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Fine-root mass, growth and nitrogen content for six tropical tree species

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Abstract Although fine roots might account for 50% of the annual net primary productivity in moist tropical forests, there are relatively few studies of fine-root dynamics in this biome. We examined fine-root distributions, mass, growth and tissue N and C concentrations for six tree species established in 16-year-old plantations in the Caribbean lowlands of Costa Rica in a randomized-block design ($n = 4$). The study included five native species (*Hyeronima alchorneoides*, *Pentaclethra macroloba*, *Virola koschnyi*, *Vochysia ferruginea* and *Vochysia guatemalensis*) and one exotic (*Pinus patula*). Under all species >60% of the total fine-root mass to 1 m deep was located in the uppermost 15 cm of the soil. Fine-root live biomass and necromass (i.e., the mass of dead fine-roots) varied significantly among species but only within the uppermost 15 cm, with biomass values ranging from 182 g m^{-2} in *Pinus* to 433 g m^{-2} in *Hyeronima* plots, and necromass ranging from 48 g m^{-2} in *Pinus* to 183 g m^{-2} in *Virola* plots. Root growth, measured using ingrowth cores, differed significantly among species, ranging from 304 g m^{-2} $year^{-1}$ in *Pinus* to 1,308 g m^{-2} $year^{-1}$ in *Hyeronima*. These growth rates were one to five times those reported for moist temperate areas. Turnover rates of fine-root biomass ranged from 1.6 to 3.0 $year^{-1}$ in *Virola* and *Hyeronima* plots, respectively. Fine-root biomass was significantly and positively correlated with fine-root growth ($r = 0.79$, $P < 0.0001$), but did not correlate with fine-root turnover ($r = 0.10$, $P = 0.20$), suggesting that fine-root accumulation is a function of growth rate rather than mortality. Fine-root longevity was not correlated ($r = 0.20$, $P = 0.34$) and growth was negatively correlated with root N concentration across species ($r = –0.78$, $P < 0.0001$), contrary to reported trends for leaves, perhaps because N was relatively abundant at this site.

Keywords Fine-root biomass · Fine-root necromass · Fine-root turnover · Root ingrowth · Tropical plantations

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Introduction

Fine roots account for a significant proportion of energy and nutrient fluxes in most terrestrial

ecosystems (Jackson et al. 1997). More than 50% of the annual net primary productivity is allocated belowground in many forests (Burke and Raynald 1994; Fahey and Hughes 1994; Hendrick and Pregitzer 1993; Vogt et al. 1983). Nutrient inputs to soils from root litter equal or surpass the return from the aboveground counterpart (Aerts et al. 1992; Sanford Jr and Cuevas 1996), and thereby constitute the main pathway of organic carbon to soil, which is the largest pool of terrestrial carbon (Jobbágy and Jackson 2000). In moist tropical forests fine-root systems have been described as shallow (e.g., Gower 1987; Jackson et al. 1996; but see Nepstad et al. 1994), highly variable spatially (Carvalheiro and Nepstad 1996; Ostertag 1998) and small in comparison with aboveground biomass (Cairns et al. 1997). Nevertheless, this ecosystem has the largest root biomass and one of the highest rates of fine-root production globally (Gill and Jackson 2000; Jackson et al. 1996; Vogt et al. 1996). Even so, measures of fine-root mass and growth have been lacking in most tropical studies, preventing proper quantification of primary productivity and nutrient cycling in those forests (Clark et al. 2001; Lauenroth and Gill 2003; Raich et al. 2006).

Plantations in the tropics have been established to meet an increasing demand for soil protection, improvement of soil fertility and ecosystem recovery in parallel with timber demand (Kobayashi 2004; Parrota et al. 1997). Several studies in tropical plantations have demonstrated that species differ in important aspects such as tissue quality (Lugo 1992; Stanley and Montagnini 1999), nutrient use efficiency (Bigelow et al. 2004; Hiremath et al. 2002; Smith et al. 1998) and growth (González and Fisher 1994); as well as in their influence on ecosystem traits such as soil fertility (Fisher 1995) or understory biodiversity (Parrota et al. 1997; Powers et al. 1997). Nonetheless, most studies have focused on aboveground traits; relatively little attention has been paid to belowground processes such as fine-root dynamics. Studies that included this component, however, indicate that species vary strongly in growth rates and that these differences can significantly affect nutrient availability and soil carbon accrual in ecosystems (Binkley and Ryan 1998; Russell et al. 2004).

Annual production of fine roots often exceeds their mean biomass (Gill and Jackson 2000). Fine-root production and mortality appear to occur simultaneously during the year and the stocks of live and dead roots reflect only the end products of these processes. In other words, fine-root accumulation in any ecosystem is ultimately controlled by the magnitude of root growth and turnover rates in the system (Santantonio and Grace 1987). Comparing these fine-root dynamics, production and mortality, thus provides a basis for identifying contrasts among species (Burke and Raynald 1994; Ruess et al. 2003).

