

## Above- and belowground organic matter storage and production in a tropical pine plantation and a paired broadleaf secondary forest

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### Abstract

The distribution of tree biomass and the allocation of organic matter production were measured in an 11-yr-old *Pinus caribaea* plantation and a paired broadleaf secondary forest growing under the same climatic conditions. The pine plantation had significantly more mass aboveground than the secondary forest (94.9 vs 35.6 t ha<sup>-1</sup> for biomass and 10.5 vs 5.0 t ha<sup>-1</sup> for litter), whereas the secondary forest had significantly more fine roots ( $\leq 2$  mm diameter) than the pine plantation (10.5 and 1.0 t ha<sup>-1</sup>, respectively). Standing stock of dead fine roots was higher than aboveground litter in the secondary forest. In contrast, aboveground litter in pine was more than ten times higher than the dead root fraction. Both pine and secondary forests had similar total organic matter productions (19.2 and 19.4 t ha<sup>-1</sup> yr<sup>-1</sup>, respectively) but structural allocation of that production was significantly different between the two forests; 44% of total production was allocated belowground in the secondary forest, whereas 94% was allocated aboveground in pine. The growth strategies represented by fast growth and large structural allocation aboveground, as for pine, and almost half the production allocated belowground, as for the secondary forest, illustrate equally successful, but contrasting growth strategies under the same climate, regardless of soil characteristics. The patterns of accumulation of organic matter in the soil profile indicated contrasting nutrient immobilization and mineralization sites and sources for soil organic matter formation.

### Introduction

Carbon and nutrient fluxes through an ecosystem and the amounts stored in the soil profile are functionally related to the rate and allocation of primary productivity (above- and belowground) and decomposition potential of the organic materials. Forest replacement either by crops, pastures, or monospecific tree plantations can modify (either beneficially or deleteriously) the

dynamics of the regulatory processes for soil organic matter formation and nutrient availability through changes in the microclimate and the quantity and quality of organic matter (Anderson and Flanagan, 1989). The direction of change in organic matter in soils depends upon the previous amount of organic matter as well as the management given afterwards (Juma and MacGill, 1986). In general, reforesting sites of naturally low fertility, or degraded because of over-

use, has beneficial effects on the soil because of increased organic matter and nutrients inputs (McColl and Powers, 1984). These effects are related to the longer time trees protect the soil surface, thus reducing erosion, their larger biomass and nutrient stocks, and their ability for efficient nutrient recycling.

Tree plantations are being established in the tropics to meet an increasing demand for wood products and for environmental protection. Not only are they important sources of timber, but they also have the potential to serve as sinks of atmospheric carbon dioxide (Brown et al., 1986), and can become an important tool for the conservation of tropical forests (Wadsworth, 1983) and the rehabilitation of damaged lands (Lugo, 1988).

Of concern with tropical plantations is the sustainability of multiple rotations of high-yielding species because they may place a high nutrient demand on the soil. The repeated removal of plant nutrients in wood during timber harvesting may result in diminishing tree growth rates in subsequent rotations. Soil degradation caused by nutrient depletion and soil erosion are exacerbated if harvesting is done improperly.

The organic matter content in the soil is determined by the net balance between the rates of above- and belowground organic matter inputs and decomposition, the transfers to soil organic matter pools, and the mineralization rates of this fraction. Proper management practices could guarantee future rotations in nutrient-poor, weathered tropical soils, through an integrated approach for the maintenance of soil fertility (Ingram and Swift, 1989; Swift, 1986). By knowing the relationship between soil biological processes and soil fertility, the responses of plant/soil systems to changing conditions of water, nutrient, and organic inputs can be assessed and manipulated (Swift, 1986).

The specific goal of this study was to determine how a non-native plantation of *Pinus caribaea* may modify processes of nutrient and organic matter cycling and soil organic matter formation relative to a native, naturally regenerating, broadleaf secondary forest of similar age. We compared the quantity, quality, and temporal patterns of above- and belowground mass storages and fluxes and their effect on soil

organic matter formation and fertility in these two contrasting vegetation types. In this paper, we report only on organic matter cycling and its effect on soil organic matter formation.

## Methods

### Study sites

Field studies were conducted in the Luquillo Experimental Forest in Puerto Rico (lat. 18°19'N, long. 65°49'W). Two forest types were studied: a *Pinus caribaea* plantation established in 1976 and a native broadleaf secondary forest. Prior to acquisition by the U.S. Forest Service, both sites had been under agricultural use for several decades. After the land was incorporated into the Luquillo Experimental Forest, part of it was reforested with the pine plantation and the remainder was left to regenerate naturally (the secondary forest). Although the exact age of the secondary forest is unknown, observations (physiognomy, species composition, and size of trees) suggest that it is of similar age (Lugo, in press).

The two forests were adjacent to each other at about 350 m elevation. Both sites had the same aspect (generally southwest). Slopes were less than 5% in the plantation, and were mostly less than 5%, with some areas as much as 15%, in the secondary forest. Previous studies on structure, organic matter dynamics, and nutrient cycling of the forests were conducted between 1980 and 1983 when the sites were 4–7 yr-old (Lugo, in press). Our studies were done between January 1987 and June 1989.

