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Dynamics of organic matter and nutrient return from litterfall in stands of ten tropical tree plantation species

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Abstract

We studied the rates and patterns of carbon and nutrient fluxes in litterfall in ten tropical tree plantation species grown at the USDA Forest Service Arboretum in the Luquillo Experimental Forest, Puerto Rico. The stands were 26-years old and grew under similar climatic and edaphic conditions. Individual plantation species ranked differently in terms of their capacity to return mass and specific nutrients to the forest floor, and with respect to their efficiency of nutrient use. The species that returned the most mass did not return the most P, N, or cations. Moreover, species differed according to the amount of N and P resorption before leaf fall. These differences reflect the variation in the ecophysiological response of each species to edaphic and climatic conditions. The difference between average and minimum resorption values of the species studied indicate that other environmental factors, such as heavy winds or the physical effects of heavy rains, can force the shedding of non-senesced leaves. This higher quality material, although not very much in quantity, can provide a small pulse of available nutrients to the forest floor community. The same holds true for other high nutrient/low mass fractions of litterfall such as reproductive parts and miscellaneous materials.

In areas with no prevalent or strongly seasonal water limitations, temporal variations of leaf litter on the forest floor are the combined result of the rate of fall and decomposition of the falling material, and the diverse responses of species to different environmental cues. Leaf fall was inversely correlated to reduced water availability in three of the species studied. Leaf fall of the other species was correlated either to daylight duration or minimum temperatures. The results highlight the importance of understanding species performance relative to nutrient and mass metabolism before selection for plantation use, or for rehabilitation of degraded lands. © 1998 Elsevier Science B.V. All rights reserved.

Keywords: Plantation species; Litterfall; Nutrient fluxes; P and N resorption; Environmental triggers

1. Introduction

It is becoming increasingly obvious that human beings will have to manage the landscape more intensively as a result of the increased pressure on space and natural resources caused by the increasing human population (Lugo, 1991). For the humid tropics, where

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high deforestation and land degradation rates rapidly reduce options for sustainable development solutions, future scenarios of land management must include a variety of production systems including high yielding tree plantations (National Research Council, 1993). Clearly, high population densities cannot be sustained without the contribution of systems with a high food and fiber yield. Thus, it is critical to understand the ecological properties of these ecosystems to avoid failures, minimize ecological damage, and optimize the use of soil, water, and energy resources.

This study is part of a larger effort to understand the ecology of tropical tree plantations (Lugo et al., 1990; Cuevas et al., 1991; Wang et al., 1991; Lugo, 1992; Lugo et al., 1993; Fu et al., 1996; Lugo, 1997). Our general objective is to characterize the biogeochemistry and biodiversity relationships within tree plantation designed for wood production and to compare these characteristics with natural forests of similar age. The results of these analyses advance our understanding of tropical forest ecology, help land managers in the selection and management of plantation tree species, and provide ecologically sound criteria for the management high yielding systems in the tropics. In this paper, we focus on carbon and nutrient fluxes in litterfall of ten tree plantation species in order to further our understanding of tropical forest ecology.

Differential resources uptake, and release of carbon and nutrients are important factors at the stand level, because they represent major fluxes through the system (Miller, 1984). The capability of each plant to utilize available resources is species specific (Marschner, 1995). These differences can either be genetically established or result from phenotypic responses to environment and/or resource availability (Van den Driessche, 1984).

Degree of retranslocation or resorption of nitrogen and phosphorus within the plants is also an important factor to be considered. Within-plant cycling of these elements decreases plantation dependence on the biogeochemical processes to fulfil nutrient requirements after the initial exponential phase of tree growth (Miller, 1984). It also decreases potential losses from the system due to leaching and erosion, as resorption maintains the nutrients within the living biomass.

The rate of fall and subsequent decay dynamics of litter affect soil organic matter formation and nutrient storage (Lugo et al., 1990). The effect will be determined by the type of soil upon which the plantation is growing and the climatic conditions that affect it (Swift et al., 1979; Bernhard-Reversat, 1987; Bernhard-Reversat, 1993). A knowledge of the timing of nutrient and mass return through litterfall to the forest floor is important for plantation management. Timing of inputs does not necessarily has to be ascribed to a single environmental trigger. This is especially relevant when planning multispecific plantations with species from different phytogeographical provenance and phenology under same climatic and edaphic conditions.

The objective of this study was to determine to what extent species differ in their rates and patterns of mass and nutrient return in litterfall. We examined nine tropical and one warm temperate tree species growing in monospecific stands under similar edaphic and climatic conditions. We chose these species as they are commonly used throughout the tropics, or have potential value in wood production or regeneration of degraded areas. The species provenance covers from Australia, Africa, Southeast Asia, South America and The Caribbean (Francis, 1989). The functional types are conifers, evergreens and deciduous species. We posed three questions based on their varied provenance and phenology: (1) What are the rates and patterns of litterfall and nutrient return to the forest floor of species with different phytogeographical origins and phenological characteristics when grown under similar edaphic and climatic conditions? (2) Are there differences in the degree of internal cycling of N and P (resorption) among these species?; and (3) What climatic factors regulate leaf senescence and the temporal patterns of litterfall in these tree species?

2. Study site

The study was carried out from November 20, 1986 to December 30, 1987 in the USDA Forest Service Arboretum established in 1960 in the Luquillo Experimental Forest in Puerto Rico (latitude 18°N, longitude 66°W). The arboretum was located at an elevation between 625 and 680 m.

Mean annual rainfall is 3807 mm with a mean temperature of 23°C at El Verde Field Station, located at 358 m elevation and approximately 10 km from the study site. Mean maximum temperature is 27°C and mean minimum temperature is 21.1°C at El Verde. Based on a climate diagram (Walter, 1973) of the average rainfall and air temperature from 1977 to 1987 (Fig. 1), the system could be considered as non-seasonal and very wet, as monthly rainfall is always higher than 150 mm. There is a seasonal pattern, however, based on the number of dry days per month (Cuevas et al., 1991). January–April are the driest months, with an average of 12–15 dry days and <300 mm rainfall per month. The wet season extends from July to December, when monthly rainfall is >300 mm and there are <10 dry days per month.

Fig. 2 presents monthly rainfall and number of dry days for 1987, the year of the study. Annual rainfall totalled 4540 mm with November and December having the highest rainfall. January–April were the driest months, with 16–23 dry days per month. Over the year, there is a 2 h difference in average monthly daylight duration. The longest days occur in June and July (13.18 and 13.08 h, respectively), and the shortest occur in December and January with 11.08 and 11.18 h, respectively (List, 1957).

The soils at the Arboretum are epiaquic isothermic tropohumults, with a high clay content (≈60%) and low pH (4.4–4.8). Soils in the stands have similar textures (Lugo et al., 1990). A more detailed description of the study site is found in Francis (1989) and Lugo et al. (1990).

The species studied were the widely used tropical plantation species *Pinus caribaea* var. *hondurensis*

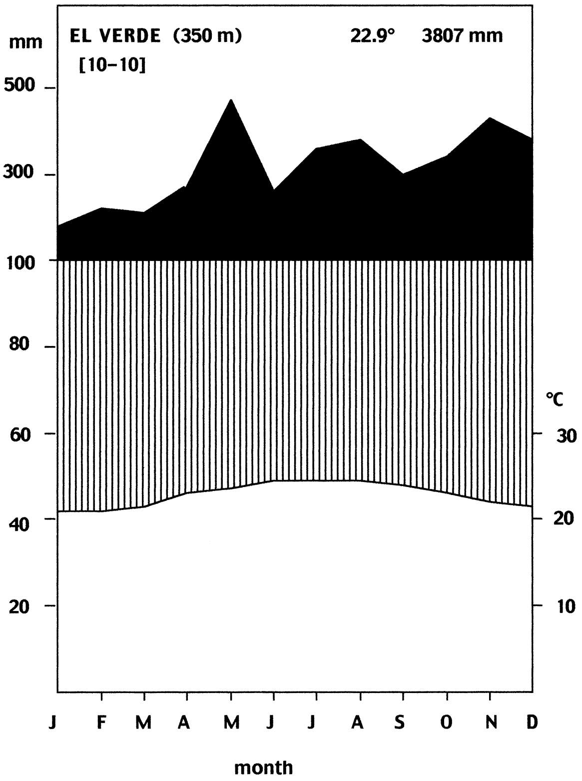

Fig. 1. Climate diagram of El Verde Field Station, Luquillo Experimental Forest, Puerto Rico. Data plotted are averages of 10 years (1977–1987). Elevation=(350 m), duration of observations in years for rainfall and temperature=[10], mean annual air temperature=22.9°C, mean annual rainfall=3807 mm.

