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Examination of Vertical Distribution of Fine Root Biomass in a Tropical Moist Forest of the Central Amazon, Brazil

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Abstract

Fine roots are an important component of the carbon flow of forests. Soil properties in tropical forest (*terra firme* forest) of the Central Amazon differ substantially along topography, and the biomass and vertical distribution of fine roots may also differ accordingly. Information on the vertical distribution of fine roots is essential to obtain unbiased estimates of fine root biomass. Accordingly, we examined fine root biomass and its vertical pattern along the gradient of topography in a typical *terra firme* forest in this region. The regressions on the cumulative fine root biomass along soil depth (at 5 cm intervals from 0-40 cm in depth) revealed significantly different vertical distribution of fine root biomass among three topographic habitats (lower-slope valley called *baixio*, mid-slope, and upper-slope plateau). A shallower rooting pattern was observed in the plateau than the other habitats, while fine root biomass was larger in the *baixio* than the plateau – a difference likely attributable to the soil physical properties than the aboveground stand structures among the sites. More than 74 and 93% of the fine root biomass was estimated to be distributed within the upper 20- and 40-cm soil layers, respectively. Our results suggested that a shallow sampling depth, which is common in fine root research in the Amazon, would be reasonable, though we should examine the consistency of our results in different regions.

Discipline: Forestry and forest products
Additional key words: contrasting soil, non-linear regression, soil depth, *terra firme* forest, topographic habitats

Introduction

Fine roots are an important component of the carbon flow of forests, since they contribute significantly to the net primary production of forest ecosystems[4,12]. While the spatial variation of fine roots is quite high[8], it is often difficult to increase the number of samples because the sampling procedures of fine roots require considerable time and effort[13], which tends to limit the accumulation of information on fine roots, particularly in tropical Amazon forests. The vertical distribution pattern of fine roots along soil depth is useful information to facilitate understanding of the matter flow in forest ecosystems[4,9]. In practical terms, determining the vertical pattern of fine roots is also important to obtain unbiased estimates of their biomass and dynamics via an optimal sampling scheme.

Jimenez *et al.*[5] revealed differences in fine root biomass (FRB) and its dynamics between sites with contrasting soil conditions in tropical forests of the Western Amazon in Colombia. The *terra firme* forest of the Central Amazon, Brazil, is also characterized by contrasting soil along its

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topography[2,6], namely nutrient-poor leached soil in lower-slope valleys (called “*baixio*”), and relatively nutritious clay-rich soil in upper-slope plateaus. Forests with differing structures and composition are distributed within a local scale, reflecting differences between the two habitats[7,11]. Though the fine roots generally aggregate within the thin and nutrient-poor topsoil of tropical forests[6], their vertical distribution pattern may differ among topographical habitats with different physical soil properties.

In the Central Amazon, pioneering work on fine roots was conducted by Klinge[6]. He revealed the FRB along soil depth and its differences between contrasting habitats. However, his discussion was based on limited sampling data. Powers et al.[10] have since revealed the FRB and its geographical differences when comparing several neotropical forest sites, including the Central Amazon. However, he pooled data from contrasting habitats and did not consider the difference in vertical distribution pattern of fine roots within the study site. Information on the vertical pattern of fine roots in the *terra firme* forest of this region remains considerably limited.

In this study, we aimed to clarify how the vertical distribution pattern of fine roots differed by topography in the Central Amazon. For this purpose, we examined the vertical distribution of FRB in the different topographic positions, including two contrasting habitats, (plateau vs. *baixio*) within a typical *terra firme* forest in the region and then applied a regression curve to estimate the cumulative fraction of the FRB with soil depth, and discussed the appropriate sampling depth of fine roots.

