# 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 nitroperchloric digests (Diaz-Romeu and Hunter 1978); N and P were measured using a Flow Injection Analyzer, while cations were measured using an Atomic Absorption Spectrophotometer. Analysis of variance and LSD tests were run to compare mean biomass ($n = 5$) and nutrient content of tree parts ($n = 5$ for each tree part) among species. Total biomass nutrient content for each species was calculated by multiplying the mean biomass of each species' plant part (leaves, branches or stems) times the mean nutrient concentration of the respective plant parts.

### *Biomass and Nutrient Concentration of Understory Vegetation*

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

### *Forest Floor Litter*

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

### *Soil Fertility*

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

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

## *RESULTS*

### *Aboveground Biomass and Nutrient Concentrations*

#### *Trees*

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

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

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

| Tree species | Dbh, cm | Height, m | Aboveground live biomass, kg/ha | | | | Mean annual increment, t $ha^{-1}yr^{-1}$ | |
|---|---|---|---|---|---|---|---|---|
| | | | Stem | Branches | Leaves | Total | Total | Stems |
| *S. microstachyum* | 12.0a | 8.9b | 35,250a | 15,250a | 4,325a | 54,825 | 13.7a | 8.8a |
| *V. ferruginea* | 10.3 | 8.1b | 24,750b | 14,250a | 5,925a | 44,925 | 11.2b | 6.2b |
| *V. guatemalensis* | 10.8a | 12.0a | 41,750a | 6,500b | 7,250a | 55,500 | 13.9a | 10.4a |
| *H. alchorneoides* | 10.8a | 9.0b | 26,250b | 12,250a | 5,350a | 43,850 | 12.0b | 6.5b |

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

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

| | 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. alchorneoides* | 1.81b | 0.15b | 1.02ab | 0.41a | 0.71a |
| Branches | | | | | |
| *S. microstachyum* | 0.93a | 0.15ab | 0.44ab | 0.15a | 0.70bc |
| *V. ferruginea* | 0.29c | 0.09b | 0.36b | 0.10a | 0.56bc |
| *V. guatemalensis* | 0.29c | 0.12b | 0.44ab | 0.16a | 0.49c |
| *H. alchorneoides* | 0.55b | 0.17ab | 0.59ab | 0.15a | 1.14a |
| Stems | | | | | |
| *S. microstachyum* | 0.49a | 0.07b | 0.81b | 0.04b | 0.20c |
| *V. ferruginea* | 0.17b | 0.09b | 1.12b | 0.10a | 0.23c |
| *V. guatemalensis* | 0.26b | 0.09b | 1.46a | 0.12a | 0.42b |
| *H. alchorneoides* | 0.32b | 0.18ab | 0.28c | 0.10a | 0.96a |

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

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

### *Understory*

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

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

(a) Nutrient concentrations of understory:[1]

| Species plots | N | P | Ca | Mg | K |
|---|---|---|---|---|---|
| | | | (%) | | |
| *S. microstachyum* | 1.70a | 0.13a | 0.33ab | 0.41b | 1.01a |
| *H. 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 (kg/ha) | P | Ca | Mg | K |
|---|---|---|---|---|---|---|
| *S. microstachyum* | 5612 | 95.1 | 4.3 | 41.6 | 8.2 | 6.6 |
| *V. ferruginea* | 17215 | 240.3 | 15.5 | 187.6 | 19.1 | 12.1 |
| *V. guatemalensis* | 11084 | 134.0 | 11.6 | 170.0 | 26.4 | 9.7 |
| *H. alchorneoides* | 4238 | 39.2 | 12.9 | 55.0 | 11.9 | 6.8 |