Fine-root dynamics can also be evaluated by considering trends already described between chemistry and demography in plant tissues (Eissenstat and Yanai 1997; Espeleta and Donovan 2002; Ryser and Lambers 1995). It is thought that plants balance growth rates, nitrogen concentration and longevity in order to maximize resource acquisition (Bloom et al. 1985). So, fast-growing structures tend to have relatively high nitrogen concentrations and short life spans, whereas slow-growing structures have relatively low nitrogen concentrations and slower turnover rates (Poorter et al. 1990). However, evidence for this hypothesis is based upon aboveground observations (Reich et al. 1992, 1997). Belowground studies are still lacking in most forest ecosystems, and little is known about the relationships among growth rates, nitrogen concentration and lifespan in fine roots, especially for tropical woody species (Pregitzer et al. 2002).

In this study we examined fine roots in single-species plantations of six tropical tree species (Table 1). Our objectives were to compare these species in terms of fine-root vertical distribution, biomass, C and N concentrations, growth and turnover rates. We hypothesized that fine-root biomass would be positively related to root production across species. Further, we hypothesized that live fine-root N concentration would correlate negatively with mean fine-root lifespan and positively with root growth rate across species, following trends previously described for foliar tissues (Poorter et al. 1990; Reich et al. 1997).

Table 1 Characteristics of the species compared in this study

Species	Family	Acronym	Tree size[a]	
			Height (m)	DBH (cm)
Hyeronima alchorneoides	Euphorbiaceae	HYAL	30.1	23.3
Pentaclethra macroloba	Fabaceae/Mimosoidae	PEMA	18.8	22.0
Pinus patula	Pinaceae	PIPA	29.2	29.1
Virola koschnyi	Myristicaceae	VIKO	24.8	23.3
Vochysia ferruginea	Vochysiaceae	VOFE	31.0	35.4
Vochysia guatemalensis	Vochysiaceae	VOGU	33.3	31.9

Tree size corresponds to maximum tree height and mean diameter in the plantations in 2005

[a] Source: http://www.nrem.iastate.edu/ECOS/species.html

Methods

Study site

Field studies were conducted at La Selva Biological Station, in the Atlantic lowlands of Costa Rica (10°26′N, 83°59′W). Mean annual rainfall is 3,960 mm with >150 mm of precipitation on average every month (Sanford Jr et al. 1994). The mean temperature is 25.8°C with minimal variation across the year. The experimental plantations were established in 1988 on a recently abandoned pasture that had been grazed intensively for approximately 30 years. The plots occupy a hilly upland area with elevations of 44–89 m. The soil was classified as a Typic Tropohumult (Ultisol) by Sollins et al. (1994), but was re-classified as a Typic Haploperox (Oxisol; Kleber et al. 2006). This residual soil in the Matabuey consociation is characterized by high organic content, low degree of base saturation, high exchangeable acidity and an argillic horizon (Sollins et al. 1994).

Originally the experiment included 11 tree species planted in monoculture and one unplanted control area established in a randomized complete block design with four replicates (González and Fisher 1994; Fisher 1995). Each block contained twelve 0.25-ha plots with 3 m × 3 m tree spacing. Soil baseline data were collected in 1987, before tree planting, and tree growth was measured from 1988 to 1994 (González and Fisher 1994). There were no maintenance activities between 1995 and 2002.

The six species considered in this study were *Hyeronima alchorneoides* Allemao, *Pentaclethra macroloba* (Willd) Kunth., *Virola koschnyi* Warb, *Vochysia ferruginea* Mart., *Vochysia guatemalensis* Donn. Sm. and the exotic species *Pinus patula* subsp. *tecunumanii* (Eguiluz and J.P. Perry) Styles (basionym, *Pinus tecunumanii* Eguiluz and J.P. Perry), hereafter referred to as *Pinus patula*. They vary in traits such as aboveground growth rates (González and Fisher 1994), canopy height (Haggar et al. 1997), understory regeneration (Powers et al. 1997) and rooting depth (Fisher 1995; Table 1). The native species are harvested from natural forests for timber purposes and, excepting *Pentaclethra macroloba*, which is the dominant species in local forests (Hartshorn and Hammel 1994), all are grown in plantations for timber production. *Vochysia guatemalensis*, *Vochysia ferruginea* and *H. alchorneoides* are the main species in Costa Rican reforestation projects whereas *Virola koschnyi* is planted just locally (Petit and Montagnini 2004; Piotto et al. 2003). *Pinus patula* is not planted in the region but it is extensively cultivated at higher elevations (Dvorak 2002).

Analysis of fine-root biomass and depth distribution

In each of the plots the two external rows of trees were buffer areas in which no sampling was done. Measurements were made inside the internal 30 m × 30 m square, which was

subdivided into four 15 m × 15 m quadrants. Samples were distributed evenly among quadrants to maintain representative plot sampling. Sample location inside each quadrant was randomly selected. Standing stock of fine roots was determined by collecting six soil cores, 15 cm deep by 5.35 cm in diameter, in each plot (24 samples per treatments) with a metal corer. Samples were collected twice (May–July in 2004 and again in 2005). In addition, we sampled to 30 cm for one sample per plot in 2004 and three samples per plot in 2005, to determine fine-root mass differences between 0–15 and 15–30 depths. Fine-root mass located below 30 cm depth was determined by sampling from the walls of soil pits dug for another study. A single 1.00 m × 0.75 m × 1.00-m-deep soil pit was excavated in each plot between February and April 2005. From each pit, four aluminum cylinders (150-ml volume each) were inserted into the wall of the pit, spaced evenly along the depth interval, to sample a total of 600 cm^3 per depth interval. Leaf-cutter ants (*Atta cephalotes*) have active nests on the plots; obvious nests were excluded in all pit sampling.

