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Fine Root Distribution in a Lower Montane Rain Forest of Panama

Dirk Hölscher[1], **Bianca Dunker, Marco Harbusch**

Tropical Silviculture and Forest Ecology, Burckhardt Institute, University of Göttingen, Büsgenweg 1, 37077 Göttingen, Germany

and

Marife Corre

Soil Science of Tropical and Subtropical Ecosystems, Büsgen Institute, University of Göttingen, Büsgenweg 2, 37077 Göttingen, Germany

ABSTRACT

In a Panamanian lower montane rain forest we: (1) analyzed the vertical and horizontal distribution of fine roots; and (2) assessed the relationship of fine root mass to thickness of the soil organic layer, soil pH, and soil-extractable nitrogen. The soil in the study area has developed on volcanic ash deposits and was classified as Hapludand. In randomly distributed samples, the median fine root mass (biomass and necromass, diam $\leq$ 2 mm) to a depth of 100 cm mineral soil was 544 g/m^2, 41 percent of which was found in the organic layer. Fine root mass was approximately twice as high in the vicinity of stems of the tree species *Oreomunnea mexicana* (1069 g/m^2) and the palm species *Colpothrinax aphanopetala* (1169 g/m^2) and was associated with thick organic layers. The median thickness of the soil organic layer in a larger random sample ($N = 64$) was 8 cm with a considerable variation (interquartile range: 7 cm). In these samples, the density of fine root biomass was correlated with the concentration of extractable nitrogen ($r = 0.33$, $P = 0.011$), and on an areal basis, fine root biomass in the organic layer increased with increasing thickness of the organic layer ($r = 0.63$, $P < 0.001$) and decreasing pH_{KCl} ($r = -0.33$, $P < 0.01$). Fine root biomass in the upper mineral soil did not show significant correlations with any of the studied parameters.

Abstract in Spanish is available at http://www.blackwell-synergy.com/loi/btp.

Key words: *Colpothrinax aphanopetala*; *Oreomunnea mexicana*; organic layer; nitrogen; pH.

FINE ROOT MASS IN TROPICAL FORESTS tends to increase with elevation while the aboveground forest biomass decreases (Leuschner *et al.* 2007, Hertel & Leuschner in press). Within montane forests, the soil organic layer is often thick and also a substrate wherein fine roots are highly abundant. In a Costa Rican upper montane forest, the organic layer was on average 19-cm thick and fine root density in the organic layer was four times as high as the fine root density in the mineral topsoil (Hertel *et al.* 2003). The soil organic layer thus seems to be a preferential rooting substrate. This is further suggested by an experimental increase of litter input and thus manipulation of the organic layer thickness in a Panamanian lowland forest where litter addition significantly promoted the root ingrowths into the organic layer (Sayer *et al.* 2006).

Locally increased litter input may also be induced by the spatial structure of the forest (Burghouts *et al.* 1998). In our study forest at La Fortuna, western Panama, the palm species *Colpothrinax aphanopetala* (Arecaceae) is abundant and reaches into the upper canopy layer. After leaffall, its large leaves accumulate around the stem that probably causes a local increase of the organic layer. In another characteristic species in the La Fortuna forest, the tree species *Oreomunnea mexicana* (Juglandaceae), the bark peals off in large strips that may also lead to a local increase of the organic layer. Influences of specific tree species on the thickness of the organic layer have been reported from a temperate oak-beech forest (Leuschner *et al.* 2001). This study revealed that the organic layer was thicker in the vicinity of oak stems, where higher fine root mass also occurred. Other factors potentially influencing fine root mass and/or soil organic layer thickness include slope steepness, distance to trees, and nutrient concentrations. Among nutrients, nitrogen may be of special importance in tropical montane forests, where soil development is often less advanced than in tropical lowland forests. Nitrogen, which is derived primarily from the atmosphere gradually accumulates as soils develop, while rock-derived nutrients (*e.g.*, phosphorus) become increasingly bound in unavailable forms in older heavily weathered soils (Walker & Syers 1976). As a consequence, productivity of forest ecosystems on young soils could be nitrogen-limited while ecosystems on highly weathered soils could be phosphorus-limited. Studies in Hawaiian montane forests on soils of different age supported this hypothesis and fertilization experiments in tropical montane forests at least did not contradict it (Vitousek & Farrington 1997, Tanner *et al.* 1998, Cavelier *et al.* 2000, Hall & Matson 2003). In our study region, the soil has developed on volcanic ash deposits and soil type is Hapludand (USDA classification). The Andept soil order typically has higher pH, organic matter, and base contents in comparison with Ultisols and Oxisols. An example of how differences in soil nutrient status may affect fine root distribution comes from lowland Amazonia (Sanford 1989), where three adjacent forest types (terra firme, caatinga, and bana) growing on different soils were studied. Terra firme, caatinga, and bana forests had 48, 39, and 23 percent, respectively, of total root biomass in the surface mat, the soil organic layer, alone. This suggests that in the relatively nitrogen-rich Oxisols supporting terra firme forests more roots are concentrated near the surface. In Spodosols, supporting

