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

**FLORENCIA MONTAGNINI**[1,*]
Yale University
School of Forestry and Environmental Studies
370 Prospect
New Haven, Connecticut 06511, USA

**CARLOS PORRAS**
FUNDECOR
Apdo. 54-3069
Puerto Viejo de Sarapiquí
Heredia, Costa Rica

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

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

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

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

---

[1] *Present address:* CATIE, 7170 Turrialba, Costa Rica.

*Author to whom correspondence should be addressed.

Environmental Management Vol. 22, No. 3, pp. 459–470

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

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

## Study Site

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

### Experimental Setting

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

## Methods

### Aboveground Tree Biomass and Carbon Accumulation

The plantations were thinned after canopy closure, which occurred approximately 2.5–3 years after planting, although some species such as *Jacaranda copaia* closed canopies within a year. For consistency, the three plantations were thinned three years after planting. With thinning, the initial 2 m × 2 m planting distance was widened to 2 m × 4 m (1250 trees/ha). This plantation density is similar to the prevalent 3 m × 3 m (1111 trees/ha), and thus it would allow for comparison with other experiences in the region. Thinning was performed in one half of each plot, leaving the other unthinned half for comparison. For thinning, all trees were cut in alternate rows. From every thinned row, two trees were randomly selected for biomass determinations, giving a total of 16 sampled trees per plot. The material from each tree was separated into its parts (stem, branches, and leaves) and weighed fresh at the site using a field scale. Subsamples of all materials, including stems (lower, middle, and top parts) were taken to the laboratory and dried at 70°C to constant weight. Dry–wet weight ratios from felled trees were used to correct the field weight determinations and obtain biomass on a per tree basis. Data from the 16 sampled trees were averaged to obtain values per plot. The average biomass per tree was multiplied by the number of trees per plot, corrected for tree mortality, and extrapolated to a hectare. Analysis of variance and LSD tests were run to compare mean biomass ($N = 4$) of tree parts among species. Comparisons were made among species in pure and mixed conditions on a per tree basis and also among pure and mixed plots on a per hectare basis.