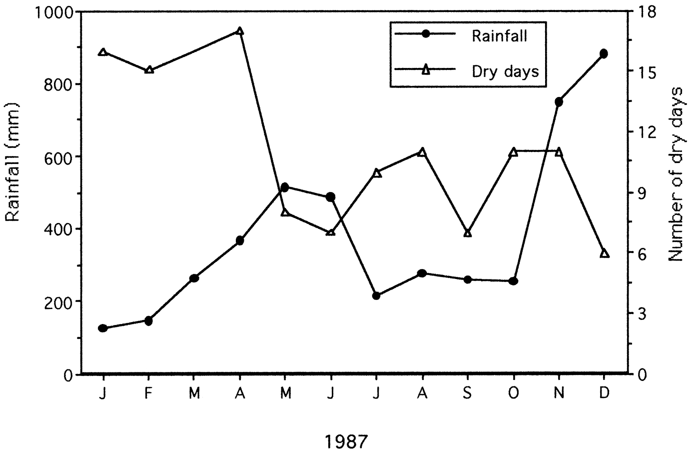

Fig. 2. Rainfall and number of dry days per month (days with $\leq$1 mm rainfall Cuevas et al., 1991) for the year 1987. Data were provided by Alejo Estrada for El Verde Field Station.

Barrett & Golfari, *Swietenia macrophylla* King, *Eucalyptus saligna* Sm., and *Eucalyptus* cf. *patentinervis*; a widely used species in the Caribbean island region, *Hibiscus elatus* Sw.; a species native to Puerto Rico, *Hernandia sonora* L.; a warm temperate pine species, *Pinus elliottii* var., *densa* Engelmann; and three tropical species that are potential alternatives to commonly used plantation species but have not been extensively tested: *Khaya nyasica* Stapf ex. Baker f., *Anthocephalus chinensis* (Lam.) A. Rich ex Walp., and *Terminalia ivorensis* A. Chev.

All stands were between 23 and 26 years of age. Each species was planted in a 400 m^2 block, with a 3 m×3 m spacing. The stands were never fertilized, but were weeded during the first 6 years after planting. A description of location, age, and growth parameters of the species studied is presented in Francis (1989) and Lugo et al. (1990) where stand age, mean total height and mean diameter breast height (dbh) are given.

3. Methods

Litter was collected in six 0.25 m^2, 2 mm mesh baskets, were randomly distributed among trees and away from the border in each stand. Each basket was horizontally placed 40 cm above the forest floor, independent of stand slope, and individually tagged. Accumulated litter was collected every 2 weeks for 58 weeks (29 samplings per basket), from late 1986 until the end of 1987. Bi-weekly collections were made in order to reduce nutrient losses due to leaching and decomposition in the basket (Cuevas and Medina, 1986). Litter from each basket was oven-dried at 65°C for a minimum of 5 days to constant weight and sorted into leaves of the plantation species (termed species leaves), other leaves (which include plantation understory leaf fall and leaf fall from adjacent plantations), five wood (<2 mm diameter wood plus bark), reproductive parts, and miscellaneous. By miscellaneous we consider anything that cannot be identified as any of the other litter fractions (i.e., insect frass).

After separation, the fractions were redried and weighed to 0.001 g. The same fractions for the six baskets per species per collection data were pooled for grinding and subsequent nutrient analyses.

We estimated resorption values for each plantation species based on the difference between nitrogen/calcium (N/Ca) or phosphorus/calcium (P/Ca) ratios of adult, fully expanded sun leaves collected at the beginning of our study, and the average ratios of recently fallen leaves of the same species (Vitousek and Sanford, 1986). Because we were also interested in whether the degree of resorption varied throughout the year, we estimated maximum resorption values from the minimum N/Ca and P/Ca in the leaf fall. We consider a leaf to be at the senescent stage when it has the minimum N/Ca and P/Ca ratios. Calcium concentration increases with age as a high proportion in the plant tissue is located in the cell walls, whereas N and P decreases due to remobilization to newly expanding tissues (Marschner, 1995). The chemistry data of the collected live, fully expanded adult sun leaves of each plantation species were provided by Dr. Ernesto Medina. The live leaves were processed in the same laboratory and with the same methodology used in our study. All concentration values were based on oven-dried weight basis.

4. Chemical analyses

Pooled samples were ground with a Wiley mill through a 0.85 mm (20 mesh) stainless steel mesh. Duplicates of each pooled sample were used for chemical analysis. Ground material was analyzed for P, K, Ca, and Mg with a Beckman plasma emission spectrometer (Spectra Span V) using the digestion method recommended by Luh Huang and Schulte (1985). Nitrogen was analyzed in samples digested with concentrated H_2SO_4 and a catalytic mixture of $CuSO_4$ and K_2SO_4 using a semi-micro Kjehldahl procedure (Chapman and Pratt, 1979).

5. Data analysis

Total nutrient content for each fraction was estimated by multiplying concentration of the pooled fraction per collection date by mass for each basket and collection date. We use the concentration of the pooled fraction as variability per basket/species was less than 1%, thus making it impractical analyzing each fraction per basket. On the other hand, variability in mass per fraction can reach up to a 100%, thus, differences in quantities of nutrients per fraction/basket/sampling date are attributed more to mass inputs than to variation in concentration values.

We used the program STATVIEW 4.5 (Abacus Concepts) for statistical analyses. ANOVA was employed to establish differences among species stands for mass and absolute nutrient amounts for total litterfall and each of its fractions. Each stand was considered to be a fixed-effect treatment. Fisher's protected least significant difference (FPLSD) was used in an a posteriori comparison to establish significant differences among means ($p<0.05$) (Steel and Torrey, 1980). Mass of leaf fall per stand was added for the sampling dates per months and simple regressions were carried out between these values and the environmental variables measured during the year of the study (day length, maximum or minimum air temperature, monthly rainfall, and amount of dry days per month).

6. Results

6.1. Litterfall mass

Litterfall ranged from 8.1 Mg ha^{-1} year^{-1} for *A. chinensis* to 14.3 Mg ha^{-1} year^{-1} for *P. caribaea* (Fig. 3) with an average of 11.1 Mg ha^{-1} year^{-1} for the ten species. There were significant differences among species and three groups could be observed. *Pinus caribaea. H. elatus*, and *E. saligna* had significantly higher total litterfall. *Pinus elliottii, E. patentinervis*, and *K. nyasica* had intermediate values, while *S. macrophylla*, *T. ivorensis*, *H. sonora*, and *A. chinensis* had the lowest values. Species leaves fraction ranged from 2.1 for *A. chinensis* to 9.7 Mg ha^{-1} year^{-1} for *P. caribaea. Anthocephalus chinensis*, *E.patentinervis*, and *E. saligna* had significantly lower mass of species leaves which accounted for around 30% of total litterfall (Fig. 3). Species leaves was the most important fraction for the other seven stands. Species leaves of *T. ivorensis* and *S. macrophylla* accounted for about 50% of total litterfall, while for the other stands, that fractions accounted for between 65% and 80% of total litterfall.

