ELSEVIER

Forest Ecology and Management 134 (2000) 257–270

Forest Ecology and Management

www.elsevier.com/locate/foreco

Accumulation in above-ground biomass and soil storage of mineral nutrients in pure and mixed plantations in a humid tropical lowland

Florencia Montagnini*

Management and Conservation of Forests and Biodiversity, Centro Agronómico Tropical de Investigación y Enseñanza, CATIE, 7170 Turrialba, Costa Rica

Received 7 May 1999; accepted 5 September 1999

Abstract

As fast-growing, short-rotation plantations are being planted in the tropics on low fertility soils, the problem of sustaining soil fertility becomes an important management issue. Above-ground biomass, nutrient concentration of above-ground tree tissues, and soil nutrients were examined in two young plantations of eight indigenous tree species grown in pure and mixed designs in a low fertility site in the humid lowlands of Costa Rica. The goal was to assess the role of nutrient accumulation in above-ground biomass on potential site nutrient decline, and to draw recommendations to conserve site nutrients in the long term.

In Plantation 1, *Jacaranda copaia* pure stands had higher above-ground tree N, P, and Mg than the other treatments, while *Vochysia guatemalensis* had the greatest accumulation of K and Ca. For *J. copaia*, stem harvest would remove about 54% of total above-ground tree N, but about 80% of P, K, Ca and Mg. For *V. guatemalensis*, stem harvest would remove less than 30% of N but from 50 to 60% of total above-ground tree Ca, K, Mg and P. Branches and foliage summed together were 25 to 35% of total above-ground tree biomass, but they generally represented about 50% of above-ground tree nutrients. In Plantation 2, the mixed stands had the highest above-ground nutrient content for all nutrients, and both the mixture and *Terminalia amazonia* pure stands had the highest stem P and Mg.

Five years after planting, decreases in soil P, K and Ca were apparent in pure plots of the fastest growing species with the largest accumulation of nutrients in above-ground biomass, such as *J. copaia* and *V. guatemalensis*. However, in other cases, beneficial effects on some soil nutrients were noted: for example, increases in soil Ca under *T. amazonia* and *Virola koschnyi*, both species with high Ca content in foliage and high rates of annual litterfall. The mixed plots showed intermediate values for the nutrients examined, and even improved soil conditions, as for P in Plantation 1. This suggests that in mixed conditions it may take longer to deplete soil nutrients than in monospecific stands of fast-growing species.

Results of continued sampling will be needed to assess the long term effects of plantation treatments on soil chemistry, especially near the end of the rotation (estimated at 12–15 years, depending on the species). The calculation of whole-stand nutrient budgets can help in the selection of tree species and plantation management strategies to favor nutrient recycling mechanisms and site nutrient conservation. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Above-ground nutrients; Humid tropics; Mixed plantations; Native trees; Soil nutrients

1. Introduction

Tropical tree plantations incorporate considerable amounts of nutrients in their biomass over a relatively

---

* Tel.: +506-556-6440; fax: +506-556-1533.
E-mail address: montagni@catie.ac.cr (F. Montagnini)

PII: S0378-1127(99)00262-5

short period of time (Bruijnzeel, 1991; Montagnini and Sancho, 1994; Fölster and Khanna, 1997; Gonçalves et al., 1997). Soil nutrients may be generally abundant early in stand growth as a result of low plant uptake, stimulation of nutrient mineralization, and low immobilization in plant biomass, but as plantations grow, decreased nutrient availability can result from immobilization into woody biomass and detritus pools, and decreased mineralization (Binkley, 1986; Binkley et al., 1997). Site fertility declines can limit sustained plantation forestry in tropical regions, especially on soils that are inherently nutrient-poor: soil fertility can be decreased through excessive removal of living biomass, particularly if nutrients in tree crowns are lost through harvest or site preparation (Jorgensen and Wells, 1986; Fölster and Khanna, 1997; Wadsworth, 1997).

Alternatives to conserve site nutrients may include preferential planting of tree species that do not place high nutrient demands on the site (Bruijnzeel, 1984; Wang et al., 1991; Montagnini and Sancho, 1994). Bruijnzeel (1984) found, for example, a higher production of wood per unit of N or P in the wood in plantations of *Pinus merkusii* compared with nearby plantations of *Agathis damara* in Java. Large differences may exist in nutrient use efficiency among tropical tree species (Wang et al., 1991; Montagnini, 1994a). For example, in Puerto Rico, Wang et al. (1991) found that *Casuarina* spp. was twice as efficient as *Leucaena* spp. for N, 3–4 times as efficient as *Albizia* and *Leucaena* for K, and about twice as efficient as all of the studied species for Mg. To design viable tropical plantations, focusing on efficient use of nutrients on a stand level may be as important as considering production rates (Wang et al., 1991).

Mixed plantations yield more diverse forest products than monospecific stands, helping to diminish farmer's risks in unstable markets. If planned with consideration for each species' response to mixed conditions, mixed designs can be more productive than monospecific systems (Smith, 1986; Binkley et al., 1992; Burkhart and Tham, 1992; Kelty, 1992; Wormald, 1992). In addition, a mixture of species, each with different nutrient requirements and different nutrient recycling properties, may be overall less demanding on site nutrients than pure stands (Binkley et al., 1997; Fölster and Khanna, 1997). In this article, above-ground nutrient accumulation and soil chemistry are compared among eight native species growing in young plantations in mixed and pure stands in the Atlantic humid lowlands of Costa Rica. In previous reports, it was shown that the growth of dominant species was faster in mixed than in pure plantation, and that mixed plantations had high volume and biomass production in comparison with pure stands (Montagnini et al., 1993, 1995; Montagnini and Porras, 1998). In other plantations of the same experiment, the mixed plantations had intermediate values of soil N, P and K, but lower soil Ca and Mg relative to pure plantations (Stanley and Montagnini, 1999). Although the young age of these plantations precludes proper extrapolation over a whole rotation, the results can suggest design and management options of tropical plantations to conserve nutrients in the long term.

2. Methods

2.1. Site description

The experiments were established on abandoned pasture at the Guaria Annex of La Selva Biological Station in the Atlantic humid lowlands of Costa Rica (10°26′N, 86°59′W, 50 m mean altitude, 24°C mean annual temperature, 4000 mm mean annual rainfall). Soils are Fluventic Dystropepts derived from volcanic alluvium. They are deep, well drained, stone-free, acid (pH in water <5.0), with low or medium organic matter prior to planting (2.5–4.5%), cation exchange capacity 10–14 cmols/kg, 10–15% base saturation, and moderately heavy texture (50–60% sand, 5–15% silt and 25–45% clay) (Sancho and Mata, 1987). Soil conditions before clearing were reported by Montagnini et al. (1993): soils were too poor for cultivation of the commercial crops commonly grown in the region (Bertsch, 1986; Sancho and Mata, 1987; Montagnini, 1994b). The area had been cleared in the mid-1950s and grazed until 1981, a sequence of land uses common in the region at the time (Montagnini, 1994b). The area is on flat, uniform terrain. The site was cleared manually and no burning was done. The slash was left on the floor, to protect against soil erosion and to delay the growth of weeds.

