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Carbon and nutrient stocks in roots of forests at different altitudes in the Ecuadorian Andes

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Abstract: Carbon and nutrient stocks in below-ground biomass have rarely been investigated in tropical montane forests. In the present study, the amounts of carbon, nitrogen, phosphorus, sulphur, potassium, calcium and magnesium in root biomass were determined by soil coring and nutrient analysis in forests at three altitudes (1900, 2400 and 3000 m) in the Ecuadorian Andes. Root biomass increased markedly from 2.8 kg m^{-2} at 1900 m and 4.0 kg m^{-2} at 2400 to 6.8 kg m^{-2} at 3000 m. The contribution of coarse roots (> 2 mm in diameter) to total root biomass increased from about 70% at 1900 m to about 80% at higher altitudes. In fine roots (≤ 2 mm in diameter), concentrations of nutrients except calcium markedly decreased with altitude. Therefore, the nutrient stocks in fine roots were similar at 1900 m and 3000 m for nitrogen and sulphur, and were even lower at higher altitudes for phosphorus, potassium and magnesium. In coarse roots of *Graffenrieda emarginata* concentrations of nutrients were substantially lower than in fine roots, and were little affected by altitude. The data suggest that the importance of coarse roots for long-term carbon and nutrient accumulation in total plant biomass increases with increasing altitude.

Key Words: Biomass, carbon sequestration, diameter, fine roots, immobilization, montane forests, nutrient cycling

INTRODUCTION

In the debate about the global carbon cycle the role of forest biomes as potential carbon sources and sinks receives increasing attention (Clark 2002, 2004; Fehse *et al.* 2002, Malhi *et al.* 1999). Considerable amounts of terrestrial C are sequestered in tropical forests (Malhi *et al.* 1999, Vogt *et al.* 1996). In 1994, these forests contributed 37% of total C sequestered worldwide in forest ecosystems. About 50% of total C in tropical forests is bound in biomass (Dixon *et al.* 1994). Roots contribute 7–34% to total biomass in tropical lowland forest ecosystems (Vogt *et al.* 1996). Thus, C stocks in root systems of tropical lowland forests are important components of the C budget on a global scale.

Within forest biomes, roots have a large impact on C and nutrient fluxes (Chen *et al.* 2001, Ostertag & Hobbie 1999). Here, the amounts of C and nutrients returned to soil from fine-root turnover may equal or exceed that from leaf litter (Joslin & Henderson 1987, Raich & Nadelhoffer 1989). Besides root tissue composition and various environmental factors, root diameter is a key factor that governs the nutrient return to soil via root turnover (Janisch *et al.* 2005, McClaughtery *et al.* 1982, Nambiar 1987, Ostertag & Hobbie 1999). Nambiar (1987) reported that root turnover of *Pinus radiata* is largely confined to roots < 1 mm in diameter.

On the other hand root biomass contributes to nutrient immobilization and may thus diminish nutrient losses from the ecosystem by leaching. This is especially true for tropical lowland forests with high precipitation rates where most potassium (K) and calcium (Ca) are stored in biomass, whereas the soil is often impoverished in these nutrients (Jordan 1985).

Data on total below-ground biomass as well as C and nutrients in below-ground biomass of tropical montane forests are scarce (Edwards & Grubb 1977, 1982; Ostertag 2001, Priess *et al.* 1999, Vance & Nadkarni 1992). Tropical montane forests are characterized by high spatial heterogeneity in climatic conditions. Usually with increasing altitude temperatures decrease while precipitation increases, causing a decrease in mineralization rates (Fabian *et al.* 2005, Holder 2003, Marrs *et al.* 1988). As a result, the amounts of C stored in the organic layer and mineral soil of montane regions are

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usually higher than in the lowlands (Edwards & Grubb 1977). It is also likely that the amounts of C and nutrients in below-ground biomass may be affected by the climatic changes along altitudinal gradients.