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[1]Corresponding author; e-mail: dhoelsc@gwdg.de

relatively phosphorus-rich caatinga and bana forests, roots are not as concentrated near the surface as are roots in terra firme forest (Sanford 1989). Compared with tropical lowland forests, fine root distributions in montane forests are rarely quantified and even fewer studies have addressed fine root biomass in relation to forest structure or soil nutrient availability.

The objectives of our study in the lower montane forest at La Fortuna, Panama were: (1) to analyze the vertical and horizontal fine root distribution; and (2) to assess the relationship of fine root mass in the organic layer and upper mineral soil to potentially related factors (thickness of the organic layer, tree distance, soil pH, slope steepness, and extractable soil nitrogen). In view of predicted future increases in nitrogen deposition to tropical forests (Galloway *et al.* 2004, Phoenix *et al.* 2006), our study may provide important baseline information on the distribution of fine roots and its relationships to factors that will be influenced by nitrogen deposition such as nitrogen availability and pH.

TABLE 1. *Soil characteristics at the study site in a lower montane forest of western Panama (mean ± SE, N = 8).*

		Mineral soil	
	Organic layer	0–5 cm	5–50 cm
Total C (g C/kg)	443.0 (18.7)	73.0 (8.3)	30.7 (5.1)
Total N (g N/kg)	22.4 (1.1)	5.0 (0.6)	1.8 (0.2)
C:N ratio (g/g)	19.9 (0.4)	14.5 (0.5)	16.5 (0.6)
Total P (g P/kg)	0.72 (0.08)	0.56 (0.05)	0.29 (0.04)
Effective cation exchange capacity ($mmol_c$/kg)		132.3 (25.4)	71.0 (18.0)
Base saturation (%)[a]		20.9 (3.6)	11.2 (4.3)
pH (H_2O)	4.1 (0.1)	4.1 (0.1)	4.6 (0.1)
Bulk density (g/cm^3)	0.07 (0.01)	0.51 (0.06)	

[a]Base saturation = (Na + K + Ca + Mg)/ECEC × 100

METHODS

STUDY SITE.—This study was conducted in the Fortuna Montane Forest Reserve, western Panama. The study site is located at 1200–1300 m asl in the Quebrada Honda area northwest of the Fortuna Lake (8°45′ N, 82°15′ W). The most common tree species in this forest are *O. mexicana* (Standl.) Leroy (Juglandaceae), *Eschweilera panamensis* Pittier (Lecythidaceae), *Vochysia guatemalensis* Donn. Sm. (Vochysiaceae), *Cassipourea elliptica* (Sw.) Poir. (Rhizophoraceae), *Hedyosmum bonplandianum* Mart. (Chloranthaceae) and *Guarea glabra* Vahl (Meliaceae). The palm species *C. aphanopetala* R. Evans is also relatively common. Stem density of trees with a diameter at breast height (dbh) ≥ 10 cm was on average 1039 stems/ha and the basal area averages 46.1 m^2/ha (M. Adamek, pers. comm.). The canopy has a height of about 20 m with only sporadic emergent trees of up to 40 m height. Mean annual precipitation is 5532 mm (1997–2007) without a pronounced dry season (no month with < 100 mm precipitation); mean annual temperature is 20°C (1999–2007). The soil (Table 1) in the research area has developed on volcanic ash deposits and is classified as Aluandic Andosol (FAO classification) or Hapludand (USDA). The study was conducted on or in the vicinity of plots established by the NITROF project, which studies the impact of elevated nitrogen input on the biogeochemistry and productivity of tropical forests (www.nitrof.forst.uni-goettingen.de).

