. Of the two, *S. excelsum*'s high rates of litterfall make it more capable of high N recycling. This species' effects on understory growth and the effects of its mulch on maize seedling growth suggest that indeed it has a positive effect on associated crops. High rates of litterfall make the potential for using this litter as mulch practical. More studies with *Stryphnodendron* mulch and litter (for example, in alley-cropping systems) would be worthwhile. Its relatively uniform root distribution in the soil may present fewer problems of root competition with nearby trees or crops.

V. hondurensis and *H. oblonga* ranked intermediate in rates of litterfall and potential for nutrient recycling. These two species may enhance recyling of cations and P.

In spite of ranking the highest in terms of tissue and litter nutrient content, *D. tucurensis* has low potential for nutrient recycling due to low litterfall under present plantation conditions. This species should be further explored, however. With appropriate pruning practices, it could probably be managed to encourage leaf production and litter recycling.

We expect that the results of these studies will be disseminated to farmers of the region through local institutions. This may take place through collaboration with DGF, for example, which is already promoting native trees among local farmers. We are continuing measurements of soil fertility to assess the long-term impacts of the tree species on soil amelioration. We are also starting more detailed studies with the most promising species and with more native species in the region, designing tree species mixtures and agroforestry combinations.

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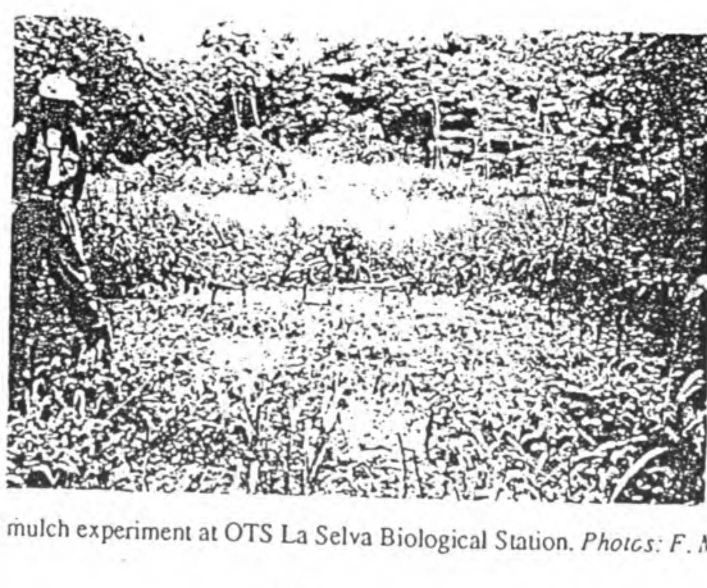
Left: *Vochysia ferruginea* Mart. (Vochysiaceae) at 3.5 years.
Right: *V. hondurensis* Sprague (Vochysiaceae) at 3.5 years.



Maize seedlings in mulch experiment at OTS La Selva Biological Station. *Photos: F. Montagnini.*

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Litterfall, litter decomposition and the use of mulch of four indigenous tree species in the Atlantic lowlands of Costa Rica

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Key words: *Stryphnodendron microstachyum, Vochysia ferruginea, Vochysia guatemalensis, Hyeronima alchorneoides,* litter, leaf mulches

Abstract. Litterfall, forest-floor litter biomass and nutrients, short-term litter decomposition and the effects of leaf mulches on initial growth of maize were studied for four indigenous tree species with agroforestry potential: *Stryphnodendron microstachyum* Poepp. et Endl. (*S. excelsum*), *Vochysia ferruginea* Mart, *Vochysia guatemalensis* Donn. Sm. (*V. hondurensis*) and *Hyeronima alchorneoides* (O), growing in a young experimental plantation in the Atlantic humid lowlands of Costa Rica. Total annual leaf litterfall was higher in *V. ferruginea* plots, followed by *S. microstachyum, V. guatemalensis* and *H. alchorneoides*; all with values comparable to those reported for other tree species grown in agroforestry combinations in humid tropical regions. Forest-floor litter accumulation was highest under *V. ferruginea* and *V. guatemalensis.* Both litterfall and forest-floor litter material had similar patterns in nutrient concentrations: N was higher in *S. microstachyum*, Ca was higher in *V. guatemalensis*, K was higher in *H. alchorneoides*; Mg was higher in *V. guatemalensis* and *H. alchorneoides*; *H. alchorneoides* and *V. guatemalensis* had the highest P. *V. ferruginea* litter decomposed more slowly, while *S. microstachyum* apparently decomposed faster than the other species. The two *Vochysia* species showed increases in N and P concentration in decomposing litter after seven weeks in the field, *H. alchorneoides* showed an increase in litter N and a decrease in litter P, and *S. microstachyum* showed a net decrease in both N and P over the same time period. The patterns found in the litter bag study were confirmed by results obtained in a tethered-leaves experiment. *S. microstachyum* and *V. ferruginea* litters lost more weight when mixed in a 1:1 proportion than either of them alone. Maize seedlings growing in plots mulched with *S. microstachyum* and *H. alchorneoides* leaves showed greatest initial growth, confirming patterns found in decomposition and nutrient release studies. The results show that these species could be used in agroforestry combinations with different advantages according to the specific objectives desired, whether these are soil protection, nutrient recycling, or enhancement of the growth of associated crops.

Introduction

The choice of tree species for plantation forestry or agroforestry is influenced by knowledge of the species' performance and their economic and environmental benefits. Most tree planting programs and subsidies promote the use of well-known, often exotic species, due to the existing knowledge on their biology, cultivation and uses. Besides, when taken to new areas, some exotics grow quickly, at least initially, probably due to the lack of natural enemies. However, several indigenous species may be more suitable than exotics [Evans, 1987] because (1) they may be better adapted to local environmental conditions; (2) seeds and other propagules are locally available; and (3) farmers are familiar with them and their uses. Additionally, the use of indigenous trees in productive systems helps preserve genetic diversity and is in better balance with the local flora and fauna.

Tree species vary in their nutrient uptake rates and recycling capacity. Litter production is a major process in the transfer of organic matter and nutrients from above-ground tree parts to the soil [Szott et al., 1991]. The addition of tree leaves and branches as mulches to soils has been shown to improve site microenvironmental conditions [Budelman, 1989] and increase the productivity of agricultural crops [Duguma et al., 1988; Gutteridge, 1990; Onim et al., 1990; Tiraa and Asghar, 1990; Yamoha and Burleigh, 1990]. The nutrient content (especially N and P) and the lignin and polyphenolic concentrations of litter strongly influence its rate of decomposition and nutrient release to the soil [Palm and Sanchez, 1990, 1991; Szott et al., 1991].

In the present article we report rates of litterfall and litter decomposition under young stands (3.5—4.5 years old) of four fast-growing, indigenous tree species in the Atlantic lowlands of Costa Rica. The four species of this study: *Stryphnodendron microstachyum* Poepp. et Endl. (*S. excelsum*), *Vochysia guatemalensis* Donn. Sm. (*V. hondurensis*), *Vochysia ferruginea* Mart and *Hyeronima alchorneoides* (O), had growth rates equal to or greater than the exotic species recommended for the region at the time [Espinoza Camacho and Butterfield, 1989]. Rates of net above-ground primary productivity of these four indigenous species were comparable to those reported for other fast-growing trees in the humid tropics, including many multiple-purpose trees commonly used in agroforestry [Montagnini and Sancho, 1993a, b]. Results of our studies on soil fertility and nutrient recycling on the same site showed that after 2.5 years, soil organic matter, nitrogen and cation levels under these species were higher than in adjacent grass, with values similar to those found in secondary forest [Montagnini and Sancho, 1990a, b]. Further studies showed that soil N availability was higher under the N-fixing *S. microstachyum* than under the other three, non-N fixing species [Montagnini et al., 1991]. Results of studies of tree biomass and nutrients [Montagnini and Sancho, 1993a, b, c] showed that *S. microstachyum* had the highest accumulation of N in tree tissue, with approximately 200 kg/ha, or 60% of above-ground biomass N in the potentially recyclable portion (leaves and branches). *V. guatemalensis* had the highest stem Ca and Mg; this species had over 120 kg/ha of Ca in the leaves + branches portion. *V. ferruginea* also had a relatively high accumulation of nutrients in above-ground biomass, with approximately 120 kg/ha of N in branches and leaves. *H. alchorneoides* had a relatively high accumulation of above-ground biomass K, with approximately 180 kg/ha in the leaves + branches portion [Montagnini and Sancho, 1993a, b, c]. Preliminary results of studies of nutrient recycling from trees to soil showed that litterfall and litter accumulation were most abundant under

V. ferruginea; *H. alchorneoides* litterfall appeared to be high but did not tend to accumulate on the floor [Montagnini et al., 1991]. These results suggested that the four species could be used to improve site quality and possibly to favor the growth of associated crops, with different advantages according to the tree species used and their management.

In this article we report rates and seasonality of litterfall, forest-floor litter accumulation, litter decomposition, and nutrient release from mulches of these four species. The influence of the trees on site microclimate (air and soil temperature), top soil compaction (bulk density) and soil moisture is also shown. The goal of this study was to provide guidelines for the use and management of these fast-growing trees in the region and in other tropical lowland, humid regions with similar soils.

Study site

The experimental plantation was established in December, 1985 on abandoned pasture at the OTS La Selva Biological Station (10°26′N, 86°59′W, 50 m m.a.s.l., 24 °C mean annual temperature, 4000 mm mean annual rainfall, with maximum in July and minimum in March) [La Selva Biological Station weather reports]. Soils are Fluventic Dystropepts derived from alluvially deposited volcanic materials; they are deep, well drained, stone-free, with low or medium organic matter content (2.5 to 4.5%), moderately heavy texture, generally very acid (pH in $H_2O < 5.0$), and infertile [Sancho and Mata, 1987]. Detailed soil chemistry has been published elsewhere [Montagnini and Sancho, 1990a, b]. The area had been cleared in the mid-1950s and grazed until 1981 [Pierce, 1992]. The site was cleaned manually before planting. The tree species were planted in a randomized block design with five replicates, each single-species plot containing seven rows of seven trees (14 m × 14 m each), with two meters between trees (2,500 trees ha^{-1}).

The tree species used for our comparisons of soil fertility and nutrient recycling are shown in Table 1. All the species have economic uses (timber of medium to high quality) and their seeds were collected from natural forests at La Selva and nearby in the region. Seed and germination characteristics of these species are given elsewhere [Gonzalez, 1991; Gonzalez et al., 1990].

Materials and methods

Litterfall

Litter was collected from 90 cm × 55.5 cm litterfall traps made of a wooden frame with fiberglass screen bottoms (1 mm^2 mesh size), set at 50 cm above the ground. Traps were located randomly in the plots but avoiding the edges;

Table 1. Native tree species studied for their effects on soils and nutrient cycling at La Selva Biological Station [Gonzalez et al., 1990; Holdridge and Poveda, 1975].

Scientific name	Common name	Family	Native range	Natural habitat
Stryphnodendron microstachyum Poepp. et Endl. (*S. excelsum*)	vainillo	Leguminosae (mimosoid)	Costa Rica	Low altitude, very humid climate. Alluvial as well as poor soils.
Vochysia guatemalensis Donn. Sm. (*V. hondurensis*)	mayo, chancho	Vochysiaceae	Mexico to Panama	Lowlands, up to 900 m, humid climate. Rich alluvial or poor soils.
Vochysia ferruginea Mart	botarrama	Vochysiaceae	Nicaragua to Brazil	Lowland forests. Well-drained, acidic, infertile soils.
Hyeronima alchorneoides Fr. Allemao	pilon	Euphorbiaceae	S. Mexico to S. Brazil	Hills, abandoned pastures. Alluvial as well as poor soils.

in most cases they were near the center of each plot. There was one trap per plot for the four species of the study; 20 traps total. The traps were emptied every two weeks, their contents oven-dried (70 °C), sorted (leaves and branches), and weighed. Collections began in April, 1989 and continued through February, 1991. Every three months, the material collected in one month was pooled to have enough sample for chemical analyses. The total N, Ca, Mg, K and P were measured on nitro-perchloric digests: N and P were measured using a Lachat Flow Injection Analyzer, while cations were measured using an Atomic Absorption Spectrophotometer. Analysis of variance and tests for differences among species using LSD ($p < 0.05$) were done for leaves and branches for each individual collection. Additionally, monthly means were calculated from biweekly collections to detect seasonal differences in leaf and branch litterfall. Finally, annual totals were calculated as the sum of all collections. Average nutrient concentrations were multiplied by annual litterfall (leaves and branches) to assess the annual nutrient input in litterfall from each species.

Forest-floor litter

The amount of litter accumulating on the ground under the species was measured in August and December, 1989, and in March, May and August 1990. These months were chosen to represent the local seasonality in rainfall, which was expected to influence the amounts of litter: August is the month of peak rainfall at La Selva, December is in the middle of a less rainy period, March is nearing the end of a relatively dry period, and May generally marks the beginning of the rainy season [La Selva Biological Station weather reports]. A 50 cm × 50 cm iron frame (one per plot) was used to demarcate an area within one meter of a randomly chosen tree stem; the location of sampling was generally near the center of the plots; plot edges were avoided when sampling. All material above the mineral soil within the frame was collected, oven-dried, sorted (leaves and branches), and weighed. Statistical analyses were performed on the results of each individual collection to compare the contribution of each litter component among species.

Litter decomposition

These experiments were designed to examine nutrient release by the species for their use as mulches; three short-term (maximum four months) experiments were conducted, which is frequently the length of mulch decomposition studies [Budelman, 1988]. The methods employed were: (a) a large litter bag decomposition experiment; (b) decomposition of tethered leaves; and (c) a mixed-leaf litter experiment using the conventional, smaller litter bags.

a. *Large litter bag experiment*

This experiment was done to compare litter decomposition among the four species. Litter bags were constructed out of plastic mesh (average mesh size 2 mm × 2 mm). Large litter bags (50 cm × 50 cm) presumably allowed for an environment for decomposition more similar to natural conditions in the forest floor than the more conventional, smaller bags (generally 10—15 cm to a side), which may tend to exclude soil macrofauna whose role in decomposition can be important [Budelman, 1988]. Approximately 2,500 g of whole, recently fallen leaves were collected from the ground in each species plot for *V. ferruginea*, *V. guatemalensis*, and *H. alchorneoides*. Leaves from *S. microstachyum*, leaflets and rachis of which are difficult to collect from the ground, were collected fresh. Due to the large volume of material, air drying was unpractical; therefore, all leaves were dried at 70 °C prior to filling litter bags. Each bag was filled with 100 g of dried leaves, weighed to 0.1 g. Two subplots were designated randomly in each of the four species plots, which were replicated five times. An area slightly larger than the litter bags was cleared of leaf litter; two bags were placed in each plot (40 bags total); and then they were covered with most of the displaced litter. The soil under the bags was exposed but not entirely bare of decomposing leaves. Litter bags were weighed and sampled on June 6 (time of initiation of the experiment), and on June 18, June 28, and July 10 and July 25; i.e., approximately every two weeks for a total of one and a half months. At each collection time, the bags were taken to the lab for weighing and subsampling. Subsampling consisted of removing 30—60 g of the field weight of the leaves, which were then dried at 70 °C to determine a field weight:dry weight ratio. These subsamples of litter from each collection were processed and analyzed for N and P as described above for other tissue. After subsampling, the bags were returned to the field. Weight loss due to decomposition was calculated by comparing the expected weight loss (loss due to sample removed) with the actual weight loss. The actual weight loss was determined by the wet:dry ratio of the subsample taken from the bag. Statistical analyses (analysis of variance and LSD for differences among means) were done to compare weight loss as a percent of the initial weight, as well as nutrient concentrations, among species for each collection.

b. *Tethered leaves experiment*

The results from this method were compared with those from the large litter bags. However, the method allowed for comparison of *V. ferruginea*, *V. guatemalensis* and *H. alchorneoides* litters only; *S. microstachyum* could not be included due to the small size of its leaflets. The tethered leaves were set loose in the litter layer instead of being enclosed in bags. Thus they were more in contact with the natural environment and provided a more realistic measure of short-term decomposition rates [La Caro and Rudd, 1985]. Recently fallen leaves collected from the litter layer below each species were dried in circulating, ambient air for about a week. All the leaves were whole, with entire margins. The leaves were tied with dental floss around their petioles to make several strings of leaves, with numbers of leaves per string depending on leaf size. The leaf strings were weighed to 0.001 g and then labeled prior to placing in the field. Subsamples were oven-dried to determine an ambient:oven dry weight ratio for calculations. Random areas of approximately 0.25 m^2 were located near the center of five plots per species, and they were cleaned of all litter. The leaf strings were placed inside these areas and anchored down with sticks, one string per mini-plot. The leaves were removed from the field two weeks later when the leaves of *H. alchorneoides* began to lose their structure and shape; leaving them longer would have made it difficult to recover them. The leaves were oven-dried at 70 °C for two days and then weighed. No chemical analyses were conducted due to the small amount of tissue recovered.

c. *Mixed-leaf litter experiment*

This experiment was done to examine the influence of mixing an N-rich litter (*S. microstachyum*) with a less N-rich, presumably more decomposition-resistant litter (*V. ferruginea*). The hypothesis was that the addition of the leguminous leaves would increase the rate of weight loss of the *V. ferruginea* litter. Fiberglass bags (1 mm^2 mesh), approximately 15 cm × 15 cm, were filled with either 5 g of *S. microstachyum* or *V. ferruginea* leaves alone, or a mixture of 2.5 g of each species. The leaves had been left to dry at ambient air temperature prior to filling the bags. Subsamples of leaves were oven-dried to determine the ambient:dry weight ratio for calculations. The bags were stapled shut and fastened together with light wire in groups of three (one of each treatment), and placed in the field on 1 August 1991. Half of the bags were randomly placed in *S. microstachyum* plots and half in *V. ferruginea* plots; each species plot, hence each treatment, was replicated five times. Thus there were a total of 60 bags (3 treatments × 5 replicates × 4 collections). The bags were collected after two weeks (15 August), one month (1 September), two months (1 October) and four months (1 December), from each plot. The bags were oven-dried and their contents weighed to 0.001 g to determine weight loss over time. As in the other two decomposition studies, statistical analysis was performed to compare weight loss as a proportion of initial weight among treatments, for each collection.

Mulch experiment

A field bio-assay was conducted to examine the influence of nutrient release from mulches of the four tree species on plant growth. Maize was used as a test species, due to its generally good growth response to added nutrients; however, this was a short-term experiment, and it was not intended to measure crop yields. Maize seedlings were grown for 40 days in small plots mulched with the litter of each of the four species. A small amount of pasture (7 m × 7 m) was cleared to soil level. In this clearing, 25 plots measuring 50 cm × 50 cm each and spaced 30 cm apart were laid out in a square, five plots on each side. Grass was cleared within 1—2 m of the plots, shade and sun patterns were consistent over the plots, and a chicken-wire fence was erected around the entire experiment area. For each treatment, including the control with no mulch, there were five replicates; all were set at random.

For mulch, 100 g of air-dried leaves of each species were broken into smaller pieces by hand, and then they were incorporated into the top 10—15 cm of soil in an appropriate plot with a trowel. After a week, each plot was planted with 25 maize seeds. The maize was a local, non-hybrid variety that had been cleaned and culled beforehand. After cleaning it exhibited a 96% germination rate in the laboratory. The seed was planted at 3-cm depth, 8—12 cm apart, using a planting dibble. Ten days after planting (approximately one week after germination), 100 g ground leaves were again laid on the soil in the maize plots. With this second application, the total addition of mulch was at a rate of 8 tons ha^{-1}; this rate was chosen based on preliminary results of litterfall measurements under the four species, to use an amount which could be possibly collected from under the tree plots. This amount also corresponds to measured production rates of pruned material from leguminous shade trees in coffee plantations [Beer, 1988]. An initial germination rate of at least 92% occurred in all but two plots. Every time the mulch was added to the treated plots, the soil in the controls was turned over, for similar cultivation effects.

Maize seedlings were measured at 10-day intervals, beginning 10 days after sowing. The height of each seedling was recorded to the highest point when the plant was held vertically against a meter stick. Forty days after planting, the maize seedlings were carefully dug up. Shoots and roots from the top 10—15 cm of soil were washed, separated (shoots from roots), oven-dried and weighed. Subsamples of shoots and roots were processed and analyzed for N and P as described above for nutrient determinations in plant materials.

Influence of tree canopies on the microenvironment

Soil temperatures at 2.5-cm depth were monitored using Weksler™ soil thermometers. The air temperature was measured with standard hardware thermometers held from sticks at 50-cm height from the ground. The soil bulk density was measured at 0—5 cm depth using a 4.8 cm diameter × 5-cm long corer equipped with an extensible hammer and a sleeve. Soil moisture was measured gravimetrically on the samples obtained for bulk density. Two replicate samples were taken from each plot. The results from the two replicate samples from each plot were averaged to obtain one value per plot. All these measurements were done in the five replicate plots of the four species, and in five of each adjacent 20-year-old secondary forest and grass sites for comparison. Analysis of variance and tests for means were conducted as described above.

Results

Litterfall

The total annual leaf litterfall was highest under *V. ferruginea*, followed by *V. guatemalensis*, *S. microstachyum* and *H. alchorneoides*, while branch litterfall was higher under *S. microstachyum* and *V. ferruginea* (Fig. 1, Table 2); these results are consistent with our earlier findings [Montagnini et al., 1991]. For leaf litterfall, annual totals from March, 1990 to February, 1991 were 4—19% lower than for the previous 12-month period, with the largest decrease in *V. ferruginea*; for branches, there were increases as well as decreases in the annual totals (although no statistics were run to compare these totals) [Montagnini and Sancho, unpublished data]. In 1989—90, *V. ferruginea* and *V. guatemalensis* exhibited peaks in leaf fall in May—June and October—December (beginning and end of rainy season, respectively) (Fig. 2). *S. microstachyum* showed a single peak in November and *H. alchorneoides* had the most even distribution, with no obvious peaks. In 1990—91, all species showed peaks in May—June; the two *Vochysia* peaked again in October—November and in January, while *S. microstachyum* and *H. alchorneoides* litterfall did not vary (Fig. 2). Seasonality in branch litterfall was similar to that of leaf fall: peaks occurred in May—June, and in October—January (Fig. 2). The differences among species noted above for peaks of leaf or branch litterfall were statistically significant ($p < 0.05$).

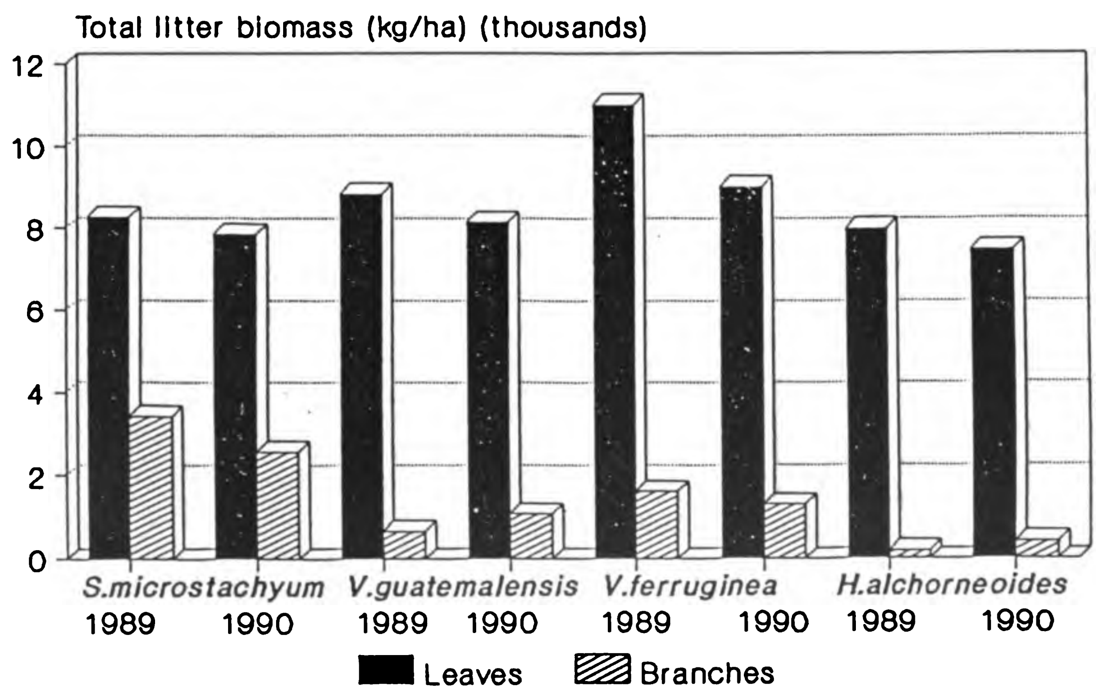
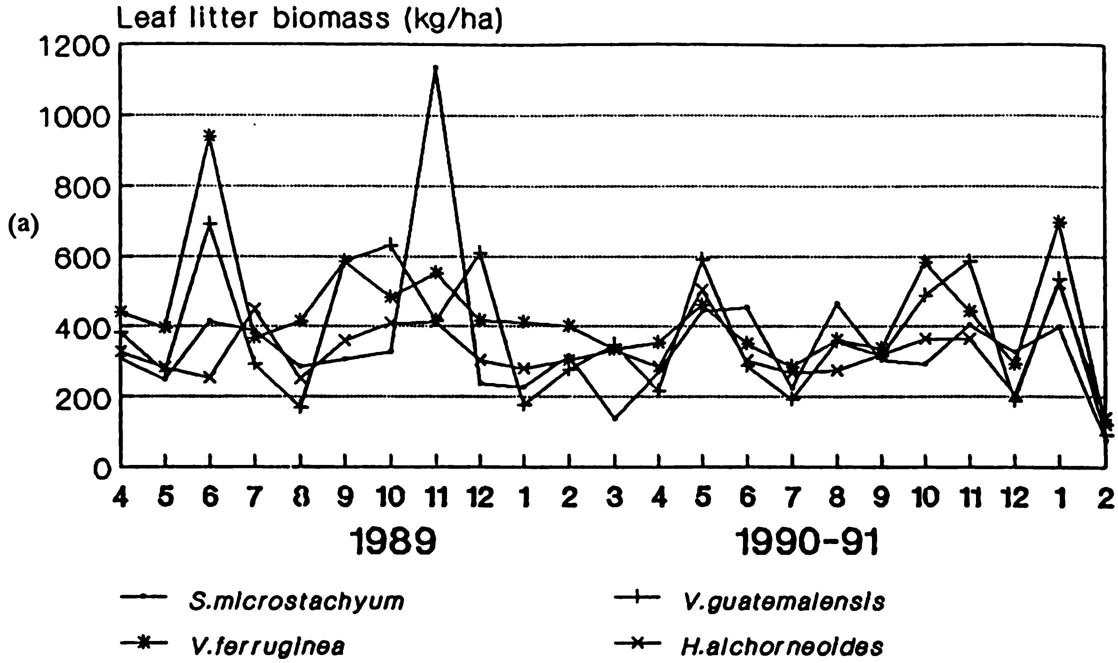


Fig. 1. Total annual litterfall (1989—1990); leaf and branch totals by species.



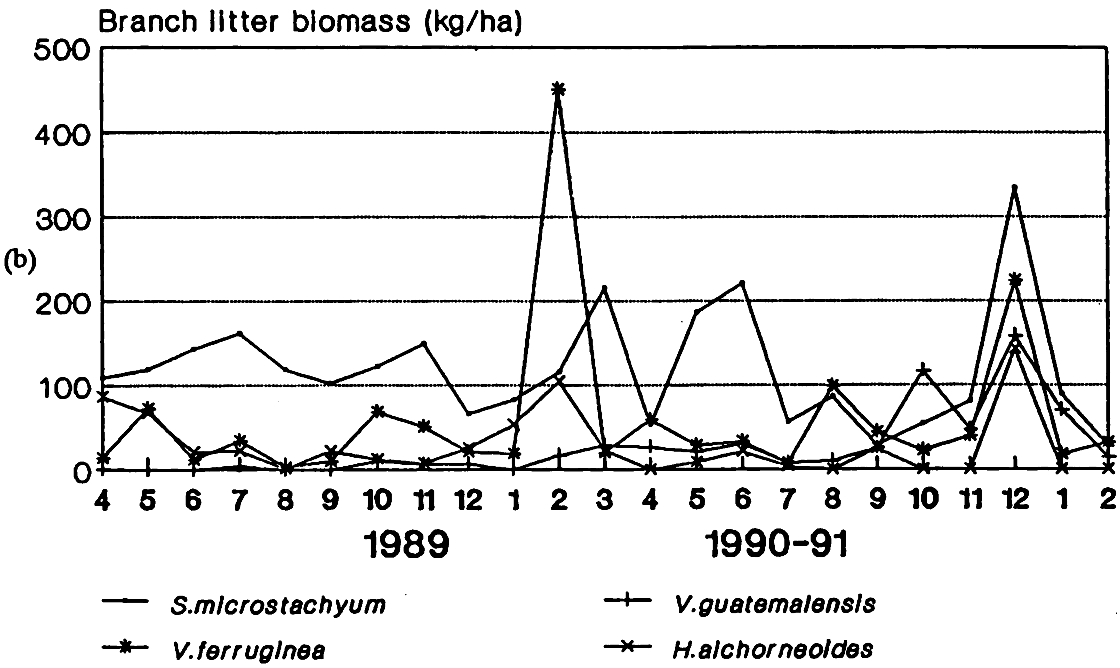


Fig. 2. Litterfall, monthly averages from April, 1989 to February, 1991. (a) Leaves; (b) Branches.

Leaf litter N concentration was 20—40% lower in October 1989 than on the other sampling dates; there were no other clear trends for Ca, Mg, K or P; differences in nutrient concentrations among species were consistent throughout the 1989—1991 sampling record [Montagnini and Sancho, unpublished data]. Results for October, 1989 were chosen for comparison because the data were more complete than for other dates, due to the high amount of litter collected for all species in that month (Fig. 2). *S. microstachyum* had the highest N concentration in leaf litter (Table 3). *H. alchorneoides* and *V. guatemalensis* had the highest Ca and Mg, *H. alchorneoides* had the highest K, and *H. alchorneoides* and *S. microstachyum* had

Table 2. Total annual litterfall biomass and nutrient content, April 1989—March 1990.

	Biomass	N	Ca	Mg	K	P
	(kg/ha)					
Leaves						
S. microstachyum	8273	106.7	142.3	24.0	13.2	15.7
V. guatemalensis	8854	65.5	201.9	36.3	12.4	9.7
V. ferruginea	11017	78.2	217.0	24.2	16.5	11.0
H. alchorneoides	8019	70.6	191.7	43.3	29.7	14.4
Branches						
S. microstachyum	3435	22.3	46.7	5.5	8.9	3.4
V. guatemalensis	664	3.3	14.5	2.0	1.4	1.8
V. ferruginea	1616	5.2	29.1	7.4	2.1	2.6
H. alchorneoides	185	1.1	2.7	0.4	0.2	0.2
Total (leaves + branches)						
S. microstachyum	11708	129.0	189.0	29.5	22.2	19.2
V. guatemalensis	12633	68.8	216.3	38.3	13.8	11.5
V. ferruginea	9518	83.4	246.1	31.7	18.6	13.6
H. alchorneoides	8204	71.7	194.4	43.7	29.9	14.6

Table 3. Litter nutrient concentrations (October 1989).[1]

	N (%)	Ca (%)	Mg (%)	K (%)	P (%)
Leaves					
S. microstachyum	1.27a	1.72d	0.29c	0.16b	0.19ab
V. guatemalensis	0.74bc	2.28ab	0.41b	0.14b	0.11b
V. ferruginea	0.71c	1.97c	0.22c	0.15b	0.10b
H. alchorneoides	0.88bc	2.39a	0.54a	0.37ab	0.18ab
Branches					
S. microstachyum	0.65a	1.36b	0.16bc	0.26b	0.10b
V. guatemalensis	0.50ab	2.18a	0.30ab	0.21b	0.27a
V. ferruginea	0.32b	1.80ab	0.46a	0.13b	0.16b
H. alchorneoides	0.59ab	1.47ab	0.21ab	1.13a	0.11b

[1] For each nutrient and tissue category (branches or litter), differences among species are statistically significant when means are followed by different letters ($p < 0.05$).

the highest P in leaf litter; these differences were statistically significant ($p < 0.05$). Nutrient concentrations of branch litter were lower than those of leaf litter (Table 3). There were no statistically significant differences in N, Ca or Mg concentrations in branch litter. *H. alchorneoides* had the highest K, and *V. guatemalensis* had the highest P; these differences were statistically significant ($p < 0.05$) (Table 3). Total annual nutrient contribution in litter is shown for April 1989—March 1990 only, because the record was more complete than that of 1990—91 (Table 2): *S. microstachyum*, with the highest N concentration and high litterfall also had the highest amount of N in annual litterfall; this species also had the highest amount of P in annual litterfall (Table 2). *V. ferruginea* and *V. guatemalensis* had approximately 25% higher contributions of Ca in annual litterfall than *S. microstachyum*, with similar values among them. *H. alchorneoides* had the highest amounts of Mg and K in litterfall.

Forest-floor litter

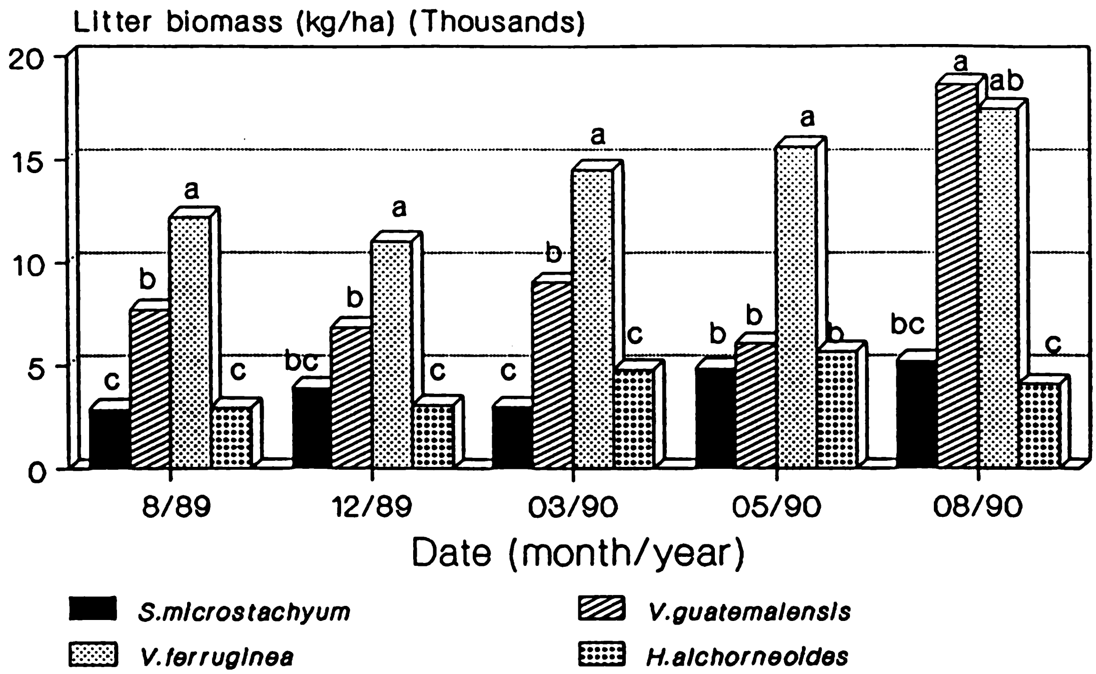
Forest-floor leaf litter accumulation was highest under *V. ferruginea* at all times except for August, 1990 when it was similar to *V. guatemalensis* (Fig. 3). The higher amount of leaves found in *V. guatemalensis* in that month was attributed to a natural cause (e.g., a full branch fell into the litterfall trap); there was no reason to reject the data. There was an apparent increase in the accumulation of leaf litter on the forest floor with time of sampling under all species, but this trend was more marked for *V. ferruginea* and *V. guatemalensis* (Fig. 3). Apparently there was a build up of litter on the forest floor under these two species, which tends to suggest both rapid tree growth with fast crown development, and relatively slow decomposition; both *Vochysia* species are self-pruning. For branch litter, again *V. ferruginea* and *V. guatemalensis* showed the highest values of accumulation on the forest floor (Fig. 3), except in March 1990, when *S. microstachyum* had the highest branch litter accumulation.

Nutrient concentrations in forest-floor material revealed a pattern similar to that of litterfall: N was higher in *S. microstachyum*; Ca was higher in *V. guatemalensis*; K was higher in *H. alchorneoides*; Mg was higher in *V. guatemalensis* and *H. alchorneoides*; *H. alchorneoides* and *V. guatemalensis* had the highest P [Montagnini and Sancho, 1993b].

Litter decomposition

a. *Litter bags*

Although the difference among decomposition rates (percent of initial weight remaining) was not significant (Table 4), the differences in weight loss among species stayed fairly consistent throughout the experiment. The variance within the treatments was larger than expected; this was attributed to the unanticipated accumulation of mud in the litter bags and problems with



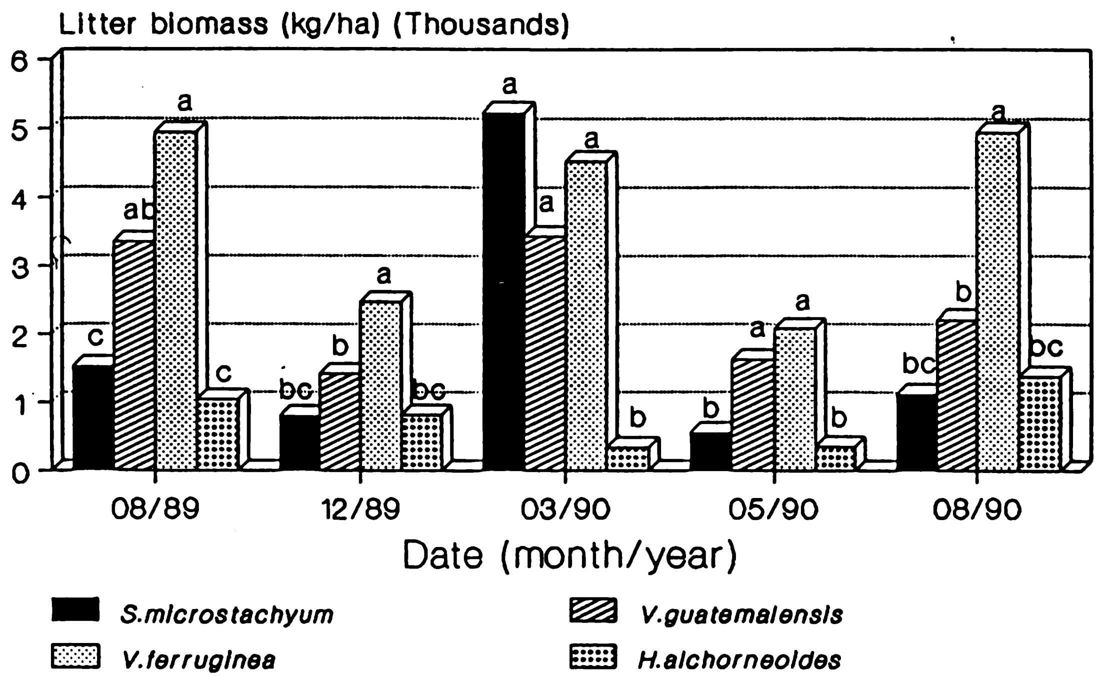


Fig. 3. Forest-floor litter, five collection dates in 1989—1990. a) Leaves; b) Branches. (For each individual collection date, different letters on the bars indicate statistically significant differences among species ($p < 0.05$)).

removing it completely from leaf fragments. Other authors have reported similar difficulties with handling small leaflets, such as those of *Leucaena leucocephala*, also encountering problems of contamination of the mulch with soil particles [Budelman, 1988]. Overall, however, the data suggest that

V. ferruginea leaves decompose more slowly, while *S. microstachyum* leaves would seem to decompose faster than the leaves of the other species.

The initial N concentrations in the leaf litter used for decomposition studies were higher, and the P values were lower (Table 4) than those reported in Table 3 for data from litter traps; this could be attributed to time of sampling and to differences in the age of the material, the litter for the decomposition study being slightly fresher than the litter collected in litter traps; however, comparing the N and P values for the four species (Tables 3 and 4) the differences among species were consistent in all cases. All changes between initial and final N and P concentrations in litter were statistically significant ($p < 0.05$), except for *H. alchorneoides'* N (Table 4). With the exception of *S. microstachyum* litter, N concentrations increased for all species. The two *Vochysia* species showed increases in litter P concentration, while the *H. alchorneoides* and *S. microstachyum* litters both showed net reduction in P concentrations when compared with initial levels. Apparently,

Table 4. Leaf litter decomposition, litter bag experiment, June—July 1990.[1]

a) Percent of initial weight remaining (since 6/6/90).

	Date of collection			
Species	6/18	6/28	7/10	7/25
S. microstachyum	96.9a	78.9a	77.1a	74.9a
V. guatemalensis	92.3a	81.8a	76.1a	77.6a
V. ferruginea	96.2a	87.6a	81.7a	83.6a
H. alchorneoides	86.6a	81.0a	78.9a	77.8a
Sig. level	< 0.2669	< 0.5874	< 0.8157	< 0.5206

b) Initial and final (after 7 weeks) N and P concentrations in litter.[2]

Species		N (%)	P (%)
S. microstachyum	init.	2.84a	0.15a
	final	2.21b	0:11b
V. guatemalensis	init.	1.26b	0.06b
	final	1.45a	0.09a
V. ferruginea	init.	1.10b	0.04b
	final	1.33a	0.05a
H. alchorneoides	init.	1.26b	0.09a
	final	1.39a	0.05b

[1] For each individual collection, differences among species are statistically significant when means are followed by different letters.
[2] Differences among initial and final nutrient concentrations for a given species are statistically significant when means are followed by different letters ($p < 0.05$).

the two *Vochysia* litters applied as mulch would tend to immobilize N and P, and *H. alchorneoides* would tend to immobilize N, at least initially; thus these nutrients would not be as readily available for crop use.

b. *Tethered leaves*

H. alchorneoides and *V. guatemalensis* litter showed the highest rate of weight loss (*S. microstachyum* was not included in the experiment), while *V. ferruginea* showed the lowest rate of loss in initial weight after two weeks (Table 5). These results confirm patterns suggested by the litter-bag experiment, as well as by the relative accumulation of forest-floor litter under these species.

Table 5. **Weight change of tethered leaves with respect to initial weight.**[1]

Species	Initial weight remaining (%)
V. guatemalensis	82.1b
V. ferruginea	93.7a
H. alchorneoides	79.8b
Sig. level	< 0.001

[1] Differences among species are statistically significant when means are followed by different letters.

c. *Mixed-leaf litter*

Non-mixed *S. microstachyum* and *V. ferruginea* litters retained 63.9% and 84.0% of their initial weight, respectively, after 4.5 months (Table 6), confirming trends found in the litter-bag experiment. Both species' litter lost more weight when mixed than alone, although differences between *V. ferruginea* alone and mixed were not statistically significant. Differences between *S. microstachyum* litter alone and mixed were statistically significant in the first three sampling dates but not in the last date (Table 6), suggesting that the effects of mixing the litters may last less than four months.

Mulch experiment

Differences in maize seedling heights between treatments were statistically significant ($p < 0.005$) and consistent throughout the experiment (Table 7). Within the treatments there was little variance. Initially, maize growing in plots with *H. alchorneoides* and *S. microstachyum* showed greatest growth, while seedlings in the unmulched control plots showed significantly inferior growth. After 20 days, maize growth in the *H. alchorneoides* plots began to slow relative to the *S. microstachyum*, but plants in those plots remained larger and stronger than the maize seedlings in either of the *Vochysia*

Table 6. Decomposition rate of *S. microstachyum* and *V. ferruginea* leaves in 1:1 mixture and alone.[1]

Treatment	Initial (1 Aug.) weight left (%)			
	15 Aug	1 Sept	1 Oct	1 Dec
Sm Alone	87.2b	80.9b	76.0b	63.9a
Sm in Mixture	79.4a	77.4a	65.6a	62.9a
Vf Alone	98.4c	96.2c	90.4c	84.0b
Vf in Mixture	97.9c	95.3c	88.9c	79.2b
Sig. Levels	< 0.0001	< 0.0001	< 0.0001	< 0.0001

[1] For each individual collection, differences among treatments are statistically significant when means are followed by different letters.

Table 7. Growth of maize seedlings in plots with mulch of four tree species.

a) Seedling growth (cm).[1]

Treatment	Date			
	6/28	7/7	7/17	7/28
S. microstachyum	17.9a	36.8a	48.9a	53.7a
V. guatemalensis	15.1b	25.2b	30.8b	39.5b
V. ferruginea	15.2b	24.2b	29.6b	35.7b
H. alchorneoides	17.9a	30.9a	38.1a	44.6a
Control	12.7c	19.8c	23.8c	25.2c
Sig. level	< 0.0002	< 0.0001	< 0.0006	< 0.0021

b) Shoot and root biomass (mean dry weight (g) per plot at the end of the experiment).[2]

Treatment	Shoots	Roots
S. microstachyum	16.5a	5.1a
V. guatemalensis	5.7b	2.7b
V. ferruginea	5.1b	2.3b
H. alchorneoides	8.2b	3.3b
Control	2.8c	1.6c
Sig. level	< 0.0465	< 0.0004

[1] For each individual date, differences among treatments are statistically significant when means are followed by different letters.

[2] For each individual parameter, differences among treatments are statistically significant when means are followed by different letters.

treatments. The control plots were slow-growing throughout the experiments and the seedlings in these plots were noticeably weaker and yellower than the plants in the other plots. Differences in dry shoot weights were statistically significant ($p < 0.05$) as well. The primary difference was between the shoots of the maize grown in *S. microstachyum* mulch and all the others (Table 7). Shoot weight of the maize grown in *S. microstachyum* plots was 2 to 8 times greater than that grown in other plots. Roots of maize grown in *S. microstachyum* mulch also had the greatest biomass.

There were no statistical differences in N concentrations in maize shoots (Table 8). Maize roots had higher N concentrations in the *S. microstachyum* mulch treatment and in control plots, than in either of the other three species (Table 8). The differences in maize P concentrations were statistically significant for both shoots and roots: the highest maize shoot P was found in the *V. ferruginea* and the lowest in the *S. microstachyum* mulch treatments; while the highest root P was in the controls. A more clear picture of the circulation of N and P from mulches to maize tissue is seen when examining the relationship between N and P uptake by maize (calculated by multiplying maize tissue nutrient content × tissue biomass at harvest), and the N and P application rates with the mulches (mulch nutrient concentrations × application rate), both extrapolated to kg/ha (Table 9). For N, maize uptake in the *S. microstachyum* treatment was over three times that in both *Vochysia*,

Table 8. Maize seedling tissue nitrogen and phosphorus concentrations, mulch experiment.[1]

Treatment	Shoots	Roots
Nitrogen		
S. microstachyum	1.99a	1.59a
V. guatemalensis	1.85a	1.17b
V. ferruginea	2.00a	1.19b
H. alchorneoides	1.69a	1.05c
Control	1.82a	1.55a
Sig. Levels	< 0.1828	< 0.0001
Phosphorus		
S. microstachyum	0.21c	0.15b
V. guatemalensis	0.25b	0.14c
V. ferruginea	0.29a	0.15b
H. alchorneoides	0.26ab	0.13c
Control	0.25b	0.19a
Sig. Levels	< 0.0421	< 0.0001

[1] For each individual nutrient and tissue category (shoots or roots), differences among treatments are statistically significant when means are followed by different letters.

Table 9. Total N and P in maize biomass and applied as mulch (kg/ha).

Treatment	N in maize	N applied as mulch
S. microstachyum mulch	16.43	22.6
V. guatemalensis mulch	5.48	10.08
V. ferruginea mulch	5.18	8.88
H. alchorneoides mulch	7.49	10.08
Control (no mulch)	3.03	0.0
Treatment	**P in maize**	**P applied as mulch**
S. microstachyum mulch	1.72	1.20
V. guatemalensis mulch	0.72	0.48
V. ferruginea mulch	0.72	0.32
H. alchorneoides mulch	1.04	0.72
Control (no mulch)	0.40	0.0

more than double that in *H. alchorneoides*, and over five times that in the controls (Table 9).

Influence of tree canopies on the microenvironment

The average air temperature tended to be at least 2 °C lower under the tree canopies than in open grass (Table 10), with no significant differences among species. The lowest average soil temperature was found under *V. ferruginea*, with a value similar to that in secondary forest and 4 °C lower than in grass; soil temperature under the other canopies was also lower (by 1.7—3 °C) than in grass. Soil moisture was higher under the two *Vochysia*, with values close to those in secondary forest, and lower under *S. microstachyum* and *H. alchorneoides*, similar to grass. The soil bulk density was lower under the tree species, except for *S. microstachyum*; the lower values were found under the two *Vochysia*, where they were intermediate between grass and secondary forest.

Discussion

Litterfall and litter decomposition

The rates of leaf litterfall of the four species of this study are comparable to others reported for pure stands in tropical humid regions: for example, our values are similar to those reported for *Acioa barteri* (9.8 ton ha^{-1} yr^{-1}) and for teak (9.0 ton ha^{-1} yr^{-1}) in Nigeria [Okeke and Omaliko, 1991]. Our values are also comparable with those reported for species grown for shade

Table 10. Influence of tree canopies on microenvironmental parameters: air and soil temperatures and soil moisture; soil bulk density (0—5 cm depth) also shown.[1]

Site	Air temp. (°C)	Soil temp. (°C)	Moisture (%)	Bulk density (g/cm³)
S. microstachyum	29.8b	27.6b	42.9bc	0.80a
V. guatemalensis	29.0b	27.3b	45.3a	0.75b
V. ferruginea	29.0b	26.4c	45.2a	0.75b
H. alchorneoides	29.1b	28.6b	41.9c	0.78ab
Grass	32.3a	30.3a	41.1c	0.81a
Secondary forest	ND	26.7c	44.6ab	0.70c

[1] For each individual parameter, differences among sites are statistically significant when means are followed by different letters ($p < 0.05$).
ND: no data available.

in agroforestry systems of humid and sub-humid climates, which range between 2 and 4 ton ha^{-1} yr^{-1} [Young, 1989] for stands generally with lower density than in the present study. For example, *S. microstachyum* at 2,500 trees ha^{-1}, with approximately 8 ton ha^{-1} yr^{-1} litterfall compares well with reports for natural litterfall from *Cordia alliodora* (2.9—3.3); *Inga jinicuil* (6.9) and *I. leptoloba* (5.3), all used for shade of crops in humid tropical regions of Latin America, although these trees were at much lower densities (185—278 trees ha^{-1}) [Beer, 1988]. The species of this study could be used with advantage in agroforestry combinations when the goal is high organic matter production to protect soils and enhance nutrient recycling; however for use as shade trees, tree densities should be much lower than the plots of this study, and therefore nutrient recycling would also be greatly reduced.

For *S. microstachyum* and *H. alchorneoides*, total annual leaf litterfall, at approximately 8 ton ha^{-1} yr^{-1} was about twice the amount of the litter on the forest floor in August, 1989, December, 1989 and March, 1990, although accumulation in the forest floor increased thereafter. For *V. ferruginea* accumulation of litter on the forest floor was larger than the total annual input. For *V. guatemalensis* the amounts of litter on the forest floor increased through the sampling period to values larger than the total annual input. This gives an approximate indication of decomposition; i.e., presumably about half the annual litter input decomposes during the same year for *S. microstachyum* and *H. alchorneoides*; in contrast litter may take over one year to decompose under both *Vochysia* species, and more so for *V. ferruginea*. The results of the decomposition studies point to similar trends. These may be influenced not only by differences in nutrient quality but also in microenvironmental conditions under the tree canopies: the below canopy environment of the *V. ferruginea* plots was both cooler (Table 10) and darker than the other plots. From a silvicultural point of view, these results suggest that at 2 m × 2 m tree spacing, after 3.5 years it would be necessary to thin the plots to allow more light and higher temperatures in the litter layer, to increase decomposition and favor tree growth.

Apparently, N and P immobilization occurred in the early stages of decomposition of the two *Vochysia* species, while N immobilization occurred in *H. alchorneoides* (Table 4). Although in many cases the litter N content is a good predictor of initial decomposition rates, apparently the amount of fiber, lignin and polyphenolic compounds play a significant role in the control of release of N and P from decomposing litter in tropical ecosystems [La Caro and Rudd, 1985; Palm and Sanchez, 1990, 1991; Rout and Gupta, 1987]. High aluminum concentrations of the two *Vochysia*'s leaf tissue [Rundell, unpublished data; Montagnini and Sancho, unpublished data] could also be involved in the observed differences; this subject deserves further attention.

The use of the species leaves for mulches

The results of the mulch experiment suggest that tree leaf mulches played a significant role in maize seedling growth. This may be in part attributed to improvements of the microsite conditions by the physical presence of the mulches: e.g., better aeration, increased water retention and lower temperatures. These effects may be significant in a compacted soil pasture as that of the experiment. However, nutrient release from the mulches was also influencing seedling growth, since the results also showed that some species had more important effects on initial maize growth. In particular, maize seedlings grown with the *Stryphnodendron* mulch were taller and visibly healthier looking than the other seedlings. The addition of mulch of leguminous leaves has been shown to have a positive influence on maize growth [Hussian et al., 1990; Kaufusi and Asghar, 1990; Tiraa and Asghar, 1990]. The lackluster growth of the seedlings grown in both *Vochysia* treatments may be due to a variety of factors; for example, Al^{+} ions released from the litter in the upper strata of soil may affect maize seedling growth. Alternatively, N immobilization in the two *Vochysia* treatments (Table 4) may result in temporary soil N deficiencies. These processes should be studied in detail if these species are to be used in tree-crop combinations where the crop species are not Al-tolerant.

With respect to N and P extraction by maize, results confirm trends suggested by the decomposition experiment, with larger N release from N-rich *S. microstachyum* leaves (Table 9) and potential N immobilization by *V. ferruginea* leaves. For P, maize grown in the *S. microstachyum* mulch treatment had extracted approximately 4 times more than in the controls. P extraction was more than double in the *H. alchorneoides* mulch treatment than in the control; while maize grown in the two *Vochysia* plots extracted less than either *S. microstachyum* or *H. alchorneoides* (Table 9). For both N and P, increased amounts added in mulches resulted in greater amounts extracted by the maize. For N, in each treatment, the amount extracted by maize was less than the rate applied; for P, the maize extracted more than applied in any treatment. Apparently, the seedlings took up additional P from the soil: if P in maize in the control (which represents what can be taken up from soil with no mulches) is subtracted from the P in maize of the mulch treatments, it is clear that the extra P provided by the mulches makes up the difference.

The desirability of a species' litter for mulch depends on the specific objective of mulching; in some cases a fast mulch decomposition rate may be needed to favor the growth of associated crops on poor soils, while in others a more persistent litter may be desired. For example, the high litter accumulation recorded under *V. ferruginea* makes it well suited for protecting the soil against erosion; the high organic matter accumulation in soil under *V. ferruginea* [Montagnini and Sancho, 1990a, b] may be related to this species' high rates of litterfall, as well as slower decomposition. In contrast, *S. microstachyum* with high N litter content and relatively faster decomposition rate may favor N recycling. *H. alchornoides* litter, although less abundant than the other three species, because of its relatively faster decomposition would tend to promote fast nutrient recycling, especially for Ca, Mg, K and P; while *V. guatemalensis* litter may be especially important for Ca recycling (Table 2). These differences should be taken into account in order to design systems so that each species' nutrient requirements and contributions can be adequately complemented. The results of the mixed *S. microstachyum/V. ferruginea* litter experiment suggest that at least initially, mixing the litters increases decomposition rates. Possibly the *V. ferruginea* leaves contributed a different microflora which was able to decompose faster the N-rich leaflets of *S. microstachyum*; or the *V. ferruginea* litter, with larger leaves, maintains a more favorable microenvironment for decompostiion than the smaller *S. microstachyum* leaflets. This is important if *V. ferruginea* is chosen to help protect soil against erosion, but at the same time a relatively faster decomposition rate is desired; this could be attained by mixing the litter with *S. microstachyum* litter; similar results could be obtained in a *S. microstachyum/ V. ferruginea*-mixed stand.

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Reciclaje de nutrientes en plantaciones jóvenes con árboles nativos: estrategias para un manejo sustentable

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RESUMEN

Se midió la biomasa arbórea y el contenido de nutrientes (nitrógeno, calcio, magnesio, potasio y fósforo) de ramas, tronco y follaje de cuatro especies arbóreas nativas, en una plantación experimental de cuatro años, situada en la Estación Biológica La Selva, de la Organización de Estudios Tropicales (OTS) situada en las tierras bajas atlánticas de Costa Rica, Centro América. Las cuatro especies —*Stryphnodendron excelsum* Harms, *Vochysia hondurensis* Sprague, *Vochysia ferruginea* Mart and *Hyeronima alchorneoides* (0), se compararon con respecto a su biomasa y contenido de nutrientes de la parte arbórea, así como a los compartimentos de la hojarasca del piso (mantillo) y vegetación de sotobosque. *S. excelsum* tuvo la mayor acumulación de nitrógeno en el tronco, ramas y total de biomasa arbórea. *V. hondurensis* tuvo la mayor acumulación de calcio y magnesio en la biomasa aérea, mientras que *H. alchorneoides* tuvo el mayor contenido de potasio y fósforo en el tronco. A pesar de su contenido relativamente menor de nitrógeno en el tejido, *V. ferruginea* y *H. alchorneoides* mostraron un mayor potencial para el reciclaje de nitrógeno, debido a su distribución más pareja de nitrógeno en el tronco, ramas y follaje. La acumulación de nutrientes en el sotobosque fue muy baja, en comparación con la biomasa arbórea y el mantillo.

Palabras clave: Especies nativas, Costa Rica, reciclaje de nutrientes, nitrógeno, fósforo, calcio, magnesio, potasio.

SUMMARY

Aboveground-tree biomass and nutrient content (nitrogen, phosphorus, calcium, magnesium and potassium) were measured in 4-year-old stands of four indigenus tree species: *Stryphnodendron excelsum* Harms, *Vochysia hondurensis* Sprague, *Vochysia ferruginea* Mart and *Hyeronima alchorneoides* (0), growing on infertile soils in an experimental plantation in the Atlantic humid lowlands of Costa Rica. Biomass and nutrient content among the species, and among above-ground tree biomass. *V. hondurensis* had the highest accumulation of Ca and Mg in the biomass, while *H. alchorneoides* had the highest stem K and P. In spite of their relatively lower N tissue concentrations, *V. ferruginea* and *H. alchorneoides* showed a high potential for N recycling due to its more even distribution of N in stems,

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branches and leaves. Nutrient accumulation by the understory represented a minor component in comparison with above-ground tree tissue and the forest-floor litter.

Key words: Native species, Costa Rica, nutrient recycling, nitrogen, phosphorus, calcium, magnesium, potassium.

INTRODUCCION

Nuestro estudio está enfocado a un área de tierras tropicales bajas y húmedas de Centro América, en Costa Rica, donde predominan las plantaciones de banano. La deforestación y la consecuente degradación del suelo a causa del manejo inadecuado — agricultura intensiva y pastoreo— son problemas comunes. Una precipitación de 4000 mm/año acelera la erosión de los suelos ya agotados por repetidas cosechas.

La restauración de suelos a su antigua productividad y balance ecológico se ha convertido en un interés primordial en la región. Existen agricultores dispuestos a dedicar una parte de sus tierras (10-15%) a plantaciones arbóreas, ya que las consideran como una forma de inversión. Los servicios forestales regionales alientan la plantación de especies exóticas: *Pinus caribaea, Eucalyptus deglupta, Gmelina arborea*, así como *Cordia alliodora*, una especie arbórea nativa de rotación de 30 años que crece en tierras fértiles, siendo inadecuada para tierras degradadas. La elección de especies adecuadas para sistemas de reforestación incluye los siguientes criterios: valor económico de las especies regionales; disponibilidad de semillas o plántulas; información sobre tasas de crecimiento; así como sus efectos sobre los suelos. Ciertas especies arbóreas nativas de la región bajo estudio tienen potencial para crecer bien en suelos pobres y degradados. Estas son especies de crecimiento rápido que contribuyen materia orgánica al suelo dentro de un período relativamente corto. En este trabajo describimos estas especies y su capacidad para crecer en plantaciones a cielo abierto y reciclar nutrientes en estadios tempranos de la rotación.

Beneficios de las plantaciones arbóreas

En la actualidad, un número de esfuerzos gubernamentales y privados están promoviendo la plantación de árboles para el desarrollo rural en los trópicos, incluyendo plantaciones mixtas de árboles y cultivos practicados en sistemas agroforestales. Los árboles son considerados fuente de dinero, ahorro y bienes para la población rural (Chambers y Leach 1990). Ya que las plantaciones tropicales manejadas para alto rendimiento pueden ser por lo menos de cuatro a diez veces más productivas que los bosques naturales no manejados (Wadsworth 1983), éstas también pueden ayudar a satisfacer la creciente demanda global de madera. Se espera que este tipo de manejo contribuya a disminuir la presión sobre los bosques naturales (Evans 1987).

El manejo sustentado de plantaciones arbóreas se convierte en una alternativa biológica y socialmente plausible en suelos que no son apropiados para la práctica continua de agricultura que usa las tecnologías locales predominantes (Gladstone y Ledig 1990). En especial, las plantaciones de árboles y las plantaciones mixtas de árboles y cultivos representan alternativas productivas para el uso de tierras deforestadas donde la regeneración natural es pobre debido a la degradación intensa o a la distancia de fuentes de propagación. La baja fertilidad, la compactación del suelo a causa del pastoreo y la invasión por malas hierbas —todos índices de degradación— pueden ser serios obstáculos en la reforestación y en la agricultura convencional. Cuanto más se expande el área de degradación, más se incrementa el énfasis en la plantación de especies arbóreas capaces de crecer en condiciones pobres y ofrecen productos con potencial financiero (madera, combustible y demás) así como también beneficios ambientales (conservación de suelos, protección de cuencas) (Evans, 1987).

La selección apropiada de especies arbóreas para la plantación forestal o agroforestal depende del conocimiento sobre el rendimiento de la especie y de los beneficios económicos y ambientales que ésta ofrezca. En situaciones locales, la selección de una especie arbórea es determinada por la disponibilidad de semillas o plántulas y por la información disponible acerca de sus características silviculturales y manejo —por ejemplo, crecimiento rápido y posibilidad de cultivo mixto durante las etapas tempranas de establecimiento. La mayoría de los programas y subvenciones de reforestación promueven el uso de especies bien conocidas y con frecuencia exóticas. Alrededor del 85% de las plantaciones forestales en los trópicos está dominada por tres géneros: *Pinus, Eucalyptus* y *Tectona* (Evans, 1987), mientras que existen miles de especies indígenas apropiadas para fines similares. Los árboles nativos pueden ser más apropiados que los exóticos ya que están mejor adaptados a las condiciones ambientales locales, las semillas y plántulas están localmente disponibles y los agricultores están familiarizados con ellos y con sus usos. Además, el uso de árboles nativos en sistemas productivos ayuda a la preservación de la diversidad genética y fomenta un mejor balance con la flora y fauna local.

Consecuencias ecológicas de las plantaciones arbóreas de crecimiento rápido

Los factores que influyen sobre la productividad de las plantaciones forestales tropicales son poco entendidos. Algunos estudios informan sobre rendimientos o producción de biomasa en relación a factores climatológicos, pero pocos refieren las características del sitio, tales como la elevación y el tipo de suelo (Lugo et al., 1988). Los árboles pueden influenciar las características del sitio a través del reciclaje de nutrientes y sus interacciones con el medio ambiente.

Los efectos beneficiosos más importantes de los árboles sobre los suelos pueden incluir el mejoramiento de la estructura del suelo y el incremento de nutrientes disponibles (Fassbender, 1984, Nair, 1989, Sánchez et al., 1985, Sánchez, 1987). La fijación simbiótica de nitrógeno por los árboles resulta, en muchos casos, en el incremento del nitrógeno disponible en el suelo (Alpízar et al., 1986, Montagnini et al., 1986, Dommergues, 1987). Por otro lado, las plantaciones jóvenes de árboles tropicales, las cuales incorporan cantidades considerables de nutrientes en su biomasa sobre un período de tiempo relativamente corto, son ecosistemas de crecimiento rápido (Bruijnzeel, 1991). Durante las etapas tempranas de desarrollo, la cantidad de nutrientes absorbida del suelo generalmente sobrepasa la cantidad de nutrientes suplementada al suelo por la hojarasca y por la lluvia (Bruijnzeel, 1991).

El deterioro de la fertilidad del suelo puede ser una limitación seria para la plantación forestal sustentada en regiones tropicales: la fertilidad del suelo puede ser disminuida a través de la eliminación excesiva de biomasa, especialmente si los nutrientes del dosel arbóreo son perdidos a través de la cosecha o de la preparación del sitio para el cultivo (Perry y Maghembe, 1989). Por otro lado, Wadsworth (1983) sugiere que, con la posible excepción del fósforo, las cosechas repetidas generalmente no resultarían en serias deficiencias de nutrientes en el suelo.

Lundgren (1980) propuso que los efectos beneficiosos de las plantaciones forestales ocurren sólo durante el período de cinco a diez años inmediatamente después del cierre del dosel (la fase de enriquecimiento por barbecho). Durante la fase de producción máxima, puede deteriorarse la calidad del sitio: los minerales nutritivos son absorbidos por los árboles mientras que la hojarasca se acumula en el suelo del bosque, pero las condiciones no son apropiadas para la descomposición de la materia orgánica (Lundgren, 1980). Sánchez et al. (1985) concluyeron que los efectos perjudiciales en los suelos ocurren sólo durante el establecimiento de la plantación, aunque también enfatizaron que la extracción de nutrientes a través de la cosecha y las pérdidas por lixiviación antes del cierre del dosel provocan un agotamiento de nutrientes claves, especialmente de potasio, que deberían ser repuestos si el nivel de rendimiento ha de ser mantenido en las rotaciones siguientes.

Las especies arbóreas varían en sus tasas de absorción y capacidad de reciclaje de nutrientes. La posibilidad de usar ciertas especies para la acumulación de nutrientes fue sugerida por Sánchez et al. (1985) quienes observaron que ciertas especies tienen la habilidad (por ejemplo, *Gmelina arborea*) de acumular calcio y magnesio, mientras que otras favorecen la acumulación de potasio y fósforo. Todavía son escasos los datos sobre segundas y terceras rotaciones, así que no tenemos suficientes indicios acerca de cuáles son los nutrientes críticos para el mantenimiento de la producción del sitio. La información sobre las tasas de absorción y capacidad de reciclaje de nutrientes por las diferentes especies arbóreas ayudará a diseñar las mejores estrategias de manejo que tomarán ventaja de los efectos beneficiosos de los árboles sobre la fertilidad del suelo o evitarán el deterioro del sitio en el momento de la cosecha.

Efectos de las plantaciones arbóreas sobre los nutrientes del sitio: un ejemplo de Costa Rica

Las pruebas locales y regionales de especies arbóreas para la reforestación muchas veces revelan rendimientos sobresalientes de los árboles nativos. Por ejemplo, de trece especies arbóreas nativas en una plantación experimental en la estación biológica La Selva de la Organización de Estudios Tropicales (OTS) situada en las tierras bajas atlánticas de Costa Rica, Centro América, por lo menos cuatro —*Stryphnodendron excelsum, Vochysia hondurensis, Vochysia ferruginea* y *Hyeronima alchorneoides*— presentaron tasas de crecimiento iguales o mayores que las especies exóticas recomendadas para la región (Espinoza y Butterfield, 1989). Este trabajo demuestra el potencial de muchos árboles nativos para uso comercial. Además se destaca que ciertas especies nativas crecen bien en sitios degradados de suelos pobres y ácidos que no podrían sustentar la agricultura convencional. Los resultados de nuestros estudios en el mismo sitio demostraron que después de dos años y medio estas especies contribuyeron a la restauración de la fertilidad del suelo a través del incremento de la materia orgánica, el nitrógeno y los niveles de cationes a valores aproximados a aquellos considerados apropiados para los cultivos agrícolas (Montagnini y Sancho, 1990a, 1990b).

En las siguientes secciones se compara la biomasa y contenido de nutrientes de estas especies, la hojarasca, la vegetación del sotobosque y las reservas de nutrientes del suelo. Esta información puede ser utilizada para diseñar estrategias de manejo que tomen ventaja de los efectos beneficiosos de los árboles sobre los suelos y para evitar el agotamiento de los nutrientes del sitio en el momento de la cosecha. Estas estrategias deberían ser valiosas para la promoción del uso de sistemas —mixtos o de plantaciones puras, sistemas agroforestales— que incluyan estas especies madereras de crecimiento rápido en la zona y en otras regiones tropicales con características ecológicas similares.

El sitio experimental

La plantación experimental fue establecida en diciembre de 1985, sobre un área de pastos abandonados en la Estación Biológica La Selva de la Organización para Estudios Tropicales (10 26'N, 86 59'O, 50 metros de altura media, 24 °C de temperatura media anual, 4000 mm de precipitación media anual, con precipitación máxima en julio y mínima en marzo) (Informes climatológicos de la Estación Biológica La Selva). Los suelos son Fluventic Dystropepts, derivados de material volcánico depositados aluvialmente; son profundos, bien drenados, y sin piedras, tienen un contenido de materia orgánica bajo o medio, textura moderadamente pesada, y son generalmente ácidos y poco fértiles (Sancho y Mata, 1987). El área se deforestó en la década del 50, y fue utilizada para pastoreo de ganado hasta 1984. Se realizó una limpieza manual del terreno antes de la plantación. Las especies arbóreas se plantaron al azar con cinco (5) réplicas, cada parcela (14 m x 14 m) con siete filas de siete árboles y con dos metros entre árboles. Cinco parcelas similares de 14 m x 14 m también fueron establecidas en un área adyacente con pastos y en un bosque secundario. Durante el primer año, se desmalezó manualmente cuatro veces. Después, este proceso se llevó a cabo mecánicamente hasta el cierre del dosel.

Las especies arbóreas

Las especies para este estudio eran de buen crecimiento inicial (Espinoza, Camacho y Butterfield, 1989, González et al., 1990), y valor comercial (González et al., 1990, Chudnoff, 1984, Holdridge y Poveda, 1975).

Stryphnodendron excelsum Harms (Leguminosae, subfamilia Mimosoideae) ("vainillo") se encuentra sólo en Costa Rica, aunque representantes de este género son nativos en todo América tropical (Brasil, Costa Rica, Guayana) (Allen y Allen, 1981). Esta especie crece en regiones de climas muy húmedos y aparentemente se adapta tanto a suelos aluviales como también a cerros bajos y a suelos degradados por el pastoreo (González et al., 1990). Su madera es primordialmente utilizada en construcción general y también para muebles pequeños y tornería (Allen y Allen, 1981). Su fruto sirve de alimento a muchas especies, sobre todo pequeños mamíferos.