Nutrient stocks in the root biomass are dependent on nutrient concentrations in root tissue. These concentrations are governed by several internal and external factors. The impact of different diameter classes of tree roots on nutrient concentration is well documented. Concentrations of N and P generally decrease with increasing root diameter, while no consistent pattern has been found for Ca, Mg and K concentrations (Edwards & Grubb 1982, Gordon & Jackson 2000, John *et al.* 2002, Klinge 1975, Nambiar 1987). Furthermore it was shown that in forest ecosystems nutrient concentrations in fine roots are influenced by season (Guevara & Romero 2004), soil age (Ostertag & Hobbie 1999), stand age (Meier *et al.* 1985) and stand density (Barron-Gafford *et al.* 2003). In many cases an increase in root nutrient concentrations is explained by an increase in soil nutrient availability (Hendricks *et al.* 2000, Ostertag & Hobbie 1999, Yin & Perry 1991).

In this study, we measured C and nutrient stocks in roots differing in diameter. We use the term 'nutrient' for the nutrient elements N, S, P, K, Ca and Mg, and the term 'element' to encompass nutrients as well as C. It may be expected that nutrient stocks in fine roots constitute a significant source of nutrient supply for plants via fine-root turnover, whereas C and nutrient stocks in coarse roots contribute to long-term sequestration of elements in plant biomass. The investigation was performed in tropical montane forest in Ecuador at 1900, 2400 and 3000 m. We hypothesized that root biomass and root C and nutrient stocks increase with altitude because nutrient limitation of plant growth increases biomass and nutrient partitioning to roots.

STUDY SITES

We selected three stands in an Ecuadorian tropical montane forest close to the provincial capital Loja. The lower stands (1900 m, S 03°58′ W 79°04′, and 2400 m, S 03°59′ W 79°04′) were situated in the Reserva San Francisco at the northern fringes of the Podocarpus National Park that protects typical mountain ecosystems of southern Ecuador. The highest stand (3000 m, S 04°06′ W 79°10′) was located in the Cajanuma area in the north-western edge of the National Park.

The three sites were situated on slopes similar in inclination (31° at 1900 m, 28° at 2400 m, and 27° at 3000 m) and were exposed north-east or north-west. All stands were old-growth forests. Precipitation was markedly lower at 1900 m (1950 mm y^{-1}) than at 2400 m (5000 mm y^{-1}) and 3000 m (4500 mm y^{-1}). Mean annual temperature decreased from 1900 m (14.9 °C) to 2400 m (12.3 °C) and 3000 m (8.6 °C) (Röderstein *et al.* 2005). Soils at 1900 m and 2400 m were classified at gleyic Cambisols, soils at 3000 m were mainly Podzols (S. Iost, pers. comm.). Soils were acid ($pH_{(CaCl_2)} < 3.5$ to a depth of 0.3 m in mineral soil) and covered by organic layers that were deeper at 3000 m (an average of 0.31 m) than at 1900 and 2400 m (an average of 0.15 m and 0.16 m, respectively). Maximum tree height decreased from 1900 to 2400 and 3000 m (19, 12 and 9 m, respectively). Further information on plant species composition that changed considerably with altitude, is given in Röderstein *et al.* (2005).

METHODS

Sampling of roots ≤ 5 mm in diameter

Sampling of roots ≤ 5 mm in diameter was conducted during the dry season of November/December 2001. At each altitude, one 20 × 20-m plot in the closed forest was established. Samples were taken from 20 randomly distributed locations. From each location, a sample of 100 × 100 mm was taken in vertical direction from the organic layer. Mineral soil was sampled vertically with a soil corer (80 mm in diameter) at depths of 0.0–0.1 m, 0.1–0.3 m, 0.3–0.5 m, 0.5–0.7 m, 0.7–0.9 m and 0.9–1.1 m. When parent soil material was reached above 1.1 m, sampling was finished earlier.

Sampling of roots > 5 mm in diameter

Sampling of roots > 5 mm in diameter was conducted in the dry season from December 2002 until January 2003. Since the sampling procedure was very destructive and the 20 × 20-m plots had to be maintained for further investigations, sampling was performed on 15 randomly distributed locations around the plots. Both soil properties and vegetation around the plots were similar to those within the plots (unpubl. data), allowing a comparison of roots smaller than and larger than 5 mm in diameter. At each of the 15 sampling locations a hole of 0.4 × 0.4 m was dug in a vertical direction. Roots within the hole were cut or sawn off and separated into roots from the organic layer, and from 0.0–0.1 and 0.1–0.3 m depths of mineral soil. In soil layers deeper than 0.3 m no coarse roots were found. Roots that grew at the interface between organic layer and mineral soil were added to the roots from the organic layer.