The other leaves fraction ranged from 0.4 for *H. sonora* to 1.6 Mg ha^{-1} year^{-1} for *P. caribaea*. Fine wood fraction ranged from 0.5 for *H. sonora* to 6.4 Mg ha^{-1} year^{-1} for *E. salinga*. The fine wood

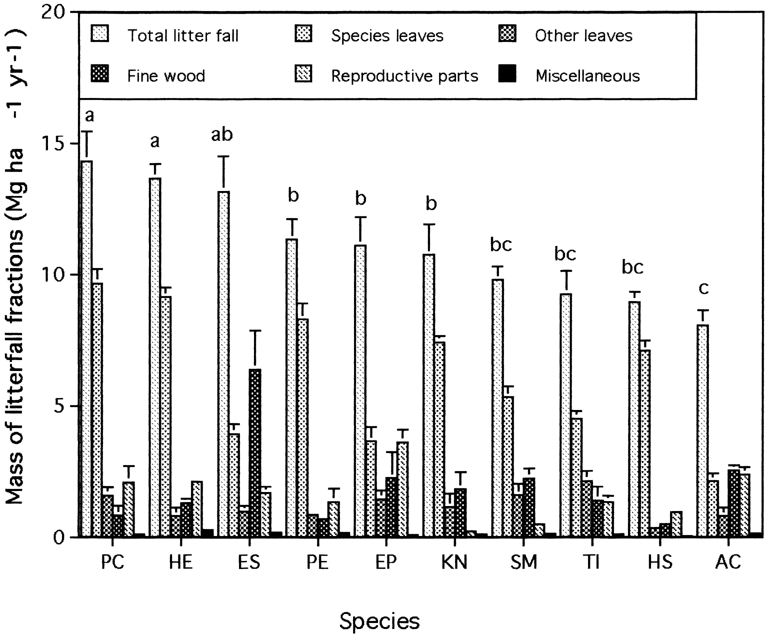

Fig. 3. Mass of total litterfall and litter fractions of ten tropical plantations species in the Luquillo Experimental Forest during the year studied. Species are ranked according to decreasing total litterfall mass. Vertical lines represent one standard error of the mean. Letters indicate significant differences at $p\leq 0.05$ (FPLSD) among means for total litterfall. ($n=6$). *Pinus caribaea* var. *hondurensis*, HE=*Hibiscus elatus*, ES=*Eucalyptus saligna*, PE=*Pinus elliottii* var. *densa*, EP=*Eucalyptus* cf. *patentinervis*, KN=*Khaya nyasica*, SM = *Swietenia macrophylla*, Tl=*Terminalia ivorensis*, HS=*Hernandia sonora*, and AC=*Anthocephalus chinensis*.

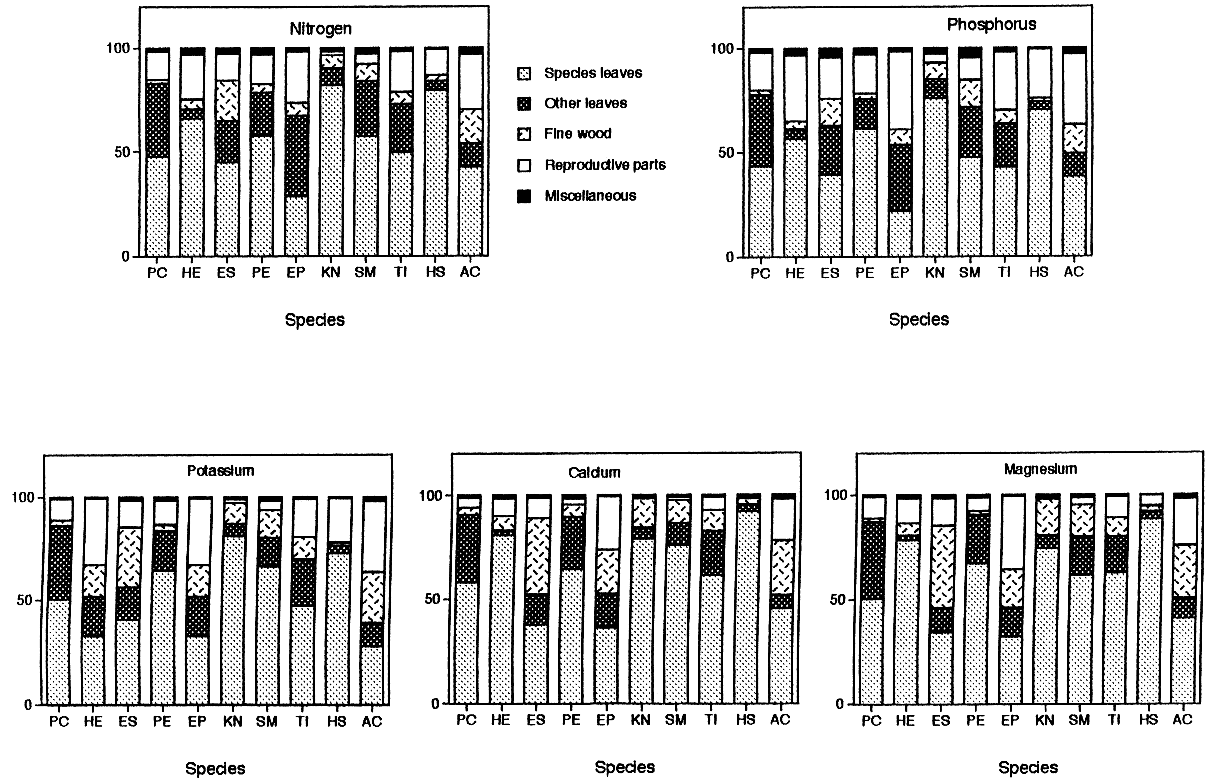

Fig. 4. Nutrient inputs of litter fractions as a percentage of the same element input in total litterfall from ten tropical tree species grown under plantation conditions in the Luquillo Experimental Forest Arboretum. Species are ranked in order of decreasing total litterfall mass. *Pinus caribaea* var. *hondurensis*, HE=*Hibiscus elatus*, ES=*Eucalyptus saligna*, PE=*Pinus elliottii* var. *densa*, EP=*Eucalyptus* cf. *patentinervis*, KN=*khaya nyasica* SM=*Swietenia macrophylla*, Tl=*Terminaliaivorensis*, HS=*Hernandia sonora*, and AC=*Anthocephalus chinensis*.

fraction of *E. saligna* was more important, mass wise, than the species leaves fraction, 48% vs. 30%, respectively (Fig. 4). Most of the fine wood fraction was mainly bark which in this species is sloughed off. In *A. chinensis* and *E. patentinervis* the reproductive parts fraction was similar to the litter input of the species leaves (32% of total). The miscellaneous fraction was less than 2% for all species studied.

6.2. *Nutrient quality of litterfall*

Nutrient concentration generally followed the pattern miscellaneous >other leaves>reproductive parts>species leaves>total litter>fine wood (Table 1). Mass-weighted concentration of N, P, K, Ca, and Mg of total litterfall varied according to stand. *Hernandia sonora* had the highest concentration of N and P with intermediate values for the other elements studied. *Hibiscus elatus* had the highest values for K and Mg. *Pinus caribaea* and *P. elliottii* had consistently lower concentrations for all the nutrients studied.

The nutrient concentrations from species leaves follow the same pattern described above, with a few exceptions. Leaves of *E. saligna*, *S. macrophylla*, *T. ivorensis*, *H. sonora*, and *A. chinensis* were considerably higher in Ca. Leaves from other species had higher N, P, K, Ca, and Mg concentrations than the species leaf litter from *P. caribaea*, *E. saligna*, *P. elliottii*, and *E. patentinervis* stands. Species leaves of the *S. macrophylla* stand also had lower N and P concentrations than other leaves that fell in the stand, but higher Ca and Mg.