All samples were placed in plastic bags, refrigerated immediately upon return to the lab and processed within 2 days following harvest. Each core was soaked at least 2 h; most of them for 12 h, before being processed in a hydropneumatic elutriation system (Smucker et al. 1982) with 530-μm mesh filters. We defined fine roots as all non-woody roots, most of which were <2 mm in diameter. *Hyeronima* and *Virola* produced non-woody, succulent roots >2 mm in diameter. Fine roots were sorted as live (hereafter 'fine-root biomass') or dead (hereafter 'fine-root necromass') based on visible appearance, texture, color and friability, oven-dried to 65°C and weighed to an accuracy of ±0.0001 g. Although the planted species wholly dominated the canopy, the plots were not monocultures; they contained other species regenerating beneath the canopy. We did not sort roots by individual species, so it must be noted that for all variables measured, the effect of 'species' refers to the entire treatment effect of the planted species, including the contribution from understory regeneration.

Analysis of fine-root ingrowth

We measured fine-root ingrowth by installing five 15-cm deep, 5.35-cm diameter ingrowth cores per plot (20 cores per treatment). Ingrowth cores were constructed of polyethylene tubing (8-mm mesh size) with 2-mm nylon mesh screens for tops and bottoms. Cylinders were filled with sieved root-free soil extracted from the same plot; cylinders were packed at the same density as the soil. In an earlier study in other plantations at La Selva, Russell et al. (2004) tested this method extensively and found that 4-month intervals were optimal for assessing ingrowth. Thus, root-free cores were installed three times in this study: June 2004; November 2004; and March–April 2005. They were removed systematically the following November 2004, March 2005 and June–July 2005. During extractions, roots outside the cylinders were cut flush and discarded. The samples were then processed in the same manner as biomass samples, except that we did not sort into live and recently senesced roots. We defined annual ingrowth production as the sum of ingrowth mass measured over the three seasons corrected to 365 days. Fine-root turnover was determined as annual fine-root ingrowth divided by the average fine-root biomass at the 0–15 cm depth, and the mean lifespan of fine-root biomass was determined as the inverse of the turnover rate (e.g., Gill and Jackson 2000).

Tissue chemistry analysis

Tissue chemistry was characterized for each treatment by analyzing live and dead roots for C and N concentration. For the biomass study, roots sampled from all the quadrants within the same plot each year were combined and ground; live and dead roots were kept as separate fractions. Ingrowth roots (live + senesced) within each plot were similarly combined and ground in each measurement. Carbon and N contents were determined using a CE Elantech Flash EA 1112 C–N elemental analyzer (CE Instruments, Milan, Italy). All data are presented as 65°C dry weights.

Statistical analyses

Vertical root distribution was modeled by the equation (Gale and Grigal 1987):

$$Y = 1 - \beta^d \quad (1)$$

where d is depth (cm), Y is the proportion of roots from the surface to depth d and β is a numerical index of rooting distribution. High values of β indicate greater proportion of roots with depth (Jackson et al. 1997). The proportional mass of roots in the profile was calculated to depths of 0, 15, 30, 50, 75 and 100 cm using mean values from each plot ($n = 4$ per species at each depth). Differences among species in root depth distribution were tested with linear regression analysis of the log-transformed β data. Species-specific differences in actual total fine-root biomass (0–100 cm depth) and dead:live root ratio were evaluated using analysis of variance (ANOVA). For the response variables fine-root biomass and necromass; fine-root nitrogen and carbon concentration; fine-root C:N; and ingrowth rate (all at 0–15 cm), a repeated-measures ANOVA was applied, with species and block as the main factors, their interaction as a random factor, and time as the repeated-measure factor. Only the necromass variable was square-root transformed to meet the ANOVA assumptions of normal distribution of residuals and equality of variance. When effects were significant, multiple comparisons were made using the Tukey–Kramer HSD test ($\alpha = 0.05$).

If fine-root biomass is a function of root production, then differences in fine-root accumulation among species would correlate significantly with differences in ingrowth rates. Alternatively, if mortality is the main factor explaining variation in fine-root accumulation we would expect a significant correlation between root biomass and turnover rates. We tested these alternatives using pair-wise correlation analyses between ingrowth rate and turnover rate of fine-root biomass, using mean values from each plot ($n = 24$). Also, we performed a similar analysis between fine-root necromass and fine-root ingrowth rates, assuming that mortality would equal root growth inputs among species. There were no differences observed in total fine-root mass between years (see below). To test our second hypothesis, pair-wise correlation analyses were performed to evaluate the relationship between fine-root nitrogen concentration with fine-root ingrowth and mean fine-root lifespan, as well as the relationship between C:N ratio with fine-root ingrowth rates. All statistical analyses were performed using JMP data analysis software (version 5.1.2, SAS Institute, NC, USA).