Analysis of roots ≤ 5 mm in diameter

For determination of root biomass, roots were sorted out from a subsample of 20–50 g (organic layer) or

100–200 g (mineral soil) of each sample. For washing of each subsample, a 0.6-mm-mesh sieve was used. From a small bowl filled with water, roots and remaining soil residue were separated with forceps. Under a binocular microscope living and dead roots were separated by colour, root elasticity and the degree of cohesion of cortex, periderm and stele (Persson 1978). Living roots were separated into the diameter classes ≤ 1 mm, > 1–2 mm, > 2–5 mm. Following Röderstein *et al.* (2005) who determined fine-root turnover at the same study sites, root ≤ 2 mm were classified as fine roots, whereas roots > 2–5 mm were included to the coarse root fraction. Roots were deep frozen for storage to allow further analysis in Germany. Afterwards, roots were dried at 50 °C for 24 h and weighed.

For the analysis of elemental composition, additional root material was sorted out from the remaining soil material of every sample. After washing, roots were sorted out directly from the mesh. This procedure allowed a shorter contact of the roots with water and a collection of sufficient root material for nutrient analysis. In a preceding analysis it was shown that this procedure was associated with negligible losses of nutrients during sample preparation (unpubl. data). Roots for nutrient analysis were separated into the same diameter classes as described above, dried at 50 °C for 24 h and ground with a flint mill (Type MM2, Retsch-GmbH & CoKG, Haan). Concentrations of C, N and S were determined with a CNS analyser (Vario Max CNS, elementar Analysesysteme, Hanau). For determination of P, K, Ca and Mg, ground samples were digested with concentrated HNO_3 under pressure (Heinrichs *et al.* 1986). Concentrations of K, Ca and Mg were measured by flame atomic absorption spectrometry (Perkin Elmer 4100, Perkin Elmer, Milano) and P concentrations were assessed with a spectral photometer (Specord 200, Analytik Jena, Jena) using the molybdenum blue procedure (Murphy & Riley 1962).

Analysis of roots > 5 mm in diameter

For determination of coarse root mass, roots from each soil layer were separated into the diameter classes > 5–10 mm, > 10–20 mm, > 20–50 mm and > 50 mm. Root samples were dried at 50 °C until constant weight was achieved. Carbon and nutrient concentrations in coarse roots were assessed only from *Graffenrieda emarginata* (Ruiz & Pav.) Triana (Melastomataceae). This species occurs at 1900–2400 m altitude, and contributes up to 11% to total tree basal area (J. Homeier, pers. comm.). Samples were obtained from the stands at 1900 and 2400 m, from three trees per altitude. Roots of each tree were divided in the same diameter classes as described above without considering soil depth. Subsamples of about 20 g were taken from every diameter class. Therefore smaller coarse roots were reduced to small pieces with help of a hedge clipper. From thicker coarse roots, representative subsamples from the bark to the root centre were taken with a borer. Carbon and nutrient analyses from these subsamples were performed as described above.

Determination of soil C stocks

Soil C stocks were determined from the 20 replicate soil cores per altitude and soil depth taken for determination of root biomass ≤ 5 mm in diameter. Therefore, four equal subsamples of the 20 replicates were bulked together in each case to obtain five replicate samples per soil depth for analysis. Samples were air dried for storage. Concentrations of total C were assessed with a CNS analyser (Vario Max CNS, Elementar Analysesysteme, Hanau). Carbon stocks in fine-root biomass were subtracted from these data to obtain C stocks in rootless soil material.

Statistical analysis

Statistical analyses were performed with help of the SPSS 13.0 software. As an exception, posthoc-tests for the non-parametric Kruskal–Wallis test (Dunn test and Nemenyi test) were calculated manually.

Root biomasses at different altitudes within one soil depth were compared by Kruskal–Wallis test for non-normally distributed replicates and subsequent Dunn test for unequal numbers of replicates (roots ≤ 5 mm in diameter) or Nemenyi test for equal numbers of replicates (roots > 5 mm in diameter).