VERTICAL DISTRIBUTION OF FINE ROOTS.—A stratified random sampling approach was applied for the assessment of vertical fine root distribution. Forty meters long transects were delineated adjacent to each of the four NITROF control plots. These plots are 40 × 40 m (side lengths corrected for inclination), are not manipulated, were randomly established, and at least 40 m apart. On each transect, three points spaced at a random distance between 1 and 40 m were selected. Each point was attributed to one of three categories: (1) random sampling; (2) sampling at 1-m distance to the trunk of a *C. aphanopetala* palm with a minimum height of 5 m; and (3) sampling at 1-m distance to the stem of a *O. mexicana* tree > 10 cm dbh. A soil profile was dug to a depth of 1 m into the mineral soil at each selected point. In the random sampling category, the soil profiles were dug directly on the transects; for the remaining two categories, a target individual closest to the selected point was chosen. Fine root samples were vertically taken with a root auger (diam.: 4 cm; height: 30 cm) from the profile side facing the target individual or in case of the random points from a randomly selected profile side. The mineral soil samples were taken at 10-cm intervals down to 100 cm, resulting in a total of 10 mineral soil samples. The thickness of the soil organic layer was measured in the same direction with a tape measure. A root sample of the entire depth of the soil organic layer was taken with the auger. We thus collected four replicates per category at 11 depth intervals. This part of the study will be referred to as the transect study.

FINE ROOT DISTRIBUTION IN THE ORGANIC LAYER AND THE UPPER MINERAL SOIL.—A quadrat measuring 35 × 35 m was established in each of the four nonfertilized NITROF control plots. On each of the four sides of a quadrat, four sampling points were randomly selected with a minimum distance of 1 m from each other. At each sampling point, fine roots were sampled from the organic layer and the upper 10-cm depth of the mineral soil using the root auger described above. This should have resulted in 64 samples for the organic layer and the upper mineral soil but, due to the loss of some root samples during processing, there were a total of 57 samples for the organic layer and 60 samples for the upper 10-cm mineral soil. This part of the study will be referred to as the quadrat study.

FINE ROOT PROCESSING.—The fine roots (≤ 2 mm diam.) were separated from the soil by sieving and washing. Roots from the organic layer and the upper mineral soil were categorized into live (biomass) and dead roots (necromass) under a dissecting microscope. Roots were identified as biomass or necromass according to the degree of cohesion of stele and periderm, root elasticity, and color (Hertel *et al.* 2003). The criteria used for dead roots are: dark periderm and

stele, white nonturgid stele and periderm, or complete loss of the stele. Fine roots were dried for 2.5 d at 60°C and were weighed.

SUPPORTING PARAMETERS.—Thickness of the organic layer, slope steepness, tree distance, pH, and soil-extractable nitrogen were measured at all sampling points in order to test their correlation with fine root mass. The steepness of the slope was measured up- and downslope from the sampling location to a distance of 1 m using an ultrasonic hypsometer (Vertex III, Haglöf, Långsele, Sweden). The two inclinations were then averaged. Distances from the sampling points to the four closest trees < 10 cm dbh were measured. Additionally, the distances to and dbh of the four closest trees ≥ 10 cm dbh were recorded. If *O. mexicana* individuals were located at a distance of < 10 m, the distances and dbh of these individuals were also measured. The same measurements were applied for *C. aphanopetala* individuals, except that their selection was based on a minimum height of 5 m (dbh would not have been an appropriate criterion in this palm species because of the lack of secondary diameter growth). Samples from the organic layer and 0–10 cm mineral soil were taken for pH determination (1:10 sample to 1M KCl ratio for the organic layer and 1:1 sample to KCl ratio for the mineral soil). Soil nitrogen was extracted immediately in the field by bringing prepared extraction bottles containing 150 ml 0.5 M K_2SO_4 solution and soil samples were put into the bottles to get an approximate solution to fresh soil ratio of 3:1. Based on the measured gravimetric moisture content of each sample (see below), the average K_2SO_4 solution to soil dry mass ratio was 4:1 for the mineral soil and 20:1 for the organic layer (due to its very low bulk density). Within approximately 4 h, the samples were brought from the site to the field station, where extraction was continued by shaking the bottles for 1 h and filtering them through K_2SO_4-prewashed filter papers (4 μm nominal pore size). The filtrates were immediately frozen and remained frozen during transport by air to Göttingen University (Germany) for analysis. NH_4^+, NO_3^-, and total nitrogen were determined using continuous flow injection colorimetry (Cenco/Skalar Instruments, Breda, Netherlands). NH_4^+ content was measured using the Berthelot reaction method (Skalar Method 155–000), NO_3^- content was determined using the copper–cadmium reduction method (Skalar Method 461–000), and total nitrogen was measured using UV-persulfate oxidation followed by hydrazine sulfate reduction (Skalar Method 473–000). The remaining soil from each sample was used for gravimetric moisture determination by drying the samples in an oven at 105°C for 24 h.