Fine wood litter had consistently lower N, P, and K concentrations than either total litter or species leaves (Table 1). Fine wood from *H. elatus*, *E. patentinervis*, and *T. ivorensis* had higher Ca concentrations than the

Table 1
Mass-weighted nutrient concentration (mg g^{-1} dry mass) of total litterfall and its fractions in ten tropical tree species grown under plantation conditions in the Luquillo Experimental Forest

	PC	HE	ES	PE	EP	KN	SM	Tl	HS	AC
Total Litter										
N	5.18	9.84	5.06	4.35	5.52	8.17	7.58	10.13	16.3	6.85
P	0.28	0.56	0.19	0.25	0.25	0.29	0.28	0.44	0.84	0.41
K	2.41	7.23	2.82	2.02	3.52	3.60	4.40	4.82	5.02	3.78
Ca	3.80	11.37	2.82	3.35	8.67	6.33	11.36	11.74	7.83	7.07
Mg	1.72	6.22	2.45	1.79	3.25	2.15	2.86	4.13	4.62	2.94
Species leaves										
N	3.55	9.67	7.38	3.43	4.76	9.58	8.01	10.06	16.40	10.92
P	0.17	0.47	0.24	0.20	0.17	0.31	0.24	0.38	0.74	0.58
K	1.76	7.08	3.83	1.76	3.55	4.14	5.40	4.52	4.58	3.89
Ca	3.26	13.70	8.17	2.93	9.60	7.09	15.85	14.50	9.12	12.12
Mg	1.24	7.27	2.69	1.63	3.17	2.24	3.24	5.19	5.15	4.51
Other leaves										
N	17.00	7.61	14.05	12.11	16.34	6.75	12.14	10.21	17.08	7.61
P	0.88	0.47	0.62	0.47	0.60	0.28	0.37	0.40	0.78	0.47
K	7.98	4.33	5.90	5.26	4.68	2.31	3.49	4.67	4.59	4.33
Ca	11.19	4.42	14.38	11.31	10.71	3.52	7.54	1.79	6.66	4.42
Mg	5.91	2.75	3.89	5.77	3.05	5.77	3.09	3.13	4.45	2.75
Fine wood										
N	1.89	5.10	2.10	2.89	1.65	3.20	2.77	4.25	7.54	3.53
P	0.11	0.24	0.05	0.12	0.09	0.14	0.17	0.21	0.24	0.18
K	1.20	3.07	1.69	1.02	2.78	2.26	2.62	3.82	1.43	2.89
Ca	2.34	8.66	5.64	3.36	8.87	5.65	5.46	8.50	3.71	5.82
Mg	0.63	3.80	2.09	0.52	3.20	2.44	1.95	2.69	2.06	2.35
Reproductive parts										
N	4.70	13.74	5.02	5.25	4.24	7.03	8.02	13.69	19.47	6.17
P	0.35	1.14	0.29	0.39	0.29	0.63	0.64	0.86	1.89	0.48
K	1.64	11.69	2.87	1.99	3.51	3.16	4.39	6.04	10.30	4.40
Ca	1.20	6.01	4.98	0.78	6.86	1.43	3.44	5.15	0.91	4.80
Mg	1.15	4.81	2.40	0.90	3.46	1.09	2.06	2.89	2.18	2.24
Miscellaneous										
N	11.16	15.29	10.04	8.82	9.73	12.91	15.23	12.92	26.87	12.16
P	0.73	0.93	0.56	0.54	0.50	0.73	0.95	0.40	1.51	0.72
K	3.50	5.98	3.65	2.28	3.21	3.87	5.03	2.41	6.78	4.44
Ca	5.13	8.85	6.59	3.72	5.92	6.78	7.29	4.46	7.53	6.99
Mg	2.20	4.39	2.79	1.68	2.81	2.18	2.99	1.65	4.02	2.94

Species are ranked in order of decreasing total litterfall mass.

PC: *Pinus caribaea* var. *hondurensis*, HE: *Hibiscus elatus*, ES: *Eucalyptus saligna*, PE: *Pinus elliottii* var. *densa*, EP: *Eucalyptus* cf. *patentinervis*, KN: *Khaya nyasica*, SM: *Swietenia macrophylla*, Tl: *Terminalia ivorensis*, HS: *Hernandia sonora*, and AC: *Anthocephalus chinensis*.

fine wood from other species. *Pinus caribaea*, *P. elliottii* and *H. sonora* had the lower Ca concentrations in the fine wood fraction, especially *P. caribaea.* The reproductive parts of *H. elatus*, *T. ivorensis*, and *H. sonora* had consistently higher concentrations of N, P, and K than the leaves from the same species. Calcium concentrations were always lower than for the species leaves. Magnesium was either lower or similar.

Nitrogen and P concentrations in the miscellaneous fraction were always higher than the species leaves fraction. The exception was *T. ivorensis* where P was similar in both fractions.

Table 2
Mass, Mg ha^{-1} year^{-1}, and nutrient return to the forest floor, in kg ha^{-1} year^{-1}, from total litterfall in ten tropical tree species grown under plantation conditions in the Luquillo Experimental Forest

	PC	HE	ES	PE	EP	KN	SM	TI	HS	AC
Mass	14.3 a	13.7 a	13.2 ab	11.4 b	11.1 b	10.8 b	9.8 bc	9.2 bc	9.0 bc	8.1 c
N	74.2 cd	134.5 a	66.6 c	49.4 e	61.4 de	87.9 bc	74.3 cd	93.7 b	146.0 a	55.3 de
P	4.0 b	7.7 a	2.5 d	2.8 c	2.8 cd	3.1 c	2.7 c	4.1 b	7.5 a	3.3 bc
K	34.5 c	98.9 a	37.1 bc	22.9 d	39.2 bc	38.8 bc	43.1 b	44.6 b	45.0 b	30.5 cd
Ca	54.4 de	155.5 a	91.9 c	38.0 e	96.4 bc	68.1 d	111.4 b	108.7 bc	70.2 d	57.1 d
Mg	24.6 d	85.2 a	32.3 c	20.3 d	36.1 bc	23.2 d	28.0 cd	38.3 bc	41.4 b	23.7 b

Values are means of six baskets per stand.

Letters in each row indicate significant differences among stands (FPLSD, p=0.05). Species are ranked in descending order according to total litterfall mass.

PC: *Pinus caribaea* var. *hondurensis*, HE: *Hibiscus elatus*, ES: *Eucalyptus saligna*, PE: *Pinus elliottii* var. *densa*, EP: *Eucalyptus* cf. *patentinervis*, KN: *Khaya nyasica*, SM: *Swietenia macrophylla*, Tl: *Terminalia ivorensis*, HS: *Hernandia sonora*, and AC: *Anthocephalus chinensis*.

6.3. Annual nutrient return from total litterfall

The rank order of the ten stands, according to amount of nutrients returned to the forest floor, is different from the order when rank is according to total mass of litterfall (Table 2). Returns of N, P, K, Ca, and Mg from *H. elatus* were two–three times higher than for *P. caribaea*, which had a similar amount of total litterfall mass. *Hernandia sonora* returned twice the amount of N and P to the forest floor than *P. caribaea*, and similar amount as *H. elatus*. In the case of *H. sonora*, the higher nutrient return was a result of higher concentrations of N and P. For *H. elatus*, it was the significantly higher mass coupled with an intermediate nutrient concentration, which in the end provided the same nutrient return to the forest floor as *H. sonora*. *Pinus elliottii* and *A. chinensis* had the lowest returns of K to the forest floor.

The ten species can be grouped into three levels of Ca return to the forest floor. *Hibiscus elatus* had the significantly higher rate of return (155.5 kg ha^{-1} year^{-1}); *E. patentinervis*, *S. macrophylla*, and *T. ivorensis* had intermediate rates (ranging from 91.9 to 111.4 kg ha^{-1} year^{-1}), while *P. caribaea*, *P. elliottii*, *K. nyasica*, *H. sonora*, and *A. chinensis* had the lowest returns to the forest floor (range was from 38 to 70.2 kg ha^{-1} year^{-1}). *Pinus elliottii* had the lowest nutrient return of all species (38 kg ha^{-1} year^{-1}). Magnesium return to the forest floor had the same pattern as Ca.

