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Soil macrofauna and litter nutrients in three tropical tree plantations on a disturbed site in Puerto Rico

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Abstract

Tree plantations are increasingly common in tropical landscapes due to their multiple uses. Plantations vary in structure and composition, and these variations may alter soil fauna communities. Recent studies have demonstrated the important role of soil fauna in the regulation of plant litter decomposition in the tropics. However, little is known about how plantation species affect soil fauna populations, which may in turn affect the biogeochemistry of the plantation system. We measured soil macroinvertebrate abundance and biomass in 9-year-old N_2-fixing *Leucaena leucocephala*, *Casuarina equisetifolia*, and non-N_2-fixing *Eucalyptus robusta* plantations on a degraded site in Puerto Rico. Nutrient concentrations and standing stocks of forest floor litter were also determined to examine the relationship between litter chemistry and soil macroinvertebrates. *Leucaena* plantations had significantly higher abundances and biomass of millipede species than *Casuarina* and *Eucalyptus*. Earthworm biomass did not differ among plantation treatments. Nitrogen, P, and K concentrations were generally higher in *Leucaena* litter, which resulted in higher standing stocks of these nutrients in fragmented, moderately decomposed litter (Oe horizon). Millipede biomass was highly correlated to N concentration and C/N ratio in the Oi litter horizon. These results suggest that plantation species differ in their influence on soil fauna, and the biomass and abundance of soil fauna can be regulated through careful selection of plantation species in degraded tropical lands.

Keywords: Diplopoda; Millipedes; Restoration; Soil fauna; Tree plantations; Tropics

1. Introduction

Tree plantations are an increasingly common land cover in tropical regions. Estimates indicate about a threefold (Evans, 1992) to sixfold (FAO, 1993) increase in the land area of tropical tree plantations from 1980 to 1990, and a present cover of about 60 million ha (FAO, 1999). Plantations are established for the commercial development of forest products (e.g. construction timber, pulpwood or fuelwood), to integrate ecological and economic benefits in agroforestry systems (Sanchez, 1987), for ecological services such as atmospheric CO_2 sequestration (Brown et al., 1986), or as a management strategy to rehabilitate degraded land (see Fisher, 1995; Lugo, 1997; Parrotta, 1997; Parrotta et al., 1997).

Land degradation can pose edaphic and biological limitations to secondary succession such as soil erosion and compaction, nutrient losses, changes in microclimate, changes in disturbance regime, competition with exotic species, and a reduced supply of plant propagules (Lugo, 1997). Tree plantations have

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been shown to mitigate these barriers to secondary succession by re-establishing nutrient cycles, providing habitat for seed dispersers, and improving the microclimate for native species establishment in the understory (Parrotta, 1993a; Hagger et al., 1997; Binkley and Resh, 1998).

Recent plantation research has focused primarily on biomass assessments (Brown et al., 1986; Cuevas et al., 1991; Lugo, 1992; Bernardo et al., 1998), nutrient cycling (Bernhard-Reversat, 1988; Binkley, 1997; Bashkin and Binkley, 1998; Binkley and Ryan, 1998; Smith et al., 1998; Binkley et al., 2000; Kaye et al., 2000), and understory regeneration (Parrotta et al., 1997). The impact of soil organisms on soil fertility in tropical tree plantations remains largely unexplored, despite the recognition that soil fauna are an important factor contributing to the decomposition of organic matter in the humid tropics (Lavelle et al., 1993; Henegan et al., 1999; González and Seastedt, 2001), and that the fertility of tropical soils largely depends on the maintenance of biological systems for regulation of decomposition. Individual plantation species may have direct and indirect effects on soil fauna, affecting the mineralization and humification of organic matter, which largely determine the nutrient status of the soil. The direct effects of plantation species on soil fauna include the quality and quantity of the litter substrate. Indirect effects may include changes in microclimatic conditions such as temperature, moisture, and physical habitat.