### Climate

The study sites are located within a subtropical wet forest life zone (*sensu* Holdridge, 1967). Although designated as subtropical by Holdridge (who divides the tropics into two latitudinal zones), the area is still within the tropical latitudes. There is no pronounced dry season in the annual pattern of rainfall as all months receive more than 180 mm (Fig. 1a), but a seasonal pattern is exhibited. The driest months occur between January to April with respect to absolute amounts (<280 mm/mo) and the highest

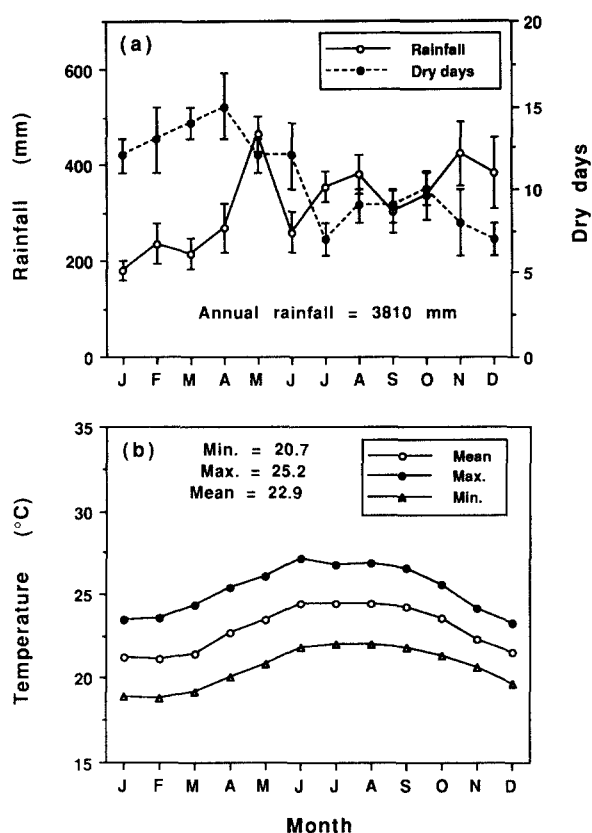


Fig. 1. (a) Mean monthly rainfall and number of dry days ( $\pm 1$  SE) and (b) mean monthly temperatures for the period 1977–1987 for the El Verde Field Station in the Luquillo Experimental Forest, Puerto Rico.

number of dry days per month (12–15 days; a dry day is defined as rainfall  $\leq 1$  mm (Cuevas and Medina, 1986) or when evaporation exceeds precipitation (Heuvelink, 1979)). The wet season extends from July–December when monthly rainfall is higher than 300 mm and the number of dry days is about 7–10/mo. Mean monthly temperatures vary little within the year, ranging from a minimum of 21°C to a high of 25°C (Fig. 1b). Daylight duration varies from 11 hours in December–January to 13 hours during the summer months.

### Soils

The soils of the plantation are classified as a clayey, mixed isothermic tropohumult. The secondary forest site was originally thought to be

located on the same soil type as the plantation (Lugo, in press). However, Sánchez (1989) found that the site is on an old, but well stabilized, landslide, which exposed less weathered soils and contained a diabase intrusion. The soils under the secondary forest, therefore, are most likely younger than those under the plantation.

The two study sites had soils that were similar in bulk density and % sand, but different with respect to % clay and % silt, although the differences were less pronounced in the top 15 cm (Table 1). Parton et al. (1987) have suggested that the potential for soil organic matter accumulation is directly related to the sum of clay and silt for soils of the Great Plains, USA. Lugo et al. (1986) found a similar trend for tropical agricultural soils in Puerto Rico, whereas Brown and Lugo (1990a) found no correlation between soil organic matter content and the clay-plus-silt fraction for soils under tropical forests. The relationship between texture and soil organic matter of tropical soils remains unclear. However, we expect the textural differences between our sites to have little effect on biomass production and allocation, although there is the likelihood that they may influence soil organic matter accumulation.

Despite the textural differences in the soils of the two sites, organic matter, nitrogen (N), and available phosphorus (P) concentrations were similar between the two sites. Concentrations of all other elements measured were higher in the secondary forest for both depths than in the pine plantation, reflecting the differences in age of the soils. An exception was available aluminum (Al) which was higher in the latter. This can be partly explained by the lower pH in the plantation than in the secondary forest (4.5 vs 5.3).

### Study design

Both study sites were 0.25 ha in area (50 m  $\times$  50 m), divided into four 20 m  $\times$  20 m plots with each plot surrounded by a buffer strip. All measurements described below were carried out within these plots. Only two plots were used for the in-growth cylinder study; the other two were used for litter decomposition studies (not presented in this paper), so as to prevent excessive trampling and loss of samples.