Table 1
Characteristics of tree species grown in mixed and pure plantations at La Selva Biological Station (Montagnini et al., 1995)

Scientific name	Common name	Family	Native range	Growth, habitat
Plantation 1				
S. microstachyum Poepp. et Endl.	vainillo	Leguminosae (Mimosoid)	Costa Rica, Nicaragua, Panama	Upper canopy of mature forest. Also on secondary forest. Fast growth
V. guatemalensis Donn. Sm.	mayo, chancho	Vochysiaceae	Mexico to Panama	Upper canopy, early-mid successional. Fast growth
J. copaia(Aubl.) D. Don.	jacaranda	Bignoniaceae	Guatemala to Brazil	Pioneer, early successional. Secondary forest. Very fast growth
C. brasiliense Cambess.	cedro Maria	Guttiferae (Clusiaceae)	Mexico to N. South America	Mature forest. Slower growth
Plantation 2				
A. guachapele (H.B.K.) Little	cenizaro, guayaquil	Leguminosae (Mimosoid)	Guatemala to Ecuador	Pioneer. Common in low secondary forest. Fast growth
T. amazonia (J.F.Gmel.) Exell.	roble coral	Combretaceae	S. Mexico to N.South America	Upper canopy, mid-successional. Relatively slow growth
V. koschnyi Warb	fruta dorada	Myristicaceae	Central America	Upper canopy, mid-successional. Moderate growth
D. panamensis (Pittier) Record & Mell	almendro	Leguminosae (Papilionoid)	Nicaragua to Colombia	Upper canopy, mid-to late successional. Slower growth

2.2. Experimental design

A total of eight native tree species of actual or potential economic value were tested in two plantations, each with four species: Plantation 1: *Stryphnodendron microstachyum* Poepp. et Endl.; *Vochysia guatemalensis* D.Sm., *Jacaranda copaia* (Aubl.) D. Don, and *Callophylum brasiliense* Cambess; Plantation 2: *Albizia guachapele* (H.B.K.) Little, *Terminalia amazonia* (Gmell.) Exell., *Virola koschnyi* Warb., and *Dipteryx panamensis* (Pittier) Record and Mell. Ecological characteristics of the eight species of this study are given in Table 1. The criteria for species selection were: growth rate and economic value, potential impacts on soils and nutrient cycling, and seedling availability (Montagnini et al., 1995). In each plantation of four tree species there was at least one nitrogen-fixing tree, one relatively fast-growing species, and a slower-growing species. Both plantations were established in 1991. The plantations were in randomized blocks, with four replicates and six treatments: four pure plantation plots of each species, a mixed-species plot (with the four species), and a fallow (natural regrowth) plot. Each plot was 32 m × 32 m. Initial planting distance was 2 m × 2 m to speed canopy closure and obtain early impacts on soils, with 50% thinning planned after canopy closure. Within each mixed-tree plot, trees of the four species were planted alternating two species per row. The sequential order of the species within rows was systematically reversed every other row. In that manner, each column contained the four species of the mixture in a sequence.

2.3. Above-ground tree biomass and nutrients

Biomass values were calculated from data obtained at the time of thinning. The plantations were thinned after canopy closure, which occurred approximately 3 years after planting. With thinning, the initial 2 m × 2 m planting distance was widened to 2 m × 4 m (1250 trees per hectare). Thinning was performed in one half of each plot, leaving the other non-thinned half for comparison. For thinning, all trees were cut in alternate rows. From every thinned row, two trees were randomly selected for biomass determinations, giving a total of 16 sampled trees per plot. Data from the 16 sampled trees were averaged to obtain values per plot. Biomass data from these plantations were also used for a separate study of the role of the plantations on carbon accumulation (Montagnini and Porras, 1998).

Portions of stems (lower, middle and top parts) and tip, medium and bottom parts of branches of the sampled trees were collected. Foliage from the tip, medium, and lower portions of each branch were pooled to obtain one sample of each tissue type and species for laboratory analysis. In mixed plots, foliage samples were collected to compare nutrient concentrations between trees growing in mixed and in pure plantations. These foliar nutrient concentrations were used in subsequent calculations for species in mixed plots. Due to limitations in the number of chemical analyses that could be performed with the available resources, stem and branch samples were not collected in mixed plots. Although there was no background information to substantiate this assumption, concentrations of nutrients in those tissues were assumed to be very similar to nutrient concentrations found in pure plots.

All tissue types were oven-dried at 70°C to constant weight and then ground. Dry : wet weight ratios from felled trees were used to correct the field weight determinations and obtain biomass on a per tree basis. The average biomass per tree was multiplied by the number of trees present in each plot before thinning, and extrapolated to a hectare. The data from the four plots of each treatment were then used for analysis of variance and LSD tests for means ($n = 4$, $P < 0.05$).

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

2.4. Soil chemistry

Soils were sampled before clearing the land, and annually thereafter. Soil conditions up to 4 years after planting had been reported by Montagnini and Porras (1998). Results of sampling from 1996, 5 years after planting, are reported here, and compared with those of previous years. Composite samples were taken in each of the four replicate plots per treatment, at 0–5, 5–15, 15–30 and 30–60 cm depth. The pH was measured in a 1 : 2.5 mixture of soil : deionized water. The exchangeable Ca and Mg were extracted with a 1N KCl solution, while the exchangeable P and K were extracted with a modified Olsen solution, which is a mixture of 0.5N $NaHCO_3$, 0.01N bi-sodium EDTA and Superfloc 127 (a commercial flocculant) (Díaz-Romeu and Hunter, 1978). A 1 : 5 proportion of soil : extractant was used in all cases. Cations were measured using an Atomic Absorption Spectrophotometer. Extractable P was measured colorimetrically after reaction with $(NH_4)_2MoO_4$ and $SnCl_2$, using a spectrophotometer. Organic matter was measured with the Walkley-Black technique (Allison, 1975) and total N was measured using a semi-Micro-Kjeldahl technique (Bremner and Mulvaney, 1982). Analysis of variance and LSD tests were run to compare the means for each variable and soil depth ($n = 4$, $P < 0.05$) among sites.

3. Results

3.1. Above-ground tree biomass and nutrient concentrations

In Plantation 1 the total above-ground biomass was higher in *J. copaia* pure plots, followed by the mixture of four species and *V. guatemalensis*. About 87% of total biomass of *J. copaia* and 70% of total biomass of *V. guatemalensis* was found in stems, while 78% of total biomass of the mixture was in stems. In Plantation 2, the highest total above-ground biomass per hectare was found in the mixed plots, *T. amazonia, Dipteryx panamensis* and *V. koschnyi,* with values 2.5–

Table 2
Above-ground biomass of tree tissues in pure plots and in mixture of eight species on a per hectare basis. Means, standard errors (SE), and statistical significance (Sig.)[a]

Species	Above-ground biomass (Mg/ha)											
	Stems			Branches			Foliage			Total tree		
	Mean	SE	Sig.	Mean	SE	Sig.	Mean	SE	Sig.	Mean	SE	Sig.
Plantation 1												
J. copaia	40.9	0.84	a	3.48	0.13	b	2.23	0.13	c	46.6	0.94	a
V. guatemalensis	19.0	0.89	c	4.25	0.22	b	4.03	0.38	b	27.3	1.38	b
C. brasiliense	7.2	1.46	d	5.71	0.71	a	5.89	0.52	a	18.8	2.67	c
S. microstachyum	1.7	1.26	e	0.56	0.42	c	0.20	0.14	d	2.5	1.82	d
Four sps. mixture	25.3	1.38	b	3.86	0.24	b	3.13	0.23	bc	32.3	1.53	b
Plantation 2												
T. amazonia	22.4	3.46	a	5.96	0.47	b	4.19	0.38	a	32.5	4.23	ab
D. panamensis	19.1	2.21	a	6.84	0.83	ab	3.22	0.49	a	29.1	3.05	ab
V. koschnyi	17.8	2.39	a	4.28	1.00	bc	3.61	0.75	a	25.7	3.54	b
A. guachapele	7.9	0.85	b	1.92	0.24	c	0.54	0.14	b	10.3	1.10	c
Four sps. mixture	24.8	2.58	a	9.66	1.72	a	4.68	0.63	a	39.1	4.41	a

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

3 times those found in *A. guachapele* (Table 2). For *T. amazonia* and *D. panamensis,* almost 70% of total biomass was in the stems, while for the mixture of four species, 63% of total biomass was in the stems.