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

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

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

### *Soil Fertility*

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

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

| Site | Depth (cm) | OM (%) | N (%) | P (mg/kg) | pH | Ca (cmol/kg) | Mg (cmol/kg) | K (cmol/kg) |
|---|---|---|---|---|---|---|---|---|
| *S. microstachyum* | 0-15 | 4.50a | 0.278a | 2.4a | 5.1a | 0.66b | 0.44a | 0.13a |
| | 15-30 | 3.29a | 0.224a | 2.1a | 5.1ab | 0.52bc | 0.22bc | 0.14a |
| | 30-60 | 1.88a | 0.196a | 1.8b | 5.1a | 0.54a | 0.16a | 0.14a |
| *V. ferruginea* | 0-15 | 5.08a | 0.320a | 3.24a | 5.0a | 0.63bc | 0.53a | 0.18a |
| | 15-30 | 3.66a | 0.248a | 2.48a | 5.0c | 0.35d | 0.20c | 0.10a |
| | 30-60 | 2.94a | 0.200a | 2.50b | 5.1a | 0.33a | 0.16a | 0.15a |
| *V. guatemalensis* | 0-15 | 4.30a | 0.304a | 2.30a | 5.2a | 0.47bc | 0.50a | 0.10a |
| | 15-30 | 3.16a | 0.232a | 1.82a | 5.1ab | 0.38cd | 0.22bc | 0.07a |
| | 30-60 | 2.42a | 0.232a | 2.00b | 5.1a | 0.38a | 0.15a | 0.08a |
| *H. alchorneoides* | 0-15 | 5.16a | 0.232a | 1.5a | 5.1a | 0.31c | 0.21b | 0.88a |
| | 15-30 | 2.77a | 0.248a | 1.5a | 5.1ab | 0.45bcd | 0.19c | 0.10a |
| | 30-60 | 1.21a | 0.158a | 1.7b | 5.2a | 0.46a | 0.20a | 0.10a |
| *Grass* | 0-15 | 3.98a | 0.200a | 4.1a | 5.2a | 0.57bc | 0.38a | 0.22a |
| | 15-30 | 2.94a | 0.236a | 3.4a | 5.1ab | 0.51bcd | 0.27bc | 0.17a |
| | 30-60 | 2.46a | 0.194a | 8.9a | 5.2a | 0.47a | 0.20a | 0.13a |
| *Forest* | 0-15 | 5.11a | 0.248a | 2.3a | 5.2a | 1.16a | 0.49a | 0.21a |
| | 15-30 | 3.83a | 0.244a | 2.0a | 5.2a | 0.92a | 0.45a | 0.17a |
| | 30-60 | 2.46a | 0.206a | 1.4b | 5.2a | 0.92a | 0.27a | 0.12a |

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

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

## *DISCUSSION*

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

### *Aboveground Tree Biomass*

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

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

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

### *Nutrient Concentrations in Tree Tissue*

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

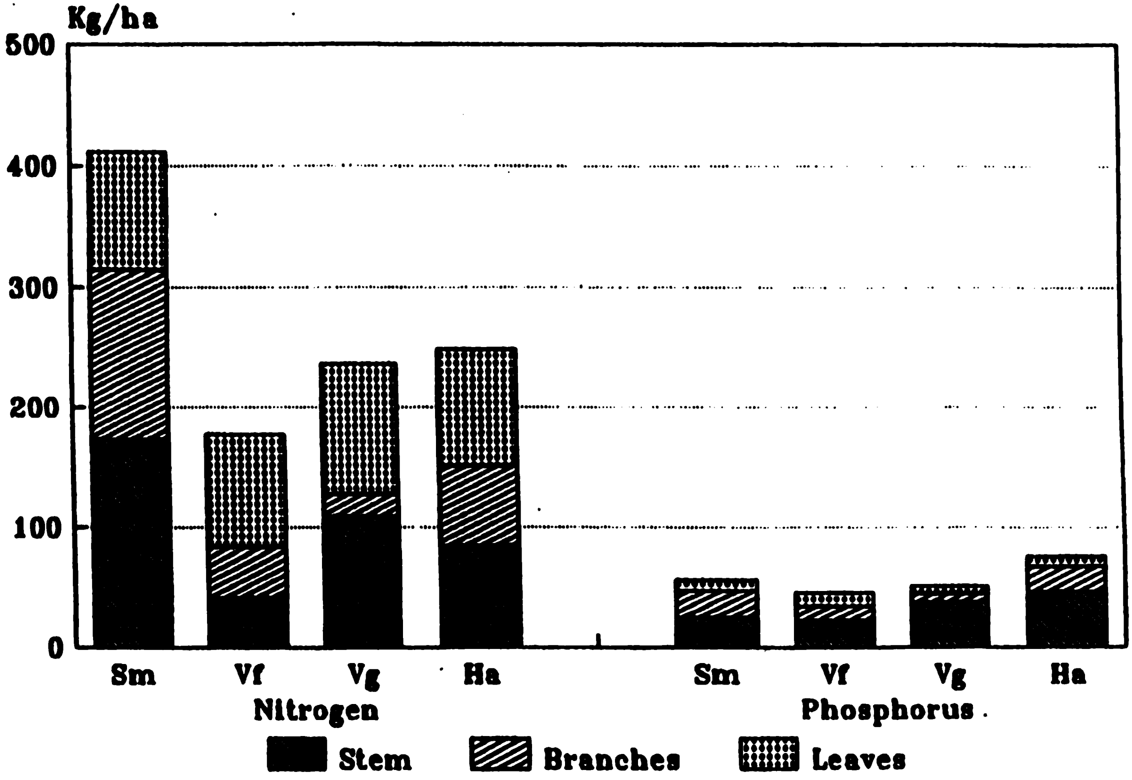
*neoides* had higher leaf Ca, similar to values reported in the literature for non-N-fixing tropical trees. The two *Vochysia* species' higher leaf Mg was not comparable to other reports in the literature (Young, 1989; Wang et al. 1991). The leaf nutrient values reported here for *S. microstachyum*,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