STATISTICAL ANALYSES.—The data from the transect study were analyzed by category ($N = 4$ per category). The equation proposed by Gale and Grigal (1987) was used to describe the decrease of fine root mass with soil depth

$$y = 1 - \beta^d,$$

where y is the cumulative fraction of total fine root mass down to a specific soil depth (d). For this analysis, the surface of the organic layer was appointed as the zero point of the curve. β values of forests typically range between 0.80 and 0.99. Low β values indicate a superficial root distribution with a sharp decrease along the soil profile, while high β values indicate a less-pronounced decrease of fine root mass with depth. Medians and interquartile ranges (IQR, 75th–25th percentile) are reported as measures of central tendency and dispersion. Pairwise comparisons among groups were conducted with the nonparametric Wilcoxon rank sum test, with a standard level of significance of $P \leq 0.05$. The relationships between fine root mass and control variables were analyzed using Spearman' rank correlation. For this purpose the data from the four plots of the quadrat study were pooled resulting in a maximum of 64 observations. Additionally, multiple linear regression models were applied to this data pool to test for relationships between fine root biomass and potentially related factors such as thickness of the organic layer and tree distance. The statistical analyses were conducted with SAS software (SAS Institute Inc., Cary, NC, version 8.2).

RESULTS

VERTICAL DISTRIBUTION OF FINE ROOTS.—In the transect study at randomly selected locations, the median fine root mass to a mineral soil depth of 100 cm was 544 g/m^2 (IQR: 463 g/m^2). Forty-one percent of the root mass was located in the organic layer and 20 percent in the upper mineral soil (0–10 cm depth; Fig. 1). Fine root mass tended to be higher close to the base of *O. mexicana* trees

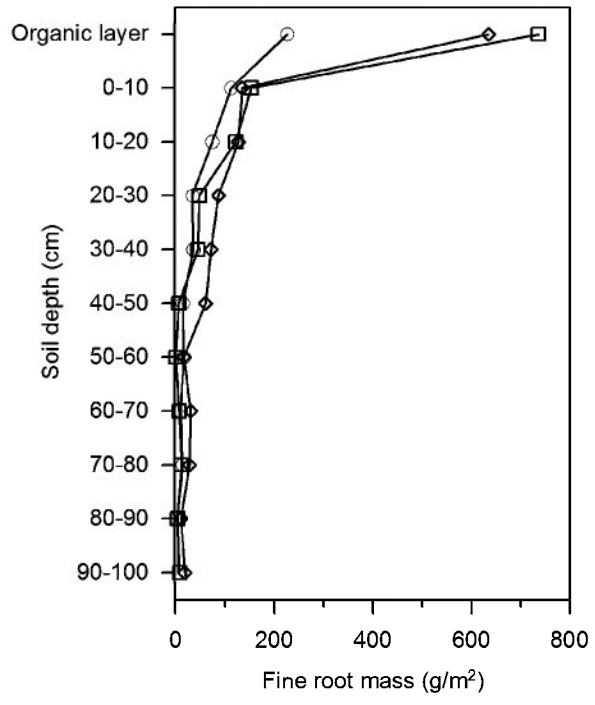

FIGURE 1. Depth profile of fine root mass (medians, $N = 4$) at fully randomly selected locations (circle) and at locations close to individuals of the palm *Colpothrinax aphanopetala* (diamond) and the tree *Oreomunnea mexicana* (square).