Materials and Methods

This study was conducted at a tropical moist forest in a 30-ha permanent plot (2° 36’ S, 60° 8’ W), around 50 km north of Manaus in the Central Amazon. Three sampling positions were randomly selected in each of the three topographic habitats, namely upper-slope plateau, mid-slope, and lower-slope valley (*baixio*). These three habitats were part of a series of sequentially appearing plateaus and *baixios* (typical of the topography in this region), and located within around 300 m of each other, with a 28-m difference in relative elevation. Soil, including fine roots, was sampled with a 400 cm^3 steel cylinder (5-cm high), at depth intervals of every 5 cm from 0 to 40 cm (8 depth classes) in each sampling position, carefully cutting the roots surrounding the cylinder with sharp knives and scissors. Each coring sample was rinsed in water on a 2-mm mesh steel sieve, removing soil having adhered to the root surface, and picking the fine roots with forceps. We separated dead and living roots by inspecting their colors and textures[13], and confirmed that the fraction of dead root mass against total fine root mass within each core (median = 0.134) showed no significant differences among habitats and depth classes (Kruskal-Wallis rank sum tests; $p > 0.05$). We thus used the value of total fine root mass (i.e. pooled dead and live fine roots) in the following analysis. These procedures were conducted within 10 days of sample collection. The dry mass of these sample roots was measured after oven-drying at 65°C for more than 72 h until a constant value had been attained.

For the vertical distribution of fine roots along soil depth, we adopted a commonly used equation developed by Gale & Grigal[3], $Y = 1 - \beta^d$ (eq. 1), where Y is the cumulative fraction of fine roots from the surface to depth d (cm), and β is a coefficient indicating the decrement of FRB along depth. While this formula effectively describes the vertical distributional pattern of FRB with only one coefficient, it is difficult to obtain the independent variable Y without data on total fine root biomass in the whole rooting depth. We thus modified this equation, and the cumulative fine root biomass (W_c ; Mg ha^{-1}) at depth d was regressed using the following equation:

$$W_c = W_t (1 - \beta^d), \quad \text{(eq. 2)}$$

in which the total fine root biomass (W_t ; Mg ha^{-1}) is one of the unknown coefficients in non-linear regressions with the least-square method (“*nls*” procedure on R2.14.1). Regressions were conducted for the data of each sampling point, the pooled data of each habitat, and all data, and the significance of the regressed coefficients was examined by t-tests. The differences in the regressed equations among each of the sampling points within and among three habitats were examined by F-tests based on residuals[1,11]. The cumulative FRB fraction was calculated for each habitat using the regressed equation, and their 95% confidence intervals (CI) was obtained from 999 bootstrap iterations.

Results

The vertical distribution of the cumulative fine root biomass (W_c) fitted well on eq. 2 for each of the 9 sampling points ($r^2 = 0.868 \sim 0.995$). All the coefficients β and W_t in the regressions on the pooled data of each habitat and on all data were significant (Fig. 1, Table 1; t-tests, $p < 0.05$).

The range of 95% CI of the coefficients W_t and β obtained from 999 bootstrap iterations for each habitat was larger in the mid-slope and *baixio* than the plateau (Table 1), reflecting the significant difference in vertical distribution of the FRB within these habitats. The value of coefficient β was larger in the mid-slope (0.93; 0.84−0.98, 95% CI) and *baixio* (0.94; 0.89−0.97) than the plateau (0.89; 0.86−0.92), which indicated that fine roots were distributed more deeply in the former. The coefficient W_t, which corresponded to the estimated total FRB for the whole rooting depth, was twice as large in the *baixio* (19.8 Mg ha^{-1}) than that in the plateau (8.7 Mg ha^{-1}), and their 95% CI (7.9−9.5