Table 1. Physical and chemical characteristics of the top soil layers (0–15, 15–30 cm depth) in a *Pinus caribaea* plantation and paired secondary forest. Sample size = 9, except bulk density where  $n = 18^a$ . Values in parentheses are standard errors of the means (SE) (data from Sánchez, 1989)

	Pine plantation		Secondary forest	
	0–15 cm	15–30 cm	0–15 cm	15–30 cm
Bulk density ( $\text{g cm}^{-3}$ )	0.90(0.03)	0.93(0.01)	0.85(0.03)	0.84(0.03)
Sand (%)	24(2)	18(4)	27(3)	22(2)
Silt (%)	33(1)	29(1)	41(2)	40(1)
Clay (%)	43(3)	53(4)	32(3)	38(3)
Organic matter (%)	3.8(0.3)	2.2(0.2)	4.6(0.6)	2.0(0.5)
pH ( $\text{H}_2\text{O}$ )	4.5	4.5	5.3	5.4
Nitrogen (%)	0.22(0.01)	0.14(0.01)	0.23(0.04)	0.11(0.4)
Phosphorus ( $\mu\text{g g}^{-1}$ )	5.4(0.7)	2.2(1.4)	6.2(1.7)	4.5(1.3)
ECEC ( $\text{meq}/100\text{ g}$ ) <sup>b</sup>	6.6(0.3)	5.9(0.3)	27.6(3.7)	23.1(4.5)
Sodium ( $\text{meq}/100\text{ g}$ )	0.1(0.01)	0.1(0.01)	0.6(0.07)	0.7(0.1)
Potassium ( $\text{meq}/100\text{ g}$ )	0.3(0.03)	0.1(0.03)	3.8(0.73)	1.0(0.13)
Calcium ( $\text{meq}/100\text{ g}$ )	2.4(0.2)	1.8(0.13)	5.1(0.47)	3.8(0.73)
Magnesium ( $\text{meq}/100\text{ g}$ )	2.4(0.2)	1.6(0.17)	17.4(2.7)	17.4(2)
Aluminum ( $\text{meq}/100\text{ g}$ )	1.5(0.23)	2.2(0.27)	0.7(0.23)	1.3(0.17)

<sup>a</sup> Three parallel and evenly spaced transects were established in each site and three soil samples were taken along each transect for all measurements, except bulk density for which six were taken; each sample was a composite of five subsamples.

<sup>b</sup> Effective cation exchange capacity (ECEC) = Sum of bases + aluminum.

#### Stand structure and aboveground biomass

The diameter, height, and identification to species of all trees with diameter at breast height (dbh)  $\geq 4.0$  cm in each plot of both study sites were recorded. These data served as the basis for calculations of species richness, stem density, basal area, and biomass estimates. The biomass of pine trees was calculated from a regression equation developed for *Pinus caribaea* growing in Puerto Rico (Lugo, in press). The biomass of the hardwood trees in both sites were calculated from the regression equation for the wet forest life zone reported in Brown et al. (1989).

#### Wood production

We estimated wood production as follows: total aboveground biomass was adjusted for leaves to obtain wood biomass (leaves = 7% of total biomass for hardwood trees and 25% of total for pine trees; Lugo, in press). Assuming that wood biomass accumulated at a linear rate since establishment (based on data presented in Brown and Lugo, 1990b and Lugo et al., 1988), we divided standing biomass of wood by the age of the stands.

#### Litter fall and litter standing stock

Twenty  $0.25\text{ m}^2$  litter traps, five per plot, were placed in each study site in January 1987. Litter fall was collected every two weeks for a period of 2 yr. The collected litter was separated into pine needles and other leaves for the plantation, all leaves for the secondary forest, fine wood ( $\leq 2$  cm diameter), reproductive parts, and miscellaneous. Each component was dried at  $65^\circ\text{C}$  to constant weight and weighed separately per basket per sampling date.

Standing stock of fine litter was sampled every 6 mo for a period 1.5 yr. Litter was collected from 24  $0.25\text{ m}^2$  quadrats, six per plot randomly located. The samples were sorted into the same components and dried as for litter fall.

#### Fine root biomass and production

Standing stock of fine roots ( $\leq 2$  mm diameter) was determined by randomly collecting 5 soil cores/plot to 30-cm depth, in 10-cm increments, in both forest types (20 per forest). Samples were collected every 6 mo, for 1.5 yr (three sample dates), approximately at the end of the dry and wet seasons. The samples were placed in a freezer until ready for separation.

Ultrasonic washing in fine-mesh bags for 3 hr was used to separate the roots from the soil. The contents of each bag were then passed through a series of sieves under running water. All roots were separated into live and dead (based on morphological characteristics such as elasticity, friability, and color) and sorted by diameter class ( $\leq 2$  mm,  $>2$ ,  $\leq 5$  mm,  $>5$  mm), dried at 65°C to constant weight, and their weight determined. In this paper only the results for the  $\leq 2$  mm diameter roots, which we call fine roots, will be reported.

In-growth cylinders made of polypropylene (10 cm tall, 7-cm diameter, 8-mm<sup>2</sup> mesh) were used to measure fine root growth in the 0–10 cm layer (Cuevas and Medina, 1983; 1988). The cylinders were filled with dry-sieved, root-free soil from the same horizon, packed to approximate bulk density, and placed in holes of the same diameter and height. Five cylinders per plot were removed every 2 mo the first year, and every 6 mo for the next 3 yr. Here we present the results of the first year of study. During collection, roots outside the cylinders were cut flush before removing the cylinder from the ground. The samples were treated and separated as for standing stock determination. Annual fine root production and turnover in the soil cores were determined according to Fairley and Alexander (1985), using maximum growth in the in-growth cylinders (Cuevas and Medina, 1988).