Lyford (1943) and Kheirallah (1979) demonstrated feeding preferences of different temperate millipede species, implying that substrate palatability can influence the distribution and abundance of the organisms. Results from Anderson et al. (1985) suggest that litter feeding organisms accelerate N mineralization in temperate, deciduous woodland. Furthermore, Anderson et al. (1983) demonstrated that the millipede *Glomeris marginata* reduced nutrient immobilization in temperate deciduous litter and soils, enhancing nutrient fluxes. The effects of these organisms on mineralization may be amplified in the tropics where the abundance of soil macrofauna is highest, and climate is a less important determinant of decomposition rate (Swift et al., 1979; Anderson et al., 1985; Lavelle et al., 1993; González et al., 2001). In the tropics, Tian et al. (1993) clearly showed that soil fauna populations were affected by the application of plant residues of various qualities (determined by percentage of N and lignin/N ratio), and that the decomposition of the residues was accelerated with the inclusion of earthworms and millipedes (Tian et al., 1995). Increased decomposition rates associated with soil macrofauna resulted in enhanced nutrient mobilization (Tian and Brussaard, 1992), corroborating the findings of Anderson et al. (1983). In their study, Tian et al. (1993) found that plant residues of various quality induced microclimatic changes in soil temperature and moisture to various degrees, however, environmental factors alone did not explain differences in populations of soil fauna (Tian et al., 1993). Recently, Henegan et al. (1999) concluded that the effects of soil microarthropods on the mass loss of a common substrate were only significant in the tropics. The studies from temperate systems, with the evidence available from the tropics, indicate that plantation species that vary in litter quality and quantity, may affect soil macrofauna populations, resulting in differential nutrient mobilization thereby affecting nutrient cycling and soil fertility.

The objectives of this study were to quantify the effects of three contrasting plantation species (non-N_2-fixing *Eucalyptus robusta*, and N_2-fixing *Casuarina equisetifolia* and *Leucaena leucocephala*) on soil fauna on a degraded site in Puerto Rico. Furthermore, to elucidate correlations between the presence of soil fauna and nutrient status in decomposing surface litter. We ask the following questions: (1) How do plantation species vary in the quality and quantity of fine litter on the forest floor, and does this affect the biomass and abundance of soil macrofauna? (2) Do nutrient standing stocks in the forest floor differ between plantation species and does this relate to the abundance of soil macrofauna?

2. Study site

The study area is located on the northern coast of Puerto Rico at the University of Puerto Rico's Toa Baja experimental station (18°27′N, 66°10′W). The area receives an average 1600 mm of precipitation annually (Parrotta, 1995), and is classified as subtropical moist forest (Holdridge system; Ewel and Whitmore, 1973). Annual temperature normally varies between 20.9 and 30.3 °C. Forest clearing, conver-

Table 1
Soil characteristics (0–10 cm) of the plantation site

	Mean (S.E.), $n = 9$
pH	7.60 (0.14)
%C	1.96 (0.12)
%N	0.13 (0.01)
P (mg kg^{-1})	5.64 (0.34)
K (mg g^{-1})	0.10 (0.01)
Ca (mg g^{-1})	1.28 (0.09)
Na (mg g^{-1})	0.06 (0.01)
Mg (mg g^{-1})	0.20 (0.03)
Fe (mg g^{-1})	0.02 (0.01)
Mn (mg g^{-1})	0.02 (0.01)

sion to agriculture, periodic fires, cattle grazing, sand excavation and leveling have been frequent, creating severe disturbances to the soils and vegetation (Parrotta, 1995). Soils are poorly developed, well drained, alkaline, calcareous sands (isohypothermic Typic Tropopsamments) (Boccheciamp, 1978; Parrotta, 1993b). The grasses *Panicum maximum* and *Sporobolus jacquemontii* dominated the site before plantation establishment (Parrotta, 1999). Three replicate $16 \times 16\,m^2$ plots of *E. robusta*, *C. equisetifolia*, and *L. leucocephala* were established in 1989 in monoculture and intercropped treatments, using a randomized block design. Only monoculture treatments were considered in this study, and all samples were taken from February to April 1998 (for a complete description of plantation establishment and design, see Parrotta, 1995). Soil pH, exchangeable cations, and total C and N do not differ among treatments, and are summarized in Table 1.

3. Materials and methods

3.1. Organisms

Organisms were collected by hand sorting using a randomly located $0.25\,m^2$ sampling frame, and two samples were taken per plot. Litter was carefully removed and all macroinvertebrate organisms in litter and on the mineral soil surface were collected. Organisms collected on the surface of mineral soil were included in the 0–10 cm soil layer. Soil was excavated to 10 and 10–25 cm, placed on a plastic tarpaulin, and sorted using a $1\,cm^2$ mesh sieve. All macroscopic organisms were collected. Fresh weight biomass for each individual was determined on the day of collection by rinsing the organism, drying on absorbent paper, and weighing. Organisms' fresh weight biomass in species plots were compared using general linear model analysis of variance (ANOVA) tests. Heteroscedastic *t*-tests were used to compare the biomass of organisms in the 0–10 and 10–20 cm soil layers for each treatment, and Pearson's correlation analysis was used for relationships between biomass and litter nutrients. All analyses were done using Minitab statistical software (Minitab, 1991).