Nutrients stocks in different root diameter classes ≤ 5 mm were calculated from the average root biomass of the respective diameter class and the replicate nutrient concentrations within this diameter class. ANOVA and Tukey test or t-test were used to assess significant differences in total fine- and coarse-root biomass, nutrient stocks or nutrient concentrations between altitudes or between diameter classes. Additionally, two-way ANOVA was applied to nutrient concentrations in roots to compare the impact of altitude and diameter class. Data were log-transformed when necessary.

RESULTS

Root biomass

Total root biomass steadily increased from 1900 to 3000 m (Table 1). At 3000 m, biomass of fine roots and coarse roots was significantly higher than at 2400 and 1900 m. The fraction of fine roots in total root biomass

Table 1. Root biomass (g m^{-2}) at different altitudes (n = 20 for fine roots ≤ 2 mm in diameter, n = 15 for coarse roots > 2 mm in diameter) of Ecuadorian montane forests. Data shown are mean ± SE. Different lowercase letters indicate significant differences between altitudes (Tukey test, $P < 0.05$).

Altitude (m)	Fine-root biomass (g m^{-2})	Coarse-root biomass (g m^{-2})	Total root biomass (g m^{-2})	Proportion of root biomass in total biomass[1] (%)
1900	890 ± 70^{a}	1910 ± 264^{a}	2800	14
2400	729 ± 90^{a}	3286 ± 567^{a}	4015	29
3000	1503 ± 127^{b}	5340 ± 473^{b}	6843	38

[1]Data on above-ground biomass were derived from G. Moser (pers. comm.).

decreased from 32% at 1900 m to 18% at 2400 m and 22% at 3000 m. In contrast to root biomass, above-ground biomass as estimated from dbh, tree height and wood density (Chave *et al.* 2005) decreased with increasing altitude (G. Moser, C. Leuschner and D. Hertel, unpubl. data). Correspondingly, the proportion of root biomass in total biomass strongly increased with increasing altitude (Table 1).

At all altitudes, the largest proportion of root biomass was located in the organic layer (Figure 1). This was most pronounced at 3000 m and 2400 m, where about 80% of total root biomass was located in this layer, in contrast to about 59% at 1900 m. Below 0.1 m depth of mineral soil, about 10% of total coarse-root and 38% of total fine-root biomass were found at 1900 m, compared with only 1% of total coarse-root and about 6% of total fine-root biomass at 2400 and 3000 m. This indicates that nutrient cycling between plant roots and soil via fine roots and, in the long term, release of C and nutrients into the soil by decaying coarse roots, are mainly confined to the uppermost soil layers, particularly at high altitudes.

Element concentrations in roots

The element concentrations of roots ≤ 5 mm in diameter were not affected by the soil layer or soil depth (data not shown). Thus, only element concentrations in roots from the organic layer are shown in this study. The root concentrations of elements with the exception of Ca were significantly ($P < 0.05$) influenced by altitude (Table 2), showing strong decreases (40–60%) of N, S, P, K and Mg from 1900 m to 3000 m (Table 3). Furthermore, the root concentrations of elements with the exception of Mg were significantly influenced by root diameter (Table 2) showing marked decreases in the concentrations of N, S and P and marked increases in the concentrations of K and Ca with increasing root diameter (Table 3).

The concentrations in roots > 5 mm, which were only measured in *G. emarginata*, with the exception of Ca were not significantly influenced by altitude (Table 4). The Ca concentrations were higher at 2400 m than at 1900 m (Table 5). Increasing coarse-root diameter significantly decreased the concentrations of N, S and P (Table 4 and 5).

The concentrations of N, S, P and Mg in coarse roots > 5 mm of *G. emarginata* were markedly lower than concentrations of these elements in roots ≤ 5 mm that were bulked from all species growing in the forests stands (cf. Tables 3 and 5). Concentrations of C and K did not strongly vary between these root pools, whereas Ca concentrations were substantially higher in roots > 5 mm than in roots with smaller diameter.

Stocks of carbon and nutrients in root biomass

In fine roots up to 2 mm in diameter, stocks of all elements except Ca were significantly influenced by altitude (Table 6). Element stocks in fine roots were lowest at 2400 m, i.e. at the altitude, where lowest fine-root biomass was associated with intermediate element concentrations (Table 3). Highest P and K stocks were observed at 1900 m because of high concentrations of these nutrients at this altitude. The stocks of N, S and Mg were not significantly different between 3000 m and 1900 m.