6.4. Annual nutrient return by the different litter fractions

Differences in nutrient concentrations among the litter fractions accounted for nutrient amounts not following the pattern established by their respective mass (Fig. 4). The highest amount of N, P, K, Ca, and Mg return was in the species leaves fraction. Nitrogen return from species leaves ranged from 29% of the total for *E. patentinervis* to 80% of the total for *H. sonora* and *K. nyasica*. *Hernandia sonora* and *K. nyasica* leaves had the highest N and P returns. Leaves of *Khaya nyasica* always had significantly higher K and Ca return than all the other species. In the case of *P. caribaea*, the other leaves fraction accounted for more than 30% of the return of all nutrients measured. As for *E. patentinervis*, the other leaves fraction was important for N and P. The fine wood fraction in *E. saligna* returned similar amount of Ca and Mg as species leaves to the forest floor (Fig. 4). In this case it was the sloughed bark rather than small branches that accounted for the input. For *A. chinensis*, the fine wood fraction returned an average of 25% of the total flux of K, Ca, and Mg to the forest floor. For the other species, the return of all nutrients in the fine wood fraction ranged between 2% and 20% of the total.

Nutrient return from the reproductive part's fraction was as important as the species leaves fraction in *A. chinensis* and *E. patentinervis* (Fig. 4). In the case of *H. elatus* and *A. chinensis*, P return from the

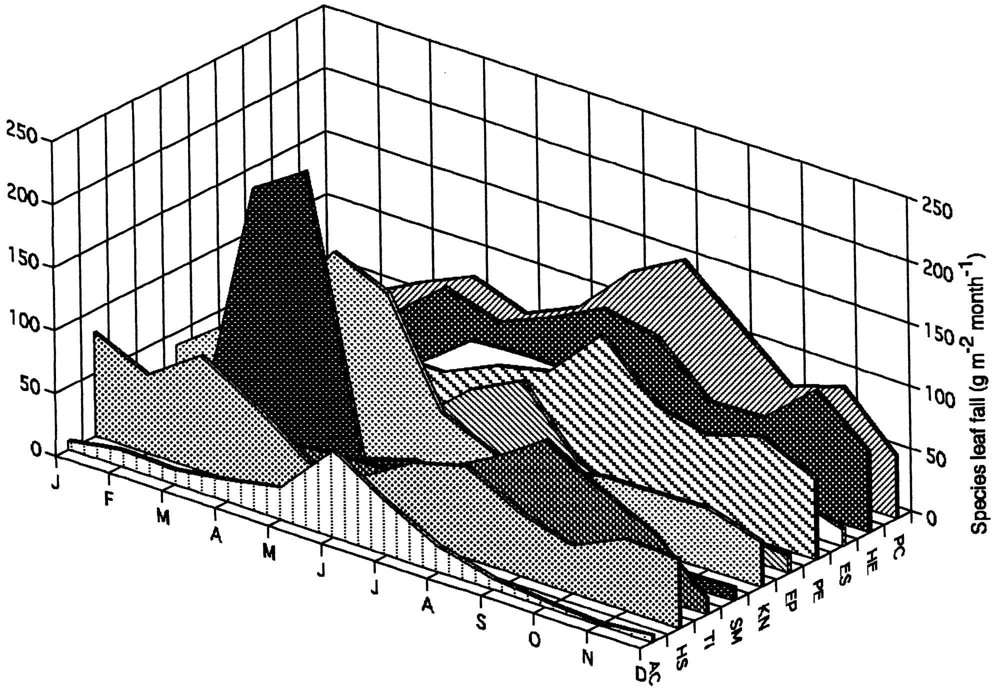

Fig. 5. Species leaf fall input throughout the year studied of ten tropical tree species from the Luquillo Experimental Forest Arboretum. *Pinus carbaea* var. *densa*, EP=*Eucalyptus* cf. *patentinervis*, KN=*Khaya nyasica*, SM=*Swietenia macrophylla*, Tl=*Terminalia ivorensis*, HS=*Hernandia sonora*, and AC=*Anthocephalus chinensis*.

reproductive parts's fraction accounted for 32% and 34% of the total return, respectively. The nutrient return in the miscellaneous fraction accounted for 1–4% of the total return for all nutrients.

6.5. Mass and nutrient dynamics of species leaves

The pattern of leaf fall varied according to the species considered. Strong to mild seasonality was observed in all stands, however, timing and intensity of maximum peak fall varied among species (Fig. 5). *Swietenia macrophylla* peaked between March and April, while *K. nyasica* peaked between April and May. *Eucalyptus saligna* peaked from May to July, *A. chinensis* in June, and *E. patentinervis* and *H. elatus* in July. *Pinus caribaea* and *P. elliottii* peaked in August, while *T, ivorensis* peaked in September. *Hernandia sonora* had two peaks of maximum leaf fall, the first in March and the second in August.

Minimum concentrations of N and P were measured in all species during periods of maximum peak fall (Fig. 6). In *H. sonora*, minimum concentrations were found at the second period of maximum leaf fall between July and September (Fig. 6(c)).

Leaf fall seemed to be triggered by different environmental factors (Table 3). We did a simple regression–correlation analysis between monthly leaf fall and either number of dry days per month, daylight duration, and average maximum of minimum air temperature of the month. Leaf fall of *H. sonora*, *S. macrophylla*, and *K. nyasica* were positively correlated with increased number of dry days (r=0.71, 0.64, and 0.62, respectively). On the other hand, leaf fall of *A. chinensis*, *E. saligna*, and *E. patentinervis* significantly correlated with increased daylight duration (r=0.79, 0.75, and 0.80, respectively). Leaf fall of *P. caribaea*, *T. ivorensis*, *P. elliottii* and *H. elatus* was significantly correlated with changes in minimum air temperature (r=0.82, 0.76, 0.71 and 0.60, respectively).