Results

Vertical pattern of fine-root distribution and stand biomass and necromass

All the species had relatively shallow fine-root systems with >60% of the total mass (live plus dead) situated in the upper 15 cm and 77–89% located in the first 30 cm. Fine-root mass declined exponentially with depth for all species with β values averaging 0.943. *Hyeronima* plots had the lowest index of rooting distribution (0.941), whereas *Pinus* had the highest (0.946); nevertheless, values of β did not differ significantly among species ($P = 0.36$; Fig. 1). The index of root distribution among plots ($\beta = 0.943$) was lower than the average estimate for tropical evergreen

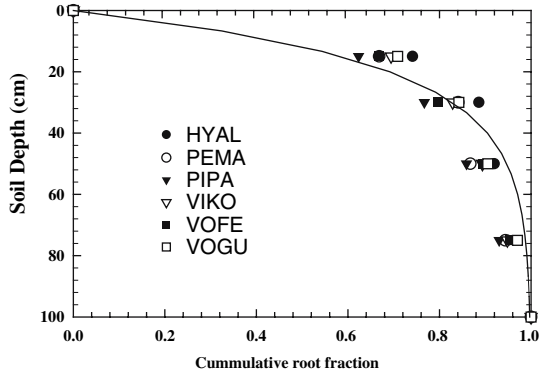

Fig. 1 Cumulative root distribution as a function of root depth for six tropical species in 16-year-old plantations in lowland Costa Rica. Fit equation is $Y = 1 - \beta^d$, where Y is the cumulative root fraction (proportion between 0 and 1) with depth (d in cm) and β is the fitted parameter (Gale and Grigal 1987). The *curve* indicates the least square fit of β for all species ($\beta = 0.943$). *Acronyms* for species are defined in Table 1

forests (β = 0.972; Jackson et al. 1997), indicating that the fine-root systems in the study site were relatively shallow in comparison with the average for this biome.

Total fine-root mass, the live:dead fine-root proportion and live fine-root N and C mass differed among species, but only in the uppermost 15 cm ($P < 0.0001$ for total fine-root mass, $P = 0.006$ for live:dead ratio, Table 2; $P < 0.0001$ for both N and C live fine-root mass, Table 3). The total amount of roots in the uppermost layer did not differ significantly between years (time $P = 0.26$; time × species $P = 0.52$). *Hyeronima* plots with 602 g m^{-2} had the largest total fine-root biomass, although not significantly different from *Virola* or *Vochysia guatemalensis* plots, which contained 597 and 580 g m^{-2}, respectively. *Pinus* plots with 286 g m^{-2} had significantly lower fine-root biomass than *Hyeronima*, *Virola* and *Vochysia guatemalensis* plots, but were similar to *Pentaclethra* and *Vochysia ferruginea* plots, which had 488 and 392 g m^{-2} on average, respectively ($P < 0.05$; Table 2). *Virola* plots had the highest fine-root necromass, which accounted for 29% of the total fine-root mass. Dead fine-roots in *Vochysia guatemalensis* plots comprised only 13% of the total fine-root mass, the lowest proportion among species ($P < 0.005$; Table 2). Mean dead:live root ratio was higher in *Virola* (0.40) than in *Vochysia guatemalensis* plots (0.15), whereas the remaining species had intermediate values (Table 2). Total N in fine-root systems averaged 5.34 g N m^{-2} in the uppermost 15 cm, differing significantly among species. *Vochysia ferruginea* and *Pinus* plots had the lowest fine-root N stocks (4.33 and 2.91 g N m^{-2}, respectively, Table 3).

Fine-root ingrowth and turnover rates

Ingrowth rates in the uppermost 15 cm did not differ through time under any of the species ($P = 0.30$), indicating no seasonality in root growth over the year of this study. Species differed significantly in fine-root growth rates, however ($P = 0.0001$; Table 4). *Hyeronima* and *V. guatemalesis* plots had the highest ingrowth rates, up to 1,300 g m^{-2} year^{-1}, 3.4 times higher on average than that of *Pinus* plots. Across species, fine-root ingrowth rate was correlated with fine-root biomass ($P < 0.0001$, $r = 0.79$, $n = 24$; Fig. 2), but uncorrelated with necromass ($P = 0.20$, $r = 0.26$, $n = 24$). This suggests that fine-root biomass was closely related to growth rates, but that dead fine-root mass was not related to the detritus inputs. Fine-root biomass turnover rates also differed among species ($P = 0.03$) with rates in *Hyeronima* plots nearly twice as fast as

Table 2 Fine-root biomass and necromass (g m^{-2}) in five soil depths and dead:live fine-root ratio for six tropical tree species in 16-year-old single-species plantations in lowland Costa Rica

Species depth (cm)	HYAL	PEMA	PIPA	VIKO	VOFE	VOGU
Live roots						
0–15	433 (34)^{A}	311 (42)^{AB}	182 (21)^{B}	386 (42)^{A}	247 (19)^{B}	405 (59)^{A}
15–30	84 (12)	86 (31)	42 (9)	71 (20)	49 (12)	78 (7)
30–50	23 (12)	16 (7)	24 (8)	47 (20)	50 (14)	40 (3)
50–75	22 (7)	43 (12)	17 (7)	44 (21)	25 (14)	38 (14)
75–100	40 (11)	30 (20)	21(4)	49 (26)	20 (11)	19 (7)
Dead roots						
0–15	125 (18)^{AB}	93 (17)^{BC}	48 (4)^{D}	183 (20)^{A}	88 (12)^{BCD}	73 (7)^{CD}
15–30	25 (7)	42 (17)	12 (3)	43 (14)	17 (1)	10 (2)
30–50	3 (3)	0 (0)	9 (5)	6 (3)	2 (2)	1 (<1)
50–75	<1 (<1)	3 (3)	9 (4)	1 (1)	6 (5)	3 (2)
75–100	<1 (<1)	2 (2)	4 (3)	1 (<1)	5 (3)	<1 (<1)
Dead:live ratio						
0–100	0.26 (0.01)^{AB}	0.28 (0.03)^{AB}	0.29 (0.04)^{AB}	0.40 (0.03)^{A}	0.32 (0.06)^{A}	0.15 (0.01)^{B}