In Plantation 1, *J. copaia* and *S. microstachyum* had the highest foliar N concentrations, *S. microstachyum* had the highest foliar P concentrations, and *V. guatemalensis* had significantly higher foliar Ca, Mg and K concentrations than any of the other three species (Table 3). *S. microstachyum* had the highest stemwood N concentrations, and *J. copaia* and *V. guatemalensis* had the highest stemwood Mg and K concentrations. Similar trends as for stemwood were found for branch nutrient concentrations (Table 3).

In Plantation 2, *A. guachapele* and *D. panamensis* had the highest foliar N, P and K concentrations, *V. koschnyi* and *T. amazonia* had the highest foliar Ca, and *A. guachapele* had higher foliar Mg concentrations than any of the other three species (Table 4). Comparing foliar nutrient concentrations for each species grown in pure and mixed stands, differences were found for only one species: *T. amazonia* had higher N concentration in foliage in mixed (1.96%), than in pure stands (1.65%). *A. guachapele* had the highest stemwood N concentrations, *A. guachapele* and *V. koschnyi* had significantly higher stemwood Mg concentrations, and there were no statistically significant differences in stemwood P, Ca or K concentrations among the four species. Again, similar trends as for stemwood were found for branch nutrient concentrations (Table 4).

3.2. Nutrient content of above-ground tree biomass

In Plantation 1, on a per hectare basis, *J. copaia* stands had higher total tree N, P, and Mg than the other treatments, while *V. guatemalensis* stands had the greatest accumulation of K and Ca (Fig. 1). The four species mixture had the second greatest total tree nutrient content for all nutrients. Due to lower tree biomass, *S. microstachyum* stands had the lowest nutrient content per hectare. Due to relatively high stem biomass, coupled with high nutrient concentrations, *J. copaia* had significantly higher stem N, P, K, Ca and Mg than any of the other pure stands, followed by the mixture of four species, and by *V. guatemalensis* pure stands, in that order (Fig. 1). Similar trends to those of stemwood were found for branch nutrient content (Fig. 1). *V. guatemalensis* had greater foliar biomass N, P, Mg, and K than the other pure stands, and *V. guatemalensis* and *C. brasiliense* had the greatest foliar biomass Ca (Fig. 1).

In Plantation 2, on a per hectare basis, the mixed stands had the highest nutrient content for all nutri-

Table 3
Nutrient concentrations in tissues of four indigenous tree species of Plantation 1. Means, standard errors (SE), and statistical significance (Sig.)[a]

Tissue/Species	Nutrient concentrations (%)														
	N			P			K			Ca			Mg		
	Mean	SE	Sig.	Mean	SE	Sig.	Mean	SE	Sig.	Mean	SE	Sig.	Mean	SE	Sig.
Leaves															
J. copaia	2.68	0.09	a	0.18	0.01	b	0.58	0.03	c	0.40	0.02	c	0.21	0.01	b
V. guatemalensis	1.73	0.17	b	0.14	0.01	b	1.01	0.05	a	1.01	0.10	a	0.40	0.02	a
S. microstachyum	2.35	0.11	a	0.23	0.23	a	0.87	0.04	b	0.37	0.01	c	0.18	0.01	b
C. brasiliense	0.99	0.03	c	0.75	0.03	c	0.35	0.03	c	0.68	0.03	b	0.09	0.01	c
Branches															
J. copaia	0.66	0.04	b	0.16	0.02	b	0.64	0.05	c	0.54	0.04	a	0.13	0.01	b
V. guatemalensis	0.77	0.10	b	0.18	0.02	b	3.06	0.41	a	0.59	0.03	a	0.16	0.01	ab
S. microstachyum	1.10	0.10	a	0.26	0.02	a	1.51	0.09	b	0.36	0.01	b	0.17	0.02	a
C. brasiliense	0.38	0.04	c	0.07	0.00	c	0.38	0.03	c	0.65	0.07	a	0.08	0.00	c
Stems															
J. copaia	0.25	0.01	b	0.09	0.01	ab	0.52	0.07	b	0.2	0.04	a	0.09	0.00	a
V. guatemalensis	0.24	0.02	bc	0.1	0.02	a	0.87	0.09	a	0.26	0.01	a	0.08	0.00	a
S. microstachyum	0.49	0.08	a	0.12	0.02	a	0.55	0.02	b	0.21	0.02	a	0.06	0.01	b
C. brasiliense	0.12	0.01	c	0.05	0.01	b	0.12	0.01	c	0.3	0.05	a	0.04	0.00	c

[a] Differences between species for a given tissue are statistically significant ($P < 0.05$) when means are followed by different letters. SE < 0.01.

ents, while the reverse was true for *A. guachapele* stands (Fig. 2). Due to relatively high stem biomass, coupled with high nutrient concentrations, the mixed stands had significantly higher stem N and Ca than any of the other pure stands, and both the mixture and *T. amazonia* pure stands had the highest stem P and Mg (Fig. 2). The mixture, *T. amazonia* and *V. koschnyi* pure stands had the highest stem K. The mixed stands and *D. panamensis* had significantly greater branch N, P, K and Ca content, while the mixture, *A. guachapele* and *T. amazonia* had the greatest branch Mg (Fig. 2). The mixed stands had significantly higher foliar N and K than any of the other pure stands, and the mixture, *T. amazonia* and *V. koschnyi* had the highest foliar P, Ca and Mg (Fig. 2).

3.3. Soil chemistry

In Plantation 1, 5 years after planting, statistically significant differences in soil nutrients between treatments were found only for P (Table 5). The mixture and the *C. brasiliense* plots had the highest while the *V. guatemalensis* and the *J. copaia* plots had the lowest concentrations of soil P at all depths ($P < 0.05$). In Plantation 2, 5 years after planting there were no statistically significant differences among treatments for any depth or nutrient (Table 6).

4. Discussion

4.1. Above-ground tree biomass in pure and mixed plantations

Converting the above-ground biomass accumulation for 3 years to an annual basis for the fastest growing species of these experiments: *V. guatemalensis, J. copaia, T. amazonia, D. panamensis* and *V. koschnyi*, yields a range from 6.2 to 15.5 Mg/ha per year. These values are within the range found for several tree species in young plantations in humid tropical regions. For example, for sites in Brazil and Costa Rica, Lugo et al. (1988) reported tropical species above-ground biomass accumulation rates of 1.6–29.8, with most in the range from 6–15 Mg/ha per year. For *Gmelina arborea,* Halenda (1993) reported total above-ground biomass accumulation rate of 13 Mg/ha per year in a 7 year-old plantation in

Table 4
Nutrient concentrations in tissues of four indigenous tree species of Plantation 2. Means, standard errors (SE), and statistical significance (Sig.)[a]. For leaves, an additional comparison is presented among pure and mixed stands (Ag: *A. guachapele*, Vk: *V. koschnyi*, Ta: *T. amazonia*, Dp: *D. panamensis*)