Vochysia ferruginea Mart (Vochysiaceae) ("botarrama") crece en los bosques de tierras bajas desde Nicaragua hasta Brasil (Whitmore y Hartshorn, 1969). Se encuentran en suelos ácidos, bien drenados, y de baja fertilidad, aunque se puede adaptar a una variedad de suelos (González et al., 1990). Es una especie pionera que se autopoda y forma rodales uniformes, de edad pareja en campos abandonados su madera se usa para madera contrachapada y construcción.

Vochysia hondurensis Sprague (Vochysiaceae) ("mayo") se encuentra desde Méjico hasta Panamá, en elevaciones hasta de 900 m (Whitmore y Hartshorn, 1969). Usualmente crece en áreas húmedas y de baja altitud, en suelos aluviales o residuales (menos fértiles). Como es considerado un substituto de la caoba, su madera es muy apreciada para carpintería, madera contrachapada y mueblería.

H. alchorneoides (O) (Euphorbiaceae) ("pilón") abarca desde el sur de Méjico hasta el sur de Brasil (Chudnoff, 1984). Esta especie crece bien en cerros y en pastos abandonados, pero no se sabe mucho sobre sus requisitos edáficos. Su madera es usada en construcción pesada, mueblería, enchapados decorativos y tornería (Chudnoff, 1984). Las características botánicas de estas especies están descritas en Holdridge y Poveda (1975), Hartshorn (1983), Standley (1937-38) y Hartshorn y Hammel (no publicado). Estudios detallados sobre las semillas y las características de germinación son presentados en González (1991).

METODOS

Los procedimientos de muestreo y métodos químicos están descritos en Montagnini y Sancho (1990a, 1990b), y en Montagnini et al. (1991). Los suelos se muestrearon bajo las cuatro especies arbóreas mencionadas, en área de pastos libre de árboles y en bosque secundario de veinte años. La biomasa de los árboles y el contenido de nutrientes en tallos, ramas y hojas fueron medidos al momento del raleo de las parcelas, cuando la plantación tenía cuatro años. También se midió la biomasa y la concentración de nutrientes del sotobosque. El reciclaje de nutrientes fue calculado multiplicando la biomasa de cada compartimento por la concentración de nutrientes en el mismo (nitrógeno, calcio, magnesio, potasio, fósforo).

RESULTADOS Y DISCUSION

Biomasa arbórea

Los valores de la biomasa de árboles enteros presentados aquí (Tabla 1) son mayores que los reportados para *Albizia lebbek* de cuatro años (Parrota, 1989) y para *Leucaena leucocephala* de cinco años y medio (Wang et al., 1991), ambos creciendo en plantaciones densas para la producción de biomasa en Puerto Rico. Los valores de productividad (biomasa arbórea dividida por la edad del árbol) concuerdan con otros valores presentados en la literatura para plantaciones monoespecíficas en los trópicos húmedos. El valor para *V. hondurensis* es similar al valor reportado para *Gmelina arborea* (12,8 toneladas/ha/año) en la región amazónica del Brasil (Russell, 1987) así como también al valor para *Gmelina arborea* (12,7 toneladas/ha) y para *Albizia falcataria*, ambos en las Filipinas (11,3) (Kawajara et al., 1981, en Young, 1989). Sin embargo, los incrementos presentados aquí son menores que aquellos reportados para algunas especies de crecimiento rápido, tales como *Acacia mangium* (15,5 a 18,0 toneladas/ha en Malasia) y *Leucaena leucocephala* (20,0 a 30,0, y hasta 80,0 toneladas/ha en Hawaii y en otros sitios tropicales, Young, 1989).

Los incrementos anuales en madera para especies latifoliadas en los trópicos

Tabla 1. Promedio de diámetros a la altura del pecho (dap), altura, biomasa aérea y crecimiento anual.

Anual medio	Dap (cm)	Altura (m)	Biomasa aérea viva Fuste	Ramas (kg/ha)	Hojas	Total	Crecimiento Total (t/ha/año)	Fuste
S. exc.	12,0a	8,9b	35.250a	15.250a	4.325a	54.825	13,7	8,8
V. fer.	10,3a	8,1b	24.750b	14.250a	5.925a	44.925	11,2	6,2
V. hon.	10,8a	12,0a	41.750a	6.500b	7.250a	55.500	13,9	10,4
H. alc.	10,8a	9,0a	26.250b	12.250a	5.350a	43.850	12,0	6,5

Nota: En ésta y las siguientes tablas, las diferencias entre sitios para un parámetro dado son estadísticamente significativas cuando los promedios son seguidos por letras diferentes.

varía entre 1 y 28 toneladas/ha/año. Las especies de crecimiento rápido como *Gmelina arborea* y *E. saligna* varían entre 10 y 20 y entre 8 y 28 toneladas/ha respectivamente, y las especies de crecimiento relativamente más lento como *Swietenia* sp. y *Tectona grandis* varían entre 1 y 4 y entre 3 y 12 toneladas/ha respectivamente (Wadsworth, 1983). Otros valores para árboles de crecimiento rápido en regiones tropicales húmedas incluyen varias especies de *Eucalyptus* cultivadas en las Américas y en el Asia (entre 7,2 y 11,9 toneladas/ha); *Gmelina arborea* en Costa Rica (11,8 toneladas/ha) (Lugo et al., 1988); de 1,3 a 5,3 *Leucaena leuocephala* en sitios premontanos y en tierras bajas húmedas (entre 2,8 y 15,9 toneladas/ha); *Prosopis juliflora*, en sitios húmedos de India (9,4 toneladas/ha), y *Populus deltoides*, en sitios subtropicales de India (6,4 toneladas/ha) (Lugo et al., 1990). De modo que el promedio anual de los incrementos en madera para las especies en este estudio cae dentro de los valores reportados para otras especies arbóreas de crecimiento rápido en los trópicos húmedos.

Acumulación de nutrientes en la biomasa arbórea

Nitrógeno

Las mayores concentraciones de nitrógeno en tallos, en ramas y biomasa arbórea se encontraron en *S. excelsum*. Aproximadamente 200 kg/ha, o 60% del nitrógeno de la biomasa arbórea de *S. excelsum* (Figura 1) permanecería en el sitio al momento de la cosecha si se dejaran las ramas y hojas en el suelo. *V. hondurensis* tenía una proporción similar de nitrógeno en su porción de hojas y ramas; al igual que en *S. excelsum* más del 50% del nitrógeno de la biomasa arbórea podría ser reciclado si se dejan los restos en el sitio al momento de la cosecha. *V. ferruginea*, con una biomasa de tallos relativamente menor, proporcionalmente tenía más nitrógeno en hojas (52,9%) y en ramas (42,1%), mientras que *H. alchorneoides* tenía una distribución más pareja en la biomasa arbórea (Figura 1).

Calcio

V. hondurensis, con una mayor biomasa de tronco y una concentración elevada de calcio (Ca), también tenía la mayor cantidad de calcio en la madera (más de 600 kg/ha, equivalente a 84% del Ca de la biomasa arbórea), aproximadamente el doble de la cantidad de *S. excelsum* y de *V. ferruginea*, y varias veces más que *H. alchorneoides* (Figura 2). En consecuencia, la cosecha total de árboles de *V. hondurensis* podría reducir considerablemente la cantidad de calcio en el sitio. Sin embargo, mientras los árboles de *V. hondurensis* estén vivos, cantidades relativamente grandes de calcio podrían ser recicladas porque, aunque sólo represente el 16% de la biomasa de la parte aérea, la cantidad conjunta de calcio en las hojas y las ramas sobrepasaba 100 kg/ha.

La proporción de calcio en el tronco en relación a la biomasa total fue similar para

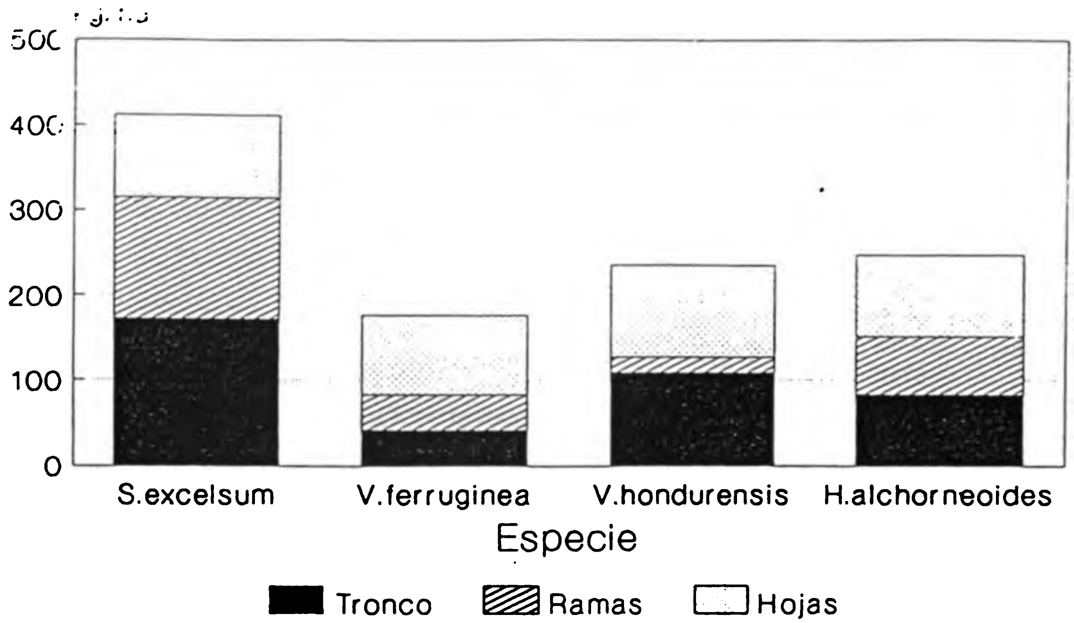

Figura 1. Nitrógeno en la biomasa arbórea.

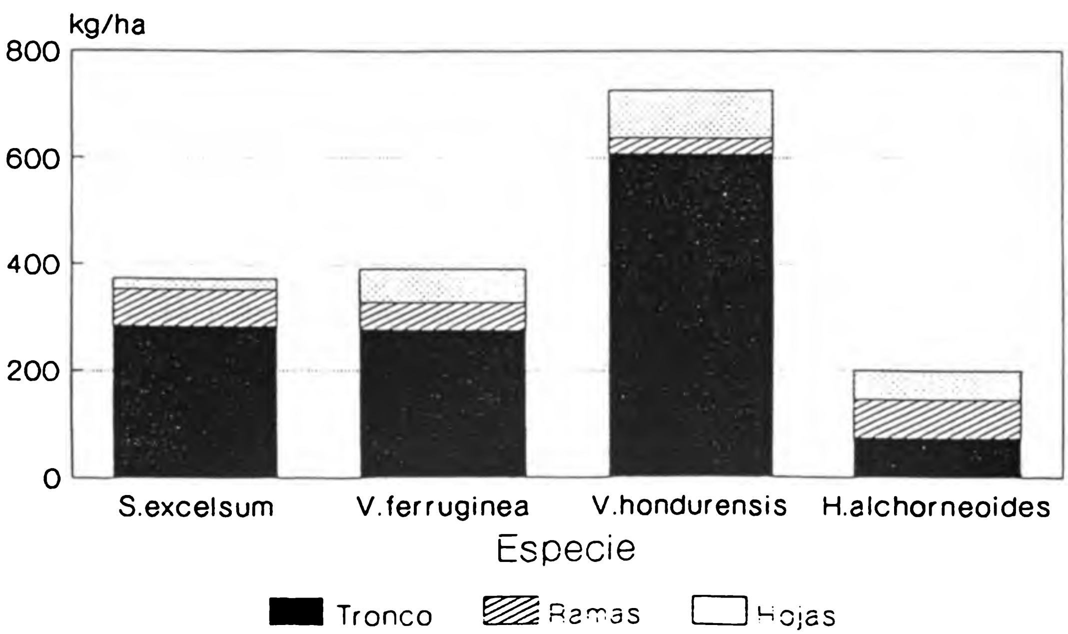

Figura 2. Calcio en la biomasa arbórea.

S. excelsum y para *V. ferruginea* (76,6% y 70,8% respectivamente) (Figura 2), pero las cantidades absolutas fueron menores que la mitad de la cantidad de *V. hondurensis*. *H. alchorneoides* otra vez tuvo una mejor distribución de calcio en los tallos, las hojas y las ramas.

Magnesio

V. hondurensis, con su alta biomasa de tronco y alta concentración de magnesio (Mg), también tuvo la mayor cantidad de Mg en la madera (55% del total del Mg contenido en la biomasa arbórea, aproximadamente 30 kg/ha) (Figura 3). En consecuencia, si se retiran los troncos de *V. hondurensis* se afectaría el reciclaje de Mg en el sitio de una manera más dramática que cualquiera de las otras especies, especialmente si se realiza una cosecha total (Figura 3).

Potasio

El panorama cambia con el potasio (K): la mayor acumulación de K en tallos fue hallado en *H. alchorneoides* (252 kg/ha, Figura 4), representando 58,7% del K arbóreo: Esta cantidad fue seguida por *V. hondurensis* con 175 kg/ha, la cual representa 76,8% del K arbóreo. En consecuencia, la cosecha total de árboles de *H. alchorneoides* y de *V. hondurensis* podría tener los mayores efectos en el reciclaje de K. *S. excelsum* y *V. ferruginea* tenían 33,6% y 35,4% respectivamente, de K en los tallos. El reciclaje de K en las hojas y las ramas podría ser relativamente más importante cuando se considera estas últimas dos especies.

Fósforo

V. hondurensis y *H. alchorneoides* tuvieron las mayores proporciones de fósforo (P) en la madera (72,4% y 62,1% respectivamente) (Figura 5). *S. excelsum* y *V. ferruginea* tuvieron relativamente menores cantidades de P en los tallos (43,9% y 48,7% respectivamente).

Nuestros resultados confirman reportes anteriores sobre los efectos negativos de la cosecha total de árboles sobre las reservas de nutrientes del sitio: por ejemplo, Bruijnzel y Wiersum (1985) estudiaron las entradas/salidas de nutrientes en plantaciones de *Agathis dammara* en las tierras altas de Java. Sus resultados, calculados para una rotación de treinta años, indicaron que la cosecha total de los árboles eliminaría una cantidad de nutrientes equivalente a las entradas de potasio y calcio, casi la mitad de la entrada de magnesio, y el doble de la

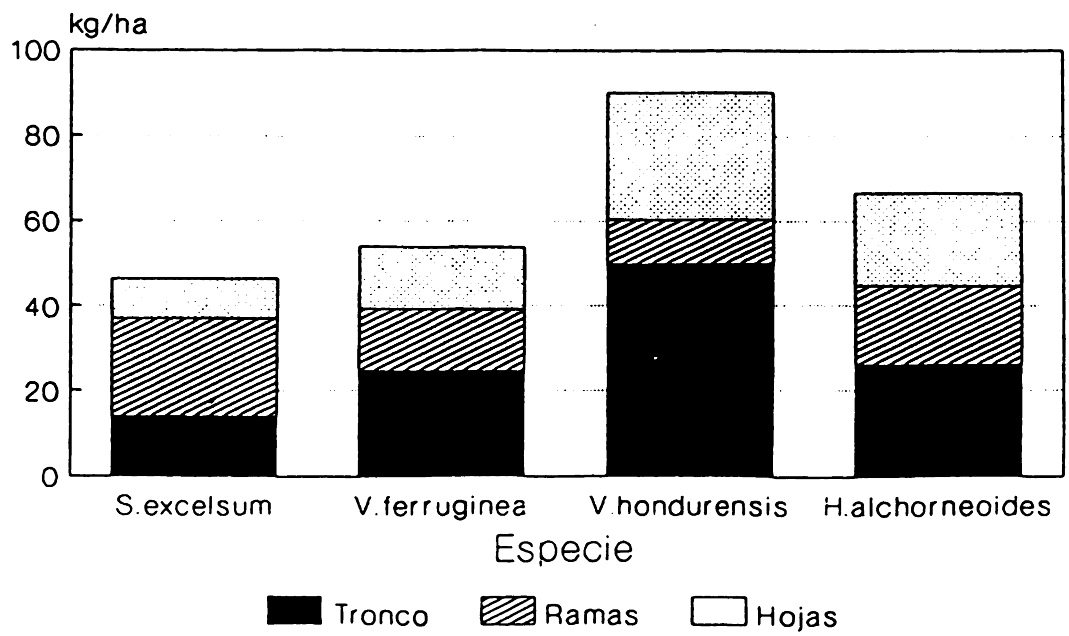

Figura 3. Magnesio en la biomasa arbórea.

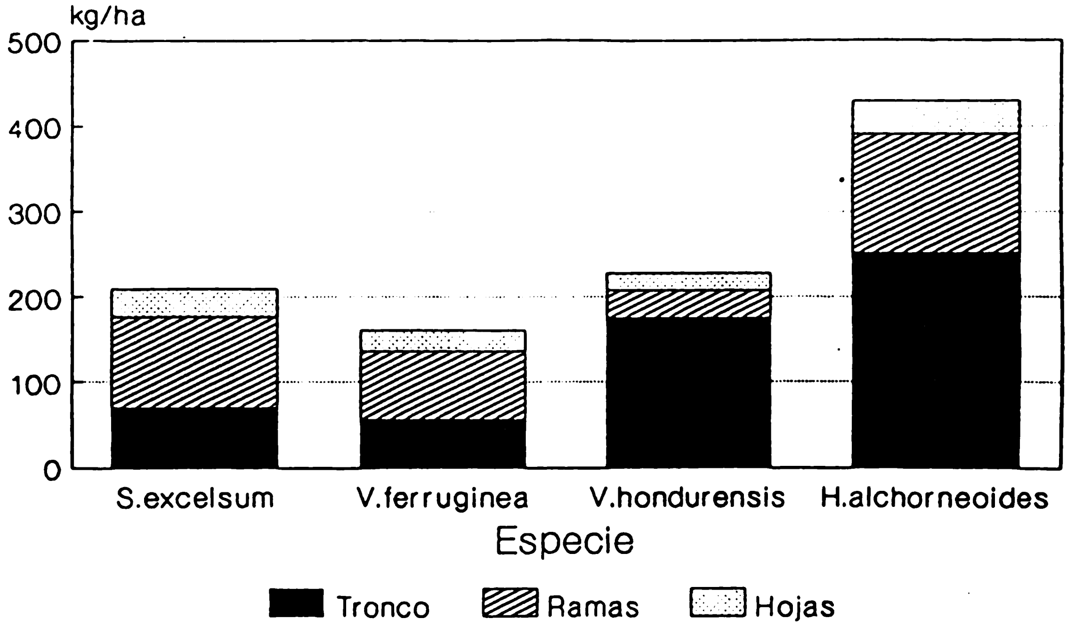

Figura 4. Potasio en la biomasa arbórea.

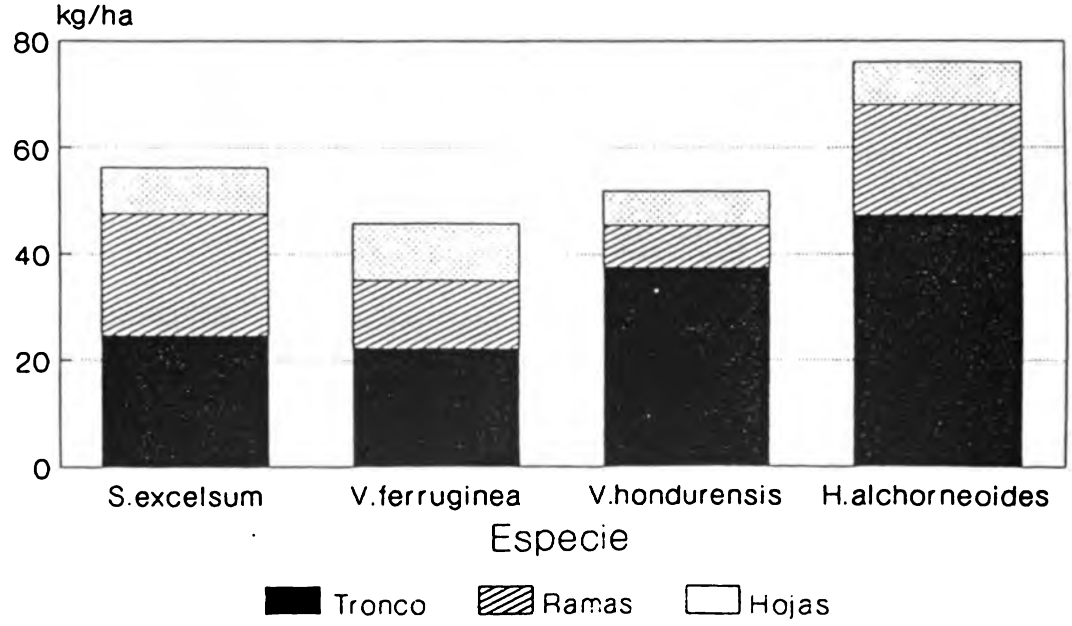

Figura 5. Fósforo en la biomasa arbórea.

Tabla 2. Materia orgánica, cantidades totales de N, P, pH, Ca, Mg y K en suelos bajo las cuatro especies arbóreas nativas en la plantación, en el área de pasto y en el bosque secundario; Mayo 1989. (1)

Sitio	Prof. (cm)	MO	N	P	pH	Ca	Mg	K
		(%)		(mg/kg)			(cmol/kg)	
S.	0-15	4,50a	0,278a	2,4a	5,1a	0,68b	0,44a	0,13a
exc.	15-30	3,29a	0,224a	2,1a	5,1ab	0,52bc	0,22bc	0,14a
	30-60	1,88a	0,196a	1,8b	5,1a	0,54a	0,16a	0,14a
V.	0-15	5,06a	0,320a	3,24a	4,98a	0,63bc	0,53bc	0,16a
fer.	15-30	3,66a	0,248a	5,03c	5,03c	0,35d	0,20c	0,10a
	30-60	2,94a	09,200a	2,50b	5,07a	0,33a	0,16a	0,15a
V.	0-15	4,30a	0,304a	2,30a	5,20a	0,47bc	0,50bc	0,10a
hon.	15-30	3,16a	0,232a	1,82a	5,08ab	0,38cd	0,22bc	0,07a
	30-60	2,42a	0,202a	2,00b	5,13a	0,36a	0,15a	0,06a
H.	0-15	5,16a	0,232a	1,5a	5,1a	0,31c	0,21a	0,09a
alc.	15-30	2,77a	0,248a	1,5a	5,1ab	0,45bcd	0,19c	0,10a
	30-60	1,21a	0,158a	1,7b	5,2a	0,46a	0,20a	0,10a
Pasto	0-15	3,98a	0,296a	4,1a	5,2a	0,57bc	0,38a	0,22a
	15-30	2,94a	0,236a	3,4a	5,1ab	0,51bcd	0,27bc	0,17a
	30-60	2,46a	0,194a	8,9a	5,2a	0,47a	0,20a	0,13a
Bosque	0-15	5,11a	0,288a	2,3a	5,2a	1,16a	0,49a	0,21a
	15-30	3,83a	0,244a	2,0a	5,2a	0,92a	0,45a	0,17a
	30-60	2,48a	0,206a	1,4b	5,2a	0,62a	0,27a	0,12a

1. Existen diferencias estadísticamente significativas entre los sitios para una profundidad dada y los parámetros cuando los promedios son seguidos por letras diferentes.

entrada de fósforo. Los autores concluyeron que para evitar la escasez de nutrientes, especialmente de fósforo, la cosecha total de árboles no debería ser practicada. Nuestros resultados también sugieren que dejando los restos de ramas y hojas en el sitio podrían disminuir considerablemente los impactos negativos de la cosecha, con diferentes consecuencias según las especies.

Impacto de los árboles sobre los nutrientes del suelo

Los mayores niveles de materia orgánica y de N en el suelo se encontraron en la plantación arbórea, con cantidades aproximadas a los del bosque secundario (Tabla 2), aunque estas diferencias no son estadísticamente significativas ($P < 0,05$). El contenido de P fue mayor en el área de pasto que en la plantación o que en el bosque (Tabla 2). Dentro de la plantación arbórea, no hubo diferencias significativas en el contenido de cationes entre las especies. Sin embargo, sí hubo una tendencia a niveles más altos de Ca bajo *S. excelsum* y niveles menores bajo *H. alchorneoides*. Los mayores niveles de Mg fueron registrados bajo las dos especies de *Vochysia*, con contenidos menores en *H. alchorneoides* (Tabla 2). Estos resultados confirman datos de mediciones anteriores realizados en 1988 (Montagnini y Sancho, 1990a, 1990b).

Mediciones similares tomadas en mayo de 1990 y nuevamente en mayo de 1991, revelaron tendencias en la acumulación de nutrientes en el suelo similares a aquellas encontradas en 1988 y 1989. Al examinar los datos entre 1988 y 1991, no se detectaron tendencias de aumento o reducción a través del tiempo para ninguno de los nutrientes (Montagnini y Sancho, datos no publicados). Aparentemente, el aumento del nivel de nutrientes del sitio fue observado en 1988, cuando los árboles tenían dos años y medio y habían cerrado el dosel, pero después de este efecto inicial no se pudo detectar ningún otro cambio positivo.

Los impactos de la plantación de especies arbóreas sobre las reservas de nutrientes del suelo dependerán de la absorción de nutrientes por los árboles en relación a la capacidad del suelo para suplir nutrientes, del reciclaje de nutrientes (mientras los árboles estén vivos), y de las partes cosechadas del árbol, ya sea el árbol entero o la madera, y su biomasa y contenido de nutrientes al momento de la cosecha. Esto se puede ilustrar tomando como ejemplo estas relaciones para *V. hondurensis*, la especie de crecimiento más rápido y aparentemente de mayores requerimientos nutricionales en este estudio. La retención de nutrientes por *V. hondurensis* (calculado dividiendo el total de nutrientes en la biomasa por la edad de la plantación) fue un promedio de 58 kg de N, 181 kg de Ca, 57 kg de K, 22 kg de Mg y 13 kg de P/ha/año. Las cantidades de N, Ca, Mg y K son el doble de aquellas reportadas por Wadsworth (1983) para plantaciones de teca, pero el valor de P es similar. Aunque estas cantidades de nutrientes son altas, éstas deberían ser comparadas con la capacidad del suelo para suplir nutrientes. Por ejemplo, Wadsworth (1983) comparó datos de la tasa de absorción anual de nutrientes de varios cultivos agrícolas en suelos Ultisoles y Oxisoles en Puerto Rico (N = 90 - 120 kg/ha/año, K = 50 - 90, Ca = 86 - 109, Mg = 68 - 98), con las tasas de retención media anual de nutrientes de plantaciones de teca y de pino. Al examinar esos datos se concluye que la capacidad de los suelos para suplir nutrientes era suficiente para las necesidades de las plantaciones, y que los árboles podían ser cosechados sin crear deficiencias en el suelo, con la posible excepción de P. Wang et al. (1991) también repotaron que la tasa anual de absorción de N, P, Ca, Mg y K para plantaciones de *Casuarina* y *Albizia* en Puerto Rico era similar a la tasa de absorción de cultivos como el maíz y el sorgo.

En nuestro análisis, no estamos considerando la capacidad para suplir nutrientes de los suelos, pues no se dispone hasta la fecha de registros que permitan esta comparación.

Biomasa y concentración de nutrientes en la vegetación del sotobosque

La acumulación de nitrógeno en la biomasa aérea del sotobosque fue mayor bajo las parcelas de *S. excelsum* (14,9 kg/ha), aunque esta cantidad representa sólo 3,6% del N en la biomasa arbórea (Tabla 3). Para

Tabla 3. Biomasa y contenidos de nutrientes en la vegetación del sotobosque y la hojarasca del suelo del bosque (1)

(a) Vegetación del sotobosque

	Biomasa (kg/ha)	N	Ca	Mg (kg/ha)	K	P
S. exc.	874	14,9 (3,6)	2,9 (0,8)	3,6 (7,7)	8,8 (4,2)	1,1 (2,0)
H. alc.	425	5,7 (2,3)	3,3 (1,6)	1,9 (2,9)	3,3 (0,8)	3,1 (4,1)

(b) Hojarasca del suelo del bosque (2)

	Biomasa (kg/ha)	N	Ca	Mg (kg/ha)	K	P
S. exc.	5 612	95,1 (23,0)	41,6 (11,1)	8,2 (17,6)	6,6 (3,1)	4,3 (7,6)
V. fer.	17 215	240,3 (137,0)	187,6 (47,9)	19,1 (35,5)	12,1 (7,5)	15,5 (33,8)
V. hond.	11 084	134,0 (57,0)	170,0 (23,4)	26,4 (24,3)	9,7 (4,2)	11,6 (22,3)
H. alc.	4 238	39,2 (15,8)	55,0 (27,0)	11,9 (17,9)	6,8 (1,6)	12,9 (16,9)

1. Los números entre paréntesis son porcentajes en relación a la biomasa total de nutrientes del árbol.
2. Totales, incluyendo hojas, fragmentos y ramas.

H. alchorneoides, el N en la biomasa del sotobosque fue 5,7 kg/ha, o 2,3% de la biomasa arbórea. Para los otros nutrientes, la acumulación en la biomasa del sotobosque bajo *S. excelsum* varió entre 0,8% y 7,7%, y bajo *H. alchorneoides*, varió entre 0,85% y 4,1% (Tabla 3).

Ya que la vegetación del sotobosque aparentemente representa una proporción relativamente pequeña de nutrientes en relación al árbol entero, las manipulaciones del sotobosque deberían tener poco efecto sobre el reciclaje de nutrientes en el sitio. Por ejemplo, el desmalezado debería tener un efecto relativamente menor sobre el reciclaje de nutrientes, a menos que el sotobosque sea eliminado varias veces al año. Esta hipótesis también sugiere que el intercultivo de especies herbáceas anuales que alcanzan cantidades similares de biomasa a las del sotobosque bajo *S. excelsum* o *H. alchorneoides* no tendrán un efecto negativo considerable en el balance de nutrientes del sitio. Debido a que las muestras de biomasa del sotobosque fueron tomadas cuando la biomasa estaba en su apogeo, las cantidades reportadas aquí son consideradas una aproximación a las que podrían ser obtenidas en cultivos. Sin embargo, este factor merece más estudio, ya que los requerimientos de nutrientes y las partes de plantas y árboles eliminados con la cosecha variarán con los cultivos. Nuestros resultados, sin embargo, tienden a concordar con Bruijnzel y Wiersum (1985), quienes concluyeron que el uso de intercultivos en plantaciones arbóreas en Java, acompañado de medidas preventivas para reducir la erosión del suelo, era una manera aceptable de conservar nutrientes. Ellos argumentan que además de sus beneficios socioeconómicos, el uso de prácticas "taungya" podrían también resultar ventajoso ya que los agricultores podrían estar dispuestos a usar fertilizantes para los cultivos y los efectos dispuestos a usar fertilizantes para los cultivos y los efectos residuales de estos nutrientes aplicados podrían incrementar la producción de los árboles.

Acumulación de nutrientes en la hojarasca del bosque

La mayor acumulación de nutrientes y biomasa de hojarasca del suelo fue bajo *V. ferruginea*. El N en la hojarasca bajo *V. ferruginea* fue mayor que en la biomasa arbórea de la misma (Tabla 3). Como fue notado anteriormente, la biomasa de las hojas y ramas de *V. ferruginea* representa una gran porción de su biomasa arbórea. Esta especie de auto-poda, una característica que aumenta el despoje de hojas y ramas, y la poda ocasional puede haber añadido aún más hojarasca al suelo forestal. Los resultados de nuestros estudios de tasas de caída de hojarasca y de la descomposición de la misma (Montagnini et al., 1991) sugieren que la descomposición de la hojarasca es relativamente lenta bajo *V. ferruginea*, un factor que explica las altas acumulaciones mencionadas anteriormente. *V. hondurensis, H. alchorneoides* y *S. excelsum* exhibieron tasas de descomposición de hojarasca más aceleradas. El Ca, Mg y P de la hojarasca bajo *V. ferruginea* eran considerables (Tabla 3), un dato especialmente relevante para P, ya que existen probabilidades de deficiencias de este elemento en el sitio, tal como fue mencionado anteriormente. Los nutrientes de la biomasa del suelo forestal también fueron mayores bajo *V. hondurensis*. De nuevo, este resultado fue más significativo para N, Ca, Mg y P. Por ende, a pesar del crecimiento rápido de esta especie, el reciclaje de nutrientes proveniente de la hojarasca puede por lo menos compensar parcialmente el agotamiento de nutrientes del suelo. Mientras que lo contrario es cierto para P, el N de la hojarasca del suelo forestal fue más que el doble bajo *S. excelsum* que bajo *H. alchorneoides*, a pesar de que ambas especies tenían cantidades similares de biomasa en la hojarasca (Tabla 3).

Estos resultados sugieren que el suelo forestal es un compartimiento importante para la acumulación y el reciclaje de nutrientes, particularmente para el N, Ca, Mg y P, pero menos para el K, con marcadas diferencias entre especies arbóreas. Si el suelo forestal es afectado por quemas o las limpiezas, puede ocurrir una pérdida sustancial de materia orgánica y nutrientes. Wang et al. (1991) también encontraron que con la excepción de K, los nutrientes en la hojarasca eran equivalentes a una gran porción (16-50%) de los nutrientes contenidos en la biomasa arbórea. Ellos concluyeron que si la hojarasca fuera dejada sobre el suelo después de la cosecha, esto representaría una reserva sustancial de nutrientes para la siguiente rotación.

CONCLUSIONES Y RECOMENDACIONES

1. Algunas especies arbóreas nativas maderables de buen valor comercial pueden crecer en plantaciones abiertas, en sitios de baja fertilidad y pueden exhibir crecimiento rápido y efectos potencialmente beneficiosos sobre los nutrientes del suelo. Además, sus efectos sobre los nutrientes del suelo pueden ser observados en una etapa temprana de la rotación, al cierre del dosel.

2. Las especies arbóreas varían en sus contenidos de nutrientes en los tejidos y en sus tasas de acumulación de nutrientes en la biomasa. Para una especie dada, las mismas tendencias no son aplicables a todos los nutrientes: por ejemplo, una especie puede tener el mayor efecto sobre el Ca del sitio, pero su influencia sobre el K o el N puede ser mínima; otra especie puede tener una influencia más significativa sobre el K o el P del sitio.

3. El establecimiento de plantaciones arbóreas mixtas debería ser una estrategia apropiada para combinar los requerimientos de nutrientes de diferentes especies arbóreas con sus efectos sobre los nutrientes del suelo, de manera que no se creen deficiencias serias de ningún nutriente en particular. Sin embargo, aun con la mezcla de especies arbóreas es posible esperar deficiencias de K y P en el sitio a largo plazo.

4. La cosecha total de los árboles tendrá efectos negativos mayores sobre los nutrientes del sitio que la cosecha de los troncos. Los efectos variarán de acuerdo a la especie y a las partes cosechadas del árbol. El agotamiento de nutrientes del sitio será mayor con rotaciones cortas porque los árboles jóvenes tienen una proporción mayor de tejido de hojas y ramas en relación a sus troncos que los árboles viejos, en otras palabras, la porción potencialmente "reciclable" del árbol es mayor en árboles jóvenes; y la cosecha de rotaciones cortas aumentará la frecuencia de la eliminación de nutrientes del sitio así como también las perturbaciones al sitio asociadas con las operaciones de cosecha (erosión del suelo, compactamiento, perturbación de la hojarasca del suelo, etc.).

5. Aparentemente, el crecimiento de la vegetación del sotobosque y la correspondiente acumulación de nutrientes juega un rol relativamente pequeño en el reciclaje de nutrientes del sitio. Por eso, las prácticas que afectan al sotobosque, tales como el desmalezado y el intercultivo con especies anuales, pueden no ser críticos para la preservación de nutrientes en el sitio. Esta situación variará con las especies cultivadas y con su manejo. El intercultivo durante etapas tempranas del crecimiento arbóreo, mientras que los requerimientos de nutrientes de los cultivos y su manejo no provoquen otros efectos adversos (erosión del suelo, eliminación excesiva de nutrientes con cosechas repetidas), es una alternativa para acelerar el retorno del capital invertido y por consiguiente actúa como un estímulo para la plantación de árboles.

6. La hojarasca representa un componente mayor en la acumulación de nutrientes y en el reciclaje de los mismos. Las prácticas que afectan a la hojarasca, tales como la quema para el control de las malezas, la cosecha de la hojarasca para utilizarla como leña o "mulch" (mantillo), etc., pueden tener efectos adversos serios sobre los nutrientes del suelo.

7. La medición de la biomasa arbórea y de las concentraciones de nutrientes en etapas tempranas de la rotación (por ejemplo, durante el raleo) pueden ofrecer una buena indicación del impacto potencial de las prácticas de manejo sobre la conservación de nutrientes del sitio.

8. Las referencias a las tasas de extracción de nutrientes por cultivos agrícolas

comunes en la región pueden servir como indicadores de la capacidad para suplir nutrientes de los suelos y ser comparados con las tasas de absorción de nutrientes de las especies arbóreas, para poder estimar las deficiencias potenciales de nutrientes en el sitio.

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Net nitrogen mineralization in soils under six indigenous tree species, an abandoned pasture and a secondary forest in the Atlantic lowlands of Costa Rica

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Abstract

Nitrogen mineralization, nitrification potentials, pH, total N, C, extractable P and cations were measured in soils under 4-year-old, mono-specific stands of six fast-growing, native tree species, an abandoned pasture, and a 20-year-old secondary forest, as part of a study on the use of indigenous tree species for rehabilitation of soil fertility on degraded pastures at the La Selva Biological Station in the Atlantic humid lowlands of Costa Rica. Soil net nitrification potential rates were higher under two N-fixing, leguminous species, *Stryphnodendron microstachyum* Poepp. et Endl. (1.1–1.9 mg kg^{-1} day^{-1}) and *Dalbergia tucurensis* Donn. Smith (0.7–1.5 mg kg^{-1}day^{-1}), than under the non-N-fixing trees in the plantation, *Vochysia guatemalesis* Don. Sm., *Vochysia ferruginea* Mart, *Dipteryx panamensis* (Pittier) Record and Mell and *Hyeronima alchorneoides* Fr. Allemao (0.2–0.8 mg kg^{-1} day^{-1}). Values under the N-fixing trees were comparable to those found in secondary forest. There were no statistically significant differences in soil total N or in other nurtients between the species. Results of pH measurements done before and after incubation did not show any clear evidence of a pH drop attributable to nitrification.

Introduction

The incorporation of N-fixing trees in production systems is frequently followed by higher yields of associated crops or trees (Alpizar et al., 1986; Dommergues, 1987; Szott et al., 1991). Symbiotic N fixation by trees often results in increased soil N mineralization and nitrification, with consequent higher availability of mineral forms of N (ammonium, NH_4^+, and nitrate, NO_3^-) in the soil and solution (Binkley et al., 1982; Montagnini et al., 1986; 1991a; Van Miegroet and Cole, 1984). Increased soil nitrification may also result in lower soil pH (Binkley and Sollins, 1990; Van Miegroet and, Cole 1984). The acidifying effects of nitrification may be of concern because low pH can affect soil cation exchange capacity and nutrient availability (Uehara and Gillman, 1981).

As in many other regions of the lowland humid tropics, soils in the Sarapiqui district of the Costa Rican Atlantic humid lowlands have low fertility because of low pH (<5.5), high Al saturation (10–50%), low cation exchange capacity (<4 μmol kg^{-1} and low extractable P (<10 mg kg^{-1}) (Berstch, 1986). Nitrogen is not usually included among the soil fertility parameters evaluated in regional land-use capability assessments (Berstch, 1986); however, N fertilizers are heavily used in agriculture in the Atlantic lowlands, indicating that low N availability may be and additional factor in the region's generally low fertility (Montagnini, 1994).

We have been evaluating the potential of indigenous tree species for soil fertility rehabilitation on abandoned pastures at the La Selva Biological Station in the Sarapiqui district of the Atlantic humid lowlands of Costa Rica since 1987. The study focused on two N-fixing leguminous trees: *Stryphnodendron microstachyum* Poepp. et Endl. (ex *S. excelsum* Harms) and *Dalbergia tucurensis* Donn. Smith, and four non-

N-fixing trees: *Vochysia guatemalensis* Donn. Sm. (ex *V. hondurensis* Sprague), *Vochysia ferruginea* Mart, *Dipteryx panamensis* (Pittier) Record and Mell and *Hyeronima alchorneoides* Fr. Allemao, all growing in a young plantation on abandoned pasture soils. Results of previous studies showed that after 2.5 years, soils in the tree plantation had higher organic matter and higher total N, exchangeable K and Mg than adjacent areas of abandoned pasture (Montagnini and Sancho, 1990). Among the species in the plantation, the highest soil total N was found under *V. ferruginea*, a non-N fixing tree (Montagnini and Sancho 1990). However, preliminary results showed that soil NO_3^- concentrations and net nitrification potential rates were highest under the two N-fixing species in the plantation than under the other species (Montagnini and Sancho, 1990). Apparently, soil total N measurements were not enough to assess the influence of the trees on soil N availability. The goal of the present study was to compare N mineralization and nitrification potentials, as a measure of N availability (Keeney, 1982) in soils under 4-year-old, mono-specific stands of the six fast-growing, native tree species named above, an adjacent abandoned pasture, and a 20-year-old secondary forest. The potential effects of nitrification on soil pH were also examined.

Study site

The experimental plantation where the present study was conducted was established in December 1985 on abandoned pasture at the La Selva Biological Station of the Organization for Tropical Studies (10°26'N, 86°59'W, 50 meters mean elevation, 24°C mean annual temperature, 4000 mm mean annual rainfall, with maximum in July and minimum in March) (La Selva Biological Station weather reports). Soils are Fluventic Dystropepts derived from alluvially deposited volcanic materials; they are deep, well drained, stone-free, of low or medium organic matter content, of moderately heavy texture, and generally acidic and infertile (Sancho and Mata, 1987). The area had been cleared in the mid-1950s and grazed until 1981. The dominant species in the pastures were grasses (*Cynodon* spp., *Paspalum fasciculatum*, *Brachiaria* spp., *Melinis minutiflora*, and *Panicum maximum*), herbs (*Desmodium* spp., *Mimosa pudica*, among others), ferns (*Nephrolepis viscerata*, *Hylepis repens*) and bushes (*Psidium guajava* and *Piper culebranum*). In the pastures there were patches of approximately 20-year-old forest with *Pentaclethra macroloba* (a mimosoid, N-fixing legume dominant in the primary forest at La Selva), *Piper culebranum*, species of the Melastomataceae family, ferns and tree seedlings in the understory. The tree plantation had a randomized block design with five replicates, each single-species plot containing seven rows of seven trees (14 m × 14 m each), with two meters between trees. There were also five 14 m × 14 m plots in an adjacent abandoned pasture, and in a nearby patch of secondary forest.

General characteristics of the tree species of this study are shown in Table 1. All the species are of medium (e.g., *S. microstachyum*, *V. ferruginea*) to high (e.g., *Hyeronima alchorneoides*, *V. guatemalensis*) timber value (Gonzalez et al., 1990; Holdridge and Poveda, 1975).

Materials and methods

Superficial roots (0–15 cm depth) of the three leguminous species of this study (*S. microstachyum*, *D. tucurensis* and *Dipteryx panamensis*) were excavated and examined for the presence of root nodules. At least five trees per plot, located along diagonal transects, were examined to give 25 trees for each species.

Net nitrogen mineralization and nitrification potentials

These measurements were taken in March (end of the dry season), May and August (beginning and middle of the rainy season, respectively) of 1990, i.e. when the plantation trees were 4–4.5-years old. Nitrogen mineralization and nitrification potentials were measured in aerobic laboratory incubations (Keeney, 1982). Buried polyethylene bags for in-situ measurements (Montagnini and Buschbacher, 1989; Westermann and Crothers, 1980) were damaged by insects after two or three days in the field, although we had used bags of different thickness (Gordon et al., 1987), and thus were not used. Soils were sampled at 0-15 cm with a 2.5-cm diameter soil corer near the center of each plot. Soils were also sampled at random locations in the five abandoned pasture and five secondary forest plots. In the forest plots, samples were taken within a circle of one meter radius from a tree trunk. Two samples were composited into one sample per plot, 40 composite samples total. NO_3^- and NH_4^+ were extracted with 2*N* KCl, using a proportion of 1:4 soil:extracting solution, and measured using a Lachat Flow Injection Analyser. One subset of samples was extracted immediately after sampling; another subset was incu-

Table 1. Native tree species studied for their effects on soils and nutrient cycling at La Selva Biological Station (Gonzalez et al. 1990, Holdridge and Poveda 1975)

Scientific name	Common name	Family	Native range	Natural habitat
Stryphnodendron microstachyum Poepp. et Endl.	Vainillo	Leguminosae (mimosoid)	Costa Rica	Low altitude, very humid climate. Alluvial as well as poor soils
Dalbergia tucurensis Donn. Sm.	Granadillo	Leguminosae (papilionoid)	Belize, Honduras, Costa Rica	Low to mid-elevation, humid and very humid climate (no information on soils)
Vochysia guatemalensis Donn. Sm.	Mayo	Vochysiaceae	Mexico to Panama	Lowlands, up to 900m, humid climate. Rich alluvial or poor soils.
Vochysia ferruginea Mart	Botarrama	Vochysiaceae	Nicaragua to Brazil	Lowland forests. Well-drained, acidic, infertile soils
Dipteryx panamensis (Pittier) Record & Mell	Almendro	Leguminosae (papilionoid)	Nicaragua to Colombia	Low elevations, very moist climate. Flat terrain, alluvial soils. Not reported to nodulate
Hyeronima alchorneoides Fr. Allemao	Pilon	Euphorbiaceae	S. Mexico to S. Brazil	Hills, abandoned pastures. Alluvial as well as poor soils

bated in plastic cups in the laboratory (Keeney, 1982) at room temperature in the dark for seven days. Cups were opened daily to maintain aerobic conditions. Soil percent moisture was measured gravimetrically before incubation. Soils were at approximately field capacity at the time of sampling; moisture levels remained constant during the short incubation time used. The difference between final (after incubation) and initial NO_3^- concentrations or NO_3^- + NH_4^+ concentrations gave the net nitrification or net N mineralization potential rates, respectively (Keeney 1982).

Soil pH was measured on separate sub-samples before and after incubation, in deionized water and in 1*N* KCl using a 1:2.5 mixture of soil:water or KCl solution. Analysis of variance and test of means (LSD, $p < 0.05$) were done to compare soil parameters between pasture, forest and the six species in plantation for each sampling date. For the pH, ANOVAS were done on H^+-ion concentrations and the calculated means were then converted back to pH values.

Soil fertility

For general chemical characteristics of the soils, samples were taken with a 'Dutch type' auger at 0–15, 15–30 and 30–60 cm depth. Composite samples were taken in each of the five replicate plots for each species, and in the secondary forest and pasture plots. Soils were sampled in May (end of dry season) of 1989, 1990 and 1991. Chemical analyses were performed at the Soils Laboratory of the College of Agriculture, University of Costa Rica, following standard methods currently used by soil testing laboratories in the country. The pH was measured in a 1:2.5 mixture of soil:deionized water. Ca and Mg were extracted with a 1*N* KCl solution, while P, K and micronutrients were extracted with a modified Olsen solution (Diaz

Romeu and Hunter, 1978). Cations were measured using an Atomic Absorption Spectrophotometer. P was measured colorimetrically after reaction with acid $(NH_4)_2MoO_4$ and $SnCl_2$, using a Spectrophotometer. Organic matter was measured with the Walkley-Black technique (Allison, 1975) and total N was measured using a semi-Micro-Kjeldahl technique (Bremner and Mulvaney, 1982). Analysis of variance and LSD tests were run to compare the means for each parameter and soil depth (n=5) among sites.

Results

Root nodules were evident on all trees examined for *S. microstachyum* and *D. tucurensis*; these were apparently active N-fixing nodules as suggested by their reddish coloration in laboratory observations (J Gordon, pers. comm.). No nodules were found in any of the *D. panamensis* trees examined; this species has not been reported to nodulate (Allen and Allen, 1981; Halliday, 1984).

Soil N mineralization and nitrification

Results of measurements taken in 1990 (Table 2) confirmed the preliminary results reported for May 1989 (Montagnini and Sancho, 1990): although there were differences among the 1990 sampling dates, there was a trend of higher soil mineral N and higher net nitrification potential rates under the two leguminous, N-fixing species (*S. microstachyum* and *D. tucurensis*), as well as under secondary forest and sometimes under pasture. In March (Table 2a), soil NO_3^- concentrations. Net nitrification potentials were significantly higher under pasture than under either forest or plantation species *D. tucurensis* and *S. microstachyum*. There were no significant differences in net N mineralization potential rates. For *D. panamensis, H. alchorneoides*, pasture and forest, net N mineralization was less than net nitrification because final NH_4^+ values were smaller than the initial ones; this suggests that a portion of the NH_4^+ had been nitrified, and another portion had been taken up (immobilized) by other microorganisms in the soil. Although March is a relatively dry month at La Selva, soil moisture was high because it had rained during the three days preceeding sampling. Gravimetric soil moisture was highest in the forest and lowest under *D. panamensis*. In May (Table 2b), NO_3^- and NH_4^+ concentrations were higher under the forest. The highest net nitrification was under *S. microstachyum*. With the exception of *H. alchorneoides*, all N mineralization values were negative, suggesting again immobilization of NH_4^+ by soil microorganisms. Soil moisture was higher than in March, and it was again higher in forest. In August (Table 2c), NO_3^- was significantly higher under *S. microstachyum* and forest, while NH_4^+ was highest under *H. alchorneoides*. Both net nitrification and N mineralization potentials were highest under *S. microstachyum*. In all cases except *H. alchorneoides* and pasture, N mineralization was higher than nitrification, possibly indicating a plentiful supply of NH_4^+ to soil nitrifiers. Gravimetric soil moisture was less than in May, and it was again higher in the forest.

Soil pH before and after incubation

In March (Table 2a), initial and final (after incubation) water pH were highest in *V. ferruginea, V. guatemalensis* and *D. panamensis* soils. The pH was less after incubation than before in *S. microstachyum, D. tucurensis* and forest soils; the greatest decrease in soil water pH was in the forest soil. In May (Table 2b), initial water pH was higher in *V. ferruginea, V. guatemalensis* and *D. panamensis*, pasture and forest soils; there were no significant differences in final soil water pH. There was a slight trend of a decrease in final water pH in pasture and forest soils. In August (Table 2c), there were no significant differences in initial soil water pH. Soil water pH tended to be lower after incubation in all soils except *H. alchorneoides* and forest; the greatest decrease in soil water pH were in pasture and in *D. tucurensis* incubated soils. Soil KCl pH showed similar trends as water pH, but with overall lower values.

Soil fertility

Analysis of samples collected in 1989 showed similar trends of differences in organic matter and N among sites as in 1988 (Montagnini and Sancho, 1990), but unlike 1988, these differences were not statistically significant ($p < 0.05$) (Table 3). Soils under secondary forest had higher exchangeable Ca than either pasture or plantation plots in the 0–15 - and 15–30 cm depths. Within the tree plantation, there were no significant differences among species in soil nutrient concentrations. Results of soil measurements done in 1990 and 1991 showed trends similar to those found in 1988 and 1989. When examining data from 1988 to 1991, no increasing or decreasing trends with time were apparent for any individual nutrient (Montagnini and Sancho, 1994b).

Table 2. Soil NO_3^- and NH_4^+ concentrations, net nitrification and N mineralization potentials, gravimetric moisture and soil water pH for the six tree species of this study, an abandoned pasture and a secondary forest; sampling done in March, May and August, 1990[a]

Site	Soil parameter						
	NO_3^- (mg kg^{-1})	NH_4^+ (mg kg^{-1})	Net Nitrification Potential (mg NO_3^- kg.day^{-1})	Net N Mineralization Potential (mg NO_3^- + NH_4^+ kg.day^{-1})	%H_2O	Initial pH-H_2O	Final pH-H_2O
a. March 1990							
S. microstachyum	2.36b	4.30a	1.44ab	1.76a	38.9bc	4.65ab	4.53b
D. tucurensis	3.63b	2.15a	1.55a	3.81a	39.0b	4.61ab	4.51b
V. ferruginea	0.64b	2.18a	0.40c	0.59a	39.2ab	4.80a	4.78a
V. guatemalensis	0.28b	1.10a	0.35c	0.98a	39.2ab	4.91a	4.88a
D. tucurensis	0.47b	2.10a	0.50c	0.33a	39.9ab	4.82a	4.83a
H. alchorneoides	1.06b	4.16a	0.64bc	0.33a	36.0c	4.51b	4.55b
Pasture	15.2a	2.19a	0.61bc	0.55a	38.6bc	4.50b	4.46b
Forest	3.40b	2.90a	1.02ab	0.69a	42.1a	4.71ab	4.55b
b. May 1990							
S. microstachyum	3.80ab	15.8ab	1.08a	–0.74ab	39.8b	4.65ab	4.10a
D. tucurensis	2.63b	15.3ab	0.74abc	–1.17abc	39.8b	4.68ab	4.72a
V. ferruginea	1.09b	13.5bc	0.37bcd	–1.29abc	40.8ab	4.77a	4.78a
V. guatemalensis	0.75b	13.6bc	0.22d	–1.44bc	39.8b	4.91a	4.90a
D. panamensis	1.03b	12.9bc	0.41bcd	–1.18abc	40.3b	4.84a	4.87a
H. alchorneoides	2.96ab	6.3c	0.45bcd	0.16a	42.3ab	4.52b	4.63a
Pasture	4.15ab	14.9bc	0.25cd	–1.56bc	42.6ab	4.78a	4.73a
Forest	6.36a	24.7a	0.78ab	–2.49c	46.1a	4.90a	4.80a
c. August 1990							
S. microstachyum	3.45a	3.86bc	1.98a	3.77a	37.4bc	4.46a	4.30bc
D. tucurensis	1.81ab	0.45bc	1.03bc	1.42ab	37.3bc	4.57a	4.35abc
V. ferruginea	0.15b	0.58bc	0.43c	0.83c	38.6b	4.52a	4.36abc
V. guatemalensis	0.02b	0.36c	0.44c	0.82c	37.8bc	4.49a	4.40abc
D. tucurensis	0.17b	2.84bc	0.70c	1.31ab	36.7bc	4.50a	4.47abc
H. alchorneoides	0.51b	10.5a	0.80c	-0.20c	36.2c	4.54a	4.54ab
Pasture	0.87ab	5.04b	1.05bc	0.83c	36.3c	4.72a	4.29c
Forest	3.61a	5.11b	1.72ab	1.97ab	41.3a	4.38a	4.60a

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

Discussion

Soil N mineralization and nitrification potentials

The presence of the N-fixing *Pentaclethra macroloba* may account for the high soil mineral N and net nitrification found in the secondary forest; abundant nodulation was found in superficial roots of adult individuals and seedlings of this species. *Pentaclethra macroloba* is considered a promising N-fixing tree of economic value (Nichols and Rodriguez, 1990). High rates of N mineralization and nitrification in the pasture may be explained by the presence of leguminous herbs (*Mimosa pudica, Desmodium ovalifolium*) which were also observed to be nodulated.

Although no statistical analysis was performed to discern differences among sampling times, values of total soil mineral N concentrations (NO_3^- + NH_4^+) were

Table 3. Organic matter (OM), total N, extractable P, pH, exchangeable Ca, Mg, and K in soils under six native tree species in plantation, an abandoned pasture and a secondary forest; sampling done in May, 1989

Site	Depth (cm)	OM (%)	N	P (mg kg^{-1})	pH	Ca	Mg	K (cmol kg^{-1})
S. microstachyum	0–15	4.50a	0.278a	2.40a	5.1.a	0.68b	0.44ab	0.13a
	15–30	3.29a	0.224a	2.10a	5.1ab	0.52bc	0.22bc	0.14a
	30–60	1.88a	0.196a	1.80b	5.1a	0.54a	0.16a	0.14a
D. tucurensis	0–15	4.77a	0.278a	3.08a	4.9a	0.55bc	0.32bc	0.13a
	15–30	3.45a	0.224a	2.30a	5.0c	0.50bcd	0.18c	0.13a
	30–60	2.46a	0.202a	1.74b	5.1a	0.44a	0.14a	0.09a
V. ferruginea	0–15	5.06a	0.320a	3.24a	4.9a	0.63bc	0.53a	0.16a
	15–30	3.66a	0.248a	2.48a	5.0c	0.35d	0.20c	0.10a
	30–60	2.94a	0.200a	2.50b	5.1a	0.33a	0.16a	0.15a
V. guatemalensis	0–15	4.30a	0.304a	2.30a	5.2a	0.47bc	0.50ab	0.10a
	15–30	3.16a	0.232a	1.82a	5.1ab	0.38cd	0.22bc	0.07a
	30–60	2.42a	0.202a	2.00b	5.1a	0.36a	0.15a	0.06a
D. panamensis	0–15	4.28a	0.290a	3.38a	5.3a	0.63bc	0.59a	0.14a
	15–30	2.62a	0.214a	2.02a	5.3a	0.54b	0.30b	0.11a
	30–60	2.45a	0.206a	1.38b	5.3a	0.66a	0.27a	0.10a
H. alchorneoides	0–15	5.16a	0.232a	1.50a	5.1a	0.31c	0.21bc	0.09a
	15–30	2.77a	0.248a	1.50a	5.1ab	0.45bcd	0.19c	0.10a
	30–60	1.21a	0.158a	1.70b	5.2a	0.46a	0.20a	0.10a
Pasture	0–15	3.98a	0.296a	4.10a	5.2a	0.57bc	0.38ab	0.22a
	15-30	2.94a	0.236a	3.40a	5.1ab	0.51bcd	0.27bc	0.17a
	30–60	2.46a	0.194a	8.90a	5.2a	0.47a	0.20a	0.13a
Forest	0–15	5.11a	0.288a	2.30a	5.2a	1.16a	0.49ab	0.21a
	15–30	3.83a	0.244a	2.00a	5.2a	0.92a	0.45a	0.17a
	30–60	2.48a	0.206a	1.40b	5.2a	0.62a	0.27a	0.12a

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

generally higher in May (Table 2), while net nitrification potentials tended to be higher in August. The lower soil mineral N pools found in March may indicate slower decomposition rates during a relatively drier month. The smaller soil mineral N pool found in August may be due to higher rainfall leading to greater NO_3^- leaching. Alternatively, lower NO_3^- + NH_4^+ pools may be the result of more rapid uptake by plants and microorganisms after the rains began, or by losses to denitrification. Root and leaf litter decomposition may be also higher in August than in May, resulting in faster N mineralization and nitrification.

Nitrification is generally controlled by the availability of ammonium in most humid tropical ecosystems (Montagnini and Buschbacher, 1989; Robertson, 1984; Vitousek, 1984; Vitousek and Denslow, 1985). As all the NH_4^+ was consumed during the incubation of soils from all sites in this study, it appears that NH_4^+ availability controls nitrification in these soils as well. Thus, an increase in soil ammonium as an indirect result of N fixation is expected to enhance nitrification. Although nitrification rates were higher under the N-fixing species, overall the rates were relatively low. For example, values reported here for secondary forest were lower than those reported for a successional forest on volcanic soils near Turrialba, Costa Rica (Matson et al., 1987). Soils at the Turrialba site were Typic Dystrandepts with large amounts of organic carbon and nitrogen (Matson et al., 1987), therefore although Matson et al. did not report soil chemistry, we suspect that the soils at our site are less fertile, with lower pH, lower exchangeable P and cations and lower available N. With respect to general soil chemical characteristics, the results of the present study suggest that after the initial site improvement found in 1988, approximately one year after canopy closure (Montagnini and Sancho, 1990), no further positive or negative changes in soil chemistry were detected. Continued soil measurements at the La Selva site will be needed to confirm the trends reported for 1988–1991.

Our values of soil net mineralization and nitrification potentials were also generally lower than those reported for successional and mature forest at La Selva (Robertson, 1984); again the site of Robertson's study was on alluvial soils, more fertile than ours. However, the rates reported in this study were higher than those found in an Amazon forest and successional sites on poorer, more acidic soils near San Carlos de Rio Negro, Venezuela (Montagnini and Buschbacher, 1989).

Changes in soil pH during incubation

Results of pH measurements taken before and after incubation do not show any clear evidence of a pH drop attributable to nitrification. Probably the incubation time was too short to show any clearer trends. Alternatively, other factors which determine soil acidification, such as base saturation, the quantity of weak acids, and acid strength (Binkley and Sollins, 1990), may have greater influence on the pH of these soils than H^+-ion production from nitrification.

Implications for the use of S. microstachyum *and* D. tucurensis *in mixed-production systems*

Of the species studied, *S. microstachyum* and *D. tucurensis* increased soil N availability, as shown by the higher N mineralization and nitrification potential rates measured in soils under these species (Table 2). Results of other studies showed that *S. microstachyum* had fast growth (over 3.0 cm diameter at breast height per year), high N concentration in leaf (2.25%) and branch (0.93%) tissue, high rates of litter fall, and relatively fast leaf litter decomposition rates (Montagnini et al., 1993). *D. tucurensis* had slower growth rate (Gonzalez et al., 1990) and lower rates of litter fall than *S. microstachyum*, but it also had high N concentrations in leaf and branch tissue (Montagnini et al., 1991b). Additionally, results of other research also showed that total above-ground biomass N accumulation by *S. microstachyum* was 176 kg ha^{-1} larger than *V. guatemalensis*, a non-N fixing tree species with similar growth in the same plantation (Montagnini and Sancho, 1994a,b). Furthermore, maize seedlings grown in soils mulched with *S. microstachyum* leaves showed better growth and extracted more N from the soil than those mulched with non-N-fixing tree species, or than the unmulched controls (Montagnini et al., 1991b, 1993). Because of its better growth and its nutrient recycling characteristics, *S. microstachyum* showed greater potential than *D. tucurensis* for its incorporation into mixed-production systems. Apparently *S. microstachyum's* faster litter decomposition rates and higher litter N concentration (Montagnini et al., 1993) resulted in the observed higher mineralization and nitrification rates in the soil. Farmers in the La Selva region are already planting this species with good results (Maroto Villalobos, 1990) in terms of initial tree growth and yields of associated crops, mainly cassava (*Manihot esculenta* Crantz). However, experiences in the region are still too recent for generalizations on the success of these systems. We are currently using *S. microstachyum* as part of mixed-tree plantation experiments at La Selva (Montagnini, 1992). We expect that mixed-species plantations, if designed with a consideration on the nutrient demands and potential impacts of each species on soils, will grow better and will have more long-term beneficial impacts on site nutrient conservation.

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Aboveground Biomass and Nutrients in Young Plantations of Indigenous Trees on Infertile Soils in Costa Rica: Implications for Site Nutrient Conservation

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ABSTRACT. Aboveground-tree biomass and nutrient content (nitrogen, phosphorus, calcium, magnesium and potassium) were measured in 4-year-old stands of four indigenous tree species: *Stryphnodendron microstachyum* Poepp. et Endl. (ex *S. excelsum* Harms), *Vochysia guatemalensis* Donn. Smith (ex *V. hondurensis* Sprague), *Vochysia ferruginea* Mart and *Hyeronima alchorneoides* (O), growing on infertile soils in an experimental plantation in the Atlantic humid lowlands of Costa Rica. Biomass and nutrient content among the species, and among aboveground tree parts, forest-floor litter and understory vegetation were compared, as key factors that can be manipulated with different effects on site nutrient conservation. Biomass and stemwood annual increments of the four species were similar to those reported for other

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tropical tree plantations in the humid tropics. *S. microstachyum* had the highest accumulation of N in stem, branch and total aboveground tree biomass. *V. guatemalensis* had the highest accumulation of Ca and Mg in the biomass, while *H. alchorneoides* had the highest stem K and P. In spite of their relatively lower N tissue concentrations, *V. ferruginea* and *H. alchorneoides* showed a high potential for N recycling due to its more even distribution in stems, branches and leaves. Nutrient accumulation by the understory in *S. microstachyum* and *H. alchorneoides* plots was 0.8-7.7% of aboveground tree biomass nutrients. The forest-floor litter represented a major compartment for nutrient accumulation and recycling under the four species, especially for N, Ca, Mg and P.

INTRODUCTION

The sustained management of tree plantations becomes a biologically and socially feasible alternative on soils that are unsuitable for the continuous practice of agriculture that uses prevailing local technologies (Gladstone and Ledig 1990). In particular, tree plantations and tree-crop combinations represent productive alternatives for uses of deforested lands that have poor regeneration of natural forests due to long distance to sources of propagules or intense site degradation. As the area of degraded lands expands, there is increasing emphasis on the planting of tree species which can grow in such conditions and yield potentially profitable products (timber, fuelwood and other) as well as environmental benefits (soil conservation, watershed protection) (Evans 1987). On the other hand, young tropical tree plantations are rapidly aggrading ecosystems which incorporate considerable amounts of nutrients in their biomass over a relatively short period of time (Bruijnzeel 1991). Site fertility declines can be a serious limitation to sustained plantation forestry in tropical regions; soil fertility can be decreased through excessive removal of living biomass, particularly if nutrients in tree crowns are lost through harvest or site preparation (Jorgensen and Wells 1986; Perry and Maghembe 1989). However, tree species vary in their nutrient uptake rates and capacity for nutrient recycling. Data on different tree species' nutrient acquisition rates and recycling capabilities will help in the design of management strategies that either can take advantage of the ameliorating effects of trees on soil fertility or avoid site deterioration at harvest.

In the present article we report on aboveground biomass and nutrient content (nitrogen, phosphorus, calcium, magnesium and potassium) for 4-year-old stands of four indigenous tree species: *Stryphnodendron microstachyum* Poepp. et Endl. (ex *S. excelsum* Harms), *Vochysia guatemalensis* Donn. Smith (ex *V. hondurensis* Sprague), *Vochysia ferruginea* Mart, and *Hyeronima alchorneoides* (O), growing on infertile soils in an experimental plantation in the Atlantic humid lowlands of Costa Rica. Results from earlier studies had shown that, after 2.5 years, soils under these species had higher organic matter, N, K and Mg than adjacent areas of abandoned pastures (Montagnini and Sancho 1990a, 1990b; Montagnini et al. 1991). Here we compare biomass and nutrient content among the species, and among aboveground tree parts, forest-floor litter and understory vegetation, as key factors that can be manipulated with different effects on site nutrient conservation. These strategies should be useful for promoting the use of these species in production systems (mixed or pure plantations, agroforestry) in the area as well as in other tropical lowland regions with similar ecological characteristics.

STUDY SITE

The experimental plantation was established in December 1985 on abandoned pasture at the La Selva Biological Station of the Organization for Tropical Studies (10°26'N, 86°59'W; 50 m mean altitude; 24°C mean annual temperature; 4000 mm mean annual rainfall, with maximum in July and minimum in March–La Selva Biological Station weather reports). Soils in the experimental area are Fluventic Dystropepts derived from volcanic alluvium; they are deep, well drained, stone-free, with low or medium organic matter content, moderately heavy texture, and are generally acid and infertile (Sancho and Mata 1987). The area had been cleared in the mid-1950s and grazed until 1981 (Pierce 1991). The site was cleaned manually before planting. The experimental area was on flat, uniform terrain. The design consisted on complete blocks, with five replicates, and tree plots (14 m × 14 m each) were set at random within the blocks. The tree species plots contained seven rows of seven trees, with 2 m between trees. Five 14 m × 14 m plots were also established in an adjacent open area with grass, and in a nearby patch of secondary forest. During the first year, weeds were manually cut four times; weeding was done mechanically thereafter until canopy closure made it no longer necessary. The grass was weeded simultaneously to keep it free of trees, with comparable treatments.

The Tree Species

The criteria for species selection for this study were: growth rate during the first 3-4 years of the plantation (Espinoza Camacho and Butterfield 1989; Gonzalez et al. 1990); presence of root nodules in the leguminous species (field observations); and economic value (Chudnoff 1984; Gonzalez et al. 1990). *S. microstachyum* (Leguminosae, sub-family Mimosoidae) ("vainillo") is found only in Costa Rica, although representatives of this genus are native to tropical South America (Brazil, Costa Rica, Guyana) (Allen and Allen 1981). It grows in low altitude with very humid climates and apparently adapts to alluvial soils as well as to slopes and abandoned pastures with poor soils (Gonzalez et al. 1990). Its timber is primarily used for general construction, and also small furniture and turnery (Allen and Allen, 1981). *V. ferruginea* (Vochysiaceae) ("botarrama") grows in lowland forests from Nicaragua to Brazil (Whitmore and Hartshorn 1969); it is found on well-drained, acidic, infertile soils, but it can adapt to a variety of soils (Gonzalez et al. 1990). It is a self-pruning pioneer species that forms uniform, even-aged stands in abandoned fields, and its wood is used for plywood and construction. *V. guatemalensis* (Vochysiaceae) ("mayo") is found from Mexico to Panama, at up to 900 m altitude (Whitmore and Hartshorn, 1969); it usually grows on humid, low altitude areas, on either rich alluvial or poor soils; its timber is used for carpentry, plywood, and furniture, and has been considered a substitute for mahogany. *H. alchorneoides* (Euphorbiaceae) ("pilon") ranges from southern Mexico to southern Brazil (Chudnoff 1984); it grows well on hills and on abandoned pastures, but not much is known about its edaphic requirements. Its timber is used for heavy construction, furniture, cabinet work, decorative veneers and turnery (Chudnoff 1984).

METHODS

Tree Aboveground Biomass and Nutrients

Taking advantage of plot thinning performed in December 1989, we chose two trees per plot of *S. microstachyum*, *V. ferruginea* and

V. guatemalensis for biomass determinations and chemical analysis. *H. alchorneoides* plots were thinned in July 1990, at which time we also chose trees for the same purpose. From each plot, we selected trees of diameter close to the average for each respective plot, as calculated by the foresters in charge of tree measurements and thinning. The material was separated into its parts (stem, branches and leaves) and weighed fresh at the site using a field scale. Subsamples of all materials, including stems (lower, medium and top parts) were taken to the laboratory and dried at 70°C until a constant weight was obtained. Dry:wet weight ratios from felled trees were used to correct the field weight determinations. The stem samples were used for chemical analysis. In order to obtain a broader sample of other tissue, leaves and branches were obtained from five more trees per species, using a pole pruner. Three whole branches of opposite orientation from the upper portion of the canopy of each tree were sampled. Leaves from the tip, medium, and lower portions of each branch were pooled to obtain one sample per tree. Portions of tip, medium and bottom parts of branches of the sampled trees were cut and pooled in the same manner. The material was oven-dried at 70°C and then ground for chemical analysis. The total N, P, Ca, Mg and K were measured on nitro-perchloric digests (Diaz-Romeu and Hunter 1978); N and P were measured using a Flow Injection Analyzer, while cations were measured using an Atomic Absorption Spectrophotometer. Analysis of variance and LSD tests were run to compare mean biomass ($n = 5$) and nutrient content of tree parts ($n = 5$ for each tree part) among species. Total biomass nutrient content for each species was calculated by multiplying the mean biomass of each species' plant part (leaves, branches or stems) times the mean nutrient concentration of the respective plant parts.