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

### Soil Chemistry

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

## Results

### Aboveground Tree Biomass

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

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

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

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

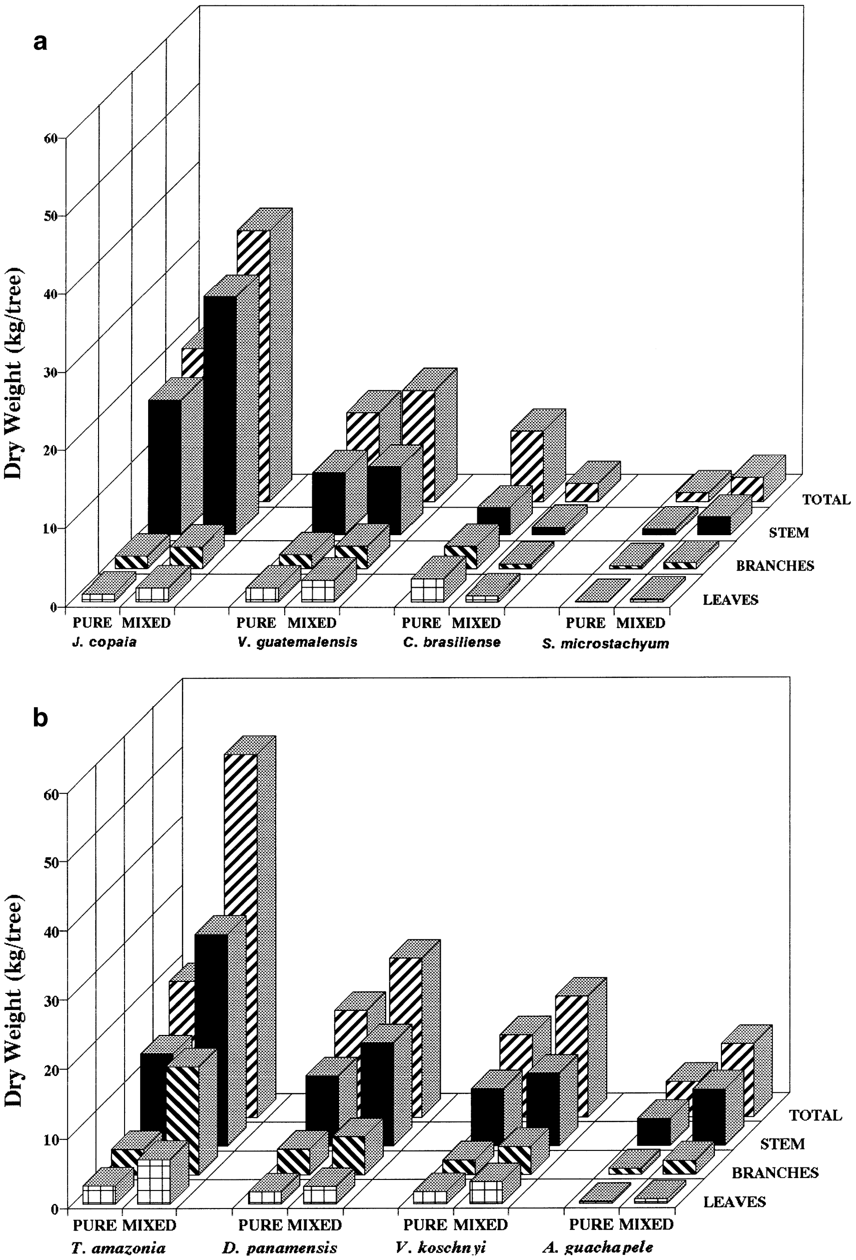

**Figure 1.** **(a)** Aboveground tree biomass (leaves, branches, stem, and total) of *Jacaranda copaia, Vochysia guatemalensis, Calophyllum brasiliense,* and *Stryphnodendron microstachyum* in pure and mixed plots. **(b)** Aboveground tree biomass (leaves, branches, stem, and total) of *Terminalia amazonia,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