Tissue/Species	Nutrient concentrations (%)														
	N			P			K			Ca			Mg		
	Mean	SE	Sig.	Mean	SE	Sig.	Mean	SE	Sig.	Mean	SE	Sig.	Mean	SE	Sig.
Leaves															
A. guachapele	4.09	0.13	a	0.23	0.01	a	1.34	0.11	a	0.39	0.04	b	0.29	0.01	a
V. koschnyi	1.57	0.13	c	0.12	0.01	d	0.63	0.06	c	0.86	0.09	a	0.23	0.02	b
T. Amazonia	1.65	0.03	c	0.16	0.01	c	0.72	0.09	c	0.74	0.11	a	0.27	0.02	ab
D. panamensis	2.48	0.1	b	0.2	0.00	b	1.09	0.02	b	0.46	0.04	b	0.14	0.00	c
Mixed versus pure leaves:															
Ag	4.1	0.13	a	0.23	0.00	a	1.35	0.11	a	0.39	0.04	a	0.29	0.01	a
Ag mix	4.43	0.13	a	0.25	0.01	a	1.46	0.12	a	0.49	0.03	a	0.34	0.02	a
V k	1.57	0.13	a	0.12	0.01	a	0.63	0.06	a	0.86	0.09	a	0.23	0.02	a
V k mix	1.64	0.1	a	0.12	0.01	a	0.71	0.06	a	0.9	0.11	a	0.18	0.02	a
Ta	1.65	0.03	b	0.16	0.01	a	0.72	0.09	a	0.74	0.11	a	0.27	0.02	a
Ta mix	1.96	0.08	a	0.16	0.01	a	0.87	0.1	a	0.82	0.15	a	0.29	0.02	a
Dp	2.48	0.1	a	0.2	0.00	a	1.09	0.02	a	0.46	0.04	a	0.14	0.00	a
Dp mix	2.21	0.1	a	0.2	0.01	a	0.96	0.06	a	0.44	0.06	a	0.16	0.01	a
Branches															
A. guachapele	1.21	0.23	a	0.18	0.02	a	1.11	0.29	a	0.41	0.06	a	0.14	0.02	b
V. koschnyi	0.71	0.25	ab	0.09	0.02	b	1.05	0.34	a	0.49	0.06	a	0.18	0.02	a
T. amazonia	0.31	0.05	b	0.1	0.01	b	0.44	0.15	a	0.23	0.04	b	0.06	0.01	c
D. panamensis	0.67	0.08	ab	0.12	0.02	b	0.73	0.18	a	0.38	0.04	ab	0.05	0.00	c
Stems															
A. guachapele	0.64	0.08	a	0.1	0.01	a	0.4	0.07	a	0.29	0.04	ab	0.08	0.01	a
V. koschnyi	0.23	0.03	b	0.07	0.01	a	0.42	0.07	a	0.2	0.02	bc	0.08	0.01	a
T. amazonia	0.24	0.01	b	0.08	0.01	a	0.34	0.05	ab	0.17	0.03	c	0.03	0	b
D. panamensis	0.27	0.04	b	0.08	0.01	a	0.22	0.03	b	0.32	0.04	a	0.04	0.00	b

[a] Differences between species for a given tissue are statistically significant ($P < 0.05$) when means are followed by different letters. SE < 0.01.

Sarawak. However, all these values were for plantations of relatively young age; values will also vary with climate and site fertility (Lugo et al., 1988).

The value for *C. brasiliense* in the present research is similar to ranges reported for relatively slower-growing species in the humid tropics, such as *Swietenia macrophylla* and *Tectona grandis* (Wadsworth, 1983). On the other hand, in the present research the nitrogen-fixing species of each plantation (*S. microstachyum,* Plantation 1, and *A. guachapele,* Plantation 2) gave the lowest biomass values, a finding that contrasts with the more general good performance of N-fixing species found in a variety of tropical environments. For example, Wang et al. (1991) reported biomass production rates of 9.8 Mg/ha per year for *Albizia lebbek* and 11 Mg/ha per year for *Leucaena leucocephala* in Puerto Rico. In the present research, the poor performance of *S. microstachyum* was due to a fungal disease, anthracnosis, caused by *Glomerella* spp. (Montagnini et al., 1995). This disease resulted in complete mortality of *S. microstachyum* in pure plots, while 42% of the trees survived in mixed plots at 4 years. The poor performance of *A. guachapele* was due to attacks by root gophers (*Orthogeomys* spp.) (Montagnini et al., 1995). Initially the trees apparently recovered from the damage, but after 4 years their poor performance became apparent. In another plantation in the same experimental setting, the nitrogen-fixing species, *Pithecellobium elegans,* was among the most productive of the species tested, both in pure and in mixed designs (Stanley and Montagnini, 1999).

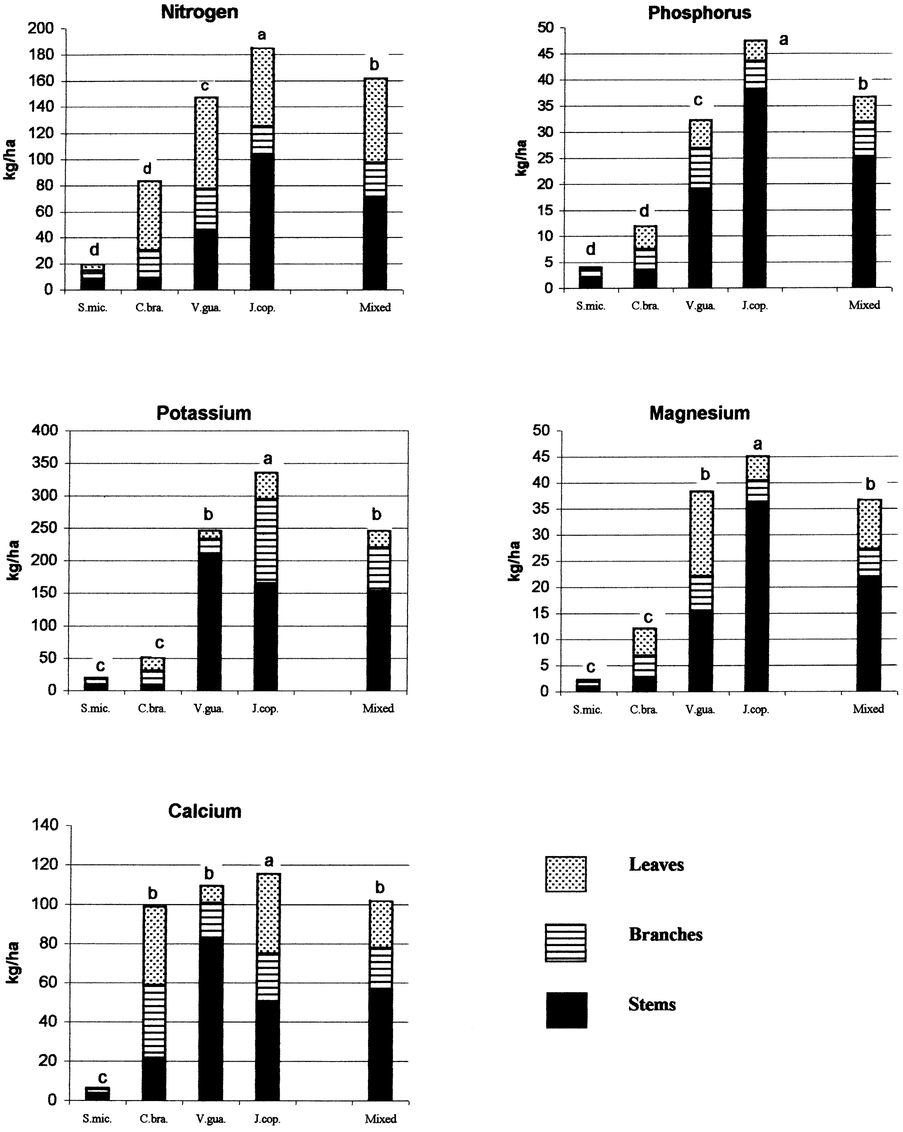

Fig. 1. Total above-ground nutrient content per hectare of *J. copaia*, *V. guatemalensis*, *C. brasiliense*, and *S. microstachyum* grown in pure plantation, and a mixture of the four species. Total nutrient content differs among treatments when bars are topped by different letters ($P < 0.05$).