Biomass and Nutrient Concentration of Understory Vegetation

Biomass and nutrient concentrations of herbaceous vegetation growing under the four tree species were measured in August (time of peak understory growth) 1989. Grass and other herbaceous vegetation from the five replicate plots of each species were cut at ground level by hand using 50 cm × 50 cm iron frames to define the sample area. One sample per plot was taken, because both the understory and forest-floor litter were very homogeneous in these mono-specific plots. The material was oven-dried and sub-samples were analyzed in the same manner as tree tissue. Statistical analyses (analysis of variance and LSD tests) were done to compare biomass (n = 5) and nutrient concentrations of understory vegetation among the tree species.

Forest Floor Litter

The amount of litter accumulating on the ground under the five replicate plots of the four species was measured in August 1989, December 1989, and in March, May and August 1990, as part of another study on litter dynamics (Montagnini et al. 1993). A 50 cm × 50 cm iron frame (one per plot) was used to demarcate an area in which all material to the top of the mineral soil was collected. The material was oven-dried, sorted (whole leaves, fragments and branches), and weighed. Chemical analysis was performed as described above for other tissue. Analysis of variance and LSD tests were used to compare the amounts of forest-floor litter among species, for each collection. The average amounts of each litter portion for each species (n = 5) was multiplied times the mean of nutrient concentration of each portion (n = 5), for the results obtained in August 1989; August results were used because the understory had also been sampled on that date. Then the nutrient contents (kg/ha) of all forest-floor litter fractions were summed to get the total nutrient accumulation in forest-floor litter.

Soil Fertility

For general chemical characteristics of the soils, samples were taken with a "Dutch type" auger at 0-15, 15-30, and 30-60 cm depths. Composite samples were taken in each of the five replicate plots for each species. Soils were sampled in May (end of dry season) of 1989, 1990 and 1991. Chemical analyses were performed at the Soils Laboratory of the College of Agriculture, University of Costa Rica, following standard methods currently used by soil testing laboratories in the country. The pH was measured in a

1:2.5 mixture of soil:deionized water. Ca and Mg were extracted with a 1N KCl solution, while P, K and micronutrients were extracted with a modified Olsen solution (Diaz Romeu and Hunter 1978). Cations were measured using an Atomic Absorption Spectrophotometer. P was measured colorimetrically after reaction with acid $(NH_4)_2MoO_4$ and $SnCl_2$, using a Spectrophotometer. Organic matter was measured with the Walkley-Black technique (Allison 1975) and total N was measured using a semi-Micro-Kjeldahl technique (Bremmer and Mulvaney 1982). Analysis of variance and LSD tests were run to compare the means for each parameter and soil depth ($n = 5$) among sites.

RESULTS

Aboveground Biomass and Nutrient Concentrations

Trees

V. guatemalensis and *S. microstachyum* had the highest stem and total aboveground biomass; these differences were statistically significant ($P < 0.05$) (Table 1). *V. guatemalensis* had the lowest branch biomass; no significant differences were found among the other three species ($P < 0.05$). There were no statistically significant differences ($P < 0.05$) in leaf biomass among the species, although values ranged from 4.3 tons/ha for *S. microstachyum* to 7.2 tons/ha for *V. guatemalensis* (Table 1).

The leguminous, N-fixing *S. microstachyum* had the highest N concentrations in leaf tissue (Table 2). *V. ferruginea* and *V. guatemalensis* had the lowest leaf N concentrations, but they had relatively high leaf Ca concentrations. *H. alchorneoides* had low or intermediate concentrations of most nutrients in leaves. *S. microstachyum* had relatively low Ca, K and Mg leaf concentrations. Similar trends of differences in nutrient concentrations among species held for branch tissue, with lower general values than those for leaves (Table 2). Stems had lower N concentrations than either leaves or branches (10-20% of leaf values), with the highest value found in *S. microstachyum*. The Ca values in stems were similar or greater than those of leaves, with the highest in *V. guatemalensis*; this species

TABLE 1. Means of tree diameter at breast height (dbh), height, aboveground biomass and annual increments[1].

Tree species	Dbh, cm	Height, m	Aboveground live biomass, kg/ha				Mean annual increment, $t\ ha^{-1}yr^{-1}$	
			Stem	Branches	Leaves	Total	Total	Stems
S. microstachyum	12.0a	8.9b	35,250a	15,250a	4,325a	54,825	13.7a	8.8a
V. ferruginea	10.3	8.1b	24,750b	14,250a	5,925a	44,925	11.2b	8.2b
V. guatemalensis	10.8a	12.0a	41,750a	6,500b	7,250a	55,500	13.9a	10.4a
H. alchorneoides	10.8a	9.0b	26,250b	12,250a	5,350a	43,850	12.0b	6.5b

[1]Differences between sites for a given parameter are statiscally significant ($P < 0.05$) when means are followed by different letters.

TABLE 2. Nutrient content in tissues of four indigenous trees grown in plantation at La Selva Biological Station, Costa Rica.[1]

	Nutrient content, %				
Tissue/species	N	P	Ca	Mg	K
Leaves					
S. microstachyum	2.25a	0.20ab	0.47c	0.22b	0.76a
V. ferruginea	1.58c	0.18ab	1.06ab	0.25b	0.41b
V. guatemalensis	1.49c	0.09c	1.22a	0.41a	0.29b
H. alchomeoides	1.81b	0.15b	1.02ab	0.41a	0.71a
Branches					
S. microstachyum	0.93a	0.15ab	0.44ab	0.15a	0.70bc
V. ferruginea	0.29c	0.09b	0.36b	0.10a	0.56bc
V. guatemalensis	0.29c	0.12b	0.44ab	0.16a	0.49c
H. alchomeoides	0.55b	0.17ab	0.59ab	0.15a	1.14a
Stems					
S. microstachyum	0.49a	0.07b	0.81b	0.04b	0.20c
V. ferruginea	0.17b	0.09b	1.12b	0.10a	0.23c
V. guatemalensis	0.26b	0.09b	1.46a	0.12a	0.42b
H. alchomeoides	0.32b	0.18ab	0.28c	0.10a	0.96a

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

also had high stem K and Mg. *H. alchorneoides* had the highest stem K and P, but it had low Ca and Mg.

Understory

There was no understory vegetation in either *V. ferruginea* or *V. guatemalensis* plots, probably because these two species had completely closed canopies at the time of sampling and light levels underneath were very low. Abundant growth was found under *S. microstachyum* (Table 3), whose small leaves and open crown allowed considerable light penetration. In understory vegetation, the highest N concentrations were found under *S. microstachyum* and

TABLE 3. Nutrient concentrations, biomass and nutrient content of understory vegetation of indigenous tree species growing in plantation.

(a) Nutrient concentrations of understory:[1]

Species plots	N	P	Ca	Mg	K
			(%)		
S. microstachyum	1.70a	0.13a	0.33ab	0.41b	1.01a
H. alchorneoides	1.35ab	0.73a	0.77a	0.45ab	0.79a

[1]For a given nutrient, means followed by a different letter are significantly different ($P < 0.05$).

(b) Biomass and nutrients of understory:

Species plots	Biomass (kg/ha)	N	P	Ca	Mg	K
				(kg/ha)		
S. microstachyum	874	14.9	1.1	2.9	3.6	8.8
H. alchorneoides	425	5.7	3.1	3.3	1.9	3.3

the highest Ca was found under *H. alchorneoides*; differences in Mg, K and P were not statistically significant (Table 3).

Forest-Floor Litter

Results of August 1989 showed that overall forest-floor biomass and nutrient accumulation was highest under *V. ferruginea* and *V. guatemalensis* (Table 4). Similar patterns of differences among species were observed from August 1989 to August 1990 (Montagnini et al. 1991, 1993). Nutrient concentrations in forest-floor material revealed a pattern similar to that of living tissue: in whole leaves, N was higher beneath *S. microstachyum*; Ca was higher beneath *V. guatemalensis*; K was higher beneath *H. alchorneoides*; Mg was higher beneath *V. guatemalensis* and *H. alchorneoides*; there were no statistically significant differences in P (Table 5). Branch and fragments in forest-floor litter showed similar trends of differences in nutrient content among species as whole leaves (Table 5).

TABLE 4. Biomass and nutrients of forest-floor litter; Totals include leaves, fragments and branches.

Species	Total Biomass (kg/ha)	Total nutrients N	P	Ca (kg/ha)	Mg	K
S. microstachyum	5612	95.1	4.3	41.6	8.2	6.6
V. ferruginea	17215	240.3	15.5	187.6	19.1	12.1
V. guatemalensis	11084	134.0	11.6	170.0	26.4	9.7
H. alchorneoides	4238	39.2	12.9	55.0	11.9	6.8

TABLE 5. Nutrient concentrations of forest-floor litter under four indigenous tree species in plantation.[1]

Tissue/species	N	Ca	K %	Mg	P
Leaves					
S. microstachyum	2.10a	0.82c	0.12bc	0.16b	0.02a
V. ferruginea	1.79ab	1.34b	0.05c	0.09c	0.04a
V. guatemalensis	1.56b	1.92a	0.13bc	0.39a	0.10a
H. alchorneoides	1.05c	1.40b	0.25a	0.37a	0.08a
Fragments					
S. microstachyum	1.93a	0.89d	0.15ab	0.21cd	0.10a
V. ferruginea	1.41a	1.07cd	0.06c	0.12e	0.09a
V. *guatemalensis*	1.33a	1.59a	0.08c	0.24bc	0.10a
H. alchorneoides	1.19a	1.44ab	0.15ab	0.31a	0.09a
S. microstachyum	1.61abc	0.71d	0.12bc	0.12cd	0.05a
V. ferruginea	1.18c	0.92bc	0.08c	0.10d	0.11a
V. guatemalensis	1.29bc	1.19abc	0.10c	0.20bc	0.14a
H. alchorneoides	0.60d	1.12c	0.18a	0.24ab	1.04ab

[1]For a given nutrient and tissue, means followed by a different letter are significantly different ($P < 0.05$).

Soil Fertility

Analysis of samples collected in 1989 showed similar trends of differences in organic matter and N among sites as in 1988 (Montagnini and Sancho 1990a, 1990b), but unlike 1988, these differences were not statistically significant ($P < 0.05$) (Table 6). Soils under secondary forest had almost twice as much Ca as under *V. guatemalensis*, *V. ferruginea* or *H. alchorneoides*. Within the tree plantation, there were no significant differences among species in soil cation content. Results of similar soil measurements done in

TABLE 6. Organic matter (OM), total N, P, pH, Ca, Mg, and K in soils under the four native tree species in plantation, grass and secondary forest[1].

Site	Depth (cm)	OM (%)	N (%)	P (mg/kg)	pH	Ca (cmol/kg)	Mg (cmol/kg)	K (cmol/kg)
S. microstachyum	0-15	4.50a	0.278a	2.4a	5.1a	0.68b	0.44a	0.13a
	15-30	3.29a	0.224a	2.1a	5.1ab	0.52bc	0.22bc	0.14a
	30-60	1.88a	0.196a	1.8b	5.1a	0.54a	0.16a	0.14a
V. ferruginea	0-15	5.06a	0.320a	3.24a	5.0a	0.63bc	0.53a	0.16a
	15-30	3.66a	0.248a	2.48a	5.0c	0.35d	0.20c	0.10a
	30-60	2.94a	0.200a	2.50b	5.1a	0.33a	0.16a	0.15a
V. guatemalensis	0-15	4.30a	0.304a	2.30a	5.2a	0.47bc	0.50a	0.10a
	15-30	3.16a	0.232a	1.82a	5.1ab	0.38cd	0.22bc	0.07a
	30-60	2.42a	0.202a	2.00b	5.1a	0.36a	0.15a	0.06a
H. alchorneoides	0-15	5.16a	0.232a	1.5a	5.1a	0.31c	0.21b	0.09a
	15-30	2.77a	0.248a	1.5a	5.1ab	0.45bcd	0.19c	0.10a
	30-60	1.21a	0.158a	1.7b	5.2a	0.46a	0.20a	0.10a
Grass	0-15	3.98a	0.296a	4.1a	5.2a	0.57bc	0.38a	0.22a
	15-30	2.94a	0.236a	3.4a	5.1ab	0.51bcd	0.27bc	0.17a
	30-60	2.46a	0.194a	8.9a	5.2a	0.47a	0.20a	0.13a
Forest	0-15	5.11a	0.296a	2.3a	5.2a	1.16a	0.49a	0.21a
	15-30	3.83a	0.244a	2.0a	5.2a	0.92a	0.45a	0.17a
	30-60	2.48a	0.296a	1.4b	5.2a	0.62a	0.27a	0.12a

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

1990 and 1991 showed trends similar to those found in 1988 and 1989. When examining data from 1988 to 1991, no increasing or decreasing trends with time were apparent for any individual nutrient (Montagnini and Sancho, unpublished data).

DISCUSSION

Annual diameter increment (calculated by dividing diameter at breast height at time of measurement by tree age) was 3 cm/yr for *S. microstachyum* and just over 2.5 cm for the other species. These rates are within the expected range for tropical tree plantations (Lugo et al., 1990). Our values are consistent with reports by Espinoza Camacho and Butterfield (1989) and Gonzalez et al. (1990), who measured tree diameters periodically and calculated increments based on differences between consecutive measurements.

Aboveground Tree Biomass

The values of aboveground tree biomass reported here are greater than those reported for 4-year-old *Albizia lebbek* (Parrotta 1989), and for 5.5-year-old *Leucaena leucocephala* (Wang et al. 1991), both growing in dense plantations for biomass production in Puerto Rico. Mean annual increments for aboveground biomass (Table 1) lie within the ranges reported elsewhere for monospecific plantations in the humid tropics; for example, *Eucalyptus citridiora* (11.8 tons/year) in Brazil, *E. deglupta* (13.1) in Costa Rica, and *Gmelina arborea* (12.9) in Costa Rica (Lugo et al. 1988). Our values are similar to those reported for *E. robusta* (12.2), but less than *Albizia procera* (22.5) and *Casuarina equisetifolia* (36.2) planted at 2m × 2m distance in Puerto Rico; growth rates in this Puerto Rican site were higher than those reported for other tropical sites (Lugo et al. 1990). However, the increments shown here (Table 1) are lower than those reported for some of the fastest growing trees in the humid tropics such as *Acacia mangium* and *Leucaena leucocephala* (Young 1989).

Annual increments of stemwood biomass for broadleafs ranges from 1 to 28 tons/ha/yr (Wadsworth 1983). Fast growing species such as *Gmelina arborea* and *E. saligna* range from 10-20 and 8-28 tons/ha, respectively, and relatively slower growing species such as *Swietenia* spp. and *Tectona grandis* range from 1-4 and 3-12 tons/ha, respectively (Wadsworth 1983). Thus, the mean annual stem-wood biomass increments for the species of this study (Table 1) also fall within the ranges reported for other fast-growing tree species in the humid tropics.

These comparisons are useful to put our data in perspective; however, to assert real differences in growth rates of tree species, data should be compared among species grown under similar conditions, including life zone and characteristics of site and management. Investigations to assess the growth rates of the species of this study on different sites are under way. The relatively fast growth rates reported here tend to confirm predictions by Lugo et al. (1988), who suggested that tree plantations increase biomass production with increasing water availability, provided the climate is not excessively wet. High annual rainfall, such as that registered at La Selva, may decrease soil cation availability, which can in turn affect tree growth. For example, a substantial decrease in extractable cations, with a corresponding increase in soil acidity occurred during the month of peak rainfall (Montagnini and Sancho 1990a). However, we do not know if these changes in soil nutrient content have any negative effects on tree productivity.

Nutrient Concentrations in Tree Tissue

Nitrogen content of *S. microstachyum* leaves was similar to values reported for many N-fixing trees; values summarized by Young (1989) range from 1.63% for *Acacia auriculiformis* to 4.4% for *Gliricidia sepium*, with a majority of N-fixing trees in the 2-3% N range. The same can be said for *S. microstachyum*'s leaf P content, which was similar to other N-fixing species (Young 1989). Leaf Ca and K content of *S. microstachyum* was approximately half of most values reported for N-fixing trees (Young 1989); Mg was also relatively low, about half the values reported for *Albizia procera* and *Leucaena leucocephala* in Puerto Rico (Wang et al. 1991). The leaf N value reported here for *S. microstachyum* was similar, while P and cations were higher than in another species of the same genus, *S. adstringens* Harms, growing in a drier region in San Pablo, Brasil (Pagano et al. 1982). The two *Vochysia* species and *H. alchor-*

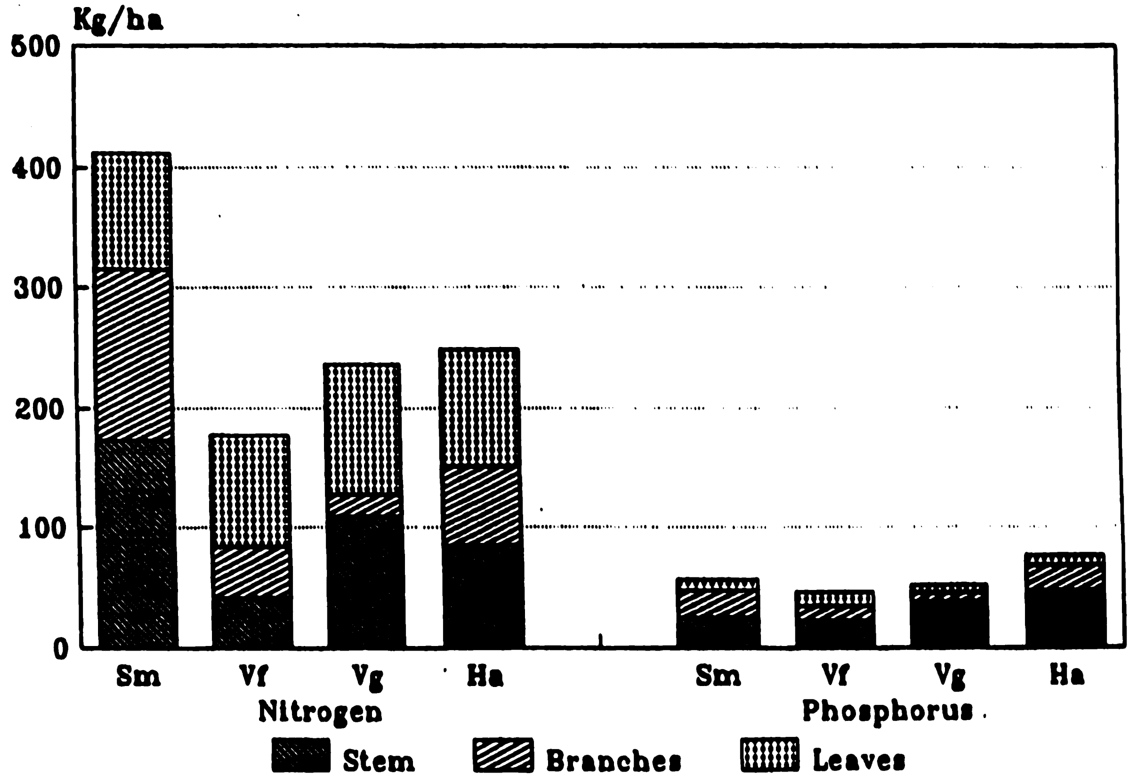
neoides had higher leaf Ca, similar to values reported in the literature for non-N-fixing tropical trees. The two *Vochysia* species' higher leaf Mg was not comparable to other reports in the literature (Young, 1989; Wang et al. 1991). The leaf nutrient values reported here for *S. microstachyum*, *V. guatemalensis* and *V. ferruginea* were similar to those found in August 1990 when leaves from a total of seventeen tree species growing in 2-4 year-old mixed-stands were sampled as part of another research project at La Selva (Montagnini and Sancho, unpublished data). *H. alchorneoides* was not included in such study.

S. microstachyum's stem N was greater than values reported for other N-fixing trees, including *Leucaena* spp. (Young, 1989; Wang et al. 1991), but it was lower than that of *S. adstringens* (Pagano et al., 1982). The other three species had lower N stem contents, with values comparable to those reported for other non-N-fixing tree species, including *E. robusta* in Puerto Rico (Wang et al. 1991), and *Gmelina arborea* in Nigeria (Chijiocke 1980, in Young 1989). *S. microstachyum* had similar stem P and K, higher Ca and lower Mg than *S. adstringens* (Pagano et al. 1982). With respect to stem cation content, the most outstanding finding was the high values of stem Ca found in the two *Vochysia* species and the high stem K found in *H. alchorneoides*, which are all above those reported in the literature (Wadsworth 1983; Young 1989; Wang et al. 1991). Stem Mg was similar to other species reported in the literature.

Nutrient Accumulation in Aboveground Tree Biomass

Consistent with trends found in N tissue concentrations, *S. microstachyum* had the highest accumulation of N in stem and branch biomass (Figure 1). Taking leaves and branches together, approximately 200 kg/ha, or 60% of *S. microstachyum*'s aboveground biomass N would be left on the site at time of harvest if only stems were removed. *V. ferruginea* and *H. alchorneoides* showed a higher potential for N recycling than *V. guatemalensis*, due to their more even distribution of N in stems, branches and leaves. *H. alchorneoides* had the highest aboveground tree biomass P; the other species had all similar values, equivalent to 60-70% those of *H. alchorneoides* (Figure 1).

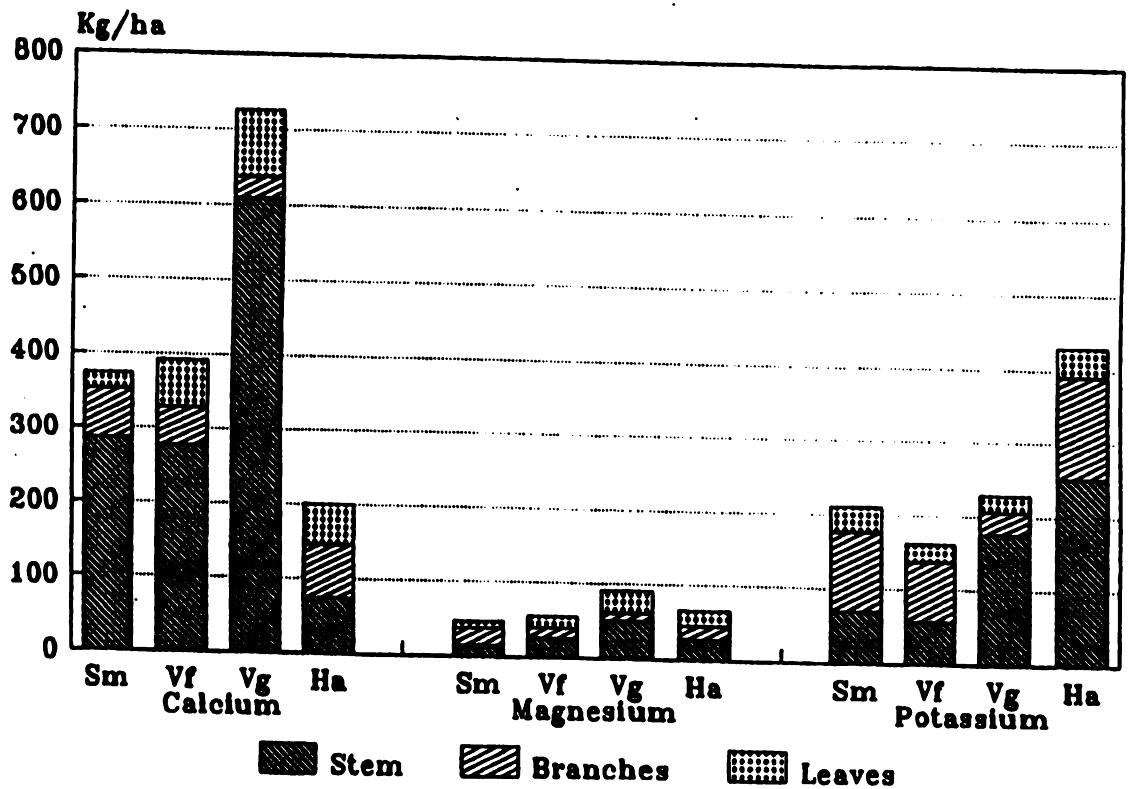
FIGURE 1. Aboveground tree nutrients in a 4-yr-old plantation of indigenous trees at La Selva Biological Station, Costa Rica: nitrogen and phosphorus.
Sm: *S. microstachyum*, Vf: *V. ferruginea*, Vg: *V. guatemalensis*, Ha: *H. alchorneoides*



V. guatemalensis, with the highest stem biomass and Ca concentration, also had the highest stemwood Ca (over 600 kg/ha, or 84% of aboveground tree biomass Ca), approximately twice as much as either *S. microstachyum* or *V. ferruginea*, and several times more than *H. alchorneoides* (Figure 2). Therefore, the harvest of *V. guatemalensis* trees could substantially reduce the amount of Ca in the site. However, the potentially recyclable portion (leaves+branches) for this species was relatively large (over 100 kg/ha), although it represented just 16% of aboveground tree biomass. The proportion of Ca in stems relative to aboveground tree biomass was similar for *S. microstachyum* and *V. ferruginea*, but the absolute amounts were less than half those of *V. guatemalensis*. *H. alchorneoides* again showed a more even distribution of Ca in stems, leaves and branches, with aboveground tree biomass Ca slightly over half those of *S. microstachyum* and *V. ferruginea*. Similar to Ca levels, *V. guatemalensis*, with its high stem biomass and high Mg concentration also had the highest Mg in stemwood (Figure 2). Again, removal of *V. guatemalensis* stems would affect the sites's Mg budget more dramatically than would the other species, especially if the whole tree was harvested. The other species showed lower proportions of aboveground tree biomass Mg in their stems (Figure 2). For K the picture changed; the highest accumulation of K in stems was found in *H. alchorneoides* (Figure 2), followed by *V. guatemalensis*. Thus, whole-tree harvest of *H. alchorneoides* and *V. guatemalensis* may have the greatest affects on the site's K budget. *S. microstachyum* and *V. ferruginea* had proportionally more K (over 65%) in the leaves + branches portion; however, *H. alchorneoides*'s absolute amounts of K in the recyclable tree parts was the largest of the four (over 180 kg/ha).

These results confirm previous reports on the negative effects of whole-tree harvest on site nutrient pools; for example, Bruijnzeel and Wiersum (1985) calculated that total tree harvest of a 40-year-old plantation of *Agathis dammara* in upland Java would remove the entire input of K and Ca, almost half of the Mg input and twice as much the input of P. Our results suggest that leaving tree residues in the site could greatly decrease the negative impacts of nutrient removal at harvest, with different consequences depending on the species. For example, slash from *V. guatemalensis* will be more rich

FIGURE 2. Aboveground tree nutrients in a 4-yr-old plantation of indigenous trees at La Selva Biological Station, Costa Rica: calcium, magnesium and potassium.
Sm: *S. microstachyum*, Vf: *V. ferruginea*, Vg: *V. guatemalensis*, Ha: *H. alchorneoides*



in Ca and Mg, residues from *S. microstachyum* will return appreciable amounts of N, and so on.

Our results are based on nutrient concentrations for a young plantation; the conclusions may change if younger trees had higher nutrient concentrations than older trees. However, Bruijnzeel and Wiersum (1985) found that stemwood P concentrations of 35-year-old *Agathis dammara* were lower than those of younger trees, whereas no such differences were found for other nutrients. Altering the rate of nutrient removal in products is probably one of the most important design considerations in planning sustainable plantations (Wang et al. 1991). The tree species and parts of the tree removed from the site will determine the nutrient "cost" of removal. This can be assessed before hand with nutrient and biomass sampling and estimation.

Nutrient Accumulation in Understory Vegetation

Nitrogen accumulation in the total understory biomass was higher under *S. microstachyum* (14.9 kg/ha), although this amount represented only 3.6% of aboveground tree biomass N (Table 3). For *H. alchorneoides*, understory biomass N was 5.7 kg/ha or 2.3% of aboveground tree biomass N. For the other nutrients, accumulation in understory biomass under *S. microstachyum* ranged from 0.8 to 7.7%, and under *H. alchorneoides* it ranged from 0.8 to 4.1% of aboveground tree biomass nutrients (Table 3). Since vegetation in the understory apparently accounts for a relatively small proportion of nutrients, as compared to the whole tree, manipulations of the understory should have little effect on nutrient cycling at the site. For example, weeding should have a relatively minor effect on nutrient recycling, unless the understory is removed or turned over many times per year. This also suggests that intercropping with annual, herbaceous species that attain similar biomass as the understory found under *S. microstachyum* or *H. alchorneoides* may not have a substantially negative effect on the balance of nutrients at the site. Since samplings of understory biomass were taken at a time when the quantity of biomass was at its peak, the amounts reported here are considered to approximate those that could be attained by crops. However, an accurate assessment of the influence of intercropping should involve measurements of the crop's nutrient requirements and parts removed at harvest. Bruijnzeel and Wiersum (1985) also concluded that the use of controlled intercropping in tree plantations in upland Java, with care to minimize soil erosion, was acceptable from a nutrient conservation point of view. Additionally, they argue that farmers may be willing to use fertilizers for the crops, and the residual effects of the nutrients applied may even increase the growth of the trees in early stages.

Nutrient Accumulation in Forest-Floor Litter

Forest-floor biomass and nutrient accumulation were highest under *V. ferruginea*; N in forest-floor litter under this species was greater than its aboveground tree biomass N (Table 4 and Figure 1). As noted above, *V. ferruginea's* leaf and branch biomass account for a large proportion of aboveground tree biomass. This species is self-pruning, a characteristic that enhances shedding of branches and leaves, and occasional prunings may have added even more tree litter to the forest floor. Litter decomposes relatively slowly under *V. ferruginea*, contributing to the high accumulation noted above (Montagnini et al. 1991, 1993). Forest-floor litter Ca, Mg and P were also considerable under *V. ferruginea* (Table 4), a finding especially relevant for P, because of the potential site deficiencies in this element mentioned earlier. Forest-floor biomass nutrients were also high under *V. guatemalensis*, and again this was more important for N, Ca, Mg and P. Thus, in spite of this species' fast growth rate, nutrient recycling from litter may at least partially compensate for soil nutrient depletion. Forest-floor litter N was more than double under *S. microstachyum* than under *H. alchorneoides*, although both species had similar forest-floor litter biomass (Table 4); the reverse was true for P.

These results show that the forest floor is an important compartment for nutrient accumulation and recycling, particularly for N, Ca, Mg and P, but less for K, with marked differences among tree species. If the forest floor is burned or collected for fuelwood, a substantial loss of organic matter and nutrients may occur. Wang et al. (1991) also found that with the exception of K, nutrients in forest-floor litter were equivalent to a large proportion (16-50%) of the nutrients contained in the aboveground tree biomass, and they concluded that if the litter were left on the floor after harvest, it would represent a substantial reservoir for the next rotation.

Impacts of Trees on Soil Nutrients

The impacts of plantation trees on soil nutrients depend on: (1) the annual nutrient uptake by the trees in relation to the nutrient supplying capacity of the soil, (2) nutrient recycling, (3) the parts of the tree removed, whether the whole tree or stemwood, and their biomass and nutrient content at harvest, and (4) the total/available soil nutrient pools. A look at these relationships for *V. guatemalensis*, the fastest-growing, and seemingly the most nutrient-demanding species of this study, will illustrate this point. Nutrient retention by *V. guatemalensis* (calculated by dividing biomass nutrients by plantation age) averaged 58 kg of N, 181 kg of Ca, 57 kg of K, 22 kg of Mg and 13 kg of P/ha/yr. The N, Ca, Mg and K values are all twice those reported by Wadsworth (1983) for teak plantations; the P value is similar. Although these nutrient values are high, they should be compared with the nutrient-supplying capacity of the soil. For example, Wadsworth (1983) compared data from the rates of annual nutrient uptake of various agricultural crops on upland Ultisols and Oxisols in Puerto Rico (N = 90-120 kg/ha/year, K = 50-90, Ca = 86-109, Mg = 68-98), with the mean rates of annual nutrient retention for fast-growing teak and pine plantations. He concluded that the capacity of the soils to supply nutrients was enough for the needs of the plantations and that plantation trees could be harvested without creating soil deficiencies, except maybe for P.

At present, no data are available on the nutrient-supplying capacity of the soils of this study. Long-term soil fertility measurements, as well as comparisons of vegetation and soil nutrient pools (Montagnini and Sancho 1993) may show specific trends of soil nutrient accumulation or deficiencies. Our results show that following the initial site improvement which was found in 1988, approximately one year after canopy closure (Montagnini and Sancho 1990a, 1990b), no further positive or negative changes in soil chemistry were detected. Lundgren (1980) proposed that ameliorating effects of plantation forests on soils occur only during the 5-10 year period immediately following canopy closure (the "fallow enrichment phase"). During the maximum-production phase an actual deterioration of site quality would occur, as mineral nutrients are taken up by the trees and litter accumulates on the floor due to unfavorable conditions for organic matter decomposition (Lundgren 1980). However, Sanchez et al. (1985) reviewed the information available at the time to test Lundgren's model, and concluded that deleterious effects on soils occur only during plantation establishment. Continued soil measurements at the La Selva site will be needed to confirm the trends reported for 1988-1991.

To obtain a more realistic picture on soil nutrient budgets, other components and transfers should be considered. Weathering inputs are unlikely to be of major importance in these soils; atmospheric deposition is expected to be small in magnitude, although it may be important over long spans of time (Szott et al. 1991). Additionally, we are not considering the ability of the trees to absorb nutrients from below 60 cm soil depth; or leaching losses, which may be considerable under the high rainfall conditions at La Selva. However, our results so far tend to agree overall with the conclusions of Wadsworth (1983), and Bruijnzeel and Wiersum (1985), pointing to P as the most critical element with a potential for depletion from soils following cultivation and harvest of relatively fast-growing trees in monospecific plantations. Finally, as tree species differ in their nutrient demands, as well as in their effects on soils, mixed-species designs can be more advantageous for site nutrient conservation if designs are planned so as to complement each species' nutrient demands and effects.

CONCLUSIONS

Biomass and stemwood annual increments in young stands of the indigenous tree species *S. microstachyum*, *V. guatemalensis*, *V. ferruginea* and *H. alchorneoides*, growing on infertile soils in the Atlantic humid lowlands of Costa Rica, were comparable to those reported for other tree species in the humid tropics. The four species differed in their tissue nutrient content and nutrient accumulation in aboveground biomass. *S. microstachyum* had the highest accumulation of N in stem, branch and total aboveground tree biomass. *V. guatemalensis* had the highest accumulation of Ca and Mg in the biomass, while *H. alchorneoides* had the highest stem K and P.

Whole-tree harvest will have more negative effects on site nutrients than stem harvest only; although the effects will vary according to the species and tree parts removed. Nutrient accumulation by the understory had a relatively small role on the site's nutrient budget. The forest-floor litter was a major compartment for nutrient accumulation and recycling.

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CHAPTER 10

NUTRIENT BUDGETS OF YOUNG PLANTATIONS WITH NATIVE TREES: STRATEGIES FOR SUSTAINED MANAGEMENT

Florencia Montagnini
Freddy Sancho

INTRODUCTION

Our research focuses on a specific area in the humid lowland tropics of Central America in Costa Rica where banana plantations are predominant. Deforestation and the consequent degradation of land from mismanagement—shifting agriculture and cattle grazing—are common problems. Unpalatable native grasses and ferns reclaim abandoned land. A 4000 mm/yr rainfall hastens erosion of soil that has been depleted of nutrients from repeated harvesting.

Restoration of the soil to its former productivity and ecological balance has become a predominant concern of the government. There are local low- to medium-income farmers who are willing to risk some part of their land to raise trees, for they consider trees as a form of savings or investment under conditions of high inflation. They may reserve 10% to 15% of their land for trees as a future cash value. Regional forest services encourage farmers to plant exotic species—*Eucalyptus deglupta*, *Gmelina arborea*, and *Cordia alliodora*. Fungus usually infects the eucalyptus, and *Cordia alliodora* is a 30-year rotation species that grows on fertile soil, but it is not suitable for degraded lands. Such governmental policies need to be reconsidered. Local people should have a role in policy-making to insure appropriate choices of land use, species, and management, for they have specific knowledge about conditions in which they live.

We advocate a strategy of gathering criteria about each local region: the economic value of the regional species; the availability of seeds or seedlings; the growth rate data of regional species; and the indications of species' effects on soil nutrients. We have found that certain native tree species have a potential to grow well on poor, degraded soils. These trees are fast-growing and contribute organic matter to the soil within three years. Their litter and small branches may be managed to obtain nutrients: the litter may be used as mulch for agriculture (for maize crops) or left on the forest floor to return

[M]ontagnini, F. & Sancho, F. 1994. Nutrient budgets of young plantations with native trees: strategies for sustained management. pp. 213-233 In Bentley, W. & Gowen, M. (eds.). Forest resources and wood-based biomass energy as rural development assets. Winrock International and Oxford & IBH Publishing Co. New Delhi. 347 pp.

nutrients to the surface layers of degraded soils as well as prevent soil erosion. Our discussion describes these species and their combined nutrient recycling capacities.

BENEFITS OF TREE PLANTATIONS

Currently, a number of governments and private efforts in rural development throughout the tropics are promoting tree planting, including tree-crop combinations as practiced in agroforestry. Trees are regarded as a source of cash, savings, and assets for the rural poor (Chambers and Leach 1990). Since tropical plantations managed for high yields can be at least four to ten times more productive than unmanaged natural forests (Wadsworth 1983), they also can help to meet the growing global demand for timber. This type of management is expected to help decrease the pressure on natural forests (Evans 1987).

The sustained management of tree plantations becomes a biologically and socially feasible alternative on soils that are unsuitable for the continuous practicing of agriculture that uses prevailing local technologies (Gladstone and Ledig 1990). Particularly, tree plantations and tree-crop combinations represent productive alternatives for the uses of deforested lands that have poor regeneration of natural forests since they are either intensely degraded or distant from sources of propagules. Low soil fertility, soil compaction from cattle grazing, and invasion by grasses and other aggressive vegetation—all evidences of site degradation—can be serious obstacles to both forest regeneration and conventional agriculture. As the area of degradation expands, there is increasing emphasis on the planting of tree species that can grow in such poor conditions to yield potentially profitable products (timber, fuelwood and other) as well as environmental benefits (soil conservation, watershed protection) (Evans 1987).

The choice of appropriate tree species for plantation forestry or agroforestry is influenced by knowledge of a species' performance as well as by economic and environmental benefits. In local situations, the choice of a tree species is determined by the availability of its seeds or seedlings and by information on its silvicultural characteristics and management—for instance, fast growth and the possibility of intercropping during early establishment. Most reforestation or tree-planting programs and subsidies promote the use of well-known, often exotic, species. About 85% of plantation forestry in the tropics is dominated by three genera: *Pinus*, *Eucalyptus*, and *Tectona* (Evans 1987), while there may be thousands of indigenous species suitable for similar purposes. Native trees can be more appropriate than exotics because they are better adapted to local environmental conditions, seeds and propagules are locally available, and farmers are familiar with them and their uses. In addition, the use of indigenous trees in productive systems helps to preserve genetic diversity and fosters a better balance with the local flora and fauna than exotics.

Ecological Consequences of Fast-Growing Tree Plantations

The factors that influence the productivity of tropical forest plantations are poorly understood. Some studies report yield or biomass productivity in relation to climatic factors, but few refer to site characteristics such as elevation or soil type (Lugo et al. 1988). Trees can influence site characteristics through their recycling of nutrients and their interactions with the microenvironment.

The most important beneficial effects of trees on soils can include improvement of soil structure and increased availability of nutrients (Fassbender 1984, Nair 1989, Sanchez et al. 1985, Sanchez 1987). Symbiotic nitrogen fixation by trees often results in increased soil nitrogen availability (Alpizar et al. 1986, Montagnini et al. 1986, Dommergues 1987). On the other hand, young tropical tree plantations which incorporate considerable amounts of nutrients in their biomass over a relatively short period of time are rapidly aggrading ecosystems (Bruijnzeel 1991). In early stages of growth, the amount of nutrient uptake from the soil usually exceeds the amount of nutrients supplied to the soil by litterfall and wash from the canopy (Bruijnzeel 1991).

Decline of site fertility can be a serious limitation to sustained plantation forestry in tropical regions: soil fertility can be decreased through excessive removal of living biomass, particularly if nutrients in tree crowns are lost through harvesting or site preparation (Perry and Maghembe 1989). On the other hand, Wadsworth (1983) suggests that, with the possible exception of phosphorus, repeated harvests usually would not result in serious deficiencies of soil nutrients.

Lundgren (1980) proposed that the ameliorating effects of plantation forests on soils occur only during the five-to-ten-year period immediately following canopy closure (the "fallow enrichment phase"). During the maximum-production phase, actual deterioration of site quality can occur: mineral nutrients are absorbed by the trees while litter accumulates on the forest floor, but conditions are unfavorable for the decomposition of organic matter (Lundgren 1980). Sanchez et al. (1985) concluded that deleterious effects on soils occur only during plantation establishment, but they also stressed that the extraction of nutrients by harvesting and the leaching losses incurred prior to canopy closure lead to a depletion of key nutrients, particularly potassium, that should be replaced if yields are to be sustained on subsequent rotations.

Tree species vary in their rates of nutrient uptake and in their capacity for nutrient recycling. The possibility of using particular species to accumulate nutrients was suggested by Sanchez et al. (1985) from their observations that certain species have the ability (e.g., *Gmelina arborea*) to accumulate calcium and magnesium, while others favor potassium and phosphorus. Little data is available on second and third rotations, so we do not have enough clues about what the critical nutrients for maintaining site productivity are. Data on different plantation species' rates of nutrient acquisition and recycling capabilities will help to design the best management strategies that either can take advantage of the ameliorating effects of trees on site fertility or avoid site deterioration at harvest.

Assessing the Impacts of Trees on Site Nutrients: An Example from Costa Rica

Local and regional trials of tree species for reforestation often reveal outstanding performances from indigenous trees. For example, out of 13 native tree species in an experimental plantation at La Selva Biological Station of the Organization for Tropical Studies (OTS) in the Atlantic lowlands of Costa Rica, Central America, at least four—*Stryphnodendron excelsum*, *Vochysia hondurensis*, *Vochysia ferruginea*, and *Hyeronima alchorneoides*—had growth rates equal to or greater than the exotic species that were currently recommended for the region (Espinoza and Butterfield 1989). This research demonstrates the potential of many native trees for commercial purposes. Most interestingly, it shows how certain indigenous species are able to grow well on degraded sites with poor, acid soils that could not sustain conventional agriculture, and how some of the species may have positive effects on soil fertility at an early stage (Montagnini and Sancho 1990a, 1990b, Montagnini et al. 1991). Results of our studies at the same site showed that after 2.5 years, these species contributed to the restoration of soil fertility by increasing organic matter, nitrogen, and soil cation levels to values close to those considered adequate for agricultural crops (Montagnini and Sancho 1990a, 1990b).

In the following sections, we present results from our studies of nutrient budgets in the same experimental plantation as an example of how biomass measurements, coupled with information on tissue nutrients, can be used to understand the potential environmental impacts of trees on site nutrients. We compare biomass and nutrient content among the species as well as among the trees' above-ground parts, forest-floor litter, understory vegetation, and soil nutrient pools. This information can be used to design management strategies to take advantage of the trees' ameliorating effects on soils and to avoid depletion of site nutrients at harvest. These strategies should be valuable for promoting the use of systems—mixed or pure plantations, agroforestry—that include these fast-growing timber species in the area and in other tropical lowland regions with similar ecological characteristics.

THE STUDY SITE

The experimental plantation was established in December, 1985, on abandoned pasture at the OTS La Selva Biological Station (10°26'N, 86°59'W, 50 meters mean elevation, 24°C mean annual temperature, 4000 mm mean annual rainfall, with maximum in July and minimum in March) (La Selva Biological Station weather reports). Soils are Fluventic Dystropepts, derived from alluvially deposited volcanic materials; they are deep, well drained, and free of stones, with low or medium organic-matter content, moderately heavy textured, and generally acid and infertile (Sancho and Mata 1987). The area had been cleared in the 1950s, and cattle had grazed there until 1984. The dominant species in the pastures were grasses (*Olyra latifolia, Melinis minutiflora*), ferns (*Pteridium* sp.), and bushes (*Psidium guajava* and *Piper culebranum*). In the pastures, there were patches of approximately 20-year-old adjacent forest with: *Pentachlethra macroloba*, a mimosoid, nitrogen-fixing legume dominant in the primary forest at La Selva; *Piper culebranum* and species of the melastomataceae family; ferns (*Pteridium* spp.); and tree seedlings in the understory.

The site was cleaned manually before planting. The tree species were planted randomly in a block design with five replicates, each plot containing seven rows of seven trees (14 m x 14 m each), with two meters between trees. Five similar 14 m x 14 m plots were also established in an adjacent open area with grass and in a nearby patch of secondary forest. During the first year, weeds were cut manually four times. Thereafter, weeding was done mechanically until canopy closure made it no longer necessary. The grass was also similarly weeded to keep it free of trees at the same time.

The Tree Species

The criteria for species selection for this study were good growth, as determined during the first three to four years of the plantation (Espinoza Camacho and Butterfield 1989, Gonzalez et al. 1990), presence of root nodules in the leguminous species (field observations), and economic value (Gonzalez et al. 1990, Chudnoff 1984, Holdridge and Poveda 1975). *Stryphnodendron excelsum* Harms (Leguminosae, subfamily Mimosoideae) ("vainillo") is found only in Costa Rica, although representatives of this genus are native to all of tropical South America, i.e. Brazil, Costa Rica, Guiana (Allen and Allen 1981). This species grows in low elevations with very humid climates and apparently adapts to alluvial soils as well as to slopes and abandoned pastures with degraded soils (Gonzalez et al. 1990). Its timber is primarily used for general construction, and, because of its ability to take high polish, small furniture and turnery (Allen and Allen 1981). Its fruits are eaten by many species of wildlife, mostly small mammals.

Vochysia ferruginea Mart (Vochysiaceae) ("botarrama") grows in lowland forests from Nicaragua to Brazil (Whitmore and Hartshorn 1969). It is found usually on acidic, well drained, and low-fertility soils, although it can adapt to a variety of soils (Gonzalez et al. 1990). It is a self-pruning pioneer species that forms uniform, even-aged stands in abandoned fields, and its wood is used for plywood and construction.

Vochysia hondurensis Sprague (Vochysiaceae) ("mayo") is found from Mexico to Panama, at elevations up to 900 m (Whitmore and Hartshorn 1969). It usually grows in humid, low altitude areas on either alluvial or residual (less fertile) soils. Considered a substitute for mahogany, its timber is highly desirable for carpentry, plywood, and furniture.

H. alchorneoides (O) (Euphorbiaceae) ("pilon") ranges from southern Mexico to southern Brazil (Chudnoff 1984). This species grows well on hills and on abandoned grasses, but not much is known about its edaphic requirements. Its timber is used for heavy construction, furniture, cabinet work, decorative veneers, and turnery (Chudnoff 1984). Botanical characteristics of the species were described by Holdridge and Poveda (1975), Hartshorn (1983), Standley (1937-38) and Hartshorn and Hammel (unpublished). Detailed studies on seed and germination characteristics are presented by Gonzalez (1991).

METHODS

Sampling procedures and chemical methods are described in Montagnini and Sancho (1990a, 1990b), and Montagnini et al. (1991). The soils under the species, in a grassy area free of trees and in a 20-year-old secondary forest, were sampled for soil fertility, and their nitrogen availability was also measured. Tree biomass and nutrient content from stems, branches, and leaves were measured at the time of plot thinning when the plantation was four years old. The biomass and nutrient concentrations of the understory vegetation and the forest floor under the trees were also measured. Nutrient budgets were calculated by multiplying the biomass of each compartment times its nutrient concentration (nitrogen, calcium, magnesium, potassium, phosphorus).

RESULTS AND DISCUSSION

Tree Biomass

The values of whole-tree biomass reported here (table 10.1) are greater than of those reported for four-year-old *Albizia lebbek* (Parrota 1989) and of five-and-a-half-year-old *Leucaena leucocephala* (Wang et al. 1991), both growing in dense plantations for biomass production in Puerto Rico. Values shown here of the total tree above-ground net primary productivity (calculated by dividing whole-tree biomass by tree age) lie within the ranges reported elsewhere for monospecific plantations in the humid tropics. The value for *V. hondurensis* is close to that reported for *Gmelina arborea* (12.8 tons/ha/yr) in the Brazilian Amazon (Russell 1987) as well as to *Gmelina arborea* (12.7 tons/ha) and to *Albizia falcataria*, both found in the Philippines (11.3) (Kawajara et al. 1981). However, the increments shown here are lower than those reported for some of the fastest-growing trees in the humid tropics, such as *Acacia mangium* (15.5 to 18.0 tons/ha in Malaysia) and *Leucaena leucocephala* (20.0 to 30.0, and even up to 80.0 tons/ha in Hawaii and in other tropical sites, Young 1989).

Table 10.1. Means of Tree Diameter at Breast Height (dbh), Height, Aboveground Biomass and Annual Increment

	Dbh	Height	Above-ground live biomass				Mean annual increment	
			Stem	Branches	Leaves	Total	Total	Stems
	(cm)	(m)	(kg/ha)				(t ha -1 yr -1)	
S. exc.	12.0a	8.9b	35,250a	15,250a	4,325a	54,825	13.7	8.8
V. fer.	10.3a	8.1b	24,750b	14,250a	5,925a	44,925	11.2	6.2
V. hon.	10.8a	12.0a	41,750a	6,500b	7,250a	55,500	13.9	10.4
H. alc.	10.8a	9.0a	26,250b	12,250a	5,350a	43,850	12.0	6.5

Note: In this and in following tables, differences between sites for a given parameter are statistically significant when means are followed by different letters.

Annual increments of stemwood biomass for broadleafs range from 1 to 28 tons/ha/yr. Fast-growing species such as *Gmelina arborea* and *E. saligna* range from 10 to 20 and from 8 to 28 tons/ha, respectively, and relatively slower-growing species such as *Swietenia* sp. and *Tectona grandis* range from 1 to 4 and 3 to 12 tons/ha, respectively (Wadsworth 1983). Other values for fast-growing trees in tropical humid regions include various eucalyptus species grown in the Americas and in Asia (from 7.2 to 11.9 tons/ha); *Gmelina arborea* in Costa Rica (11.8 tons/ha) (Lugo et al. 1988); 1.3- to 5.3 *Leucaena leucocephala* growing in premontane and lowland humid sites (2.8 to 15.9 tons/ha); *Prosopis juliflora*, on a moist site in India (9.4 tons/ha), and *Populus deltoides*, on a subtropical site in India (6.4 tons/ha) (Lugo et al. 1990). Thus, the mean annual increments of stemwood biomass for the species in this study also fall within the ranges reported for other fast-growing tree species in the humid tropics.

Nutrient Accumulation in Above-Ground Tree Biomass

Nitrogen

Consistent with trends found in nitrogen (N) tissue concentrations (Montagnini et al. 1991), *S. excelsum* had the highest stem, branch, and total above-ground tree biomass N. Although *S. excelsum* had higher N-leaf concentrations than the other species, it had similar N-leaf biomass because its leaf biomass was relatively lower (figure 10.1). Taking leaves and branches together, approximately 200 kg/ha, or 60% of *S. excelsum*'s above-ground tree biomass

N (figure 10.1) would be left on the site at the time of harvest if only stems were removed. *V. hondurensis* had a similar proportion of N to that of *S. excelsum* in its leaves and branches portion. Again, over 50% of above-ground tree biomass N could be recycled if left at the site at the time of harvest. *V. ferruginea*, with relatively lower stem biomass, had proportionally more N in leaves (52.9%) and branches (42.1%), while *H. alchorneoides* showed a more even distribution of above-ground tree biomass N in stems (39%), branches (27%), and leaves (33.8%).

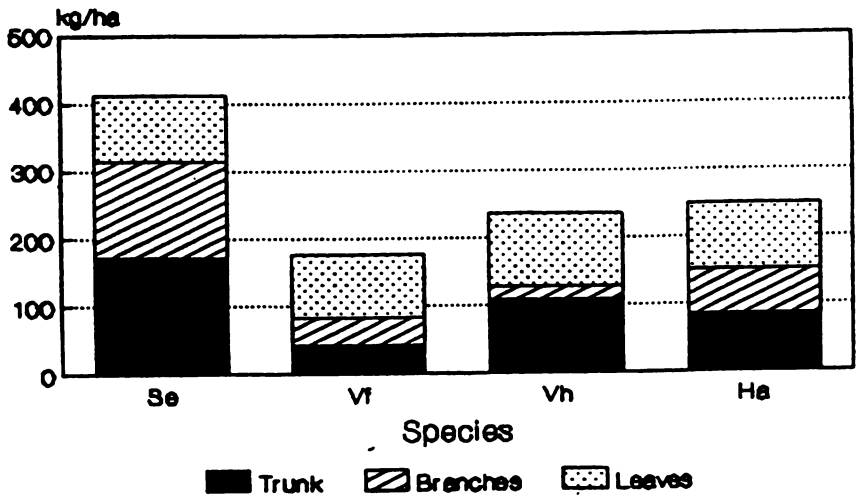

Figure 10.1. Nutrients in Tree Biomass - Nitrogen.

Calcium

V. hondurensis, with the highest stem biomass and calcium (Ca) concentration, also had the highest stemwood Ca (over 600 kg/ha, or 84% of above-ground tree biomass Ca), approximately twice as much as either *S. excelsum* or *V. ferruginea*, and several times more than *H. alchorneoides* (figure 10.2). Therefore, the harvest of *V. hondurensis* trees could substantially reduce the amount of Ca in the site. However, while the *V. hondurensis* trees are living, relatively large amounts of Ca could be recycled because, although it represented only 16% of above-ground tree biomass, the amount of Ca in leaves and branches together was over 100 kg/ha.

The proportion of Ca in stems relative to above-ground tree biomass was similar for *S. excelsum* and *V. ferruginea* (76.6% and 70.8% respectively) (figure 10.2), but the absolute amounts were less than half those of *V. hondurensis*. *H. alchorneoides* again showed a more evenly distributed quantity of Ca in stems, leaves, and branches, with above-ground tree biomass Ca slightly over half that of *S. excelsum* and *V. ferruginea*.

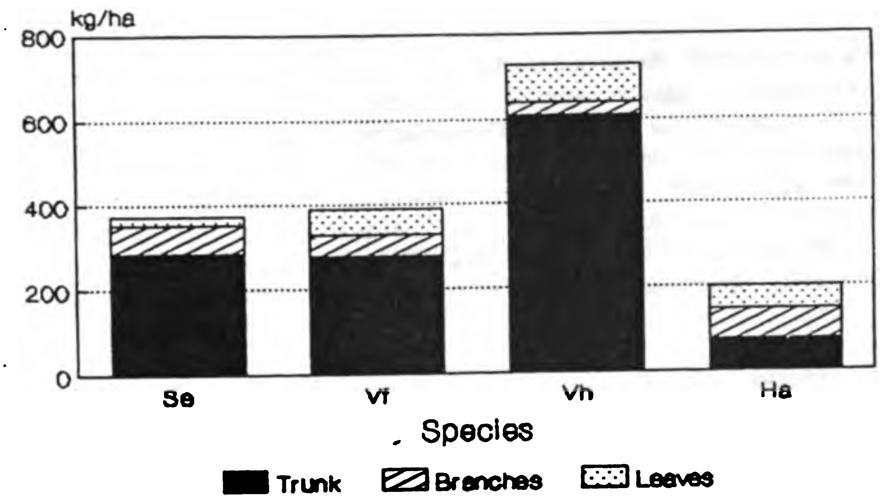

Figure 10.2. Nutrients in Tree Biomass - Calcium.

Magnesium

V. hondurensis, with its high stem biomass and high magnesium (Mg) concentration, also had the highest Mg in stemwood (55% of above-ground tree biomass, or approximately 30 kg/ha) (figure 10.3). Again, removal of *V. hondurensis* stems would affect the site's Mg budget more dramatically than for any of the other species, especially if the whole tree is harvested. The other species showed lower proportions of above-ground tree biomass Mg in their stems (30% to 46%) (figure 10.3).

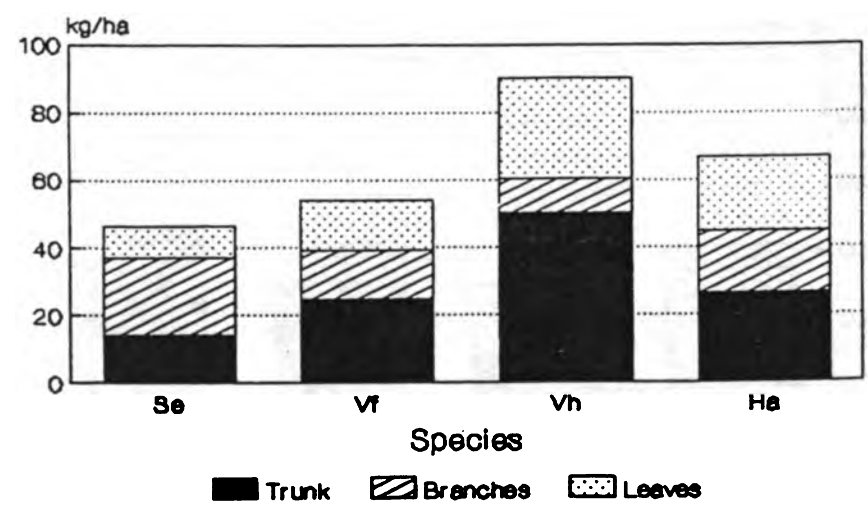

Figure 10.3. Nutrients in Tree Biomass - Magnesium.

Potassium

For potassium (K) the picture changed: the highest accumulation of K in stems was found in *H. alchorneoides* (252 kg/ha, figure 10.3), accounting for 58.7% of above-ground tree biomass K. This quantity was followed by *V. hondurensis* with 175 kg/ha, which represents 76.8% of above-ground tree biomass K. Thus, whole-tree harvest of *H. alchorneoides* and *V. hondurensis* may have the greatest effects on the K budget. *S. excelsum* and *V. ferruginea* had 33.6% and 35.4%, respectively, of K in the stem. The recycling of K from leaves and branches could be relatively more important when considering these latter two species.

Phosphorus

V. hondurensis and *H. alchorneoides* had the highest proportions of stemwood phosphorus (P) (72.4% and 62.1%, respectively) (figure 10.4). *S. excelsum* and *V. ferruginea* had relatively lower amounts of stem P, also correlating with proportions of above-ground tree biomass P (43.9% and 48.7% respectively).

Our results confirm earlier reports on the negative effects of the harvest of whole trees on site nutrient pools: for example, Bruijnzel and Wiersum (1985) studied nutrient input/output budgets for *Agathis dammara* plantations in upland Java. Their results, calculated for a thirty-year rotation, showed that total harvesting of the trees would remove the entire inputs of K and Ca, almost half of the Mg input, and twice the input of P. The authors concluded that, in order to avoid shortages of nutrients, especially P, harvesting of whole-tree biomass should not be practiced. Our results also suggest that leaving plant residues in the site could greatly decrease the negative impacts of nutrient removal at harvest, with varying consequences that would depend on the individual species.

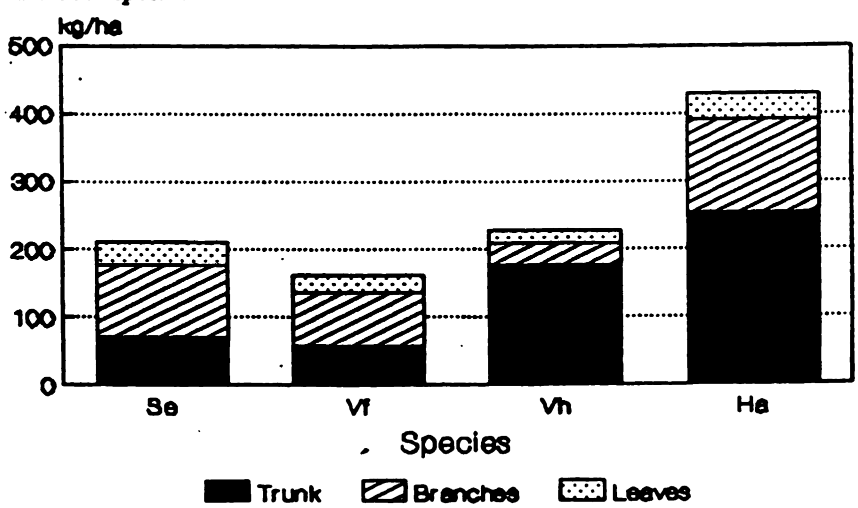

Figure 10.4. Nutrients in Tree Biomass - Potassium.

Altering the rate of nutrient removal from the site is probably one of the most important design considerations when planning sustainable plantations (Wang et al. 1991). The tree species as well as the parts of the tree removed will determine the nutrient "cost" of removal. This "cost" can be assessed in advance by nutrient and biomass sampling and estimation. By comparing the quantities of nutrients removed from a variety of species in numerous tropical sites, these authors argue that nutrient removal increases from 13% to 253%, while biomass removal increases less than 50%, when harvesting of whole-tree biomass, rather than harvesting only stems, is practiced. Additionally, they argue that shorter rotations will be more affected by this difference because the fractions of leaves and small branches of the total biomass tend to decrease with tree size. Bruijnzel and Wiersum (1985) found that stemwood P concentrations of 35-year-old *Agathis dammara* were lower than those of younger trees, whereas no such differences were found for other nutrients, and they suggest that the main effects of shorter rotations will be an increase in site disturbance.

Impacts of Trees on Soil Nutrients

Similar to the 1988 findings, higher levels of soil organic matter and N were found in the tree plantation than in grass, with values close to those of secondary forest (table 10.2), but unlike 1988, these differences were not statistically significant ($P<0.05$). P content was higher in grass than in the plantation or in the forest (table 10.2). Within the tree plantation, there were no significant differences among species in soil cation content. However, there was a trend of higher Ca under *S. excelsum* and lower Ca in *H. alchorneoides*. Higher Mg was recorded under the two *Vochysia* species, with lower values again in *H. alchorneoides* (table 10.2).

Results of similar measurements taken in May, 1990, and again in May, 1991, revealed trends like those found in 1988 and 1989. When examining data from 1988 to 1991, no increasing or decreasing trends over time were detected for any individual nutrient (Montagnini and Sancho, unpublished data). Apparently, site improvement was observed in 1988, when the trees were 2.5 years old and had developed closed canopies. Following this initial site improvement, further testing could not detect any additional positive changes in soil chemistry. In fact, as trees approach their maximum-production phase and as the "recyclable" portion (leaves and branches) of the tree decreases in relation to that of the stem, a decrease in soil nutrients can be expected (Lundgren 1980).

The impacts of plantation tree species on soil nutrient reserves will depend on the annual nutrient uptake of the trees in relation to the nutrient-supplying capacity of the soil, nutrient recycling (while the trees are living), and the parts of the tree removed, whether the whole tree or stemwood, and their biomass and nutrient content at the time of harvest. A look at these relationships for *V. hondurensis*, the fastest-growing and seemingly the most

Table 10.2. Organic Matter, Total N, P, pH, Ca, Mg, and K in Soils Under the Four Native Tree Species in Plantation, Grass and Secondary Forest, May 1989[1].

Site	Depth (cm)	OM	N (%)	P (mg/kg)	pH	Ca	Mg (cmol/kg)	K
S. exc.	0-15	4.50a	0.278a	2.4a	5.1a	0.68b	0.44a	0.13a
	15-30	3.29a	0.224a	2.1a	5.1ab	0.52bc	0.22bc	0.14a
	30-60	1.88a	0.196a	1.8b	5.1a	0.54a	0.16a	0.14a
V. fer.	0-15	5.06a	0.32a	3.24a	4.98a	0.63bc	0.53bc	0.16a
	15-30	3.66a	0.248a	2.48a	5.03c	0.35d	0.20c	0.10a
	30-60	2.94a	0.200a	2.50b	5.07a	0.33a	0.16a	0.15aa
V. hon.	0-15	4.30a	0.304a	2.30a	5.20a	0.47bc	0.50bc	0.10a
	15-30	3.16a	0.232a	1.82a	5.08ab	0.38cd	0.22bc	0.07a
	30-60	2.42a	0.202a	2.00b	5.13a	0.36a	0.15a	0.06a
H. alc	0-15	5.16a	0.232a	1.5a	5.1a	0.31c	0.21a	0.09a
	15-30	2.77a	0.248a	1.5a	5.1ab	0.45bcd	0.19c	0.10a
	30-60	1.21a	0.158a	1.7b	5.2a	0.46a	0.20a	0.10a
Grass	0-15	3.98a	0.296a	4.1a	5.2a	0.57bc	0.38a	0.22a
	15-30	2.94a	0.236a	3.4a	5.1ab	0.51bcd	0.27bc	0.17a
	30-60	2.46a	0.194a	8.9a	5.2a	0.47a	0.20a	0.13a
Forest	0-15	5.11a	0.288a	2.3a	5.2a	1.16a	0.49a	0.21a
	15-30	3.83a	0.244a	2.0a	5.2a	0.92a	0.45a	0.17a
	30-60	2.48a	0.206a	1.4b	5.2a	0.62a	0.27a	0.12a

[1]. Differences between sites for a given depth and parameter are statistically significant when means are followed by different letters.

nutrient-demanding species of this study, will illustrate this point. Nutrient retention by *V. hondurensis* (calculated by dividing biomass nutrient by plantation age) was an average of 58 kg of N, 181 kg of Ca, 57 kg of K, 22 kg of Mg, and 13 kg of P/ha/yr. The N, Ca, Mg, and K values are all twice as much as those reported by Wadsworth (1983) for teak plantations but the value of P is similar. Although these nutrient values are high, they should be compared with the nutrient-supplying capacity of the soil. For example, Wadsworth (1983) compared data from the rates of annual nutrient uptake of various agricultural crops on upland Ultisols and Oxisols in Puerto Rico (N = 90 - 120 kg/ha/yr, K = 50 - 90, Ca = 86 - 109, Mg = 68 - 98), with the rates of mean annual nutrient retention for fast-growing teak and pine plantations. He concluded that the capacity of the soils to supply nutrients was enough for the needs of the plantations and that plantation trees could be harvested without creating soil deficiencies, except maybe for P. Wang et al. (1991) also reported that the rate of removal of N, P, Ca, Mg and K on an annual basis for

Casuarina and *Albizia* plantations in Puerto Rico was similar to that of crop systems such as maize and sorghum.

In our analysis, we are not considering "nutrient-supplying capacity" of soils, but rather we are comparing the stocks of above-ground nutrients for each tree species with those in the soil. These quantities were calculated by multiplying the average soil nutrient concentrations for each soil layer under each species to a depth of 60 cm (table 10.2) times the weight of a hectare of the soil for the corresponding layer. Values were corrected by estimating soil bulk density for each type of vegetation (Montagnini and Sancho, unpublished data). If we assume that the nutrient content of the grassy area—where there are no trees—represents the quantity of nutrient stocks before the establishment of the plantation, and if we compare these values with nutrient concentrations found under trees, we can obtain an approximation of the effects of tree uptake on soil reserves.

Comparing soil nutrient budgets (figures 10.1-10.5) with nutrient content of tree biomass (figures 10.6-10.10), we observe that after four years, soil Ca reserves tended to decrease under all the species except for *S. excelsum*. In contrast, soil under the secondary forest appears to have almost twice as much Ca as under *V. hondurensis*, *V. ferruginea*, or *H. alchorneoides* (figure 10.7). Mg and K tended to be lower under *H. alchorneoides* (figures 10.8 and 10.9). However, the most notable overall decrease in soil nutrients occurred for P (figure 10.10), where values under all of the tree species were lower than those under grass and similar to those under the secondary forest. (We do not discuss statistically significant differences here because these measurements are already shown for soil nutrient concentrations, table 10.2). The figures for N are more difficult to compare because soil N was calculated from total N (TKN) values, which tend to be approximately 100 times larger than available N (NO_3 +NH_4), and because N fixation by *S. excelsum* is an additional input that needs to be examined separately. We are not considering other factors affecting nutrient concentration levels such as weathering or rain, the ability of the trees to absorb nutrients from below 60 cm soil depth, or recycling mechanisms (which we will examine next). However, our results tend to agree with the conclusions of Wadsworth (1983) and Bruijnzel and Wiersum (1985) that P, with its potential for depletion, is the most critical element to be considered. Our results also underscore the importance of promoting nutrient-recycling mechanisms through management practices, both in the living stand and at the time of harvest.

Biomass and Nutrient Concentration of Understory Vegetation

Nitrogen accumulation in the total understory biomass was higher under *S. excelsum* plots (14.9 kg/ha), although this amount represented only 3.6% of whole-tree biomass N (table 10.3). For *H. alchorneoides*, understory biomass N was 5.7 kg/ha, or 2.3% of above-ground tree biomass N. For the other nutrients, accumulation in understory biomass under *S. excelsum* ranged from

0.8% to 7.7%, and under *H. alchorneoides*, it ranged from 0.85% to 4.1% of above-ground tree biomass nutrients (table 10.3).

Table 10.3. Biomass and Nutrient Content of Understory Vegetation and Forest-Floor Litter[1]

(a) Understory vegetation

	Biomass (kg/ha)	N	Ca	Mg (kg/ha)	K	P
S.exc.	874	14.9(3.6)	2.9(0.8)	3.6(7.7)	8.8(4.2)	1.1(2.0)
H. alc.	425	5.7(2.3)	3.3(1.6)	1.9(2.9)	3.3(0.8)	3.1(4.10

(b) Forest-floor litter[2]

	Biomass (kg/ha)	N	Ca	Mg (kg/ha)	K	P
S. exc.	5612	95.1(23.0)	41.6(11.1)	8.2(17.6)	6.6(3.1)	4.3(7.6)
V. fer.	17215	240.3(137.0)	187.6(47.9)	19.1(35.5)	12.1(7.5)	15.5(33.8)
V. hon.	11084	134.0(57.0)	170.0(23.4)	26.4(24.3)	9.7(4.2)	11.6(22.3)
H. alc.	4238	39.2(15.8)	55.0(27.0)	11.9(17.9)	6.8(1.6)	12.9(16.9)

[1]. Numbers between parentheses are percent in relation to whole-tree biomass nutrients.
[2]. Totals, including leaves, fragments, branches.