To obtain a rough estimate of element stocks in coarse roots > 2 mm in diameter, coarse root biomass of forest stands was multiplied with average element concentrations from 1900 m and 2400 m measured in coarse roots of *G. emarginata*. To obtain a rough estimate of element stocks in total root biomass, measured element

Table 2. Significance levels for differences in root element concentrations (≤ 5 mm in diameter) from root diameter and altitude calculated by two-way ANOVA (n = 5).

	C	N	S	P	K	Ca	Mg
Altitude	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	0.175	0.001
Diameter	0.001	< 0.001	< 0.001	< 0.001	< 0.001	0.021	0.106

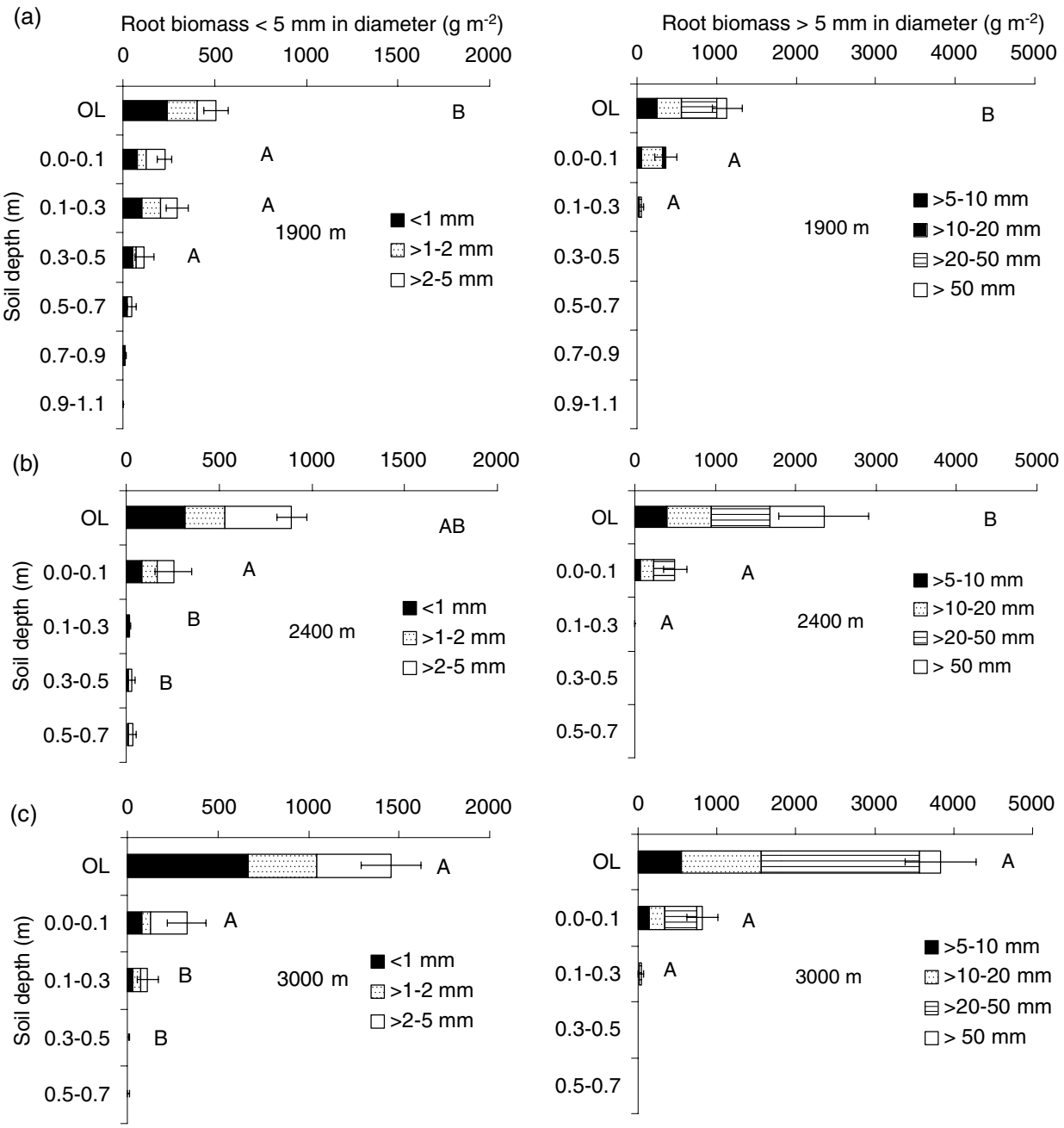

Figure 1 Root biomass (g m^{-2}) of different diameter classes in different soil depths at (a) 1900 m, (b) 2400 m and (c) 3000 m; OL = organic layer. Error bars indicate standard errors. Different upper-case letters indicate significant differences of root biomass between altitudes within one soil depth (root biomass ≤ 5 mm in diameter: n = 9–20, Dunn test, $P < 0.05$; root biomass > 5 mm in diameter: n = 15, Nemenyi test, $P < 0.05$).

stocks in fine roots and estimated element stocks in coarse roots were summed up. Element stocks in coarse root and total root biomass increased with altitude (Table 6). The only exception was the root stocks of P which were very similar at 1900 and 3000 m.

Compared to data from literature, carbon stocks at 3000 m were about three times higher. At 3000 m also Ca stocks were substantially higher, whereas the stocks of all other elements in the present study were similar to the range found for the other tropical forests.