Acronyms for species are defined in Table 1. Values are means (standard error; $n = 4$). Different letters indicate significant differences among species for a given depth (Tukey–Kramer HSD test; $\alpha = 0.05$)

Table 3 Live fine-root nitrogen and carbon mass (g m^{-2}) in five soil depths for six tropical tree species in 16-year-old single-species plantations in lowland Costa Rica

Species depth (cm)	HYAL	PEMA	PIPA	VIKO	VOFE	VOGU
Nitrogen mass						
0–15	5.90 (0.41)^{A}	6.43 (0.50)^{A}	2.91 (0.29)^{B}	6.05 (0.50)^{A}	4.33 (0.28)^{AB}	6.44 (0.72)^{A}
15–30	1.15 (0.12)	1.82 (0.67)	0.68 (0.16)	1.12 (0.30)	0.85 (0.22)	1.24 (0.12)
30–50	0.28 (0.13)	0.22 (0.07)	0.27 (0.09)	0.68 (0.28)	0.48 (0.14)	0.43 (0.08)
50–75	0.24 (0.08)	0.63 (0.14)	0.11 (0.06)	0.64 (0.27)	0.24 (0.14)	0.37 (0.13)
75–100	0.41 (0.08)	0.41 (0.21)	0.25 (0.07)	0.64 (0.33)	0.21 (0.12)	0.19 (0.06)
Carbon mass						
0–15	194 (19)^{A}	147 (14)^{AB}	79 (7)^{C}	181 (16)^{A}	109 (10)^{BC}	174 (21)^{A}
15–30	38 (5)	41 (15)	18 (4)	33 (9)	21 (6)	33 (3)
30–50	10 (5)	7 (2)	11 (4)	22 (10)	23 (7)	17 (1)
50–75	10 (3)	19 (4)	7 (3)	21 (10)	12 (6)	16 (6)
75–100	18 (5)	13 (6)	8 (2)	23 (13)	9 (5)	8 (3)

Acronyms for species are defined in Table 1. Values are means (standard error; $n = 4$). Different letters indicate significant differences among species for a given depth (Tukey–Kramer HSD test; $\alpha = 0.05$)

Table 4 Annual fine-root ingrowth and turnover rates for six tropical species in 16-year-old single-species plantations in lowland Costa Rica

Species	Ingrowth rate (g m^{-2} $year^{-1}$)	Turnover rate ($year^{-1}$)	
		Biomass	Carbon
Hyeronima alchorneoides	1,304 (159)^{A}	2.98 (0.15)^{A}	2.93 (0.19)^{A}
Pentaclethra macroloba	641 (73)^{BC}	2.12 (0.20)^{AB}	2.12 (0.25)^{AB}
Pinus patula	382 (44)^{C}	2.21 (0.41)^{AB}	2.21 (0.40)^{AB}
Virola koschnyi	614 (83)^{BC}	1.60 (0.16)^{B}	1.56 (0.14)^{B}
Vochysia ferruginea	518 (18)^{C}	2.13 (0.17)^{AB}	2.18 (0.18)^{AB}
Vochysia guatemalensis	1,068 (219)^{AB}	2.64 (0.34)^{AB}	2.82 (0.38)^{A}

Values are means (standard error, $n = 4$) for the uppermost 15 cm of soil only. Different letters indicate significant differences among species (Tukey–Kramer HSD test; $\alpha = 0.05$)

those of *Virola* (Table 4). The remaining species had intermediate values. Turnover rates were uncorrelated with fine-root biomass across plots ($P = 0.63$, $r = 0.10$).

Root C and N concentration

Live root N concentration decreased with depth ($P > 0.0001$), which is consistent with observed trends in temperate broadleaf fine-root systems (Pregitzer et al. 1998). Among species, live root C and N concentrations were significantly different in the uppermost 15 cm ($P < 0.0001$ for both elements; Table 5). Mean live root N concentration was 1.67% among species. *Pentaclethra*, an N-fixing tree, had the highest root N concentration while *Hyeronima* had the lowest (Table 5). Carbon concentration averaged 44.8% among species with the highest values in *Virola* and *Pentaclethra* plots (Table 5). The C:N values were relatively narrow for fine roots. Indeed, the C:N ratio range in this study (22–32) was narrower than the global average reported for roots ≤2 mm in diameter (43–45; Gordon and Jackson 2000; Jackson et al. 1997) but similar to ratios reported for first- and second-order roots of temperate broadleaf-species (Pregitzer et al. 2002). As reported in previous studies (Aerts 1990; Nambiar 1987) we found no difference in fine-root N concentration or C:N ratio between live and dead fine-roots. The only exception was in the *Virola* plots, where dead-root N concentration was slightly higher than live fine-roots (*t*-test; $P < 0.01$; Table 5).