3.2. Forest floor mass/litter analysis

Two litter samples were taken from each plot using a randomly located $25 \times 25\,cm^2$ ($0.0625\,m^2$) sampling frame. Samples were oven dried at 65 °C until constant weight. Litter was separated into three categories representing organic horizons in three stages of decomposition (Brady, 1990): identifiable intact slightly decomposed (Oi), identifiable fragmented moderately decomposed (Oe), and unidentifiable highly decomposed (Oa). Horizons were separated by sequentially passing the samples through 10 and 3 mm sieves, and manual sorting. Identifiable litter could be recognized as a leaf, twig or reproductive structure. Each layer was weighed and ground in a Wiley mill (20 mesh size), and sent to the International Institute of Tropical Forestry (IITF) laboratory for chemical analysis. The digestion method of Huang et al. (1985) was used to determine Ca, P, Al, Fe, Mn, K, and Mg concentrations. Samples were analyzed using a Beckman plasma emission spectrometer. Total C and N were determined by dry combustion (LECO CNS-2000 analyzer). Nutrient concentration, C/N and C/P ratios, and nutrient standing stock (g m^{-2}) were determined for each species and litter layer. Nutrient pools were compared among treatments and between litter layers using general linear model ANOVA (Minitab, 1991).

4. Results

4.1. Organisms

All plantations were clearly dominated by the millipede species *Leptogoniulus nearsii* and *Trigoniulus lubricinus*. The earthworm *Pontoscolex corethrurus*

Table 2
Abundance and biomass of soil fauna in plantation treatments

	Mean (S.E.)[a]		
	Casuarina	*Leucaena*	*Eucalyptus*
Abundance (individuals m^{-2})			
Millipedes	19.33 (5.97) b	56.00 (14.05) a	15.33 (7.04) b
Earthworms	32.67 (22.26)	56.00 (36.15)	8.67 (4.55)
Other	10.67 (5.43)	15.67 (6.66)	8.00 (2.31)
Total	62.67 (27.72)	127.67 (60.49)	32.00 (12.00)
Biomass (g m^{-2})			
Millipedes	5.58 (2.59) b	15.60 (1.49) a	6.41 (3.61) b
Earthworms	7.97 (7.54)	16.03 (16.03)	4.70 (2.84)
Other	0.32 (0.12)	0.66 (0.24)	0.22 (0.08)
Total	13.87 (4.94) b	32.34 (15.61) a	11.33 (3.27) b

[a] Different letters following values indicate significance at $p = 0.05$ ($n = 3$).

was also common, however, distribution was patchy, and samples varied from 0 to 196 individuals m^{-2}. Scarabadiae (Coleoptera), and Cicadea (Homoptera) larvae were also present in low numbers, and a few Blattidae species were found. For statistical analysis, Coleopterans, Homopterans, and Blattidae are grouped as ''other'' due to their relatively low abundance and biomass. Soil macroinvertebrate abundances and biomass (Table 2) were consistently higher in *Leucaena* plots than *Casuarina* and *Eucalyptus*. The average abundance (individuals m^{-2}) of millipedes was significantly greater in the *Leucaena* treatment (mean = 56.00 individuals m^{-2}; $p = 0.02$) than *Casuarina* or *Eucalyptus* treatments (mean = 19.33 and 15.33 individuals m^{-2}, respectively), and the difference was consistent with millipede biomass ($p = 0.04$); *Leucaena* averaged 15.60 g m^{-2}, while *Eucalyptus* averaged 6.41 g m^{-2} and *Casuarina* averaged 5.58 g m^{-2}. Although earthworm abundance and biomass were also higher in the *Leucaena* plots, there was considerable sample variance (see standard errors, Table 2) and the difference was not significant. Biomass of all organisms combined (Table 2) was marginally significantly higher in *Leucaena* plots ($p = 0.05$), where total biomass averaged 32.34 g m^{-2}, compared to 13.87 g m^{-2} for *Casuarina* and 11.33 g m^{-2} for *Eucalyptus*. No differences in macroinvertebrate abundance and biomass were found between *Casuarina* and *Eucalyptus*.

Biomass of millipedes and other organisms was generally greater in the top 10 cm of soil than the 10–20 cm depth (Fig. 1). Millipede biomass was significantly higher in the top 10 cm of *Casuarina* and *Leucaena* soil ($p = 0.02$, and 0.005, respectively). *Leucaena* plots averaged 15.60 g m^{-2} of millipede biomass in the top 10 cm of soil compared to 0.07 g m^{-2} at 10–20 cm. Biomass of other organisms was also significantly greater in the top 10 cm of soil in *Leucaena* plots ($p = 0.04$). Millipedes in *Casuarina* plantations averaged 5.47 g m^{-2} in the top 10 cm layer compared to 0.13 g m^{-2} in the 10–20 cm layer. No significant differences were observed between soil depths in the *Eucalyptus* plots.