Carbon stocks in soil

Soil carbon stocks differed significantly between the sites at different altitudes (Table 7). Higher C stocks at 1900 and 3000 m than at 2400 m were the result of the

Table 3. Element concentrations (mg g^{-1}) in roots ≤ 5 mm in diameter (n = 5) at different altitudes of Ecuadorian montane forests. Data shown are mean ± SE.

Element	Altitude (m)	Diameter class (mm)			
		≤ 1	> 1–2	> 2–5	Mean[1]
C	1900	500 ± 3	504 ± 5	500 ± 2	501 ± 1
	2400	511 ± 1	514 ± 3	501 ± 1	509 ± 4
	3000	544 ± 1	532 ± 3	513 ± 1	530 ± 9
N	1900	15.4 ± 0.6	12.0 ± 1.1	9.1 ± 0.7	12.2 ± 1.8
	2400	12.3 ± 0.1	9.1 ± 1.0	8.0 ± 1.0	9.8 ± 1.3
	3000	10.4 ± 0.6	6.4 ± 0.2	4.9 ± 0.4	7.2 ± 1.6
S	1900	1.82 ± 0.10	1.40 ± 0.09	1.22 ± 0.15	1.48 ± 0.18
	2400	1.18 ± 0.14	1.02 ± 0.08	0.88 ± 0.09	1.03 ± 0.09
	3000	1.13 ± 0.05	0.87 ± 0.08	0.60 ± 0.06	0.87 ± 0.15
P	1900	1.03 ± 0.06	0.85 ± 0.19	0.61 ± 0.08	0.83 ± 0.12
	2400	0.57 ± 0.09	0.28 ± 0.07	0.29 ± 0.06	0.38 ± 0.10
	3000	0.55 ± 0.05	0.26 ± 0.02	0.22 ± 0.03	0.34 ± 0.10
K	1900	3.43 ± 0.27	5.09 ± 0.75	6.57 ± 0.96	5.03 ± 0.91
	2400	1.99 ± 0.09	3.15 ± 0.75	4.31 ± 0.87	3.15 ± 0.67
	3000	1.70 ± 0.14	2.13 ± 0.29	3.52 ± 0.73	2.45 ± 0.55
Ca	1900	2.32 ± 0.81	2.35 ± 0.59	2.62 ± 0.56	2.43 ± 0.10
	2400	2.14 ± 0.41	3.50 ± 0.38	5.65 ± 2.32	3.76 ± 1.02
	3000	1.80 ± 0.64	3.88 ± 0.54	4.14 ± 1.37	3.27 ± 0.74
Mg	1900	1.49 ± 0.28	1.32 ± 0.19	2.03 ± 0.45	1.61 ± 0.23
	2400	0.94 ± 0.04	2.26 ± 0.66	1.27 ± 0.23	1.49 ± 0.40
	3000	0.79 ± 0.05	1.06 ± 0.14	1.25 ± 0.17	1.03 ± 0.13

[1]Simple mean is shown.