### Statistical analyses

To determine whether significant differences between stocks and annual flows of organic matter occurred between the two sites, Student-t tests ( $p = 0.05$ ) were used. Differences over time between flows and storages of organic matter were determined by ANOVA, followed by the Least Significant Difference (LSD) test ( $p = 0.05$ ).

## Results

### Community structure

The native secondary forest was dominated by *Tabebuia heterophylla* (almost 50% of the stems). Other species commonly found were

*Psidium guajava*, *Miconia prasina*, and *Casearia sylvestris* (accounting for about 30% of the stems). The total number of tree species (dbh  $\geq 4$  cm) found in all plots of the secondary forest was 23, with an average number per plot of 10 (Fig. 2a). The total number of tree species encountered in the plantation was significantly lower than in the secondary forest: total of eight species with an average number per plot of less than four. *Pinus caribaea* accounted for 88% of the stems, followed by *Casearia sylvestris* and *Didymopanax morototoni* (a further 7% of the stems). A well developed understory of native species (e.g. Melastomataceae and Piperaceae) (C. Domínguez, 1987, Institute of Tropical Forestry, personal communication, and Lugo, in press) was present in the plantation.

The major difference between the structure of the two sites was in tree height and diameter. Plantation trees were taller (4–26 m in the plantation versus 4–12.5 m for the secondary forest) and had significantly larger diameters (Fig. 2b). The larger diameters, but same stem density (Fig. 2c) as the secondary forest resulted in a basal area in the plantation that was almost four times higher than in the secondary forest (Fig. 2d).

The aboveground biomass of trees in the plantation was significantly higher than that of the secondary forest (Fig. 2e). The biomass of the native secondary forest was comparable to that reported for other similar age forests growing in the tropical wet forest life zone (about 40–50 t ha<sup>-1</sup>), whereas the biomass of the pine plantation was comparable to similar-age forests growing in the tropical moist forest life zone and to other pine plantations of the same age (about 80–90 t ha<sup>-1</sup>) (Brown and Lugo, 1990b; Lugo et al., 1988).

### Litter fall

There were significant differences in the quantity of litter fall between the plantation and the secondary forest (Figs. 3 and 4), but no significant differences between the two years studied for any of the litter components and totals within each forest type (Figs. 3a and 3b). Total annual litter fall, total leaf fall, and the fall of reproduc-