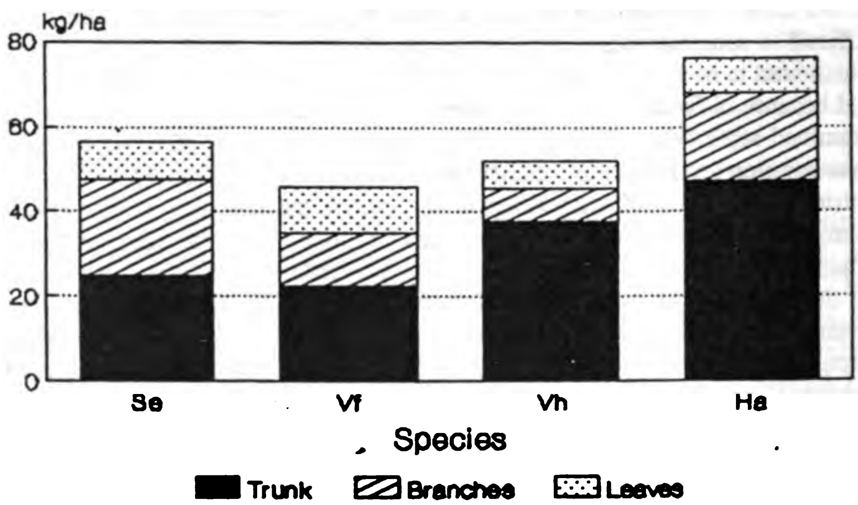

Figure 10.5. Nutrients in Tree Biomass - Phosphorus.

Since vegetation in the understory apparently accounts for a relatively small proportion of nutrients, as compared to the whole tree, manipulations of the understory should have little effect on nutrient recycling at the site. For example, weeding should have a relatively minor effect on nutrient recycling, unless the understory is removed many times a year. This hypothesis also suggests that intercropping with annual, herbaceous species that attain similar amounts of biomass as that of the understory found under *S. excelsum* or *H. alchorneoides* will not have a substantially negative effect on the balance of nutrients at the site. Since samplings of understory biomass were taken at a time when the quantity of biomass was at its peak, the amounts reported here are considered to approximate those that could be attained by crops. However, this factor deserves further research, since nutrient requirements and parts of plants and trees removed at harvest will vary according to the crops. Our results, however, tend to agree with Bruijnzel and Wiersum (1985), who concluded that the use of controlled intercropping on tree plantations of upland Java, coupled with precautionary measures to minimize soil erosion, was an acceptable way to conserve nutrients. They argue that, in addition to their socioeconomic benefits, the use of such "taungya" practices could also prove advantageous since farmers may be willing to use fertilizers for the crops and the residual effects of these applied nutrients may increase the yield of the trees.

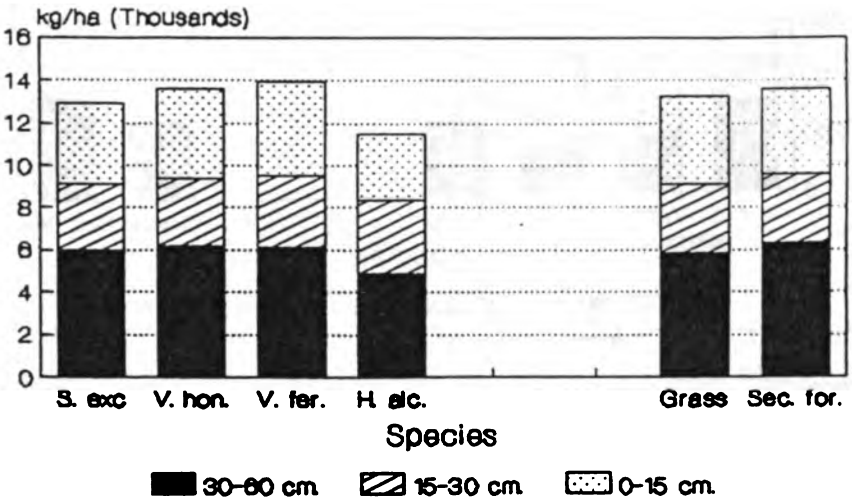

Figure 10.6 Soil Nutrient Balances - Nitrogen.

Nutrient Accumulation in Forest-floor Litter

The nutrient accumulation and forest-floor biomass were highest under *V. ferruginea*. N in forest-floor litter under *V. ferruginea* was greater than this species' above-ground tree biomass N (table 10.3). As noted above, *V. ferruginea*'s leaf-and-branch biomass accounts for a large proportion of its above-ground tree biomass. This species is self-pruning, a characteristic which enhances shedding of branches and leaves, and occasional prunings may have added even more tree litter to the forest floor. Results of our studies on the rates of litterfall and litter decomposition (Montagnini et al. 1991) suggest that litter decomposes relatively slowly under *V. ferruginea*, a factor explaining the high accumulations noted above. *V. hondurensis*, *H. alchorneoides*, and *S. excelsum* show faster rates of litter decomposition. Forest-floor litter Ca, Mg and P were also considerable under *V. ferruginea* (table 10.3), a finding especially relevant for P, since there is a potential deficiency of this element at the site, as mentioned earlier. Nutrients from forest-floor biomass were also higher under *V. hondurensis*. Again, this result was more significant for N, Ca, Mg and P. Thus, in spite of this species' fast growth rate, nutrient recycling from litter may at least partially compensate for depletion of soil nutrients. While the reverse was true for P, forest-floor litter N was more than double under *S. excelsum* than under *H. alchorneoides*, even though both species had similar forest-floor litter biomass (table 10.3).

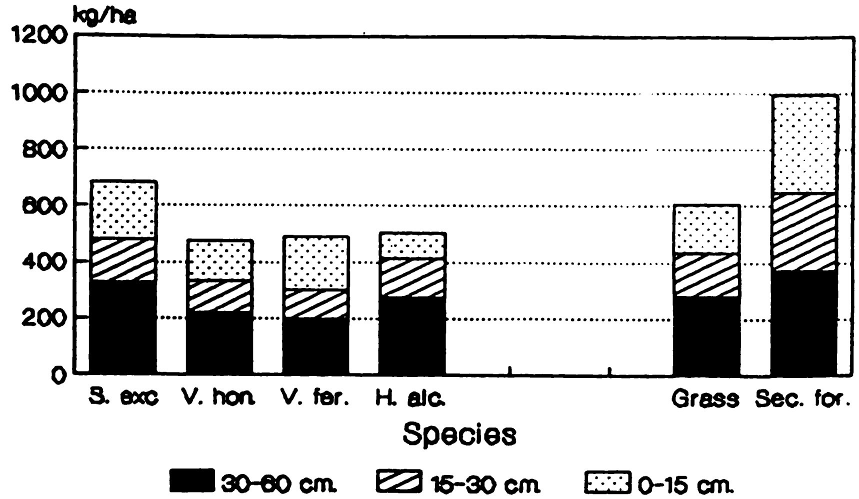

Figure 10.7. Soil Nutrient Balances - Calcium.

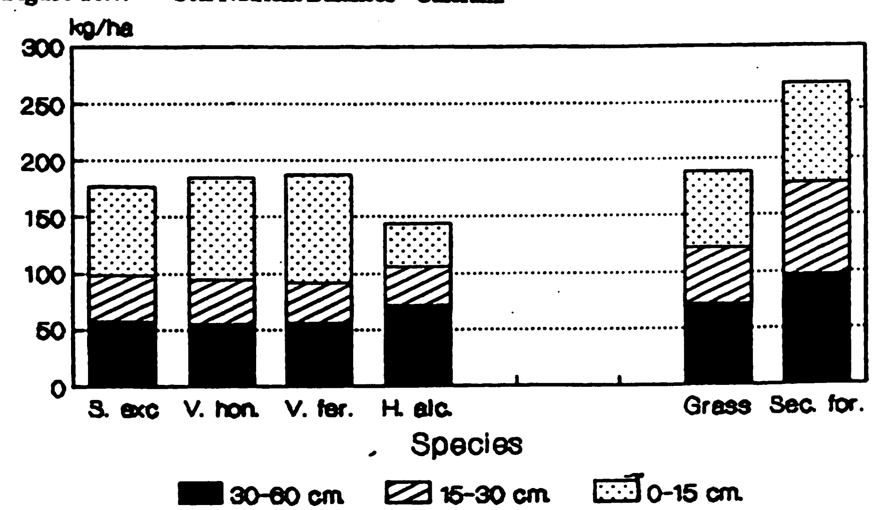

Figure 10.8. Soil Nutrient Balances - Magnesium.

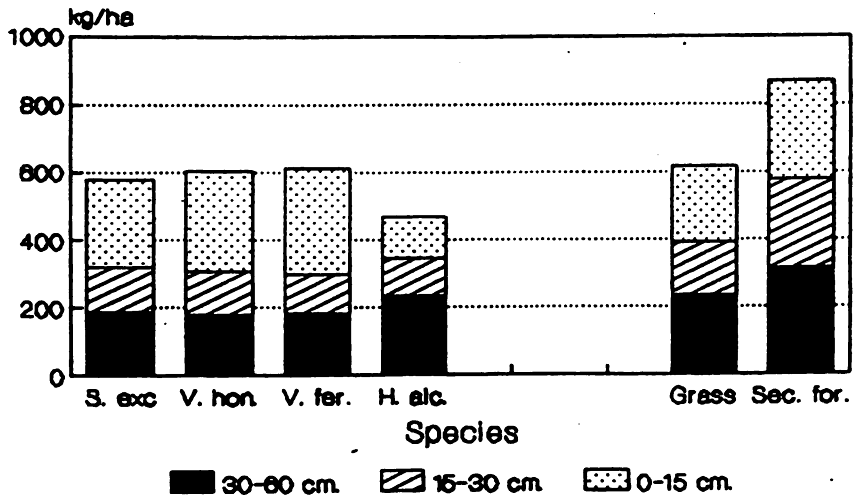

Figure 10.9. Soil Nutrient Balances - Potassium.

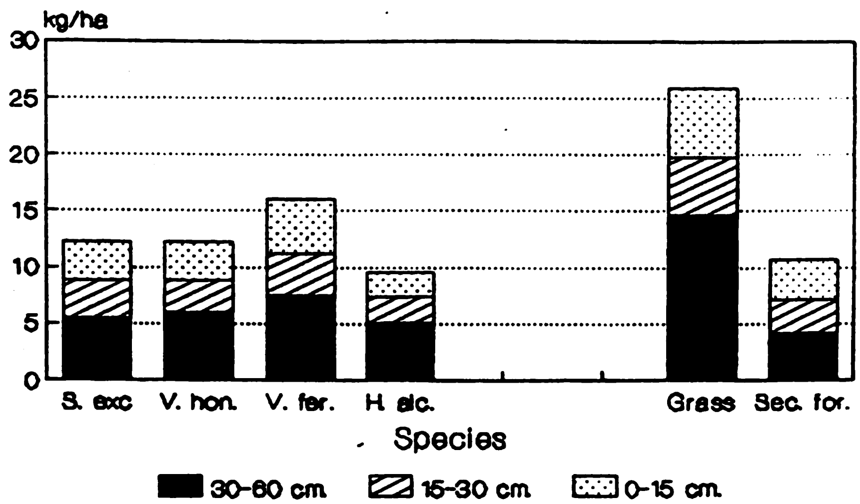

Figure 10.10. Soil Nutrient Balances - Phosphorus.

These results show that the forest floor is an important place for the accumulation and recycling of nutrients, particularly for N, Ca, Mg and P, but less for K, with marked differences among tree species. If the forest floor is affected by burning or during weeding, a substantial loss of organic matter and nutrients may occur. Wang et al. (1991) also found that with the exception of K, nutrients in forest-floor litter were equivalent to a large proportion (16-50%) of the nutrients contained in the above-ground tree biomass. They concluded that if the litter were left on the floor after harvest, it would represent a substantial reservoir of nutrients for the next rotation.

CONCLUSIONS AND RECOMMENDATIONS

1. Many indigenous tree species with good timber value can grow in open plantations on sites of low fertility and can exhibit fast growth and potential beneficial effects on soil nutrients. Moreover, their effects on soil nutrients may be observed early in the term of rotation, at canopy closure.

2. Tree species differ in their rates of nutrient accumulation in their biomass and in their tissue nutrient content. For a given species, the same trends do not hold for all nutrients: for example, a species may have the greatest effect on site Ca, but its influence on K or N may be minimal; another species may have a more significant influence on site K or P.

3. The establishment of mixed-tree plantations should be an appropriate strategy for combining the nutrient requirements of different tree species with their effects on site nutrients, so that a site may not become depleted of any particular nutrient. However, even with mixtures of trees, site deficiencies are possible for K and P in the long run.

4. Harvest of whole trees will have more negative effects on site nutrients than stem harvest only. The effects will vary according to the species and tree parts removed. Depletion of site nutrients will be greater with shorter rotations because younger trees have a larger proportion of leaf+branch tissue in relation to their stems than older trees, i.e., the potentially "recyclable" portion of the tree is greater in young trees; and harvesting shorter rotations will increase the frequency of removing nutrients from the site as well as the site disturbances associated with harvest operations (soil erosion, compaction, disturbance of the forest-floor layer, etc.).

5. Apparently, growth of understory vegetation and the corresponding accumulation of nutrients plays a relatively small role in affecting the site's nutrient budget. Therefore, agroforestry practices in the understory, such as weeding and intercropping with annual species, may not be that critical for the preservation of nutrients in the site. This situation will vary with the species planted and their management. Intercropping during early stages of tree growth, as long as the crops' nutrient requirements and their management do not provoke other deleterious effects (i.e., soil erosion, excessive nutrient removal with repeated harvests), is an alternative way to accelerate capital returns on the land and thus to stimulate local farmers to plant trees.

6. Forest-floor litter represents a major component of nutrient accumulation and recycling. Practices that affect the forest-floor litter, such as burning for weed control, harvest of litter for fuelwood or mulch, etc., can have serious deleterious effects on site nutrients.

7. The measurement of tree-tissue biomass and nutrient concentrations early in a rotation (for example, when thinning) can give a good indication of the potential impact of management practices on the conservation of site nutrients.

8. References to the rates of nutrient extraction by agricultural crops common in the region can serve as indicators of the "nutrient-supplying capacity" of soils to be compared with the rates of tree ecies' nutrient uptake in order to assess potential nutrient ficiencies in the site.

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REHABILITATING FOREST ECOSYSTEMS IN THE HUMID TROPICS: RECENT EXPERIENCES FROM LATIN AMERICA

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SUMMARY

This article reports results from a seven-year research program on forest rehabilitation in three tropical humid regions of Latin America, with emphasis on the impacts of native trees on soil fertility and nutrient cycling. In Costa Rica, increased level of soil nitrogen, carbon, Ca and Mg were found under some of the tree species than under grass, with values close to those found in 20-year-old forest. Among the tree species, the highest soil C, N and cations were found under *Vochysia ferruginea*, while results of nutrient cycling studies revealed important effects of other species on soil N and P availability and Ca and Mg recycling. In Bahia, Brazil, positive effects were found in at least five soil parameters under 15 out of 20 tree species, in comparison with primary and secondary forest. Several species contributed to increased C and N: *Inga affinis, Parapiptadenia pterosperma, Plathymenia foliolosa* (leguminous, N-fixing species), *Caesalpinia echinata, Copaifera luscens* (leguminous, non-N-fixing), *Eschweilera ovata, Pradosia lactescens* (of other families). In Misiones, NE Argentina, soils under *Bastardiopsis densiflora* had the highest levels of organic matter, N, cations and pH. Nutrient use efficiencies (stem biomass increments per unit of nutrient taken up) were calculated for each species to help to integrate results and design management recommendations geared to sustaining productivity of systems including these species.

Keywords: soil rehabilitation, native trees, nutrient use efficiency, lowland humid tropics

INTRODUCTION

The initial step in ecosystem rehabilitation projects is to identify the most important constraints to crop or tree productivity, as well as defining the specific land restoration objectives. Some soils can be recovered through the use of fertilizers, others need more drastic rehabilitation techniques, and there are situations of extreme degradation where soils cannot be recovered at all (Dedecek 1992). The recovery of the soils' productive capacity is frequently very expensive, thus the techniques involved must produce financial returns to ensure their

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

adoptability by the local farmers. In addition to financial and socio-cultural reasons, tree species choice is determined by seedling availability and information on silvicultural characteristics and management. This article focuses on the rehabilitation of lands abandoned from extensive agriculture or cattle in the humid tropics. A total of 30 indigenous tree species were evaluated in three forest regions of Latin America. The principal focus of this article is on the impacts of trees on soils, their nutrient recycling abilities and the lessons that can be learned for the implementation and sustainable management of forestry systems including these species.

METHODS

A research program to develop alternatives for the rehabilitation and use of abandoned lands started in 1987 in three humid forest regions of Latin America: the Atlantic lowlands of Costa Rica, the Atlantic rainforest of Bahia, NE Brazil and the sub-tropical forest of Misiones, NE Argentina (Table 1). In these regions, common situations of rapid deforestation, loss of biodiversity, resource misuse and land degradation persist. Similar methods were used in the three locations: soil chemistry and nutrient cycling parameters were measured in pure stands of selected indigenous species, using adjacent areas free of trees (abandoned agricultural field or pasture, secondary/primary forest) for comparison. The size of each project varied with the sites: in Costa Rica the studies started earlier and were the most complete (soils, above- and below-ground biomass, litterfall and forest-floor litter biomass and tissue chemistry), while in Bahia and Misiones the trees were part of a forest reserve or were in private farms and thus destructive sampling was not possible. Methods for sampling and analysis are found in Montagnini and Sancho 1990a, b, 1994a, b, Montagnini et al. 1991, 1993a, b, c.

As a means of integrating results accross sites and summarizing recommendations for the design and management of systems including these species, nutrient use efficiencies were

Table 1. Site characteristics.

Location	Mean annual rainfall, temp.	Soils	Previous land use	Experimental setting
La Selva Biol. Sta., Atlantic lowlands of Costa Rica	4,000mm, 24°C	Fluventic Dystropepts pH 4.3-4.6	1-3 yrs. agriculture, cattle	Pure plantation, 2mx2m, 2-6 yrs. old
Pau Brasil Ecol. Station Porto Seguro, Bahia, Brazil	1,700mm, 23°C	Oxisols (Haplorthox) pH 4.5-5.0	Shifting agriculture	Pure plantation, 2mx2m, 14-15 yrs. old
Eldorado, Misiones, NE Argentina (private farms)	1,700-2,400mm 22°C	Acid, clayey Ultisols pH 4.5-5.0	Agriculture, pine plantations	Pure stands from natl. regen., 10-20 yrs. old

calculated as the amount of biomass produced per unit of nutrient taken up (Vitousek 1984, Binkley 1992) for the species studied in Costa Rica and Brazil, where data were more complete. Because the interest in forestry is timber production, annual stem biomass increments were used in the calculations. Since no direct measurements of nutrient uptake are usually available, litterfall nutrients have been used as an estimate by several authors (Grubb 1989). Litterfall data were not available for Bahia; however, it was expected that for the fast-growing tree species of this study, in a humid tropical climate, the annual litterfall had reached equilibrium with its accumulation on the forest-floor after 14-15 years, thus the forest-floor leaves nutrient concentrations were used instead of litterfall nutrients for the calculations.

RESULTS AND DISCUSSION

Impacts of Trees on Soils

La Selva, Costa Rica

At the La Selva site, improved soil conditions were found starting just after tree canopy closure: soil nitrogen and carbon were generally higher under the trees than in abandoned pasture, with values close to those found in 20-year-old forest (Table 2). The highest values for soil carbon, total N, calcium and phosphorus were found under *Vochysia ferruginea*, a species of the Vochysiaceae family, abundant in mature and secondary forests in the region (Montagnini and Sancho 1990a, 1990b). Similar results were obtained in the three subsequent years (Montagnini and Sancho 1994a).

The effects of trees on soil N and P may not be apparent when using standard soil tests, in part due to difficulties in detecting the chemical forms available for plant uptake. Measurements of soil total N may not indicate the influence of young trees on soil N availability (Montagnini and Sancho 1994b), because available N ($NO_3^- + NH_4^+$) generally comprises less than 10% of the total soil N pool. For example, soil total N was not increased under *Stryphnodendron microstachyum*, a leguminous, N-fixing species (Baker and Montagnini 1994) (Table 2). However, this species'N- rich litter decomposed faster than the other species, resulting in increased soil mineral N under its canopy (Montagnini et al. 1991, 1993a, Montagnini and Sancho 1994b). Difficulties in evaluating the effects of trees on soil P availability are even greater: experiments involving the response of test crops to the addition of tree parts may be needed. For example, maize seedlings in plots mulched with *S. microstachyum* and *Hyeronima alchorneoides* leaves had greatest initial growth and higher N and P uptake than maize mulched with the other species' litter (Montagnini et al. 1991, 1993a).

The impacts of trees on soils depend on their nutrient recycling characteristics, hence the evaluation of key nutrient cycling parameters, such as litter chemistry and decomposition can

Table 2. Topsoil chemical characteristics in pure stands of 24 indigenous tree species at La Selva, Costa Rica and Porto Seguro, Bahia, Brazil.

Site/Tree species	pH	C (%)	N (%)	P (cmol.kg^{-1})	K	Ca	Mg
a- La Selva, Costa Rica							
Stryphnodendron microstachyum	5.4ab	3.42ab	0.29b	5.6a	0.27a	0.45a	0.63ab
Vochysia ferruginea	5.4ab	3.76a	0.32a	7.1a	0.22a	0.73a	0.61ab
Vochysia guatemalensis	5.3ab	3.13ab	0.29b	5.2a	0.11a	0.25a	0.37ab
Hyeronima alchorneoides	5.1b	2.96c	0.22b	1.5b	0.09a	0.31b	0.21b
Abandoned pasture	5.3ab	2.73c	0.22b	4.9a	0.19a	0.32b	0.27b
Secondary forest	5.3ab	4.33a	0.33a	3.6b	0.17a	0.68a	0.55ab
b- Porto Seguro, Bahia, Brazil							
N-fixing leguminous species:							
Bowdichia virgilioides	4.9	1.98def	0.16def	1.32def	0.06bcd	1.35bc	0.39de
Centrolobium minus	4.6	1.87efg	0.16def	1.19efg	0.05fgh	0.53hi	0.21i
Centrolobium robustum	4.5	1.65ij	0.13f	1.07fgh	0.05fgh	0.40i	0.16i
Inga affinis	4.9	2.10cde	0.18cd	3.64a	0.07bcd	0.76gh	0.49bc
Parapiptadenia pterosperma	4.9	2.38ab	0.20bc	0.78ij	0.08b	1.40bc	0.60a
Pithecellobium elegans	4.8	1.67hij	0.15ef	0.59kl	0.05efg	0.79gh	0.40de
Platymenia foliolosa	4.7	2.08cde	0.18bcd	0.13m	0.05efg	1.05cde	0.42cd
Non-N fixing leguminous species:							
Arapatiella psilophylla	4.7	1.94def	0.18bcd	1.45de	0.06bcd	0.38i	0.37de
Caesalpinia echinata	5.1	2.41a	0.17cde	1.54de	0.07bcd	1.17bcd	0.39de
Cassia spp.	4.7	1.94def	0.16def	1.40def	0.07bcd	0.56hi	0.34de
Copaifera luscens	5.0	2.02cde	0.17cde	0.63jk	0.06cde	1.15bcd	0.34de
Dimorphandra jorgei	4.9	1.97def	0.19bc	0.97ghi	0.03j	0.98def	0.32efg
Hymenaea aurea	4.4	2.00def	0.16def	2.03c	0.06bcd	0.26i	0.24hi
Macrolobium latifolium	4.7	1.90efg	0.16def	0.67jk	0.04hij	0.36i	0.25fg
Of other families:							
Bombax macrophyllum	4.8	1.78ghi	0.13f	1.42de	0.06bcd	0.84efg	0.33ef
Buchenavia grandis	4.6	2.06cde	0.14f	2.09c	0.06bcd	0.80fg	0.33ef
Eschweilera ovata	5.3	1.82fgh	0.31a	0.58kl	0.11a	1.38bc	0.53ab
Lecythis pisonis	5.3	1.99def	0.18bcd	0.23lm	0.04ghi	1.46b	0.32ef
Licania hypoleuca	5.0	1.63j	0.14f	1.61d	0.07bcd	1.31bcd	0.35de
Pradosia lactescens	4.9	2.15bcd	0.18bcd	0.81ij	0.05fgh	0.84efg	0.24gh
Primary forest	4.9	1.99def	0.15ef	0.96hi	0.08bc	1.23bcd	0.36de
Secondary forest	5.1	2.15abc	0.22b	2.46b	0.07bcd	2.20a	0.62a

Note: for each site, differences among means are statistically significant when followed by different letters ($p<0.05$).

suggest the species' potential as a soil improver. Tree litter can act as mulch for different objectives: high rates of litterfall and slower decomposition resulted in high litter accumulation and high soil carbon under *V. ferruginea*, making this species well suited for protecting soils against erosion. *H. alchorneoides*' litter was less abundant but it decomposed faster and had higher nutrient content, while *Vochysia guatemalensis*' litter was relatively more important for Ca and Mg recycling (Montagnini et al. 1993a, Montagnini and Sancho 1994a,c).

Porto Seguro, Bahia, Brazil

In Bahia, positive effects on at least five soil parameters were found under 15 out of the 20 species of the experiment, in comparison with primary and secondary forest (Montagnini et al. 1994). Several species contributed to increased C and N, among others: *Inga affinis, Parapiptadenia pterosperma, Plathymenia foliolosa* (leguminous, N-fixing species), *Caesalpinia echinata, Copaifera luscens* (leguminous, non-N-fixing), *Eschweilera ovata, Pradosia lactescens* (of other families) (Table 2). Others increased soil pH and/or some cations, such as *Copaifera luscens, Eschweilera ovata, Lecythis pisonis and Licania hypoleuca*. The highest amounts of forest-floor litter were found under *Licania hypoleuca, Arapatiella psilophylla, Inga affinis, Bombax macrophyllum* and *Pithecellobium elegans*; positive effects on soils were found under these species (Montagnini et al. 1994a,b).

Misiones, NE Argentina

The greatest differences in soil C and N levels were found under *Bastardiopsis densiflora*, where they were twice those in areas beyond the canopy influence (Fernández et al. 1994). The pH was higher under *Bastardiopsis densiflora* and *Cordia trichotoma*, while the sum of bases (Ca+Mg+K) was highest under *Cordia trichotoma, Bastardiopsis densiflora* and *Enterolobium contortisiliquum*. These results were substantiated with data from biomass chemical analyses, which helped to explain the trends shown above through nutrient recycling mechanisms (Montagnini et al. 1994b). *Bastardiopsis densiflora* has interesting possibilities because it is a forest pioneer which colonizes areas abandoned from agriculture, forming dense even-aged stands which can reach commercial size in 10-14 years. *Cordia trichotoma* with a slower growth rate is however a valuable timber species known to participate successfully in plantation and agroforestry systems. The potential of *Enterolobium contortisiliquum* as a soil improver with its N-fixing capacity needs to be verified.

Nutrient Use Efficiencies

Assessing potential long-term impacts

As shown above, a number of native timber species which combine good economic value with important soil rehabilitation properties were found in the three tropical and subtropical humid regions of this study. The potential of the species for rehabilitation of degraded areas sometimes was obvious through their direct impacts on soil fertility parameters such as organic matter or cations. In other cases their effects only became evident through more detailed studies such as litter decomposition, N mineralization, or by studying the response of test plants to the tree species mulch or litter.

The calculation of nutrient use efficiencies proved a useful means of integrating results for drawing recommendations for system design and management. At both the La Selva and Bahia sites, phosphorus and potassium showed the broadest ranges and the highest values of use efficiency (Table 3). Conversely, nitrogen and calcium showed narrower ranges and lower efficiency values, with magnesium in an intermediate position. These results confirm the expectation that the most scarce nutrients (P, K) were used more efficiently than the most abundant and easily recyclable nutrients (N, Ca, Mg).

Comparing among species, at La Selva *S. microstachyum* (a N-fixing species), showed relatively low efficiency (high recycling) for N and P, but comparatively high efficiencies for cations, thus confirming this species' role in nutrient cycling discussed above. *V. ferruginea* showed comparatively low efficiency values for all the nutrients considered, again sustaining the assessment of this species as beneficial in terms of organic matter recycling and positive impacts on soil fertility. *H. alchorneoides* had a similar response, with generally low values, especially for K and P. In contrast, *V. guatemalensis* with its relatively faster growth rates apparently tended to accumulate large amounts of nutrients in stem biomass, resulting in higher efficiency values and comparatively less recycling capacity, especially for N, P and K.

Among the 20 species in Bahia, *Cassia spp.*, with the highest annual stem increment and small accumulation of forest-floor litter (Montagnini et al. 1994a, b) showed the highest use efficiencies for the five nutrients considered (Table 3). This species would be particularly suited for relatively poor soils. *Dimorphandra jorgei*, with comparatively lower stem biomass increment but also with low forest-floor value, also showed high efficiencies for the five nutrients considered. *P. foliolosa* showed the highest values for Ca and Mg. Among the species with lowest use efficiencies, i.e., higher potential for recycling for the five nutrients considered were *L. hypoleuca, A. philophylla* and *H. aurea*. Within the N-fixing species, the lowest efficiencies were for *P. elegans, I. affinis, B. virgilioides*, among others.

Comparing these results with the impacts of the Bahia tree species on soils shown in Table 2, the data on nutrient use efficiencies provided additional clues on the long-term influence of the species on ecosystem nutrients. This is especially useful when additional knowledge on nutrient cycling processes is not available as was the case for the Bahia site. However, the assumptions involved in the calculations (e.g., the use of forest-floor data instead of litterfall) limit the interpretation of these findings: low amounts of forest-floor litter may result from either low litterfall, or very fast litter decomposition, thus at least some reference or indication of litterfall amounts and decomposition is needed for proper interpretation of these results.

The information on nutrient use efficiencies should be useful in matching species with sites: species with high efficiency can produce high biomass on poor sites, and species with low efficiencies would be preferred for nutrient recycling, focusing on the nutrients which are most scarce at each location. In comparing several species for a given site, interpretation of nutrient use efficiencies should include consideration of the species' growth rates and amounts of litterfall. In the absence of litterfall data, forest-floor litter data could be used for mature stands, however with more limitations.

Table 3. Nutrient use efficiencies: stem increments ($Mg.ha^{-1}year^{-1}$) / nutrients in litterfall (La Selva) or in forest-floor litter leaves (Bahia) ($kg.ha^{-1}$).

Site/Tree species	Nutrients N	Ca	Mg	K	P
a- La Selva, Costa Rica					
Stryphnodendron microstachyum	0.08	0.06	0.34	0.63	0.53
Vochysia ferruginea	0.08	0.03	0.26	0.38	0.56
Vochysia guatemalensis	0.16	0.05	0.28	0.83	1.07
Hyeronima alchorneoides	0.09	0.03	0.15	0.22	0.45
b- Porto Seguro, Bahia, Brazil					
N-fixing leguminous species:					
Bowdichia virgilioides	0.05	0.09	0.72	1.25	6.51
Centrolobium minus	0.15	0.21	1.29	0.88	8.16
Centrolobium robustum	0.22	0.28	1.94	4.37	8.74
Inga affinis	0.09	0.11	1.13	1.62	3.68
Parapiptadenia pterosperma	0.16	0.22	1.57	5.34	8.90
Pithecellobium elegans	0.02	0.08	0.36	0.90	1.81
Platymenia foliolosa	0.11	0.49	10.1	5.03	6.71
Non-N fixing leguminous species:					
Arapatiella psilophylla	0.02	0.03	0.27	0.29	0.89
Caesalpinia echinata	0.04	0.03	0.60	0.98	1.78
Cassia spp.	3.96	7.04	56.8	100.8	260.5
Copaifera luscens	0.05	0.05	0.62	0.78	1.80
Dimorphandra jorgei	0.16	0.43	3.26	7.66	16.3
Hymenaea aurea	0.03	0.04	0.26	0.39	1.00
Macrolobium latifolium	0.06	0.06	0.29	1.41	4.06
Of other families:					
Bombax macrophyllum	0.20	0.12	0.53	4.87	12.3
Buchenavia grandis	0.05	0.04	0.42	0.78	1.72
Eschweilera ovata	0.06	0.05	0.26	0.50	2.44
Lecythis pisonis	0.06	0.06	0.64	1.10	2.00
Licania hypoleuca	0.02	0.01	0.10	0.11	0.53
Pradosia lactescens	0.06	0.06	0.34	0.50	2.43

Lessons for system design and long-term management

In the design of productive forest systems, to decrease site deterioration with consecutive harvests, species choice and management should ensure the maintenance of adequate levels of ecosystem nutrients in the long term. To attain this goal, it is evident from the results shown above that species with low efficiency (high potential for recycling) for a given set of nutrients (e.g., N, Ca, Mg) should be complemented with others with low efficiencies for different nutrients (K, P). Alternative designs may involve planting different species in successive rotations. Another option is the use of tree species mixtures. Mixed-species designs can be more advantageous than tree monocultures for site nutrient rehabilitation if systems are planned so as to complement each species' nutrient demands and effects. As part of the same research program, additional studies at La Selva and Misiones involved comparisons of growth and impacts on soils of monospecific and mixed-tree plantations of indigenous species of economic value (Montagnini 1992, Montagnini et al. 1993b, Montagnini et al. this volume).

In the long term, the impacts of plantation trees on soil nutrients depend on: (1) the annual nutrient uptake by the trees in relation to the nutrient supplying capacity of the soil, (2) amounts of leaf litterfall and decomposition, (3) differential nutrient allocation in tree parts: stems, foliage, roots, and (4) the parts of the tree removed at harvest, whether the whole tree or stemwood, and their biomass and nutrient content. To help understanding these relationships, biomass nutrients were compared among tree parts for the four species of the La Selva site. For the nutrients with lowest use efficiency values (N, Ca, Mg) (Fig. 1) the forest-floor comprised a relatively high proportion of the total. Therefore for N, Ca and Mg the forest-floor appears as an important compartment for nutrient accumulation and recycling, although with marked differences among the species considered (Fig. 1). If the forest-floor is burned or collected for fuelwood, a substantial loss of organic matter and nutrients may occur, while if the litter is left on the floor after harvest, it represents a significant reservoir for the next rotation.

In contrast, for K and P, which were more scarce and showed higher use efficiency values, a higher proportion was stored in live tree biomass (Fig. 2). Although the forest-floor was still a substantial compartment, it was proportionally smaller than for N, Ca and Mg. In comparison, especially for *V. ferruginea* and *S. microstachyum*, root biomass K and P was relatively more important than forest-floor K and P (Fig. 2). Under tropical humid conditions K and P recycling from roots could be particularly important because root turnover is expected to be relatively fast. The roots are less likely to be affected during manual timber harvest operations than the forest-floor, while mechanical site operations could seriously affect the root system and its nutrient storing and recycling capacity. This can be especially critical for P and K, often mentioned as the nutrients which are most likely to be depleted from soils with subsequent rotations (Wadsworth 1982, Bruijnzeel 1991).

CONCLUSIONS AND RECOMMENDATIONS

A number of economically valuable native tree species were found to have positive impacts on soils in the three regions studied. The calculation of nutrient use efficiencies proved a useful tool for system design and management: to conserve nutrients in the long term, species with low use efficiency should be combined in time or space with others with high use efficiency. Evaluation of biomass nutrient allocation helped in drawing specific management recommendations: preserving the forest-floor was key for nutrient conservation, but for the most limiting nutrients, the roots were more important. For ecosystem rehabilitation, the examination of tree growth, soil chemistry and litter biomass and nutrients constitutes a minimum set of measurements needed for the design and long-term management of sustainable forest systems.

Fig. 1

Biomass nutrients, La Selva site
Nitrogen, Calcium and Magnesium

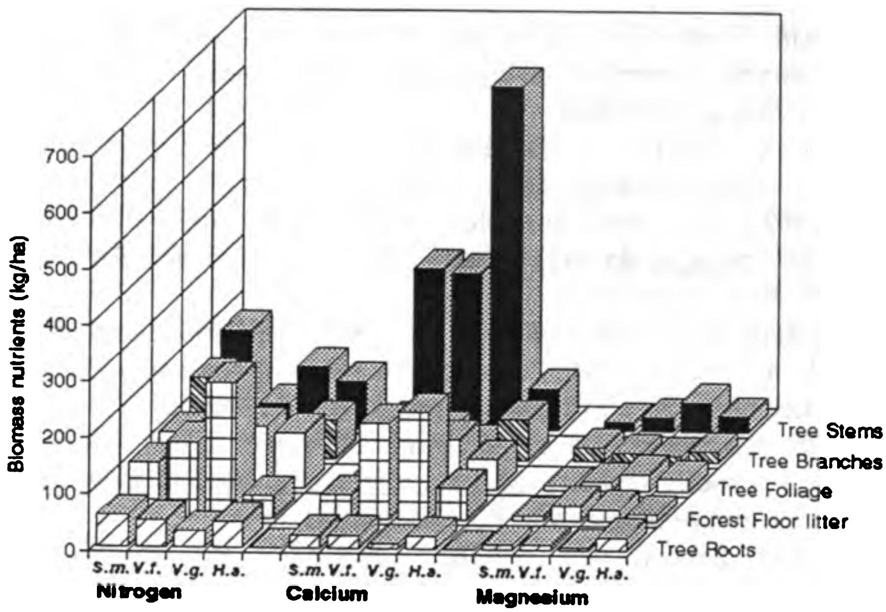
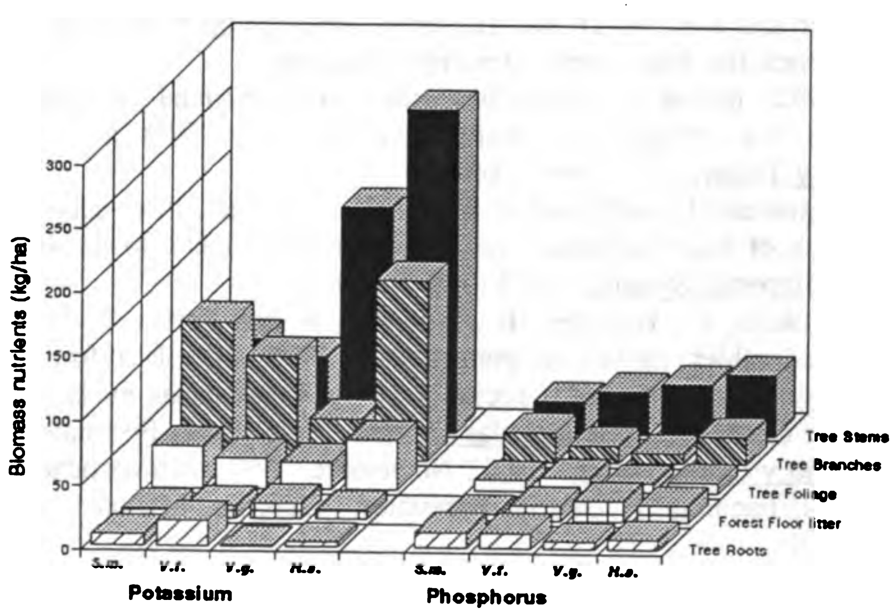


Fig. 2

Biomass nutrients, La Selva site
Potassium and Phosphorus



Note: please see Tables 2, 3 for complete names of species.

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Agricultural Systems in the La Selva Region

Florencia Montagnini

A variety of land uses representative of the Costa Rican Atlantic lowlands can be observed in the vicinity of the La Selva Biological Station, including pastures, tree plantations, home gardens, and extensive monocultures in addition to primary and secondary forests. This diversity is amenable to comparative studies of the function of agroecosystems, including evaluation of their productivity and sustainability under local conditions.

In Costa Rica the agricultural sector accounts for approximately 17.9% of the gross national product, for 28% of total employment, and for 72.3% of export income (Banco Central de Costa Rica [BCCR], Costa Rican Central Bank, 1988). The principal agricultural exports are coffee, bananas, beef, sugar, rice, and ornamentals (BCCR 1988). Costa Rica has the ecological conditions and technical capability to produce all of its own food but has not done so because of crop preferences (e.g., farmers prefer to grow coffee and other traditional crops); low yields (e.g., cacao is often imported to satisfy local demand); high costs (e.g., weed control in rice); cheaper imports (e.g., wheat, apples, grapes); and lack of incentives.

In Costa Rica most regional development programs are promoting agricultural diversification to decrease farmers' dependence on external markets, cushion against fluctuating crop yields, and increase exports. For example, when international coffee prices are low (as in 1990), farmers who have a more diverse production system (e.g., coffee with citrus) are in a better position than those who grow coffee in monocultures. Additionally, those who have planted trees may be able to sell timber at good prices during years of low crop yields. More diverse agricultural production would make the country more independent of fluctuating international prices of export products.

The Atlantic lowlands of Costa Rica include the Atlantic and Northern regions, which are administrative divisions used by the Government Office for Planning (SEPSA 1982). The Atlantic Region is a 9,756 km² area covering the eastern portion of the Atlantic lowlands, including the whole province of Limón and part of Heredia (DGEC 1987). In Heredia the Atlantic Region includes the Horquetas District up to the Sarapiquí River (fig. 23.1, chap. 23). All of La Selva except La Guaria Annex is in this region. The Northern Region includes the Sarapiquí, Puerto Viejo and La Virgen districts near La Selva and extends northwest to include the counties of San Carlos, Guatuso, and Los Chiles, and the San Isidro de Peñas Blancas and Río Cuarto districts (SEPSA 1982). In this chapter I refer to the Atlantic lowlands as a whole and emphasize the Atlantic Region near La Selva (the watershed of the Sarapiquí River and the Horquetas District in Heredia Province).

The Atlantic Region is 19.1% of the total surface of Costa Rica, but the area in farms (owned by farmers or agricultural enterprises) comprises only 9% of the country's total, which is the lowest among the country's regions. Of the total area in farms 48% is not under active cultivation and remains under forest cover; only 49.4% is in agricultural use, again the lowest value for the entire country (Flores Silva 1987). The region has until recently been so strongly dedicated to banana and cacao cultivation that other crops have received little attention. In the 1990s the region produces more than 70% of the country's total production of bananas along with 62.5% of coconuts and 20.5% of plantains but only 4% of basic grains and 5% of beef cattle. The region generates a large proportion of foreign income because bananas are grown mostly for export (Flores Silva 1987). The level of economic development in the region, however, does not reflect its significance for the country's export income. Agricultural diversification could contribute to the development of a stronger regional economy, offering options beyond employment generated by the banana companies.

In the Atlantic Region agricultural diversification has already begun to respond to the opening of new markets and to improved transportation. The paving of the road between San José and Puerto Viejo de Sarapiquí, which was completed in early 1986, significantly stimulated agriculture, forestry, and other economic activities in the region. Diversification has involved expansion of macadamia, citrus, fish culture, dwarf coconut, and other crops (Flores Silva 1987). Many of these species were chosen based on market value and presumed adaptability to the climatic conditions of the lowlands but without much previous in situ evaluation or experimentation with management practices. Most of these activities are too recent for evaluation of their economic success or ecological impact. If the region is to play a more significant role in the whole country's development, much more needs to be done to develop and implement economically productive and ecologically sustainable agricultural and forestry systems.

A number of local and international institutions such as Ministerio de Agricultura ([MAG], Ministry of Agriculture), Dirección General Forestal ([DGF] Forest Service), Junta de Administración Portuaria y de Desarrollo Económico de la Vertiente Atlántica ([JAPDEVA] Council for Harbour Administration and Economic Development of the Atlantic Lowlands), Instituto de Desarrollo Agrario ([IDA] Institute for

Agrarian Development), University of Costa Rica (UCR), Centro Agronómico Tropical de Investigación y Enseñanza ([CATIE] Tropical Agriculture Research and Training Center), Escuela Agropecuaria para la Región Tropical Húmeda ([EARTH] College of Agriculture for Humid Tropical Regions) are operating in the Atlantic lowlands. Although their objectives differ, the overall goal is to develop alternative, ecologically sound land use systems. La Selva has begun to take part in this effort, but it can have a much more significant role both in evaluating current practices and in making scientifically based recommendations for better land-use practices.

In this chapter I survey traditional and more innovative land-use systems in the La Selva region, and emphasize opportunities for improvements, summarize Organization for Tropical Studies (OTS) involvement in research on the ecological basis of sustainable and productive land-use systems, and present recommendations for future agroecological research in the region.

ECOLOGICAL CONDITIONS OF THE ATLANTIC REGION

La Selva Biological Station is in the Atlantic Region of Costa Rica at its western border with the Northern Region. Except for the northern portion of the Talamanca mountain range, a small portion of the Cordillera Central, and small, extinct volcanoes, the region lies below 100 m elevation. The average slope is 6° (11%) in the upper parts, and 1°–2° (1%–3%) in the lower areas. Because of the flat terrain, swamps and areas with poor drainage are common. The general geology consists principally of recent alluvial deposits and lahars (Madrigal and Rojas 1980). The indigenous vegetation in the region was tropical rain forest.

The Atlantic lowlands are crossed by the only rivers in Costa Rica that are navigable for any distance from the coast: the San Juan and its tributaries, the San Carlos, and the Sarapiquí. Because of the influence of the trade winds and strong convection forces, the region receives abundant precipitation, with annual means from 2,000 to 9,000 mm. In many years there is no pronounced dry season, and farmers generally need to adapt to an excess rather than to a scarcity of water. Heavy rainfall and heat made the area inhospitable to European settlers, and significant settlement occurred only in the twentieth century.

In a general soil fertility survey of Costa Rica the Sarapiquí District was diagnosed as having problems of low fertility because of low pH (<5.5), high aluminum saturation (10%–50%), low cation exchange capacity (<5 meq/100g), low calcium (<4 meq/100 g), low magnesium (<1 meq/100 g), and low extractable phosphorous (<10 μg/g) (Bertsch 1986). Levels of micronutrients and potassium were considered adequate for most agricultural crops. Nitrogen is not generally included as part of routine soil tests because levels of soil total nitrogen are not a good indicator of nitrogen availability, and nitrogen demand by crops is usually measured with fertilizer experiments. Nitrogen fertilizers are heavily used in agriculture in the Atlantic lowlands, indicating that low nitrogen may be an additional factor in the region's generally low fertility (E. Bornemisza pers. comm.). Soils of the Sarapiquí area, thus, have low fertility and potential problems with acidity and high aluminum saturation. Fifty percent of the Río Frío region has been placed in class 3 land-use capability (Tosi 1972), which corresponds to conditions of moderate to low soil fertility, strong acidity, and moderate to poor drainage. These characteristics restrict the possibilities for crop species (UCR 1984). Research on soils at La Selva is summarized in chapter four. La Selva's soils share many features with other soils of the Costa Rican Atlantic lowlands as well as with other regions of the lowland humid tropics; thus, soils research at La Selva has broad regional as well as local significance.

TRADITIONAL LAND USE IN THE ATLANTIC LOWLANDS

The present land-use pattern in the Atlantic Region is complex and is not simply related to the ecological conditions that favor each activity. Land-use patterns can be better understood by examining the history of agricultural colonization in the region as well as the socioeconomic and ecological factors influencing agricultural production. In this section I examine the traditional land uses in pre-Hispanic times and the changes resulting from colonization by Hispano-American settlers in the late-1800s to 1900s.

Pre-Columbian Period

Archaeological investigations carried out in the Atlantic lowlands reveal a cultural complex similar to that in northern South America with dietary habits and ceramics most like those of people inhabiting the coastal Caribbean plains of Colombia (Hall 1984). It is likely that a single humid tropical forest culture extended from the Amazon and Orinoco river basins along the Caribbean coast to Honduras (Snarskis 1975, 1976).

Agricultural practices in the Atlantic lowlands in pre-Columbian times apparently had a very strong South American influence: most of the crops grown in the Atlantic lowlands were native to tropical forest zones in the northern part of South America (Hall 1984). These include tuber crops, such as cassava (*Manihot esculenta*) and tiquisque (*Xanthosoma violaceum*). Cultivation of pejibaye (peach palm, *Bactris gasipaes*) spread from the Orinoco valley. Cacao (*Theobroma cacao*) was also apparently introduced from South America, and its pods were used in religious ceremonies in the Amazon and Orinoco river basins (Stone 1977). It was generally believed that corn was introduced to the region from Mexico and Guatemala. Corn with South American characteristics, dated A.D. 100–300, however, has been discovered in excavations in the Atlantic lowlands (Snarskis 1975), suggesting that the variety grown here was of South American origin. Storage of corn must have been a problem because of the very humid climate of the region. In contrast, root tubers such as cassava produce year-round and store well in the ground, from which they can be harvested as needed.

During pre-Columbian times land-use patterns allowed for the regeneration of most forests. The relatively low population density permitted long periods of forest regeneration following slash and burn agriculture (Hall 1984). It is only during the twentieth century that settlers of European descent accelerated the deforestation process.

Agricultural Colonization

Settlement of the Atlantic lowlands resulted from three principal phenomena: spontaneous migrations from other regions of the country; the establishment of banana plantations by U.S. companies; and government colonization policies such as the establishment of prison colonies in the 1950s to 1960s and the more recent settlement projects of IDA. These different sources of colonization have determined land-use and tenure systems, agricultural practices, and the market economies of the region. These historical patterns also influence the kinds of changes that are feasible as well as the mechanisms appropriate for implementing change.

The Early Settlements: Subsistence Agriculture. After three centuries of European settlements largely restricted to the Central Valley, colonists began moving out in all directions about one hundred years ago. These early settlers were few and faced isolation from the Central Valley because of rugged mountains and a nearly total lack of roads and marketing potential for their products (Sandner 1961).

During this period forest cutting by individual pioneers or small groups of settlers with machetes and axes removed the largest trees, leaving stumps and understory seedlings to dry for burning. Commercial wood exploitation was very limited because of inadequate transportation and the absence of sawmills, markets, and technologies suited for tropical forest species. Small amounts of wood were used by settlers for construction and for firewood; a few stems were sold to local industries for furniture and construction. Commercially undesirable species were burned or left to decompose (Tosi 1971, 1974). Sandner (1959) estimated that 60%–80% of the area deforested between 1860 and 1960 was initially used for shifting agriculture. Settlers could buy public lands at low prices and obtain property title once the land was under cultivation. In practice, however, many farmers settled without claiming property titles (Hall 1984).

The small subsistence farms operated very much like indigenous agriculture. After two to three years of cultivation, fields were abandoned and new areas were cleared. On subsistence farms, traditional home gardens were planted to meet household needs. These gardens grew basic foodstuffs: rice, corn, plantains, beans, "robusta" coffee (adapted to low elevations), sugar cane, and various fruits and vegetables. These small farms also had chickens, pigs, and, frequently, a few cows. Some of the products were occasionally marketed to obtain cash for other needs. With relatively low population pressure, shifting agriculture was a viable alternative for the early colonizers. In many areas of the Atlantic lowlands, however, ecological conditions were not suitable for agriculture; colonists found that yields were too low for sustained cultivation, and settlers often sold their land to speculators and moved to other areas (Lambert 1969).

The Beginnings of Extensive Cattle Ranching. Large holdings in the area were acquired in most cases through buy-outs of small settlers as described. On large properties extensive beef cattle ranching was the most feasible land use before the development of modern transportation (Sandner 1961) because live steers could be transported to markets without significant deterioration. Efforts to establish plantations in inaccessible regions such as the Sarapiquí valley often failed because of lack of railroads or paved roads for transportation of relatively fragile agricultural products to potential markets (León 1943).

The initiation of beef exports to United States markets in 1957 provided a major new economic incentive to the cattle industry in Costa Rica. Ranchers began to direct their efforts toward the colonization zones, and in one decade (1963–1973) the area in pasture in Costa Rica increased 62% (Parsons 1983). The center for ranching in Costa Rica traditionally has been Guanacaste Province because of its long dry season. With strong economic incentives after 1957 landscapes in Valle del General and Coto Brus, Turrúbares, Puriscal, Parrita, San Carlos, Sarapiquí, and Arenal became increasingly dominated by cattle pastures. The more humid areas of the Atlantic lowlands were spared from cattle encroachment, and only in the mid-1960s were cattle ranches established in this area.

In the late 1950s many farmers in the Atlantic lowlands planted rice on the flat areas of their farms. This "rice fever" lasted until the mid-1960s, when most farmers stopped growing rice because of the difficulty in controlling weeds after two to three years of cultivation. During the "rice fever" areas not suited for rice were dedicated to beef cattle. With higher beef prices in the mid-1960s ranching expanded to occupy the old rice fields.

Although these conditions promoted the establishment of ranches in the Atlantic lowlands, the region is not well-suited ecologically for extensive cattle raising, and management practices were inadequate. There were very few permanent workers on cattle ranches, and displaced farmers made up most of the labor force. Natural grasses were very unproductive, and exotic pasture species with higher yields were introduced only about fifteen years ago. As a result, productivity of cattle ranching was very low and extensive areas were degraded by inappropriate management practices and overgrazing (Parsons 1983).

Plantation Agriculture: The Beginnings of High-input Commercial Production. In the late nineteenth and early twentieth centuries, a number of plantations with similar characteristics were established in the Costa Rican Atlantic Region as well as in several other areas of the lowland humid Latin American tropics. Extensive virgin lands were then still available for agriculture, and governments exerted little control over the activities of multinational companies (Casey 1979). In the Atlantic lowlands of Costa Rica, banana plantations were started by the United Fruit Company (United Brands) in the Limón area in the late 1870s. Limón was the principal region for banana cultivation until the mid-1930s. Banana production declined after 1913 because of low prices, high incidence of fungal diseases (Sigatoka and Panama diseases caused by *Micosphaerella musicola* and *Fusarium oxysporum*, respectively), soil degradation, and labor unrest. By 1942 banana exports from Limón had ceased, and the region underwent severe economic depression. Alternative crops were planted (cacao, rubber, subsistence food crops) in the 1940s and early 1950s.

In the early 1950s considerable migration from other regions of Costa Rica to the Atlantic lowlands took place with settlers occupying new land as well as areas abandoned by

United Fruit. As the railroad system was expanded to Río Frío and Estrella, Standard Fruit Company, a subsidiary of Dole Fresh Fruit Company, installed banana plantations in 1956 in the areas near Limón previously occupied by United Fruit as well as in the Río Frío zone just east of La Selva. In the 1990s Standard Fruit expanded its operations to areas northeast of La Selva along the Río Sucio. United Fruit has moved its operations to the Pacific Coast where it grows mostly African oil palm although recently it has come back to the Atlantic Region to reinitiate banana production. In the mid-1960s the Costa Rican government gave incentives for banana production ("crédito bananero") to stimulate the establishment of plantations by local companies. By 1979 Costa Rican companies produced approximately 60% of bananas in the Atlantic Region although they still market their produce through Standard Fruit.

The banana companies established their plantations on the most fertile, well-drained riparian soils. In the early days of banana plantations (late 1800s) with intensive land use and inappropriate soil management these good soils deteriorated after seven to ten years of monoculture and had to be fallowed for about ten years before they could be put back into banana cultivation (Casey 1979). Immigrants from Jamaica and Costa Rican migrants from other regions of Costa Rica worked in the plantations. Independent banana producers also grew bananas on farms ranging from less than 10 ha to more than 20,000 ha and sold their produce to United Fruit (Casey 1979). Local farmers also had home gardens with subsistence crops, apart from bananas. Jamaican immigrants introduced Afro-Caribbean subsistence production systems, including polycultures with bread fruit, citrus, plantains, cassava, yams, and sweet potatoes for food and cacao and coconuts as cash crops. While the banana industry flourished, however, subsistence agriculture did not meet local demand for foodstuffs; most of the products for consumption by banana workers and local farmers were either imported or brought from other regions of the country (Jones and Morrison 1952). This was beneficial for the banana companies, who sold those products in their own stores.

In contrast to areas colonized by individual or group settlers, plantations were established from the start as highly specialized commercial agriculture. Standard Fruit Company grows "grand Cavendish" and "dwarf Cavendish" varieties of bananas, which are exported to the United States and Europe through Limón. Bananas are an ecologically demanding species; they require high temperature, high humidity, and abundant soil nutrients. They are a typical large-scale plantation crop because of high risk of crop failures from natural catastrophes and the high costs of site preparation, drainage, and labor administration. Banana cultivation requires intense use of agrochemicals: fertilizers are applied monthly (N, K, Mg, and micronutrients), and nematocides are applied four times per year. Fungicides and insecticides are also applied frequently. Fungicide applications are aerial; fertilizer and nematocide applications are manual. Some areas around Río Frío were abandoned by Standard Fruit because the high incidence of fungal diseases and nematode damage required such intensive application of agrochemicals that banana cultivation was no longer profitable.

In contrast to bananas, cacao has played a minor role in the development of commercial plantations in Costa Rica. In the Atlantic lowlands cacao was a major export crop in the 1940s and early 1950s (between the banana boom periods) as in the nineteenth century. With the reestablishment of the banana industry, however, cacao took a secondary position. In fact, cacao does best in areas with an extended dry season and the Atlantic lowlands are not ideal for the crop because of high annual rainfall and lack of a well-defined dry season. The strong rains and high humidity favor the spread of fungal diseases (e.g. *Monilia roreri*), delay or impede ripening of fruits, and complicate their collection and processing. The northern plains (especially Upala) are ecologically more appropriate.

In the Atlantic Region of Costa Rica cacao is mostly grown on farms managed by individuals or families with far less advanced technology than is used in bananas. In the 1990s in the Atlantic lowlands most cacao is grown on land abandoned from banana plantations or in remnants of forest. Cacao has a highly fluctuating price on the international market, and interest in its cultivation follows these price cycles. Because of high risks of crop failure and fluctuating prices, the Costa Rican Ministry of Agriculture recommends that farmers who grow cacao should diversify their production with coconuts, tuber crops (cassava, tiquisque), and spices (black pepper, ginger).

Plantation agriculture had and still has a strong socioeconomic impact in Costa Rica. As foreign companies converted land, installed drainage and transportation systems, and built ports and living facilities, they contributed to development of large areas. Until recently, however, most revenue from these enterprises left the country, yielding little benefit to the Costa Rican economy (Casey 1979). The establishment of plantations resulted in a rapid transformation of the forested landscape into fruit monocultures, but these also declined very rapidly when the banana industry was hit by fungal diseases and economic depressions. Hundreds of hectares of secondary forest developed in the areas abandoned by United Fruit in the early 1900s.

Despite past and present problems, bananas are still seen as a key crop for regional economic development owing to relatively favorable conditions in the Atlantic lowlands and the employment opportunities offered. In the 1990s the banana companies contribute much more to the local and national economy than in the past. They hire a higher proportion of local technical and administrative personnel, and the government imposes a tax on exported bananas and on company revenues (Gaceta Oficial, Government Public Document, 1978).

In the late-1950s to 1980s the construction of good roads eliminated the principal barrier to development of commercial agriculture in the Atlantic lowlands. An ongoing secondary colonization process began on land already partially deforested and populated (see chap. 23).

LAND USE IN THE ATLANTIC REGION AND FUTURE PROSPECTS

Land-use patterns in the Atlantic lowlands of Costa Rica changed over the 1980s in response to increased population, the improvement of roads, and a general trend in the country to diversify agricultural production. These changes, however, have often outstripped technical expertise and the capacity of agricultural extension agents. For example, technical problems in cacao management have restricted its expansion while enthusiasm for the cultivation of a promising ornamental, *Dracaena* spp., oversaturated the market. Thus, the transition from subsistence agriculture and extensive cattle raising to more intensive land-use systems is not complete: large areas (up to 70% of the area in farms in many districts) are still ranches. In spite of low productivity per hectare a cultural predilection for ranching sustains the practice. In many cases land is deforested and fenced, and cattle are installed just to claim the land. Additionally, lack of adequate markets and infrastructure has limited the production of food crops for local consumption (González Vega et al. 1970). In spite of better communications and more and better roads, the market structure is still not adequate to foster the production of many crops for local consumption or for export.

Land-use patterns in the Atlantic lowlands are changing continuously in response to changes in markets, agricultural technology, and economic policies. Between 1963 and 1982 the area in farms tripled, and the area in pastures increased severalfold while the forested area decreased sharply (table 24.1). Among agricultural crops, perennial crops predominate, mostly reflecting the large areas in bananas (table 24.1). I present the principal agricultural practices in the Atlantic Region, their main constraints, and potential for improvement next.

Agriculture

In the general statistics for the most commonly grown crops in the Atlantic Region presented in table 24.2 the area in cacao may be an overestimate because many plantations have been abandoned owing to fungal diseases (*Monilia*). The most frequent annual crops comprise a mix of subsistence and commercial crops (table 24.2). The data in table 24.2 are for the entire Atlantic Region, including farms of all sizes. Most farms in the region are small (table 24.3): 68% of farms are smaller than 20 ha and 19% are smaller than 4 ha. Farms less than 20 ha, however, cover only 16% of the total area. Medium (20–200 ha) and large farms (>200 ha) dominate. These areas are primarily devoted to bananas.

A different picture of crop preferences emerges if small farms are examined separately. In a survey of recently established IDA settlements (farms <20 ha) in the Río Frío region near La Selva (UCR 1984) 63% of the land owned by these farmers was under cultivation; the rest was unused principally because of inadequate economic resources (table 24.4). Of the land under cultivation 39% was planted to annual crops and 23% to perennials, and 38% was used for cattle. Small farmers grew a mix of annual and perennial subsistence crops. and more than half of these farmers combined cattle with crops. Cattle were raised for market and local consumption. Although most crops were grown in monoculture, some examples of crop combinations were cacao and cassava, corn and beans, plantains and corn, plantains and beans, and plantains with cassava and cacao.

Table 24.1 Land use in the Atlantic Region, 1963–1982

	Total Hectares Covered		
Land-use Category	1963	1973	1982
Annual crops	—	ca. 76.000	19.000
Perennial crops	39.100	44.400	78.300
Pasture	35.000	71.800	232.900
Area in farms	205.200	140.800	—
Nonagricultural land (mostly forest)	767.500	728.200	352.500

Sources: Dirección General de Estadísticas y Censos ([DGEC] National Office of Statistics and Census) 1974 and 1975: Unidad Regional de Asistencia Técnica ([IDA/RUTA] Reginal Unit for Technical Assistance) 1984 in Van Sluys et al. 1989.

Table 24.2 Principal crops in the Atlantic Region, 1973

Crops	Total Area (ha)	Farms (No.)
Perennial		
Bananas	20.698	802
Cacao	17.224	1.935
Plantains	1.551	664
Coconuts	940	781
Coffee	485	343
Annual		
Corn	5.245	1.532
Rice	753	474
Cassava	566	553
Beans	171	189
Sugarcane	146	122

Source: DGEC 1974, in Van Sluys et al. (1989).

Table 24.3 Farm size distribution in the Atlantic Region, 1984

	Distribution				
Farm Size (ha)	Number	Percentage of Total	Area (ha)	Percentage of Total	Mean Size (ha)
<4	1.754	19	3.400	1	2
4–20	4.445	49	43.000	15	10
21–200	2.577	29	125.100	44	49
>200	252	3	286.200	40	455
Total	9.028	100	286.200	100	32

Source: Preliminary results of 1984 Agricultural Census in Van Sluys et al. 1989.

Perennial Crops. *Bananas* are largely produced and exclusively marketed by foreign companies; the Costa Rican companies sell their produce through Standard Fruit. The Costa Rican Association for Banana Production (ASBANA) supports local producers with technical research and extension. As noted, bananas are not a good crop for small farmers owing to high production costs. Commercial banana plantations, however, are expanding in the region.

Plantains are grown by small farmers for home consumption, whereas the produce of midsized farms is sold to local markets, principally San José; small amounts are exported. In general, both inputs and productivity of plantains are lower than bananas. In the early-1980s plantains began to be af-

Table 24.4 Frequency of crops in the Río Frío region

Crop	Cultivated Area[a] (% of total)	Farmers[b] (% of total)
Corn	20	68
Plantains	18	38
Cacao	14	30
Beans	8	64
Cassava	7	57
Aroids	7	45
Pineapple	7	30
Rice	6	30
Bananas	5	11
Pejibaye	4	11
Coffee	2	11
Fruit crops	2	8

Source: Univerity of Costa Rica 1984.
[a]Percentage of total area cultivated by small farmers.
[b]Percentage of farmers who grow them.

fected by the Sigatoka disease, and cultivation was drastically reduced (Van Sluys et al. 1989).

Cacao was the principal crop on small and midsized farms, especially in the southern part of the Atlantic Region, until 1978 when the *Monilia roreri* fungus became a serious problem. *Monilia* attacks only the pods; it can be controlled by planting resistant hybrids, eliminating the infected fruits, and reducing shade (intense shade creates a humid microclimate that favors the spread of the fungus). These measures are costly, however, and many plantations were instead abandoned. In the 1980s, there was renewed interest in cacao cultivation and new government incentives (MIDEPLAN 1984).

Coconuts are grown for oil and fresh fruit. In the Río Frío area coconuts are grown for local consumption. Most coconut plantations are along the Caribbean coast north and south of Limón. Plantations of dwarf coconuts can be found elsewhere, but these are generally small and show low productivity (Rojas 1978).

Coffee is cultivated primarily near Volcán Turrialba and along the Siquirres-Turrialba road. Most areas of the Atlantic Region are too low in elevation for optimal productivity of coffee. In lower areas conditions are better suited for other crops such as macadamia.

Macadamia and pejibaye are new to the Atlantic Region, and both are promising. At present, they are attractive only to large-scale farmers who have access to export markets. There is, however, a small national market for pejibaye fruit and heart of palm.

Annual Crops. *Corn* is a subsistence crop grown by small farmers throughout the Atlantic Region. On midsized farms, especially near Guácimo and Cariari, it is an important crop. The produce is sold to Consejo Nacional de Producción, ([CNP] National Production Council) at subsidized prices. Corn is not very profitable, apparently because of the high costs of chemical weeding, insect control, tillage, harvesting, and transportation.

Rice is grown as a commercial crop on midsized farms, especially in the areas around Batáan-Matina (NNW of Limón). Its production is highly mechanized and costly as a result.

Cassava is grown by small farmers for subsistence and on midsized farms for the export market, especially to the United States.

Most Promising Crops for Agricultural Expansion. Among the more innovative crops the cultivation of aroids with edible tubers, including white tiquisque (*Xanthosoma sagitifolium*), red tiquisque (*X. violaceum*), and malanga (*Colocasia esculenta*) is very promising for export (especially to the United States where demand for them is increasing among the growing Hispano-American population). These crops are well adapted to the region, but they are highly susceptible to viral diseases. Because crops are propagated vegetatively, viral diseases are easily spread when new plantings are established. Investigators at the University of Costa Rica (UCR) are working to produce virus-resistant strains.

Ornamentals, principally foliage, ferns, itabo (*Yucca elephantipes*), and others are grown mainly for export to the United States; their cultivation is expanding after the opening of additional export markets (Japan, Europe). Ornamentals require intensive management and are, thus, an important source of employment.

At the UCR experimental farm in Río Frío, the adzuko bean (*Vigna angularis*) is under study; it has edible seeds and good yields, can be grown year-round and is disease tolerant. The lack of acceptance by consumers accustomed to black beans may limit its expansion.

Peach palm (pejibaye, *Bactris gasipaes*) cultivation for heart of palm was begun by Industrias de Desarrollo Agropecuario ([INDACO] Institute of Agricultural Development) for local industry and for export. This company at present absorbs most of the local crop. The species is well suited to the Atlantic Region and maybe an interesting alternative for cash income as the market expands.

Among fruit trees, citrus appears most promising. Cultivation of oranges for export to the United States is expanding, and a juice-processing plant (for oranges, pineapple, and other fruits) will soon be operating in the Sarapiquí area, built by Tico-Fruiti, a private company with Florida producers as partners.

The cultivation of bamboo (*Bambusa guadua*) for home construction and furniture is being promoted in the Atlantic Region through a project recently begun with financing from the Dutch government and the United Nations Development Program and technical assistance from IDA, DGF, and MAG.

Other crops that have been introduced or improved by UCR are fruit trees such as mamón chino (*Litchi chinensis*), carambola (*Averrhoa carambola*), water apple (*Eugenia malaccensis*), messina lemon (*Citrus aurantifolia*), and grapefruit (*Citrus grandis*). These should be well suited to the region, and they merit exploration. Examples of other innovative crops include chilis (*Capsicum* spp.), passion fruit (*Passiflora* spp.), papaya (*Carica papaya*), cardamom (*Elletaria cardamomo*), achiote (*Bixa orellana*), and medicinal plants mainly for the Costa Rican market for herb teas.

Ecological Constraints on Agricultural Production. Agricultural production in the Atlantic Region has a low yield/

cost ratio owing to problems with weed control, pests and diseases, soil drainage and fertility, and labor administration. The ecological problems are aggravated by the high costs of agricultural inputs, lack of credit, and high interest rates (Van Sluys et al. 1989).

Although the climate is relatively uniform, occasional dry periods or excessive rains may impede growth or ripening of crops. In some years, as in 1985, hurricanes may considerably damage bananas (Van Sluys et al. 1989). Drainage problems occur in large areas, limiting crop choices, increasing costs, and interfering with management practices.

Weeds are a major problem for annual crops; as mentioned, high costs of weed control in rice ended the "rice fever" in the Sarapiquí valley in the mid-1960s. Weed control is labor intensive and involves the use of toxic and expensive herbicides that may contaminate soil. Pests and diseases cause considerable losses (e.g., rotting of corn and cacao) and may increase production costs (e.g., *Monilia* control in cacao). Problems may be serious enough to discourage the cultivation of certain crops as was the case with Panama disease in bananas and *Monilia* in cacao. A few management recommendations exist to solve pest and disease problems, including selection of more favorable areas (drier areas for plantains), manipulating the microclimate (reducing shade in cacao plantations), and timing production (planting corn so that it ripens during a relatively dry period).

Management problems are related to soil characteristics (e.g., bad drainage, steep slopes) and climate (e.g., excessive rains). Problems of low soil fertility will probably increase with increasing pressure on the land and lack of appropriate practices to maintain soil fertility (Van Sluys et al. 1989).

Infrastructure and Institutional Constraints. Constraints include financing, access to agricultural inputs, availability and transfer of agricultural technology, and physical access to markets (Van Sluys et al. 1989). Many small farmers have little access to credit. Land titles are needed to obtain credit, and interest rates are high. The establishment of perennial crops, in particular, requires high initial investments and many years of interest payments before any benefits accrue. Labor costs are generally high because the large banana companies in the region pay relatively good salaries. Many farmers need to work outside the farm to supplement their incomes (Van Sluys et al. 1989).

Both farmers and government employees in charge of agricultural extension point to a lack of technical information on agricultural crops. Most of the available information comes from outside the region, which means that local experience with many crops is very limited. The foreign banana companies have developed their own technology, but they are not willing to share it with local producers. Even when local technology exists, its transfer is often inadequate. For example, as mentioned, the technology to control *Monilia* disease in cacao consists of planting resistant hybrids, pruning trees, reducing shade, and eliminating infected pods. Many farmers have heard about these techniques, a few know how to apply them, but the majority are not using these recommendations. Apparently, both research and extension are not effectively reaching farmers (Van Sluys et al. 1989).