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

### Carbon Sequestration in Pure and Mixed Plantations

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

### Soil Chemistry

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

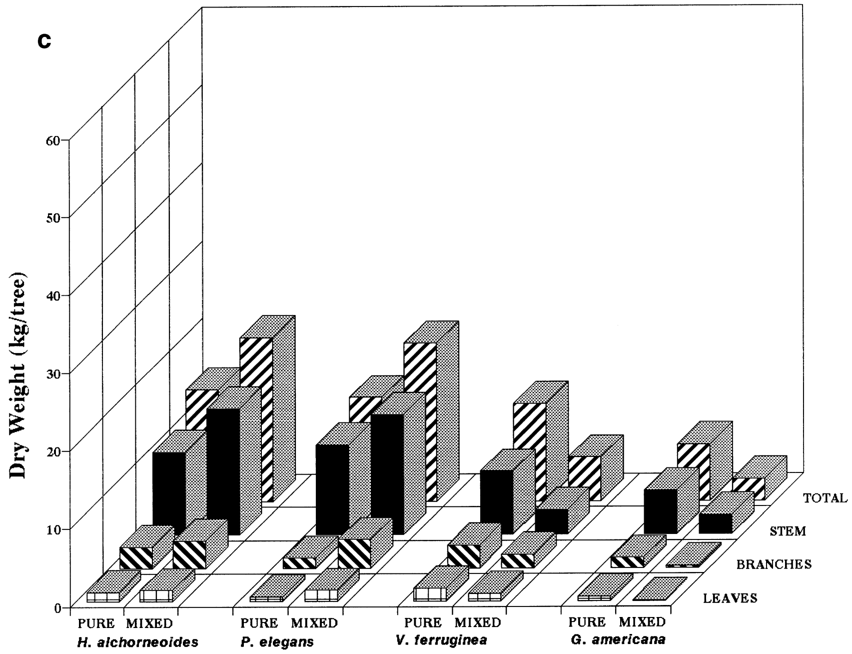

**Figure 1. (Continued)**

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

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

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

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

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

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

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

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

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

## Discussion

### Aboveground Tree Biomass in Pure and Mixed Plantations

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

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

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

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

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

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

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

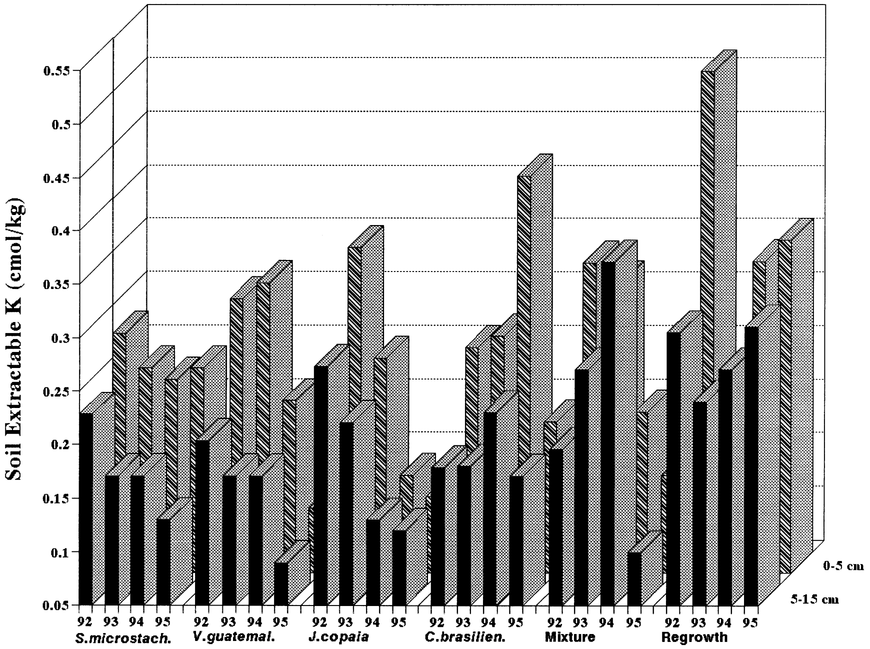

**Figure 2.** Soil potassium in plantation 1 at 0–5 cm and 5–15 cm depths, in sampling done from 1992 to 1995 (one to four years after planting), under *Stryphnodendron microstachyum, Vochysia guatemalensis, Jacaranda copia, Calophyllum brasiliense,* mixture of four species, and regeneration plots (natural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