Of all the litter characteristics measured, biomass of millipedes was most correlated to N concentration ($R = 0.77; p = 0.01$) and C/N ratio ($R = -0.75$; $p = 0.02$) in the Oi litter layer (Fig. 2). Earthworms and other organisms were not correlated with any litter parameter.

4.2. Forest floor mass

Total forest floor mass did not differ between species, and ranged between 0.80 and 3.24 kg m^{-2} with a mean of 1.47 kg m^{-2}. Mass of the Oi layer was significantly higher in the *Casuarina* (mean = 0.59 kg m^{-2}) and *Eucalyptus* (mean = 0.56 kg m^{-2}) plots than *Leucaena* (mean = 0.31 kg m^{-2}; $p = 0.02$). Litter mass in the Oe and Oa layers did not differ across tree species, although *Leucaena* litter mass tended to be less than in *Casuarina* or *Eucalyptus* treatments (Table 3). Within species treatments, mass

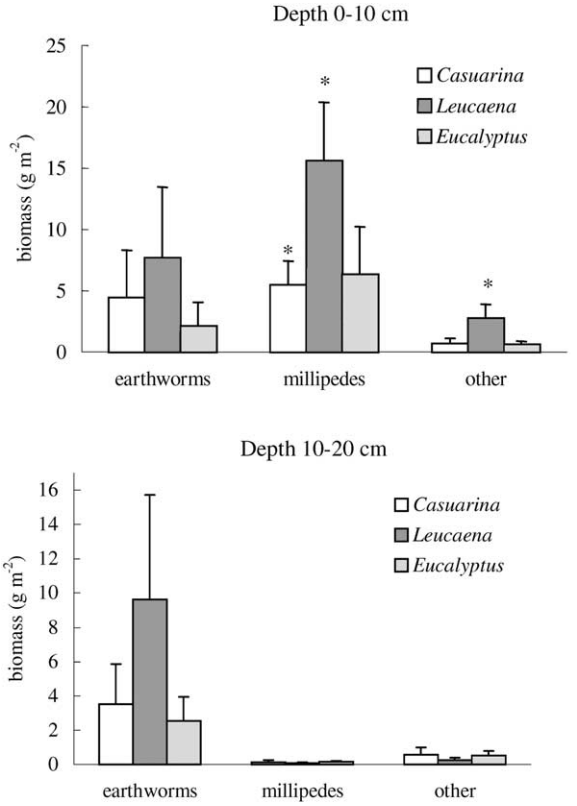

Fig. 1. Biomass of soil fauna in plantations of *C. equisetifolia*, *L. leucocephala*, and *E. robusta* at depths of 0–10 and 10–20 cm. Error bars represent standard error, * represents significant differences ($p < 0.05$) between 0–10 and 10–20 cm depths.

of the Oi, Oe, and Oa followed the general pattern Oa > Oi > Oe (Table 3), however, only *Leucaena* had significantly greater Oa litter mass than the Oi or Oe ($p = 0.03$; mean = 0.56, 0.31, and 0.28 kg m^{-2}, respectively).

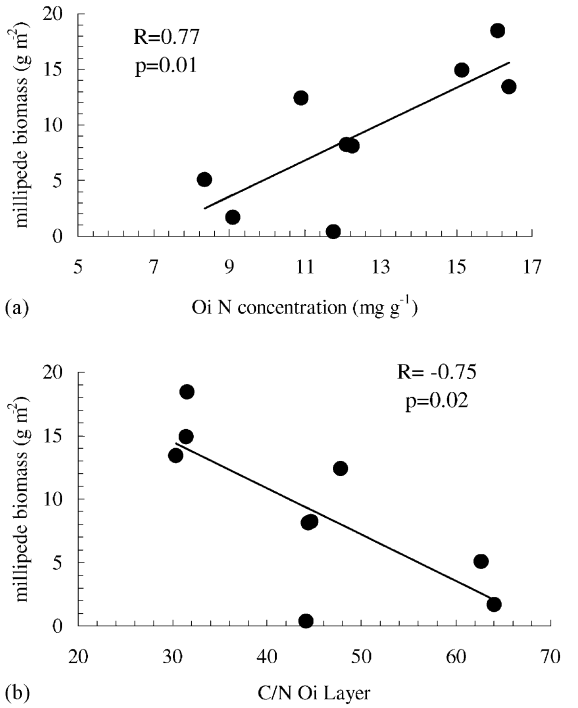

Fig. 2. Correlation of millipede biomass versus: (a) N concentration in the Oi litter layer; (b) C/N ratio in the Oi layer ($n = 9$).