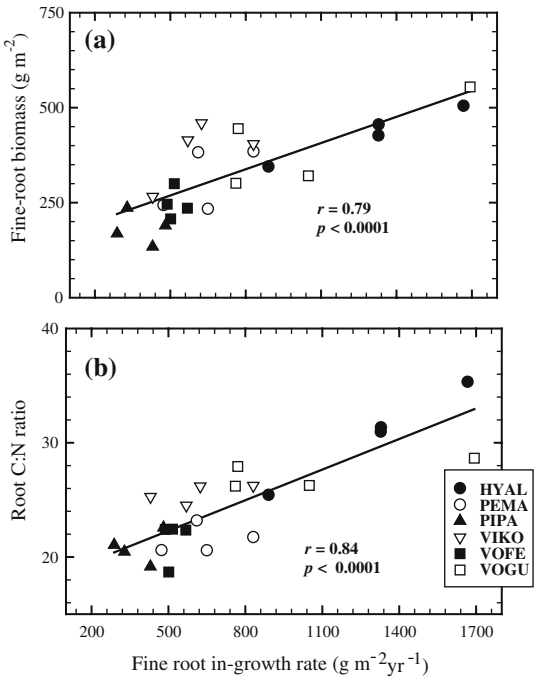

Fig. 2 Relationship of fine-root ingrowth rates with **a** live fine-root mass and **b** fine-root C:N ratio among six tropical tree species in lowland Costa Rica. Comparisons were made with mean plot values for each variable (n = 24). *Acronyms* for species are defined in Table 1

Fine-root growth was positively correlated with root C:N ratio ($P < 0.0001$, $r = 0.84$, $n = 24$; Fig. 2) and negatively correlated with fine-root N concentration ($P < 0.0001$, $r = -0.78$, $n = 24$; Fig. 3). This suggests that species with low root N concentration grew faster than species with higher N concentration. This is contrary to the hypothesized trend based on patterns described for leaves, but is consistent with trends described for fine-root systems of temperate tree species (Withington et al. 2006). Across species, mean fine-root lifespan was not correlated with live fine-root N concentration ($P = 0.34$, $r = 0.20$, $n = 24$; Fig. 3), which is inconsistent with our hypothesis that roots with higher N concentration would have a shorter lifespan.

Discussion

Our objectives were to describe fine-root systems in terms of vertical distribution, mass and root growth rates in single-species plantations of six tropical trees. Further, we determined fine-root carbon and nitrogen concentrations to test whether fine-root turnover was related to root nutrient status in a manner analogous to leaves.

Vertical distribution and mass of fine roots

Consistent with previous studies in moist tropical forests, fine-root biomass decreased exponentially with soil depth (Cairns et al. 1997; Jobbágy and Jackson 2000; Raich 1983). The index of rooting distribution in our plots indicated that fine-root systems in our plots are shallower than the average for this biome (Jackson et al. 1997). Sollins et al. (1994) reported that the clay content in this soil (Matabuey consociation) increased from 41% in the A horizon (0–18 cm) to 62% in the underlying argillic horizon, which parallels the

Table 5 Nitrogen and carbon concentrations and C:N for live and dead fine-roots in the uppermost 15 cm of six tropical species in 16-year-old single-species plantations in lowland Costa Rica

Species	Live roots			Dead roots		
	N (%)	C (%)	C:N	N (%)	C (%)	C:N
Hyeronima alchorneoides	1.39 (0.08)^{C}	44.7 (0.2)^{B}	32.6 (1.5)^{A}	1.41 (0.07)^{B}	43.6 (0.3)^{BC}	31.2 (1.3)^{A}
Pentaclethra macroloba	2.09 (0.08)^{A}	47.3 (0.5)^{A}	22.8 (0.8)^{D}	2.10 (0.12)^{A}	44.8 (0.9)^{AB}	21.8 (1.5)^{B}
Pinus patula	1.60 (0.07)^{BC}	43.8 (0.6)^{B}	27.7 (1.1)^{BC}	1.66 (0.07)^{B}	42.5 (0.4)^{C}	25.8 (1.2)^{AB}
Virola koschnyi	1.58 (0.04)^{BC}	46.8 (0.5)^{A}	29.7 (0.6)^{AB}	1.67 (0.05)^{B,a}	46.4 (0.7)^{A}	27.8 (0.8)^{AB}
Vochysia ferruginea	1.77 (0.11)^{B}	43.7 (0.7)^{B}	25 (1.2)^{CD}	1.75 (0.06)^{AB}	42.3 (0.6)^{CD}	24.2 (0.7)^{B}
Vochysia guatemalensis	1.59 (0.04)^{BC}	42.8 (0.5)^{B}	26.9 (0.6)^{BC}	1.68 (0.09)^{B}	40.25 (0.4)^{D}	24.5 (1.7)^{B}

Values are means (standard error, n = 4). Different letters within columns indicate significant differences among treatments (Tukey–Kramer HSD test; $\alpha = 0.05$)

[a] Nitrogen concentration was significantly higher than that in life fine-roots ($P < 0.01$)