(median 927 g/m^2; IQR: 222 g/m^2) than in random samples ($P = 0.062$). Fine root mass in profiles close to the palm *C. aphanopetala* (median: 1169 g/m^2; IQR: 405 g/m^2) was higher than in random samples ($P = 0.043$). *Oreomunnea mexicana* and *C. aphanopetala* samples also had a higher proportion of fine root mass in the organic layer (64% and 52%, respectively) than the random samples. The organic layer was considerably thicker close to *O. mexicana* (median: 21.0 cm; IQR: 7 cm) and *C. aphanopetala* (median: 20.5 cm; IQR: 6 cm) than in random samples (median: 10 cm; IQR: 5 cm). Median β values, describing the change in fine roots with soil depth, were 0.96 in random samples, 0.97 close to *C. aphanopetala* stems, and 0.96 close to *O. mexicana* stems, indicating similar distributions of fine root mass with soil depth.

FINE ROOT MASS IN THE ORGANIC LAYER AND THE TOP MINERAL SOIL.—In the quadrat study, total fine root density was 3.4 g/L in the organic layer and 2.4 g/L in the upper mineral soil (Table 2). In the organic layer, 32 percent of the fine roots were classified as live roots (biomass) and the remaining 68 percent were considered to be dead (necromass). A slightly higher proportion of live roots (38%) was found in the upper mineral soil. Fine root biomass densities in the organic layer and the upper mineral soil were significantly correlated with each other ($r = 0.43$, $P = 0.002$, $N = 54$). The median fine root biomass of the organic layer was 111 g/m^2 with an interquartile range of 122 g/m^2, indicating considerable variability (Table 2). For the upper mineral soil a median of 87 g/m^2 and an interquartile range of 98 g/m^2 were found.

SUPPORTING PARAMETERS AND RELATIONSHIPS WITH FINE ROOTS.—In the quadrat study (Table 3), the organic layer had slightly lower median thickness than measured from only four transect samples. The median pH_{KCl} in the organic layer and the upper mineral soil was 4.1. Abundance of small trees is reflected in the short median distances (68–116 cm) between the sampling points and the nearest trees < 10 cm dbh. In addition, the relatively high stem density of trees ≥ 10 cm dbh is reflected in the short distances (126–248 cm) between the sampling points and this tree dbh category. Nitrate was not detectable in either the organic or the mineral soil, and the extractable organic nitrogen (*i.e.*, total N – [$NH_4^+ + NO_3^-$]) was higher than NH_4^+ (Table 3).

In the quadrat study, the density of fine root biomass in the organic layer was significantly correlated with the total extractable nitrogen ($r = 0.33$, $P = 0.011$, $N = 57$), but was not related with other studied parameters. Fine root biomass (Fig. 2) and necromass (Table 4) per unit of ground area thus increased with thickness of the organic layer (Fig. 2). Fine root biomass in the organic layer also increased with decreasing pH_{KCl} in the organic layer and decreasing pH_{KCl} in the mineral soil (Table 4). The analyses of the other parameters did not reveal significant correlations with fine root biomass in the organic layer. A multiple linear regression using thickness of the organic layer and distance to the closest tree < 10 cm

TABLE 2. *Fine root mass in the soil organic layer and the upper mineral soil (0–10 cm depth).*

Fine roots	Soil layer	*N*	Median	Interquartile range
Biomass (g/m^2)	Organic layer	57	110.6	121.8
	Upper mineral soil	60	87.5	98.1
Necromass (g/m^2)	Organic layer	57	157.6	167.1
	Upper mineral soil	60	136.1	120.6
Total mass (g/m^2)	Organic layer	57	247.5	201.3
	Upper mineral soil	60	236.7	196.8
Biomass density (g/L)	Organic layer	57	1.1	1.2
	Upper mineral soil	60	0.9	1.0
Necromass density (g/L)	Organic layer	57	2.0	2.0
	Upper mineral soil	60	1.4	1.2
Total mass density (g/L)	Organic layer	57	3.4	2.9
	Upper mineral soil	60	2.4	2.0

TABLE 3. *Thickness of the organic layer, pH, extractable nitrogen concentrations, stem distances and diameters (dbh), and slope steepness at the root sampling locations.*