4.3. Nutrient concentration

Concentration of Mg, Mn, Fe and Al increased with stage of decomposition from the Oi to Oa layer for all species litter (Table 4). The Oi layer contained the lowest concentrations of these elements, and the Oa contained the highest; over sixfold increases for Fe, and fivefold increases for Al were observed for all species litter. The highest concentrations of K and Ca were found in the Oe litter layer for all species. N and

Table 3
Species litter mass (kg m^{-2}) by layer

Litter layer	Mean (S.E.)[a]		
	Casuarina	*Leucaena*	*Eucalyptus*
Oi	0.59 (0.07) a	0.31 (0.03) Ab	0.56 (0.07) a
Oe	0.28 (0.05)	0.28 (0.03) A	0.21 (0.01)
Oa	0.94 (0.29)	0.56 (0.05) B	0.67 (0.24)
Total	1.81 (0.38)	1.15 (0.04)	1.44 (0.31)

[a] Different capital letters indicate significance ($p < 0.05$) among litter layers within a species ($n = 3$). Different small letters in a row indicate significance between species.

Table 4
Mean nutrient concentration (mg g^{-1} dry mass), C/N and C/P ratios in litter layers of *Casuarina*, *Eucalyptus* and *Leucaena*[a]

Layer	Nutrient	*Casuarina*	*Leucaena*	*Eucalyptus*
Oi	N	12.03 a	15.88 b	9.45 c
	P	0.16 Aa	0.32 Ab	0.23 Ac
	K	1.36 a	2.10 Ab	1.83 Ab
	Ca	14.53 a	17.62 Aab	21.23 Ab
	Mg	1.72 Aa	2.57 Ab	2.60 Ab
	Mn	0.10 Aa	0.08 Aa	0.21 Ab
	Fe	1.14 A	1.52 A	1.03 A
	Al	0.92 A	1.15 A	1.15 A
	C	531.3 Aa	493.6 Ab	519.6 Aa
	C/N	44.40 a	31.11 b	58.17 c
	C/P	3478.69 a	1555.18 b	2311.50 c
Oe	N	14.52 a	19.90 b	14.15 a
	P	0.24 Ba	0.65 Bb	0.32 ABa
	K	1.59 a	3.24 Bb	2.22 Aa
	Ca	18.58 a	35.18 Bb	33.05 Bab
	Mg	2.47 Aa	3.74 Bb	3.02 Ab
	Mn	0.18 AB	0.18 B	0.26 A
	Fe	3.89 AB	4.63 AB	4.10 A
	Al	2.48 AB	2.89 B	1.71 A
	C	476.0 AB	383.0 A	479.1 A
	C/N	32.67 a	19.15 b	32.26 a
	C/P	2079.32 a	601.43 b	1539.95 a
Oa	N	14.70	16.88	11.57
	P	0.27 Ba	0.53 Bb	0.41 Bab
	K	1.47 a	2.14 Ab	2.11 Ab
	Ca	16.41 a	25.68 Bab	31.46 Bb
	Mg	3.41 Ba	4.59 Cb	4.10 Bb
	Mn	0.29 Ba	0.36 Cb	0.43 Bc
	Fe	7.46 B	9.62 B	9.62 B
	Al	4.76 B	5.88 B	6.03 B
	C	359.9 B	261.1 B	257.1 B
	C/N	24.66 a	15.72 b	23.77 a
	C/P	1379.86	482.96	627.43

[a] Different capital letters indicate significance ($p < 0.05$) among litter layers of the same species ($n = 3$). Different small letters in a row indicate significance between species.

P in *Leucaena* litter also followed this pattern, with the highest concentration occurring in the Oe layer. Similarly, N concentration in *Eucalyptus* litter was greatest in the Oe.

Among species, litter nutrient concentration varied the most in the Oi layer (Table 4). *Casuarina*, *Leucaena*, and *Eucalyptus* litter had distinct N and P concentrations ($p < 0.0001$), with the N-fixers *Leucaena* and *Casuarina* having higher N concentrations (15.88 and 12.03 mg g^{-1}, respectively) than *Eucalyptus* (9.45 mg g^{-1}). K concentration was lower in *Casuarina* litter (mean = 1.36 mg g^{-1}; $p = 0.001$) than *Leucaena* (2.10 mg g^{-1}) or *Eucalyptus* (1.83 mg g^{-1}). Ca concentration was marginally higher in *Eucalyptus* Oi litter (mean = 21.23 mg g^{-1}; $p = 0.05$) than *Casuarina* (14.53 mg g^{-1}), and *Leucaena* litter was intermediate (17.62 mg g^{-1}). Mg concentration was highest in *Leucaena* litter ($p < 0.0001$), and Mn concentration was highest in *Eucalyptus* litter ($p < 0.0001$). C content of *Leucaena* litter was significantly lower ($p = 0.001$) than the other two species in the Oi layer.