The values of total above-ground biomass and stem biomass for the two mixed plantations of the present research are within the ranges reported elsewhere for fast-growing, monospecific plantations of commonly used species in the humid tropics. The most successful mixed plantings are stratified mixtures composed of faster-growing, shade-intolerant species above slower-starting tolerants (Smith, 1986). If the trees in the upper canopy are not too dense, they grow more rapidly in diameter than if crowded into the single canopy of a pure plantation (Burkhart and Tham, 1992). In the present research, the dominant species of each plantation grew larger when grown with other species compared to single species plantation.

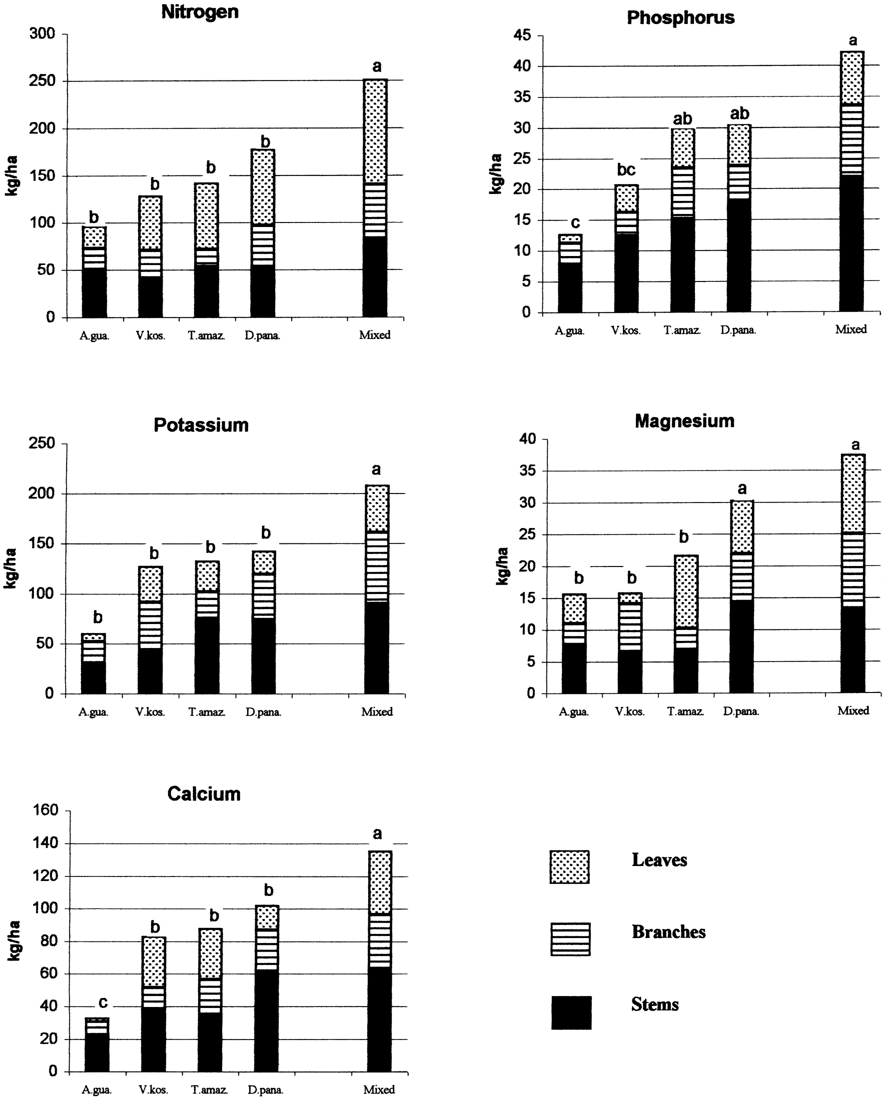

Fig. 2. Total above-ground nutrient content per hectare of *T. amazonia*, *D. panamensis*, *V. koschnyi* and *A. guachapele* grown in pure plantation, and a mixture of the four species. Total nutrient content differs among treatments when bars are topped by different letters ($P < 0.05$).

Apparently in the mixtures the dominant species, with less intra-specific competition, can attain larger diameters, as reported in earlier research (Montagnini et al., 1995; Montagnini and Porras, 1998; Stanley and Montagnini, 1999). Only one of the eight species tested here was seemingly suppressed by the dominant species and thus grew better in pure plots: *C. brasiliense* (Plantation 1). Except in the case noted, the other species associated with the faster growing dominants apparently shared resources with the dominant species and had higher biomass of plant parts in mixed than in pure plots.

The inclusion of faster and relatively slower growing species in a mixture has the advantage of providing harvestable products at different rotation times, with the relatively slower growing species (e.g., *C. brasi-*

Table 5
Nutrient concentrations, organic matter, and soil pH under indigenous tree species grown in pure stands, mixture of the four species, and natural regeneration stands in Plantation 1. Means, standard errors (SE), and statistical significance[a]. Soils were sampled in June 1996