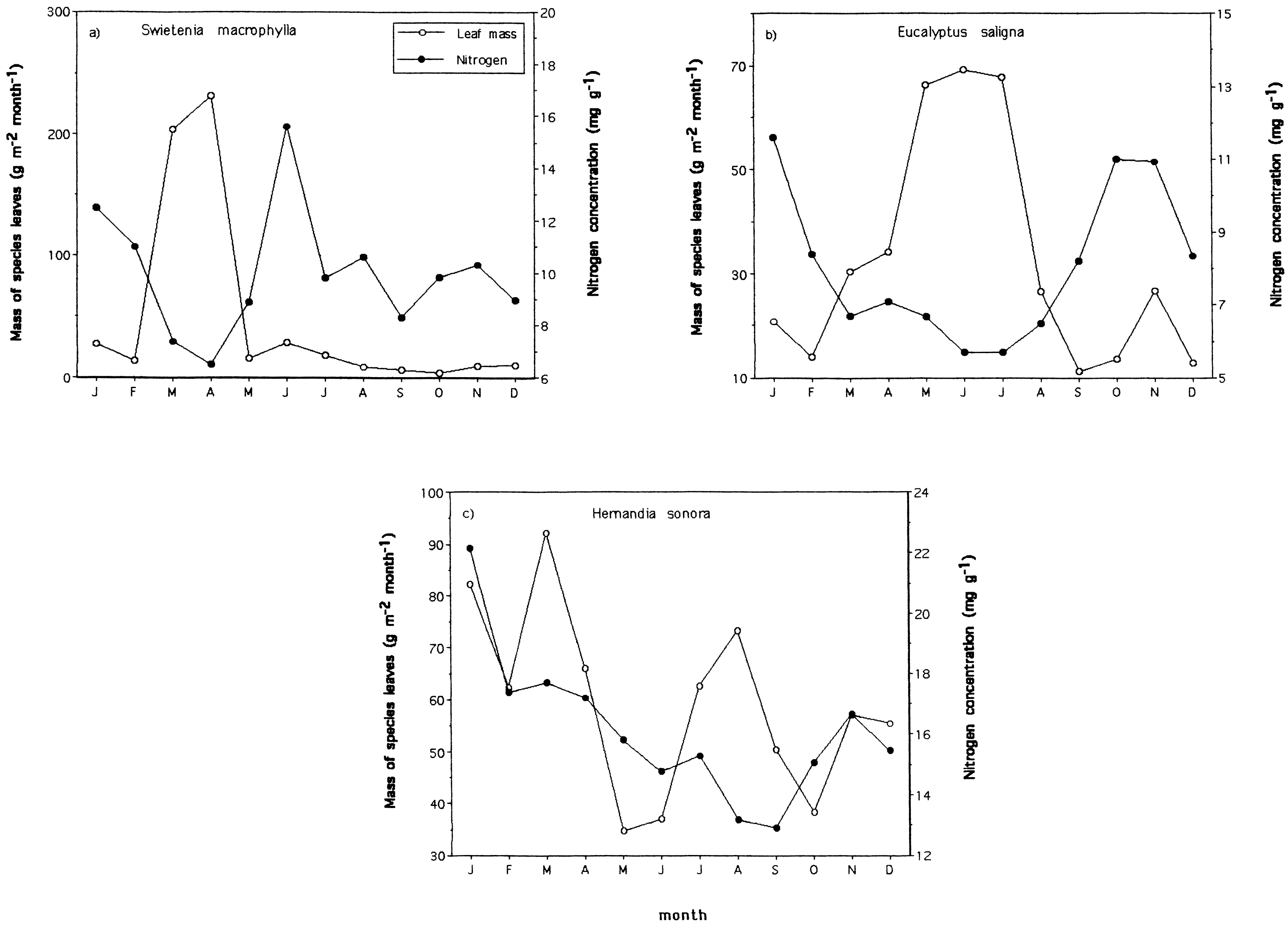

Fig. 6. Annual pattern of mass and nitrogen concentrations of the species leaves fraction of litterfall in three plantation tropical tree species in the Luquillo Experimental Forest Arboretum. The three species, *Swietenia macrophylla*, *Eucalyptus saligna* and *Hernandia sonora*, illustrate the different patterns of nitrogen concentrations observed in the ten species that were studied.

Table 3
Regression equations and correlation coefficients between either (a) amount of dry days, (b) daylight duration (hours), or (c) minimum air temperature (°C), and mass of species leaves (g m^{-2} $month^{-1}$) of the ten tree species grown under plantation conditions in the Luquillo Experimental Forest

Species	Equation	*r*
HS	$y = 3.238(\text{dry}) + 22.891$	0.71^{**}
SM	$y = 13.039(\text{dry}) - 98.66$	0.64^{*}
KN	$y = 5.658(\text{dry}) - 4.869$	0.62^{*}
ES	$y = 23.248(\text{daylight duration}) - 249.429$	0.80^{**}
AC	$y = 20.159(\text{daylight duration}) - 225.841$	0.79^{**}
EP	$y = 20.015(\text{daylight duration}) - 235.725$	0.75^{**}
PC	$y = 21.925(\text{minimum temperature}) - 367.23$	0.82^{**}
Tl	$y = 17.349(\text{minimum temperature}) - 316.95$	0.76^{**}
PE	$y = 12.967(\text{minimum temperature}) - 197.53$	0.71^{*}
HE	$y = 9.654(\text{minimum temperature}) - 122.46$	0.60^{*}

* denotes significance at $p<0.05$, ** denotes significance at $p<0.01$.

HS: *Hernandia sonora*, SM: *Swietenia macrophylla*, KN: *Khaya nyasica*, ES: *Eucalyptus saligna*, AC: *Anthocephalus chinensis*, EP: *Eucalyptus* cf. *patentinervis*, PC: *Pinus caribaea* var. *hondurensis*, Tl: *Terminalia ivorensis*, PE: *Pinus elliottii* var. *densa*, and HE: *Hibiscus elatus*.

6.6. Nutrient availability and efficiency of nutrient utilization

We estimated N and P resorption per species two ways: using the average concentration of the nutrient throughout the sampling year, and the minimum concentration of the nutrient during peak fall. In this way we were able to assess the effect if senescence played an important role in maximizing resorption in the species studied. Based on average values, P resorption or retranslocation was either higher than or similar to N resorption in all species, with the exception of *S. macrophylla* and especially *P.elliottii* which retranslocated higher amount of N than P (Fig. 7(a)). There are three groups that can be separated according to N resorption: the ones with more than 70% resorption, the ones between 40% and 65%, and the one that retranslocate less than 30%.

There were differences in the estimates of retranslocation based on the minimum concentration values in leaf fall (Fig. 7(b)). Nitrogen and P resorption increased considerably in all species; the exception was *K. nyasica* where P resorption was higher than N resorption. The spread of values, however, is completely different from the one observed in Fig. 7(a). There is a clumped distribution where seven of the ten species retranslocate more than 70% of N and P, whereas using average values there were only three species with such a high retranslocation of both N and P. Interpretation of degree of resorption as an index of nutrient limitation could be misleading if only mean resorption values are used, as the same weight is placed on periods with low leaf fall but relatively higher nutrient concentration and periods of higher leaf fall with truly senesced leaves.

Normally, biweekly measures of leaf nutrient concentration are not available, and ecologists use mean concentration values to estimate retranslocation rates. Maximum nitrogen retranslocation can be underestimated, depending on each species, ranging from 0% to 14%, with a mean of 7.5% when mean concentration values are used. Maximum P resorption can be underestimated on an average of 13%, from 3% to 22%. This difference between N and P maximum resorption could indicate a stronger limitation of P than N from senescent tissues. The wider range of P retranslocation values are also reflected in the P/N ratios of leaves of the species studied (Fig. 8). If the mean concentrations are used, P/N ratios tend to be higher than when estimated based on truly senescent leaves, however, the wide range of variation is maintained.

An index of efficiency of nutrient use (Vitousek, 1982) is the ratio of leaf fall to amount of either N or P return to the forest floor. This index is a good indicator of the amount of nutrients required in storage to support a unit of leaf fall mass. Higher ratios indicate higher nutrient use efficiency because more mass is transferred to the unit floor per unit nutrient returned.

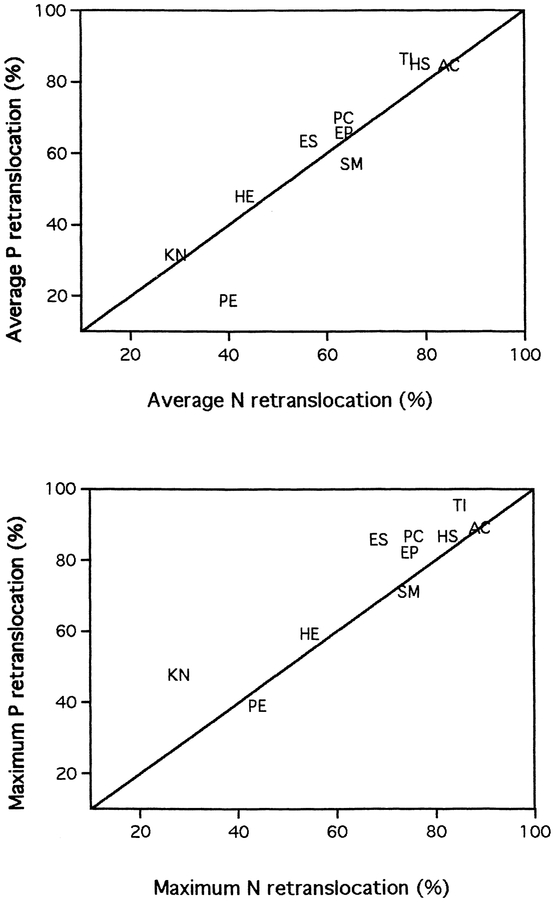

Fig. 7. Estimates of mean and maximum retranslocation values (expressed as per cent of element of mature leaf tissue) for nitrogen (a) and phosphorus (b) for the ten tropical tree species grown in plantations at the Luquillo Experimental Forest Arboretum. Mean retranslocation is based on the N/Ca or P/Ca ratios of the average concentrations (on a mg g^{-1} basis) of leaf fall mass throughout the year (59 observations) and the same ratios of live fully expanded adult leaves at the beginning of the sampling period. Maximum retranslocation is based on the minimum N/Ca and P/Ca of leaf mass at the peak of leaf fall during the dampling period. *Pinus caribaea* var. *hondurensis*, HE=*Hibiscus elatus*, ES=*Eucalyptus saligna*, PE=*Pinus elliottii* var. *dens*, EP=*Eucalyptus* cf. *patentinervis*, KN=*Khaya nyasica*, SM=*Swietenia macrophylla*, Tl=*Terminalia ivorensis*, HS=*Hernandia sonora*, and AC=*Anthocephalus chinensis*.