In the Oe litter layer, differences in N, P, K, Ca, and Mn concentrations between *Casuarina* and *Eucalyptus* were no longer present. However, *Leucaena* maintained significantly higher concentrations of N, P, K, and Mg ($p = 0.004, p < 0.0001, p < 0.0001$, $p = 0.001$, respectively) than *Casuarina* or *Eucalyptus*, and a slightly higher concentration of Ca than *Casuarina* ($p = 0.05$). In the highly decomposed Oa layer, P and K concentrations were significantly higher in *Leucaena* and *Eucalyptus* litter than *Casuarina* ($p = 0.002$ and 0.001, respectively), and Ca concentration was higher in *Eucalyptus* than *Casuarina* ($p = 0.01$). Concentrations of Mn in the Oa layer varied across species ($p < 0.0001$), the highest concentration occurring in *Eucalyptus* litter (mean = 0.43 mg g^{-1}) followed by *Leucaena* (0.36 mg g^{-1}) and *Casuarina* (0.29 mg g^{-1}). C/N and C/P ratios (Table 4) followed an inverse pattern to that of N and P concentrations, however, *Leucaena* litter in the Oa layer had a lower C/N ratio than *Casuarina* or *Eucalyptus* ($p < 0.0001$).

4.4. Nutrient standing stocks

Differences in nutrient concentrations among *Casuarina*, *Leucaena*, and *Eucalyptus* litter in the Oi layer were not an indication of a pool size difference in the nutrient standing stocks of these species (Table 5). However, the standing stock of Ca was higher in *Eucalyptus* (mean = 11.89 g m^{-2}) and *Casuarina* (8.57 g m^{-2}) than *Leucaena* (mean = 5.46; $p = 0.004$). Standing stock of Mg in the Oi layer was significantly lower in *Leucaena* than *Casuarina* or *Eucalyptus* (means = 0.80, 1.01, and 1.46 g m^{-2}, respectively; $p = 0.02$), and Mn standing stocks (Table 5) varied across all species ($p < 0.0001$).

Table 5
Mean nutrient standing stocks (g m^{-2}) in litter layers of *Casuarina*, *Eucalyptus* and *Leucaena*[a]

Layer	Nutrient	*Casuarina*	*Leuceana*	*Eucalyptus*
Oi	N	7.10 A	4.92 A	5.29 AB
	P	0.09 A	0.10 A	0.13 A
	K	0.80 A	0.65 A	1.02 A
	Ca	8.57 ABab	5.46 Aa	11.89 Ab
	Mg	1.01 Aab	0.80 Aa	1.46 Ab
	Mn	0.06 Aa	0.02 Ab	0.12 Ac
	Fe	0.67 A	0.47 A	0.58 A
	Al	0.54 A	0.36 A	0.64 A
	C	313.5 Aa	153.0 Ab	291.0 Aa
Oe	N	4.07 Aa	5.57 ABb	2.97 Aa
	P	0.07 Aa	0.18 Bb	0.07 Aa
	K	0.45 Aa	0.91 ABb	0.47 Ba
	Ca	5.20 A	9.85 AB	6.94 A
	Mg	0.69 A	1.05 A	0.63 A
	Mn	0.05 A	0.05 A	0.05 A
	Fe	1.09 A	1.30 A	0.86 A
	Al	0.69 A	0.81 A	0.36 A
	C	133.3 B	107.2 A	100.6 B
Oa	N	13.82 Ba	9.45 Ba	7.75 Bb
	P	0.25 B	0.30 C	0.27 B
	K	1.38 B	1.20 B	1.41 A
	Ca	15.43 B	14.38 B	21.08 B
	Mg	3.21 B	2.57 B	2.75 B
	Mn	0.27 B	0.20 B	0.29 B
	Fe	7.01 B	5.39 B	6.45 B
	Al	4.47 B	3.29 B	4.04 B
	C	338.3 Aa	146.2 Ab	172.3 Bb
Total	N	24.99	19.94	16.01
	P	0.41 a	0.58 b	0.47 a
	K	2.63	2.76	2.90
	Ca	29.20	29.69	39.91
	Mg	4.91	4.42	4.84
	Mn	0.38	0.27	0.46
	Fe	8.77	7.16	7.89
	Al	5.70	4.46	5.04
	C	785.1	406.4	563.9

[a] Different capital letters indicate significance ($p < 0.05$) within species litter layers ($n = 3$). Different small letters in a column indicate significance between species.