Treatment	Depth (cm)	pH			Ca (cmol/l)			Mg (cmol/l)			K (cmol/l)			P (mg/l)			OM (%)			N (%)		
		Mean	SE	Sig.	Mean	SE	Sig.	Mean	SE	Sig.	Mean	SE	Sig.	Mean	SE	Sig.	Mean	SE	Sig.	Mean	SE	Sig.
J. copaia																						
	1–5	4.05	0.10	a	0.94	0.19	a	0.40	0.06	abc	0.16	0.01	a	11.2	1.3	ab	9.73	0.93	a	0.37	0.06	a
	5–15	4.08	0.10	a	0.88	0.06	a	0.32	0.04	a	0.19	0.09	a	8.75	1.61	c	7.27	0.97	a	0.28	0.02	a
	15–30	4.13	0.11	a	0.77	0.06	a	0.30	0.02	a	0.11	0.01	ab	7.98	1.6	c	6.69	1.28	a	0.30	0.03	a
	30–60	4.1	0.15	a	0.80	0.02	a	0.31	0.05	a	0.10	0.02	ab	7.98	1.89	b	6.77	1.35	a	0.24	0.03	a
C. brasiliense																						
	1–5	4.1	0.11	a	0.52	0.10	ab	0.24	0.05	c	0.14	0.02	a	14.4	2.23	a	7.63	0.69	b	0.35	0.01	a
	5–15	3.98	0.08	a	0.44	0.07	b	0.22	0.06	a	0.14	0.02	a	13	1.19	ab	6.05	0.65	a	0.29	0.02	a
	15–30	4.08	0.08	a	0.51	0.11	a	0.23	0.07	a	0.16	0.02	ab	13.9	1.63	ab	5.29	0.94	a	0.29	0.04	a
	30–60	4.05	0.10	a	0.47	0.13	a	0.21	0.08	a	0.14	0.01	ab	13.5	0.86	a	4.76	1.32	a	0.25	0.05	a
S. microstachyum																						
	1–5	4.1	0.11	a	0.69	0.10	ab	0.39	0.04	abc	0.16	0.02	a	13.3	0.35	ab	8.17	0.81	ab	0.35	0.02	a
	5–15	4.08	0.14	a	0.61	0.13	ab	0.32	0.06	a	0.15	0.03	a	11.9	0.66	abc	6.83	1.01	a	0.3	0.02	a
	15–30	4.1	0.15	a	0.60	0.13	a	0.25	0.05	a	0.21	0.05	a	10.6	0.62	bc	5.82	1.37	a	0.26	0.04	a
	30–60	4.1	0.18	a	0.52	0.11	a	0.23	0.06	a	0.20	0.05	a	11.1	1.33	ab	5.32	1.67	a	0.25	0.06	a
V. guatemalensis																						
	1–5	4.18	0.15	a	0.89	0.17	ab	0.65	0.20	a	0.13	0.01	a	9.35	1.74	b	6.65	0.18	b	0.31	0.01	a
	5–15	4.08	0.13	a	0.58	0.09	b	0.35	0.02	a	0.10	0.02	a	8.5	1.09	c	5.85	0.91	a	0.27	0.03	a
	15–30	4.08	0.10	a	0.52	0.10	a	0.26	0.04	a	0.09	0.01	b	8.8	0.77	c	5.15	1.08	a	0.26	0.05	a
	30–60	4.13	1.38	a	0.54	0.14	a	0.23	0.08	a	0.09	0.02	b	7.45	1.46	b	4.28	1.25	a	0.22	0.06	a
Mixture																						
	1–5	4.03	0.08	a	0.61	0.08	b	0.29	0.01	bc	0.15	0.02	a	15.1	1.46	a	7.77	0.33	b	0.32	0.05	a
	5–15	4.03	0.05	a	0.61	0.11	ab	0.26	0.06	a	0.13	0.02	a	14.2	1.38	a	6.81	0.70	a	0.32	0.02	a
	15–30	4.08	0.10	a	0.52	0.06	a	0.23	0.05	a	0.13	0.01	ab	14.3	1.44	a	6.43	1.08	a	0.28	0.03	a
	30–60	4.13	0.13	a	0.58	0.13	a	0.22	0.07	a	0.12	0.02	ab	14	1.36	a	5.64	1.58	a	0.24	0.05	a
Regeneration																						
	1–5	4.18	0.13	a	0.68	0.12	ab	0.61	0.18	ab	0.32	0.17	a	11.9	1.82	ab	7.69	0.58	b	0.36	0.03	a
	5–15	4.13	0.10	a	0.62	0.12	ab	0.34	0.02	a	0.23	0.11	a	10.1	1.28	bc	6.78	0.47	a	0.29	0.01	a
	15–30	4.18	0.16	a	0.53	0.06	a	0.26	0.04	a	0.19	0.08	ab	9.95	0.88	c	5.87	1.06	a	0.25	0.04	a
	30–60	4.13	0.20	a	0.55	0.13	a	0.24	0.08	a	0.15	0.05	ab	10.4	2.35	ab	4.56	1.3	a	0.23	0.06	a

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

Table 6
Nutrient concentrations, organic matter, and pH of soil under four indigenous tree species grown in pure stands, mixture of the four species, and natural regeneration stands in Plantation 2. Mean,standard errors (SE), and statistical significance[a]. Soils were sampled in June 1996

Treatment	Depth (cm)	pH			Ca (cmol/l)			Mg (cmol/l)			K (cmol/l)			P (mg/l)			OM (%)			N (%)		
		Mean	SE	Sig.	Mean	SE	Sig.	Mean	SE	Sig.	Mean	SE	Sig.	Mean	SE	Sig.	Mean	SE	Sig.	Mean	SE	Sig.
A. guachapele																						
	0–5	4.43	0.06	a	1.02	0.51	a	0.33	0.16	a	0.16	0.04	a	12	1.00	a	6	1.33	a	0.33	0.08	a
	5–15	4.43	0.05	a	1.01	0.53	a	0.34	0.17	a	0.17	0.04	a	11.4	0.68	b	6.11	0.92	a	0.29	0.05	a
	15–30	4.40	0.04	a	0.99	0.48	a	0.30	0.15	a	0.16	0.05	a	11.7	0.56	a	5.51	1.32	a	0.30	0.06	a
	30–60	4.35	0.05	a	1.05	0.42	a	0.33	0.14	a	0.17	0.06	a	11.7	0.91	a	5.86	1.2	a	0.32	0.06	a
D. panamensis																						
	0–5	4.40	0.00	a	1.01	0.42	a	0.35	0.14	a	0.19	0.06	a	12.2	1.59	a	5.93	0.36	a	0.32	0.03	a
	5–15	4.35	0.03	a	1.02	0.41	a	0.34	0.13	a	0.18	0.06	a	11.9	0.99	b	5.83	0.17	a	0.32	0.03	a
	15–30	4.30	0.04	a	1.27	0.28	a	0.45	0.07	a	0.18	0.06	a	12.2	1.54	a	6.31	0.84	a	0.36	0.05	a
	30–60	4.30	0.04	a	1.22	0.27	a	0.44	0.07	a	0.18	0.07	a	15	3.66	a	5.81	1.36	a	0.34	0.04	a
T. amazonia																						
	0–5	4.30	0.04	a	1.13	0.31	a	0.36	0.08	a	0.17	0.04	a	11.1	0.52	a	7.41	1.00	a	0.38	0.05	a
	5–15	4.35	0.03	a	1.15	0.30	a	0.38	0.09	a	0.17	0.04	a	11.1	0.73	b	6.9	1.23	a	0.38	0.05	a
	15–30	4.40	0.04	a	1.13	0.37	a	0.37	0.10	a	0.17	0.04	a	11.9	0.38	a	7.11	1.35	a	0.36	0.05	a
	30–60	4.33	0.03	a	1.13	0.33	a	0.38	0.10	a	0.18	0.04	a	12.8	1.26	a	7.15	1.44	a	0.38	0.06	a
V. koschnyi																						
	0–5	4.40	0.07	a	1.55	0.45	a	0.52	0.12	a	0.18	0.05	a	12.8	0.97	a	6.56	1.48	a	0.36	0.08	a
	5–15	4.38	0.09	a	1.54	0.44	a	0.52	0.12	a	0.18	0.05	a	13.5	1.26	ab	7.11	2.02	a	0.35	0.08	a
	15–30	4.30	0.04	a	1.54	0.44	a	0.51	0.12	a	0.18	0.04	a	13.9	1.36	a	7.7	1.42	a	0.38	0.06	a
	30–60	4.30	0.04	a	1.47	0.38	a	0.49	0.10	a	0.18	0.05	a	14.3	2.05	a	7.43	1.11	a	0.38	0.05	a
Mixed																						
	0–5	4.40	0.12	a	0.63	0.14	a	0.24	0.07	a	0.16	0.06	a	13.4	1.29	a	5.26	1.33	a	0.24	0.05	a
	5–15	4.43	0.09	a	0.66	0.13	a	0.23	0.07	a	0.17	0.06	a	15.6	1.32	a	5.52	1.47	a	0.26	0.04	a
	15–30	4.38	0.11	a	1.12	0.44	a	0.52	0.24	a	0.17	0.06	a	13.6	0.56	a	5.08	1.5	a	0.28	0.05	a
	30–60	4.40	0.09	a	1.19	0.50	a	0.41	0.15	a	0.17	0.06	a	14.6	0.93	a	4.62	1.18	a	0.27	0.05	a
Regeneration																						
	0–5	4.35	0.05	a	1.31	0.27	a	0.44	0.07	a	0.18	0.04	a	13.8	1.43	a	6.21	1.14	a	0.33	0.05	a
	5–15	4.40	0.08	a	1.16	0.32	a	0.39	0.10	a	0.15	0.04	a	12.9	1.8	ab	5.4	1.03	a	0.30	0.04	a
	15–30	4.40	0.09	a	0.99	0.32	a	0.34	0.10	a	0.17	0.06	a	10.3	3.48	a	6.15	1.15	a	0.30	0.05	a
	30–60	4.30	0.08	a	1.15	0.45	A	0.38	0.13	a	0.18	0.05	a	11.2	0.91	a	6.11	1.66	a	0.33	0.06	a