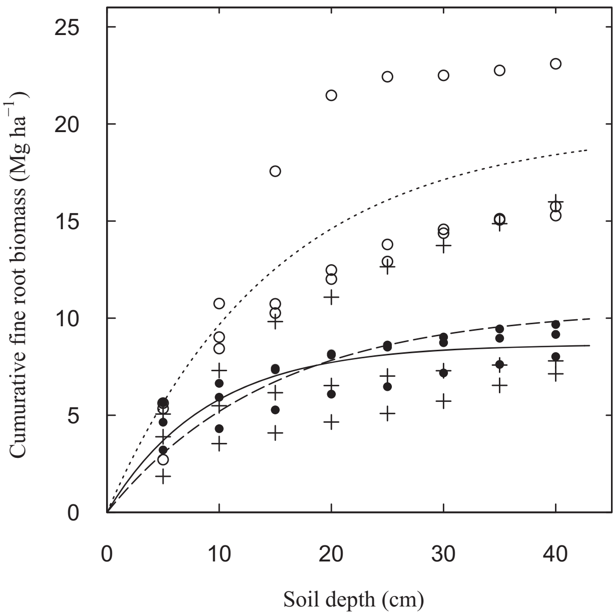

Fig. 1. Cumulative fine root biomass along soil depth (cm) in three topographic habitats in a tropical moist forest in Manaus, Brazil

Solid circles, crosses, and open circles indicate the cumulative biomass at each measurement point in the upper-slope plateau, mid-slope, and lower-slope valley (*baixio*), respectively. Solid, dashed and dotted lines indicate the regression lines (eq. 2 in the text) on pooled data of the plateau, mid-slope, and *baixio*, respectively.

Table 1. Regression coefficients of the fine root biomass along soil depth (cm; eq. 2 in the text) in a tropical moist forest in Manaus, Brazil

	Coefficients	
	β	W_t (Mg ha^{-1})
Plateau	0.89 (0.86, 0.92)	8.7 (7.9, 9.5)
Mid-slope	0.93 (0.84, 0.98)	10.5 (8.1, 24.8)
Baixio	0.94 (0.89, 0.97)	19.8 (16.5, 28.0)
All	0.93 (0.88, 0.96)	12.9 (10.9, 17.7)

The regression coefficients on pooled data of each of the three habitats and of all data collectively are indicated. Numbers in parentheses indicate 95% confidence intervals obtained by 999 bootstrap iterations.

and 16.5−28.0 Mg ha^{-1}, respectively) did not overlap. The regressed total FRB in the mid-slope was intermediate (10.5 Mg ha^{-1}; 8.1−24.8 Mg ha^{-1}). F-tests based on the residuals of the regressions showed significant differences in regressions within and among habitats ($p < 0.001$, Table 2), indicating the difference in vertical distribution pattern of the fine root biomass (FRB) within and among the habitats.

The fraction of fine roots sampled at soil depths of 5, 10, 20, 30 and 40 cm respectively (Table 3) clearly showed that more fine roots were concentrated in the shallow topsoil in the plateau than in the mid-slope and *baixio*. More than 40% of the FRB was estimated to appear at a depth of less than 5 cm in the plateau, while less than 30% appeared in that layer in the *baixio*. In the plateau, 89% of the FRB appeared at a depth of less than 20 cm, while the corresponding proportion was around 74% in the mid-slope and *baixio*. According to the regression curve, around 90% and more than 90% of the FRB was expected to be sampled down to depths of 30 and 40 cm, respectively, in all topographic habitats (Table 3).

Discussion

We observed significant differences in the FRB and its decrement pattern with soil depth (regression coefficient β) among the three topographic habitats in our study site. These differences might be primarily attributable to contrasting soil properties among the habitats. For example, the soil physical properties differ remarkably between the two habitats: sandy soil with poorer water retention prevails in the *baixio*, while harder and more clayish soil dominates the

Table 2. Results of F-tests on regressions on fine root biomass along soil depth (eq. 2 in the text) within and among three habitats in a tropical moist forest in Manaus, Brazil

F test	Separate regression		Regression on pooled data		F	p
	Sum of RSS	df	RSS	df		
Within plateau	3.12	18	23.1	22	6.06	1.42E-04
Within mid-slope	2.85	18	211	22	60.5	1.09E-12
Within baixio	36.7	18	281	22	6.26	1.15E-04
Among habitats	514	66	1309	70	2.40	2.14E-04

The total residual sum of the squares (RSS) of separate regressions at each of the sampling points is compared with the RSS of the regression on the pooled data of each habitat for tests within each habitat. The sum of RSS of the regression on the pooled data in each habitat was compared with that of the pooled data of all tests among habitats. See text for details.