Access to good markets is another constraint to agricultural production. For some products, such as corn and rice, CNP guarantees the purchasing price, but it is not certain how long this policy can be sustained by the government. For other products (e.g., plantains) there is a free market. The market for export crops, such as bananas, roots and tubers, ornamentals, and macadamia, is controlled by foreign companies, which generally have foreign headquarters. Small farmers, then, have access to these markets only through foreign companies, if at all.

Farmers need to improve this situation and have the potential to do so, but few farmers have access to capital, inputs, technology, and markets. The potential of alternative crops such as ornamentals, cardamom, macadamia, and pejibaye will not be realized as long as these constraints remain.

Livestock

Of the large increases in pasture areas in the Atlantic Region since the 1970s (table 24.1) only a small portion is used for intensive milk production. Most is used for extensive beef production with productivity values per hectare lower than many crops. The principal farming systems that include cattle are

Farms with dual purpose cattle (meat and milk) producing milk for consumption on the farm. Most such farms are small and also grow annual subsistence crops (corn, beans), as well as some perennial crops (cacao, plantains). Some may also have pigs and poultry. Sometimes part of the family's income is from sources outside the farm. Generally, productivity is very low; lack of cash and credit are the principal constraints to improvement.

Farms with dual purpose cattle producing milk for market. Dairy products are marketed locally and can generate a regular income that can be invested in improved pastures and stock and mineral supplements for cows. The most common races of cattle are Brahman, Indo-Brasil, Holstein-Frisian, and Jersey.

Specialized dairy farms. Generally, these are larger farms (up to 100 ha), with modern dairies and substantial investment in pastures, feed supplements, and veterinary care for cows. Products are generally sold commercially through large dairy companies (Borden, Dos Pinos).

Beef cattle ranches. These ranches either raise calves for sale to other ranches at about 150 kg, or eight months, or buy calves at this age and raise them to 500 kg (2–2.5 more years). Both operations occasionally take place on the same farm. Ranching at this scale requires improved pastures on fertile, well-drained soils. Such ranches often occupy recently cleared land in areas where land is still cheap.

Farms with pigs. A few specialized farms raise pigs, using banana residues and waste from dairy farms as feed.

Among the IDA farmers of Río Frío raising dairy cows for milk and cheese production generally occupies more than one-third of the area in farms, both at the subsistence level (fewer than four cows) and at the commercial level. Dairy farming has increased because many farmers in the IDA settlements came from the San Carlos valley (Northern Region in the Atlantic lowlands) and are familiar with this activity.

Dairy farming is seen as a promising activity in spite of its requirements: technological knowledge, high investments, and reliable markets (UCR 1984). CATIE and IDA promoted dairy farming in the region through credits, technical advice, and marketing facilities offered by the CATIE Dairy Farming Program in the 1970s to early 1980s; CATIE has ceased these activities.

Despite institutional efforts to promote technological improvements in dairy farming innovations are still not widespread among farmers. Mostly native grasses are used in pastures although they support only low production. Introduced grasses, such as *Cynodon nlemfuensis*, *Brachiaria decumbens*, and *Pennisetum purpureum*, are considered by UCR researchers to be most promising in yield and nutritional value for dairy cattle in the region.

In contrast to dairy cattle farming beef production is an extensive and almost exclusively commercial activity. Most beef cattle in the region are range fed, but even the more productive exotic pasture grass species are low in protein and fiber (Parsons 1983). Because of this dependence on pastures, most ranches are large and the mean stocking rate is only one animal per hectare. As a result, ranching generates few employment opportunities and promotes migration to cities. The ecological impacts of expansion of beef cattle ranching have been incalculable, including serious problems of soil deterioration (Parsons 1976). Excessive grazing may result in soil compaction, which exacerbates drainage problems and leads to soil erosion on steep slopes. With poor management productivity is low and after a few years new areas are cleared and put into pasture. Forest regeneration on abandoned pastures is often slow because of soil deterioration and distance from seed sources in large cleared areas.

Livestock Management Problems. The principal technical problems of dairy and beef cattle raising are high production costs that are not compensated by high prices, dependence on grasses of low productivity and quality, little integration with agriculture (e.g., crop residues and manure are underused as feed and fertilizer, respectively), and high incidence of cattle diseases, which are often related to the hot, humid climate and muddy pastures (Van Sluys et al. 1989).

Institutional Problems with Cattle Production. The problems encountered in livestock production mirror those encountered in agriculture (Van Sluys et al. 1989). Extension and veterinary services are few and, therefore, ranchers find little useful advice. Ranchers have little control of market institutions, which have been poorly organized (e.g., until recently, beef cattle were sold in Alajuela, and small farmers generally had to sell to middlemen). Large producers depend on the international market and confront fluctuating prices for their products. Whether selling to middlemen or directly to dairy companies, farmers must organize transportation themselves. There is little opportunity to expand the national market for dairy products because most such products are too expensive for the majority of the population to buy.

Dairy and beef cattle ranches can be most feasibly improved by intensifying management rather than by expanding onto marginal lands. Key strategies are improving pastures by planting more productive fodder species, using rotational grazing practices to avoid overgrazing and decrease risks of soil compaction and nutrient depletion, and adopting agrosilvopastoral systems that include fodder trees in pastures and in living fences. CATIE's livestock project is experimenting with these techniques near Guápiles and at the Los Diamantes Experiment Station. These more intensive practices can now be seen on a few farms in the vicinity of La Selva. If these practices are financially feasible (i.e., if increased productivity pays for the additional costs of intensive management), they may represent viable alternatives for management of ranches in the region.

FUTURE DIRECTIONS IN AGROECOSYSTEM RESEARCH IN THE ATLANTIC REGION

Apparently, there is still no clear consensus as to the most profitable agricultural activities in the Atlantic Region. Agriculture is developing quickly and in different directions depending on the initiatives of individual land owners, investors in commercial agriculture and forestry, and the national and foreign institutions dedicated to research, education, and development. Many production systems are economically and ecologically sound (e.g., cultivation of pejibaye, use of living fences in farms, intensive dairy farming). Other systems have problems but are still practiced because they are traditional in the region (e.g., cacao and rice production, extensive cattle raising). In many cases the availability of capital is the principal factor influencing the choice of a system (e.g., bananas, macadamia, and large-scale production of ornamentals require considerable capital investment). Farmers are experimenting with production systems according to their own interests (e.g., with techniques for growing macadamia). National and international institutions (MAG, UCR, CATIE) are investigating and promoting production systems for specific sectors (generally, the small farmers of the region).

Any organized effort to promote sound agricultural development should start by dividing the region into subregions of relatively homogeneous ecological and socioeconomic conditions (e.g., Horquetas, Río Frío, Guápiles, the Caribbean coast south or north of Limón). Within these subregions the sectors to which efforts are directed need to be clearly defined (small-, medium-, or large-scale farmers). Land-use capability must be assessed for each subregion, considering slope, soils, and other production factors to determine appropriate land uses (intensive agriculture, cattle, forestry, or agroforestry). Finally, research and extension should begin by examining existing ecologically and economically sound practices and should concentrate on improving them and on designing and promoting new systems if needed.

Agricultural diversification should supply farmers' needs for subsistence crops and cash by promoting cultivation of home gardens and of cash crops for local markets and for export. Agricultural research should focus on crops that are (or are expected to be) most profitable or those that contribute strongly to subsistence nutrition. In a small country such as Costa Rica it is possible to saturate markets quickly, with negative results for otherwise very promising crops such as passion fruit and chilis. Research should be concentrated on crops that are accepted by farmers, such as pejibaye and corn; those that are ecologically appropriate (macadamia, cardamom, pejibaye); those with excellent market potential even though they may have some technical problems (rice, plantains); and the traditional subsistence crops (cassava, beans, bread fruit, tiquisque, fruit trees, among many).

Agricultural diversification at both farmer and regional levels can also be attained by using agroforestry practices, ideally, combining subsistence crops with more marketable or export species. Agroforestry systems may successfully combine timber trees with cacao, rubber, coconuts, and ornamentals. Many annual crops, however, are shade intolerant and, thus, are not suited for agroforestry. Trees and crops may be profitably combined in the early stages of tree plantations (first to second year, depending on the species and planting distance) when trees do not provide much shade. Agroforestry practices should decrease the need for weeding, and trees may have positive effects on soil properties (Montagnini 1990a). Many areas in the region should be better suited for trees than for conventional or mechanized agriculture because of steep slopes, low fertility, and problems with soil compaction. On individual farms land that is not suited for agriculture can be used to grow trees in association with crops. Besides, many agroforestry practices require less labor than intensive agriculture and allow for more flexibility in management and timing of harvest (Kapp 1989). The following agroforestry systems already are present in the Atlantic Region (Kapp 1989):

- Cacao, coffee, and other perennial crops with native trees for shade, many of which are valuable timber species (for a complete list see Kapp 1989)
- Pastures with native trees (same as those with perennial crops)
- Annual crops with native trees
- Crops or pastures in alternating rotation with tree fallows
- Living fences (*Gliricidia sepium*, *Diphysa robinioides*, *Bursera simaruba*, and others)
- Mixed home gardens with food crops and many fruit and timber trees

Opportunities to improve these systems include

- The promotion of better spatial designs (e.g., planting in lines rather than haphazardly to facilitate management practices)
- Selection of tree species more appropriate for combinations with crops (eucalypts and pines, very much used in the region, are not well suited for combinations with crops; *Gmelina*, also common in the region, and many native trees are better)
- Choice of shade-tolerant crop or pasture species (cassava and other root crops are more shade-tolerant than corn or rice, among forage species legumes are more shade tolerant than grasses)
- Developing detailed management schemes (e.g., timing pruning and thinning to provide more light and increase inputs in the form of residues from pruning to the soil when crops can most use these resources).

To design improved systems that will be accepted by farmers the socioeconomic and institutional constraints described in the previous sections must also be considered.

OTS INVOLVEMENT IN EDUCATION AND RESEARCH ON SUSTAINABLE LAND-USE SYSTEMS IN THE ATLANTIC LOWLANDS

The involvement of OTS in agricultural research is a very recent phenomenon that began with small projects by participants in OTS agricultural ecology courses inaugurated in 1985. OTS offered its first agroecology course in Spanish in 1988, an outstanding promotion of agroecology education in Latin America. Research by course participants consists of projects completed in a few days although some students return for longer-term research. Topics examined are varied: herbivory, soil chemistry and microbiology, mycorrhizae, nitrogen fixation, crop ecophysiology, general surveys of socioeconomic aspects of land-use patterns, crop preferences, and land-use alternatives. Course projects also orient theses and other long-term projects. Most importantly, agroecologically oriented courses can influence the philosophy of those already involved in agricultural or forestry research, education, or practice toward greater concern for environmental issues and a more integrative, holistic approach to agriculture and forestry.

Increased interaction between OTS and Costa Rican institutions involved in agricultural and forestry research, training, and extension is desirable. Students in course projects can take advantage of data and recommendations resulting from local agricultural and forestry projects, and, in turn, provide data and innovative ideas toward solving specific problems. OTS research fellowships for students are making a good contribution by funding projects by Latin American scientists at La Selva. OTS might additionally strengthen ties between foreign researchers and local scientists by helping to identify local faculty to serve as advisers to foreign students working on applied problems at La Selva. Through its connections with its Costa Rican member institutions OTS can also facilitate collaborative research involving local and foreign scientists. Especially when one works on applied research, local expertise is valuable to ensure that the project is well-grounded in social, political, and institutional realities.

Other educational efforts can be implemented through OTS's Environmental Education Program. Initially focused on ecology and conservation, this program has recently expanded into agroecology and forestry through interaction with forestry projects at La Selva.

RECOMMENDATIONS FOR AGROECOLOGICAL RESEARCH AT LA SELVA

As noted, La Selva has soils that are representative of the Atlantic Region of Costa Rica as well as of many lowland areas in tropical America. Thus, research on soil fertility, soil/plant interactions, soil chemistry, and microbiology have potential for wide applicability. Research on management of traditional and more innovative agroecosystems could be applicable to other areas in Latin America as evidenced by the similarity of traditional cropping systems across broad areas of the lowland wet tropics.

Agroecological research at La Selva should focus on the most promising land-use systems for the economic benefit of farmers and the country, including subsistence crops. Existing forestry plots at La Selva can be used by OTS researchers and students in collaboration with the principal investigators of the projects to study management techniques, impact of trees on soils, and agroforestry uses of the species planted.

Buffer zones for protected areas offer interesting opportunities for agroecological research at La Selva, both on station property (La Guaria Annex, El Peje, La Flaminea) and elsewhere in the Atlantic lowlands (e.g., via participation in the recently funded Forest Resources for a Stable Environment Project [FORESTA]. This type of research fits well with OTS goals and is also becoming an important aspect of tropical ecological research as new areas are protected and surrounding lands need to be managed in ways that foster protection of the core. Agroforestry, management of secondary forests, and development of ecologically sound land-use systems are a frequent component of management plans for buffer zones in areas of tropical rain forest.

Whenever possible, research should be conducted in collaboration with local institutions (MAG, DGF, UCR, CATIE). Much research is currently undertaken by local institutions to design innovative land-use systems. For example, F. Bertsch and V. Vega (UCR) are conducting soil fertility research at the UCR experimental farm in Río Frío as part of a network of studies in the lowland humid tropics coordinated by North Carolina State University (Bertsch and Vega 1990). The experiment, which is in its early stages, consists of continuous cropping of a rice (*Oryza sativa*)-cowpea (*Vigna unguiculata*)-mucuna (*Styzolobium* spp., a legume fallow) sequence. Researchers from Wageningen Agricultural University (Holland) have been working at CATIE since 1986 in collaboration with MAG's "Atlantic Zone Programme" (Atlantic Zone Programme 1987). The objectives are to contribute to sustainable development in the Atlantic zone of Central America and Panama through research and training activities. Research focuses on production systems and on regional land-use planning. Other projects at CATIE could be of interest to La Selva researchers (Nitrogen-fixing Tree Project, agroforestry, wildlands management, and others). OTS researchers and course participants could take advantage of such experiments and projects to visit, exchange ideas, and, potentially, to initiate collaborative research.

Likewise, researchers involved in agroecological work at La Selva should be aware of the efforts of local institutions in the same discipline and encouraged to interact actively with their colleagues by sharing results and by collaborating on mutual projects whenever appropriate. This sort of interaction could be encouraged by organizing joint activities, such as workshops, seminars, and field trips. La Selva already facilitates local research by providing cheaper station fees for Costa Ricans. The opportunities at La Selva could be better publicized in local universities and other institutions by more frequent communication and by organizing seminars by La Selva researchers on subjects of common interest. Local researchers could supply background data and help to define priorities and goals. This type of interaction will magnify the contribution by OTS students and researchers at local and national levels.

Biologists in many projects at La Selva already interact with local researchers and employ local technicians and students, and more direct involvement of local scientists and collaborators is a highly desired next step. For example, data from local institutions that are concerned with development and with socioeconomic aspects of agriculture and forestry should be useful for defining goals and subjects of study for La Selva researchers. OTS can play a more significant role in its host country by building upon its educational and research programs and, especially, by capitalizing upon its pivotal position to improve linkages between U.S. and Latin American scientists and the general public.

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LA SELVA

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NUTRIENTES EN PLANTACIONES JOVENES CON ARBOLES NATIVOS (2a. Parte)

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METODOS

Los procedimientos de muestreo y métodos químicos están descritos en Montagnini y Sancho (1990a y 1990b) y en Montagnini et al. (1991). Los suelos se muestrearon bajo las cuatro especies arbóreas mencionadas, en área de pastos libre de árboles y en bosque secundario de veinte años.

La biomasa de los árboles y el contenido de nutrientes en tallos, ramas y hojas fueron medidos al momento del raleo de las parcelas, cuando la plantación tenia cuatro años.

También se midió la biomasa y la concentración de nutrientes del sotobosque. El reciclaje de nutrientes fue calculado multiplicando la biomasa de cada compartimento por la concentración de nutrientes en el mismo (nitrógeno, calcio, magnesio, potasio, fósforo).

RESULTADOS Y DISCUSION

Biomasa arbórea

Los valores de la biomasa de árboles enteros presentados aquí (Tabla 1), son mayores que los reportados para Albizia lebbek de 4 años (Parrota, 1989) y para Leucaena leucocephala de 5 años y medio (Wang et al. 1991), ambos creciendo en plantaciones densas para la producción de biomasa en Puerto Rico.

Los valores de productividad (biomasa arbórea dividida por la edad del árbol) concuerdan con otros valores presentados en la literatura para plantaciones monoespecíficas en los trópicon húmedos. El valor para V.hondurensises similar al valor reportado para Gmelina arborea (12,8 toneladas/ha/año) en la región amazónica del Brasil (Russell, 1987) así como también al valor para Gmelina arborea (12,7 toneladas/ha) y para Albizia falcataria, ambos en las Filipinas (11,3) (Kawahara et al., 1981, en Young, 1989).

Sin embargo, los incrementos presentados aquí son menores que aquellos reportados para algunas especies de crecimiento rápido, tales como Acacia mangium (de 15,5 a 18,0 toneladas/ha en Malasia) y Leucaena leucocephala (20,0 a 30,0 y hasta 80,0 toneladas /ha en Hawaii y en otros sitios tropicales, Young, 1989).

Los incrementos anuales en madera para especies latifoliadas en los trópicos varia entre 1 y 28 toneladas/ha/año. Las especies de crecimiento rápido como Gmelina arborea y E, saligna varían entre 10 y 20 y entre 8 y 28 toneladas/ha respectivamente, y las especies de crecimiento relativamente más lento como Swietenia sp. y Tectona grandis varían entre 1 y 4 y entre 3 y 12 toneladas/ha respectivamente (Wadsworth, 1983).

Otros valores para árboles de crecimiento rápido en regiones tropicales húmedas incluyen varias especies de Eucalytus cultivadas en las Américas y en el Asia (entre 7,2 y 11,9 toneladas/ha); Gmelina arborea en Costa Rica (11,8 toneladas/ha) (Lugo et al., 1988); de 1,3 a 5,3 Leucaena leucephala en sitios premontanos y en tierras bajas húmedas (entre 2,8 y 15,9 toneladas/ha); Prosopis juliflora, en sitios húmedos de India (9,4 toneladas/ha), y Populus deltoides, en sitios subtropicales de India (6,4 toneladas/ha) (Lugo et al., 1990).

Anual medio	Biomasa aérea viva						Crecimiento	
	Dap (cm)	Altura (m)	Fuste	Ramas (Kg/ha)	Hojas (kg/ha)	Total	Total (t/ha/año)	Fuste (t/ha/año)
S. exc.	12.0a	8.9b	35250a	15250a	4325a	54825	13.7	8.8
V. fer.	10.3a	8.1b	24750b	14250a	5925a	44925	11.2	6.2
V. hon.	10.8a	12.0a	41750a	6500b	7250a	55500	13.9	10.4
H. alc.	10.8a	9.0a	26250b	12250a	5350a	43850	12.0	6.5

Tabla 1. Promedio de diámetros a la altura del pecho (dap), altura, biomasa aérea y crecimiento anual
Nota: En ésta y las siguientes tablas, las diferencias entre sitios para un parámetro dedo son estadísticamente significativas cuando los promedios son seguidos por letras diferentes

De modo que el promedio anual de los incrementos en este estudio cae dentro de los valores reportados para otras especies arbóreas de crecimiento rápido en los trópicos húmedos.

Acumulación de nutrientes en la biomasa arbórea

Nitrogeno

Las mayores concentraciones de nitrógeno en tallos, en ramas y biomasa arbórea se encontraron en S.excelsum.

Aproximadamente 200 kg/ha, o 60% del nitrógeno de la biomasa arbórea de S. excelsum (Fig. 1) permanecería en el sitio al momento de la cosecha si se dejaran las ramas y hojas en el suelo. V.hondurensis tenía una proporción similar de nitrógeno en su porción de hojas y ramas; al igual que en S.excelsum más del 50% del nitrógeno de la biomasa arbórea podría ser reciclado si se dejan los restos en el sitio al momento de la cosecha.

V. ferruginea, con una biomasa de tallos relativamente menor, proporcionalmente tenía más nitrógeno en hojas (52,9%) y en ramas (42,1%), mientras que H.alchorneoides tenía una distribución más pareja en la biomasa arbórea (Fig.1)

Calcio

V. hondurensis, con una mayor biomasa de tronco y una concentración elevada de calcio (Ca), también tenía la mayor cantidad de calcio en la madera (más de 600 kg/ha, equivalente a 84% del Ca de la biomasa arbórea), aproximadamente el doble de la cantidad de S.excelsum y de V. ferruginea, y varias veces más que H.alchorneoides (Figura 2).

En consecuencia, la cosecha total de árboles de V. hondurensis podría reducir considerablemente la cantidad de calcio en el sitio. Sin embargo, mientras los árboles de V. hondurensis estén vivos, cantidades relativamente grandes de clacio podrían ser recicladas porque, aunque sólo represente el 16% de la biomasa de la parte aérea, la cantidad conjunta de calcio en las hojas y las ramas sobrepasaba 100 kg/ha.

La proporción de calcio en el tronco en relación a la biomasa total fué similar para S. excelsum y para V. ferruginea (76,6% y 70,8% respectivamente) (Figura 2), pero las cantidades absolutas fueron menores que la mitad de la cantidad de V.hondurensis.

H.alchorneoides otra vez tuvo una mejor distribución de calcio en los tallos, las hojas y las ramas.

Magnesio

V.hondurensis, con su alta biomasa de tronco y alta concentración de magnesio (Mg), también tuvo la mayor cantidad de Mg en la madera (55% del total del Mg contenido en la biomasa arbórea, aproximadamente 30 kg/ha) (Figura 3).

En consecuencia, si se retiran los troncos de V.hondurensis se afectaría el reciclaje de Mg en el sitio de una manera más dramática que cualquiera de las otras especies, especialmente si se realiza una cosecha total (Figura 3).

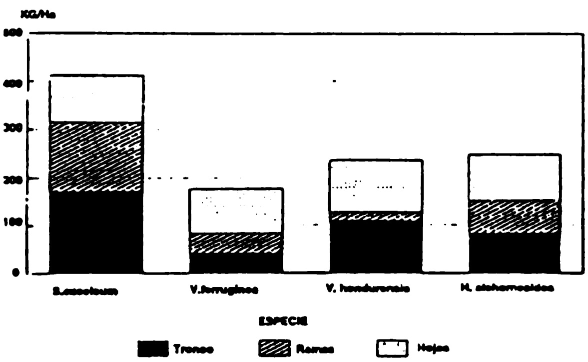

Fig. 1 - Nitrógeno en la biomasa arbórea

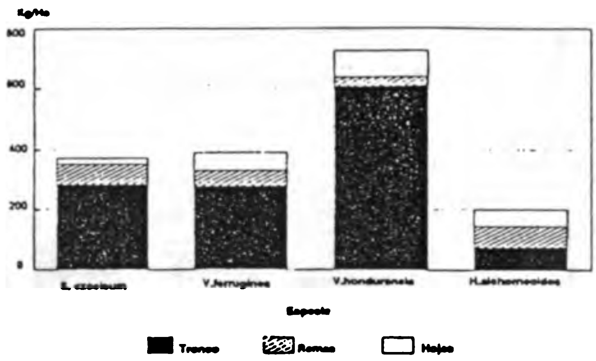

Fig. 2 - Calcio en la biomasa arbórea

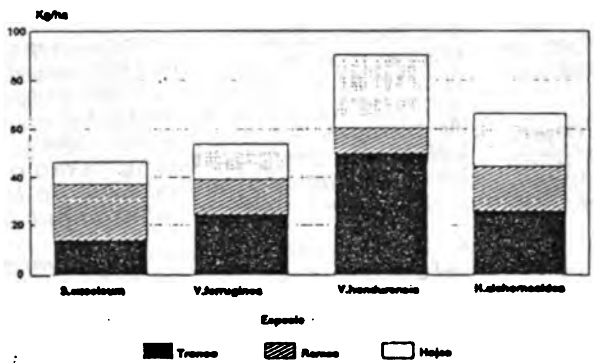

Fig. 3 - Magnesio en la biomasa arbórea

Potasio

El panorama cambia con el potasio (K): la mayor acumulación de K. en tallos fué hallado en H. alchomeoides (252 kg/ha, Figura 4), representando 58,7% del K arbóreo. Esta cantidad fue seguida por V.hondurensis con 175 kg/ha, la cual representa 76,8% del K arbóreo. En consecuencia, la cosecha total de árboles de H.alchorneoides y de V. hondurensis podría tener los mayores efectos en el reciclaje de K.

S. excelsum y V. ferruginea tenían 33,6% y 35,4% respectivamente, de K en los tallos.

El reciclje de K en las hojas y las ramas podría ser relativamente más importante cuando se considera estas últimas dos especies.

Fosforo

V.hondurensis y H.alchorneoides tuvieron las mayores proporciones de fósforo (P) en la madera (72,4% y 62,1% respectivamente) (Figura 5).

S. excelsum y V. ferruginea tuvieron relativamente menores cantidades de P en los tallos (43,9% y 48,7% respectivamente).

Nuestros resultados confirman reportes anteriores sobre los efectos negativos de la cosecha total de árboles sobre las reservas de nutrientes del sitio: por ejemplo, Bruijnzel y Wierzum (1985) estudiaron las entradas/salidas de nutrientes en plantaciones de Agathis dammara en las tierras altas de Java.

Sus resultados, calculados para una rotación de 30 años, indicaron que la cosecha total de los árboles eliminaría una cantidad de nutrientes equivalente a las entradas de potasio y calcio, casi la mitad de la entrada de magnesio, y el doble de la entrada de fósforo.

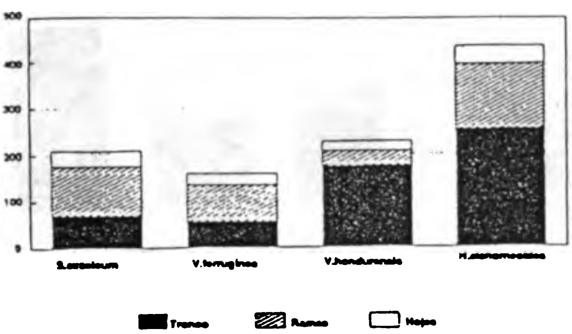

Fig. 4 - Potasio en la biomasa arbórea

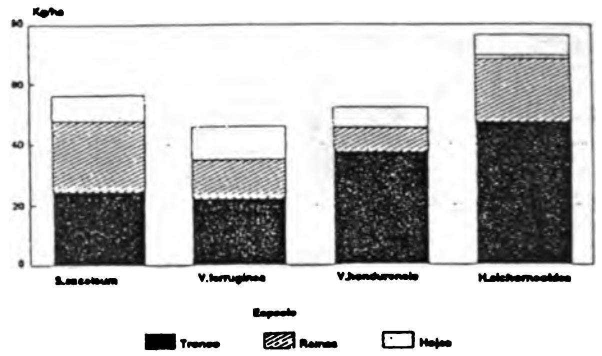

Fig. 5 - Fósforo en la biomasa arbórea

Los autores concluyeron que para evitar la escasez de nutrientes, especialmente de fósforo, la cosecha total de árboles no debería ser practicada.

Nuestros resultados también sugieren que dejando los restos de ramas y hojas en el sitio podrían disminuir considerablemente los impactos negativos de la cosecha, con diferentes consecuencias según las especies.

Impacto de los árboles sobre los nutrientes del suelo

Los mayores niveles de materia orgánica y de N en el suelo se encontraron en la plantación arbórea, con cantidades aproximadas a los del bosque secundario (Tabla 2), aunque estas diferencias no son estadísticamente significativas (P 0,05). El contenido de P fue mayor en el área de pasto que en la plantación o que en el bosque (Tabla 2).

Dentro de la plantación arbórea, no hubo diferencias significativas en el contenido de cationes entre las especies. Sin embargo, sí hubo una tendencia a niveles más altos de Ca bajo S.excelsum y niveles menores bajo H. alchorneoides.

Los mayores niveles de Mg fueron registrados bajo las dos especies de Vochysia, con contenidos menores en H. alchorneoides(Tabla 2).

Estos resultados confirman datos de mediciones anteriores realizados en 1988 (Montagnini y Sancho, 1990a, 1990b).

Mediciones similares tomadas en mayo de 1990 y nuevamente en mayo de 1991, revelaron tendencias en la acumulación de nutrientes en el suelo similares a aquellas encontradas en 1988 y 1989. Al examinar los datos entre 1988 y 1991, no se detectaron tendencias de aumento o reducción a través del tiempo para ninguno de los nutrientes (Montagnini y Sancho, datos no publicados).

Aparentemente, el aumento del nivel de nutrientes del sitio fue observado en 1988, cuando los árboles tenían dos años y medio y habían cerrado el dosel, pero después de este efecto inicial no se pudo detectar ningún otro cambio positivo.

Los impactos de la plantación de especies arbóreas sobre las reservas de nutrientes del suelo dependerán de la absorción de nutrientes por los árboles en relación a la capacidad del suelo para suplir nutrientes, del reciclaje de nutrientes (mientras los árboles estén vivos), y de las partes cosechadas del árbol, ya sea el árbol entero o la madera, y su biomasa y contenido de nutrientes al momento de la cosecha.

Esto se puede ilustrar tomando como ejemplo estas relaciones para V. hondurensis, la especie de crecimiento más rápido y aparentemente de mayores requerimientos nutricionales en este estudio.

La retención de nutrientes por V. hondurensis (calculado dividiendo el total de nutrientes en la biomasa por la edad de la plantación) fué un promedio

Sitio	Prof. (cm)	MO (%)	N (%)	P (mg/kg)	pH	Ca	Mg (cmol/kg)	K
S. exc.	0-15 15-30 30-60	4.50a 3.29a 1.88a	0.278a 0.224a 0.196a	2.4a 2.1a 1.8b	5.1a 5.1ab 5.1a	0.68b 0.52bc 0.54a	0.44a 0.22bc 0.16a	0.13a 0.14a 0.14a
V. fer.	0-15 15-30 30-60	5.06a 3.66a 2.94a	0.320a 0.248a 0.200a	3.24a 5.03c 2.50b	4.98a 5.03c 5.07a	0.63bc 0.35d 0.33a	0.53bc 0.20c 0.16a	0.16a 0.10a 0.15a
H. hon.	0-15 15-30 30-60	4.30a 3.16a 2.42a	0.304a 0.232a 0.202a	2.30a 1.82a 2.00b	5.20a 5.08ab 5.13a	0.47bc 0.38cd 0.36a	0.50bc 0.22bc 0.15a	0.10a 0.07a 0.06a
H. alc.	0-15 15-30 30-60	5.16a 2.77a 1.21a	0.232a 0.248a 0.158a	1.5a 1.5a 1.7b	5.1a 5.1ab 5.2a	0.31c 0.45bcd 0.46a	0.21a 0.19c 0.20a	0.09a 0.10a 0.10a
Pasto	0-15 15-30 30-60	3.98a 2.94a 2.46a	0.296a 0.236 0.194a	4.1a 3.4a 8.9a	5.2a 5.1ab 5.2a	0.57bc 0.51bcd 0.47a	0.38a 0.27bc 0.20a	0.22a 0.17a 0.13a
Bosque	0-15 15-30 30-60	5.11a 3.83a 2.48a	0.288a 0.244 0.206	2.3a 2.0a 1.4b	5.2a 5.2a 5.2a	1.16a 0.92a 0.62a	0.49a 0.45a 0.27a	0.21a 0.17a 0.12a

Tabla 2 - Materia orgánica, cantidades totales de N, P, pH, Ca, Mg y K en suelos bajo las cuatro especies arbóreas nativas en la plantación, en el área de pasto y en el bosque secundario; Mayo 1989 (1)

(1) Existen diferencias estadísticamente significativas entre los sitios para una profundidad dada y los parámetros cuando los promedios son seguidos por letras diferentes.

de 58 kg de N, 181 kg de Ca, 57 kg de K, 22 kg de Mg, y 13 kg de P/ha/año.

Las cantidades de N, Ca, Mg y K, son el doble de aquellas reportadas por Wadsworth (1983) para plantaciones de teca, pero el valor de P es similar.

Aunque estas cantidades de nutrientes son altas, éstas deberían ser comparadas con la capacidad del suelo para suplir nutrientes.

Por ejemplo, Wadsworth comparó datos de la tasa de absorción anual de nutrientes de varios cultivos agrícolas en suelos Ultisoles y Oxisoles en Puerto Rico (N= 90 - 120 kg/ha/año, K= 50 - 90, Ca= 86 - 109, Mg= 68 - 98), con las tasas de retención media anual de nutrientes de plantaciones de teca y de pino.

Al examinar estos datos se concluye que la capacidad de los suelos para suplir nutrientes era suficiente para las necesidades de las plantaciones, y que los árboles podían ser cosechados sin crear deficiencias en el suelo, con la posible excepción de P. Wang et al.(1991) también reportaron que la tasa anual de absorción de N. P, Ca, Mg y K para plantaciones de Casuarina y Albizia en Puerto Rico era similar a la tasa de absorción de cultivos como el maiz y el sorgo.

En nuestro análisis, no estamos considerando la capacidad para suplir nutrientes de los suelos, pues no se dispone hasta la fecha de registros que permitan esta comparación.

(continuará)

RECUPERACION DE AREAS DEGRADADAS CON LA UTILIZACION DE ARBOLES NATIVOS: EXPERIENCIAS EN TRES REGIONES DE LATINOAMERICA

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RESUMEN

Un programa de investigación para estudiar los impactos de especies arbóreas nativas de valor económico sobre la rehabilitación de la fertilidad del suelo en tierras abandonadas comenzó en 1987 en tres regiones húmedas de Latinoamérica: las tierras bajas del Atlántico de Costa Rica, el bosque lluvioso del Atlántico ("Mata Atlántica") de Bahía, NE de Brasil, y el bosque húmedo subtropical de Misiones, NE de Argentina. En las tres regiones, se comparó la fertilidad de los suelos bajo un total de 29 especies arbóreas indígenas, incluyendo leguminosas fijadoras de nitrógeno, como así también otras familias, en rodales monoespecíficos de 3 a 20 años de edad, en relación con áreas adyacentes sin cobertura arbórea, y bosques secundarios. Se encontraron mejoras en la fertilidad del suelo bajo aproximadamente la mitad de las especies estudiadas, alcanzando en muchos casos valores de materia orgánica, nitrógeno o cationes, cercanos a aquéllos encontrados en bosques secundarios de 20 años de edad. Para un subgrupo de especies de Costa Rica y Brasil de las cuales se disponía de datos de crecimiento de fuste y de los nutrientes contenidos en la hojarasca anual, se calcularon índices de eficiencia en el uso del N y el P. Estos índices fueron de utilidad para integrar resultados y como herramienta para la planificación del diseño y manejo dirijidos a la productividad sostenida de sistemas incluyendo estas especies en cada región.

Palabras clave: rehabilitación de suelos, árboles nativos, eficiencia en el uso de nutrientes

INTRODUCCION

El paso inicial en proyectos de rehabilitación de ecosistemas es identificar los impedimentos que presenta el sitio con respecto a la productividad de árboles o cultivos, como así también definir los objetivos específicos de la recuperacion del sitio. Algunos suelos pueden ser recuperados a través de la incorporación de fertilizantes, otros necesitan técnicas de rehabilitación más drásticas, y existen situaciones de extrema degradación donde los suelos ya no pueden ser recuperados (Dedecek 1992). Este artículo focaliza en la rehabilitación de tierras abandonadas después de agricultura intensiva o pastoreo en los trópicos húmedos. El propósito de la rehabilitación es recuperar la capacidad productiva a través de la implementación de sistemas de uso de la tierra adaptados a la región e incluyendo especies maderables nativas de valor económico.

La recuperación de la capacidad productiva de los suelos es frecuentemente cara, por lo tanto las técnicas involucradas deben producir retorno financiero para que los productores locales las adopten. También es importante la disponibilidad de semillas o plantines, así como poseer información sobre las características silviculturales y de manejo. En muchos casos, la posibilidad de realizar cultivos intercalares durante los primeros años de establecimiento del sistema forestal facilita su adopción, al proporcionar un retorno financiero a corto plazo.

En 1987 se comenzó un programa de investigación para desarrollar alternativas para la rehabilitación y uso de tierras abandonadas, en tres regiones de Latinoamérica: las tierras bajas húmedas del Atlántico en Costa rica, la selva lluviosa atlántica ("Mata Atlantica"), de Bahía, Brasil y el bosque húmedo subtropical de Misiones, NE de Argentina (Tabla 1). En estas regiones, persisten situaciones de deforestación, pérdida de biodiversidad, uso inadecuado de recursos y degradación de la tierra, y a la vez existe interés por parte de instituciones y productores privados en implementar usos productivos de la tierra y tendientes a la recuperación de áreas degradadas.

a- Llanura del Atlántico, Costa Rica

En Costa Rica, el área experimental está ubicada en la Estación Biológica La Selva (Tabla 1). La fertilidad del suelo fue medida bajo plantaciones monoespecíficas de cuatro especies, incluyendo leguminosas fijadoras de nitrógeno como así también especies pertenecientes a otras familias: *Striphnodendron microstachyum* Poepp. et Endl. (sinon: *excelsum*), *Vochysia ferruginea* Mart., *Vochysia guatemalensis* Donn.Sm. (sinon: *hondurensis*) y *Hyeronima alchorneoides* (O). Los resultados mostraron que cuando los árboles alcanzaron los 2.5 años de edad, las condiciones del suelo fueron mejoradas comparadas con terrenos de pasturas abandonadas: en los 15 cm superiores, los contenidos de nitrógeno total del suelo y materia orgánica fueron mayores bajo cobertura arbórea que bajo pastos, con valores cercanos a los encontrados en un bosque adyacente de 20 años de edad (Tabla 2). Los valores más altos de materia orgánica, N total, Ca y P extraible se encontraron bajo *Vochysia ferruginea*, una especie de la familia *Vochysiaceae*, abundante en bosques secundarios de la región (Montagnini y Sancho 1990a, 1990b). Otros efectos incluyen el incremento del contenido del Ca y Mg extraible en el suelo a niveles cercanos a los aceptables para la agricultura convencional en la región (Berstch 1986). Resultados similares fueron obtenidos en los tres años subsiguientes (Montagnini y Sancho 1994a).

En estos suelos, la materia orgánica fué responsable de la mayor parte de la capacidad de intercambio catiónico (Montagnini y Sancho 1990a, b): basado en la relación entre la materia orgánica del suelo y la suma de bases (Ca+Mg+K), un incremento de 1-2% en el contenido de materia orgánica del suelo en el rango de 4-6%, resultó en un incremento de más del doble en el contenido de bases. La materia orgánica del suelo tuvo también influencias positivas sobre las propiedades físicas: la densidad aparente del suelo fué menor (es decir, menor compactación) mientras que el contenido de humedad fué mayor bajo cobertura arbórea que bajo pastos (Tabla 2).

Otros efectos de las especies estudiadas sobre el N y P del suelo resultaron aparentes en los estudios de reciclaje de nutrientes y de disponibilidad de N mineral en el suelo. Por ejemplo, bajo *S. microstachyum*, una especie leguminosa fijadora de nitrógeno (Baker y Montagnini 1994), la hojarasca rica en nitrógeno se descompuso mas rápido que las demás especies, resultando en un incremento del nitrógeno mineral del suelo (Montagnini y Sancho 1994b). Asimismo, con el agregado al suelo de hojarasca de *S. microstachyum* y *H. alchorneoides*, plántulas de maíz mostraron mayor crecimiento inicial y mayor grado de absorción de N y P que plántulas con el agregado de hojarasca de las otras especies (Montagnini et al. 1991, 1993).

Los valores de caída anual de hojarasca de las cuatro especies estudiadas fueron comparables a valores reportados para otras especies utilizadas en agroforestación en regiones tropicales húmedas (Montagnini et al. 1991, 1993). La hojarasca puede actuar como agregado orgánico con diferentes objetivos: por ejemplo, debido a su descomposición más lenta, se encontró una alta acumulación de hojarasca y materia orgánica del suelo bajo *V. ferruginea*, demostrando que esta especie puede ser adecuada para la protección contra la erosión de suelos. En contraste, la hojarasca de *H. alchorneoides*, aunque menos abundante que las otras tres especies, debido a su descomposición rápida y alto contenido de nutrientes promovió el reciclaje de N y P, mientras que la hojarasca de *V. guatemalensis* fue importante para el reciclaje de Ca y Mg (Montagnini et al. 1993, Montagnini y Sancho 1994a). Por último, se registraron influencias favorables sobre el microambiente del sotobosque: las temperaturas del suelo y del aire fueron menores bajo la cobertura de los árboles que en la pastura, mientras que la humedad del suelo fué mayor bajo las dos especies de *Vochysia* (Montagnini et al. 1993).

b- Región del bosque lluvioso atlántico, Bahía, Brasil

En el sur de Bahía, los estudios fueron realizados en un área donde la vegetación original fue la "Mata Atlantica" (Tabla 1). Los estudios se focalizaron en las relaciones especie/sitio de 20 especies arbóreas nativas en rodales monoespecíficos de 14-15 años de edad. Se encontraron efectos positivos en por lo menos cinco parámetros del suelo, bajo 15 de las 20 especies del experimento, en comparación con bosque primario y secundario (Montagnini et al. 1994a) (Tabla 2). Varias especies contribuyeron a incrementar los contenidos de C y N totales del suelo: *Inga affinis, Parapiptadenia pterosperma, Platymenia foliosa* (especies leguminosas, fijadoras de nitrógeno), *Eschweilera ovata, Pradosia lactescens* (de otras familias); asimismo, bajo la mayoría de estas especies se detectó una menor compactación y mayor contenido de humedad del suelo. Bajo otras especies se detectaron incrementos en el pH del suelo y/o algunos cationes: *Copaifera luscens, Eschweilera ovata, Lecythis pisonis* y *Licania hypoleuca*; y leves aumentos en los niveles de P extraíble del suelo superficial: *Inga affinis, Arapatiella psilophylla, Caesalpinia echinata, Cassia spp., Hymenaea aurea, Bombax macrophyllum* y *Buchenavia grandis.*

Tal como en los estudios de Costa Rica, los resultados de estudios de reciclaje de nutrientes complementaron la información sobre el posible papel de las especies como mejoradoras del suelo. Entre las 20 especies estudiadas en Bahia, la mayor caída de hojarasca fué encontrada bajo *Bombax macrophyllum*, *Buchenavia grandis* y *Caesalpinia echinata* (da Vinha y Pereira 1983, da Vinha et al. 1985); bajo estas especies se encontraron efectos positivos sobre los suelos, p.e. mayor contenido de P extraíble en el suelo superficial bajo las tres especies, mayor contenido de humedad bajo *B. grandis* y *C. echinata*, y mayor espesor del mantillo, mejorando la protección del suelo, bajo *B. macrophyllum* (Montagnini et al. 1994a).

c- Misiones, NE Argentina

La investigación fué conducida en una región de bosque húmedo subtropical en la provincia de Misiones, cercana al límite con el estado brasileño de Paraná (Tabla 1). Las especies forestales nativas utilizadas en este estudio fueron: *Balfourodendron riedelianum, Cordia trichotoma, Bastardiopsis densiflora, Enterolobium contortisiliquum* y *Ocotea puberula*. Las mayores diferencias en el carbono y nitrógeno del suelo fueron encontradas bajo *Bastardiopsis densiflora*, donde fué el doble del contenido en áreas sin cobertura arbórea (Fernández et al. 1994). El pH fue mayor bajo *Bastardiopsis densiflora* y *Cordia trichotoma*, mientras que la suma de bases (Ca+Mg+K) fué mayor bajo *Cordia trichotoma, Bastardiopsis densiflora* y *Enterolobium contortisiliquum*.

Estos resultados fueron sustanciados con datos de análisis químicos de biomasa arbórea, los cuales ayudaron a explicar las tendencias halladas (Montagnini et al. 1994b). Dentro de las especies más importantes desde el punto de vista de su potencial como mejoradoras del suelo, *Bastardiopsis densiflora* posee interesantes posibilidades debido a que es una especie pionera que coloniza áreas abandonadas, formando densos rodales coetáneos que pueden alcanzar dimensiones comerciales en 10-14 años. *Cordia trichotoma*, con una tasa de crecimiento menor es sin embargo una especie maderera valiosa conocida por su participación exitosa en plantaciones y sistemas agroforestales. El potencial de *Enterolobium contortisiliquum* como mejoradora del suelo con su capacidad fijadora de nitrógeno necesita ser verificado.

EFICIENCIA EN EL USO DE NUTRIENTES

La eficiencia en el uso de nutrientes (EUN) se calculó como el cociente entre el incremento medio anual del fuste y la absorción anual de nutrientes (N y P), esta última medida como el contenido de N y P en la hojarasca anual (Grubb, 1989). Estos cálculos se realizaron para las cuatro especies de Costa Rica, y para ocho de las veinte especies de Bahía, de las cuales se disponía de datos de caída de hojarasca. Los valores de EUN indican la capacidad de las diferentes especies de producir biomasa, en relación a la cantidad de nutrientes absorbidos del suelo. La capacidad de una especie de producir madera con una menor cantidad de nutrientes (es decir, un valor relativamente alto de EUN) puede ser un criterio importante para la elección de especies para la producción de biomasa, especialmente en áreas con suelos pobres. Por otro lado, especies con valores bajos de EUN pueden ejercer una influencia importante sobre la mejora del nivel de nutrientes de un sitio degradado, dado que producen menos biomasa pero el contenido de nutrientes de su hojarasca es relativamente elevado, lo cual conlleva un mayor reciclaje.

El cálculo de la eficiencia del uso de nutrientes (EUN) probó ser un medio útil a los fines de integrar los resultados para la elaboración de recomendaciones para el diseño y manejo de estos sistemas. En ambos sitios, La Selva y Bahia, el fósforo presentó rangos más amplios y valores más elevados en la eficiencia de uso que el nitrógeno (Figs. 1 y 2).

Comparando entre especies, *S. microstachyum* (fijadora de N), mostró una eficiencia relativamente baja (alto reciclaje) para N y P, confirmando el rol de esta especie en el reciclaje de nutrientes estos nutrientes, presentado en la sección sobre Costa Rica. *V. ferruginea* mostró valores comparativamente bajos de eficiencia para ambos nutrientes considerados, reafirmando así los resultados encontrados en términos del contenido de materia órganica y efectos positivos sobre el reciclaje de nutrientes. *H. alchorneoides* tuvo una respuesta similar, con baja eficiencia. En contraste, *V. guatemalensis* con su tasa de crecimiento relativamente rápida, aparentemente tendió a acumular grandes cantidades de nutrientes en el fuste, resultando en mayores valores de eficiencia y comparativamente menor capacidad de reciclaje para N y P.

De las 8 especies en Bahía, *Bombax macrophyllum*, debido a su alta tasa de crecimiento, a pesar de presentar valores relativamente altos de caída de hojarasca mostró la mayor eficiencia de uso para N y P (Figs. 1 y 2). Esta especie sería particularmente adecuada para suelos relativamente pobres. Asimismo, *Platymenia foliolosa*, *Lecythis pisonis* y *Eschweilera ovata*, con valores de eficiencia de uso relativamente elevados para N y P, serían también especies acertadas para producir biomasa en suelos pobres. De las dos especies fijadoras de N, las mayores eficiencias de uso de N y P se encontraron en *Platymenia foliolosa*. Entre las especies con los valores más bajos de eficiencia de uso, es decir, mayor potencial para el reciclaje de los dos nutrientes considerados se encontraron *Buchenavia grandis, Caesalpinia echinata* e *Hymenaea aurea*. Estas especies podrían ser adecuadas para combinaciones agroforestales, donde los cultivos intercalares se beneficiarían por la mayor disponibilidad de nutrientes debido al alto reciclaje a través de la hojarasca de estas especies.

En conjunto con las influencias de las especies arbóreas sobre el suelo que se muestran en

la Tabla 2, los datos sobre eficiencia en el uso de los nutrientes proveen información adicional sobre la posible influencia a largo plazo de las especies sobre los nutrientes del ecosistema. Sin embargo, los supuestos involucrados en los cálculos (p.e., el uso de datos de caída de hojarasca anual en lugar de una medida directa de la absorción de nutrientes), limitan la interpretación de estos resultados.

DISEÑO DE SISTEMAS Y MANEJO A LARGO PLAZO

En el diseño de sistemas forestales productivos, para disminuir el deterioro del sitio luego de cosechas consecutivas, la elección de especies y manejo debería asegurar el mantenimiento de niveles adecuados de nutrientes del ecosistema en el largo plazo. Para lograr este objetivo, especies con baja eficiencia (alto potencial para reciclaje) para determinados nutrientes (p.e., N y P), deberian ser complementadas con otras de baja eficiencia de uso. Ciertos diseños pueden incorporar la plantación de diferentes especies en rotaciones sucesivas. Otra opción es el uso de mezclas de especies de manera simultánea sobre el terreno. Los diseños de especies mixtas pueden ser más ventajosos que monocultivos para la rehabilitación del sitio si los sistemas son planeados de manera tal de complementar las demandas y efectos de cada especie.

A largo plazo, los impactos de la plantación de árboles sobre los nutrientes del suelo dependen de: (1) la absorción anual de nutrientes por los árboles en relación a la capacidad de provisión de nutrientes del suelo, (2) la cantidad de hojarasca y su descomposición, (3) distribución diferencial de nutrientes en las partes del árbol: tallo, follaje, raíces, y (4) las partes del árbol removidas durante la cosecha, ya sea el árbol completo o fuste, y su biomasa y contenido de nutrientes. Por ejemplo, el mantillo es generalmente un compartimiento importante para la acumulación y el reciclaje de nutrientes, aunque con marcadas diferencias entre especies. Si el mantillo es quemado o recolectado para combustible, puede ocurrir una pérdida sustancial de materia orgánica y nutrientes, mientras que si la hojarasca es dejada en el suelo luego de la cosecha, representa una reserva significativa para la próxima rotación.

En contraste, para ciertos nutrientes como K y P, en ciertos casos una proporción relativamente alta es almacenada en la biomasa aérea de los árboles, o en las raíces. En comparación con el mantillo es menos probable que las raíces sean afectadas durante las operaciones manuales de extracción de los arboles, mientras que el uso de maquinaria pesada podría afectar seriamente al sistema radicular y su capacidad de almacenamiento y reciclaje de nutrientes.

CONCLUSIONES

En las tres regiones estudiadas, varias especies arbóreas nativas de valor comercial tuvieron efectos favorables sobre la fertilidad y algunas propiedades físicas de los suelos. El cálculo de la eficiencia en el uso de nutrientes probó ser una herramienta útil para el diseño y manejo de sistemas: para conservar nutrientes en el largo plazo, especies con baja eficiencia de uso deberían ser combinadas en tiempo y espacio con otras con alta eficiencia de uso. Para la rehabilitación de ecosistemas en sitios tropicales húmedos, información sobre las tasas de crecimiento de los árboles, composición química del suelo y biomasa y contenido de nutrientes de de la hojarasca, es imprescindible para el diseño y manejo a largo plazo de sistemas forestales sustentables.

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Tabla 1. Sitios de estudio en tres regiones de América Latina.

Ubicación geográfica	Precipitaciones y temp. medias	Suelos	Uso previo de la tierra	Diseño experimental
Estación Exp. La Selva Tierras bajas de Costa Rica 10°26'N, 86°59'W	4.000mm, 24°C	Fluventic Dystropepts pH 4,3-5,3	1-3 años de agricultura, pastura	Plantación pura,2mx2m, 3-6 años
Estación Ecol.de Pau Brasil, Porto Seguro, Bahía, Brasil 16°23'S, 39°11'O	1.700mm, 23°C	Oxisoles (Haplorthox) pH 4,5-5,0	Agricultura migratoria	Plantación pura, 2mx2m, 14-15 años
Eldorado,Misiones, NE de Argentina (Terrenos privados)	1.700'2.400 mm, 22°C	Ultisoles ácidos arcillosos ph 4.5-5.0	Agricultura, Plantaciones de pinos	Rodales puros de regen. nat. 10-20 años

Tabla 2. Características químicas del suelo en rodales puros de 24 especies de árboles nativos en La Selva, Costa Rica y Porto Seguro, Bahia, Brazil.

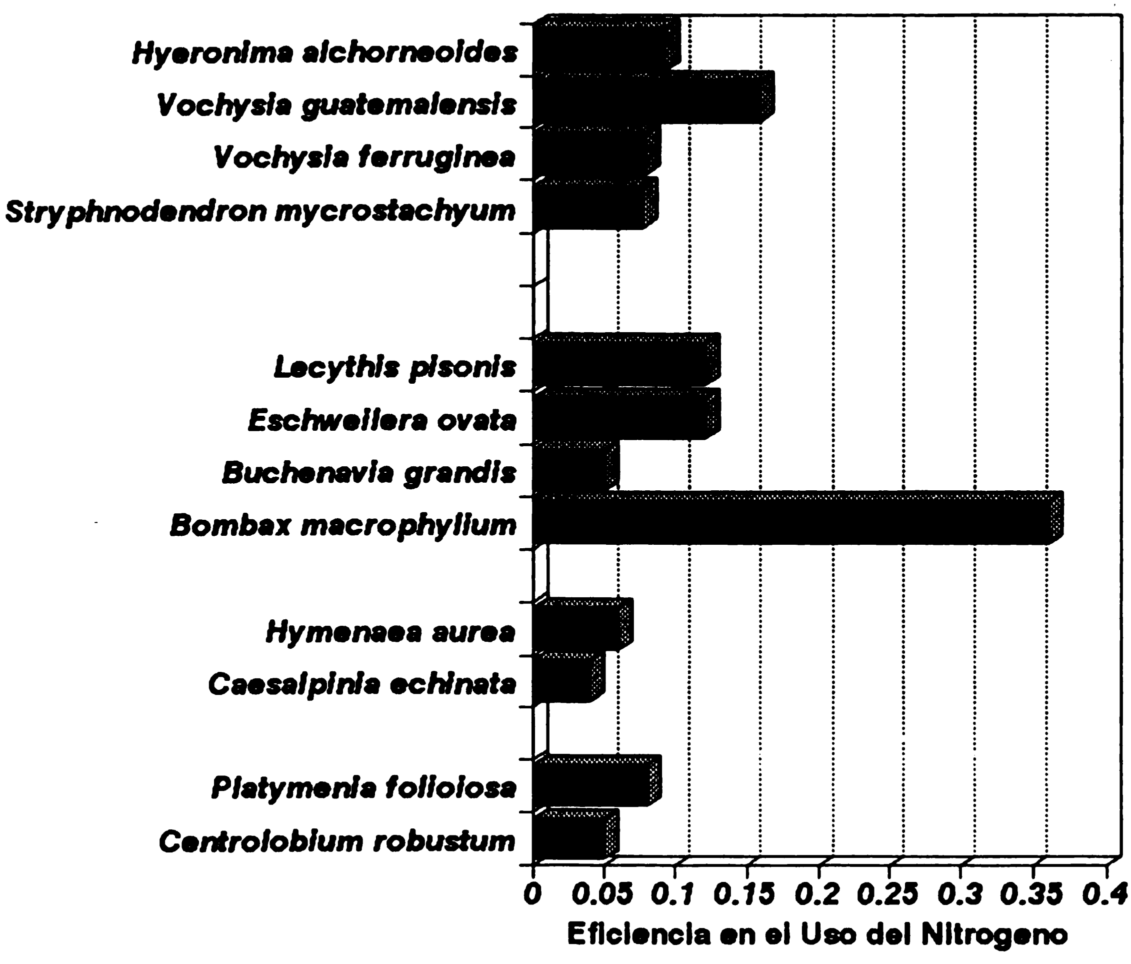
Sitio/Especies	pH	C (%)	N (%)	P (cmol.kg⁻¹)	K	Ca	Mg
a- La Selva, Costa Rica							
Stryphnodendron microstachyum	5.4ab	3.42ab	0.29b	5.6a	0.27a	0.45a	0.63ab
Vochysia ferruginea	5.4ab	3.76a	0.32a	7.1a	0.22a	0.73a	0.61ab
Vochysia guatemalensis	5.3ab	3.13ab	0.29b	5.2a	0.11a	0.25a	0.37ab
Hyeronima alchorneoides	5.1b	2.96c	0.22b	1.5b	0.09a	0.31b	0.21b
Pastura abandonada	5.3ab	2.73c	0.22b	4.9a	0.19a	0.32b	0.27b
Bosque secundario	5.3ab	4.33a	0.33a	3.6b	0.17a	0.68a	0.55ab
b- Porto Seguro, Bahia, Brasil							
Especies Leguminosas fijadoras de N:							
Bowdichia virgilioides	4.9	1.98def	0.16def	1.32def	0.06bcd	1.35bc	0.39de
Centrolobium minus	4.6	1.87efg	0.16def	1.19efg	0.05fgh	0.53hi	0.21i
Centrolobium robustum	4.5	1.65ij	0.13f	1.07fgh	0.05fgh	0.40i	0.16i
Inga affinis	4.9	2.10cde	0.18cd	3.64a	0.07bcd	0.76gh	0.49bc
Parapiptadenia pterosperma	4.9	2.38ab	0.20bc	0.78ij	0.08b	1.40bc	0.60a
Pithecellobium elegans	4.8	1.67hij	0.15ef	0.59kl	0.05efg	0.79gh	0.40de
Platymenia foliolosa	4.7	2.08cde	0.18bcd	0.13m	0.05efg	1.05cde	0.42cd
Especies Leguminosas no fijadoras de N:							
Arapatiella psilophylla	4.7	1.94def	0.18bcd	1.45de	0.06bcd	0.38i	0.37de
Caesalpinia echinata	5.1	2.41a	0.17cde	1.54de	0.07bcd	1.17bcd	0.39de
Cassia spp.	4.7	1.94def	0.16def	1.40def	0.07bcd	0.56hi	0.34de
Copaifera luscens	5.0	2.02cde	0.17cde	0.63jk	0.06cde	1.15bcd	0.34de
Dimorphandra jorgei	4.9	1.97def	0.19bc	0.97ghi	0.03j	0.98def	0.32efg
Hymenaea aurea	4.4	2.00def	0.16def	2.03c	0.06bcd	0.26i	0.24hi
Macrolobium latifolium	4.7	1.90efg	0.16def	0.67jk	0.04hij	0.36i	0.25fg
De otras familias:							
Bombax macrophyllum	4.8	1.78ghi	0.13f	1.42de	0.06bcd	0.84efg	0.33ef
Buchenavia grandis	4.6	2.06cde	0.14f	2.09c	0.06bcd	0.80fg	0.33ef
Eschweilera ovata	5.3	1.82fgh	0.31a	0.58kl	0.11a	1.38bc	0.53ab
Lecythis pisonis	5.3	1.99def	0.18bcd	0.23lm	0.04ghi	1.46b	0.32ef
Licania hypoleuca	5.0	1.63j	0.14f	1.61d	0.07bcd	1.31bcd	0.35de
Pradosia lactescens	4.9	2.15bcd	0.18bcd	0.81ij	0.05fgh	0.84efg	0.24gh
Bosque primario	4.9	1.99def	0.15ef	0.96hi	0.08bc	1.23bcd	0.36de
Bosque secundario	5.1	2.15abc	0.22b	2.46b	0.07bcd	2.20a	0.62a

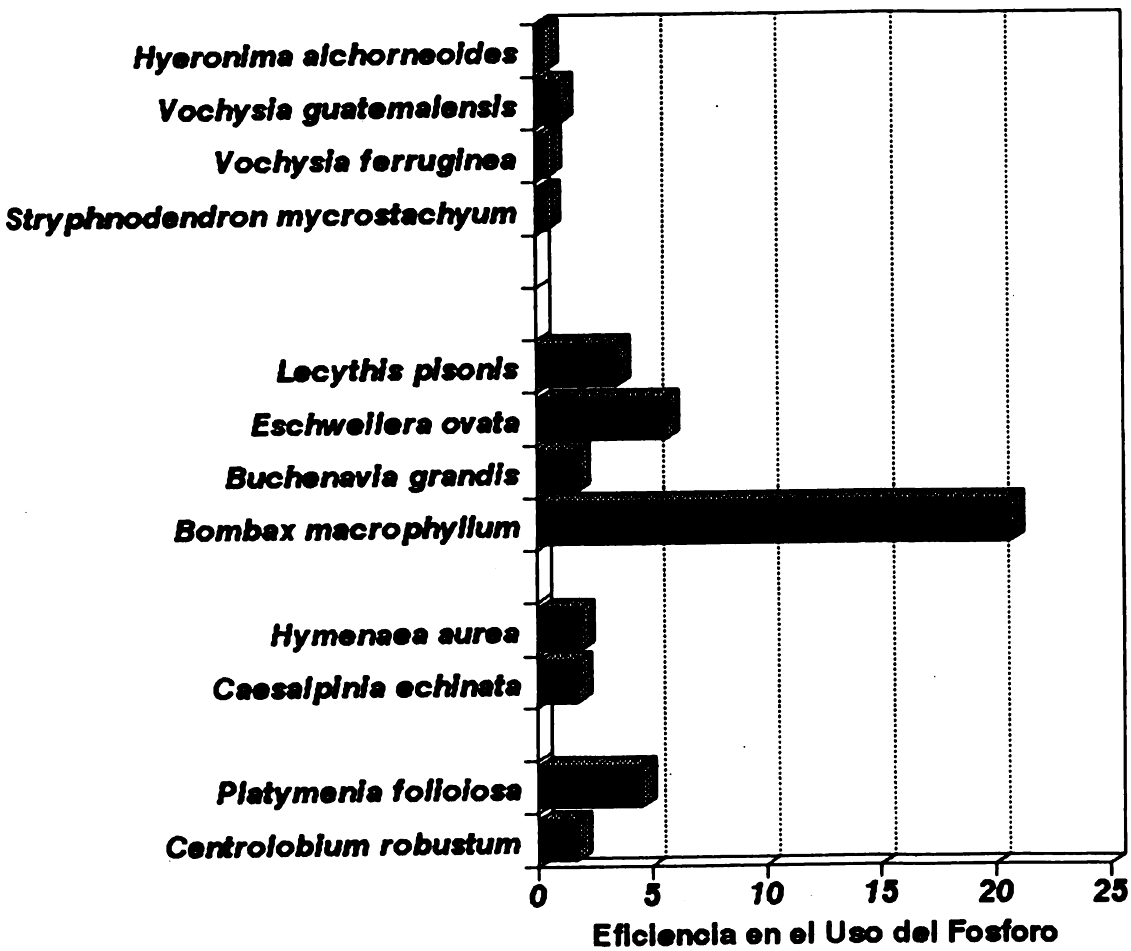
Nota: para cada sitio, las diferencias entre medias son estadísticamente significativas cuando están acompañadas por diferentes letras ($p < 0.05$).

Leyendas de las Figuras.

Fig. 1. Eficiencia en el Uso del Nitrógeno (Megagramos de incremento anual de la biomasa del fuste/kg de N en la hojarasca anual) para cuatro especies arbóreas de Costa Rica y ocho especies de Bahia, Brasil.

Fig. 2. Eficiencia en el Uso del Fósforo (Megagramos de incremento anual de la biomasa del fuste/kg de P en la hojarasca anual) para cuatro especies arbóreas de Costa Rica y ocho especies de Bahia, Brasil.


Hyeronima alchorneoides
Vochysia guatemalensis
Vochysia ferruginea
Stryphnodendron mycrostachyum
Lecythis pisonis
Eschweilera ovata
Buchenavia grandis
Bombax macrophyllum
Hymenaea aurea
Caesalpinia echinata
Platymenia foliolosa
Centrolobium robustum
0
0.05
0.1
0.15
0.2
0.25
0.3
0.35
0.4
Eficiencia en el Uso del Nitrogeno


Hyeronima alchorneoides
Vochysia guatemalensis
Vochysia ferruginea
Stryphnodendron mycrostachyum
Lecythis pisonis
Eschweilera ovata
Buchenavia grandis
Bombax macrophyllum
Hymenaea aurea
Caesalpinia echinata
Platymenia foliolosa
Centrolobium robustum
0
5
10
15
20
25
Eficiencia en el Uso del Fosforo

Tropical plantations with native trees: Their function in ecosystem restoration

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ABSTRACT

In humid tropical regions, soil nutrients are key factors influencing plant productivity and long-term sustainability of a production system. Tree planting is currently being promoted in a number of government and private efforts towards rural development throughout the tropics. As the area in degraded lands increases, emphasis is placed on the use of species which can grow in such conditions and yield economic products as well as environmental benefits (soil conservation, watershed protection).

This article reports results from research on forest rehabilitation in a humid region of Costa Rica, focused on the impacts of native trees on soil fertility and nutrient cycling. Increased levels of soil nitrogen, carbon, Ca and Mg were found under some of the tested tree species than under grass, with values close to those found in 20-year-old forest. The highest soil C, N and cations were found under *Vochysia ferruginea*, while important effects of other species were found on soil N and P availability and on Ca and Mg recycling. Nutrient use efficiencies (stem biomass increments per unit of nutrient taken up) were calculated to integrate results and design management recommendations geared to sustaining productivity of systems including these species.

INTRODUCTION

Tropical plantations can serve diverse economic, social, political and ecological functions. With considerably higher yields than managed native forests, tropical and subtropical plantations can make substantial contributions to world timber and pulp production (Wadsworth 1983, Evans 1992). Tree plantations can also be a source of cash, savings and insurance for individual farmers. Plantations may help stabilize rural populations in regions where shifting agriculture is the predominant land use. In combination with subsistence and commercial crops (agroforestry) or cattle (agrosilvopastoral systems), plantations have been used as tools in rural development projects worldwide. Plantations are often seen as alternatives to deforestation as they can provide products that otherwise would be taken from natural forests (Fearnside 1990, Mc Nabb et al. 1994).

If plantation species are chosen with knowledge of their nutrient-use efficiencies and recycling capacities, they can be highly productive and even serve a function in ecosystem restoration projects. Particularly, tree plantations and tree-crop combinations represent productive land use alternatives for deforested lands with poor natural forest regeneration due to long distance to sources of propagules or intense site degradation. Among the latter, low soil fertility, soil compaction after abandonment from cattle grazing and invasion by grasses and other agressive vegetation can be serious obstacles to both forest regeneration and conventional agriculture. As the area in degraded lands spreads out, emphasis is increasing on the use of tree species which can grow in such conditions and yield economic products (timber, fuelwood and other) as well as environmental benefits (soil conservation, watershed protection) (Evans 1992).

The choice of appropriate tree species for plantation forestry or agroforestry is influenced by knowledge on the species' performance and their economic and environmental benefits. Locally, tree species choice is determined by seed or seedling availability and information on silvicultural characteristics and management, including fast growth and the possibility of intercropping during early establishment. Most reforestation or tree planting programs and subsidies promote the use of well-known, often exotic species. About 85% of plantation forestry in the tropics is dominated by three genera: *Pinus*, *Eucalyptus* and *Tectona*, while there may be thousands of indigenous species suitable for similar purposes (Evans 1992). Native trees can be more appropriate than exotics because (1) they are better adapted to local environmental conditions, (2) seeds and other propagules are locally available, and (3) farmers are familiar with them and their uses. Besides, the use of indigenous trees in productive systems helps preserve genetic diversity and is in better balance with the local flora and fauna.

In the present article we present results from an experimental plantation with native trees at La Selva Biological Station in the Atlantic humid lowlands of Costa Rica. We compare impacts of trees on soils, tree productivity, nutrient content and nutrient use efficiency among the species. This information can be used to design management strategies to take advantage of the trees' ameliorating effects on soils and to avoid site nutrient depletion with harvest. These strategies should be useful for promoting the use of systems (mixed or pure plantations, agroforestry) including these fast growing timber species in the area and in other tropical lowland regions with similar ecological characteristics.

STUDY SITE

The experimental plantation was established in December 1985 on abandoned pasture at the Organization for Tropical Studies (OTS) La Selva Biological Station (10°26'N, 86°59'W, 50 meters mean elevation, 24°C mean annual temperature, 4000 mm mean annual rainfall, with maximum in July and minimum in March) (La Selva Biological Station weather reports). Soils are Fluventic Dystropepts derived from alluvially deposited volcanic materials; they are deep, well drained, stone-free, with low or medium organic matter content, moderately heavy texture, and generally acid and unfertile (Sancho and Mata 1987). The area had been cleared in the 1950s and grazed until 1984. The site was cleaned manually before planting. The tree species were planted in a randomized block design with five replicates, each plot containing seven rows of seven trees

(14 m x 14 m each), with two meters between trees. Five 14 m x 14 m plots were also established in an adjacent open area with grass, and in nearby patch of secondary forest. During the first year, weeds were manually cut four times; weeding was done mechanically thereafter until canopy closure made it no longer necessary. The grass was weeded simultaneously to keep it free of trees and with comparable treatments.

The tree species

The criteria for species selection for this study were: (1) good growth (as determined during the first 3-4 years of the plantation), (2) presence of root nodules in the leguminous species (field observations), and (3) economic value. *Stryphnodendron microstachyum* Poepp. Et Endl. (Leguminosae, sub-family Mimosoideae) ("vainillo") is found only in Costa Rica, although representatives of this genus are native to all tropical South America (Brazil, Costa Rica, Guiana) (Allen and Allen 1981). It grows in low elevations with very humid climates; the species apparently adapts to alluvial soils, as well as to slopes and abandoned pastures with degraded soils (Gonzalez et al. 1990). Its timber is primarily used for general construction, and also small furniture and turnery because of its ability to take high polish (Allen and Allen 1981). Its fruits are eaten by many wildlife species, mostly small mammals. *Vochysia ferruginea* Mart (Vochysiaceae) ("botarrama") grows in lowland forests from Nicaragua to Brazil (Whitmore and Hartshorn 1969); it is found on acidic, well drained, low fertility soils, but it can adapt to a variety of soils (González et al. 1990); it is a self-pruning pioneer species that forms uniform, even-aged stands in abandoned fields; its wood is used for plywood and construction. *Vochysia guatemalensis* Donn. Sm. (Vochysiaceae) ("mayo") is found from Mexico to Panama, up to 900 m (Whitmore and Hartshorn 1969); usually it grows on humid, low altitute areas, on either alluvial or residual (less fertile) soils;

its timber is highly appreciated; it is used for carpentry, plywood, and furniture. *Hieronyma alchorneoides* Fr. Allemao (Euphorbiaceae) ("pilón") ranges from southern Mexico to southern Brazil; it grows well in hills and on abandoned grasses, but not much is known about its edaphic requirements. Its timber is used for heavy construction, furniture, cabinet work, decorative veneers and turnery (Chudnoff 1984).

METHODS

Sampling procedures and chemical methods are described in Montagnini and Sancho (1990a, 1990b, 1994a, 1994b), Montagnini et al. (1991, 1993), and Montagnini (1994). The soils under the species, a grassy area free of trees and a 20-year-old secondary forest were sampled for soil fertility and nitrogen availability measurements, starting when the trees were 2.5 years old, and annually thereafter for three more years. Tree biomass and nutrient content (stems, branches and leaves) were measured at the time of plot thinning, when the plantation was 4 years-old. The biomass and nutrient concentrations of the understory vegetation and the forest floor under the trees were also measured. Nutrient budgets were calculated by multiplying the biomass of each compartment times its nutrient concentration (N, Ca, Mg, K, P). Nutrient use efficiencies (NUE) were calculated by dividing annual stem biomass increments by annual nutrient uptake by each species. As direct measurements of nutrient uptake were not available, nutrient content of annual litterfall was used for the calculations of NUE.