Control variables		*N*	Median	Interquartile range
Organic layer thickness	(cm)	64	8	7
pH (KCl)	Organic layer	60	4.1	0.8
	Upper mineral soil	63	4.1	0.4
Extractable N organic layer	NO_3^- (mg N/kg)	62	0	0
	NH_4^+ (mg N/kg)	62	54	31
	Total extractable N (mg N/kg)	62	176	71
Extractable N upper mineral soil	NO_3^- (mg N/kg)	64	0	0
	NH_4^+ (mg N/kg)	64	9	5
	Total extractable N (mg N/kg)	64	36	17
Tree < 10 dbh	Distance[a] (cm)	64	68	50
	Distance[b] (cm)	64	116	53
	dbh[a] (cm)	64	2	2
	dbh[b] (cm)	64	3	1
Tree ≥ 10 dbh	Distance[a] (cm)	64	126	115
	Distance[b] (cm)	64	248	131
	dbh[a] (cm)	64	16	11
	dbh[b] (cm)	64	21	8
O. mexicana	Distance[a] (cm)	35	428	286
	dbh[a] (cm)	35	40	21
C. aphanopetala	Distance[c] (cm)	28	524	463
	dbh[c] (cm)	16	30	3
	Height[c] (cm)	18	159	118
Slope	(%)	64	25	13

[a]Closest stem to the sampling point.

[b]Mean of the four stems closest to sampling point.

[c]Closest palm stem (> 5 m high) to the sampling point.

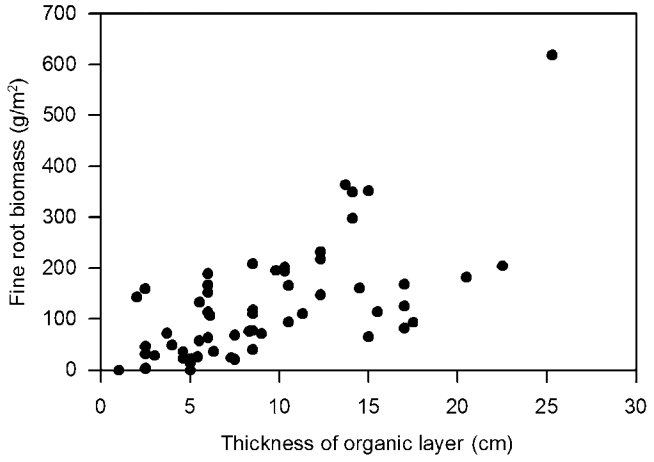

FIGURE 2. Fine root biomass in the organic layer in relation to the thickness of the organic layer ($r = 0.63$, $P < 0.001$, $N = 57$).

dbh explained 51 percent of the variation observed in fine root biomass in the organic layer. Fine root biomass in the upper mineral soil was not correlated with any of the parameters included in this study.

DISCUSSION

FINE ROOT BIOMASS IN THE PANAMANIAN STUDY FOREST.—Fine root biomass in tropical lower montane forests can vary from 112 g/m^2 to 950 g/m^2 according to 28 studies of root mass in the 10–100 cm depth interval (Hertel & Leuschner in press). At our study site, fine root biomass was 198 g/m^2 in the organic layer and the upper mineral soil (0–10 cm depth), which is at the lower end of the reported range. The cumulative total fine root mass (biomass and necromass) to a depth of 100 cm in our forest was 544 g/m^2 from random samples. In the same study region at La Fortuna, Cavelier (1992) reported a total fine root mass of 400 g/m^2 at a depth of 0–25 cm measured from the surface of the organic layer. When considering the average thickness of the organic layer and the depth distribution of the fine roots, these results are very similar.

In samples close to stems of *O. mexicana* and *C. aphanopetala* we found thick organic layers and high fine root mass, which exceeded those in random samples by twofold. These differences may be attributed to special characteristics of the studied species, or it may be a more general phenomenon of high fine root mass occurring next to stems of trees and palms in this forest. The large amount of fine root mass close to *C. aphanopetala* might be caused by the special palm root structure. However, at our study site the fine roots found at the base of *C. aphanopetala* stems did not only belong to this species, but roots of dicotyledonous trees were also abundant. The two study species may be special in respect to the litterfall close to their stem; in *O. mexicana* the bark peals off in large strips, which then increase the thickness of the organic layer close to the stem and *C. aphanopetala* has large leaves that also accumulate around the stem. In the quadrat study, we observed that pH in the organic layer decreased and thickness of the organic layer increased with decreasing distance to stems of these species. Such a correlation was not observed for other tree stems, and may be caused by litter quality and quantity. Thus, the observed patterns appear to be species-specific.