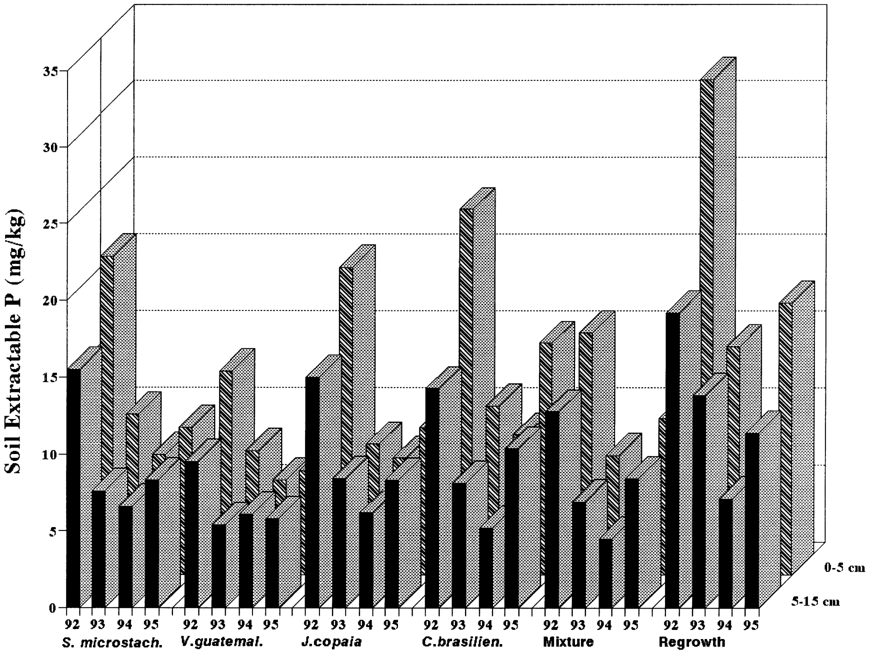

**Figure 3.** Soil phosphorus in plantation 1 at 0–5 cm and 5–15 cm depths, in sampling done from 1992 to 1995 (one to four years after planting), under *Stryphnodendron microstachyum, Vochysia guatemalensis, Jacaranda copia, Calophyllum brasiliense,* mixture of four species, and regeneration plots (natural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

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

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

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

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

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

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

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

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

NA: not available.

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

## Carbon Sequestration in Pure and Mixed Plantations

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

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

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

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

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

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

### Soil Chemical Characteristics in Pure and Mixed Plantations

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

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

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

### Potential of Tropical Tree Plantations as Carbon Sinks

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

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

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

## Acknowledgments

This project was funded by the A. W. Mellon Foundation (USA). For their collaboration, we thank Juan Romero and Henry Salas, La Selva Biological Station, and personnel of the Center for Agricultural Research, University of Costa Rica. We also thank Robin Sears for processing soils data and Tori Derr for reviewing the manuscript.

## Literature Cited

Allison, L. E. 1975. Organic carbon. Pages 1367–1378 *in* C. A. Black (ed.), Methods of soil analysis, Part 2. American Society of Agronomy, Madison, Wisconsin.

Bertsch, F. H. 1986. Manual para interpretar la fertilidad de los suelos en Costa Rica. Universidad de Costa Rica. Escuela de Fitotecnia, San José, Costa Rica, 76 pp.

Bloomfield, J., K. A. Vogt, and D. J. Vogt. 1993. Decay rate and substrate quality of fine roots and foliage of two tropical tree species in the Luquillo Experimental Forest, Puerto Rico. *Plant and Soil* 150:233–245.

Bowen, G. D., and E. K. S. Nambiar. 1984. Nutrition of plantation forests. Academic Press, New York, 516 pp.

Bremner, J. M., and C. S. Mulvaney. 1982. Nitrogen-total. Pages 595–624 *in* A. L. Page, R. H. Miller, and R. R. Keeney (eds.), Methods of soil analysis, Part 2, 2nd ed. American Society of Agronomy, Madison, Wisconsin.

Brown, K., and W. N. Adger. 1994. Economic and political feasibility of international carbon offsets. *Forest Ecology and Management* 68:217–229.

Brown, S., and A. E. Lugo. 1982. The storage and production of organic matter in tropical forests and their role in the global carbon cycle. *Biotropica* 14:161–187.

Brown, S., A. E. Lugo, and J. Chapman. 1986. Biomass of tropical tree plantations and its implications for the global carbon budget. *Canadian Journal of Forest Research* 16(2):390–394.

Bruenig, E. F. 1996. Conservation and management of tropical rainforests. An integrated approach to sustainability. CAB International, Wallingford, Oxon, UK, 339 pp.

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

Cairns, M. A., and R. A. Meganck. 1994. Carbon sequestration, biological diversity, and sustainable development: Integrated forest management. *Environmental Management* 18(1): 13–22.

Chambers, R., and M. Leach. 1990. Trees as savings and security for the rural poor. *Unasylva* 41:39–52.

Dabas, M., and S. Bhatia. 1996. Carbon sequestration through afforestation: Role of tropical industrial plantations. *Ambio* 25:327–330.