RESULTS AND DISCUSSION

Impacts of trees on soils

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 ferruginea*, a species common in mature and secondary forests in the region (Montagnini and Sancho 1990a, 1990b). 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 (Bertsch 1986), 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 (rice, beans). 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 (Montagnini and Sancho 1990a). 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 (Bertsch 1986).

Low crop yields in the humid tropics are often a result in part of unfavorable physical properties such as soil compaction (Cassel and Lal 1992). 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).

The results of standard soil fertility tests used in agriculture (such as those shown in Table 1) may not always reveal the soil's productive potential, because they do not include all chemical forms of nutrients available for plant uptake. For example, although they make up less than 10% of the total soil N pool, mineral N (NO_3^-+NH_4^+), are the forms of N available to plants. 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. 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 (Montagnini and Sancho 1994a). 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 other species' litter, showed the greatest initial growth and the highest N and P plant uptake (Montagnini et al. 1993). 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.

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 (Montagnini et al. 1993).

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 (Montagnini and Sancho 1994a, 1994b). 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.

Tree productivity

The values of whole tree biomass reported here (Table 2) are greater than those reported for 4-year-old *Albizia lebbek* (Parrota 1989), and for 5.5- year-old *Leucaena leucocephala* (Wang et al. 1991), both growing in dense plantations for biomass production in Puerto Rico. Values of total tree above-ground net primary productivity shown here (calculated by dividing whole-tree biomass by tree age) lie within the ranges reported elsewhere for monospecific plantations in the humid tropics. The value for *V. guatemalensis* is close to that reported for *Gmelina arborea* (12.8 tons per ha/yr) in the Brazilian Amazon (Russell 1987); and to *Gmelina arborea* (12.7 tons/ha) and *Albizia falcataria* in the Philippines (11.3) (Kawajara et al. (1981), in Young (1989)). The increments shown here are however lower than those reported for some of the fastest growing trees in the humid tropics such as *Acacia mangium* (15.5 to 18.0 tons/ha in Malaysia), *Leucaena leucocephala* (20.0-30.0 and even up to 80.0 tons/ha in Hawaii an other tropical sites, Young (1989)).

Stemwood biomass annual increment for broadleafs ranges from 1 to 28 tons/ha/yr. Fast growing species such as *Gmelina arborea* and *E. saligna* range from 10-20 and 8-28 tons/ha, respectively, and relatively slower growing species such as *Swietenia* sp. and *Tectona grandis* range from 1-4 and 3-12 tons/ha, respectively (Wadsworth 1983). Other values for fast-growing trees in tropical humid regions include varios eucalyptus species grown in the Americas and Asia (7.2 to 11.9 tons/ha), *Gmelina arborea* in Costa Rica (11.8) (Lugo et al 1988); 1.3 to 5.3-year-old *Leucaena leuocephala* growing in pre-montane and lowland humid sites (2.8 to 15.9); *Prosopis juliflora*, moist site in India (9.4), *Populus deltoides*, subtropical site in India 6.4 (Lugo et al 1990). Thus the mean annual stemwood biomass increments for the species of this study also fall within the ranges reported for other fast-growing tree species in the humid tropics.

Assessing potential long-term impacts: Nutrient Use Efficiencies

As shown above, a number of native timber species which combine good economic value with important soil rehabilitation properties were found in this study. The potential of the species for rehabilitation of degraded areas sometimes was obvious through their direct impacts on soil fertility parameters such as organic matter or cations. In other cases their effects only became evident through more detailed studies such as litter decomposition, N mineralization, or by studying the response of test plants to the tree species mulch or litter.

The calculation of nutrient use efficiencies proved a useful means of integrating results for drawing recommendations for system design and management. Among the nutrients examined, phosphorus and potassium showed the broadest ranges and the highest values of use efficiency (Table 3). Conversely, nitrogen and calcium showed narrower ranges and lower efficiency values, with magnesium in an intermediate position. These results confirm the expectation that the most scarce nutrients (P, K) were used more efficiently than the most abundant and easily recyclable nutrients (N, Ca, Mg). Comparing among species, *S. microstachyum* (a N-fixing species), showed relatively low efficiency (high recycling) for N and P, but comparatively high efficiencies for cations, thus confirming this species' role in nutrient cycling discussed above. *V. ferruginea* showed comparatively low efficiency values for all the nutrients considered, again sustaining the assessment of this species as beneficial in terms of organic matter recycling and positive impacts on soil fertility. *H. alchorneoides* had a similar response, with generally low values, especially for K and P. In contrast, *V. guatemalensis* with its relatively faster growth rates apparently tended to accumulate large amounts of nutrients in stem biomass, resulting in higher efficiency values and comparatively less recycling capacity, especially for N, P and K.

In the design of productive forest systems, to decrease site deterioration with consecutive harvests, species choice and management should ensure the maintenance of adequate levels of ecosystem nutrients in the long term. To attain this goal, it is evident from the results shown above that species with low efficiency (high potential for recycling) for a given set of nutrients (e.g., N, Ca, Mg) should be complemented with others with low efficiencies for different nutrients (K, P). Alternative designs may involve planting different species in successive rotations. Another option is the use of tree species mixtures. Mixed-species designs can be more advantageous than tree monocultures for site nutrient rehabilitation if systems are planned so as to complement each species' nutrient demands and effects. As part of the same research, additional studies at La Selva involved comparisons of growth and impacts on soils of monospecific and mixed-tree plantations of indigenous species of economic value (Montagnini et al. 1995, Montagnini and Porras 1997).

Biomass nutrients: implications for management

In the long term, the impacts of plantation trees on soil nutrients depend on: (1) the annual nutrient uptake by the trees in relation to the nutrient supplying capacity of the soil, (2) amounts of leaf litterfall and decomposition, (3) differential nutrient allocation in tree parts: stems, foliage, roots, and (4) the parts of the tree removed at harvest, whether the whole tree or stemwood, and their biomass and nutrient content. To help understanding these relationships, biomass nutrients were compared among tree parts for the four species of the La Selva site. Consistent with trends found in N tissue concentrations (Montagnini et al. 1991), *S.microstachyum* had the highest stem, branch and whole-tree biomass N (Fig. 1). *V. guatemalensis* had a similar proportion of N to *S.microstachyum* in its leaves+branches portion; over 50% of whole-tree biomass N could be recycled if left at he site at the time of harvest. *V. ferruginea*, with relatively lower stem biomass, had proportionally more N in leaves (52.9%) and branches (42.1%); *H. alchorneoides* showed a more even distribution of whole-biomass N in stems (39%), branches (27%), and leaves (33.8%). *V. guatemalensis* and *H. alchorneoides* had the highest proportions of stemwood P (72.4 and 62.1%, respectively) (Fig. 2).

V. guatemalensis, with the highest stem biomass and Ca concentration, also had the highest stemwood Ca (over 600 kg/ha, or 84% of whole-tree biomass Ca), approximately twice as much as either *S. microstachyum* or *V. ferruginea*, and several times more than *H. alchorneoides* (Montagnini and Sancho 1994a). Therefore, the harvest of *V. guatemalensis* trees could substantially reduce the amount of Ca in the site. However, while the *V. guatemalensis* trees are living, relative large amounts could be recycled, because although it represented only 16% of whole-tree biomass, the amount of Ca in leaves and branches together was over 100 kg/ha. Likewise, *V. guatemalensis* with its high stem biomass and high Mg concentration also had the highest Mg in stemwood (55% of whole-tree biomass, or approximately 30 kg/ha) (Montagnini and Sancho 1994a). Again, removal of *V. guatemalensis* stems would affect the sites's Mg budget more dramatically so than the other species, especially if the whole tree is harvested. For K the picture changed: the highest accumulation of K in stems was found in *H. alchorneoides* (252 kg/ha), followed by *V. guatemalensis* with 175 kg/ha, which represents 76.8% of whole-tree biomass K. Thus whole-tree harvest of *H. alchorneoides* and *V. guatemalensis* may have the greatest effects on the K budget (Montagnini and Sancho 1994a).

For the nutrients with lowest use efficiency values (ej. N) the forest-floor comprised a relatively high proportion of the total (Fig. 1). Therefore the forest-floor appears as an important compartment for N accumulation and recycling, although with marked differences among the species considered (Fig. 1). If the forest-floor is burned or collected for fuelwood, a substantial loss of organic matter and N may occur, while if the litter is left on the floor after harvest, it represents a significant reservoir for the next rotation.

In contrast, for P, which was relatively more scarce and showed higher use efficiency values, a higher proportion was stored in live tree biomass (Fig. 2). Although the forest-floor was still a substantial compartment, it was proportionally smaller than for N. In comparison, especially for *V. ferruginea* and *S. microstachyum*, root biomass P was relatively more important than forest-floor P (Fig. 2). Under tropical humid conditions P recycling from roots could be particularly important because root turnover is expected to be relatively fast. The roots are less likely to be affected during manual timber harvest operations than the forest-floor, while mechanical site operations could seriously affect the root system and its nutrient storing and recycling capacity. This can be especially critical for P and K, often mentioned as the nutrients which are most likely to be depleted from soils with subsequent rotations (Wadsworth 1983, Bruijnzeel 1991).

CONCLUSIONS AND RECOMMENDATIONS

A number of economically valuable native tree species were found to have positive impacts on soils in the region studied. The calculation of nutrient use efficiencies proved a useful tool for system design and management: to conserve nutrients in the long term, species with low use efficiency should be combined in time or space with others with high use efficiency. Evaluation of biomass nutrient allocation helped in drawing specific management recommendations: preserving the forest-floor was key for nutrient conservation, but for the most limiting nutrients, the roots were more important. For ecosystem rehabilitation, the examination of tree growth, soil chemistry and litter biomass and nutrients constitutes a minimum set of measurements needed for the design and long-term management of sustainable forest systems.

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FIGURE LEGENDS

Fig. 1. Nitrogen stocks in above ground biomass, forest-floor litter and roots of 4-year-old stands of four indigenous timber species grown in pure plantation at La Selva Biological Station, Costa Rica.

Fig. 2. Phosphorus stocks in above ground biomass, forest-floor litter and roots of 4-year-old stands of four indigenous timber species grown in pure plantation at La Selva Biological Station, Costa Rica.

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.

Species/Site	Organic Matter (%)	Total N (%)	P (mg kg)$^{-1}$	Ca (cmol kg^{-1})	Mg	K	PH	Bulk density (g cm^{-3})	H_2O (%)
Stryphnodendron microstachyum	6.0ab	0.29b	5.6a	0.45a	0.63ab	0.27a	5.4ab	0.80a	42.9bc
Vochysia ferruginea	6.6a	0.32^{a}	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 ($n = 5$, $P < 0.05$).

Table 2. Means, aboveground biomass and annual increments for the four native species in plantation at La Selva, Costa Rica[1].

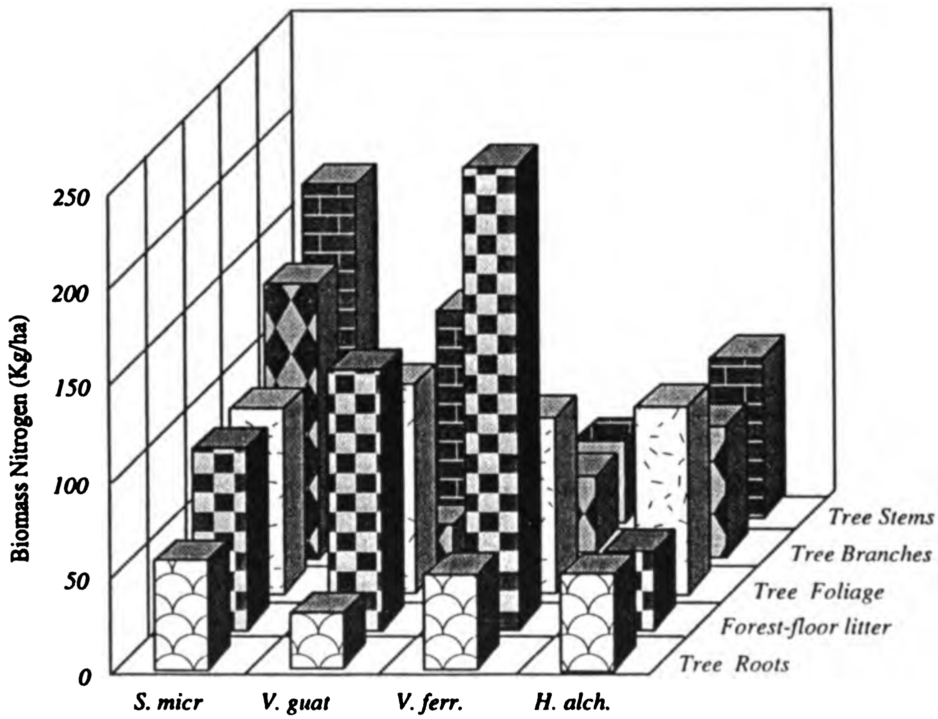
Tree species	Aboveground live biomass, kg/ha				Mean annual Increment, t $ha^{-1}yr^{-1}$	
	Stem	Branches	Leaves	Total	Total	Stems
Stryphnodendron microstachyum	35,250a	15,250^a	4,325^a	54,825a	13.7a	8.8^a
Vochysia ferruginea	24,750b	14,250^a	5,925^a	44,925	11.2b	6.2b
Vochysia guatemalensis	41,750a	6,500b	7,250^a	55,500	13.9a	10.4^a
Hyeronima alchorneoides	26,250a	12,250^a	5,350^a	43,850	12.0b	6.5b

[1] Differences between sites for a given parameter are statiscally significant ($P < 0.05$) when means are followed by different letters.

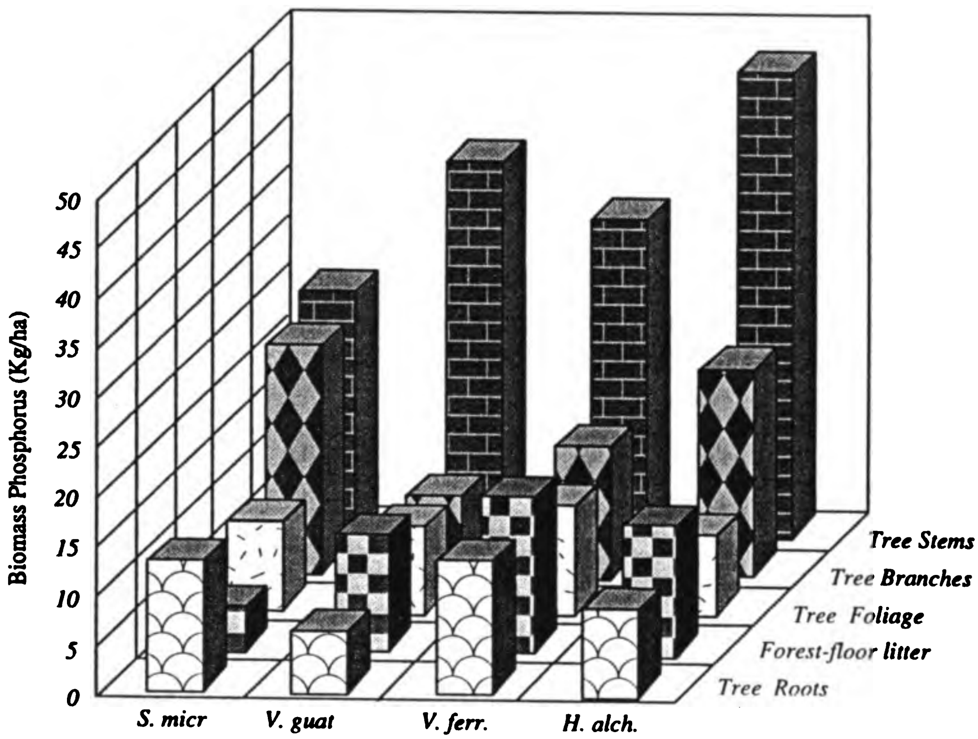
Table 3. Nutrient use efficiencies (NUE) (Megagrams of annual stem biomass increment/kg nutrient in annual litter fall) for the four native species in plantation at La Selva, Costa Rica.

Tree Species	**N**	**Ca**	**Mg**	**K**	**P**
Stryphnodendron mycrostachyum	0.08	0.06	0.35	0.63	0.53
Vochysia ferruginea	0.08	0.03	0.26	0.38	0.56
Vochysia guatemalensis	0.16	0.05	0.29	0.84	1.07
Hyeronima alchorneoides	0.09	0.03	0.15	0.22	0.45

Biomass Nitrogen



Biomass Phosphorus



Nutrient cycling and nutrient use efficiency in agroforestry systems

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INTRODUCTION

In humid tropical regions, soil nutrients are key factors influencing plant productivity and long-term sustainability of a production system. It has long been maintained that nutrient losses and increased weed invasion are the principal contributors to abandonment of fields of annual grains or root crops after 2-4 years of use (Watters 1971, Van Wambeke 1992, Bandy et al. 1993). Increased weed infestation of agricultural fields after nutrient loss results from the greater ability of weeds to take up scarce nutrients relative to most annual or root crops, thus out-competing these plants in the use of nutrients and other resources. Many "weed" species are perennials and woody species, whose ability to compete depends on a variety of mechanisms associated with roots, woody stems, and litter production. A key to increasing the sustainability of agricultural systems is to incorporate species that have these nutrient-conserving capabilities, while at the same time producing a crop that has economic and/or subsistence value. Many indigenous peoples have devised such systems through trial and error, and this chapter presents examples from the Kayapó in Brazil, and from other traditional systems from Asia and Africa.

The importance of nitrogen fixing species in agroforestry systems is widely recognized. In this chapter, we discuss this and other effects of woody species on soil fertility, the interactions between species of woody plants, and the significance for design of agroforestry systems. The concept of nutrient use efficiency by plants is brought forward as a potential tool to aid in system design and management. Finally, we stress the need for initial economic incentives to allow for system establishment and to increase the adoptability of sound agroforestry techniques by local farmers.

NUTRIENT DYNAMICS IN AGROFORESTRY SYSTEMS

Examples of Traditional Sustainable Agroforestry

Shifting agriculture has been practiced in the tropics for many centuries. Today, shifting (also called "swidden", "slash-and-burn") agriculture is the predominant land-use practice on about 30% of the arable soils of the world and provides sustenance for an estimated 300 million of the world's poorest people (Andriesse and Schelhaas 1987). Traditional shifting agriculture uses long forest fallows between short periods of farming. Long fallows make the traditional technique sustainable but also require extensive amounts of land. When land is scarce, farmers shorten forest fallows and lengthen agricultural periods, resulting in soil nutrient depletion, reduced crop yields and increased weed invasion.

Similar patterns are reported in the tropics worldwide, in spite of differences in ecological and socioeconomic conditions. For example, the "jhum" cycle is a system of shifting agriculture widely practiced by about 30 million people in the hilly, subtropical region of northeast India (Ramakrishnan 1992). A variety of versions of jhum agriculture are practiced by the different tribes in cycles that range from 10 to 30 years. However the shortening of the jhum cycle to 4-5 years during recent times has led to concerns about the resulting soil degradation and yield declines in a pattern much like that experienced in lowland humid regions of Latin America and Africa.

An Example from the Kayapó in Brazil

There are numerous examples of agricultural practices of indigenous peoples, or of pioneers such as the Amazonian caboclos, that use trees to maintain or restore soil fertility without chemical fertilizers (Anderson 1990, Gómez-Pompa and Kaus 1990, Subler and Uhl 1990, Balée 1992, Lescure et al. 1992, Nations 1992, Jordan 1995). One well-documented example is that of the Kayapó in Brazil (Posey 1982). The Kayapó live today on a 2.5 million hectare reserve in the Xingú River Basin in the Amazon region. Although the Kayapó are nomads for part of the year, cultivation of plants for food and medicine is an important part of their culture. Cultivation begins with the clearing of a circular field. Trees are felled so that the fallen stems radiate outward, and the bulk of the forest canopy biomass ends up near the perimeter of the circle. Root crops such as sweet potatoes or yams (*Dioscorea* spp.), taro (*Colocasia esculenta*) and manioc (*Manihot esculenta*) are planted in open corridors left between the fallen trees. The crops are already rooted and growing before burning occurs.

Burning is carefully managed. Tribal elders agree upon an appropriate day when winds are minimal and the fields will burn thoroughly but not too quickly. The farmers begin burning the piles of dried debris one at a time. A protracted burn minimizes the heat, so that the root crops will lose their green tops but not their viability. These pre-burn crops are given a head start on weeds that will establish in the ash.

Papaya, bananas, cotton, urucú (*Bixa orellana*), and tobacco, which require a high quantity of nutrients, are planted on the outer margins of the field, where ash concentrations are highest. A few weeks after the burn, the farmers gather up unburned sticks and limbs for a second fire. In the resulting piles of ash, other high-nutrient requiring plants like beans, squash, and melons are planted.

The fields of the Kayapó last for many years. Sweet potato and yam bear in fields that are four or five years old. Bananas and urucú, and domesticated varieties of a large vine-like plant called "kupa" commonly continue to bear edible leaves and stalks for 8 to 12 years, and some fields that are 40 years old still yield edible kupa.

Many plants useful to the Kayapó establish naturally in the old fields. Some of these spontaneously colonizing plants have important medicinal values, and others provide seeds, berries, and roots for food. Some of the colonizing plants bear fruits that make excellent fish bait. Others attract animals or birds. The animals drawn to the leafy and bushy plants in these sites are easier to hunt than those inhabiting the canopy of the high forest.

Because the Kayapó understand this process and take advantage of the species that sequentially occupy a site, they do not need to continually seek new forest to cut and burn. After many years, when an old site develops into a closed forest, it can be cut and used again, with no long term degradation of the site.

Kayapó practices contrast with the shifting cultivation in the Amazon carried out by colonists from southern and northeastern Brazil. The latter depend mainly upon crops such as corn, rice, and cassava which grow well for only two or three years. When yields decline, the colonists abandon the fields and clear new forest.

Homegardens: Traditional Low- Scale, Low-Input Agroforestry

Homegardens are systems for the production of subsistence crops for the gardener and family, with or without the addition of cash crops. They can be located immediately surrounding the home or slightly further away, but still near the residential area. It is claimed that homegardens originated in prehistoric times when hunters and gatherers accidentlaly dispersed seed of highly valued fruit trees close to their homes (Soemarwoto 1987). In the near east, homegardens are documented in paintings dated 3,000 years BC, and the practice continues in modern times. There are several well documented examples from Java, and they are also common in other parts of Indonesia, and in Malaysia, India, and in countries of Africa and Latin America. They hold great species diversity with many life forms varying from climbers to tall trees and vines, creating a forest-like, multistorey canopy structure. The canopies of most homegardens consist of 2-5 layers. Usually there are no rows, blocks or definite planting distances among components. Chemical fertilizers are generally not used; dung, household wastes and pruning residues are used instead. The use of species with anti-pest properties is also a widespread practice that decreases the need for chemical pesticides (Fernandes et al. 1989, Michon et al. 1989). They generally have stable yields and great variety of products, allowing continuous or repeated harvests during the year under a low-input system.

In west Java, the average size of homegardens is <0.1 ha, with an average of 19.0 and 24 species per garden in the dry and wet seasons, respectively. Size of homegardens decreases with altitude with highest number of species occurring at 500-1000 m. Poor people tend to grow more staples, vegetables and fruits, well-off people tend to grow more ornamentals and high-economic value cash crops. More subsistence crops are grown in remote areas, more cash crops are grown near cities. Culture and tradition influence composition: e.g., more medicinal plants are found in west Java, while tobacco and coffee are more commonly grown in Muslim districts of southern Ethiopia; animals are found in most gardens but pigs are not found in Muslim homegardens; in west Java with intense rains fishponds are usually present (Soemarwoto 1987).

Homegardens can be sustainable production systems, however this is true under low-input and low-yield conditions. For example, the homegardens of the Chagga, in Mt. Kilimanjaro

(Tanzania) represent ecologically sustainable land-use systems, but their productivity is relatively low and needs to be increased if they are expected to support larger populations (Fernandes et al. 1989). Migration of youngsters to urban areas has disrupted the traditional transmission of the knowledge and experience required for the successful management and perpetuation of the complex multicropping system. Availability of fertilizers has decreased the need for organic manures, thus greatly reducing labor inputs in homegardens and therefore reducing nutrient recyling processes. If homegardens are to be used for raising the standard of living of people to satisfactory levels, the question arises whether the yield and the income can be significantly increased without sacrificing their sustainability.

Nutrient Mobilization and Losses in Shifting Agriculture

Scientists have long believed that sharp decreases in growth of annuals like corn and rice after two or three years of shifting cultivation were due to nutrient losses such as leaching of calcium and potassium and volatilization of N. However, results from the Man and the Biosphere project at San Carlos de Río Negro in Venezuela (Jordan 1989) suggested that during the first 2-3 years of cultivation of a cleared forest, only a very small proportion of the nutrient stocks was actually lost through leaching (Figs. 1, 2). The decrease in production was instead due to binding of formerly labile phosphorus by iron and aluminum in the mineral soil, thus rendering the P unavailable to crop plants.

In undisturbed forests of the region, P appears to be readily available to the trees (Jordan 1989). Even after cutting and burning the forest, and during the first few years of cultivation, most of the soil P was kept mobile because it was chelated to Fe and Al by organic acids leached from decomposing organic matter on the soil surface. After the site was cut and burned, and as the humus and litter gradually disappeared during the three years of cultivation, liberation of organic acids decreased and an increasing proportion of P was bound in the soil. By the end of the third year, all of the humus, and most of the tree trunks were gone. The study concluded that lack of labile P caused diminishing crop productivity, and that the conversion of P from labile to bound states was due to the disappearance of humus and organic matter on the soil surface.

Despite binding of P in the soil, secondary successional vegetation invaded the site, and by the fifth year stocks of Ca, K, Mg, and N began to decline (Figs. 1, 2). There were no detectable changes in total ecosystem stocks of P during the experiment. However, there was an increase in P in biomass as the successional forest became established. Apparently, successional plant species were able to take up bound P from the soil. This P was probably in Fe- and Al-bound fractions that were unavailable to the crop plants.

What is the mechanism through which woody vegetation is able to take up the P unavailable to crops? One possibility is excretion of piscidic acid[1] from the roots (Ae et al. 1990), or leaching of citric and malic acids from the decomposing leaf litter of the trees (Han 1989). These organic acids can replace the P bound by Fe and Al the clay, liberating the P and rendering it soluble and readily available for uptake. Annual plants may not have these P recycling mechanisms, or crop plants bred for productivity may have lost the capability of taking up these forms of P (Chapin

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[1] Piscidic acid = (p-hydroxy benzyl) tartaric acid

1980, 1983).

Mobilization of bound P by woody plants accounts for sustainability of agroforestry systems such as those of the Kayapó. The tree crops are established soon after clearing and burning, before the tree trunks, branches, and organic matter in the upper soil horizons are completely decomposed. Because the new trees are already producing litter before the remains of the old ones disappear, the production of organic acids is not interrupted, and the P is kept in a labile state.

This suggests that it would be desirable to start an agroforestry system immediately after clearing a fallow or primary forest. For example, establishment of rubber trees (*Hevea brasiliensis*) in the Brazilian Amazon region has been highly successful under the partially opened canopy of a secondary forest (Mesquita 1995). At the time of planting, a thick layer of litter and humus on the forest floor supplied nutrients, improved the microclimate, prevented erosion, and was an energy source for soil microorganisms that improved the physical and chemical properties of the soil.

Unfortunately, many agroforestry systems are established on sites that have been cropped or kept in pasture for many years. In such sites, nutrient status of the soils is low. Figs. 1 and 2 show that in the experimental plots at San Carlos de Río Negro, nutrient loss continued even after cultivation was abandoned after three years, and nutrient recovery did not begin until year five. Apparently in this system with high rainfall (3600 mm/year) and low cation exchange capacity, it took a couple of years for fallow vegetation to cover the site and reestablish nutrient cycling mechanisms that lead to recovery. By the time the reversal began, nutrient stocks were only a fraction of those in the ecosystem when cultivation started.

Managed Forest Fallows

Improved fallows have been proposed as a management alternative to shifting cultivation in the tropics (Nair 1990, Kass et al. 1993). 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 (Kass et al. 1993, Denevan at al. 1984, Padoch et al. 1985, Padoch and De Jong 1987, Raintree and Warner 1986, Unruh 1990, Deal Amo and Ramos 1993, Sips 1993). Some of these systems produce crops for local consumption and for a regional market, providing substantial cash income for many farmers (Padoch et al. 1985).

The use of managed fallows based on a single species is quite widespread in the Americas, occurring from subtropical areas of Brazil to highland regions of Central America (Kass et al. 1993, Sips 1993). These systems include both biologically and economically enriched fallows. Some of the economically enriched fallows of the Amazon require more intensive management by which certain trees are protected during clearing or planted during the cropping period and maintained during the fallow (Padoch and De Jong 1987). In the planted fallows, one or more species with biological or economic value are introduced to shorten the fallow regeneration period or increase its economic value (Szott et al. 1991, Vergara 1987).

For example, in an experimental fallow system in the Peruvian Amazon, selected soil-improving tree species were planted in abandoned shifting agriculture fields (Szott et al 1991).

The species planted were acid-tolerant woody legumes, *Cajanus cajan* and *Inga edulis*. Two years after planting, the total ecosystem levels of Mg and Ca declined, while total N and K increased, and the levels of P increased after 4.5 years. In these experiences, weed control was achieved more rapidly with herbaceous species (*Pueraria phaseoloides, Desmodium ovalifolium*), however good suppression of weeds was also eventually obtained by the woody legumes.

Experiences such as those described by Szott et al. (1991) are relevant in tropical regions worldwide where land becomes scarce and the fallows are not long enough to restore soils to their productive capacity. For example, *Gliricidia sepium*, a N-fixing tree native from the Neotropics and broadly used there as shade for coffee, for living fences and as a common component of homegardes, is currently a popular fallow tree in some parts of lowland rainforest regions of western Nigeria (Adejuwon and Adesina 1990). Its poles are staked as support for training yam vines, and as the species propagates vegetatively, the staked poles coppice within a short time and at the end of the cropping cycle they become part of the fallow vegetation. Compared to natural fallows in which the development of trees is random, the progress of the cultivated fallows of *G. sepium* leads to greater organic matter build up and increases in nitrate-nitrogen and potassium concentrations in the soils. Other leguminous trees that are also becoming popular in the region such as *Leucaena leucocephala* or *Derris indica* could also be used with similar results (Adejuwon and Adesina 1990).

Other improved fallow systems rely more on the introduction of valuable species in the fallow period, in combination with other species that have soil restoring capacity. For example, in a traditional shifting cultivation system in the lowlands of Papua New Guinea, the cropping cycle is usually 18 months, consisting on mixed food crop gardens with yams, bananas, taro, sugar cane and some fruit trees. The fallow cycles last up to 30 years. Robusta coffee, a cash crop component, has been added to the fallows in some areas since the 1950s. The coffee is interplanted with *Leucaena leucocephala* as shade, and food crops are planted in the establishment phase. This seems to be a promising enriched fallow alternative, and the local fallow gardeners appear to be willing to take on such innovations (Allen 1985).

Nutrient Dynamics in More Recent Agroforestry: Alley Cropping

In the mid-1980s, considerable research focused on the development of low-input technologies for sustainable food production by small-hold farmers. Results from this research suggest that in situations where planted fallows are not feasible because land is scarce, techniques such as alley cropping and the application of mulch (green covers) may become practical alternatives (Kang and Wilson 1987, Kang et al. 1990). In alley cropping, annual crops are grown between hedgerows of preferably N-fixing leguminous shrubs and trees, which are periodically pruned to prevent shading of companion crops. The prunings can then be used as mulch and green manure to improve soil fertility and produce high-quality fodder. Alley cropping is regarded as an improved bush-fallow system with the following potential advantages: 1) Cropping and fallow phases are combined; 2) Cropping periods are longer, and land is used more intensively; 3) Soil fertility is effectively maintained with the use of species selected for that purpose; and 4) The need for external inputs is reduced (Kang and Wilson 1987).

In areas of Nigeria and in other forest-savanna transition regions of Africa with non-acid soils, results of field and on-farm trials have shown that alley cropping with corn, cowpea, rice and cassava between hedgerows of *Leucaena leuocephala* and *Gliricidia sepium* allowed higher levels of crop production than monocultures (Kang and Wilson 1987). Cowpea and rice showed no significant increase in yield in comparison with monocultures, but when planted in alley cropping with *Leucaena*, they did not respond to N fertilization, indicating that the N supply from prunings was adequate, and additional fertilizers were not necessary.

When used in regions of low soil fertility, the addition of green manure from the trees grown in the hedgerows can significantly increase the yield of the crops grown in the alleys. For example, in western Kenya, experiments carried on red, acid soils showed that maize and bean yields were higher when grown in alley cropping with *Leucaena leucocephala*, *Cajanus cajan* and *Sesbania sesban*. These responses were still significant in the third testing season (Onim et al. 1990).

However, in some instances although the tree prunings can add substantial amounts of nutrients and organic matter to the soil, these quantities may not be enough to reach the levels required by the associated crops. For example in experiments conducted in Ibadan, Nigeria, prunings from *Gliricidia sepium* hedgerows yielded the highest N while prunings from *Cassia* spp. yielded the highest organic matter. N supplementation was needed to optimize the yield of maize, with higher amounts required in *Flemingia* alleys than in *Gliricidia* or *Cassia* alleys (Yamoha et al. 1986).

Agroforestry techniques such as alley cropping are better able to increase available stocks of nutrients than monocultures. The following examples illustrate the contributions of this agroforestry system to P and N dynamics. Fig. 3 compares total labile P in a replicated alley-cropping system (*Albizia julibrissin* as the hedge, *Sorghum bicolor* as the grain crop) on an Ultisol in the state of Georgia, U.S.A., with plots without alleys that otherwise had received the same treatment. Both alley-cropped and monocultured sorghum were previously green-manured in summer with velvet bean (*Mucuna deeringiana*) and in winter with crimson clover (*Trifolium incarnatum*). There was a gradual increase in labile P between the two systems, but even by the third year, sorghum production in the agroforestry system was not greater than that in the monoculture (Matta-Machado and Jordan 1995).

This study was carried out on soil degraded by a century of cotton and soybean farming. While agroforestry can increase nutrient stocks compared to non-agroforestry plots, this increase comes slowly. A better strategy, if it is affordable, might be to initially fertilize the agroforestry system to enable faster production. An even better strategy, if a suitable site is available, is to start the system following a fallow. When an agroforestry system begins with high levels of nutrients, the system has a higher chance of maintaining itself.

Research at the Tropical Agricultural Research and Training Center (CATIE) in Turrialba, Costa Rica has addressed the role of N in alley cropping annual crops with trees used in agroforestry throughout the humid tropics. Results of long term experiments with maize grown with *Erythrina poeppigiana* and *Gliricidia sepium* hedgerows showed that after seven years, maize productivity and N uptake were more than twice as high in alley cropping with either species than in monoculture (Haggar et al. 1993). Higher rates of soil N mineralization in the alley cropping systems led to faster maize establishment in comparison with the single crop. These higher rates of soil N mineralization resulted from the build up of readily mineralizable organic N compounds in the soil after seven years of tree mulch application. The long term accumulation of mineralizable N was more important than the synchrony of mulch N release and crop uptake in determining the higher yields and N uptake by maize in the alley cropping system compared with the sole crop. In spite of higher yields, total recovery of mulch N by the maize in a single year was only about 10 kg/ha, with most of it taken up during the first two months following planting; however this initial effect led to faster establishment of maize in the alley crop. This again points to the need for long-term studies that assess the benefits of alley cropping to crop yields. This also serves to stress that early results may not be outstanding, and that other external inputs may be necessary initially to ensure the system's successful establishment.

The use of alley cropping can also help ameliorate the detrimental effects caused by certain soil management practices. For example, experiments in Ibadan, Nigeria have shown overall nutrient declines in soils through a four year cropping cycle, with the highest depletion of soil nutrients in plow-till systems and the least severe in *Leucaena* based systems (Lal 1989).

In alley cropping systems sometimes competition between trees and crops can significantly reduce yields by the crop (Haggar 1994). Other research on non-acid, alluvial soils in Yurimaguas, in the Peruvian Amazon, showed that rice yield reductions from light competition were evident up to 1.5 meters from the hedgerows of all tree species tried (*Inga* spp., *Leucaena* spp. and *Erythrina* spp.), with the greatest decrease in yield found with *Leucaena* hedgerows (Salazar et al. 1993). Weed control was better achieved with the slowly decomposing *Inga* mulch, but rice yields (at a distance >1.5 m from the hedgerows) were higher with *Leucaena* and *Erythrina*.

Species choice strongly influences the success and overall applicability of alley cropping techniques. For example, many plant species contain allelochemicals that suppress weeds and other plants. Allelopathic interactions are useful when the suppressed plants are considered weeds, but care must be exercised when the mulch is applied to crop plants (Regnier and Janke

1990). Finally, on very acid soils with high aluminum saturation, some of the tree species preferred for alley cropping, such as *Leucaena* spp. and *Gliricidia* spp., do not grow well, and they have to be replaced by other species more adapted to those conditions (e.g., *Calliandra* spp., *Cassia* spp., *Inga* spp., *Flemingea* spp., or *Paraserianthes* spp.).

Modified Traditional Systems: Trees Used for Shade of Perennial Crops

At CATIE, Costa Rica, research has long intended to modify the predominant traditional systems of the region--coffee or cacao with shade trees--to improve their productivity and sustainability. This research started with examination of nutrient cycling variables in the existing systems in the region and was followed by experimental systems where nutrient cycling could be examined in controlled experiments. For example, on a farm near CATIE, Beer (1988) compared the annual nutrient return in litter fall and prunings in systems of coffee with *Erythrina poeppigiana* (poró), and coffee with poró and *Cordia alliodora* (laurel). Both trees are common in agroforestry systems with perennial crops in Latin America. The total annual input of litter fall plus pruning residues was similar in both systems. Total annual litter fall input from poró was less than half in association with laurel than without laurel, but litter fall from laurel compensated for the reduced litter fall from poró. In addition, the inclusion of laurel with poró and coffee resulted in a more even distribution of annual nutrient input. Annual inputs of Ca and Mg in litter fall and prunings were larger in the system including laurel than in the system with poró alone. There were no differences in the total input of N or P between the two systems, and the system including laurel had a smaller annual input of K. In spite of these differences among the two systems, the amounts of nutrients recycled by the associated trees reached the recommended levels of fertilizer required for coffee production in both cases.

Which system to choose will depend on the most limiting nutrients in each case. In the previous example, the system with laurel was preferred by many farmers because, apart from a more even nutrient input throughout the year, the value of the laurel timber added an economic incentive. In addition, laurel is a self pruning species while poró has to be pruned to increase biomass recycling; the system including laurel is therefore less costly than the system with poró alone. Results of experiments at CATIE confirmed these findings. Recommendations were also drawn to modify the traditional systems in order to take advantage of the nutrient cycling benefits from the shade trees and to consider labor availability and timber value (Fassbender et al. 1991).

Other research on similar traditional systems have also demonstrated the importance of nutrient cycling by shade trees and perennial crops. In Ocumare de la Costa, Venezuela, Aranguren et al. (1982) concluded that shade trees of cacao plantations contributed about half of the total annual litter fall. The rate of N transfer to the soil via litter fall was 321 kg/ha. N output with the harvest of cacao pods was 45 kg/ha, with approximately 20 kg returned to the field after processing from pod shells. The authors concluded that the net harvest output of N could be compensated by inputs of N in shade-tree leaf litter from species of *Inga* and *Erythrina*.

Agroforestry in Semi-arid Environments

The semi-arid tropics cover an area of about 20 million km^2 and are inhabited by about 700 million people, nearly half of them in India (Vandenbeldt 1990). It covers most of western, eastern, and south-central Africa; most of India, northeastern Burma, northeastern Thailand, and northern Australia; large parts of eastern and central south America, and western parts of Central

America. In all, about 34% of the land area of 48 countries is included in the semi-arid tropics. They are characterized by low standards of living and low and erratic crop yields due to defficient and strongly seasonal and undependable precipitation (Swindale 1982, in Vandenbeldt 1990). The climate is characterized by high atmospheric water demand; high mean anual temperatures (>18°C); and low, variable annual rainfall (400-1900mm). The climate of most of the semi-arid tropics is monsoonal, with over 90% of the rainfall occurring in the period of April-October in the northern hemisphere and October-April in the southern hemisphere.

In arid and semi-arid environments, agroforestry systems help to provide greater insurance against weather abnormalities (Swaminathan 1987). Some multiple purpose trees commonly used in agroforestry such as species of *Acacia*, *Prosopis*, and *Casuarina*, can grow well in arid areas and can be conbined with grain crops. Perennial shrubs such as *Sesbania grandiflora* and *Cajanus cajan* are also promising for producing food, fodder and fuelwood. In semi-arid regions, browsing from shrubs and trees, more resistant to dry periods than herbaceous forage, can represent as much of 20-25% of the total intake for livestock (Le Houérou 1987). This provides stability and productivity to livestock and is a main source of income to farmers.

In Africa, shrubland, woodland (open dry forest with more than 50% canopy cover) and savanna (annual or perennnnial grass or herb cover with <50% canopy cover) cover about 10 million km^2, or about 35% of the continent (Le Houérou 1987). Trees, shrubs and palms have always played important ecological and economic roles semi-arid Africa. In ancient Egypt, certain species of trees and palms (e.g., *Balanites aegyptica*, *Phoenix dactylifera*) were worshiped as sacred trees (von Maydell 1987). The baobab (*Adansonia digitata*) and *Acacia albida* are other trees of great significance to people in Saharan, Sahelian, and Sudan savannas.

A. albida, a N-fixing tree widespread in arid and semi-arid Africa, keeps its foliage through the dry season and only sheds its leaves at the beginning of the growing season, therefore there is no competition for water or nutrients with the associated crops. In fields where *A. albida* grows naturally at densities of 20-40 trees/ha, the most common intercrops are with millet, sorghum, maize, and peanuts. The pods of *A. albida* are good fodder during the dry season, and the tree also produces good firewood, thorny fencing material, tannins, gum, and bee forage (von Maydell 1987).

In India, the extent of the arid and semi-arid region is about 300,000 km^2, mostly in the northwest (Shankarnarayan 1989). The *Prosopis cineraria* based systems of semi-arid India are similar to the *A. albida* systems of semi-arid Africa. *P. cineraria*, also a N-fixer, is an important source of animal feed, fuel and timber. As *A. albida*, *P. cineraria* has a very deep tap root and it can be lopped at a young age (about 8 years) with yields of 40-70 kg of fuelwood, 20-30 kg of leaves and 5 kg of pods per year (Singh 1987). In fields with relatively low densities of *P. cineraria* (about 120 trees per ha, depending on soil type and rainfall), it is usually intercropped with millet and legumes. Improved soil fertility and higher moisture content have been found in *P. cineraria* intercropped systems, along with higher grain yield and forage biomass production (Singh 1987).

In semi-arid ecosystems, soils under tree canopies apparently have greater levels of organic matter, calcium, magnesium, potassium and phosphorus than those in open grass (Belsky *et al.* 1993, Campbell *et al.* 1994, Isichei and Moughalu 1992, Kellman 1989). However, in these systems the direct effects of trees cannot be easily distinguished from other, indirect effects, because higher fertility underneath the trees is often associated with a more favorable microenvironment (Belsky *et al.* 1993). Additionally, because the trees in savanna ecosystems have generally been in place for a relatively long time before crops are interplanted and soils are sampled, it is hard to determine cause and effect relationships between the presence of the trees and improved soil conditions under their canopies.

The Role of Animals: Agrosilvopastoral Systems

Agrosilvopastoral systems--the combination of timber, fuelwood or fruit trees with animals, with or without crops--are practiced at many scales. A large scale system may include timber plantations with grazing to control weeds and to obtain a more immediate return from the sale of animal products. Cattle raising can also complement subsistence agriculture, with animals integrated in home gardens or in systems of fodder production to feed animals in stables. In farms where alley cropping is practiced, animal manure can be added to mulch to contribute rapidly available nutrients to crops. Mulches of manure can also serve as a nutrient source for microbial decomposers, speeding up the decomposition of plant materials. In some regions, the incorporation of trees--especially MPTS--can change cattle raising from an inefficient use of land to a more ecologically and economically feasible activity. The incorporation of trees can improve system productivity either by increasing pasture yields or through the production of tree fodder from leaves and fruits (Gill et al. 1990, Cobbina 1994/1995).

Though the presence of animals in a tree plantation may accelerate nutrient cycling, if the animal load is too high, soil compaction may affect tree growth (Montagnini 1992). It is often difficult to separate the effects of soil compaction and nutrient recycling by animals from the impacts of trees and forage grasses or legumes. In experimental systems in the Atlantic region of

Costa Rica, a fast-growing leguminous tree species (*Erythrina berteroana*) was introduced in native grass pastures. Over a three-year study period, soil organic C increased in two non-grazing treatments, and soil bulk density decreased in the control areas with no grazing and no trees (Cooperband and Logan 1993). Changes in soil pH, exchangeable cations, Al and P levels were not clearly a result of the impacts associated with grazing, or of changes associated with site preparation.

Other experiments on eroded marginal lands in subtropical India compared soil erosion in agrosilvopastoral systems with *Leucaena leucocephala* (used for fuelwood and fodder) and *Pennisetum purpureum* (used for fodder) with the traditional rainfed crop sequence of *Sesamum indicum* followed by *Brassica napus* (Grewal et al. 1994). Results suggested that the agrosilvopastoral systems were more effective in conserving soil than the traditional cropping system. However, animal grazing did not have an influence on soil variables because the animals were kept outside of the system.

Agrosilvopastoral systems require careful management to take advantage of nutrient cycling and to avoid soil compaction and trampling by cattle. This can be achieved at a small scale where manual recycling of manure, managing and rotating pastures and hauling fodder to feed animals in stables or enclosures are more feasible. However, these practices are labor intensive and will only be adopted when the benefits and returns are attractive to the farmers.

THE EFFECTS OF TREES ON SOIL FERTILITY

Agroforestry systems have often been regarded as having protecting functions on soil physical and chemical properties. It can be argued that erosion control can be achieved through the use of soil covers, independently of the presence of trees. A number of herbaceous species were used in early attempts to improve fallows in tropical areas, but in the more seasonal climates, the herbaceous crops with their shallow roots were not able to sustain the dry season very well. Some herbaceous, leguminous species such as *Pueraria phaseoloides* and *Centrosema pubescens* are still used with success as green covers of commercial tree plantations (rubber, cacao) in several tropical humid regions. In the 1970s and 1980s, as selective herbicides became more accessible and the "minimun tillage" practices became popular in tropical regions, the use of cover crops such as *Pueraria phaseoloides* and *Mucuna utilis* became widespread as in-situ mulches. However, small shrubs such as *Crotalaria* spp. and *Cajanus cajan* were found to be more adequate than herbaceous species because they could stand drier periods and competed less with the associated herbaceous crops. Tree or shrub species that stand pruning, have high rates of organic matter production and good nutrient cycling abilities can be combined in agroforestry systems with agricultural crops or cattle, with the added advantage of yielding products such as fuelwood, timber, fruits or fodder.

In addition, in agroforestry all system components including trees, crops, and their litter can contribute to nutrient cycling and soil protection. For example, a summary of erosion rates under tropical forest, tree crops and some agroforestry systems is given in Table 1. If the rates of soil loss shown are considered low (<2tons/ha/yr), moderate (2-10 tons/ha/yr) and high (>10 tons/ha/yr), then the lowest erosion rates correspond to natural rain forest, forest fallows, multistorey tree gardens, and undisturbed forest plantations; intermediate or moderate to high rates are found for cropping periods of shifting agriculture and taungya systems; and the highest rates are recorded for tree plantation crops and for forest plantations, both under intense management. The wide ranges shown by the data indicate the importance of management rather than the intrinsic nature of the systems. Additionally, it can be seen that the highest erosion rates were recorded for the two intensively managed systems in which there was no surface cover (Young 1989).

A key to the success of agroforestry systems is the choice of fast-growing woody components with positive impacts on soil properties (Sanchez et al. 1985, Nair 1989, Young 1989, Montagnini 1992). A number of publications compile characteristics, uses, and properties of Multiple-Purpose Tree Species (MPTS) for their application worldwide (e.g., NAS 1979, NAS 1980, Glover and Adams 1990, Lantican and Taylor 1991). The majority of the MPTS lists and data- bases include information on the role of trees on soil fertility or nutrient cycling. These guides emphasize the N-fixing ability and nodulating status of leguminous trees and actynorrhizal plants with few statements on their potential effect on other ecosystem nutrients.

Several indigenous and exotic tree species show potential for improving soil chemical, biological and physical characteristics, and could be advantageous in agroforestry combinations. For example, out of about 30 economically valuable tree species tested in experimental conditions in humid lowland regions of Costa Rica, Brazil and Argentina, nearly half had a positive influence on soil total N, organic matter, and/or exchangeable cations and P, in comparison with nearby pasture (Table 2). In several cases the values of the parameters tested under the tree canopies were close to those found in adjacent young secondary forests. Most of the other species tested did not appear to change soil conditions substantially, and they could be used on non-degraded soils (Table 2).

A number of constraints limit the broad utilization of results, such as those shown in Table

2, as a single criterion for species selection for agroforestry. Primarily, the results of standard soil fertility tests used in agriculture may not always reveal the soil's productive potential because they do not include all chemical forms of nutrients available for plant uptake. For example, although mineral N (NO_3^- and NH_4^+) makes up less than 10% of the total soil N pool, it is the form of N available to plants. Data on N mineralization rates under tree species are frequently not available because their estimation requires time-consuming laboratory or field incubation of soil samples. Evaluating the effects of trees on soil P availability is even more difficult, although P release from litter and its uptake by test crops can give an indirect indication of impacts on soil P availability.

The impacts of trees on soil fertility depend on nutrient recycling characteristics such as litter chemistry and decomposition rates. Tree litter can be used as mulch with different outcomes: a fast mulch decomposition rate may accelerate the growth of associated crops on poor soils, while in other cases a more persistent litter may provide a steady source of nutrients and a better soil cover year round. In the example shown in Table 2, high rates of litter fall and slower decomposition resulted in high litter accumulation and high soil organic matter under *V. ferruginea*, making this species well suited for protecting soils against erosion. In contrast, litter from *V. guatemalensis* may be especially important for Ca and Mg recycling (Montagnini et al. 1993). Although the litter of *H. alchorneoides* was less abundant than the other three species, it had a relatively faster decomposition rate and higher nutrient content. These characteristics promoted fast nutrient recycling, especially of N, Ca, Mg, K and P.

Additional factors influencing nutrient release from litter are its polyphenol and lignin content, as both compounds lower the quality of plant materials. The polyphenol to N ratio, for example, may serve as an index for short-term immobilization patterns observed for legumes with relatively high polyphenol content, and the lignin plus polyphenol to N ratio may serve as an index for longer-term release patterns (Palm 1995). The timing of nutrient release by trees is also important so that nutrients will be supplied in synchrony with crop needs (Palm 1995). Yet as discussed in the previous section, synchronizing nutrient supply may not be as important as the long-term build up of tree litter mulch and soil organic matter in influencing crop yields and, equally important, in maintaining soil productivity.

It has been argued that the ability of agroforestry systems to enhance nutrient availability is very limited on infertile soils compared to systems on fertile soils, although they can indeed play an important role in reducing nutrient losses in both situations (Szott et al. 1991). Litter production and quantities of nutrients recycled in litter are greater on fertile than infertile soils; however, use of prunings to accelerate nutrient fluxes may increase plant productivity on infertile soils (Szott et al. 1991).

Inclusion of woody components in a production system can provide benefits from the tree products themselves (timber, fuelwood, leaf mulches, and other tree products) and from their potential ecological advantages, especially their nutrient cycling abilities. The choice of a tree species will often depend on whether both productive and ecological advantages can be achieved in the same system, and in some cases one prevailing function may be desired.

NUTRIENT USE EFFICIENCY AND SPECIES CHOICE

The nutrient use efficiency (NUE) concept has been employed to describe the differential ability of tree species to accumulate organic matter in relation to nutrients taken up from the soil. NUE has been defined on different scales of space and time. At the plant population and community levels, NUE is generally defined as the amount of biomass produced per unit of nutrient taken up (Grubb 1989, Binkley et al. 1992, Medina 1995). Since direct measurements of nutrient absorption are not usually made for mature tree stands, leaf litter fall nutrients are generally used as an estimate of annual nutrient uptake (Vitousek 1984, Grubb 1989, Binkley et al. 1992). Ideally, efforts should be made to measure total production by stems, branches and roots and to consider nutrient uptake plus losses to herbivory and leaching of nutrients (Grubb 1989). Differences in nutrient cycling and efficiency of use may result from an ability to use various nutrient conserving mechanisms, from physiological to mutualistic interactions (Chapin 1980, 1983).

It is also important to consider the relationship between the recycling ability of the species and its potential short and long-term impacts on soil nutrient amelioration. A "nutrient cycling index" (NCI), taken as the inverse of NUE, i.e., the amount of nutrients in annual litterfall/annual tree biomass production, has been used to assess suitability of tree species for agroforestry combinations. For example, Fassbender et al. (1991) found that the P recycling index was about six times higher in combinations of cacao with *Erythrina poeppigiana* than with *Cordia alliodora* in agroforestry systems in Turrialba, Costa Rica. *Cordia*, a timber species, accumulated much P in stem biomass, while *Erythrina*, a shade tree with good nutrient cycling properties, produced large amounts of leaves and branches resulting in greater P recycling.

When put in context with nutrient recycling characteristics of a species, NUE can indicate appropriate system design and management to maintain productivity and recover or conserve nutrients over the long term. The ability of a species to produce large amounts of biomass with less nutrients may be an important consideration in choosing species for degraded, nutrient-poor sites.

Applicability of NUE in System Design and Management

From the 24 tree species shown in Table 2, data on tree productivity, leaf litter fall and litter chemistry of eight species in Bahia, Brazil and four species at La Selva, Costa Rica were used to calculate NUE values (Table 3). Because the species were part of a forestry project with fast-growing timber trees, NUE values were calculated as the annual stem biomass increments/nutrients in annual leaf litter fall (Montagnini 1995). There were not enough data on litter fall or productivity for the other species shown in Table 2. At both Bahia and La Selva, the highest efficiencies were for K and P, and the lowest were for N, Ca and Mg (Table 3).

Results from Bahia suggest that *B. macrophyllum* and *P. foliolosa*, with overall high NUE values, would grow well on relatively nutrient-poor soils, and thus could be good alternatives for reforestation of degraded sites following the abandonment from agriculture and pasture that is frequent in the region. *B. macrophyllum* tended to accumulate high amounts of litter under its canopy while *P. foliolosa* stands had relatively high amounts of organic matter and total N in the topsoil in comparison with adjacent areas of secondary forest (Montagnini et al. 1994). These features indicate that these species may be well suited for soil rehabilitation, including increasing soil organic matter content and protecting against soil erosion. Also at Bahia, species such as *B. grandis* and *H. aurea*, with overall lower NUE values, would be most appropriate for agroforestry combinations where crops could benefit from nutrient recycling from litter.

At La Selva, *V. ferruginea* showed comparatively low efficiency values for all the nutrients considered, confirming the beneficial role of this species in recycling organic matter and positively impacting soil fertility as shown in Table 2. The relatively low efficiency (high recycling) of N and P found for *S. microstachyum* and *H. alchorneoides* was also shown in experiments where maize grown with mulch of these species grew better and absorbed more N and P than with mulch of other species (Montagnini et al. 1993).

In projects that aim to recover soil nutrients in degraded sites, species with high nutrient use efficiency should be combined in time or space with species with low use efficiency. However, NUE values alone may not be enough to assess the role of a tree species on ecosystem nutrients. For example, in spite of high NUE values, a tree species may pose high demands on soil nutrients over the long term. In humid tropical regions nutrients are expected to be critical factors influencing tree productivity, while in regions with a marked dry season water use efficiency rather than NUE would be a more important factor influencing species choice and system design. Still other ecological adaptations of the species (e.g., light use efficiency, root architecture, resistance to pests and diseases) could be more important in selecting species for agroforestry combinations.

ADOPTABILITY OF AGROFORESTRY SYSTEMS

The introduction of trees in a production system will only be beneficial if competition between trees and crops for resources is minimized while positive effects on soil fertility are enhanced: examples of such systems include parklands with N-fixing species such as *Faidherbia albida* in the Sahel, and some sequential systems of relay intercropping and improved fallows (Sanchez 1995). Apart from their beneficial effects on soils, tree species with rapid canopy closure may decrease the growth of weeds, thus the canopy characteristics of the trees will affect their suitability for interplanting with annual crops and will dictate the management practices required when used in agroforestry systems. Finally, decisions to change any system must take into account the objectives that the change is seeking to achieve, thus species selection for agroforestry must be based on several factors apart from their positive influence on soils and crop yields (Wood 1990). Furthermore, species choices for forestry and agroforestry systems are mandated by local people's preferences, which in turn depend on seedling availability, official incentives, and markets.

Choice of suitable crop species is also important for the success of alley cropping systems. Maize and rice, for example, are more light demanding than beans or cassava and thus more affected by shading by trees. The height of pruning and the width of alleys can be adjusted to avoid excessive competition between crops and trees: in experiments at CATIE, for example, Kass (1989) found that maize yield was higher when planted farther away from *Gliricidia* hedgerows. Results of economic analyses for the same systems indicated that the alley cropping system was not as profitable for N, with a lower market cost for fertilizer, as for K and P, with relatively higher market fertilizer prizes.

The adoption of alley cropping systems appears widespread in low income areas of eastern Indonesia, southern Philippines, and Sri Lanka (Kang and Wilson 1987). In Nigeria, researchers from the International Institute of Tropical Agriculture (IITA) have found that although labor for pruning hedges is a major constraint, alley cropping with *Calliandra* spp. has given good results (Plucknett 1990). However the application of alley cropping techniques has its limitations: sometimes crop monocultures are preferred for practical reasons, and sometimes the value of prunings from the hedgerows is higher than the value of crops. Planting the hedgerow trees at high density favors biomass production by trees, but may result in lower crop yields because of competition with trees for light and nutrient resources. On highly weathered soils, successful alley cropping may require the use of external inputs (e.g., liming to increase soil pH) to maintain levels of soil fertility adequate for the desired crop yields (Evensen et al. 1995).

The Need for Initial Economic Incentives to Facilitate System Establishment

When nutrient stocks are low, it may take a number of years for an agroforestry system to build up nutrients and soil carbon to the point where the system is profitable compared with monocultures. For example, three years after the establishment of the *Albizia*-sorghum alley cropping system previously discussed, production of the grain crop was still less than the control, despite the slow but continuous rise in available soil P in the agroforestry system. Because of the low initial productivity of agroforestry systems established on degraded soil, sometimes it is not economically feasible for a farmer to begin agroforestry systems.

Since the adoption of agroforestry systems involves the planting of selected trees, some initial capital will be needed to cover the first 2-3 years of establishment costs. This requirement can be a problem if farmers have no access to capital. In the Atlantic lowlands of Costa Rica, enriched fallow systems are more profitable than conventional agriculture or cattle; however, some assistance may be required to help farmers make the initial expenditures needed to plant the trees (Montagnini and Mendelsohn 1997). Small subsistence farmers often have no access to loans and so cannot afford to make even profitable investments. In Costa Rica, programs such as the Forestry Development Fund (FDF) provide loans for planting trees to small farmers. The farmers repay the loan by giving 30% of the income from harvesting the trees at maturity. Such programs could make sustainable development a reality by allowing small farmers to make sound long-term investments in their land.

CONCLUSIONS

One of the most important reasons for adoption of agroforestry systems in regions where commercial fertilizers are expensive or unavailable is the ability of such systems to recover, recycle, or efficiently utilize nutrients. This ability is often linked to mechanisms associated with woody or perennial species. While agroforestry systems can be profitable if established immediately after forest clearing, they often require a number of years to become profitable when established on degraded lands. For this reason, capital-limited farmers on poor soils may require subsidies to encourage establishment of agroforestry systems.

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Table 1. Rates of erosion in tropical forest and tree crop systems (Wiersum 1984, in Young 1989).

Land use system	Erosion (ton/ha/yr)
Multistorey tree gardens	0.01-0.14
Natural rain forest	0.03-6.16
Fallow period of shifting cultivation	0.05-7.40
Undisturbed forest plantations	0.02-6.20
Tree crops with cover crop or mulch	0.10-5.60
Cropping period of shifting cultivation	0.40-70.05
Cultivation period of taungya system	0.63-17.37
Tree crops, clean weeded	1.20-182.90
Forest plantations, burned or litter removed	5.92-104.80

Table 2. Topsoil chemical characteristics in pure stands of 24 indigenous tree species at La Selva, Costa Rica; Porto Seguro, Bahia, Brazil; and Misiones, Argentina.

Site/Tree species

	pH	C (%)	N (%)	P (cmol.kg^{-1})	K	Ca	Mg
a- La Selva, Costa Rica[1]							
Stryphnodendron microstachyum	5.4ab	3.42ab	0.29b	5.6a	0.27a	0.45a	0.63ab
Vochysia ferruginea	5.4ab	3.76a	0.32a	7.1a	0.22a	0.73a	0.61ab
Vochysia guatemalensis	5.3ab	3.13ab	0.29b	5.2a	0.11a	0.25a	0.37ab
Hyeronima alchorneoides	5.1b	2.96c	0.22b	1.5b	0.09a	0.31b	0.21b
Abandoned pasture	5.3ab	2.73c	0.22b	4.9a	0.19a	0.32b	0.27b
Secondary forest	5.3ab	4.33a	0.33a	3.6b	0.17a	0.68a	0.55ab
b- Porto Seguro, Bahia, Brazil[2]							
N-fixing leguminous species:							
Bowdichia virgilioides	4.9	1.98def	0.16def	1.32def	0.06bcd	1.35bc	0.39de
Centrolobium minus	4.6	1.87efg	0.16def	1.19efg	0.05fgh	0.53hi	0.21i
Centrolobium robustum	4.5	1.65ij	0.13f	1.07fgh	0.05fgh	0.40i	0.16i
Inga affinis	4.9	2.10cde	0.18cd	3.64a	0.07bcd	0.76gh	0.49bc
Parapiptadenia pterosperma	4.9	2.38ab	0.20bc	0.78ij	0.08b	1.40bc	0.60a
Pithecellobium elegans	4.8	1.67hij	0.15ef	0.59kl	0.05efg	0.79gh	0.40de
Platymenia foliolosa	4.7	2.08cde	0.18bcd	0.13m	0.05efg	1.05cde	0.42cd
Non-N fixing leguminous species:							
Arapatiella psilophylla	4.7	1.94def	0.18bcd	1.45de	0.06bcd	0.38i	0.37de
Caesalpinia echinata	5.1	2.41a	0.17cde	1.54de	0.07bcd	1.17bcd	0.39de
Cassia spp.	4.7	1.94def	0.16def	1.40def	0.07bcd	0.56hi	0.34de
Copaifera luscens	5.0	2.02cde	0.17cde	0.63jk	0.06cde	1.15bcd	0.34de
Dimorphandra jorgei	4.9	1.97def	0.19bc	0.97ghi	0.03j	0.98def	0.32efg
Hymenaea aurea	4.4	2.00def	0.16def	2.03c	0.06bcd	0.26i	0.24hi
Macrolobium latifolium	4.7	1.90efg	0.16def	0.67jk	0.04hij	0.36i	0.25fg
Of other families:							
Bombax macrophyllum	4.8	1.78ghi	0.13f	1.42de	0.06bcd	0.84efg	0.33ef
Buchenavia grandis	4.6	2.06cde	0.14f	2.09c	0.06bcd	0.80fg	0.33ef
Eschweilera ovata	5.3	1.82fgh	0.31a	0.58kl	0.11a	1.38bc	0.53ab
Lecythis pisonis	5.3	1.99def	0.18bcd	0.23lm	0.04ghi	1.46b	0.32ef
Licania hypoleuca	5.0	1.63j	0.14f	1.61d	0.07bcd	1.31bcd	0.35de
Pradosia lactescens	4.9	2.15bcd	0.18bcd	0.81ij	0.05fgh	0.84efg	0.24gh
Primary forest	4.9	1.99def	0.15ef	0.96hi	0.08bc	1.23bcd	0.36de
Secondary forest	5.1	2.15abc	0.22b	2.46b	0.07bcd	2.20a	0.62*
c- Misiones, Argentina[3]							
Balfourodendron riedelianum	5.8	2.6b	0.34ab	n.d.	0.55bc	7.1bc	1.7c
Bastardiopsis densiflora	7.1	6.3a	0.65a	n.d.	1.28a	20.4a	3.4ab
Cordia trichotoma	6.4	4.0ab	0.46ab	n.d.	0.79b	13.6ab	2.6abc
Enterolobium contortisiliquum	6.1	3.4ab	0.39ab	n.d.	0.67b	8.7bc	3.5a
Ocotea puberula	6.1	4.4ab	0.59a	6.09a	1.11a	17.3a	4.7a
Grass control	5.8	2.2b	0.0.27b	n.d.	0.26c	6.3c	2.4bc

Sources: [1] Montagnini and Mendelsohn (1996), [2] Montagnini et al. (1994), [3] Fernández et al. (1995).
Note: For each site, differences among means are statistically significant when followed by different letters ($p<0.05$).
n.d.: not detected

Table 3. Nutrient use efficiencies (NUE) (Megagrams of annual stem biomass increment/kg nutrient in annual litter fall).

Porto Seguro, Bahia, Brazil:	**N**	**Ca**	**Mg**	**K**	**P**
N-fixing leguminous species:					
Centrolobium robustum	0.05	0.05	0.37	0.87	1.74
Platymenia foliolosa	0.08	0.34	7.00	3.51	4.66
Non N-fixing leguminous species:					
Caesalpinia echinata	0.04	0.03	0.54	0.78	1.81
Hymenaea aurea	0.06	0.09	0.45	0.64	1.91
Species of other families:					
Bombax macrophyllum	0.36	0.20	0.88	20.70	20.70
Buchenavia grandis	0.05	0.04	0.38	0.68	1.70
Eschweilera ovata	0.12	0.10	0.44	0.96	5.73
Lecythis pisonis	0.12	0.11	0.89	1.58	3.56

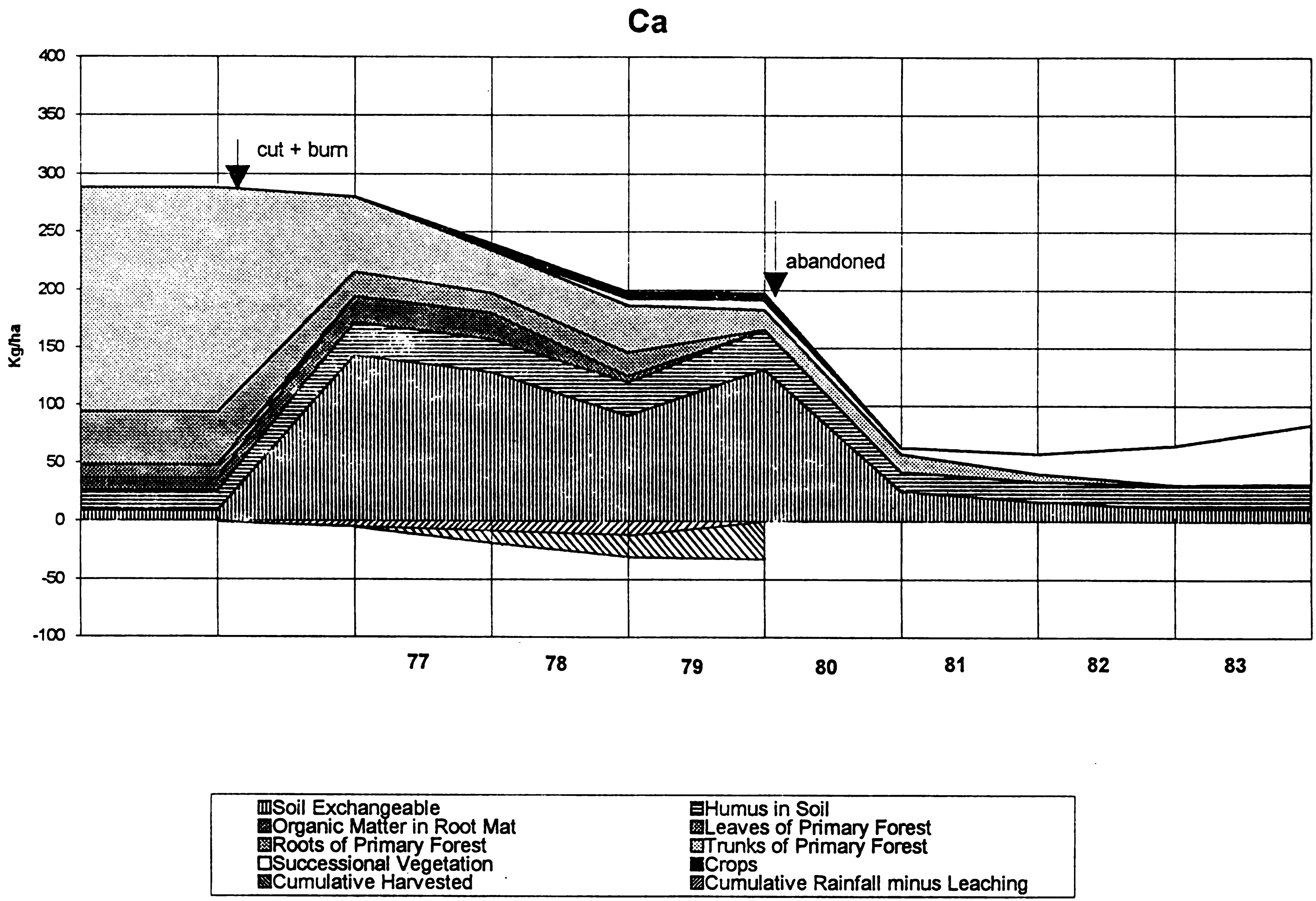
La Selva, Costa Rica:	**N**	**Ca**	**Mg**	**K**	**P**
Stryphnodendron mycrostachyum	0.08	0.06	0.35	0.63	0.53
Vochysia ferruginea	0.08	0.03	0.26	0.38	0.56
Vochysia guatemalensis	0.16	0.05	0.29	0.84	1.07
Hyeronima alchorneoides	0.09	0.03	0.15	0.22	0.45

Figure Legends

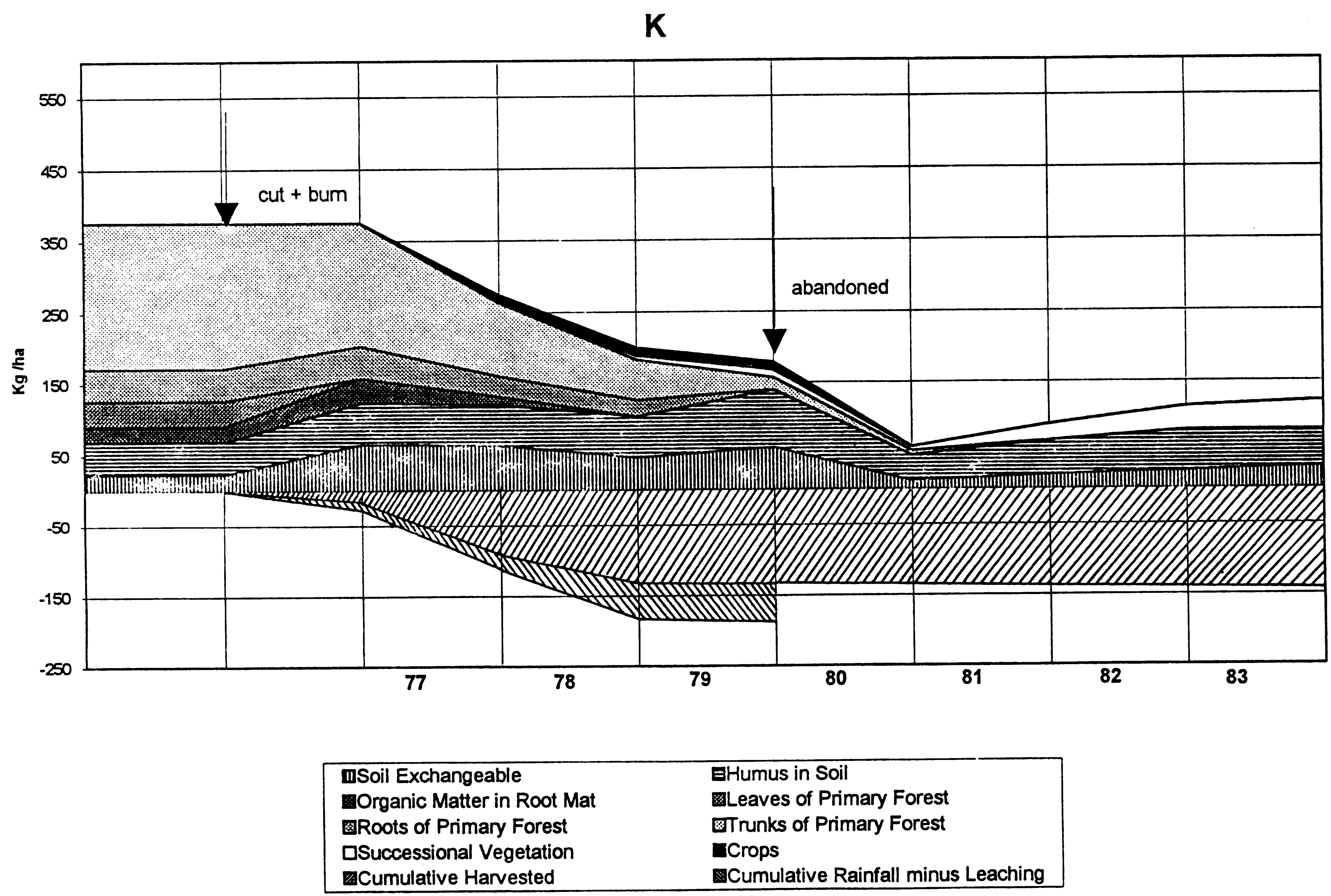
Fig. 1. Stocks and cumulative losses of calcium and potassium as a function of time in the experimental plot at San Carlos de Rio Negro, Venezuela.