There were differences in the efficiency of N or P utilization among the ten species when this index was used (Fig. 9). We found a wider range of P use efficiency in the species studied when compared to the efficiency of N utilization. *Pinus caribaea*, *P. elliottii*, and *E. patentinervis* had higher N use efficiency than the other seven species which appeared to fluctuate around values of 100. These differences seem to indicate that P utilization depends on the different phosphorus requirements of the species, rather than P availability Per se, because all species were grown under the same climatic and edaphic conditions.

7. Discussion and conclusions

The study of the Arboretum had the advantage of having the stands under a known land use for a set time (26-year old plantation growth), proximity of stands to each other, and similarity of edaphic and climatic conditions. Lacking replication by not having more stands of each species limits the breadth of statistical inferences between and among these ten stands. Also, having only 1 year of results, when the rainfall was nearly 20% more than average rainfall in the area, limits the possible generalization about average flux of carbon and nutrients to the system. This, however, does not subtract any merit to the study, as long term ecological research shows that 'average' is a relative term which depends on the length of the period studied. Years with higher rainfall are common and relevant in the temporal continuum of the ecosystem. We feel that the information obtained allows us to detect (a) relationships between litter and nutrient fluxes among contrasting species stands, (b) species-specific effects on nutrient use efficiency and maintenance of nutrient reservoirs within the plant via resorption, and (c) the possible phenotypic responses to different environmental cues.

The proximity of other plantations caused leaves from one to fall on baskets located in another. We took the precaution of separating and accounting this input by identifying the leaf litter to species. In addition, this flux was small both in terms of litter input (results) and accumulation as measured by Lugo et al. (1990) who found that less than 20% of the accumulated litter came from understory vegetation and surrounding plantation stands.

Total litterfall mass for all stands falls within the high range of values for moist tropical forests (Vitousek and Sanford, 1986). Our average rate of litterfall is higher than the one reported by Vitousek and Sanford (1986) (11.1 Mg ha^{-1} year^{-1} vs.

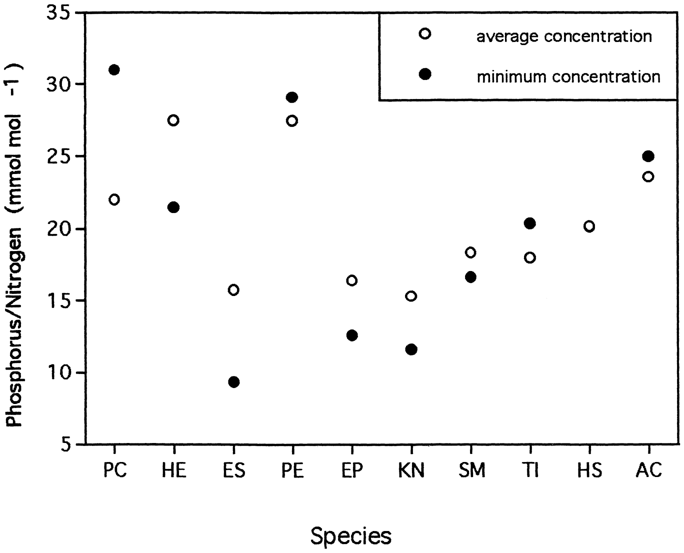

Fig. 8. Phosphorus/nitrogen (P/N) ratios, on a mmol mol^{-1} basis, of the species leaf fall of ten tropical tree plantations in the Luquillo Experimental Forest. *Pinus caribaea* var. *hondurensis*, HE=*Hibiscus elatus*, ES=*Eucalyptus saligna*, PE=*Pinus elliottii* var. *densa*, EP=*Eucalyptus* cf. *patentinervis*, KN=*Khaya nyasica*, SM=*Swietenia macrophylla*, Tl=*Terminalia ivorensis*, HS=*Hernandia sonora*, and AC=*Anthocephalus chinensis*.

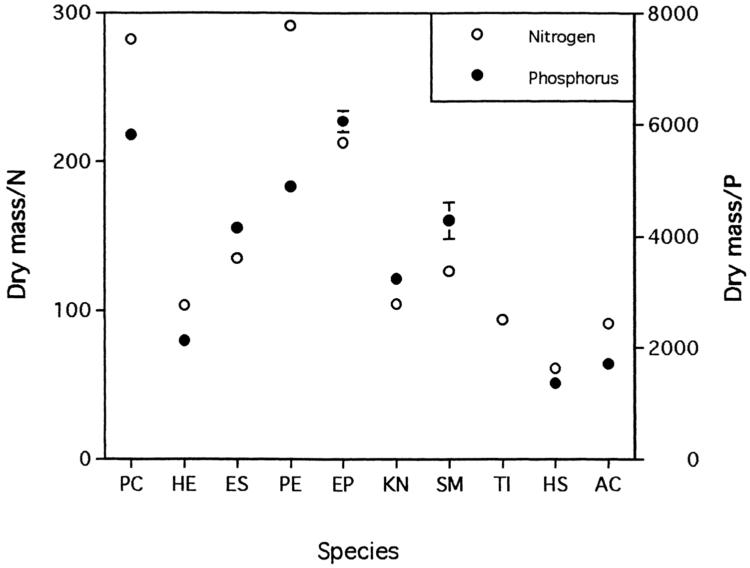

Fig. 9. Efficiency of nitrogen or phosphorus utilization (Vitousek, 1982) of ten tropical plantation species. Vertical lines are one standard error of the mean (n=6). *Pinus caribaea* var. *hondurensis*, HE=*Hibiscus elatus*, ES=*Eucalyptus saligna*, PE=*Pinus elliottii* var. *densa*, EP=*Eucalyptus* cf. *patentinervis*, KN=*Khaya nyasica*, SM=*Swietenia macrophylla*, Tl=*Terminalia ivorensis*, HS=*Hernandia sonora*, and AC=*Anthocephalus chinensis*.

10.4 Mg ha^{-1} year^{-1}) and three of our species, i.e., *P. caribaea*, *H. elatus*, and *E. saligna*, exceed the highest value reported by them. This underscores the high production of plantations relative to natural forests (Lugo, 1992). Cuevas et al. (1991) corrected for belowground productivity and showed that the apparently higher productivity of plantations was due to more allocation of biomass to aboveground wood and not to a greater total biomass production.

The ten species used in this study differed in the amount of littermass and nutrient return to the forest floor under similar environmental conditions reflecting variation in the ecophysiological response. Nutrient return via litterfall can be regulated by the combination of high mass and intermediate or low nutrient concentrations or low mass and high nutrient concentration. Such was the case here. *Hibiscus elatus* is an example of the first case, while *H. sonora* is an example of the second. *Pinus caribaea*, on the other hand, is an example of a third situation where high litterfall, coupled with low nutrient concentration, yield a low nutrient return. These different rates and amounts of nutrient return to the forest floor have a measurable impact on soil nutrient characteristics, especially in the surface layers (Lugo et al., 1990). In fact, there is a very significant and negative correlation between quality of species leaves fraction, based on the C/N and C/P ratio, and both soil N concentration and bicarbonate extractable P in the soil of these stands (Fig. 10).

The phosphorus to nitrogen (P/N) ratio of a plant leaf can be related to the relative demand of one or both elements (Penning de Vries and Krul, 1980). In general, P/N ratios in litterfall are always lower than in living canopy leaves due to the higher retranslocation of P, as compared to N, before leaf shedding (Medina, 1984; Cuevas and Medina, 1991; Medina and Cuevas, 1994). Vitousek (1982) proposed that mass/nutrient ratios can be used as index of resource availability at the ecosystem level. Medina and Cuevas (1994) found that P/N ratios are inversely related to P-use efficiency as measured by the litterfall mass/P ratio at the ecosystem level. We find that the latter relationship does not hold at the species level. Although all species appear to internally regulate both P and N, the degree of regulation is apparently determined by specific nutrient requirements, in this case phosphorus.