Díaz-Romeu, R., and A. Hunter. 1978. Método para el muestro de suelos, análisis químico de suelos y tejido vegetal e investigación en invernaderos. CATIE, Turrialba, Costa Rica.

Dixon, R. K., J. K. Winjum, K. J. Andrasko, J. J. Lee, and P. E. Schroeder. 1994. Integrated land-use systems: Assessment of promising agroforest and alternative land-use practices to enhance carbon conservation and sequestration. *Climatic Change* 27(1):71–92.

Evans, J. 1992. Plantation forestry in the tropics. Tree planting for industrial, social, environmental, and agroforestry purposes, 2nd ed. Clarendon Press, Oxford, England, 403 pp.

Fearnside, P. M. 1995. Global warming response options in Brazil's forest sector: Comparison of project-level costs and benefits. *Biomass and Bioenergy* 8:309–322.

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

Halenda, C. J. 1993. Aboveground biomass production and nutrient accumulation of a *Gmelina arborea* plantation in Sarawak, Malaysia. *Journal of Tropical Forest Science* 5(4):429–439.

Houghton, R. A. 1996. Converting terrestrial ecosystems from sources to sinks of carbon. *Ambio* 25(4):267–272.

Jorgensen, J. R., and C. G. Wells. 1986. Tree nutrition and fast-growing plantations in developing countries. *International Tree Crops Journal* 3:225–244.

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

Lugo, A. E., S. Brown, and C. G. Chapman. 1988. An analytical review of production rates and stemwood biomass of tropical forest plantations. *Forest Ecology and Management* 23:179–200.

Montagnini, F. 1994. Agricultural systems in the La Selva region. Pages 307–316 *in* L. A. McDade, K. Bawa, H. A. Hespenheide, and G. S. Hartshorn (eds.), La Selva: Ecology and natural history of a neotropical rainforest. University of Chicago Press, Chicago.

Montagnini, F., and R. Mendelsohn. 1996. Managing forest fallows: improving the economics of swidden agriculture. *Ambio* 26(2):118–123.

Montagnini, F., and F. Sancho. 1994. Aboveground biomass and nutrients in young plantations of four indigenous tree species: implications for site nutrient conservation. *Journal of Sustainable Forestry* 1:115–139.

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

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

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

Murdiyarso, D. 1993. Policy options to reduce $CO_2$ release resulting from deforestation and biomass burning in Indonesia. *Chemosphere* 27(6):1109–1121.

Myers, N., and T. J. Goreau. 1991. A management response to the greenhouse effect. *Climatic Change* 19:215–225.

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

Rotmans, J., and R. S. Swart. 1991. Modeling tropical deforestation and its consequences for global climate. *Ecological Modelling* 58:217–247.

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

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

Schroeder, P. 1992. Carbon storage potential of short rotation tropical tree plantations. *Forest Ecology and Management* 50:31–41.

Sedjo, R. A. 1989. Forests: a tool to moderate global warming? *Environment* 31(1):14–21.

Smith, D. M. 1986. The practice of silviculture,8th ed. John Wiley & Sons, New York, 527 pp.

Vogt, K., H. Asbjornsen, A. Ercelawn, F. Montagnini, and M. Valdes. 1997. Roots and mycorrhizas in plantation ecosystems. *In* E. K. S. Nambiar and A. G. Brown (eds.), Better management of soil, water and nutrients in tropical plantation forests (in press).

Wadsworth, F. H. 1983. Production of usable wood from tropical forests. Pages 279–288 *in* F. B. Golley (ed.), Tropical Rain forest ecosystems: structure and function. Ecosystems of the world 14A. Elsevier, New York.

Wang, D., F. H. Bormann, A. E. Lugo, and R. D. Bowden. 1991. Comparison of nutrient-use efficiency and biomass production in five tropical tree taxa. *Forest Ecology and Management* 46:1–21.

Wormald, T. J. 1992. Mixed and pure forest plantations in the tropics and subtropics. FAO Forestry Paper 103. FAO, Rome, 152 pp.