The bulk of fine roots in a forest is typically concentrated in the organic layer and the first few centimeters of the mineral soil and diminishes rapidly with increasing depth (*e.g.*, Jackson *et al.* 1996). The β values calculated according to Gale and Grigal (1987) for the three sampling categories in our study forest (random, close to *O. mexicana,* close to *C. aphanopetala*) ranged between 0.96 and 0.97, suggesting a similar decrease of fine root mass with soil depth in all categories. The values are also very similar to β values given as a mean for tropical evergreen forest (0.962; Jackson *et al.* 1996). For old-growth forest on Sulawesi, Indonesia at a comparable altitude to our forest an average β value of 0.90 is reported (Hertel *et al.* 2007), which indicates deeper rooting profiles than in our study forest.

INFLUENCES ON FINE ROOT DISTRIBUTION.—The heterogeneity in fine root mass in both the upper mineral soil and the organic layer was considerable. In the upper mineral soil, however, simple and multiple regressions did not yield any significant relationships between fine root biomass and the other parameters measured. We thus assume that there exist either other influencing parameters, which were not included in this study (*e.g.*, soil phosphorus concentrations), or that live fine roots in the upper mineral soil are distributed randomly.

In the organic layer fine root biomass correlated with pH, extractable nitrogen, and organic layer thickness. The thickness of the organic layer in our study also increased with increasing fine

TABLE 4. *Correlation coefficients between fine root mass (g/m^2) and control variables (Spearman's rank correlation; *, **, *** indicate significance at* $P \leq 0.1$, $P \leq 0.05$, *and* $P \leq 0.01$, *respectively).*

	Parameter	*N*	Biomass	Necromass	Total mass
Organic layer	Thickness of the organic layer	57	0.63***	0.54***	0.64***
	pH_{KCl} in the organic layer	55	–0.33***	–0.18	–0.26***
	Total extractable N in the organic layer	57	0.25*	0.20	0.24*
Upper mineral soil	pH_{KCl}	60	0.21	0.27**	0.20

root necromass, which is in accordance with the suggestion that fine root necromass can contribute significantly to the organic layer (Sanford & Cuevas 1996, Röderstein *et al.* 2005).

From comparisons among sites, it is well known that fine root biomass may increase with soil acidity (Vogt *et al.* 1995, Leuschner & Hertel 2003, Hertel & Leuschner in press). Vogt *et al.* (1995) suggested that the total amount of fine roots may increase in base-poor acidic sites to compensate for lower nutrient availability in the soil. It is also possible that due to decreasing pH_{KCl} values and thus thicker organic layers, new space for fine root growth is provided, resulting in preferential exploitation of the organic layer (Leuschner *et al.* 2004). It has previously been discussed that fine root growth in the organic layer is promoted by plant available nutrients such as nitrogen (Cavelier 1992, Hertel *et al.* 2003, Sayer *et al.* 2006). In our study, fine root biomass density was correlated with extractable total nitrogen. Stewart (2000) suggested that higher biomass densities with increasing nitrogen supply indicate a limitation of plant available nitrogen in a stand.

Thick and densely rooted organic layers are common in tropical montane forests, and altitude seems to be a major controlling factor of humus layer thickness (Grieve *et al.* 1990, Tanner *et al.* 1998, Hafkenscheid 2000, Wilcke *et al.* 2002). Variation in organic layer thickness may be explained by plant species composition, each species producing different quantities and qualities of litter (Burghouts *et al.* 1998). In an Ecuadorian forest at an altitudinal range of 1900–2200 m asl, Wilcke *et al.* (2002) found that the thickness of the organic layer ranged from 2 to 43 cm with a mean of 16 cm. From further studies on nutrient storage and turnover, they concluded that this layer contains large nutrient stocks, which is heterogeneously distributed and released (Wilcke *et al.* 2002). At our study site, fine root mass correlated with humus layer thickness, and we are not aware of other studies that compare humus layer thickness and fine root mass within a given tropical montane forest. However, along a successional gradient in an upper montane forest in Costa Rica, average humus layer thickness increased from early secondary forest over mid-successional forest to old-growth forest with a corresponding increase in fine root biomass in this layer (Hertel *et al.* 2003).

In conclusion, we found significant relationships between fine root biomass, nitrogen concentration, pH, and thickness of the organic layer. A future increase in nitrogen deposition may change plant nitrogen availability and lead to a decrease in pH, which will change the organic layer and the fine root biomass.

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