Standing stock of C (Table 5) in *Leucaena* litter was less than the other two species ($p = 0.01$). In the Oe litter layer, standing stocks of N, P, and K (Table 5) were significantly higher in *Leucaena* plots ($p = 0.001, p < 0.0001$, and $p = 0.001$, respectively). In the Oa, standing stock of N (Table 5) was lower in *Eucalyptus* plots ($p = 0.004$), and C stocks were almost twice as high ($p < 0.0001$) in *Casuarina* plots (mean = 33.83 g m^{-2}) than *Leucaena* (mean = 14.62 g m^{-2}) or *Eucalyptus* (mean = 17.23 g m^{-2}).

5. Discussion

5.1. Organisms

The two millipede species *L. nearsii* and *T. lubricinus* were the most abundant organisms in all three plantations, and millipede numbers were substantially greater in *Leucaena* plots. The occurrence of large numbers of millipedes in the *Leucaena* plots may be due to higher substrate palatability. The tendency for millipedes to feed preferentially has been well documented for temperate, deciduous forests (Lyford, 1943; Kheirallah, 1979), and food preference may be an important regulatory factor of millipede populations. *Leucaena* litter may be more palatable to millipedes due to higher litter quality reflected in the relatively low C/N and C/P ratios in all litter layers, higher concentration of N and P in Oi litter, and higher N, P, K, Ca, and Mg concentration in the Oe layer compared with the other two species. Overall forest floor mass did not vary, and litter quantity had no significant correlations with soil macroinvertebrate abundance or biomass, suggesting that soil macroinvertebrates were associated with litter quality more than litter quantity. Earthworm distribution was highly variable and patchy throughout the study site. Although *Leucaena* plots had higher earthworm abundance and biomass, treatments did not account for a significant proportion of the variation. The quality of litter substrate has been shown to significantly affect earthworm populations in tropical regions (Zou, 1993; Tian et al., 1995; González and Zou, 1999). However, in the well-drained sandy soils of our study area, spatial variation in soil moisture and texture were probably more important than litter quality in the determination of earthworm abundance and biomass.

Litter decomposition rates are determined by climate, chemical composition of the litter, and soil organisms (Swift et al., 1979). At the global to continental scale, climate and litter chemistry are considered to be the most important factors in the regulation of decomposition rate, and many decomposition studies concentrate on these factors alone as

dependant variables (Meentenmeyer, 1978; Aerts, 1997). In the humid tropics, where climatic variation tends to be less extreme at the landscape scale, litter chemistry and soil organisms play an increasingly important role in decomposition processes (Lavelle et al., 1993; Tian et al., 1993, 1995; Vitousek et al., 1994; González and Seastedt, 2001; Henegan et al., 1999; González et al., 2001). Although biological systems of regulation of decomposition are acknowledged in the humid tropics (Lavelle et al., 1993), little is known about these systems, and how they vary in time and space across resource gradients. The results from this site suggest that millipedes may be influenced by litter chemistry at fairly small spatial scales (meters to decameters), and earthworms are probably more affected by higher order controls such as physical soil conditions. Earthworm populations may respond to plantation species over a sufficient period of time, when litter input and chemistry differences affect soil physical and chemical properties such as soil moisture, pH, and organic matter content.

The abundance of millipedes in the *Leucaena* plots, could have many effects on the biogeochemistry of the plantation system, specifically by influencing the mineralization pathway of organic material. Temperate millipedes have been found to increase the mobilization of nutrients (Anderson et al., 1983), and to be an important factor in a model of nitrogen mineralization (Anderson et al., 1985). Immobilization of nutrients by soil microbes may be reduced or eliminated where millipedes are abundant, due to increasing nitrogen concentration and decreasing C/N ratio between millipede food and feces (Edwards, 1974; Anderson et al., 1983). Increased decomposition and mobilization of nutrients due to millipede activity in *Leucaena* plots may result in higher turnover of litter and nutrients. Using litterfall production data for this site from Parrotta (1999), the litter turnover ratio (k_L) can be roughly estimated using the equation: $k_L = L/X_L$, where k_L is the litter turnover ratio, L the litterfall production and X_L the litter standing crop (Swift et al., 1979). By this estimate, the k_L value is about twice as high in *Leucaena* plantations (0.84) than *Casuarina* (0.48) or *Eucalyptus* (0.38) suggesting a higher decomposition rate. Estimates of N and P turnover ratio are also substantially higher for *Leucaena* litter. N turnover ratio for *Leucaena* litter is approximately 0.97, compared to 0.42 for *Casuarina* and 0.26 for *Eucalyptus*, and P turnover ratio was 0.78 for *Leucaena*, 0.53 for *Casuarina* and 0.23 for *Eucalyptus*. These estimates of litter and nutrient turnover are meant to serve as a useful comparison among plantation treatments, however, should be interpreted with caution. Long term data on litter production and forest floor mass are unavailable to substantiate the assumption of steady state in these plantations.