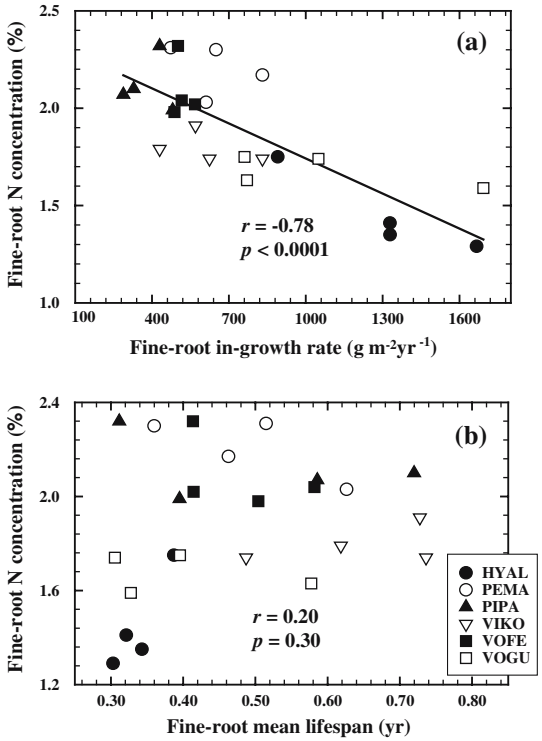

Fig. 3 Relationship of fine-root nitrogen concentration with **a** fine-root ingrowth and **b** fine-root lifespan among six tropical tree species in lowland Costa Rica. Comparisons were made with mean plot values for each variable (n = 24). *Acronyms* for species are defined in Table 1

abrupt decrease in root biomass observed for all the species. Further, the soil organic carbon content among plots had a similar trend with the highest values in the first 15 cm and an exponential decline with depth (Russell et al., submitted for publication). These data suggest that increasing clay content with depth might impede fine-root growth deeper in the profile. Thus, we hypothesize that soil texture plays a role in confining fine-root growth to a shallow depth, and that this abiotic factor overrides species-specific differences in rooting-depth patterns.

Fine-root biomass in the upper 15 cm across all study plots averaged 328 g m^{-2} (Table 2), which is higher than previous values at similar depth for fine-root biomass in La Selva (Gower 1987; Raich 1980), but consistent with the averaged 330 g m^{-2} reported for tropical evergreen forests (Jackson et al. 1997). The low fine-root biomass values observed in the *Pinus* plots are consistent with other tropical studies that compared *Pinus* plantations with broad-leaved species (Cavelier and Santos 1999; Cuevas et al. 1991). The fine-root biomass values for the broadleaf-species in our study are similar to those reported for similar soils (Ultisol–Oxisol) and depths in 9-year-old *Eucalyptus robusta*, *Leucaena leucocephala* and *Casuarina equisetifolia* plantations (Parrota 1999) and 11-year-old secondary forests (Cuevas et al. 1991). Several authors have found consistent differences in fine-root biomass between adjacent successional and mature forests, even after several decades of succession (Cavelier et al. 1996; Hertel et al. 2003; Sanford Jr 1989). The differences are normally attributed to differences in stand age rather than species composition. The significant positive relationship between fine-root growth and biomass that we found indicates that species-specific variations in fine-root growth contribute to stand-level differences in fine-root biomass. Thus, we conclude that species identity can be an important factor explaining fine-root biomass differences among stands, especially in plantations or secondary succession where a single species can account for most of the stand biomass (Guariguata and Ostertag 2002).

Fine-roots dynamics

The ingrowth core technique has been recommended for estimating root productivity in fast-growing root systems (Vogt et al. 1998) and has been repeatedly used in tropical soils (Cuevas et al. 1991; Cuevas and Medina 1988; Ostertag 1998; Russell et al. 2004). Among our studied species, fine-root ingrowth rates averaged 754 g m^{-2} $year^{-1}$, which is in the upper range of rates observed in tropical ecosystems (Lauenroth and Gill 2003). Similar to results from temperate (Aerts et al. 1992; Coleman et al. 2000; Espeleta and Donovan 2002; Matamala et al. 2003) and tropical areas (Binkley and Ryan 1998; Russell et al. 2004), tree species differed substantially in root growth. The slow root growth rates observed for *Pinus* in this study were similar to other tropical *Pinus* ingrowth rates in plantations (Cuevas et al. 1991). The high root growth rates we observed for other species, notably *Hyeronima* and *Vochysia guatemalensis*, >1,000 g m^{-2} $year^{-1}$,

were similar to those reported in Amazonian forests growing on highly weathered soils (Cuevas and Medina 1988; Sanford Jr and Cuevas 1996).

High fine-root growth was coupled with rapid turnover rates in our study. Although rapid fine-root turnover is expected in tropical lowlands (Lauenroth and Gill 2003), the observed rates in this study, which ranged from 1.6 to 3.0 year^{-1}, were higher than those reported for other tropical forests (average 0.8 year^{-1}; Gill and Jackson 2000). In fact, mean biomass turnover coefficients for *Hyeronima* and *Vochysia guatemalensis* plots are among the highest ever reported. Cuevas and Medina (1988) found that fine-root growth rates were considerably higher on weathered soils because nutrients such as Ca, P and Mg can be easily leached or occluded in these soils. In this setting, shallow, highly dynamic root systems would be advantageous for capturing nutrients from fresh litter (Jordan and Escalante 1980; Whitmore 1998). A consequence of a shallow root system is that it increases the exposure of roots to higher temperatures, drought, physical damage and pathogens, potentially decreasing their life-span (Eissenstat et al. 2000). These concepts are consistent with our findings.