The calculation of maximum resorption values, as compared to average ones, underscores the species-specific maximum capability for nutrient retranslocation, an important ecological adaptation. Based on N resorption, the species can be separated into three groups, the ones that mostly depend on physiological cycling, a group which cycles both internally and externally (via the litter-decomposition-nutrient uptake pathway), and the species which depend mostly on external cycling. These differences point towards species-specific mechanisms of maintenance of nutrient reservoirs and effective nutrient cycling.

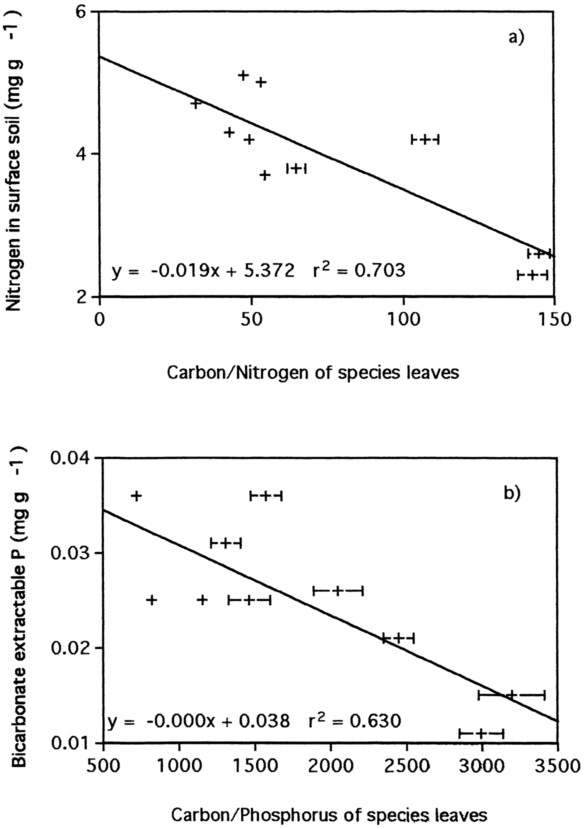

Fig. 10. Relationship between quality of leaf fall (based on C/N and C/P ratios) and availability of (a) nitrogen and (b) phosphorus in surface soil layer of the ten plantation tree species studied in the Luquillo Experimental Forest Arboretum.

Variation in retranslocation values throughout the year, as expressed by the differences between the average and the maximum retranslocation values, in the species leaves fraction of all the species studied seem also to indicate that other environmental factors, such as heavy winds of the physical effects of heavy rains can force non-senesced leaves to break and fall to the forest floor. This higher quality material, although not very much in quantity, can provide a small pulse of available nutrients to the decomposing community and the plants. The same holds true for other high nutrient but low mass fractions of litterfall such as reproductive parts and miscellaneous materials.

When a climatic factor, such as strongly seasonal water availability, is the principal constraint in an ecosystem, plants will mainly respond to water stress (Frankie et al., 1974; Medina, 1983; Reich and Borchert, 1984; Martínez-Yrizar, 1995 among others). However, in tropical systems without prevalent or strongly seasoal water limitations, which we can consider to be our case here, spatial and temporal heterogeneity of mass of leaf litter on the forest floor can result from the rate of fall and decomposition of the falling material (Cuevas and Medina, 1988), and by the diverse responses of species to different environmental cues (Alvin and Alvin, 1978; Williams-Linera and Tolome, 1996).

Since leaves account as a major component of total litterfall, the general pattern of litterfall will depend mostly on factors responsible for leaf senescence and abscission. Leaf fall seems to be triggered by reduced water availability, brought about by increased number of dry days even in months with rainfall higher than 150 mm, in two of the deciduous species studied, *S. macrophylla* and *K. nyasica*, and also in *H. sonora*, an evergreen. In the case of our study year the high amount of rainfall between January and April resulted from single high rainfall events rather than continuous rain throughout the month. So it is not the total amount of water that is received but its distribution to which plants physiologically respond to. Our results are in accordance with Cuevas and Medina (1986) and Cuevas et al. (1991) who found the same relationship in systems growing in highly humid non-seasonal conditions.

The other plantation species responded more to small but continuous increase or decrease in daylight, either directly or indirectly via changes in minimum air temperature throughout the year. Changes in photoperiodicity have been proven to exert a response in flowering and bud break in plants. Njoku (1963, 1964) demonstrated that there was a significant effect of daylength on bud dormancy. Williams-Linera and Tolome (1996) found that there were differences in the tree's response to minimum and maximum temperature depending on phytogeographical origin of the species: holarctic species had a negative correlation between leaf fall and precipitation and minimum temperature, whereas tropical species had a significant positive correlation with maximum temperature. In our case out of the nine tropical species studied, six responded to changes in either photoperiod or minimum temperatures, indicating that even under tropical provenance, there are species-specific responses to a range of environmental cues.

While most attention is usually placed on the leaf fraction because of its dominance of the literfall process, our results suggest that other litterfall fractions can be very important both in terms of magnitude of flux (bark in *E. saligan*; reproductive parts in *E. patentinervis*, *T. ivorensis*, *H. sonora*, and *A. chinensis*), and the quality of inputs (fine wood of *H. sonora*; miscellaneous fraction in all stands; reproductive parts in *H. elatus*, *T. ivorensis*, and *H. sonora*). The wide range in litter quality has implications to the speed of use and availability to litter and soil consumers and to the overall function of the plantation system. Clearly, some high quality fractions are available much quicker to consumers and could prime the decomposition process, thus accelerating the use of other lower quality litter fractions.

The other species leaves fraction show greater nutrient concentration (and in five of the cases lower N or P use efficiency) than plantation species. Same results were found by Lugo (1992) in a comparative study of two species of tree plantations (*P. caribaea* and *S. macrophylla*) and secondary forests of similar age. These two species were included in our study and the result were confirmed with the difference being greatest in *Pinus*. However, we also observed the pattern with other plantation species as well.

Because of the greater nutrient concentration we consider that most of the other species leaves fractions comes from plants in the understory.

The higher nutrient concentrations in understory litter markedly increase its percentage contribution to the total nutrients in litterfall (Gosz, 1984). For this reason we can not rule out the importance of the other leaves fraction in plantation management as it is definitely an added resource, either via understory inputs or advective inputs from adjacent stands.

Individual plantation species are ranked differently in terms of their capacity to return mass, specific nutrients, or their efficiency of use. The species that return the most mass are not necessarily the ones that return the most P, N, or cations. Moreover, species can adjust their performance though differences in retranslocation rates before leaf fall. Because all species were growing under similar conditions, our results highlight the importance of understanding species performance relative to nutrient and mass metabolism before they are planted. Species such as *P. caribaea*, *P. elliottii*, *E. patentinervis* and *E. saligan*, can produce large amounts of Organic matter with low use of nutrients, especially P, a strategy that adapts them to nutrient poor soils. others, like *H. elatus*, *T. ivorensis*, and *H. sonora*, produce less organic material and return large quantities of nutrients, a characteristic that adapts them to nutrient rich soils, but not necessarily to nutrient poor ones.

Our study provides evidence that species' selection can make a difference in the management strategies proposed to ensure efficient use of available resources and improvement of ecosystem fertility. We have also seen that species differences influence rate and timing of nutrient return to the forest floor. Therefore, the nutrient recycling characteristics of a species are an important selection criteria when evaluating suitability to particular environmental conditions.

Ewel et al. (1991) found that similar soil-nutrient dynamics can be achieved by both successional vegetation and human-built mimics of that vegetation. Based on the differences of nutrient resources use and returns, we can create structures to establish and maintain nutrient pools within human-designed ecosystems, or human-directed successional situations. Species selection should be determined based on effectiveness of resource utilization and degree of nutrient limitation. The selection of foster species, i.e., those that improve either water or nutrient conditions within the stand, for restoration projects, should be based on this criteria, thus assuring faster ecosystem recovery.

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