Table 4. Significance levels for differences in element concentrations in coarse roots > 5 mm in diameter of *Graffenrieda emarginata* from root diameter and altitude calculated by two-way ANOVA (n = 3).

	C	N	S	P	K	Ca	Mg
Altitude	0.619	0.664	0.302	0.540	0.114	< 0.001	0.262
Diameter	0.168	0.001	0.015	0.043	0.073	0.128	0.209

high C concentrations in mineral soil. In the upper 0.3 m of mineral soil, C concentrations were 7.7% at 1900 m, 7.2% at 3000 m, and only 1.6% at 2400 m. The relative contribution of mineral soil and organic layer to soil carbon storage also differed between sites at different altitudes. At 1900 m and 3000 m more than 75% of total soil C was stored in mineral soil, whereas at 2400 m about 55% of total soil C was stored in mineral soil.

The contribution of plant biomass C in roots and shoots to total C stocks (C in plant biomass and soil) varied between 18% at 3000 m, 23% at 1900 m and 35% at 2400 m. Thus, no consistent pattern with altitude became apparent (Table 7). The contribution of root C stocks to

Table 5. Element concentrations (mg g^{-1}) in coarse roots > 5 mm in diameter of *Graffenrieda emarginata* (n = 3). Data are mean ± SE.

Element	Altitude (m)	Diameter class (mm)				
		> 5–10	> 10–20	> 20–50	> 50	Mean[1]
C	1900	495 ± 1	491 ± 4	490 ± 1	486 ± 2	490 ± 2
	2400	490 ± 4	491 ± 3	488 ± 1	488 ± 1	489 ± 1
N	1900	4.3 ± 0.4	4.6 ± 1.4	2.3 ± 0.2	2.4 ± 0.1	3.4 ± 0.6
	2400	5.2 ± 0.3	3.0 ± 0.3	2.6 ± 0.1	2.1 ± 0.1	3.2 ± 0.7
S	1900	0.70 ± 0.04	0.72 ± 0.26	0.33 ± < 0.01	0.31 ± 0.01	0.51 ± 0.11
	2400	0.76 ± 0.28	0.33 ± 0.01	0.30 ± 0.02	0.26 ± 0.01	0.41 ± 0.12
P	1900	0.081 ± 0.012	0.086 ± 0.033	0.040 ± 0.005	0.037 ± 0.002	0.061 ± 0.013
	2400	0.087 ± 0.012	0.042 ± 0.001	0.033 ± < 0.001	0.056 ± 0.026	0.054 ± 0.012
K	1900	3.0 ± 0.2	3.2 ± 0.7	2.0 ± 0.1	1.9 ± 0.1	2.5 ± 0.3
	2400	4.5 ± 1.0	2.4 ± 0.1	2.5 ± 0.4	3.2 ± 0.7	3.2 ± 0.5
Ca	1900	9.2 ± 0.8	15.7 ± 6.9	6.8 ± 1.1	7.7 ± 0.3	9.9 ± 2.0
	2400	11.8 ± 0.8	12.5 ± 0.9	13.2 ± 1.4	18.8 ± 3.1	14.1 ± 1.6
Mg	1900	0.78 ± 0.40	0.22 ± 0.05	0.23 ± 0.04	0.66 ± 0.24	0.47 ± 0.14
	2400	0.43 ± 0.21	0.35 ± 0.04	0.24 ± 0.01	0.26 ± 0.04	0.32 ± 0.04

[1]Simple mean is shown.

Table 6. Element stocks (g m^{-2}) in fine roots ≤ 2 mm in diameter (n = 5) and coarse roots > 2 mm in diameter from Ecuadorian montane forests and data from other tropical forests. Different lower-case letters indicate significant differences in nutrient stocks between altitudes (Tukey test, $P < 0.05$).