Although there is evidence that fine-root dynamics vary among tree species (Aerts et al. 1992; Coleman et al. 2000; Matamala et al. 2003), most studies in the tropics have focused on external factors controlling root appearance and disappearance, such as nutrient availability (Giardina et al. 2004; Gower 1987), soil moisture (Yavitt and Wright 2001), rainfall seasonality (Green et al. 2005) or litterfall inputs (Sayer et al. 2006) rather than in inherent differences among species in root production and longevity. This study demonstrated that tropical tree species vary in fine-root production. Further, it indicated that live fine-root mass is closely related to differences in growth rates among species whereas turnover is not, suggesting that root accumulation is controlled by root production rather than mortality, as reported previously (Pregitzer et al. 2000). There is increasing evidence that species vary in fine-root architecture and that differences in root branching patterns influence root chemistry and dynamics (Guo et al. 2004; Pregitzer et al. 2002). Further studies could disclose patterns in fine-root dynamics not observed in our study.

A remarkable result in our study was the differences found among species in necromass. Although Jackson et al. (1997) reported that necromass comprises on average 40% of the total fine-root mass in moist tropical forest this compartment is infrequently quantified. In our case fine-root necromass ranged from 13 to 29% of total biomass, with significant differences among species. This indicates that dead roots have accumulated at different rates depending upon the dominant species. Since fine-root biomass was similar among years in this study, fine-root growth and detritus production must be similar. Thus, it is possible to determine whether fine-root necromass is more a function of dead-root inputs or dead-root decay. We found a poor correlation between fine-root necromass and fine-root ingrowth rates, suggesting that dead-root stocks across species are not related to fine-root mortality. Thus, we hypothesize that differences in decomposition rates explain the differences among species in necromass stocks. Root decomposition studies from the tropics are scarce (Silver and Miya 2001), and the data that do exist may be inaccurate due to methodological bias (Dornbush et al. 2002). These studies provide only scarce reference to species composition (Ostertag and Hobbie 1999); hence, this is a promising field for future research.

Differences in fine-root growth and turnover among species might drive important belowground processes. For instance, Matamala et al. (2003) described the impact of fine-root turnover on soil carbon pools for temperate tree plantations. They reported that a *Liquidambar styraciflua* plantation produced 45–50% more fine roots that turned over twice as fast as those in a *Pinus taeda* plantation, leading to a significant increase in soil C concentration. Fine-root ingrowth rates observed in our 16-year-old *Hyeronima* plots were three to six times higher than those reported from two 9-year-old *Hyeronima* plantations at La Selva on alluvial soils, using identical techniques (Russell et al. 2004), suggesting that soil properties have a large effect on fine-root growth rates. Soil organic carbon concentrations in those plots were between 33 and 37 g kg^{-1} (Russell et al.,

submitted for publication) compared with 49 g kg^{-1} in our plots, indicating a proportional relationship between fine-root carbon inputs and SOC accrual.

Nutrient availability might also be influenced by fine-root dynamics and tissue traits. For instance, live fine-root N mass was similar between *Hyeronima* and *Virola* plots and relatively lower than that in *Pentaclethra* plots. However, when fine-root turnover is considered, *Hyeronima* plots cycled the largest amount of N via fine-root inputs to the ecosystem, whereas *Pentaclethra* and *Virola* plots cycled on average 20 and 40% less N, respectively. Differences detected in dead-root accumulation could also affect nutrient availability. The presence of dead roots may influence not only mineralization rates but also the dominant forms of N in the soil (Ehrenfeld et al. 1997), which would have an important role in nitrogen availability (Roy and Singh 1995) and soil biological activity (Wardle et al. 2004). Further investigation is necessary to understand the extent to which dominance of single tropical species can modify those processes.

Root dynamics and N content

Because leaves are more readily observed than roots and theories are better developed, trends for leaves have been used as a framework to interpret fine-root dynamics (Eissenstat and Yanai 1997; Reich et al. 1998; Ryser 1996). Leaf lifespan and growth rates have been repeatedly associated with tissue nitrogen concentration (Reich et al. 1992, 1997). If the same relationship holds for fine roots, then we would expect fine-root lifespan to decline as root N increases among species. The results of our study did not support this hypothesis, but are consistent with trends reported by Withington et al. (2006), who used a similar approach. One possible reason for this finding could be that nitrogen is not a limiting nutrient at this site. The high N concentration in roots as well as the remarkably high flux of N in litterfall in these plots (Raich et al., in press) indicates that N is particularly abundant. In contrast, Gower (1987) found in the same study area a negative relationship between fine-root biomass and soil P availability, whereas Silver and Miya (2001) found a global positive relationship between fine-root decomposition and root Ca content. Both studies suggest that those elements rather than N might be important in defining fine-root dynamics in some tropical ecosystems (e.g., Vitousek and Sanford Jr 1986).

In conclusion, our findings indicate that species identity plays an important role in defining fine-root biomass pools in tropical ecosystems, and that different tree species produce fine roots with different turnover rates. Results suggest that differences among species in root growth rates determine equivalent differences in live fine-root storage, whereas decomposition may be more critical in explaining fine-root necromass. In contrast with the global negative relationship between tissue longevity and N concentration found in leaves (Reich et al. 1997), among-species differences in fine-root lifespan did not correlate with root N concentration, but growth rates did correlate positively with root C:N.

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