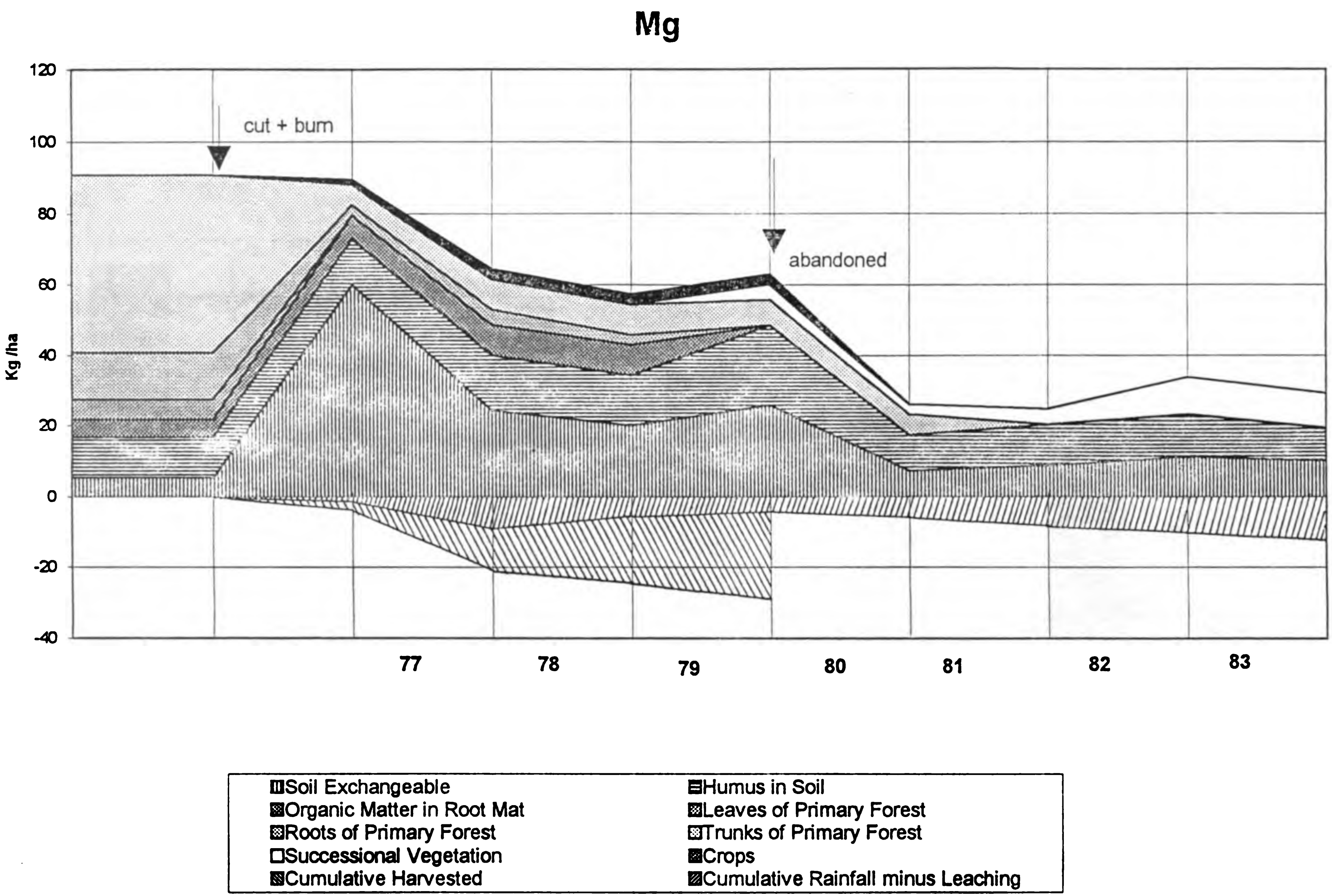
Fig. 2. Stocks and cumulative losses of magnesium and nitrogen as a function of time in the experimental plot at San Carlos de Rio Negro, Venezuela. Keys as for Fig. 1

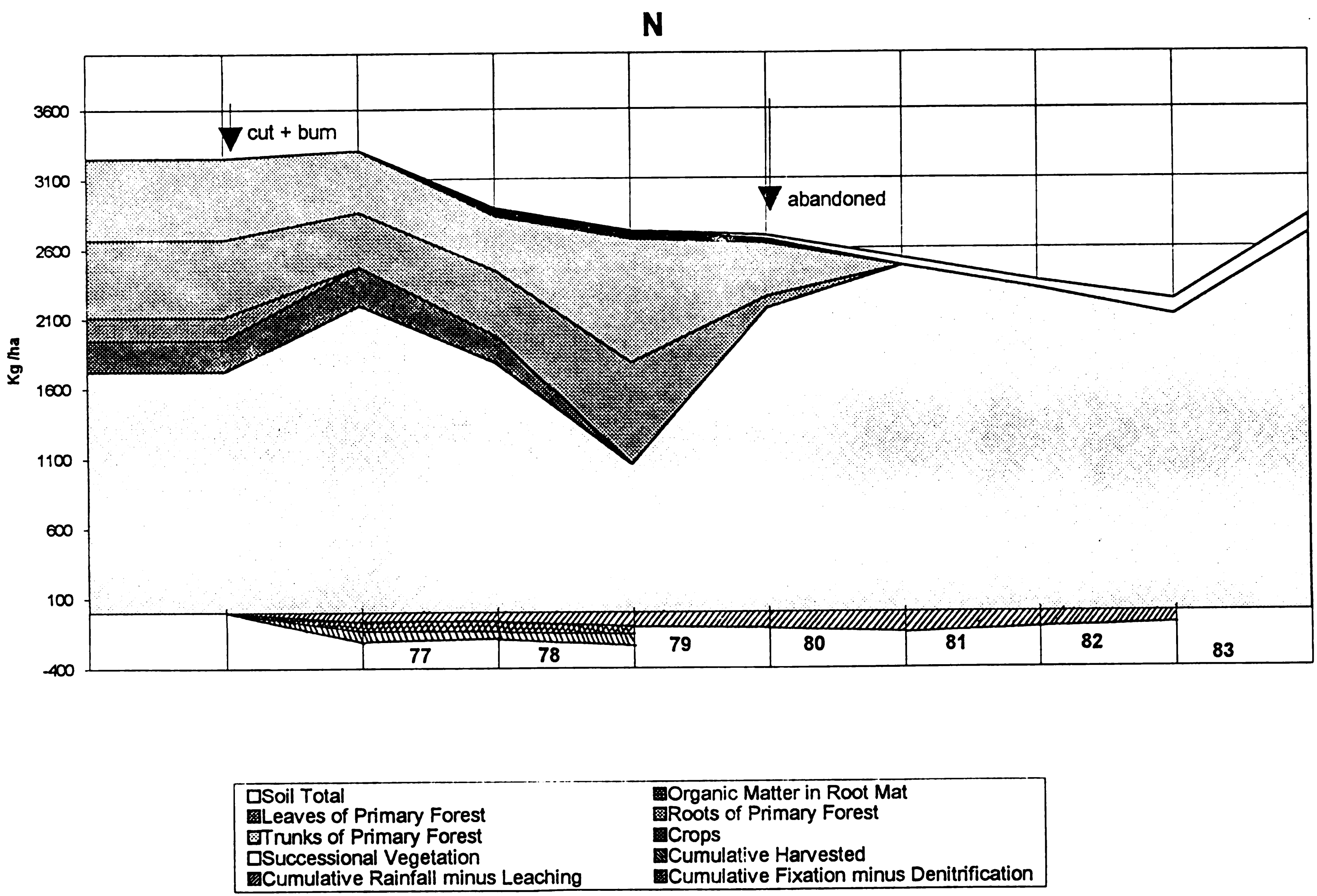
Fig. 3. Labile phosphorus stocks in fractions of the upper 75 cm of soil and in the aboveground biomass in an experimental alley cropping system (AC), and in a monoculture control of sorghum (NA). There is a trend of gradually increasing differences between the two systems throughout the three-year experimental period. Due to large variability, differences were not significant except between those fractions labeled "a" and "b". PO is organic phosphorus, PI is inorganic phosphorus, NaOH and NaHCO3 are the extractants. ABOVEBIO is aboveground biomass.



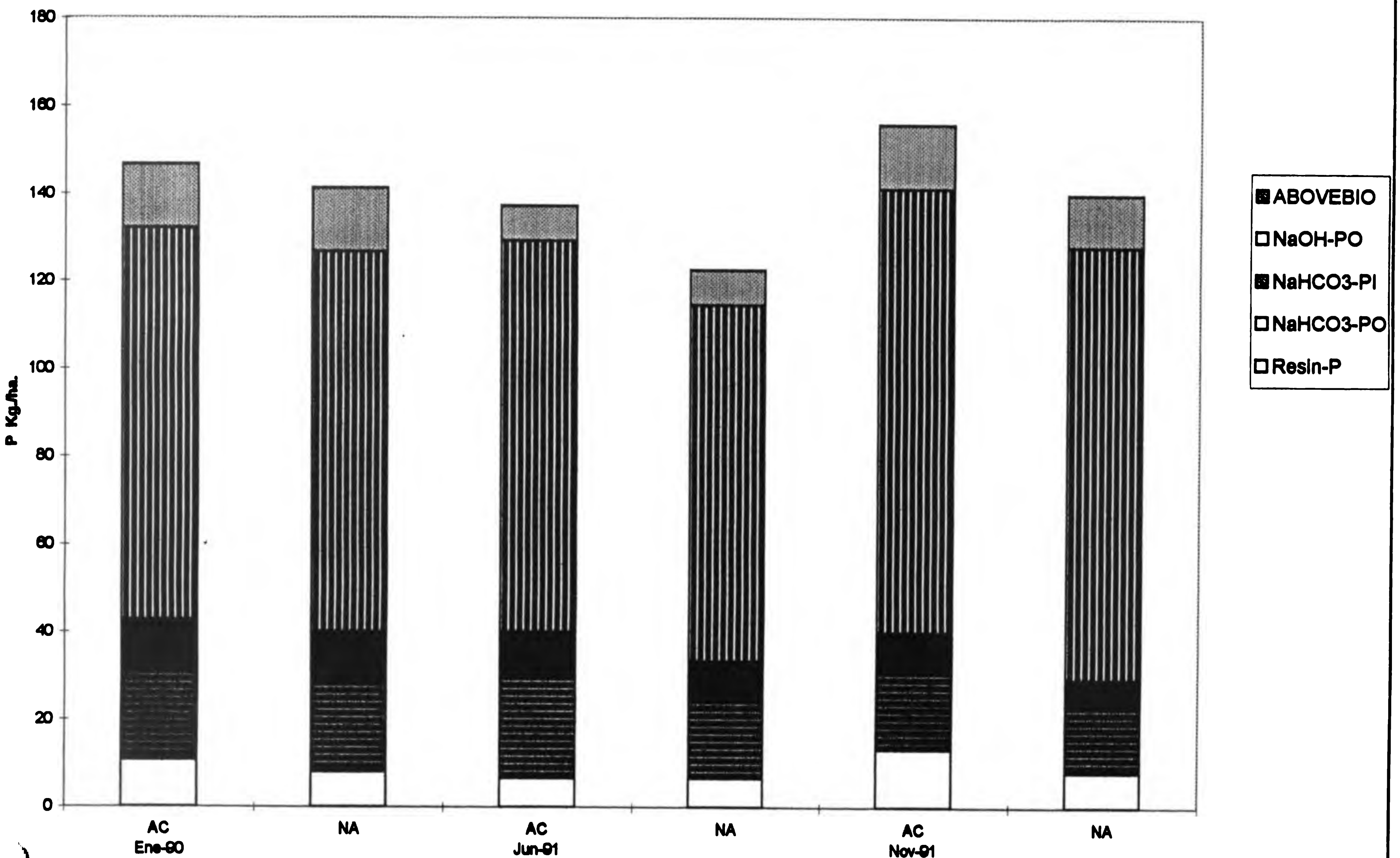
Ca
400
350
300
250
200
150
100
50
0
-50
-100
Kg/ha
cut + burn
abandoned
77
78
79
80
81
82
83
Soil Exchangeable
Humus in Soil
Organic Matter in Root Mat
Leaves of Primary Forest
Roots of Primary Forest
Trunks of Primary Forest
Successional Vegetation
Crops
Cumulative Harvested
Cumulative Rainfall minus Leaching


K
Kg /ha
550
450
350
250
150
50
-50
-150
-250
cut + burn
abandoned
77
78
79
80
81
82
83
Soil Exchangeable
Humus in Soil
Organic Matter in Root Mat
Leaves of Primary Forest
Roots of Primary Forest
Trunks of Primary Forest
Successional Vegetation
Crops
Cumulative Harvested
Cumulative Rainfall minus Leaching


Mg
120
100
80
60
40
20
0
-20
-40
Kg /ha
cut + burn
abandoned
77
78
79
80
81
82
83
Soil Exchangeable
Humus in Soil
Organic Matter in Root Mat
Leaves of Primary Forest
Roots of Primary Forest
Trunks of Primary Forest
Successional Vegetation
Crops
Cumulative Harvested
Cumulative Rainfall minus Leaching


N
Kg /ha
3600
3100
2600
2100
1600
1100
600
100
-400
cut + burn
abandoned
77
78
79
80
81
82
83
Soil Total
Leaves of Primary Forest
Trunks of Primary Forest
Successional Vegetation
Cumulative Rainfall minus Leaching
Organic Matter in Root Mat
Roots of Primary Forest
Crops
Cumulative Harvested
Cumulative Fixation minus Denitrification

Labile Phosphorus Stocks in Fractions of the Upper 75 cm. of Soil and in the Aboveground Biomass in an Experimental Alley Cropping System (AC) and in a Monoculture Control of Sorghum (NA)



Reciclaje y Eficiencia en el Uso de Nutrientes en Sistemas Agroforestales

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RESUMEN

En regiones tropicales húmedas, los nutrientes del suelo son factores claves que influyen sobre la productividad de las plantas y la sustentabilidad a largo plazo de un sistema de producción. Un aspecto clave en el incremento de la sustentabilidad de sistemas agrícolas es la incorporación de especies que poseen adaptaciones dirigidas a una mejor captura y conservación de nutrientes, mientras que al mismo tiempo producen una cosecha de valor económico o de subsistencia. Se presentan ejemplos de sistemas tradicionales con estas características, y se sugieren sistemas agroforestales con selección de especies y diseños que promuevan la conservación de nutrientes. Se presenta la eficiencia en el uso de nutrientes como un concepto integrador que puede contribuir a la elección de especies y su diseño espacial o temporal en sistemas agroforestales. Se agregan consideraciones de tipo socioeconómico que deben tomarse en cuenta al promover sistemas agroforestales sostenibles, especialmente para pequeños agricultores.

ABSTRACT

In tropical humid regions, soil nutrients are key factors affecting plant productivity and the sustainability of production systems. A key element in promoting the sustainability of agricultural systems is the use of species that have good nutrient conserving mechanisms, and that at the same time yield economic or subsistence products. Examples of such systems are presented, and agroforestry systems are suggested where species selection and system design promote nutrient conservation. The nutrient use efficiency of species is advanced as an integrative concept that can be useful in species choice and design of agroforestry systems. Additional considerations are presented on the socioeconomic factors that must be taken into account in the promotion of sustainable agroforestry systems, especially for small farmers.

INTRODUCCION

En regiones tropicales húmedas, los nutrientes del suelo son factores claves que influyen sobre la productividad de las plantas y la sustentabilidad a largo plazo de un sistema de producción. Por mucho tiempo se ha afirmado que las pérdidas de nutrientes y el incremento en la invasión de malezas son los principales factores que contribuyen al abandono de campos de cultivos anuales después de 2-4 años de uso (Watters 1971, Van Wambeke 1992, Bandy et al. 1993). El incremento en la invasión de malezas en terrenos de agricultura luego de la pérdida de nutrientes, resulta de una mayor habilidad de las mismas para absorber escasos nutrientes en comparación con la mayoría de los cultivos anuales, eliminando a éstos en la competencia por el uso de nutrientes y otros recursos. Muchas especies de malezas son leñosas perennes cuya habilidad para competir depende de una variedad de mecanismos de absorción y conservación de nutrientes, a su vez dependientes de la estructura y adaptaciones de su aparato radicular, la presencia de tallos leñosos, y la producción de hojarasca. Un aspecto clave en el incremento de la sustentabilidad de sistemas agrícolas es la incorporación de especies que poseen este tipo de adaptaciones dirigidas a una mejor captura y conservación de nutrientes, mientras que al mismo tiempo producen una cosecha de valor económico o de subsistencia. Muchas poblaciones indígenas han desarrollado estos sistemas a través del proceso de prueba y error, y este artículo presenta un ejemplo de los Kayapó, en el Amazonas de Brasil.

La importancia de la fijación de nitrógeno en especies de sistemas agroforestales está ampliamente reconocida. En este artículo, discutimos éste y otros efectos de las especies leñosas sobre la fertilidad del suelo, las interacciones entre especies de plantas leñosas, y la importancia del diseño adecuado de sistemas agroforestales. Finalmente, el concepto de la eficiencia en el uso de nutrientes en las plantas es presentado como una herramienta potencial útil para el diseño y manejo de los sistemas agroforestales.

DINAMICA DE NUTRIENTES EN SISTEMAS AGROFORESTALES

Características Generales del Ciclaje de Nutrientes en Sistemas Agroforestales

La Fig. 1 muestra un diagrama del ciclaje de nutrientes en la situación básica de los sistemas agroforestales, con los componentes árboles y cultivos, adaptado de Young (1989). El ciclo contiene cajas que representan almacenajes o reservorios de nutrientes, flujos dentro del sistema, y ganancias y pérdidas. Los reservorios son los tallos y raíces de árboles y cultivos, residuos vegetales, fauna del suelo, materia orgánica del suelo, minerales de arcilla, y el almacenaje de nutrientes disponibles en forma mineral en la solución del suelo. Los principales flujos internos se dirigen desde el componente plantas al componente de residuos vegetales, y por medio de la fauna del suelo al humus. A través del proceso de mineralización, los nutrientes llegan a la solución del suelo en forma mineral, y retornan a las plantas por la absorción de las raíces. Las entradas o ganancias del sistema son los nutrientes contenidos en la lluvia y polvo atmosférico, residuos orgánicos traídos de fuera del sistema, fertilizantes, meteorización de las rocas, y, para el nitrógeno, la fijación simbiótica y asimbiótica. Las pérdidas incluyen lixiviación, erosión, cosecha (incluído el pastoreo de animales), más las pérdidas gaseosas en las quemas, la volatilización y la denitrificación.

Las principales pérdidas ocasionadas por las quemas se limitan al nitrógeno y el azufre, mientras que la mayoría de los otros nutrientes son retenidos en las cenizas y otros restos de la quema. Por otro lado, la lixiviación y la erosión pueden ocasionar pérdidas de cualquier nutriente. La inmovilización por fijación en minerales secundarios de arcillas puede ser importante para el fósforo y algunos microelementos. Un aspecto importante es la gran proporción de nutrientes que se encuentra retenido en forma orgánica en un momento dado. Por ejemplo, para el nitrógeno, solamente un 1% se encuentra disponible en forma mineral en la solución del suelo. Una vez mineralizados los nutrientes son disponibles para la absorción por parte de las raíces, pero al mismo tiempo pueden perderse por lixiviación.

El objetivo del diseño y manejo de los sistemas agroforestales es modificar el ciclaje de nutrientes de manera de hacer un uso más eficiente de los mismos, sea que éstos provengan de fuentes naturales o fertilizantes. Específicamente, es deseable reducir la relación entre entradas-salidas y el reciclaje interno. Los sistemas agrícolas son ampliamente abiertos, con entradas y salidas de hasta un 40% del reciclaje, mientras que los ecosistemas de bosques son más cerrados, con entradas y salidas a veces llegando a no más del 10% del reciclaje interno (Young 1989). Si se puede reducir esta relación, los nutrientes son re-utilizados más frecuentemente por las plantas antes de perderse del sistema. En general, los sistemas agroforestales pueden promover ciclajes de nutrientes más cerrados que los sistemas agrícolas, por medio del reciclaje en los residuos de hojas y raíces. Además, es posible sincronizar la liberación de nutrientes con los requerimientos de los cultivos, controlando la calidad, tiempo y forma de adición de los residuos vegetales. En las siguientes secciones se presentan ejemplos en los cuales se mejora el reciclaje de nutrientes por medio de prácticas tendientes a aumentar o mejorar la liberación de nutrientes y su sincronización con los requerimientos de los cultivos, a la vez que se minimizan las pérdidas del ecosistema.

Ejemplos de Sistemas Agroforestales Tradicionales

La agricultura migratoria ha sido practicada en los trópicos por muchos siglos. Actualmente, la agricultura migratoria (también llamada "de corta y quema") es la práctica de uso de la tierra predominante en aproximadamente un 30% de los suelos arables del mundo y provee alimentos para un estimado de 300 millones de la población más pobre del mundo (Andriesse y Schelhaas 1987). La agricultura migratoria tradicional utiliza largos períodos de recuperación de los terrenos abandonados (barbechos) entre períodos cortos de cultivo. Estos largos períodos de abandono, hacen que la técnica tradicional sea sostenible pero también requiere de mayores extensiones de tierra. Cuando la tierra es escasa, los agricultores disminuyen el período de recuperación de los terrenos y aumentan la duración de los períodos de cultivo, resultando en una disminución de los nutrientes del suelo, caída de la productividad y aumento de la invasión de malezas.

Una alternativa que ha sido adoptada con cierto éxito es el uso de "barbechos mejorados" (Nair 1990, Kass et al. 1993). Por ejemplo, en sistemas experimentales de barbechos en el Amazonas peruano, especies arbóreas mejoradoras del suelo fueron plantadas en terrenos abandonados de agricultura migratoria (Szott et al. 1991). Se plantaron dos leguminosas leñosas tolerantes a la acidez del suelo, *Cajanus cajan* e *Inga edulis*. Dos años después de plantadas, los niveles totales de Ca y Mg del ecosistema habían declinado, sin embargo el N y K total habían aumentado. Los niveles de P también aumentaron aunque sólo luego de 4.5 años. En general, el sistema de "barbecho mejorado" resultó en aumentos netos de varios nutrientes importantes en la nutrición de las plantas del ecosistema. De manera adicional, aunque el uso de especies herbáceas inicialmente resultó en un rápido control de las malezas, sólo se obtuvo una supresión efectiva de las malezas a través de la implantación de leguminosas leñosas. Experiencias tales como las descriptas por Szott et al. (1991) son de relevancia especial en Centro América y otras regiones donde la tierra es escasa y los períodos de barbecho no son lo suficientemente prolongados como para restaurar la capacidad productiva de los suelos (Watters 1971, Sips 1993, Montagnini and Mendelsohn 1996).

El ejemplo de los Kayapó en Brasil

Existen numerosos ejemplos de prácticas agrícolas llevadas a cabo por pueblos indígenas, o por pioneros tales como los caboclos del Amazonas, que utilizan árboles para mantener o restaurar la fertilidad del suelo sin utilizar ningún fertilizante químico (Anderson 1990, Gómez-Pompa y Kaus 1990, Subler y Uhl 1990, Balée 1992, Lescure et al. 1992, Nations 1992, Jordan 1995). Un ejemplo bien documentado es el de los Kayapó en Brasil (Posey 1982). Los Kayapó viven hoy en una reserva de 2.5 millones de hectáreas en la cuenca del Rio Xingú en la región del Amazonas. Aunque los Kayapó son nómadas por la mayor parte del año, el cultivo de plantas para alimentos y medicinas es una parte importante de su cultura. El proceso de cultivo comienza con el aclareo de un área de terreno de forma circular. Los árboles son cortados de tal manera que los troncos apuntan hacia la periferia, y la mayor parte de la biomasa de la copa termina cerca del perímetro del círculo. Cultivos de raíces tales como la batata o ñame (*Dioscorea* spp.), el taro (*Colocasia esculenta*) y la mandioca (*Manihot esculenta*) son plantados en corredores abiertos que quedan entre los árboles caídos. Los cultivos ya se encuentran enraizados y creciendo antes de que se lleve a cabo la quema de los residuos.

La quema es manejada cuidadosamente. Los ancianos de la tribu coinciden en el día apropiado cuando los vientos son mínimos y los campos van a quemar por completo pero no demasiado rápido. Los campesinos comienzan quemando las pilas de hojarasca seca una a la vez. Una quema lenta minimiza el calor, de tal manera que los cultivos de raíces pierden la parte aérea pero no la viabilidad. Estos cultivos, luego de la quema tienen ventaja inicial sobre las malezas que se establecerán sobre la ceniza.

La papaya, las bananas, el algodón, el urucú (*Bixa orellana*), y el tabaco, los cuales requieren una alta cantidad de nutrientes, son plantados en las márgenes externas del terreno, donde las cantidades de cenizas son mayores. Unas pocas semanas después de la quema, los campesinos recogen los palos y ramas sin quemar para realizar una segunda quema. Otros cultivos de alto requerimiento de nutrientes son plantados sobre la pila resultante de cenizas.

Los cultivos de los Kayapó perduran por varios años. La batata y el ñame crecen en campos de cuatro o cinco años. Las bananas y el urucú, y variedades domésticas de una planta leguminosa llamada "kupa" comúnmente continúan produciendo hojas y tallos comestibles por 8 a 12 años, y algunos campos de 40 años aun rinden "kupa" comestible.

Muchas plantas útiles para los Kayapó se establecen naturalmente en los campos abandonados. Algunas de esta plantas de colonización espontánea poseen importantes valores medicinales, otras proveen semillas, frutos, y raíces comestibles. Algunas de estas especies de plantas pioneras producen frutas que son excelentes como carnada para peces. Otras atraen animales o pájaros. Los animales atraídos por las plantas de mucho follaje en estos sitios son más fáciles de cazar que aquéllos que habitan el dosel superior del bosque.

Puesto que los Kayapó comprenden este proceso y toman ventaja de las especies que secuencialmente ocupan estos sitios, no necesitan buscar continuamente nuevos rodales para cortar y quemar. Después de muchos años, cuando un sitio abandonado se convierte nuevamente en bosque cerrado, éste puede ser cortado y usado nuevamente, sin seguir el proceso de degradación de largo plazo del sitio.

Las prácticas de los Kayapó contrastan con las prácticas de cultivos migratorios llevadas a cabo en el Amazonas por colonizadores del sur y el noreste de Brasil. Estos últimos dependen principalmente de cultivos tales como maíz, arroz, y mandioca, los cuales crecen satisfactoriamente sólo por dos a tres años. Cuando los rindes decrecen, los colonizadores abandonan el sitio y aclarean una nueva porción de bosque.

Movilización y Pérdidas de Nutrientes en la Agricultura Migratoria

Los científicos han pensado por mucho tiempo que las disminuciones bruscas de la productividad de cultivos anuales tales como maíz y arroz, luego de dos o tres años de cultivos en parcelas de agricultura migratoria, son debidos a la pérdida de nutrientes del suelo, tales como la percolación de calcio y potasio y la volatilización de N. Sin embargo, los resultados del proyecto de "El Hombre y la Biosfera" en la región amazónica, cerca de San Carlos de Río Negro en Venezuela (Jordan 1989) sugieren que durante los 2-3 primeros años de cultivo luego del aclareo del bosque, sólo una pequeña parte de los nutrientes almacenados es perdida debido a la lixiviación (Figs. 2-5). La disminución de la producción fue debida en cambio a la fijación del fósforo previamente disponible, por el hierro y el aluminio del suelo mineral, inmovilizando el fósforo y haciéndolo inutilizable por las plantas.

En los bosques intactos de la región, aparentemente el P se encuentra en formas disponibles para los árboles (Jordan 1989). Inclusive luego de cortar y quemar el bosque, y durante los primeros 1-2 años de cultivo, la mayor parte del fósforo del suelo fue mantenido en formas móviles, debido a que se encontraba quelado al Fe y el Al por ácidos orgánicos percolados de la materia orgánica en descomposición del mantillo del suelo. Luego de que el sitio fue cortado y quemado, y el humus y la hojarasca gradualmente desaparecieron durante los tres primeros años de cultivo, la liberación de ácidos orgánicos disminuyó, y una mayor proporción de P fue inmovilizado en el suelo. Al final del tercer año, todo el humus y la mayor parte de los troncos de los árboles había desaparecido. El estudio concluye en que la falta de P disponible causó la disminución de la productividad del cultivo, y que la conversión del P de estado disponible a inmóvil fue debido a la desaparición del humus y la materia orgánica de la superficie del suelo.

A pesar de la inmovilización del P en el suelo, la vegetación sucesional secundaria invadió el sitio, y para el quinto año, los niveles de Ca, K, Mg, y N comenzaron a declinar (Figs. 2-5). No hubieron cambios detectables en los niveles totales de nutrientes del ecosistema durante el experimento. Sin embargo, hubo un incremento de P en la biomasa a medida que el bosque sucesional se establecía. Aparentemente, las especies sucesionales fueron capaces de tomar el P inmóvil del suelo. Este P probablemente se encontraba en fracciones de enlaces de Fe y Al no disponibles para los cultivos.

¿Cuál es el mecanismo a través del cual la vegetación leñosa es capaz de absorber el P no disponible para los cultivos? Una posibilidad es la excreción de ácido psídico[1] de las raíces (Ae et al. 1990), o el lavado de ácidos cítricos y málicos de la hojarasca en descomposición de los

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[1] Acido psídico = (p-hidroxi benzil) ácido tartárico

árboles (Han 1989). Estos ácidos orgánicos pueden reemplazar al P ligado al Fe y al Al de la arcilla, liberando al P y haciéndolo soluble y disponible para su absorción. Es posible que las plantas anuales no posean este mecanismo de reciclaje de P, o puede que las mismas hayan perdido esa capacidad en el proceso de selección genética para favorecer la productividad (Chapin 1980, 1983).

La movilización del P ligado por las plantas leñosas podría explicar, al menos en parte, la sustentabilidad de los sistemas agroforestales tales como los de los Kayapó. Los árboles de cultivo son establecidos inmediatamente después del aclareo y quema, antes de que la materia orgánica de los horizontes de suelo superiores se descomponga completamente. Puesto que los árboles implantados se encuentran produciendo hojarasca antes de que los residuos anteriores desaparezcan completamente, la producción de ácidos orgánicos no es interrumpida, y el P es mantenido en un estado disponible para las plantas. Sin embargo, la mayor disponibilidad del P es sólo un factor que contribuye a la sostenibilidad de estos sistemas. Otros factores tales como relaciones alelopáticas, índices de actividad fotosintética, tasas de reciclaje de otros nutrientes, control de patógenos, en conjunto, influyen sobre la sostenibilidad a largo plazo.

Esto sugiere que sería deseable comenzar con un sistema agroforestal inmediatamente después del aclareo del bosque, ya sea éste secundario o primario. Por ejemplo, en un sitio localizado en la región central del Amazonas brasileño, se establecieron experimentalmente árboles de caucho (*Hevea brasiliensis*) bajo el dosel parcialmente abierto de un bosque secundario (Mesquita 1995). Al momento de la plantación, el estrato de hojarasca y humus del suelo forestal mejoró el microclima, disminuyó la erosión, y contribuyó a mejorar las propiedades físicas y químicas del suelo, favoreciendo el establecimiento de las plántulas del caucho.

Desafortunadamente, muchos sistemas agroforestales son establecidos en sitios que han sido cultivados o mantenidos en pasturas por muchos años. En tales sitios, la situación de los nutrientes del suelo ha sido deteriorada. Las Figuras 2-5 muestran que en las parcelas experimentales de San Carlos de Río Negro, la pérdida de nutrientes continuó inclusive después de tres años de abandono del cultivo, y la recuperación de nutrientes no comenzó sino hasta el quinto año. Aparentemente en este sistema de altas precipitaciones anuales (3.600 mm) y con suelos de baja capacidad de intercambio catiónico, tomó un par de años para que la regeneración de la vegetación cubriera el sitio y reestableciera los mecanismos de reciclaje de nutrientes.

Dinámica de Nutrientes en Sistemas Agroforestales Modernos: Cultivos en Callejones

A mediados de los años 1980, un esfuerzo considerable de investigación se concentró en el desarrollo en tecnologías de bajos insumos dirigidas a la producción sustentable de alimentos para pequeños productores. Los resultados de estas investigaciones sugieren que en situaciones donde los "barbechos mejorados" no son factibles debido a la escasez de tierras, técnicas tales como el cultivo en callejones con la aplicación de "mulch" (mantillo o abono verde) pueden constituir alternativas de agricultura viables (Kang y Wilson 1987, Kang et al. 1990). En los cultivos en callejones, los cultivos anuales son plantados entre hileras de árboles, preferiblemente de especies leguminosas fijadoras de nitrógeno, las cuales son periódicamente podadas para prevenir que produzcan sombra sobre los cultivos anuales. Las podas pueden ser usadas como abono verde para mejorar la fertilidad del suelo y producir alimento de alta calidad para ganado. Los cultivos en callejones son considerados como un sistema de agricultura migratoria mejorado, con las siguientes ventajas potenciales: 1) Las fases de cosecha y recuperación del suelo son combinadas; 2) Los períodos de cosecha son más largos, y la tierra es usada de manera más intensiva; 3) La fertilidad del suelo es mantenida de manera efectiva con el uso de especies seleccionadas para ese propósito; y 4) Se reduce la necesidad de insumos externos (Kang and Wilson 1987).

En áreas de Nigeria y otras regiones de transición de bosque-sabana de Africa, resultados de experimentos de campo y ensayos en tierras de agricultores han mostrado que los cultivos en callejones con maíz, frijoles, arroz y mandioca entre hileras de *Leucaena leuocephala* y *Gliricidia sepium* permitieron un nivel más alto de producción que los monocultivos (Kang and Wilson 1987). El frijol y arroz no siempre mostraron incrementos significativos en la producción en comparación con monocultivos, pero al ser plantados en cultivos de callejones con *Leucaena*, no respondieron a la fertilización con N, indicando que el abastecimiento de N a través del material proveniente de las podas fue adecuado, y la adición de fertilizantes no fue necesaria. En los sistemas de cultivos en callejones la competencia entre árboles y cultivos puede a veces reducir significativamente la producción del cultivo (Haggar 1994). Otras investigaciones en suelos aluviales en Yurimaguas, en el Amazonas peruano, mostraron que las reducciones en la producción del arroz debido a competencia por luz eran evidentes hasta los 1,5 metros de distancia desde las hileras de todas las especies de árboles ensayadas (*Inga* spp., *Leucaena* spp. y *Erythrina* spp.), con la mayor disminución en producción encontrada en las hileras de *Leucaena* (Salazar et al. 1993). El control de malezas tuvo mayor éxito con el "mulch" de descomposición lenta de *Inga*, pero las cosechas de arroz (a una distancia > 1,5 m de las líneas) fueron mayores con *Leucaena* y *Erythrina*.

Las técnicas agroforestales tales como la de cultivos en callejones tienen mayor potencial para incrementar las reservas de nutrientes que los monocultivos. Los siguientes ejemplos ilustran las contribuciones de estos sistemas agroforestales a la dinámica del P y el N. La Fig. 6 muestra el P total disponible en un sistema replicado de cultivo en callejones (*Albizia julibrissin* en las hileras, *Sorghum bicolor* como cultivo) en un Ultisol en el estado de Georgia, U.S.A., en comparación con parcelas de sorgo en monocultivo. Ambos tratamientos, ya sea el cultivo en callejones como el sorgo en monocultivo fueron previamente provistos de abono verde, en el verano con poroto (frijol) (*Mucuna deeringiana*) y en el invierno con trébol (*Trifolium incarnatum*). Hubo un incremento gradual en el fósforo disponible en los dos sistemas, a pesar de que inclusive hasta el tercer año, la producción de sorgo en el sistema agroforestal no fue mayor que en el monocultivo (Matta-Machado and Jordan 1995).

Este estudio se llevó a cabo en un suelo degradado por un siglo de cultivos de algodón y soja. Mientras que los sistemas agroforestales pueden incrementar las reservas de nutrientes comparados con parcelas de sistemas no agroforestales, este incremento se produce de una manera lenta. Una mejor estrategia, si es económicamente factible, podría ser fertilizar inicialmente el sistema agroforestal para favorecer una producción mas rápida. Una estrategia inclusive mejor, si se dispone de un sitio adecuado, sería comenzar el sistema después de un "barbecho", puesto que cuando un sistema agroforestal comienza con niveles altos de nutrientes, el sistema tiene una mayor posibilidad de mantenerse productivo a largo plazo.

Investigaciones llevadas a cabo en el Centro Agronómico Tropical de Investigación y Enseñanza (CATIE) en Turrialba, Costa Rica han examinado el rol del N en cultivos anuales en callejones con árboles usados en sistemas agroforestales en zonas tropicales húmedas. Los resultados de experiencias a largo plazo con maíz en cultivos en callejones con *Erythrina* *poeppigiana* y *Gliricidia sepium* mostraron que después de siete años, la productividad del maíz y la absorción del N fueron más del doble en cultivos en callejones con cualquiera de las dos especies que en monocultivo (Haggar et al. 1993). Mayores porcentajes de mineralización de N del suelo en los sistemas de cultivo en callejones llevaron a un establecimiento mas rápido del maíz en comparación con el cultivo sin asociar. Estos mayores porcentajes de mineralización del N del suelo resultaron de la acumulación de compuestos de N orgánico disponibles para mineralización luego de siete años de aplicación de abono verde de los árboles. En el sistema de cultivo en callejones, la acumulación a largo plazo de N mineralizable en el suelo influyó más sobre la producción y absorción de N por el maíz, que la sincronización de la liberación de N del abono verde y la absorción de N por los cultivos. A pesar de la mayor producción, la recuperación total del N del abono verde por el maíz en un año fue sólo de 10 kg/ha, la mayor parte del cual fue absorbido durante los dos primeros meses después de la siembra; sin embargo, este efecto inicial llevó a un establecimiento más rápido del maíz en el cultivo en callejones. Esto de nuevo señala la necesidad de estudios de largo plazo que demuestren los beneficios de cultivos en callejones con el objetivo de una mayor producción. Esto sirve también para recalcar que los resultados tempranos pueden no ser muy evidentes, y que otros insumos externos pueden ser necesarios inicialmente para asegurar el establecimiento exitoso del sistema.

La elección de especies influye de gran manera sobre el éxito y aplicabilidad general de las técnicas de cultivos en callejones. Por ejemplo, muchas especies contienen sustancias aleloquímicas que suprimen malezas y otras plantas. Las interacciones alelopáticas son útiles cuando las especies suprimidas son consideradas malezas, pero se debe tener cuidado cuando el abono verde es aplicado a los cultivos anuales (Regnier y Janke 1990). Por último, en suelos muy

ácidos con alta saturación de aluminio, algunas de las especies arbóreas preferidas para el cultivo en callejones, tales como *Leucaena* spp. y *Gliricidia* spp., no crecen bien, y tienen que ser reemplazadas por otras especies más adaptadas a esas condiciones (e.g., *Calliandra* spp., *Cassia* spp., *Inga* spp., *Flemingea* spp., o *Paraserianthes* spp.).

Sistemas Tradicionales Modificados: Arboles para Sombra de Cultivos Perennes

En CATIE, Costa Rica, numerosas investigaciones han intentado por largo tiempo modificar los sistemas tradicionales de la región--café o cacao con árboles de sombra--para mejorar la productividad y sustentabilidad. Estas investigaciones comenzaron con el examen de las variables del reciclaje de nutrientes en los sistemas existentes en la región y fue continuada con sistemas experimentales donde el reciclaje de nutrientes podía ser examinado en experimentos controlados. Por ejemplo, en una finca cercana al CATIE, Beer (1988) comparó el retorno anual de nutrientes proveniente de la hojarasca y las podas en sistemas de café con *Erythrina poeppigiana* (poró), y café con poró y *Cordia alliodora* (laurel). Ambos árboles son comunes en sistemas agroforestales con cultivos perennes en Latinoamérica. La contribución total anual de la hojarasca más los residuos de las podas fue similar en ambos sistemas. La producción anual de hojarasca del poró fue menos de la mitad cuando éste se encontraba en asociación con laurel, que en el sistema con poró solo, pero la hojarasca del laurel compensó esta reducción. Por otro lado, la inclusión de laurel con el poró y el café, resultó en una distribución más pareja de la contribución anual de nutrientes. Las contribuciones anuales de Ca y Mg en la hojarasca fueron mayores en el sistema que incluía al laurel que en el sistema con poró solamente. No hubieron diferencias en la contribución total de N o de P entre los dos sistemas, y el sistema que incluía

laurel tuvo una incorporación anual menor de K. A pesar de estas diferencias entre los dos sistemas, las cantidades de nutrientes reciclados por los árboles en asociación alcanzó los niveles recomendados de fertilización requerida para la producción de café en ambos casos.

Qué sistema elegir dependerá del nutriente más limitante en cada caso particular. En el ejemplo previo, el sistema con laurel fue preferido por muchos agricultores debido a que, aparte de una incorporación más pareja de nutrientes a lo largo del año, el valor de la madera del laurel agregaba un incentivo económico. Además, como el laurel es una especie de poda natural, mientras que el poró necesita ser podado para incrementar el reciclaje de biomasa, el sistema que incluye laurel es menos costoso que el sistema con poró solo. Los resultados de otros experimentos posteriores en el CATIE confirmaron estos hechos (Fassbender et al. 1991).

Otras investigaciones en sistemas tradicionales similares también demostraron la importancia del reciclaje de nutrientes en sistemas agroforestales con cultivos perennes. En Ocumare de la Costa, Venezuela, Aranguren et. al. (1982) concluyeron que los árboles de sombra de las plantaciones de cacao contribuían con aproximadamente la mitad del aporte anual de hojarasca. La cantidad de N transferida al suelo a través de la hojarasca fue de 321 Kg/ha. La salida de N del sistema a través de las cosechas de cacao fue de 45 Kg/ha., con aproximadamente 20 Kg retornados al suelo luego del procesamiento. Los autores concluyeron que la extracción neta de N podía ser compensada por la incorporación de N a través de la hojarasca de árboles de sombra de las especies *Inga* y *Erythrina*.

El Rol de los Animales: Sistemas Agrosilvopastoriles

Los sistemas agrosilvopastoriles--la combinación de árboles para la producción de madera, leña o árboles frutales con animales, con o sin la incorporación de cultivos--son practicados a varias escalas. Ejemplos de sistemas de gran escala incluyen plantaciones de árboles con la incorporación de pastos para controlar malezas y obtener un retorno más inmediato de la venta de productos animales. En la zona subtropical húmeda de Misiones, Argentina la práctica de aclarar un bosque para aprovechar madera de especies valiosas, y mantener un ambiente adecuado para los animales, además de conservar árboles valiosos para su aprovechamiento futuro, se denomina "parqueo"; en algunos casos se realizan rotaciones de potreros y siembra de pasturas bajo los árboles. La cría de ganado puede además complementar la agricultura de subsistencia, con animales integrados en huertos caseros, o en sistemas de producción de alimento para ganado para su alimentación en establos.

En establecimientos donde se practican cultivos en callejones, el abono proveniente del ganado puede adicionarse al abono verde de los árboles para así aumentar la disponibilidad de nutrientes para los cultivos. El estiércol agregado al suelo puede también servir como una fuente de nutrientes para los microorganismos descomponedores, acelerando así la incorporación de nutrientes al suelo provenientes de la descomposición del abono verde. En algunas regiones, la incorporación de árboles--especialmente árboles de uso múltiple--puede tornar la cría de ganado de un uso ineficiente de la tierra a una actividad económica y ecológicamente factible. La incorporación de árboles puede mejorar el sistema incrementando la productividad de pasturas, o a través de la producción de forraje proveniente de hojas y/o frutas (Gill et al. 1990, Cobbina 1994/1995). En las zonas de altura (1300-2500 msnm) en los alrededores de San José, Costa Rica, son comunes los sistemas de *Alnus acuminata* (jaúl), en asociación con pastos, principalmente *Pennisetum clandestinum* (pasto kikuyo) y *Pennisetum purpureum* (pasto elefante), que sirven de forraje para el ganado de leche. Se estima que este sistema agrosilvopastoril tradicional se practica en aproximadamente 50.000 hectáreas en este país (Russo 1990).

Aunque la presencia de animales en una plantación de árboles puede acelerar el reciclaje de nutrientes, si la carga animal es muy alta, la compactación del suelo puede afectar el crecimiento de los árboles (Montagnini 1992). Generalmente es difícil separar los efectos de la compactación del suelo y el reciclaje de nutrientes generados por los animales, de los impactos de los árboles y pastos o leguminosas. En sistemas experimentales en la región Atlántica de Costa Rica, una especie leguminosa arbórea de rápido crecimiento (*Erythrina berteroana*) fué introducida en pasturas nativas. Por un período de estudio de tres años, el C orgánico del suelo aumentó en los tratamientos sin pastoreo, y la densidad aparente del suelo disminuyó en las áreas de control sin pastoreo y sin árboles (Cooperband and Logan 1993).

Otros experimentos en tierras marginales erosionadas de India subtropical compararon la erosión del suelo en sistemas agrosilvopastoriles con *Leucaena leucocephala* (usada para leña y forraje) y *Pennisetum purpureum* (usado para forraje) con la secuencia tradicional de cultivos de *Sesamum indicum* seguidos por *Brassica napus* (Grewal et al. 1994). Los resultados sugirieron que los sistemas agrosilvopastoriles fueron más efectivos en la conservación del suelo que los sistemas tradicionales de cultivo. Sin embargo, el pastoreo animal no tuvo influencia sobre las variables del suelo debido a que los animales fueron mantenidos fuera del sistema.

En América Central se destaca el uso de cercas vivas de *Gliricidia sepium*, sobre todo como fuente de forraje para el ganado durante la época seca. Las cercas vivas son establecidas por medio de la plantación de estacas grandes (generalmente de 2,5 m de largo y entre 8 y 20 cm de diámetro), que enraizan fácilmente, y sobre las cuales se atan varios hilos (generalmente tres) de alambre de púas (Budowski 1987). Para el mantenimiento de estos sistemas es necesaria mucha mano de obra permanente. En las cercas vivas se utilizan numerosas especies, de acuerdo con las condiciones climáticas y culturales. Las cuatro especies más comunes en América Central, norte de América del Sur y muchos países del Caribe son *Gliricidia sepium, Bursera simaruba, Spondias purpurea* y *Erythrina berteroana* (Budowski 1987).

El uso de follaje de árboles y arbustos en la alimentación de rumiantes es una práctica conocida por los productores de América Central desde hace siglos. Los estudios realizados en el CATIE desde 1980 se orientaron a la valoración como fuente de forraje de árboles y arbustos y su incorporación a sistemas de producción (Benavídez 1989). El follaje de la mayoría de las especies leñosas muestra contenidos de proteína cruda del doble o el triple de los pastos tropicales y, en varios casos, superiores a los alimentos concentrados. Se destaca la calidad nutricional de dos especies de euforbiáceas, chicasquil ancho (*Cnidoscolus acotinifolius*) y chicasquil fino (*C. chayamansa*), cuyo follaje contiene más de un 30% de proteína cruda. También sobresalen los valores forrajeros de dos moráceas, la morera (*Morus* sp.) y una especie de *Ficus* (amate); de malváceas como la amapola (*Malviscus arboreus*) y el clavelón (*Hibiscus rosa-sinensis*); del sauco negro *Sambucus mexicana*) y del sauco amarillo (*S. canadensis*), que pertenecen a la familia caprifoliácea, y de tres especies de la familia compositae, chilca (*Senecio* sp.), tora blanca (*Verbesina turbacensis*), y tora morada (*V. myriocephala*), todas ellas con valores de proteína cruda superiores al 20% (Benavídez 1994).

Con las especies de mayor contenido de nutrimentos, trabajando con rumiantes menores (ganado caprino) se han obtenido valores de producción de leche más elevados, y se ha observado una respuesta muy significativa al incrementar el nivel de follaje en animales recibiendo una dieta a base de pasto. Tal es el caso del follaje de amapola y morera, con los que se han observado rendimientos de 2.2 y 2.5 kg de leche por animal y por día, respectivamente, valores normalmente posibles sólo con el uso de concentrados. Además con el follaje de morera se han encontrado respuestas crecientes de ganancia de peso al aumentar su proporción en la dieta (Benavídez 1994).

Los sistemas agrosilvopastoriles requieren de un manejo cuidadoso para poder aprovechar el reciclaje de nutrientes y evitar la compactación del suelo. Esto puede lograrse a pequeña escala donde son más factibles el reciclaje manual del estiércol, el manejo y rotación de las pasturas y el transporte de forraje para alimentar los animales en establos o corrales. Sin embargo, estas prácticas requieren una labor intensiva y sólo serán adoptadas cuando los beneficios y retornos económicos sean atractivos para los agricultores.

LOS EFECTOS DE LOS ARBOLES SOBRE LA FERTILIDAD DEL SUELO

Una clave en el éxito de los sistemas agroforestales es la elección de componentes leñosos de rápido crecimiento con impactos positivos sobre las propiedades del suelo (Sánchez et al. 1985, Nair 1989, Young 1989, Montagnini 1992). Varias publicaciones compilan características, usos, y especies Arbóreas de Uso Múltiple (AUM) para su aplicación en diferentes regiones del mundo (e.g., NAS 1979, NAS 1980, Glover y Adams 1990, Lantican y Taylor 1991). La mayoría de las listas y bases de datos de AUM incluyen información sobre el rol de las especies sobre la fertilidad del suelo o el reciclaje de nutrientes. Estas guías enfatizan la fijación de N y las características de nodulación de especies leguminosas y plantas actinorrícicas, generalmente ofreciendo pocos detalles sobre su efecto potencial sobre otros nutrientes del ecosistema.

Numerosas especies arbóreas nativas y exóticas presentan potencial como mejoradoras de las características químicas, fisicas y biológicas del suelo y pueden ser muy útiles en combinaciones agroforestales. Por ejemplo, de 30 especies arbóreas de valor económico probadas en condiciones experimentales en regiones de las planicies húmedas de Costa Rica, Brasil y Argentina, aproximadamente la mitad tuvieron un efecto positivo sobre el N total del suelo, materia orgánica y/o cationes intercambiables y P, en comparación con una pastura aledaña (Tabla 1). En varios casos los valores de los parámetros probados fueron muy similares a aquéllos encontrados en bosques secundarios adyacentes. La mayoría de las otras especies probadas no parecieron cambiar sustancialmente las condiciones del suelo, y podrían ser utilizadas en suelos no degradados (Tabla 1).

Ciertas limitaciones disminuyen el amplio uso de los resultados tales como los mostrados en la Tabla 1, como un único criterio para la selección de especies para agroforestación. Primeramente, los resultados de pruebas estándar de fertilidad del suelo usadas en agricultura puede que no siempre revelen el potencial productivo del suelo, porque generalmente no incluyen todas las formas químicas de los nutrientes disponibles para su absorción por las plantas. Por ejemplo, aunque el N mineral (NO_3^- y NH_4^+) constituye menos del 10% de la cantidad total de N del suelo, ésta es la forma de N disponible para las plantas. Datos en porcentajes de mineralización de N bajo especies arbóreas frecuentemente no se hallan disponibles porque su estimación requiere procedimientos cuidadosos de laboratorio o de muestreo a campo. La evaluación de los efectos de los árboles sobre la disponibilidad de P en el suelo es inclusive más difícil, aunque la liberación de P de la hojarasca y su absorción por cultivos en experimentos de invernadero pueden dar una indicación indirecta de los impactos sobre la disponibilidad de P en el suelo.

Los impactos de los árboles sobre el suelo dependen de las características de reciclaje de nutrientes tales como la cantidad de hojarasca producida, su composición química y su tasa de descomposición. La hojarasca de los árboles puede ser usada como abono verde con diferentes resultados: la rápida descomposición del abono verde puede acelerar el crecimiento de cultivos asociados en suelos pobres, mientras que en otros casos una hojarasca más persistente puede constituir una fuente más constante de nutrientes y una mejor cobertura del suelo a lo largo del año. En el ejemplo de la Tabla 1, los altos porcentajes de caída de hojarasca y de descomposición más lenta resultaron en una elevada acumulación de hojarasca y alto contenido de materia orgánica en el suelo bajo *V. ferruginea*, haciendo a esta especie apropiada para la protección contra la erosión del suelo. En contraste, la hojarasca de *V. guatemalensis* puede ser especialmente importante para el reciclaje de Ca y Mg (Montagnini et al. 1993). Por otro lado, la hojarasca de *H. alchorneoides* fue menos abundante que las otras tres especies, pero su contenido de nutrientes fué mayor. Estas características promovieron el reciclaje, especialmente de N, Ca, Mg, K y P.

Factores adicionales que influencian la liberación de nutrientes de la hojarasca son sus contenidos de polifenoles y lignina, ya que ambos compuestos disminuyen la calidad de los materiales vegetales. La proporción polifenol/N por ejemplo, puede servir como un índice para tendencias de inmovilización a corto plazo observado en leguminosas con un alto contenido de polifenol, y la proporción lignina+polifenol/N puede servir como índice para patrones de largo plazo (Palm 1995). También es importante que los nutrientes sean provistos en sincronía con la necesidad de los cultivos (Palm 1995).

Se ha discutido que la habilidad de los sistemas agroforestales de facilitar la disponibilidad de nutrientes es muy limitada en suelos infértiles comparada con suelos fértiles, aunque pueden sin duda jugar un rol importante en la reducción de la pérdida de nutrientes en ambas situaciones (Szott et al. 1991). La producción de hojarasca y la cantidad de nutrientes reciclados en la hojarasca son mayores en suelos fértiles que en suelos infértiles; sin embargo, el uso de podas para acelerar el flujo de nutrientes puede incrementar la productividad de las plantas en suelos infértiles (Szott et al. 1991).

La incorporación de componentes leñosos en un sistema de producción puede proveer de beneficios provenientes de los productos arbóreos en sí (madera, leña, abono verde, y otros) y de sus potenciales ventajas ecológicas, especialmente sus habilidades en el reciclaje de nutrientes. La elección de una especie depende de que ambas ventajas productivas y ecológicas puedan lograrse en el mismo sistema, y en algunos casos una determinada función puede ser preferida.

EFICIENCIA EN EL USO DE NUTRIENTES Y ELECCION DE ESPECIES

El concepto de eficiencia en el uso de nutrientes (EUN) ha sido empleado para describir la habilidad diferencial de especies arbóreas para acumular materia orgánica en relación a los nutrientes tomados del suelo. La EUN ha sido definida a diferentes escalas de espacio y tiempo. En los niveles de poblaciones y comunidades vegetales, la EUN es definida generalmente como la cantidad de biomasa producida por unidad de nutriente absorbido (Grubb 1989, Binkley et al.

1992, Medina 1995). Puesto que usualmente no se efectúan mediciones de absorción de nutrientes en rodales de árboles maduros, se utiliza la caída de hojarasca como un estimador de la absorción anual de nutrientes (Vitousek 1984, Grubb 1989, Binkley et al. 1992). Idealmente, deberían hacerse esfuerzos para medir la producción total por tallos y raíces y considerar la absorción de nutrientes más las pérdidas debido a plagas y lixiviación de nutrientes (Grubb 1989). Las diferencias en el reciclaje y eficiencia de uso pueden ser el resultado de varios mecanismos de conservación de nutrientes, mediados por interacciones fisiológicas o mutualísticas (Chapin 1980, 1983).

También es importante considerar la relación entre la habilidad de reciclaje de las especies y sus potenciales impactos a corto y largo plazo en la mejora de nutrientes del suelo. Un "índice de reciclaje de nutrientes" (IRN), tomado como la inversa de EUN, es decir, la cantidad de nutrientes en la producción anual de hojarasca/producción anual de biomasa, ha sido usado para evaluar la adaptabilidad de especies arbóreas para combinaciones en sistemas agroforestales. Por ejemplo, Fassbender et al. (1991) encontraron que el índice de reciclaje de P era aproximadamente 6 veces mayor en combinaciones de cacao con *Erythrina poeppigiana* que con *Cordia alliodora* en sistemas agroforestales en Turrialba, Costa Rica. *Cordia*, una especie maderera, acumuló mucho P en la biomasa del tronco, mientras que *Erythrina*, un árbol de sombra con buenas propiedades de reciclaje de nutrientes, produjo grandes cantidades de hojas y ramas resultando en un mayor reciclaje de P.

Cuando se pone en contexto con las características de reciclaje de nutrientes de una especie, la EUN puede indicar el diseño y manejo apropiados de un sistema tendientes a mantener la productividad y recuperar o conservar nutrientes a largo plazo. La habilidad de una especie para producir grandes cantidades de biomasa con menos nutrientes puede ser una consideración importante en la selección de especies para sitios degradados y pobres en nutrientes.

Aplicabilidad del Concepto de EUN en el Diseño y Manejo de Sistemas Agroforestales

De las 24 especies mostradas en la Tabla 1, datos sobre productividad de árboles, caída de hojarasca, y química de la hojarasca de ocho especies de Bahía, Brasil y cuatro especies de La Selva, Costa Rica fueron usados para calcular valores de EUN (Tabla 2). Debido a que las especies fueron parte de proyectos de ensayos de especies arbóreas forestales, los valores de EUN fueron calculados como el incremento anual de biomasa del tronco/nutrientes en la caída anual de hojarasca (Montagnini 1995). No hubieron datos suficientes sobre caída de hojarasca o productividad de las otras especies mostradas en la Tabla 1. En ambos sitios, Bahía y La Selva, las mayores eficiencias fueron para el K y el P, y las menores para el N, Ca y Mg (Tabla 2).

Los resultados de Bahía sugieren que *Bombax macrophyllum* y *Plathymenia foliolosa*, con altos valores de EUN, crecerían bien en suelos relativamente pobres en nutrientes, y por lo tanto podrían ser buenas alternativas para la reforestación de sitios degradados luego del abandono después de actividades agrícolas o ganaderas, situaciones frecuentes en la región. *B. macrophyllum* tendió a acumular altas cantidades de hojarasca bajo su copa mientras que rodales de *P. foliolosa* tuvieron relativamente altas cantidades de materia orgánica y N total en el horizonte superior del suelo, en comparación con áreas adyacentes a bosques secundarios (Montagnini et al. 1994). Estas características indican que estas especies pueden ser adecuadas para proyectos de rehabilitación de suelos, incluyendo el incremento del contenido de materia orgánica y la protección contra la erosión. En Bahía, otras especies tales como *Buchenavia* *grandis* y *Hymenaea aurea*, con valores bajos de EUN, serían más apropiadas para sistemas agroforestales donde los cultivos se beneficiarían con el reciclaje de nutrientes de la hojarasca.

En La Selva, *Vochysia ferruginea* mostró comparativamente bajos valores de eficiencia para todos los nutrientes considerados, confirmando el rol beneficioso de esta especie en el reciclaje de materia orgánica y su impacto positivo sobre la fertilidad del suelo como se muestra en la Tabla 1. La relativamente baja eficiencia (alto reciclaje) de N y P encontrado para *Stryphnodendron microstachyum* y *Hyeronima alchorneoides* coinciden con resultados de experimentos donde plántulas de maíz cultivadas con abono verde de estas especies crecieron mejor y absorbieron más N y P que con abono verde de otras especies (Montagnini et al. 1993).

En proyectos que apuntan a la recuperación de los nutrientes en suelos degradados, las especies con alta eficiencia en el uso de nutrientes deberían ser combinadas en tiempo o espacio con especies con baja eficiencia de uso de nutrientes. Sin embargo, los valores de EUN por sí solos puede que no sean suficientes para determinar el rol de una especie arbórea sobre los nutrientes del ecosistema. Por ejemplo, a pesar de los altos valores de EUN, una especie arbórea puede presentar alta demanda de nutrientes del suelo a largo plazo. En las regiones tropicales húmedas se considera que los nutrientes son un factor crítico para la productividad de los árboles, mientras que en regiones con una marcada estación seca la eficiencia de uso del agua sería un factor más importante que la EUN, influyendo sobre la elección de especies y el diseño de sistemas. Finalmente, otras adaptaciones ecológicas de las especies (p.e., eficiencia del uso de luz, arquitectura radicular, resistencia a plagas y enfermedades) pueden ser más importantes en la selección de especies para combinaciones agroforestales.

FACTIBILIDAD DE SISTEMAS AGROFORESTALES

La introducción de árboles en sistemas de producción es ventajosa sólo si la competencia entre árboles y cultivos por recursos es minimizada mientras que son favorecidos los efectos positivos sobre la fertilidad del suelo: ejemplos de tales sistemas incluyen la introducción de especies fijadoras de N tales como *Faidherbia albida* en el Sahel, y algunos sistemas secuenciales de barbechos mejorados (Sánchez 1995). Aparte de sus efectos benéficos sobre el suelo, muchas especies arbóreas con rápido cierre del dosel disminuyen el crecimiento de malezas, por lo tanto las características de copa de los árboles afectarán su elección y dictarán las prácticas de manejo requeridas en sus usos en sistemas agroforestales. Por último, las decisiones para cambiar cualquier sistema deben tomar en cuenta los objetivos que el cambio pretende lograr, por lo tanto la selección de especies para sistemas agroforestales debe estar basada en varios factores además de sus influencias positivas sobre suelos y la producción de los cultivos (Wood 1990). La elección de especies para forestación y para sistemas agroforestales es regida en última instancia por la preferencia de los pobladores locales, lo cual a su vez depende de la disponibilidad de plantines, incentivos oficiales y de los mercados.

La elección de especies de cultivo anuales adecuadas es importante para el éxito de sistemas de cultivos en callejones. El maíz y el arroz por ejemplo, demandan más luz que los frijoles o la mandioca y son por lo tanto más afectados por la sombra de los árboles. La altura de poda y el ancho de los callejones pueden ser ajustados para evitar una competencia excesiva entre árboles y cultivos. En experimentos del CATIE por ejemplo, Kass (1989) encontró que la producción de plantas de maíz era mayor cuando se encontraban a mayor distancia de las hileras de *Gliricidia* dentro de los callejones. Los resultados de los análisis económicos para los mismos sistemas indicaron que el cultivo en callejones no era conveniente para N, con un costo de mercado bajo de fertilizantes.

La adopción de sistemas de cultivos en callejones es de amplia difusión en áreas de bajos ingresos en el este de Indonesia, el sur de las Filipinas, y en Sri Lanka (Kang y Wilson 1987). En Nigeria, investigadores del Instituto Internacional de Agricultura Tropical (IITA) encontraron que aunque la mano de obra para la poda de las hileras es una gran limitante, cultivos en callejones con *Calliandra* spp. han dado buenos resultados (Plucknett 1990). Sin embargo la aplicación de la técnica de cultivos en callejones tiene sus limitaciones: a veces los monocultivos son preferidos por razones prácticas, y a veces el valor de los productos de las podas de las hileras de árboles es mayor que el valor de los cultivos. La plantación de los árboles en las hileras favorece la producción de biomasa por los árboles, pero puede resultar en una menor producción de los cultivos debido a la competencia con los árboles por luz y nutrientes. En suelos altamente lavados, un cultivo en callejones exitoso puede requerir el uso de insumos externos (p.e., agregado de cal para incrementar el pH) para mantener niveles de fertilidad del suelo adecuados para las producciones deseadas de cultivos (Evensen et al. 1995).

Cuando la existencia de nutrientes es baja, puede tomar varios años para que un sistema agroforestal acumule nutrientes y materia orgánica en el suelo hasta un punto en el cual el sistema se torne conveniente en comparación con monocultivos. Por ejemplo, tres años después del establecimiento del sistema de cultivo en callejones de *Albizia*-sorgo discutido previamente, la producción del cultivo de grano en el sistema era menor que en el control, a pesar del lento pero continuo aumento en P del suelo disponible en el sistema agroforestal. Debido a la baja productividad inicial de los sistemas agroforestales establecidos en suelos degradados, algunas veces éstos no son económicamente factibles para los agricultores.

Como la adopción de sistemas agroforestales involucra la plantación de árboles seleccionados, se necesitará capital inicial para cubrir los costos de establecimiento de los 2-3 primeros años. Este requerimiento puede constituirse en un problema si los agricultores no tienen acceso a capital. En las tierras bajas del Atlántico de Costa Rica, los sistemas de barbechos enriquecidos pueden ser más convenientes que la agricultura o ganadería convencional; sin embargo, se requiere de asistencia para ayudar a los agricultores a cubrir los gastos iniciales que se necesitan para plantar los árboles (Montagnini y Mendelsohn 1996). Los agricultores de subsistencia generalmente no tiene acceso a préstamos y no pueden solventar los gastos aún cuando lo consideran una inversión conveniente. Los programas de préstamos de bajos intereses para la reforestación pueden hacer realidad el desarrollo sostenido permitiendo a pequeños productores hacer una sólida inversión a largo plazo en sus tierras.

CONCLUSIONES

El objetivo del diseño y manejo de los sistemas agroforestales es modificar el ciclaje de nutrientes de manera de hacer un uso más eficiente de los mismos, sea que éstos provengan de fuentes naturales o fertilizantes. Experiencias descritas en este trabajo con barbechos mejorados son de relevancia especial en Centro América y otras regiones donde la tierra es escasa y los períodos de barbecho no son lo suficientemente prolongados como para restaurar la capacidad productiva de los suelos. Se destacan ejemplos de prácticas agrícolas llevadas a cabo por pueblos indígenas, tales como el de los Kayapó en Brasil, que utilizan árboles para mantener o restaurar la fertilidad del suelo sin utilizar ningún fertilizante químico. En situaciones donde los "barbechos mejorados" no son factibles debido a la escasez de tierras, técnicas tales como el cultivo en callejones con la aplicación de "mulch" (mantillo o abono verde) pueden constituir alternativas de agricultura viables.

En estudios realizados por CATIE en Costa Rica, se ha comprobado que las cantidades de nutrientes reciclados por los árboles en asociación con cultivos permanentes como el café, alcanzaron los niveles recomendados de fertilización requerida para la producción. En sistemas agrosilvopastoriles, el uso de follaje de árboles y arbustos en la alimentación de rumiantes es una práctica conocida. El follaje de la mayoría de las especies leñosas muestra contenidos de proteína cruda del doble o el triple del de los pastos tropicales y su utilización redunda en ahorros considerables y aumentos significativos en la producción de carne y leche.

Una clave en el éxito de los sistemas agroforestales es la elección de componentes leñosos de rápido crecimiento con impactos positivos sobre las propiedades del suelo. Numerosas especies arbóreas nativas y exóticas presentan potencial como mejoradoras de las características químicas, fisicas y biológicas del suelo y pueden ser muy útiles en combinaciones agroforestales. Cuando se pone en contexto con las características de reciclaje de nutrientes de una especie, el concepto de eficiencia en el uso de nutrientes (EUN) puede indicar el diseño y manejo apropiados de un sistema tendientes a mantener la productividad y recuperar o conservar nutrientes a largo plazo. La habilidad de una especie para producir grandes cantidades de biomasa con menos nutrientes puede ser una consideración importante en la selección de especies para sitios degradados y pobres en nutrientes.

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Tabla 1. Características químicas del horizonte superior del suelo en rodales puros de 24 especies arboreas nativas en La Selva,Costa Rica; Porto Seguro, Bahia, Brasil; y Misiones, Argentina.