Table 3. Cumulative fraction of fine root biomass (FRB) at specific soil depths (cm) and their 95% confidence intervals (indicated in parentheses) in a tropical moist forest in Manaus, Brazil

	Cumulative fraction of FRB at specific soil depths (cm)				
	5	10	20	30	40
Plateau	0.427 (0.336, 0.526)	0.672 (0.559, 0.776)	0.892 (0.806, 0.950)	0.965 (0.915, 0.989)	0.988 (0.962, 0.997)
Mid-slope	0.288 (0.079, 0.586)	0.494 (0.151, 0.829)	0.744 (0.279, 0.971)	0.870 (0.388, 0.995)	0.934 (0.48, 0.999)
Baixio	0.285 (0.154, 0.444)	0.489 (0.285, 0.690)	0.739 (0.489, 0.904)	0.866 (0.634, 0.970)	0.932 (0.738, 0.991)
All	0.315 (0.179, 0.476)	0.530 (0.325, 0.725)	0.779 (0.545, 0.924)	0.896 (0.693, 0.979)	0.951 (0.793, 0.994)

The estimated fractions and their confidence intervals are obtained by regressions on fine-root biomass along soil depth (eq. 2 in the text) and 999 bootstrap iterations, respectively.

plateau[2]. Accordingly, it may be easier for tree roots to grow more deeply into the sandy soil of *baixio* than the clayish soil of the plateau.

The soil nutrient condition is another major factor affecting the spatial distribution of fine roots. Jiménez et al.[5] found significantly higher FRB in nutrition-poor sandy sites (10.94 ± 0.33 Mg C ha^{-1}) than clayish sites (3.04 ± 0.18 Mg C ha^{-1}) in the Colombian Amazon. Klinge[6] also found higher FRB values in the nutrient-poor Podzolic sandy site (8.4 Mg ha^{-1}) than in the Latosolic site (5.7 Mg ha^{-1}) in the vicinity of our study site. The FRB estimates in our study site, ranging from 8.7 Mg ha^{-1} (around 4.3 Mg C ha^{-1}) in the plateau to 19.8 Mg ha^{-1} (around 9.9 Mg C ha^{-1}) in the *baixio*, fall within the range of estimates obtained in the tropical forest of Colombia and a previous study reported by Klinge[6]. Besides, the difference of the FRB by soil type found in our study (i.e. larger FRB in sandy soils) is also the same as those previous studies.

Conversely, the between-sites differences in FRB and its vertical pattern were unlikely to be associated with those in the aboveground stand structure. For example, the aboveground biomass which can be estimated using allometric regression (eq. 6 by Suwa et al.[11]) and the data of tree census in the two contrasting habitats of our study forest does not differ greatly: 283 Mg ha^{-1} in the *baixio*, versus 316 Mg ha^{-1} in the plateau (Suwa et al. *unpublished data*). This fact implies that fine roots may respond to soil conditions more strongly than aboveground parts in terms of biomass growth. To discuss this possibility in detail, however, further studies are required by considering other stand structure characteristics, such as the differences in species composition between the two habitats (Suwa et al. *pers. comm.*).

From a technical perspective, it is often difficult to increase the number of samples, as sampling and processing the fine roots generally requires tremendous time and effort[13]. Accordingly, an optimized sampling scheme based on information on the vertical distribution of FRB and an effective means of analysis is required. By combining nonlinear regressions, *F*-tests, and bootstrap iterations, we could detect clear differences in the FRB and its vertical distribution pattern among the habitats. A small modification in the widely used equation of Gale and Grigal[3] (eq. 2) allowed us to conduct these analyses from data obtained from a feasible sampling depth (0-40 cm). This approach could also provide information on the fraction of fine roots at specific soil depths in each habitat, and revealed that most FRB appeared within shallow topsoil in all habitats. The nature of superficial fine root distribution is also likely common to other tropical forest sites in the Amazon[5,10]. Considering this fact, a sampling depth of less than 30 cm would suffice to estimate FRB effectively by saving time and effort. However, this inferred depth of appropriate fine root sampling should be examined in different Amazon regions.

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