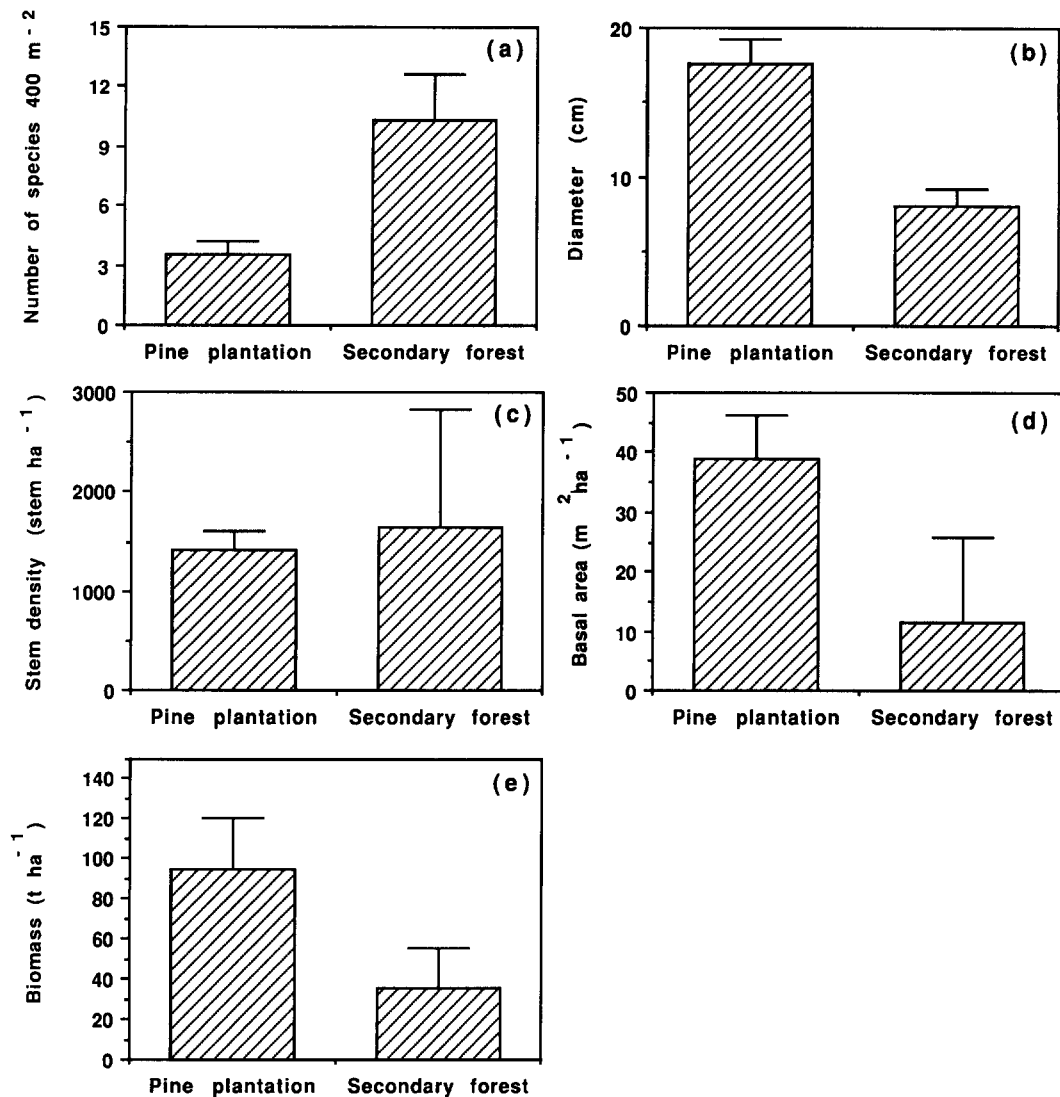


Fig. 2. Mean ( $\pm 95\%$  confidence intervals) structural characteristics of a *Pinus caribaea* plantation and a paired native secondary forest. All values based on trees with diameter at breast height (dbh)  $\geq 4.0$  cm.

tive parts were significantly higher in the pine plantation than in the secondary forest. Leaves accounted for more than 80% of total litter fall in both forests.

There was no well defined pattern of leaf fall in the pine plantation (Fig. 4a), even though the total annual amount was the same for the two years. The peaks in leaf fall ( $\geq 7.1 \text{ g m}^{-2} \text{ d}^{-1}$ ) and overall average rates ( $2.5 \text{ g m}^{-2} \text{ d}^{-1}$ ) were higher in the pine plantation than in the secondary forest (cf, Fig. 4a and 4b). The peaks in pine leaf fall coincided with peaks in wood-

fruit- and flower fall (Fig. 4c) suggesting that physical factors like wind or heavy rainfall produce the fall of litter.

In contrast, total leaf fall in the secondary forest during the 2 yr of study had a very defined and repeatable pattern (Fig. 4b). Maximum leaf fall (about  $5.7 \text{ g m}^{-2} \text{ d}^{-1}$ ) was between late April to early May, in a 4-week period immediately after the month with the largest number of dry days (see Fig. 1a). Other litter fall components, particularly wood, responded to winds or heavy rainfall, like in the plantation.

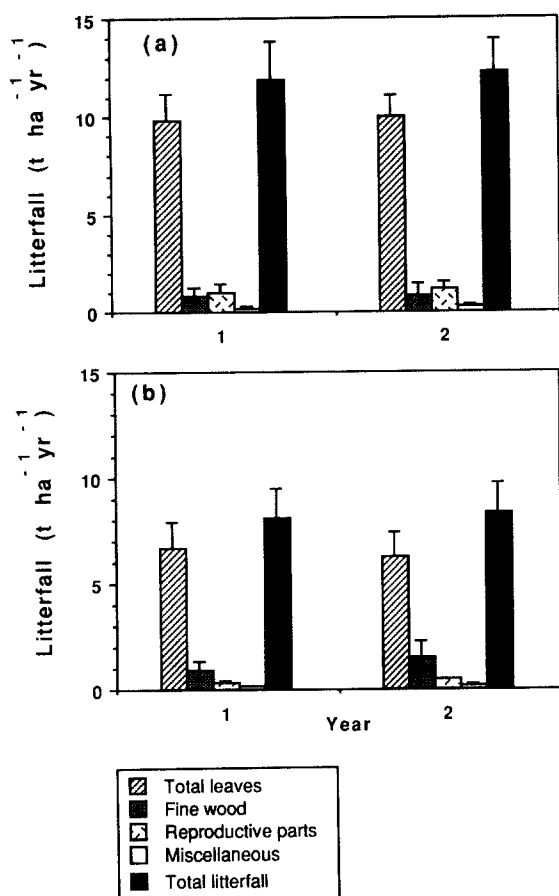


Fig. 3. Mean annual litter fall rates by component ( $\pm 95\%$  confidence intervals) for a (a) *Pinus caribaea* plantation and (b) a paired native secondary forest.

#### Standing stock of litter

There were significant differences in the seasonal pattern of standing stock of total litter and leaf litter between the two forest types (Fig. 5). In general, there was twice the amount of litter on the ground in the pine plantation than in the secondary forest (average of 1054 and 503 g m<sup>-2</sup>, respectively; Fig. 6). There were no significant differences in standing stock of leaves and total litter between sampling dates in the secondary forest, but differences occurred between some time intervals in the plantation (Fig. 5).

Leaf litter accounted for most of the standing crop in both sites (about 60%, Fig. 6). Fine wood fraction was similar in both sites, but there were always higher amounts of the other litter fractions in the pine plantation.

#### Fine root distribution in the soil profile

Standing stock of fine roots in the secondary forest was significantly higher than in the plantation for both dead and live mass (Fig. 7). In both forests the majority of fine roots were in the top 10 cm of soil. Live root fraction in the secondary forest was about four times higher at all depths than in the pine plantation. Dead root mass was always higher than live root mass in the secondary forest (60% of total), regardless of depth, whereas the reverse was true for the plantation.