Sitio/Especie arborea

	pH	C (%)	N (%)	P (cmol.kg⁻¹)	K	Ca	Mg
a- La Selva, Costa Rica[1]							
Stryphnodendron microstachyum	5.4ab	3.42ab	0.29b	5.6a	0.27a	0.45a	0.63ab
Vochysia ferruginea	5.4ab	3.76a	0.32a	7.1a	0.22a	0.73a	0.61ab
Vochysia guatemalensis	5.3ab	3.13ab	0.29b	5.2a	0.11a	0.25a	0.37ab
Hyeronima alchorneoides	5.1b	2.96c	0.22b	1.5b	0.09a	0.31b	0.21b
Pastura Abandonada	5.3ab	2.73c	0.22b	4.9a	0.19a	0.32b	0.27b
Bosque secundario	5.3ab	4.33a	0.33a	3.6b	0.17a	0.68a	0.55ab
b- Porto Seguro, Bahia, Brasil[2]							
Especies leguminosas fijadoras de N:							
Bowdichia virgilioides	4.9	1.98def	0.16def	1.32def	0.06bcd	1.35bc	0.39de
Centrolobium minus	4.6	1.87efg	0.16def	1.19efg	0.05fgh	0.53hi	0.21i
Centrolobium robustum	4.5	1.65ij	0.13f	1.07fgh	0.05fgh	0.40i	0.16i
Inga affinis	4.9	2.10cde	0.18cd	3.64a	0.07bcd	0.76gh	0.49bc
Parapiptadenia pterosperma	4.9	2.38ab	0.20bc	0.78ij	0.08b	1.40bc	0.60a
Pithecellobium elegans	4.8	1.67hij	0.15ef	0.59kl	0.05efg	0.79gh	0.40de
Platymenia foliolosa	4.7	2.08cde	0.18bcd	0.13m	0.05efg	1.05cde	0.42cd
Especies leguminosas no fijadoras de N:							
Arapatiella psilophylla	4.7	1.94def	0.18bcd	1.45de	0.06bcd	0.38i	0.37de
Caesalpinia echinata	5.1	2.41a	0.17cde	1.54de	0.07bcd	1.17bcd	0.39de
Cassia spp.	4.7	1.94def	0.16def	1.40def	0.07bcd	0.56hi	0.34de
Copaifera luscens	5.0	2.02cde	0.17cde	0.63jk	0.06cde	1.15bcd	0.34de
Dimorphandra jorgei	4.9	1.97def	0.19bc	0.97ghi	0.03j	0.98def	0.32efg
Hymenaea aurea	4.4	2.00def	0.16def	2.03c	0.06bcd	0.26i	0.24hi
Macrolobium latifolium	4.7	1.90efg	0.16def	0.67jk	0.04hij	0.36i	0.25fg
De otras familias:							
Bombax macrophyllum	4.8	1.78ghi	0.13f	1.42de	0.06bcd	0.84efg	0.33ef
Buchenavia grandis	4.6	2.06cde	0.14f	2.09c	0.06bcd	0.80fg	0.33ef
Eschweilera ovata	5.3	1.82fgh	0.31a	0.58kl	0.11a	1.38bc	0.53ab
Lecythis pisonis	5.3	1.99def	0.18bcd	0.23lm	0.04ghi	1.46b	0.32ef
Licania hypoleuca	5.0	1.63j	0.14f	1.61d	0.07bcd	1.31bcd	0.35de
Pradosia lactescens	4.9	2.15bcd	0.18bcd	0.81ij	0.05fgh	0.84efg	0.24gh
Bosque primario	4.9	1.99def	0.15ef	0.96hi	0.08bc	1.23bcd	0.36de
Bosque secundario	5.1	2.15abc	0.22b	2.46b	0.07bcd	2.20a	0.62a
c- Misiones, Argentina[3]							
Balfourodendron riedelianum	5.8	2.6b	0.34ab	n.d.	0.55bc	7.1bc	1.7c
Bastardiopsis densiflora	7.1	6.3a	0.65a	n.d.	1.28a	20.4a	3.4ab
Cordia trichotoma	6.4	4.0ab	0.46ab	n.d.	0.79b	13.6ab	2.6abc
Enterolobium contortisiliquum	6.1	3.4ab	0.39ab	n.d.	0.67b	8.7bc	3.5a
Ocotea puberula	6.1	4.4ab	0.59a	6.09a	1.11a	17.3a	4.7a
Control con pastos	5.8	2.2b	0.0.27b	n.d.	0.26c	6.3c	2.4bc

Fuentess: [1] Montagnini y Mendelsohn (1996), [2] Montagnini et al. (1994), [3] Fernández et al. (1995).
Nota: Para cada sitio, las diferencias entre medias son estadisticamente diferentes cuando se encuentran seguidas de diferentes letras ($p<0.05$).
n.d.: no detectado

Tabla 2. Eficiencia del uso de nutrientes (EUN) (Megagramos de incremento anual de biomasa del tallo)

	N	Ca	Mg	K	P
Porto Seguro, Bahia, Brasil:					
Especies leguminosas fijadoras de N:					
Centrolobium robustum	0.05	0.05	0.37	0.87	1.74
Platymenia foliolosa	0.08	0.34	7.00	3.51	4.66
Especies leguminosas no fijadoras de N:					
Caesalpinia echinata	0.04	0.03	0.54	0.78	1.81
Hymenaea aurea	0.06	0.09	0.45	0.64	1.91
Especies de otras familias:					
Bombax macrophyllum	0.36	0.20	0.88	20.70	20.70
Buchenavia grandis	0.05	0.04	0.38	0.68	1.70
Eschweilera ovata	0.12	0.10	0.44	0.96	5.73
Lecythis pisonis	0.12	0.11	0.89	1.58	3.56
	N	**Ca**	**Mg**	**K**	**P**
La Selva, Costa Rica:					
Stryphnodendron mycrostachyum	0.08	0.06	0.35	0.63	0.53
Vochysia ferruginea	0.08	0.03	0.26	0.38	0.56
Vochysia guatemalensis	0.16	0.05	0.29	0.84	1.07
Hyeronima alchorneoides	0.09	0.03	0.15	0.22	0.45

Leyendas de las Figuras

Fig. 1. Diagrama del ciclaje de nutrientes en sistemas agroforestales (adaptado de Young 1989)

Fig. 2. Existencias y pérdidas acumulativas de calcio en función del tiempo en la parcela experimental de San Carlos de Rio Negro, Venezuela.

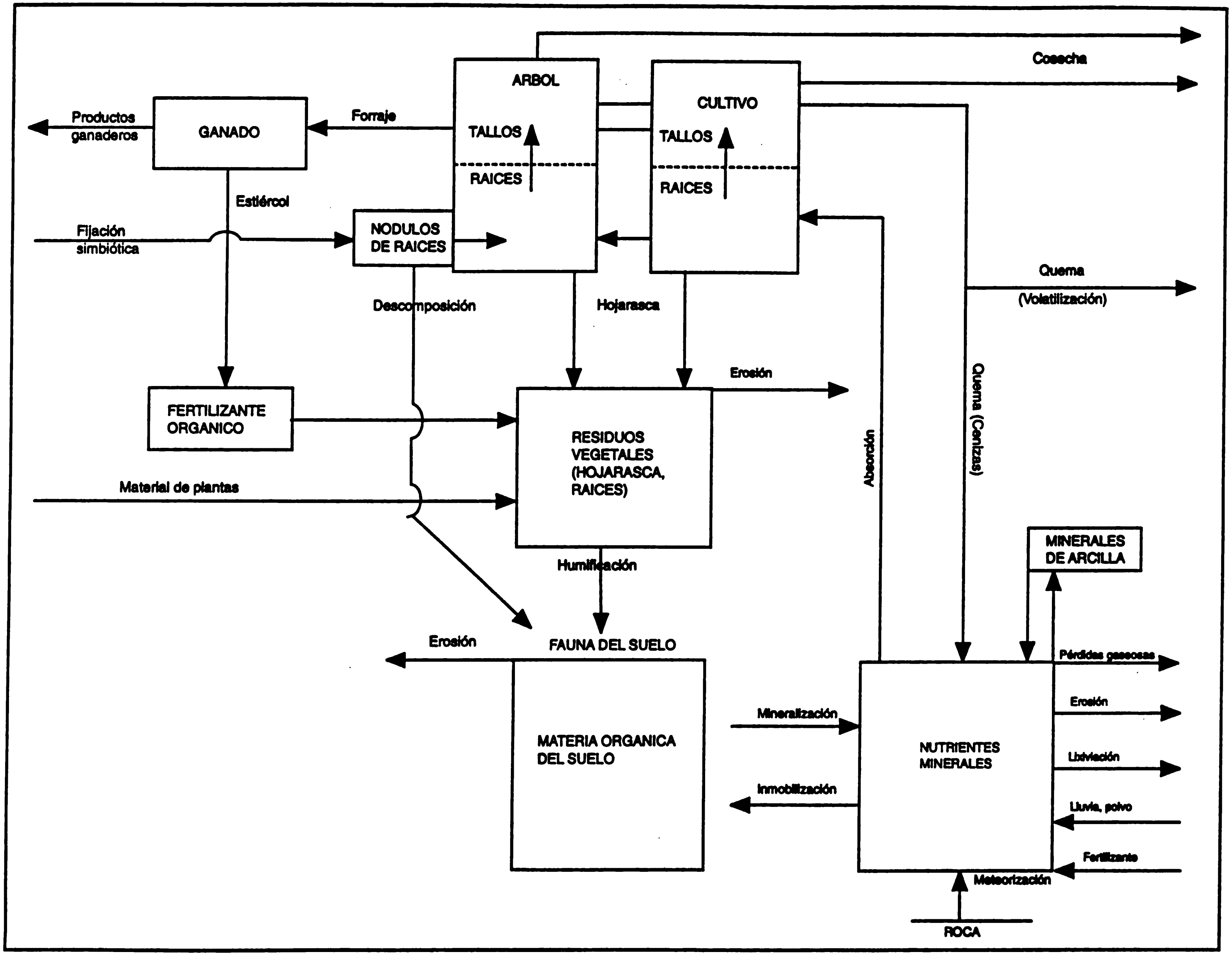
Fig. 3. Existencias y pérdidas acumulativas de potasio en función del tiempo en la parcela experimental de San Carlos de Rio Negro, Venezuela.

Fig. 4. Existencias y pérdidas acumulativas de magnesio en función del tiempo en la parcela experimental de San Carlos de Rio Negro, Venezuela.

Fig. 5. Existencias y pérdidas acumulativas de nitrógeno en función del tiempo en la parcela experimental de San Carlos de Rio Negro, Venezuela.

Fig. 6. Existencias de fósforo lábil en fracciones de suelo de los 75 cm superiores y en la biomasa aérea en un sistema experimental de cultivo en callejones (AC), y en un control de monocultivo de sorgo (NA). Hay una tendencia de incrementos de diferencias graduales entre los dos sistemas a lo largo de los tres años del período experimental. Debido a la gran variabilidad, las diferencias no fueron significativas con excepción de las fracciones marcadas con "a" y "b". PO es fósforo orgánico, PI es fósforo inorgánico, NaOH y NaHCO3 son los extractivos. ABOVEBIO es la biomasa aérea.

Fig 1



Cosecha
ARBOL
TALLOS
RAICES
CULTIVO
TALLOS
RAICES
GANADO
Productos ganaderos
Forraje
Estiércol
Fijación simbiótica
NODULOS DE RAICES
Descomposición
Hojarasca
Quema
(Volatilización)
Erosión
FERTILIZANTE ORGANICO
RESIDUOS VEGETALES (HOJARASCA, RAICES)
Material de plantas
Absorción
Quema (Cenizas)
MINERALES DE ARCILLA
Humificación
FAUNA DEL SUELO
Erosión
MATERIA ORGANICA DEL SUELO
Mineralización
Inmobilización
NUTRIENTES MINERALES
Pérdidas gaseosas
Erosión
Lixiviación
Lluvia, polvo
Fertilizante
Meteorización
ROCA

Fig 2

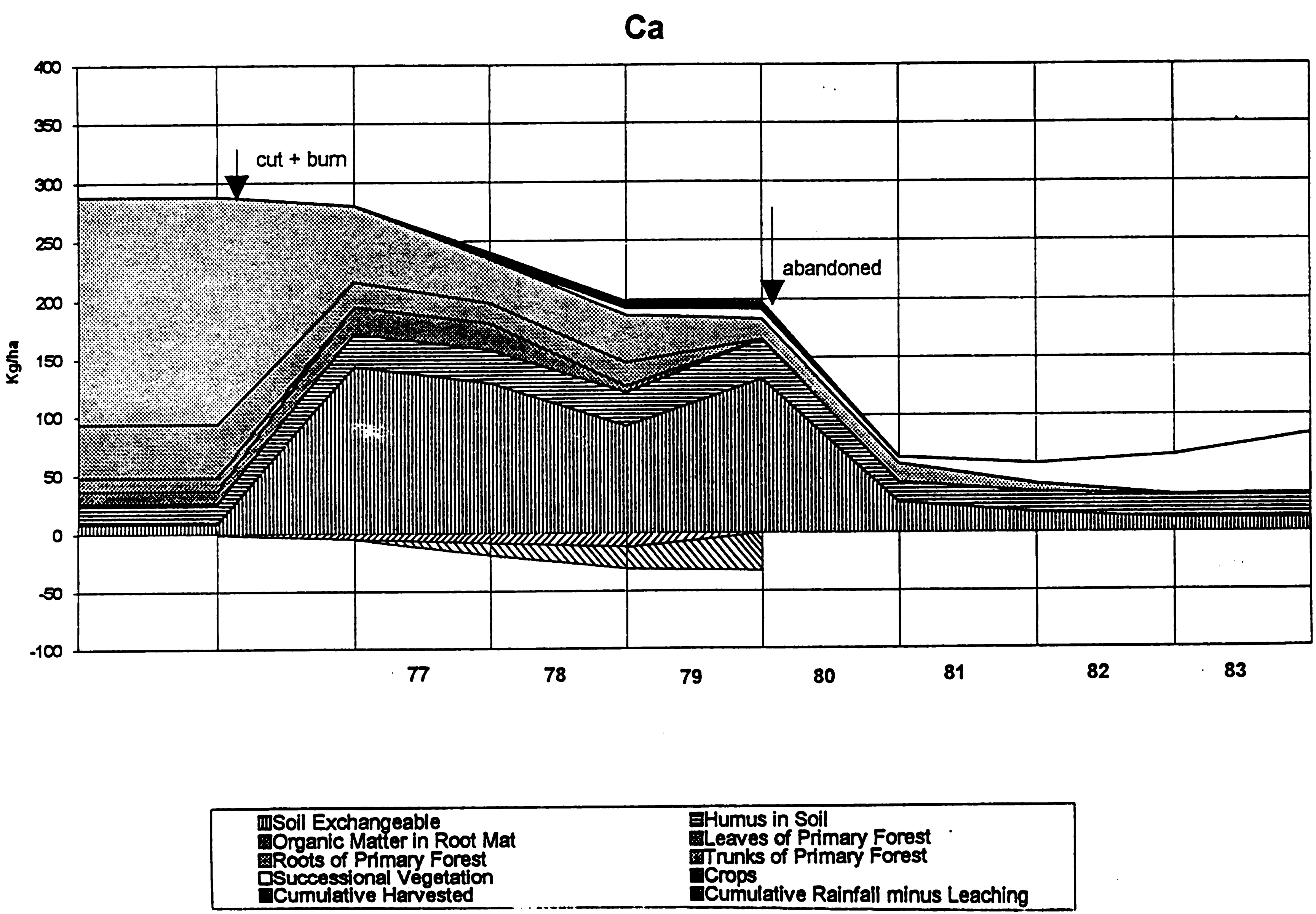

Ca
cut + burn
abandoned
Kg/ha
400
350
300
250
200
150
100
50
0
-50
-100
77
78
79
80
81
82
83
Soil Exchangeable
Organic Matter in Root Mat
Roots of Primary Forest
Successional Vegetation
Cumulative Harvested
Humus in Soil
Leaves of Primary Forest
Trunks of Primary Forest
Crops
Cumulative Rainfall minus Leaching

Fig 3

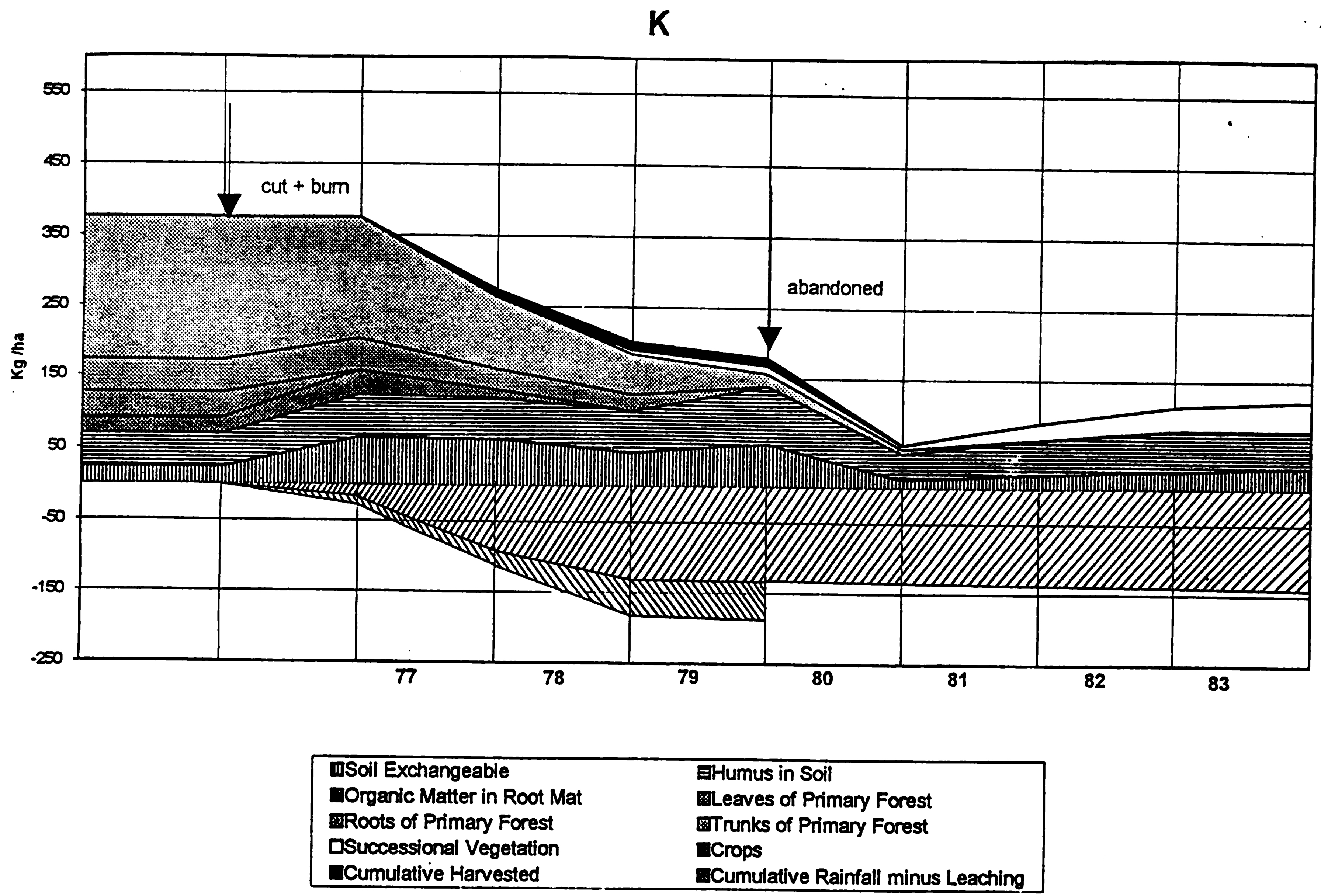
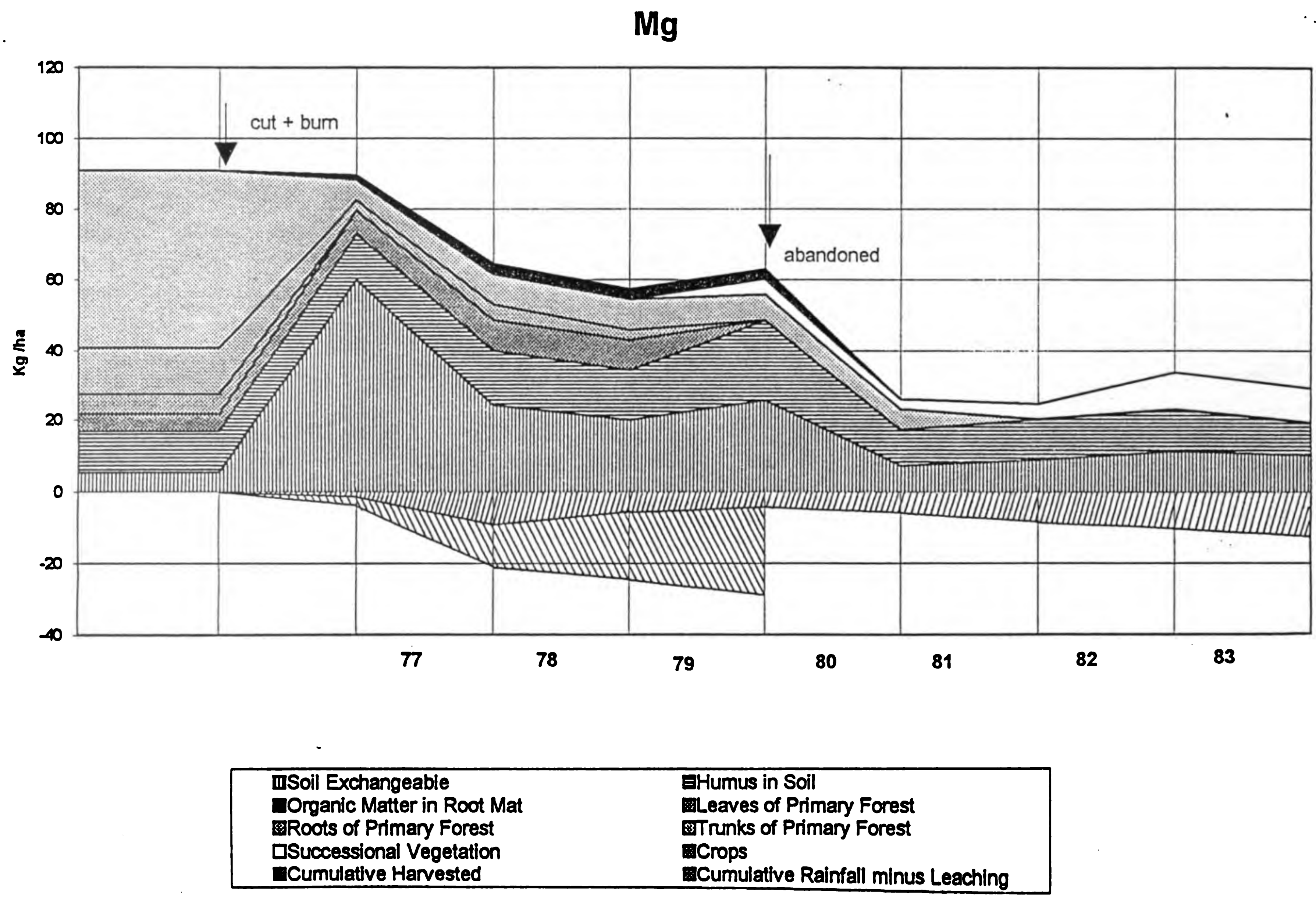
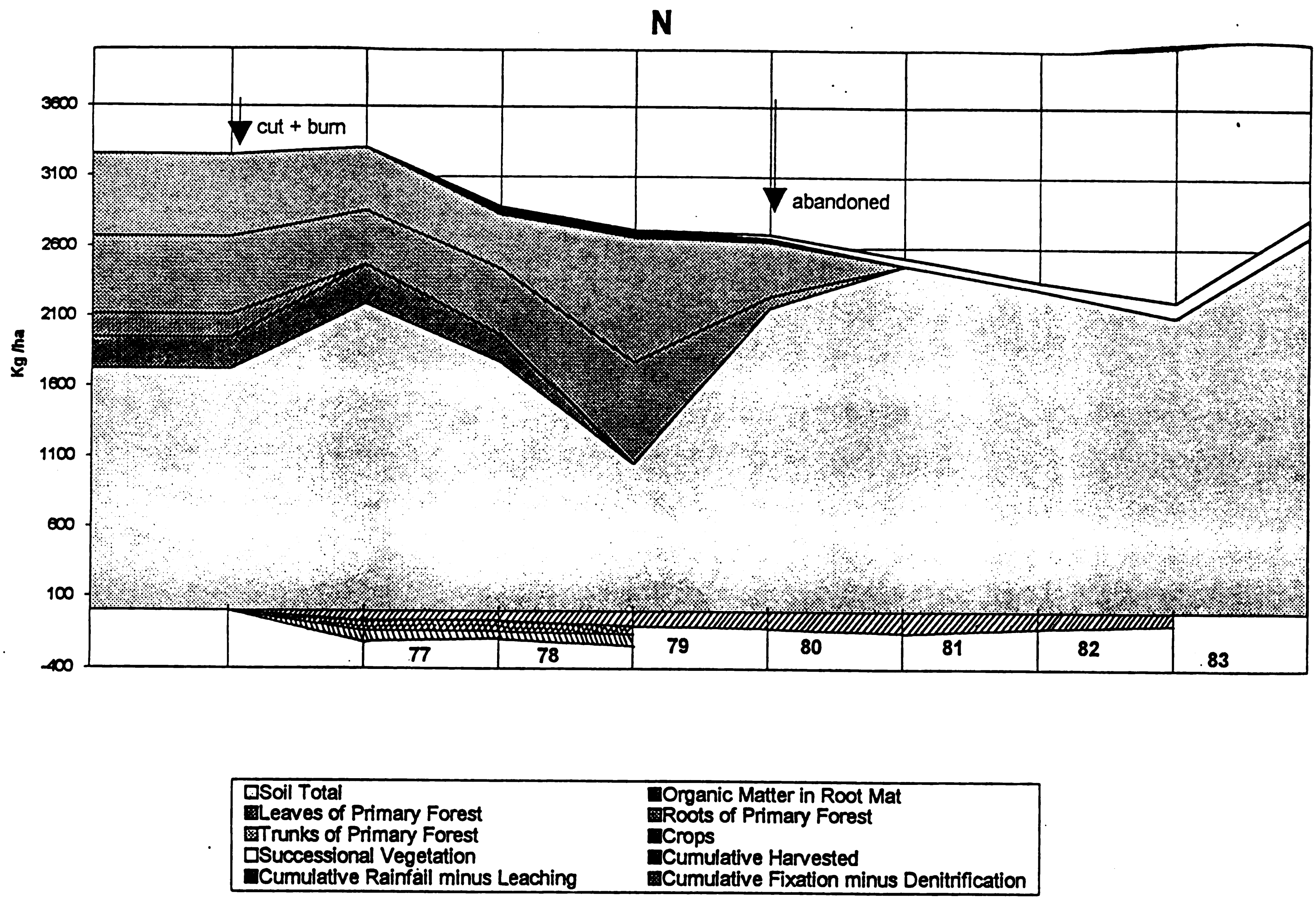

K
550
450
350
250
150
50
-50
-150
-250
Kg /ha
cut + burn
abandoned
77
78
79
80
81
82
83
Soil Exchangeable
Organic Matter in Root Mat
Roots of Primary Forest
Successional Vegetation
Cumulative Harvested
Humus in Soil
Leaves of Primary Forest
Trunks of Primary Forest
Crops
Cumulative Rainfall minus Leaching

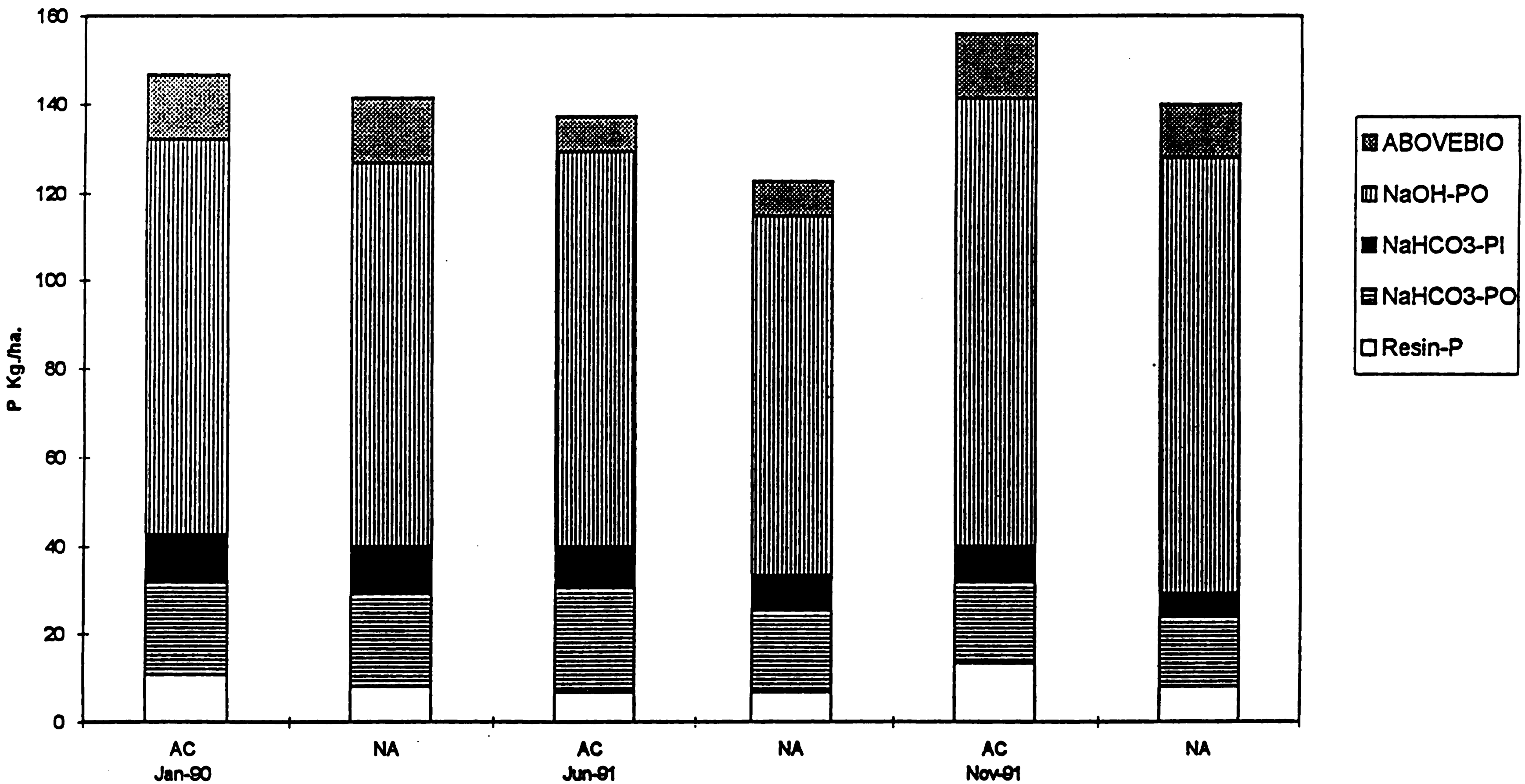
Fig 4


Mg
Kg /ha
120
100
80
60
40
20
0
-20
-40
cut + burn
abandoned
77
78
79
80
81
82
83
Soil Exchangeable
Humus in Soil
Organic Matter in Root Mat
Leaves of Primary Forest
Roots of Primary Forest
Trunks of Primary Forest
Successional Vegetation
Crops
Cumulative Harvested
Cumulative Rainfall minus Leaching


N
Kg /ha
3600
3100
2600
2100
1600
1100
600
100
-400
cut + burn
abandoned
77
78
79
80
81
82
83
Soil Total
Leaves of Primary Forest
Trunks of Primary Forest
Successional Vegetation
Cumulative Rainfall minus Leaching
Organic Matter in Root Mat
Roots of Primary Forest
Crops
Cumulative Harvested
Cumulative Fixation minus Denitrification

'126

Labile Phosphorus Stocks in Fractions of the Upper 75 cm. of Soil and in the Aboveground Biomass in an Experimental Alley Cropping System (AC) and in a Monoculture Control of Sorghum (NA)



Tropical plantations with native trees: Their function in ecosystem restoration

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ABSTRACT

Tree planting is currently being promoted in a number of government and private efforts towards rural development throughout the tropics. As the area in degraded lands increases, emphasis is placed on the use of species which can grow in such conditions and yield economic products as well as environmental benefits (soil conservation, watershed protection).

This chapter focuses on the impacts of native trees on soil fertility and nutrient cycling, using examples from land rehabilitation programs from tropical humid regions of Latin America. In Costa Rica, increased level of soil nitrogen, carbon, Ca and Mg were found under the tree plantations than under grass, with values close to those found in 20-year-old forest. Among the tree species, the highest soil C, N and cations were found under *Vochysia ferruginea*, while results of nutrient cycling studies revealed important effects of other species on soil N and P availability and Ca and Mg recycling. In Bahia, Brazil, positive effects were found in at least five soil parameters under 15 out of 20 tree species, in comparison with primary and secondary forest. Several species contributed to increased C and N concentrations in the top-soil: *Inga affinis*, *Parapiptadenia pterosperma*, *Plathymenia foliolosa* (leguminous, N-fixing species), *Caesalpinia echinata*, *Copaifera luscens* (leguminous, non-N-fixing), *Eschweilera ovata*, *Pradosia lactescens* (of other families). In Misiones, NE Argentina, soils under *Bastardiopsis densiflora* had the highest levels of organic matter, N, cations and pH.

Nutrient use efficiencies (biomass increments per unit of nutrients in annual litterfall) were calculated for each species to help to integrate results and design management recommendations geared to sustaining productivity of plantation systems including these species. In addition, analysis

of nutrient stocks in soils and in forest litter, and information on nutrient release from litter, is brought forward to stress the importance of the soil-litter system on plantation nutrient conservation.

Keywords: soil rehabilitation, native trees, nutrient use efficiency, lowland humid tropics

INTRODUCTION

Tropical plantations can serve diverse economic, social, political and ecological functions. With considerably higher yields than managed native forests, tropical and subtropical plantations can make substantial contributions to world timber and pulp production (Wadsworth 1983, Evans 1992). Tree plantations can also be a source of cash, savings and insurance for individual farmers. Plantations may help stabilize rural populations in regions where shifting agriculture is the predominant land use. In combination with subsistence and commercial crops (agroforestry) or cattle (agrosilvopastoral systems), plantations have been used as tools in rural development projects worldwide. Plantations are often seen as alternatives to deforestation as they can provide products that otherwise would be taken from natural forests (Fearnside 1990, Mc Nabb et al. 1994).

If plantation species are chosen with knowledge of their nutrient-use efficiencies and recycling capacities, they can be highly productive and also serve a function in ecosystem restoration projects. Particularly, tree plantations and tree-crop combinations represent productive land use alternatives for deforested lands with poor natural forest regeneration due to long distance to sources of propagules or intense site degradation. Among the latter, low soil fertility, soil compaction after abandonment from cattle grazing, and invasion by grasses and other agressive vegetation can be serious obstacles to both forest regeneration and conventional agriculture. As the area in degraded lands spreads out, emphasis is increasing on the use of tree species which can grow in such conditions and yield economic products (timber, fuelwood and other) as well as environmental benefits (soil conservation, watershed protection) (Evans 1992).

The initial step in ecosystem rehabilitation projects is to identify the most important constraints to crop or tree productivity, as well as defining the specific land restoration objectives. Some soils can be recovered through the use of fertilizers, others need more drastic rehabilitation techniques, and there are situations of extreme degradation where soils cannot be recovered at all (Dedecek 1992). The recovery of the soils' productive capacity is frequently very expensive, thus the techniques involved must produce financial returns to ensure their adoptability by the local farmers.

The choice of appropriate tree species for plantation forestry or agroforestry is influenced by knowledge on the species' performance and their economic and environmental benefits. Locally, tree species choice is determined by seed or seedling availability and information on silvicultural characteristics and management, including fast growth and the possibility of intercropping during early establishment. Most reforestation or tree planting programs and subsidies promote the use of well-known, often exotic species. About 85% of plantation forestry in the tropics is dominated by three genera: *Pinus*, *Eucalyptus* and *Tectona*, while there may be thousands of indigenous species suitable for similar purposes (Evans 1992). Native trees can be more appropriate than exotics because (1) they are better adapted to local environmental conditions, (2) seeds and other propagules are locally available, and (3) farmers are familiar with them and their uses. Besides, the use of indigenous trees in productive systems helps preserve genetic diversity and is in better balance with the local flora and fauna.

In the present chapter, examples are presented from experimental plantations with native trees that had been established with the purpose of rehabilitating lands abandoned from extensive agriculture or cattle in the humid tropics. A total of 30 indigenous tree species were evaluated in three forest regions of Latin America. The principal focus of this chapter is on the impacts of trees on soils, their nutrient recycling abilities and the lessons that can be learned for the implementation and sustainable management of plantation systems including these species. This information can be used to design management strategies to take advantage of the trees' ameliorating effects on soils and to avoid site nutrient depletion with harvest. These strategies should be useful for promoting the use of systems (mixed or pure plantations, agroforestry) including these fast growing timber species in the area and in other tropical lowland regions with similar ecological characteristics.

REHABILITATING ABANDONED LANDS IN THE LATIN AMERICAN HUMID TROPICS

A research program to develop alternatives for the rehabilitation and use of abandoned lands took place from 1987 to 1998 in three humid forest regions of Latin America: the Atlantic lowlands of Costa Rica, the Atlantic rainforest of Bahia in NE Brazil, and the sub-tropical forest of Misiones, NE Argentina (Table 1). In these regions, common situations of rapid deforestation, loss of biodiversity, resource misuse and land degradation persist. Similar methods were used in the three locations: soil chemistry and nutrient cycling parameters were measured in pure stands of selected indigenous species, using adjacent areas free of trees (abandoned agricultural field or pasture, secondary/primary forest) for comparison. The size of each project varied with the sites: in Costa Rica the studies were the most complete (soils, above- and below-ground tree biomass, litterfall and forest-floor litter biomass and tissue chemistry), while in Bahia and Misiones the trees were part of a forest reserve or were in private farms and thus destructive sampling was not possible.

Sampling procedures and chemical methods are described in Montagnini (1994), Montagnini and Sancho (1990a, 1990b, 1994a, 1994b), and Montagnini et al. (1991, 1993, 1994, 1995a, b, c). The soils under the species, grassy areas free of trees and adjacent young secondary forest were sampled for soil fertility and nitrogen availability measurements at the three research sites. Litterfall was mesured biweekly with litter traps, and forest-floor litter accumulation was sampled every three months at La Selva, while at Bahia data from existing studies was used. No litter data was available from the Misiones site. For both La Selva and Bahia, nutrient use efficiencies (NUE) were calculated by dividing annual biomass increments by nutrients in annual litterfall for each species.

IMPACTS OF TREES ON SOILS AND NUTRIENT RECYCLING FROM LITTER

La Selva, Costa Rica

Soil fertility

At La Selva, in just 2.5 years soil conditions improved in the tree plantations 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 2). The highest values for soil organic matter, total N, Ca and P were found under *Vochysia ferruginea*, a species common in mature and secondary forests in the region (Montagnini and Sancho 1990a, 1990b). 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 (Bertsch 1986), 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 (rice, beans). 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 (Montagnini and Sancho 1990a). 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 (Bertsch 1986).

Low crop yields in the humid tropics are often a result in part of unfavorable physical properties such as soil compaction (Cassel and Lal 1992). 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 (Montagnini and Mendelsohn 1996).

The results of standard soil fertility tests used in agriculture (such as those shown in Table 2) may not always reveal the soil's productive potential, because they do not include all chemical forms of nutrients available for plant uptake. For example, although they make up less than 10% of the total soil N pool, mineral N (NO_3^-+NH_4^+), are the forms of N available to plants. 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. From the results shown in Table 2, *Stryphnodendron 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 (Montagnini and Sancho 1994a). 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 *Hieronyma alchorneoides* versus the other species' litter, showed the greatest initial growth and the highest N and P plant uptake (Montagnini et al. 1993). 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.

Nutrient recycling from litter

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 (Montagnini et al. 1993).

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 (Montagnini and Sancho 1994a, 1994b). 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.

Bahia, Brazil

Soil fertility

In Bahia, positive effects on at least five soil parameters were found under 15 out of the 20 species of the plantations, in comparison with primary and secondary forest (Table 2). Several species contributed to increased C and N, among others: *Inga affinis, Parapiptadenia pterosperma, Plathymenia foliolosa* (leguminous, N-fixing species), *Caesalpinia echinata, Copaifera luscens* (leguminous, non-N-fixing), *Eschweilera ovata, Pradosia lactescens* (of other families) (Table 2). Others increased soil pH and/or some cations, such as *Copaifera luscens, Eschweilera ovata, Lecythis pisonis and Licania hypoleuca* (Table 2, Montagnini et al. 1994, Montagnini et al. 1995a).

Nutrient recycling from litter

Total litter accumulation (whole leaves, branches and fragments) was higher under secondary than under primary forest and mixed plantation (Montagnini et al. 1994, 1995a). This is similar to findings by Silva (1990) in Barrolandia, another experimental site located near Porto Seguro, also in Bahia. Litter nutrients were also higher than in primary forest, suggesting that in secondary forest, forest-floor litter is an important source of nutrients to the soil.

Among the 20 species in the arboretum, the highest amounts of forest-floor litter were found under *Arapatiella psilophylla, Bombax macrophyllum, Inga affinis, Licania hypoleuca* and *Pithecellobium pedicellare*; positive effects on soils were found under all these species, with *Pithecellobium pedicellare* having the least influence. This suggests that forest-floor nutrients were incorporated into the soil via decomposition under these species. Da Vinha and Pereira (1983) reported high rates of litterfall under *Bombax macrophyllum, Buchenavia grandis, Caesalpinia echinata, Hymenaea aurea, Lecythis pisonis* and *Plathymenia foliolosa*, in the same arboretum. Of this group of species, leaf-litter decomposition was faster under *Buchenavia grandis, Hymenaea aurea* and *Bombax macrophyllum*, in that order (da Vinha et al. 1985).

The total N stocks (kg/ha) in the topsoil (0-5 cm depth) were higher than the total N stocks in forest-floor litter in all the tree species and forest sites (Table 3). The highest topsoil N stocks were in *Eschweilera ovata*, a non N-fixing species, where they were even higher than in secondary forest. Other species with high topsoil N stores were *Arapatiella psilophylla, Dimorphandra jorgei, Lecythis pisonis* and *Pradosia lactescens*, all non N-fixing species; and *Parapiptadenina pterosperma* and *Platynemia foliolosa* among the leguminous, N-fixing trees. Several species had higher forest-floor N stores than secondary forest: *Arapatiella psillophyla, Bombax macrophyllum, Buchenavia grandis, Hymenaea aurea, Inga affinis, Licania hypoleuca, Macrolobium latifolium* and *Pithecellobium pedicellare.*

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

The comparison of topsoil and forest-floor nutrient stores presented in Table 3 contributes further to interpretation of results on impacts of tree species in land rehabilitation. For example, litter under *Licania hypoleuca* had low nutrient concentrations, but due to its relatively high mass it resulted in large nutrient stores, and positive effects on soils. Under the species with high litter nutrient concentrations and slower decomposition, forest-floor litter may serve as a nutrient reservoir. Forest-floor litter with slower decomposition may also serve to protect the soil against erosion.

Misiones, NE Argentina

Soil fertility

The greatest differences in soil C and N levels under tree species and grass were found under *Bastardiopsis densiflora*, where they were twice those in areas beyond the canopy influence (Table 2) (Fernández et al. 1997). The pH was higher under *Bastardiopsis densiflora* and *Cordia trichotoma*, while the sum of bases (Ca+Mg+K) was highest under *Cordia trichotoma, Bastardiopsis densiflora* and *Enterolobium contortisiliquum*.

Data from biomass chemical analyses helped to explain the trends shown above through nutrient recycling mechanisms (Montagnini et al. 1994b). *Bastardiopsis densiflora* has interesting possibilities because it is a forest pioneer which colonizes areas abandoned from agriculture, forming dense even-aged stands which can reach commercial size in 10-14 years. *Cordia trichotoma* with a slower growth rate is however a valuable timber species known to participate successfully in plantation and agroforestry systems. The potential of *Enterolobium contortisiliqum* as a soil improver with its N-fixing capacity needs to be verified.

ASSESSING POTENTIAL LONG-TERM IMPACTS: NUTRIENT USE EFFICIENCIES

As shown above, a number of native timber species which combine good economic value with important soil rehabilitation properties were found in this program. The potential of the species for rehabilitation of degraded areas sometimes was obvious through their direct impacts on soil fertility parameters such as organic matter or cations. In other cases their effects only became evident through more detailed studies such as litter decomposition, N mineralization, or by studying the response of test plants to the tree species mulch or litter.

The calculation of nutrient use efficiencies is a useful means of integrating results for drawing recommendations for system design and management. The nutrient use efficiency (NUE) concept has been employed to describe the differential ability of tree species to accumulate organic matter in relation to nutrients taken up from the soil. NUE has been defined on different scales of space and time. At the plant population and community levels, NUE is generally defined as the amount of biomass produced per unit of nutrient taken up (Grubb 1989, Binkley et al. 1992, Medina 1995). Since direct measurements of nutrient absorption are not usually made for mature tree stands, leaf litter fall nutrients are generally used as an estimate of annual nutrient uptake (Vitousek 1984, Grubb 1989, Binkley et al. 1992). Ideally, efforts should be made to measure total production by stems, branches and roots and to consider nutrient uptake plus losses to herbivory and leaching of nutrients (Grubb 1989). Differences in nutrient cycling and efficiency of use may result from an ability to use various nutrient conserving mechanisms, from physiological to mutualistic interactions (Chapin 1980, 1983).

It is also important to consider the relationship between the recycling ability of the species and its potential short and long-term impacts on soil nutrient amelioration. A "nutrient cycling index" (NCI), taken as the inverse of NUE, i.e., the amount of nutrients in annual litterfall/annual tree biomass production, has been used to assess suitability of tree species for agroforestry combinations. For example, Fassbender et al. (1991) found that the P recycling index was about six times higher in combinations of cacao with *Erythrina poeppigiana* than with *Cordia alliodora* in agroforestry systems in Turrialba, Costa Rica. *Cordia*, a timber species, accumulated much P in stem biomass, while *Erythrina*, a shade tree with good nutrient cycling properties, produced large amounts of leaves and branches resulting in greater P recycling.

When put in context with nutrient recycling characteristics of a species, NUE can indicate appropriate system design and management to maintain productivity and recover or conserve nutrients over the long term. The ability of a species to produce large amounts of biomass with less nutrients may be an important consideration in choosing species for degraded, nutrient-poor sites.

Applicability of NUE in plantation design and management

From the 24 tree species shown in Table 2, data on tree productivity, leaf litter fall and litter chemistry of eight species in Bahia, Brazil and four species at La Selva, Costa Rica were used to calculate NUE values (Table 4). Because the species were part of a forestry project with fast-growing timber trees, NUE values were calculated as the annual stem biomass increments/nutrients in annual leaf litter fall (Montagnini 1994). There were not enough data on litter fall or productivity for the other species shown in Table 2.

At both Bahia and La Selva, the highest efficiencies were for K and P, and the lowest were for N, Ca and Mg (Table 4). Results from Bahia suggest that *Bombax macrophyllum* and *Platymenia foliolosa*, with overall high NUE values, would grow well on relatively nutrient-poor soils, and thus could be good alternatives for reforestation of degraded sites following the abandonment from agriculture and pasture that is frequent in the region. *B. macrophyllum* tended to accumulate high amounts of litter under its canopy while *P. foliolosa* stands had relatively high amounts of organic matter and total N in the topsoil in comparison with adjacent areas of secondary forest (Montagnini et al. 1995a). These features indicate that these species may be well suited for soil rehabilitation, including increasing soil organic matter content and protecting against soil erosion. Also at Bahia, species such as *Buchenavia grandis* and *Hymenaea aurea*, with overall lower NUE values, would be most appropriate for agroforestry combinations where crops could benefit from nutrient recycling from litter.

At La Selva, *Vochysia ferruginea* showed comparatively low efficiency values for all the nutrients considered, confirming the beneficial role of this species in recycling organic matter and positively impacting soil fertility as shown in Table 2. The relatively low efficiency (high recycling) of N and P found for *Stryphnodendron microstachyum* and *Hieronyma alchorneoides* was also shown in experiments where maize grown with mulch of these species grew better and absorbed more N and P than with mulch of other species (Montagnini et al. 1993).

In projects that aim to recover soil nutrients in degraded sites, species with high nutrient use efficiency should be combined in time or space with species with low use efficiency. However, NUE values alone may not be enough to assess the role of a tree species on ecosystem nutrients. For example, in spite of high NUE values, a tree species may pose high demands on soil nutrients over the long term. In humid tropical regions nutrients are expected to be critical factors influencing tree productivity, while in regions with a marked dry season water use efficiency rather than NUE would be a more important factor influencing species choice and system design. Still other ecological adaptations of the species (e.g., light use efficiency, root architecture, resistance to pests and diseases) could be more important in selecting species for agroforestry combinations.

TREE PRODUCTIVITY IN PLANTATIONS USED FOR LAND REHABILITATION

As stated earlier in this chapter, land rehabilitation programs must use species and designs that not only help in soil recovery but also are productive. If a land rehabilitation system is productive it may represent an economic incentive for the local farmers. At La Selva, the values of whole tree biomass for the plantations (Table 5) were greater than those reported for 4-year-old *Albizia lebbek* (Parrota 1989), and for 5.5- year-old *Leucaena leucocephala* (Wang et al. 1991), both growing in dense plantations for biomass production in Puerto Rico. Values of total tree above-ground net primary productivity (calculated by dividing whole-tree biomass by tree age) lie within the ranges reported elsewhere for monospecific plantations in the humid tropics. The value for *V. guatemalensis* is close to that reported for *Gmelina arborea* (12.8 tons per ha/yr) in the

Brazilian Amazon (Russell 1987); and to *Gmelina arborea* (12.7 tons/ha) and *Albizia falcataria* in the Philippines (11.3) (Kawajara et al. (1981), in Young (1989)). The increments shown here are however lower than those reported for some of the fastest growing trees in the humid tropics such as *Acacia mangium* (15.5 to 18.0 tons/ha in Malaysia), *Leucaena leucocephala* (20.0-30.0 and even up to 80.0 tons/ha in Hawaii an other tropical sites, Young (1989)).

Stemwood biomass annual increment for broadleafs ranges from 1 to 28 tons/ha/yr. Fast growing species such as *Gmelina arborea* and *E. saligna* range from 10-20 and 8-28 tons/ha, respectively, and relatively slower growing species such as *Swietenia* sp. and *Tectona grandis* range from 1-4 and 3-12 tons/ha, respectively (Wadsworth 1983). Other values for fast-growing trees in tropical humid regions include varios eucalyptus species grown in the Americas and Asia (7.2 to 11.9 tons/ha), *Gmelina arborea* in Costa Rica (11.8) (Lugo et al 1988); 1.3 to 5.3-year-old *Leucaena leuocephala* growing in pre-montane and lowland humid sites (2.8 to 15.9); *Prosopis juliflora*, moist site in India (9.4), *Populus deltoides*, subtropical site in India 6.4 (Lugo et al 1990a). Thus the mean annual stemwood biomass increments for the species of this land rehabilitation program also fall within the ranges reported for other fast-growing tree species in the humid tropics.

NUTRIENTS IN PLANTATION BIOMASS: IMPLICATIONS FOR MANAGEMENT

In the long term, the impacts of plantation trees on soil nutrients depend on: (1) the annual nutrient uptake by the trees in relation to the nutrient supplying capacity of the soil, (2) amounts of leaf litterfall and decomposition, (3) differential nutrient allocation in tree parts: stems, foliage, roots, and (4) the parts of the tree removed at harvest, whether the whole tree or stemwood, and their biomass and nutrient content. To help understanding these relationships, biomass nutrients were compared among tree parts for the four species of the La Selva site. Consistent with trends found in N tissue concentrations (Montagnini et al. 1991), *S.microstachyum* had the highest stem, branch and whole-tree biomass N (Fig. 1). *V. guatemalensis* had a similar proportion of N to *S.microstachyum* in its leaves+branches portion; over 50% of whole-tree biomass N could be recycled if left at he site at the time of harvest. *V. ferruginea*, with relatively lower stem biomass, had proportionally more N in leaves (53%) and branches (42%); *H. alchorneoides* showed a more even distribution of whole-biomass N in stems (39%), branches (27%), and leaves (34%). *V. guatemalensis* and *H. alchorneoides* had the highest proportions of stemwood P (72 and 62%, respectively) (Fig. 2).

V. guatemalensis, with the highest stem biomass and Ca concentration, also had the highest stemwood Ca (over 600 kg/ha, or 84% of whole-tree biomass Ca), approximately twice as much as either *S. microstachyum* or *V. ferruginea*, and several times more than *H. alchorneoides* (Montagnini and Sancho 1994b). Therefore, the harvest of *V. guatemalensis* trees could substantially reduce the amount of Ca in the site. However, while the *V. guatemalensis* trees are living, relative large amounts could be recycled, because although it represented only 16% of whole-tree biomass, the amount of Ca in leaves and branches together was over 100 kg/ha. Likewise, *V. guatemalensis* with its high stem biomass and high Mg concentration also had the highest Mg in stemwood (55% of whole-tree biomass, or approximately 30 kg/ha) (Montagnini and Sancho 1994b). Again, removal of *V. guatemalensis* stems would affect the sites's Mg budget more dramatically so than the other species, especially if the whole tree is harvested. For K the picture changed: the highest accumulation of K in stems was found in *H. alchorneoides* (252 kg/ha), followed by *V. guatemalensis* with 175 kg/ha, which represents 77% of whole-tree biomass K. Thus whole-tree harvest of *H. alchorneoides* and *V. guatemalensis* may have the greatest effects on the K budget (Montagnini and Sancho 1994b).

For the nutrients with lowest use efficiency values (ej. N) the forest-floor comprised a relatively high proportion of the total (Fig. 1). Therefore the forest-floor appears as an important compartment for N accumulation and recycling, although with marked differences among the species considered (Fig. 1). If the forest-floor is burned or collected for fuelwood, a substantial loss of organic matter and N may occur, while if the litter is left on the floor after harvest, it represents a significant reservoir for the next rotation.

In contrast, for P, which was relatively more scarce and showed higher use efficiency values, a higher proportion was stored in live tree biomass (Fig. 2). Although the forest-floor was still a substantial compartment, it was proportionally smaller than for N. In comparison, especially for *V. ferruginea* and *S. microstachyum*, root biomass P was relatively more important than forest-floor P (Fig. 2). Under tropical humid conditions P recycling from roots could be particularly important because root turnover is expected to be relatively fast. The roots are less likely to be affected during manual timber harvest operations than the forest-floor, while mechanical site operations could seriously affect the root system and its nutrient storing and recycling capacity. This can be especially critical for P and K, often mentioned as the nutrients which are most likely to be depleted from soils with subsequent rotations (Wadsworth 1983, Bruijnzeel 1991).

MANAGEMENT OF PLANTATION FLOOR LITTER

The relative importance of the litter layer in plantation nutrient conservation has been shown by Lugo et al. (1990b), who reported that the amount of litter in 10 tropical plantations ranged from 5 to 28 Mg ha^{-1}. Results of the present research program at La Selva show that plantation floor leaf litter represented up to 59% of the aboveground tree nutrient content (Fig. 1). This figure emphasizes 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 several regions, 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, at La Selva, floor leaf litter represented between 40% and 45% of the aboveground N found in the plantations. Furthermore, in some of the studied plantations up to 54% of the aboveground K, and 56 % of the Mg, were in floor leaf litter (Stanley and Montagnini 1999). 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 reincoporated 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.

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 *Vochysia ferruginea*, provide ground cover that reduces susceptibility to soil erosion and are an important nutrient source in subsequent rotations. *Vochysia ferruginea* also has a dense canopy, which helps to deter the growth of understory vegetation and decrease costs of weeding (Horn and Montagnini 1998; Montagnini and Mendelsohn 1996). In situations where soil fertility is severely depleted and rotations are short, species characterized by quick nutrient recycling become more desirable. If more than one benefit is sought, a mixture of species may offer an attractive option.

CONCLUSIONS AND RECOMMENDATIONS

A number of economically valuable native tree plantation species were found to have positive impacts on soils in three regions of the Latin American humid tropics. The calculation of nutrient use efficiencies proved a useful tool for system design and management: to conserve nutrients in the long term, species with low use efficiency should be combined in time or space with others with high use efficiency. Evaluation of biomass nutrient allocation helped in drawing specific management recommendations: preserving the forest-floor was key for nutrient conservation, but for the most limiting nutrients, the roots were more important. For ecosystem rehabilitation, the examination of tree growth, soil chemistry and litter biomass and nutrients constitutes a minimum set of measurements needed for the design and long-term management of sustainable forest systems.

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Table 1. Characteristics of the study sites mentioned in this chapter.

Location	Mean annual rainfall and temperature	Soil type	Previous land use	Experimental setting
La Selva Biological Station, Atlantic Lowlands of Costa Rica	4,000mm, 24°C	Fluventic Dystropepts pH 4.3-4.6	1-3 yrs. agriculture, cattle	Pure plantation, 2mx2m, 2-6 yrs. old
Pau Brasil Ecological Station Porto Seguro, Bahia, Brazil	1,700mm, 23°C	Oxisols (Haplorthox) pH 4.5-5.0	Shifting agriculture	Pure plantation, 2mx2m, 14-15 yrs. old
Eldorado, Misiones, NE Argentina (private farms)	1,700-2,400mm 22°C	Acid, clayey Ultisols pH 4.5-5.0	50 yrs. of agriculture, pine plantations	Pure stands from natural regeneration, 10-20 yrs. old

Table 2. Topsoil chemical characteristics in pure stands of indigenous tree species at La Selva, Costa Rica; Porto Seguro, Bahia, Brazil; and Misiones, Argentina.

Site/Tree species

	pH	C (%)	N (%)	P (cmol.kg⁻¹)	K	Ca	Mg
a- La Selva, Costa Rica[1]							
Stryphnodendron microstachyum	5.4ab	3.42ab	0.29b	5.6a	0.27a	0.45a	0.63ab
Vochysia ferruginea	5.4ab	3.76a	0.32a	7.1a	0.22a	0.73a	0.61ab
Vochysia guatemalensis	5.3ab	3.13ab	0.29b	5.2a	0.11a	0.25a	0.37ab
Hyeronima alchorneoides	5.1b	2.96c	0.22b	1.5b	0.09a	0.31b	0.21b
Abandoned pasture	5.3ab	2.73c	0.22b	4.9a	0.19a	0.32b	0.27b
Secondary forest	5.3ab	4.33a	0.33a	3.6b	0.17a	0.68a	0.55ab
b- Porto Seguro, Bahia, Brazil[2]							
N-fixing leguminous species:							
Bowdichia virgilioides	4.9	1.98def	0.16def	1.32def	0.06bcd	1.35bc	0.39de
Centrolobium minus	4.6	1.87efg	0.16def	1.19efg	0.05fgh	0.53hi	0.21i
Centrolobium robustum	4.5	1.65ij	0.13f	1.07fgh	0.05fgh	0.40i	0.16i
Inga affinis	4.9	2.10cde	0.18cd	3.64a	0.07bcd	0.76gh	0.49bc
Parapiptadenia pterosperma	4.9	2.38ab	0.20bc	0.78ij	0.08b	1.40bc	0.60a
Pithecellobium elegans	4.8	1.67hij	0.15ef	0.59kl	0.05efg	0.79gh	0.40de
Platymenia foliolosa	4.7	2.08cde	0.18bcd	0.13m	0.05efg	1.05cde	0.42cd
Non-N fixing leguminous species:							
Arapatiella psilophylla	4.7	1.94def	0.18bcd	1.45de	0.06bcd	0.38i	0.37de
Caesalpinia echinata	5.1	2.41a	0.17cde	1.54de	0.07bcd	1.17bcd	0.39de
Cassia spp.	4.7	1.94def	0.16def	1.40def	0.07bcd	0.56hi	0.34de
Copaifera luscens	5.0	2.02cde	0.17cde	0.63jk	0.06cde	1.15bcd	0.34de
Dimorphandra jorgei	4.9	1.97def	0.19bc	0.97ghi	0.03j	0.98def	0.32efg
Hymenaea aurea	4.4	2.00def	0.16def	2.03c	0.06bcd	0.26i	0.24hi
Macrolobium latifolium	4.7	1.90efg	0.16def	0.67jk	0.04hij	0.36i	0.25fg
Of other families:							
Bombax macrophyllum	4.8	1.78ghi	0.13f	1.42de	0.06bcd	0.84efg	0.33ef
Buchenavia grandis	4.6	2.06cde	0.14f	2.09c	0.06bcd	0.80fg	0.33ef
Eschweilera ovata	5.3	1.82fgh	0.31a	0.58kl	0.11a	1.38bc	0.53ab
Lecythis pisonis	5.3	1.99def	0.18bcd	0.23lm	0.04ghi	1.46b	0.32ef
Licania hypoleuca	5.0	1.63j	0.14f	1.61d	0.07bcd	1.31bcd	0.35de
Pradosia lactescens	4.9	2.15bcd	0.18bcd	0.81ij	0.05fgh	0.84efg	0.24gh
Primary forest	4.9	1.99def	0.15ef	0.96hi	0.08bc	1.23bcd	0.36de
Secondary forest	5.1	2.15abc	0.22b	2.46b	0.07bcd	2.20a	0.62*
c- Misiones, Argentina[3]							
Balfourodendron riedelianum	5.8	2.6b	0.34ab	n.d.	0.55bc	7.1bc	1.7c
Bastardiopsis densiflora	7.1	6.3a	0.65a	n.d.	1.28a	20.4a	3.4ab
Cordia trichotoma	6.4	4.0ab	0.46ab	n.d.	0.79b	13.6ab	2.6abc
Enterolobium contortisiliquum	6.1	3.4ab	0.39ab	n.d.	0.67b	8.7bc	3.5a
Ocotea puberula	6.1	4.4ab	0.59a	6.09a	1.11a	17.3a	4.7a
Grass control	5.8	2.2b	0.0.27b	n.d.	0.26c	6.3c	2.4bc

Sources: [1] Montagnini and Mendelsohn (1996), [2] Montagnini et al. (1994), [3] Fernández et al. (1995).
Note: For each site, differences among means are statistically significant when followed by different letters ($p<0.05$).
n.d.: not detected

Table 3.
Soil and forest floor nutrient stocks of N and P under plantations and forests at Bahia (kg/ha).

	N		P	
Species	Soil	Forest-floor	Soil	Forest-floor
Leguminous, N-fixing species				
Bowdichia virgilioides	952	147.6	0.79	1.24
Centrolobium minus	976	97.0	0.73	1.59
Centrolobium robustum	799.5	23.4	0.66	0.60
Inga affinis	981	388.7	1.98	8.96
Parapiptadenia pterosperma	1060	210.6	0.41	3.50
Pithecellobium pedicellare	930	339.4	0.37	3.79
Platymenia foliolosa	1044	140.6	0.08	1.98
Leguminous, non-N-fixing species				
Arapatiella psilophylla	1044	307.5	0.84	7.08
Caesalpinia echinata	960.5	128.6	0.87	2.88
Cassia spp.	992	9.3	0.87	0.15
Copaifera luscens	935	102.4	0.35	2.83
Dimorphandra jorgei	1178	60.3	0.60	0.60
Hymenaea aurea	856	212.2	1.09	5.67
Macrolobium latifolium	744	192.2	0.31	3.35
Species of other families				
Bombax macrophyllum	689	233.1	0.75	4.05
Buchenavia grandis	735	192.8	1.10	5.44
Eschweilera ovata	1798	156.7	0.34	3.72
Lecythis pisonis	1116	130.1	0.14	3.63
Licania hypoleuca	798	277.9	0.92	8.21
Pradosia lactescens	1107	137.5	0.50	3.62
Mixed plantation	896	87.1	1.10	1.30
Primary forest	802.5	182.3	0.51	3.07
Secondary forest	1078	137.5	1.21	2.06

Table 4. Nutrient use efficiencies (NUE) (Megagrams of annual stem biomass ncrement/kg nutrient in annual litter fall).

Porto Seguro, Bahia, Brazil:	N	Ca	Mg	K	P
N-fixing leguminous species:					
Centrolobium robustum	0.05	0.05	0.37	0.87	1.74
Platymenia foliolosa	0.08	0.34	7.00	3.51	4.66
Non N-fixing leguminous species:					
Caesalpinia echinata	0.04	0.03	0.54	0.78	1.81
Hymenaea aurea	0.06	0.09	0.45	0.64	1.91
Species of other families:					
Bombax macrophyllum	0.36	0.20	0.88	20.70	20.70
Buchenavia grandis	0.05	0.04	0.38	0.68	1.70
Eschweilera ovata	0.12	0.10	0.44	0.96	5.73
Lecythis pisonis	0.12	0.11	0.89	1.58	3.56

La Selva, Costa Rica:	N	Ca	Mg	K	P
Stryphnodendron mycrostachyum	0.08	0.06	0.35	0.63	0.53
Vochysia ferruginea	0.08	0.03	0.26	0.38	0.56
Vochysia guatemalensis	0.16	0.05	0.29	0.84	1.07
Hyeronima alchorneoides	0.09	0.03	0.15	0.22	0.45

Table 5. Means, aboveground biomass and annual increments for the four native species in plantation at La Selva, Costa Rica[1].

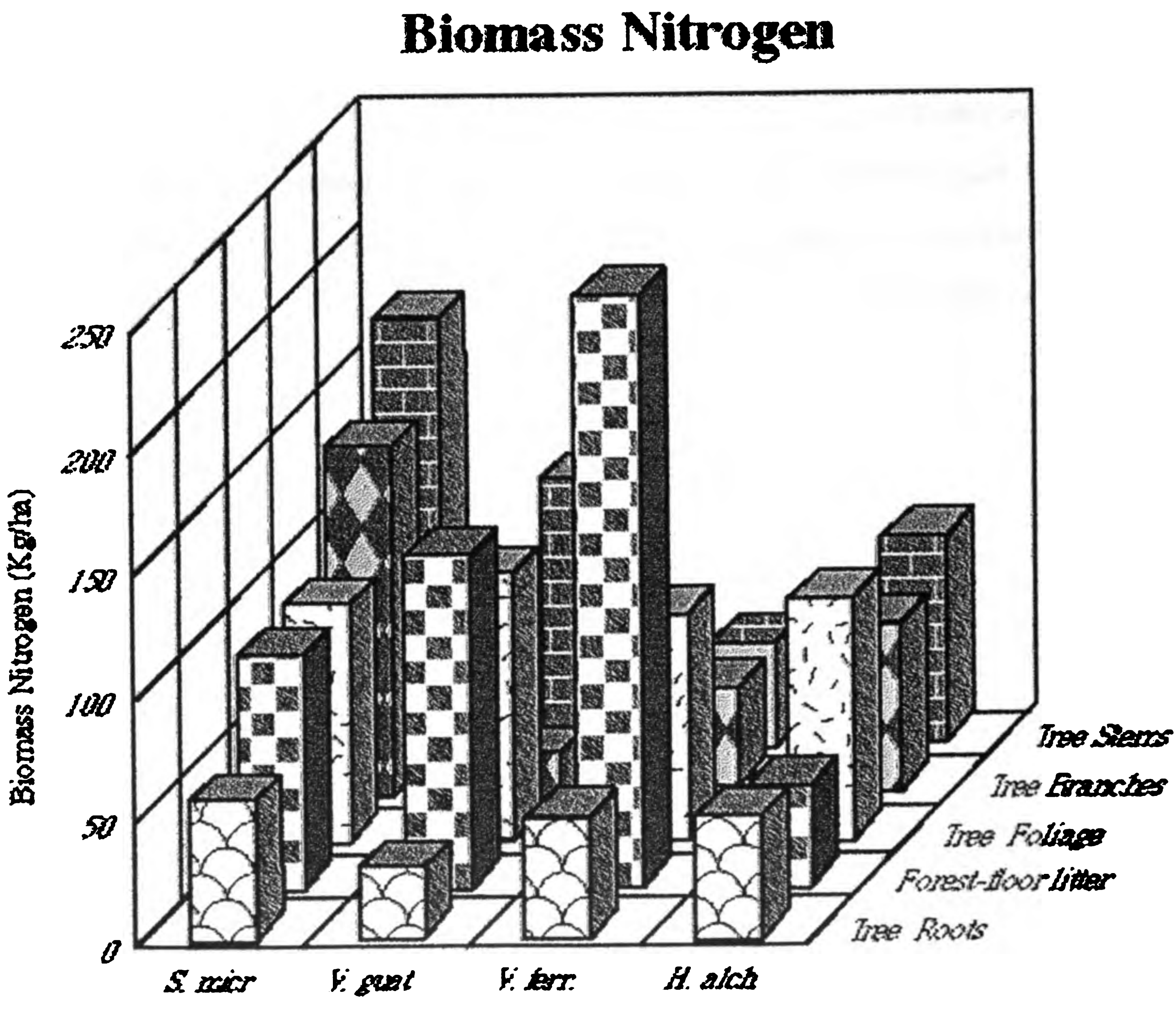
Tree species	Aboveground live biomass, kg/ha				Mean annual Increment, t $ha^{-1}yr^{-1}$	
	Stem	Branches	Leaves	Total	Total	Stems
Stryphnodendron microstachyum	35,250a	15,250[a]	4,325[a]	54,825a	13.7a	8.8[a]
Vochysia ferruginea	24,750b	14,250[a]	5,925[a]	44,925	11.2b	6.2b
Vochysia guatemalensis	41,750a	6,500b	7,250[a]	55,500	13.9a	10.4[a]
Hyeronima alchorneoides	26,250a	12,250[a]	5,350[a]	43,850	12.0b	6.5b

[1] Differences between sites for a given parameter are statiscally significant ($P < 0.05$) when means are followed by different letters.

FIGURE LEGENDS

Fig. 1. Nitrogen stocks in above ground biomass, forest-floor litter and superficial roots of 4-year-old stands of four indigenous timber species grown in pure plantation at La Selva Biological Station, Costa Rica.

Fig. 2. Phosphorus stocks in above ground biomass, forest-floor litter and superficial roots of 4-year-old stands of four indigenous timber species grown in pure plantation at La Selva Biological Station, Costa Rica.


Biomass Nitrogen
Biomass Nitrogen (Kg/ha)
250
200
150
100
50
0
S. micr
V. guat
V. ferr.
H. alch
Tree Stems
Tree Branches
Tree Foliage
Forest-floor litter
Tree Roots

Biomass Phosphorus