5.2. Litter chemistry

By separating litter on the forest floor into Oi, Oe, and Oa components, it was our objective to obtain an instantaneous chronosequence of litter in different stages of decay (Brady, 1990). With the exception of C, nutrients tend to increase or remain constant from the Oi to Oa layers (Table 4), suggesting that nutrients remain in an immobilized form in the decomposing litter. Nutrient standing stocks (Table 5) also tend to increase as decomposition progresses, while there are no significant increases in litter mass at each layer. In fact, the highest values of N, P, K, and Ca standing stocks were found in Oe litter in the *Leucaena* plantation (Table 5), which had a relatively low mass (Table 2). The general increase of nutrient standing stocks from the Oi to Oa litter layers further suggest nutrient immobilization in the decaying litter.

N concentration remained constant in litter at each stage of decay, while P concentrations increased from the Oi to the Oe and Oa (Table 4). *Casuarina* litter had a relatively low P content in all litter layers, resulting in a higher C/P ratio. C/P ratio in the Oi was 3478.69 for *Casuarina*, compared to 2311.50 for *Eucalyptus* and 1555.18 for *Leucaena.* The availability of N apparently influenced P mineralization evidenced by the turnover rates of N and P. Sufficiency of N in *Casuarina* and *Leucaena* litter was associated with independent N and P turnover ratios. In *Casuarina* litter, where C/P ratios were the highest, P turnover ratio was higher than that of N (0.53 and 0.42, respectively). The limited availability of P in *Casuarina* litter may be a constraint on N mineralization. High N and P concentrations in *Leucaena* litter resulted in high N turnover ratio (0.97) and high P turnover (0.78) respective to *Casuarina* and *Eucalyptus*.

In contrast, *Eucalyptus* litter maintained C/N ratios similar to *Casaurina*, with lower C/P ratios. Turnover ratios of N and P in *Eucalyptus* litter were similar (0.26 and 0.23, respectively) and much lower than *Casuarina* and *Leucaena*, suggesting N limitation on P mineralization in the decaying litter of *Eucalyptus*.

Although differences in nutrient standing stocks among species treatments (Table 5) are in accordance with values reported by Parrotta (1999), our estimates are much higher due to differences in forest floor mass. The discrepancy is probably due to the accretion of forest floor mass as the plantations matured. Forest floor mass was sampled by Parrotta (1999) when the plantations were 3 years old, as opposed to 9 years old in the present study. Differences in sampling procedure may also have contributed to the differences in litter nutrient standing stocks.

6. Conclusions

Forest floor litter in *Leucaena*, *Casuarina*, and *Eucalyptus* plantations varied in quality, but not quantity. Variation in litter chemistry was highest in the Oi litter layer, where material was intact, and slightly decomposed. N and P concentration in *Leucaena* was higher than *Casuarina* and *Eucalyptus* in the Oi and Oe litter layers, however, litter nutrient concentrations tended to converge by the advance stages of decay. Differences among species in nutrient concentration resulted in differences of nutrient standing stocks of N, P, and K in the Oe layer, and N in the Oi layer of *Leucaena* litter. Higher litterfall productivity (Parrotta, 1999) and higher nutrient concentration in the Oi layer of *Leucaena* litter did not result in higher nutrient standing stocks in this layer, suggesting a faster turnover ratio of these nutrients. In general, nutrient standing stocks for all species increased with later stages of decay.

The fresh weight biomass and abundance of millipedes, and the total fresh weight biomass of soil fauna were higher in *Leucaena* plantations than *Casuarina* or *Eucalyptus*. Millipede biomass was significantly correlated to N concentration and C/N ratio in the Oi litter layer. Earthworm biomass and abundance was not affected by plantation species, and distribution was patchy. Millipede biomass was significantly greater in the top 10 cm of soil than 10–20 cm in *Leucaena* and *Casuarina* plantations, and biomass of other soil macroinvertebrates was also higher in the top 10 cm of *Leucaena* plantations.

The results from our study suggest that the distributions of millipedes and other soil macroinvertebrates are associated with litter quality in these plantations. Macroinvertebrate populations may be an important factor regulating the turnover of nutrients on the forest floor, emphasizing the importance of biological systems of regulation of decomposition in the tropics. Future studies are recommended to investigate litter chemistry and soil fauna communities as interacting controls on decomposition rates in tropical regions. Research integrating soil fauna communities, decomposition, and nutrient cycling is needed to evaluate the effectiveness of present methodology for studying decomposition in the tropics, and to obtain a better understanding of the role of soil macrofauna in litter decomposition in tropical ecosystems.

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