The pine plantation had live root mass and distributions similar to those of a former *Theobroma cacao* plantation in Costa Rica (Gower, 1987), while values for the secondary forest were similar to those reported by Klinge and Herrera (1978) for Amazon caatinga forests in southern Venezuela.

#### Organic matter budgets

Total storage (including soil organic matter) of organic matter was the same in both forest types, but its allocation among pools was markedly different (Table 2). The total organic matter pool in the plantation was about evenly divided between live and dead components, whereas in the secondary forest, twice as much was in the dead pool as in the live. Within the living components, practically all of the biomass was allocated aboveground in the plantation, whereas about 10% of the live biomass was allocated to fine roots in the secondary forest. Furthermore, the size of the detrital pools (above- plus belowground) were the same in both forests, but the origin of the detritus differed. Aboveground litter was more than 35 times the dead root fraction in the plantation, whereas for the secondary forest, the standing stock of dead roots was higher than aboveground litter.

Both forests had similar rates of total organic matter production (Table 2), but allocation was significantly different between the two: 44% was allocated to fine roots in the secondary forest, while only 6% was allocated to roots in the pine plantation. Litter fall and wood production in the plantation were approximately 1.5 and 2 times higher, respectively, than in the secondary

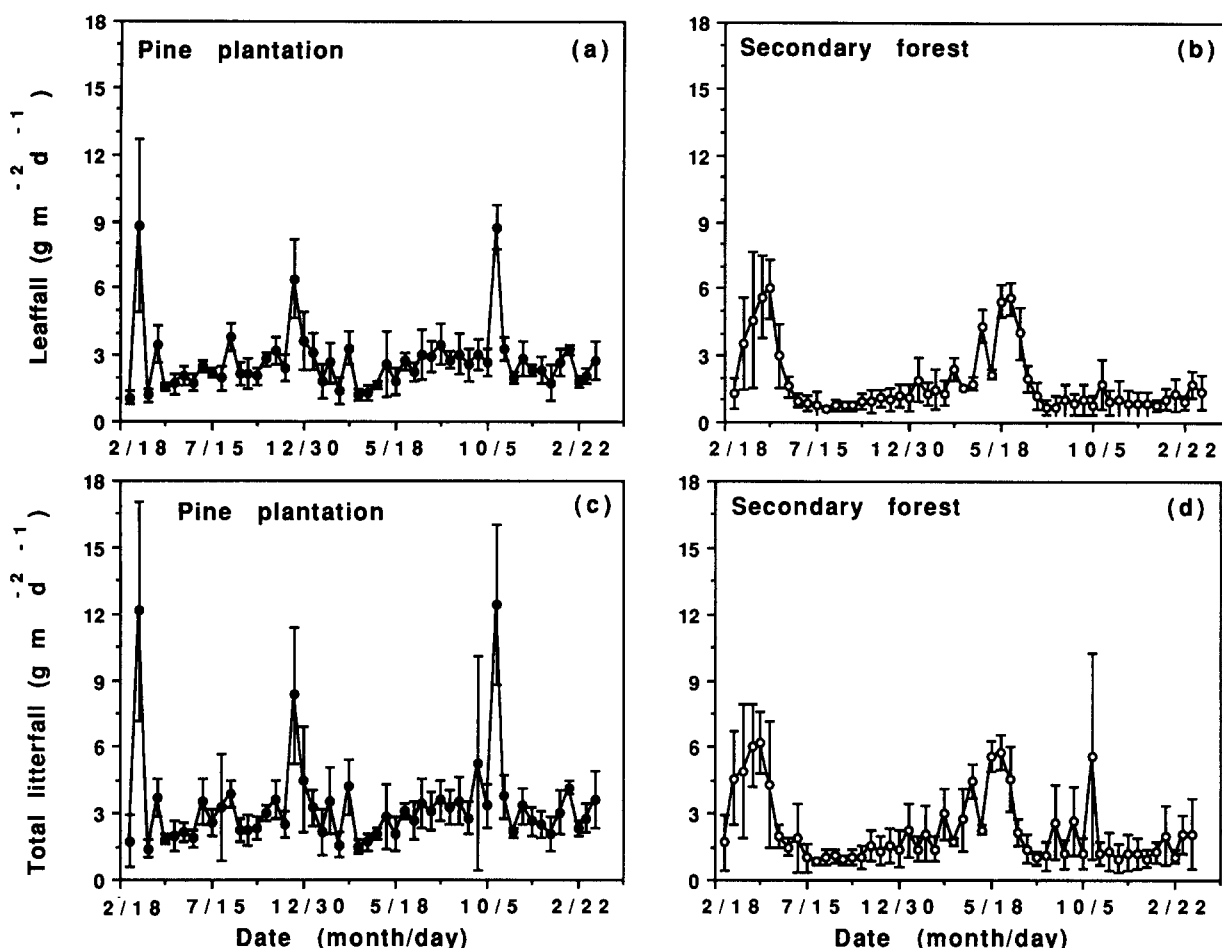


Fig. 4. Pattern of mean ( $\pm 95\%$  confidence intervals) leaf fall (a–b) and total litter fall (c–d) for the period of February 22, 1987 to February 22, 1989 in a *Pinus caribaea* plantation and a paired native secondary forest. Values are means of 20 baskets per sampling date.

forest. However, root production in the secondary forest was almost a magnitude higher than in the pine plantation. Fine root production was equal to aboveground litter production in the secondary forest, but in the pine plantation litter production was 12 times higher than fine root production.