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

### *Nutrient Accumulation in Aboveground Tree Biomass*

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

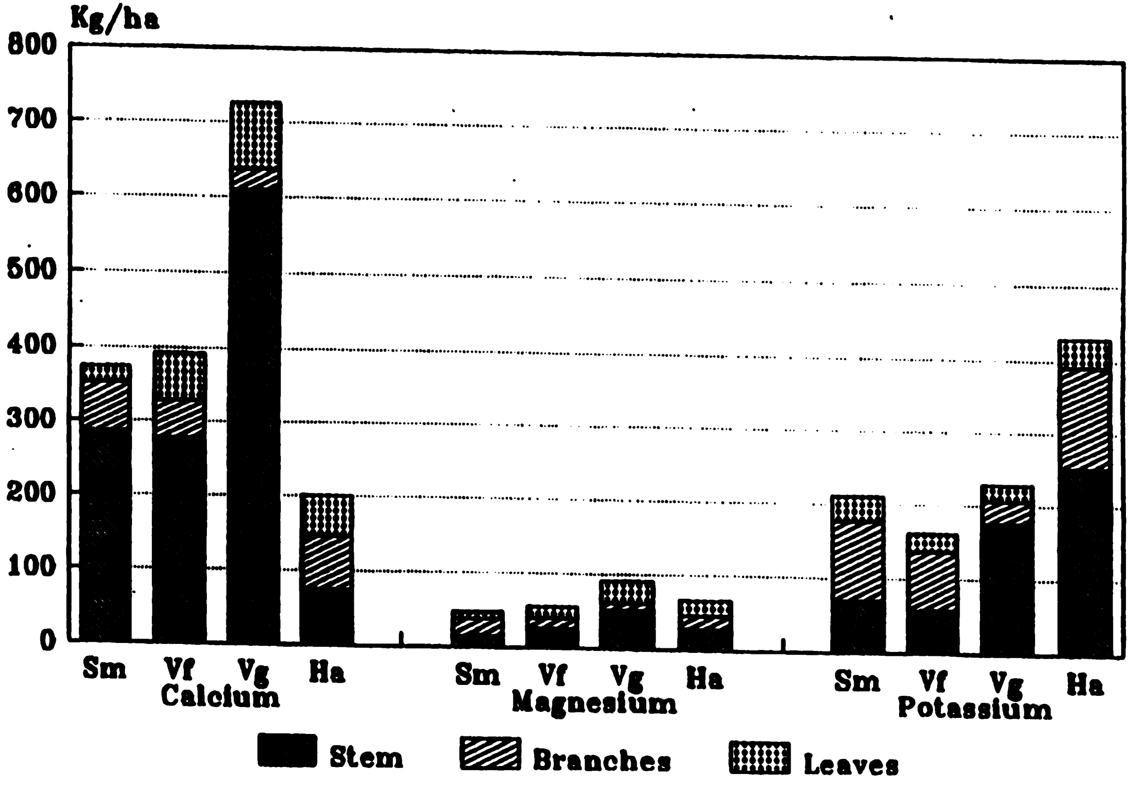
FIGURE 1. Aboveground tree nutrients in a 4-yr-old plantation of indigenous trees at La Selva Biological Station, Costa Rica: nitrogen and phosphorus.
Sm: *S. microstachyum*, Vf: *V. ferruginea*, Vg: *V. guatemalensis*, Ha: *H. alchorneoides*



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

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

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



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

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

### *Nutrient Accumulation in Understory Vegetation*

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

### *Nutrient Accumulation in Forest-Floor Litter*

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

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

### *Impacts of Trees on Soil Nutrients*

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

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

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

## CONCLUSIONS

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

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

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