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

liense, D. panamensis) producing more valuable wood. For the slower growing species, establishment costs are less in mixed than in pure plots, because the need for weeding is substantially less in mixed plots (Montagnini et al., 1995). Additionally, because the different species of the mixture have different rotation lengths, the land is in use for a longer period than if planted with just one fast-growing, short-rotation species (such as *J. copaia*). This diminishes incentives for changing to other land uses, keeps a vegetative cover that protects the soil, and serves other environmental purposes as well (Montagnini and Mendelsohn, 1996).

4.2. Nutrient accumulation in above-ground tree biomass in pure and mixed plantations

In Plantation 1, high foliar N found in *S. microstachyum,* the N-fixing species of the plantation, coincides with results of previous studies in other plantations at La Selva (Montagnini and Sancho, 1994). The high N concentration in foliage found in *J. copaia,* a tree of the Bignoniaceae family, is a result consistent with earlier studies of leaf litter decomposition and nutrient release from litter at La Selva by Byard et al. (1996). Likewise, high cation concentrations in foliage and stemwood of *V. guatemalensis* coincide with earlier findings by Montagnini and Sancho (1994). In Plantation 2, the highest foliar N was found in the N-fixing component of the plantation, *A. guachapele,* and the second highest was found in another leguminous species, *D. panamensis*. No evidence of nodulation was found in this or in earlier research involving *D. panamensis* (Montagnini and Sancho, 1994; Kershnar and Montagnini, 1998), and no reports exist of its nodulation in other environments. However, symbiotic N fixation has been shown for other non-nodulating legumes, and recent evidence of its occurrence in *D. panamensis* has been found (Bryan et al., 1996).

The higher N concentration of leaves of *T. amazonia* when grown in mixed plantation, in comparison with leaves of trees of this species in the pure plots, could be attributed to additional uptake of N released by its N-fixing neighbors (*A. guachapele, D. panamensis*) (Kershnar and Montagnini, 1998). A similar trend was found in *V. koschnyi,* but the smaller difference in N concentration between leaves of mixed and pure stands was not statistically significant.

At the time of plantation harvest, the amount of nutrients represented by foliage or branches which may be left behind varies between nutrients, species, and sites. The results of the present research are from young plantations; crowns form a high proportion of total biomass in young stands, but their importance decreases as the stand ages (Fölster and Khanna, 1997). However, these early results can point out to potential effects of stem harvest on site nutrients by each species. For example, stems of *J. copaia* and *V. guatemalensis* represented 88 and 70% of total above-ground tree biomass, respectively. For *J. copaia,* stem harvest would remove about 54% of total above-ground tree N, but about 80% of P, K, Ca and Mg. For *V. guatemalensis,* stem harvest would remove less than 30% of N but from 50 to 60% of total above-ground tree Ca, K, Mg and P. On the other hand, branches and foliage summed together represented about 25–35% of total tree biomass (Table 2), but they generally represented about 50% of total tree nutrients (Figs. 1 and 2). For broad leaved species, the proportion of nutrients in branches and foliage may range from 15 to 46% of total tree nutrients (Fölster and Khanna, 1997). Leaving branches and leaves on the site, rather than harvesting the whole tree, can generally reduce nutrient losses by one-half, a result consistent with earlier findings on other species at La Selva (Stanley and Montagnini, 1999).

4.3. Influence of nutrient accumulation in above-ground tree biomass on soil nutrients

In Plantation 1, five years after planting, the pure plots of the two fastest growing species, *V. guatemalensis* and *J. copaia,* had the lowest values of soil P concentration. This result could be attributed to high accumulation of P in above-ground biomass of these two species. This trend is consistent with results from the previous years (Montagnini and Porras, 1998). In addition, this result was more marked in the present research: in 1995, significant differences for P had only occurred in the top soil (0–5 cm depth) (Montagnini and Porras, 1998), while in 1996 the differences were detected at all depths studied (Table 5).

Although there were no statistically significant differences in other soil nutrients among treatments, some differences were found with respect to results of the previous years. For example, under *V. guatema-*

lensis values of soil K and Ca in 1996 were about half those found in 1995 (Montagnini and Porras, 1998). These results are again consistent with findings on nutrient accumulation in above-ground biomass by the tree species: *V. guatemalensis* had the greatest accumulation of K and Ca of the four species of this plantation.

In Plantation 2 there had been changes with respect to the levels measured the previous years as well (Montagnini and Porras, 1998). For example, in 1996 soil K concentrations had decreased in all treatments with respect to 1995, while soil Mg had decreased in all treatments except for *V. koschnyi*. However, in other cases, beneficial effects on some soil nutrients were noted: for example, about 30% increases in soil Ca were found under *T. amazonia* and *V. koschnyi* with respect to the previous year (Montagnini and Porras, 1998).

Knowledge of the nutrient cycling characteristics of the species can also help in choosing management strategies to conserve site nutrients. For example, *J. copaia* and *V. guatemalensis* had the highest annual litterfall of the four species of Plantation 1, and they also had the highest accumulation of litter on the ground, therefore these two species can provide good soil protection (Byard et al., 1996). The mixed designs provided intermediate to fast decomposition rates, releasing nutrients to the soil and allowing a litter layer to protect the soil (Byard et al., 1996).

Likewise, in Plantation 2, both *T. amazonia* and *V. koschnyi* had the highest Ca content in foliage, and they also had high rates of annual litterfall (*T. amazonia*: 853 g/m^2, *V. koschnyi*: 620 g/m^2) (Kershnar and Montagnini, 1998). *T. amazonia* had the fastest litter decomposition of the species studied, while *V. koschnyi* decomposed the slowest (Kershnar and Montagnini, 1998). *T. amazonia* can have beneficial effects on soil nutrients, as suggested by results of the present research; while *V. koschnyi* can contribute to better soil protection. Again, the mixed plots exhibited the most consistent litterfall and plantation-floor litter throughout the year, and mixed litter had an average decomposition rate and performed well as a mulch (Kershnar and Montagnini, 1998).

Apparently some decreases in soil nutrients with time were detected for K and P, the two nutrients more likely to be depleted from plantation soils (Wadsworth, 1983; Bowen and Nambiar, 1984). These decreases were most apparent under the fastest growing species with the highest nutrient accumulation in above-ground biomass, such as *V. guatemalensis* and *J. copaia*. This suggests that rapid uptake and accumulation of nutrients in tree biomass served as the main mechanism responsible for this decrease. Results of continued sampling will be needed to assess the long term effects of plantation treatments on soil chemistry, especially near the end of the rotation (estimated at 12–15 years, depending on the species).

On the other hand, beneficial effects on soil nutrients were noted under pure stands of some of the studied species, therefore nutrient cycling characteristics must also be taken into account when assessing the potential impacts of plantation species on site nutrients. The mixed plots showed intermediate values for the nutrients examined, and even improved soil conditions, as for P in Plantation 1. This suggests that in mixed conditions it may take longer to deplete soil nutrients than in monospecific stands of fast-growing species.