Litter turnover ( $k_L$ ) was somewhat faster in the secondary forest than in the pine plantation (Table 2). Estimated decay rates for fine roots ( $k_R$ ) in the plantation were almost three times faster than for fine roots in the secondary forest.

## Discussion

This study shows that two different forest ecosys-

tems can function under the same environmental conditions and exhibit the same rate of primary productivity but have different effects on the soil compartment. The area had been cultivated prior to the establishment of the two forest stands and, while one of the stands was planted, the other developed under natural conditions. Both forests had similar amounts of soil organic matter and similar accumulation of organic matter in the soil (including litter, dead roots, and soil organic matter, i.e.  $93\text{--}96 \text{ t ha}^{-1}$ ). However, the stands had different biomass allocation and inputs to the soil. The plantation had more litter accumulation and aboveground biomass. The secondary forest accumulated more root mass (both live and dead fractions) at the expense of aboveground litter. Thus the input of organic



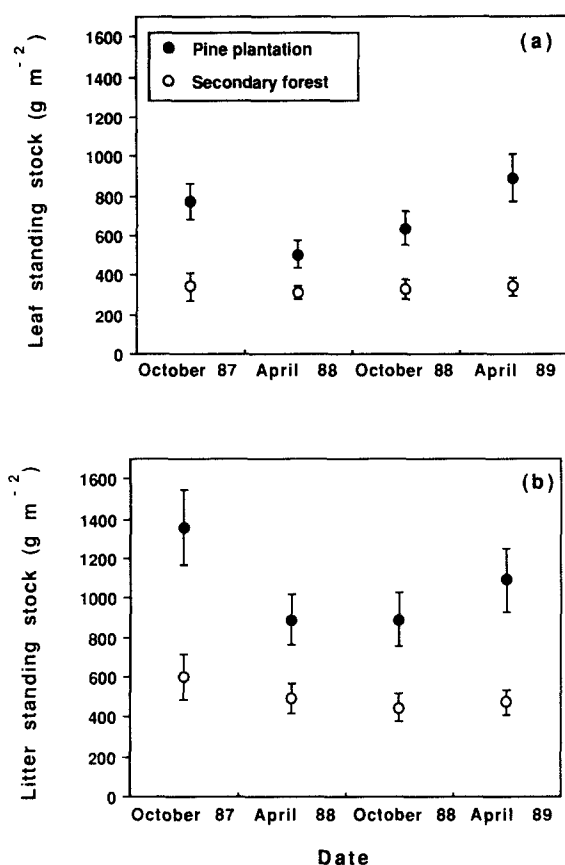


Fig. 5. Seasonal pattern of standing stock of (a) leaf litter and (b) total litter in a *Pinus caribaea* plantation and a paired native secondary forest. Values are means  $\pm 95\%$  confidence intervals ( $n = 24$ ).

matter to soils followed different pathways in these two forest stands with the result that the quality of the organic matter reaching the soil was also different.

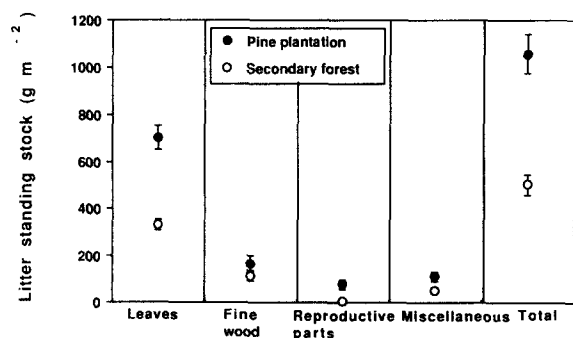


Fig. 6. Mean ( $\pm 95\%$  confidence intervals) standing stock of litter components for the duration of the study in a *Pinus caribaea* plantation and paired native secondary forest.

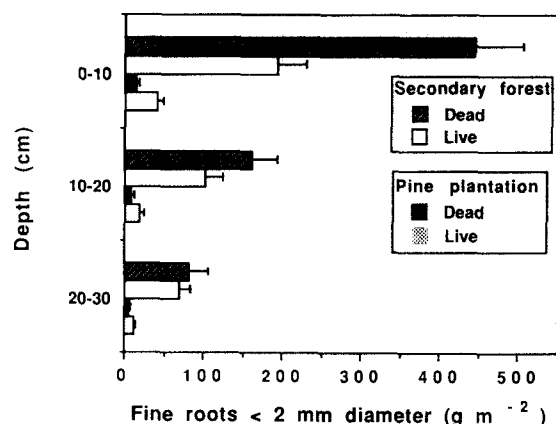


Fig. 7. Distribution of mean mass ( $\pm 95\%$  confidence intervals) of fine dead and live roots in the soil profile, 0–30 cm depth, in a *Pinus caribaea* plantation and a paired native secondary forest.