Acknowledgements

This project was funded by the A.W. Mellon Foundation (USA). For their collaboration, I thank La Selva Biological Station; personnel of the Center for Agricultural Research, University of Costa Rica; and C. Jordan for his comments.

References

Allison, L.E., 1975. Organic carbon. In: Black, C.A. (Ed.), Methods of Soil Analysis, part 2. American Society of Agronomy, Madison, WI, pp. 1367–1378.

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, p. 76.

Binkley, D., 1986. Forest Nutrition and Management. Wiley, New York.

Binkley, D., Dunkin, K.A., DeBell, D., Ryan, M.G., 1992. Production and nutrient cycling in mixed plantations of *Eucalyptus* and *Albizia* in Hawaii. For. Sci. 38, 393–408.

Binkley, D., O'Connell, A.M., Sankaran, K.V., 1997. Stand development and productivity. In: Nambiar, E.K.S., Brown, A.G. (Eds.), Management of Soil, Nutrients and Water in Tropical Plantation Forests. ACIAR/CSIRO/CIFOR, ACIAR, Canberra, Australia, pp. 419–442.

Bowen, G.D., Nambiar, E.K.S., 1984. Nutrition of Plantation Forests. Academic Press, New York, p. 516.

Bremner, J.M., Mulvaney, C.S., 1982. Nitrogen-total. In: Page, A. L., Miller, R.H., Keeney, R.R. (Eds.), Methods of Soil Analysis, 2nd. ed., part 2. American Society of Agronomy, Madison, Wisconsin, pp. 595–624.

Bruijnzeel, L.A., 1984. Immobilization of nutrients in plantation forests of *Pinus merkusii* and *Agathis damara* growing on volcanic soils in central Java, Indonesia. In: Tajib, A., Pushparajah, E. (Eds.), Proc. Int. Conf. on Soils and Nutrition of Perennial Crops. Malaysian Soil Science Society, Kuala Lumpur, pp. 19–29.

Bruijnzeel, L.A., 1991. Nutrient input-output budgets of tropical forest ecosystems: a review. J. Trop. Ecol. 7, 1–24.

Bryan, J.A., Berlyn, G.P., Gordon, J.C., 1996. Toward a new concept of symbiotic nitrogen fixation in the Leguminosae. Plant Soil 186, 151–159.

Burkhart, H.E., Tham, Å., 1992. Predictions from growth and yield models of the performance of mixed-species stands. In: Cannell, M.G.R., Malcolm, D.C., Robertson, P.A. (Eds.), The Ecology of Mixed-Species Stands of Trees. Blackwell Scientific, Boston, pp. 21–34.

Byard, R., Lewis, K.C., Montagnini, F., 1996. Leaf litter decomposition and mulch performance from mixed and monospecific plantations of native tree species in Costa Rica. Agric. Ecosys. Environ. 58, 145–155.

Díaz-Romeu, R., Hunter, A., 1978. Método para el Muestreo de Suelos, Análisis Químico de Suelos y Tejido Vegetal e Investigación en Invernaderos. CATIE, Turrialba, Costa Rica, pp. 9–11, 15–27.

Fölster, H., Khanna, P.K., 1997. Dynamics of nutrient supply in plantation soils. In: Nambiar, E.K.S., Brown, A.G. (Eds.), Management of Soil, Nutrients and Water in Tropical Plantation Forests. ACIAR/CSIRO/CIFOR, ACIAR, Canberra, Australia, pp. 338–378.

Gonçalves, J.L.M., Barros, N. F., Nambiar, E.K.S., Novais, R.F., 1997. Soil and stand management for short-rotation plantations. In: Nambiar, E.K.S., Brown, A.G. (Eds.), Management of Soil, Nutrients and Water in Tropical Plantation Forests. ACIAR/CSIRO/CIFOR, ACIAR, Canberra, Australia, pp. 379–417.

Halenda, C.J., 1993. Above-ground biomass production and nutrient accumulation of a *Gmelina arborea* plantation in Sarawak, Malaysia. J. Trop. For. Sci. 5, 429–439.

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

Kelty, M.J., 1992. Comparative productivity of monocultures and mixed-species stands. In: Kelty, M.J., Larson, B.C., Oliver, C.D. (Eds.), The Ecology and Silviculture of Mixed-Species Forests. Kluwer Academic Publishers, Dordrecht, pp. 125–141.

Kershnar, R., Montagnini, F., 1998. Leaf litter decomposition, litterfall and effects of leaf mulches from mixed and monospecific plantations in Costa Rica. J. Sustainable For. 7, 95–118.

Lugo, A.E., Brown, S., Chapman, C.G., 1988. An analytical review of production rates and stemwood biomass of tropical forest plantations. For. Ecol. Manage. 23, 179–200.

Montagnini, F., Sancho, F., González, E., Moulaert, A., 1993. Mixed-tree plantations with indigenous trees in the Atlantic lowlands of Costa Rica. In: Parrotta, J.A., Kanashiro, M. (Eds.), Proc. Int. Symp. on Management and Rehabilitation of Degraded Lands and Secondary Forests in Amazonia. Santarem, Pará, Brazil, 18–22 April, 1993, IITF, USDA Forest Service, Puerto Rico, pp. 161–169.

Montagnini, F., 1994a. Rehabilitating forest ecosystems in the humid tropics: recent experiences from Latin America. In: Proc. from IUFRO Int. Symp. on Growth and Yield of Tropical Forests. September 26–October 1, 1994, Tokyo University of Agriculture and Technology, Fuchu, Tokyo, Japan, pp. 224–234.

Montagnini, F., 1994b. Agricultural systems in the La Selva region. In: McDade, L.A., Bawa, K., Hespenheide, H.A., Hartshorn, G.S. (Eds.), La Selva: Ecology and Natural History of a Neotropical Rainforest. University of Chicago Press, Chicago, pp. 307–316.

Montagnini, F., Sancho, F., 1994. Above-ground biomass and nutrients in young plantations of four indigenous tree species: implications for site nutrient conservation. J. Sustainable For. 1, 115–139.

Montagnini, F., González, E., Rheingans, R., Porras, C., 1995. Mixed and pure forest plantations in the humid neotropics: a comparison of early growth, pest damage and establishment costs. Commonwealth For. Rev. 74, 306–314.

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

Montagnini, F., Porras, C., 1998. Evaluating the role of plantations as carbon sinks: an example of an integrative approach from the humid tropics. Environ. Manage. 22, 459–470.

Sancho, F., Mata, R., 1987. Estudio Detallado de Suelos. Estación Biológica La Selva. Organización Estudios Tropicales, San José, Costa Rica, p. 162.

Smith, D.M., 1986. The Practice of Silviculture, 8th ed. Wiley, New York, p. 527.

Stanley, W., Montagnini, F., 1999. Biomass and nutrient accumulation in pure and mixed plantations of indigenous tree species grown on poor soils in the humid tropics of Costa Rica. For. Ecol. Manage. 113, 91–103.

Wadsworth, F.H., 1983. Production of usable wood from tropical forests. In: Golley, F.B. (Ed.), Tropical Rain Forest Ecosystems: Structure and Function. Ecosystems of the World 14A. Elsevier, New York.

Wadsworth, F.H., 1997. Forest Production for Tropical America. United States Department of Agriculture Forest Service. Agriculture Handbook 710. Washington, DC.

Wang, D., Bormann, F.H., Lugo, A.E., Bowden, R.D., 1991. Comparison of nutrient-use efficiency and biomass production in five tropical tree taxa. For. Ecol. Manage. 46, 1–21.

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