An indication of differences in organic matter quality can be determined from lignin to nitrogen ratios (L/N). These ratios for pine and secondary forest leaf litter were similar to each other (37.5 and 31.1, respectively; unpublished data of authors). In contrast, L/N for secondary forest fine roots was 70.4, almost double that for pine fine roots (44.7) and double the ratios for leaves.

Our study allowed us to describe the rates and patterns of ecosystem processes that resulted in the dissimilar routes of organic matter input into the soil compartment. For example, there were significant differences in the amounts and pattern of litter production between the two forests. The pine plantation always had higher litter production than the secondary forest and the rate of litter fall had no discernible pattern. However, not all needles fell to the ground at any one time; a considerable amount was intercepted by branches and understory vegetation. Peaks in litter fall in the pine plantation were explained by wood- and fruit fall and the raining-out of suspended senescent needles caused by strong winds and/or heavy rains.

There was a repeatable pattern of litter fall in the secondary forest during the two years studied. Maximum leaf fall occurred after the driest months of the year. *Tabebuia heterophylla*, the dominant species in the secondary forest, is a facultative deciduous species, so senescence and

Table 2. Above and belowground (0–30 cm depth) standing stocks and production of organic matter in a 12-yr-old *Pinus caribaea* plantation and paired secondary forest. Values in parentheses are 95% confidence intervals

	Pine plantation	Secondary forest
<b>Standing stocks: t ha<sup>-1</sup></b>		
Biomass of trees	94.9(25.8)	35.6(19.7)
Fine roots < 2 mm diam.	1.0(0.1)	10.5(0.9)
Live	0.7(0.1)	3.6(0.5)
Dead	0.3(0.1)	6.9(0.9)
Aboveground litter	10.5(0.8)	5.0(0.4)
Soil organic matter	82.0(1.2)	83.9(5.6)
Total organic matter	188.4(27.9)	135.0(26.6)
Above- + belowground litter	10.8(0.9)	11.9(1.3)
Shoot/live fine roots	135.6	9.9
Above/belowground litter	35.0	0.7
<b>Production: t ha<sup>-1</sup> yr<sup>-1</sup></b>		
Aboveground litter	12.1(1.3)	8.2(1.0)
Wood	6.0(1.5)	2.8(1.5)
Fine roots <sup>a</sup> :		
(a)	1.1(0.3)	8.5(0.4)
(b)	1.1(0.6)	8.4(2.5)
Total production	19.2(3.4)	19.4(5.0)
Belowground/total	0.06	0.44
Litter fall/standing stock (k <sub>L</sub> )	1.5	1.64
Root production/dead root mass (k <sub>R</sub> )	3.67	1.23

<sup>a</sup> Method (a) based on differences in standing stocks between sampling dates, and (b) maximum biomass in in-growth cylinders.

leaf fall may be triggered by periods of potentially low water availability.

Although litter fall throughout the two years studied indicated two peaks of leaf fall in the secondary forest, there was no significant difference in the standing stock of leaves on the forest floor between sampling dates. The sampling dates for forest floor litter either preceded the litter fall peak, or were nearly 5 mo after the peak had occurred. There were, however, differences in the total amount of litter on the forest floor, which reflected significant differences in the miscellaneous fraction between sampling dates. Significant temporal differences in the standing stock of litter in the pine plantation reflected higher litter fall inputs due to heavy winds and rain.

The pine plantation had an amount of litter on the ground twice that of the secondary forest, even though turnover rates were similar for both forests. Higher rates of litter fall in the pine plantation resulted in a higher proportion of aboveground litter in the total soil organic matter storage.

Fine root production was higher than aboveground litter production in the secondary forest. This high organic matter allocation belowground makes this process as important or more so to soil organic matter formation and nutrient cycling as aboveground litter fall. In contrast, aboveground litter production was the major source of organic matter to the forest floor in the pine plantation. The fine root compartment could be more important for labile nutrients in the pine plantation (Sánchez et al., 1989; Vogt et al., 1986) because they turn over nearly four times per year.

Differences in production and accumulation of organic matter in the soil profile between the two sites point toward contrasting nutrient immobilization and mineralization sites and different sources of soil organic matter. Fine roots were produced throughout the year in both forests. The slower turnover of fine roots in the secondary forest coupled with the higher rate of root production resulted in the observed accumulation of dead roots. This accumulation may act as a nutrient sink due to immobilization

because the root material was more lignified than was leaf litter (35.2% lignin for roots and 17.4% for leaves; unpublished data of authors). In contrast, the pine plantation always had a higher amount of live than dead fine roots (24.6% lignin), suggesting higher mineralization rate of roots and concomitant release of nutrients.

The predominantly belowground allocation of biomass in the secondary forest suggests that these plants were allocating a considerable portion of photosynthate to nutrient-absorbing organs. In contrast, the faster turnover rate of fine roots, the obligately ectomycorrhizal nature of Caribbean pine, and the observed well developed mycelia within the litter layers, allowed efficient nutrient uptake to occur with a lower allocation of biomass to roots. In the long run, the two contrasting biomass allocation strategies allow the two types of forests to grow with equal rates of organic matter production under similar climatic and edaphic conditions.

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