Root fraction	Altitude (m)	Element stocks (g m^{-2})						
		C	N	S	P	K	Ca	Mg
Fine roots	1900	431[b]	12.0[a]	1.42[a]	0.82[a]	3.49[a]	1.99[a]	1.53[a]
	2400	379[c]	8.1[b]	0.82[b]	0.33[c]	1.83[b]	2.01[a]	0.81[b]
	3000	680[a]	11.2[a]	1.31[a]	0.55[b]	2.34[b]	3.24[a]	1.12[ab]
Coarse roots[1]	1900	938	8.6	1.18	0.31	6.69	19.40	1.27
	2400	1621	12.7	1.64	0.29	9.75	36.21	1.63
	3000	2630	17.9	2.39	0.38	14.70	54.21	4.19
Total root biomass[1]	1900	1369	20.6	2.60	1.13	10.18	21.40	2.81
	2400	1999	20.8	2.46	0.62	11.58	38.22	2.44
	3000	3310	29.1	3.70	0.93	17.04	57.45	5.31
Total root biomass	Lower montane							
	New Guinea[2]	–	13.7	–	0.6	18.6	33.3	6.1
	Puerto Rico[2]	–	30.0	–	1.6	23.0	30.0	8.5
	Lowland							
	Brazil[3]	–	55.3	–	0.7	6.2	8.3	5.5
	Ghana[2]	–	32.6	–	2.4	14.3	26.8	6.5
	Brazil[4]	1023–1260	11–40	–	0.3–1.1	–	–	–

[1]Data are estimated with help of element concentrations in coarse root biomass of *Graffenrieda emarginata*.
[2]From Edwards & Grubb (1982).
[3]From Klinge (1975).
[4]From Silver *et al.* (2000).

Table 7. Carbon stocks in soil (n = 5) and contribution of soil, shoot and roots to total carbon stocks at different altitudes of Ecuadorian montane forests. Data shown are mean ± SE. Different lower-case letters indicate significant differences between altitudes (Tukey test, $P < 0.05$).

Altitude (m)	Soil C stocks (g m^{-2})	Relative contribution to total carbon stocks (%)		
		Soil	Shoots[1]	Roots
1900	34200 ± 4100[a]	77	20	3
2400	13100 ± 400[b]	65	25	10
3000	40200 ± 8200[a]	82	11	7

[1]Carbon stocks in shoot biomass are derived from shoot biomass data (G. Moser, pers. comm.), assuming 500 mg g^{-1} as average C concentration in biomass (Gordon & Jackson 2000, Wilcke *et al.* 2005).

total plant C stocks increased with increasing altitude from 14% at 1900 m to 29% at 2400 m and 38% at 3000 m.

DISCUSSION

Impact of altitude on root biomass

Fine- and coarse-root biomass was substantially higher at 3000 m than at 1900 and 2400 m. This is in agreement with results of Röderstein *et al.* (2005) obtained from the same study sites for fine roots down to a soil depth of 0.2 m. It is worth mentioning that absolute amounts of coarse-root biomass may be somewhat underestimated by our approach because very high coarse-root densities occurred underneath the stem bases where sampling was not possible.

The absolute increase of total root biomass with increasing altitude was accompanied by increased biomass partitioning to roots at high altitudes (Table 1). It is well documented that biomass partitioning between above- and below-ground organs is dependent on environmental conditions, such as light intensity (Sultan 2003), soil moisture content (Bell & Sultan 1999), root zone temperature (Engels 1993) and wind speeds (Cordero 1999). Theoretically, biomass partitioning is regulated by plants to optimize capture of above-ground and below-ground resources (Farrar & Jones 2003, McConnaughay & Coleman 1999). Environmental conditions leading to growth limitation by water and mineral nutrients should increase biomass partitioning to roots whereas environmental conditions leading to growth limitation by photosynthesis should increase allocation to shoots. At high altitudes, capture of below-ground resources may be reduced, e.g. due to soil nutrient availability (Bruijnzeel *et al.* 1993, Edwards & Grubb 1977, Tanner *et al.* 1998) and low nutrient uptake ability of roots due to low oxygen availability in soil (Bruijnzeel & Veneklaas 1998). Capture of above-ground resources may be reduced by increased cloudiness, i.e. low light intensity (Bruijnzeel & Veneklaas 1998) and low photosynthetic activity of leaves due to low air temperatures (Kitayama & Aiba 2002). According to the theory of functional equilibrium between roots and shoots (Brouwer 1983), increased biomass partitioning to roots at high altitudes would indicate that environmental conditions at high altitudes limit nutrient uptake activity

more than photosynthetic activity. In accordance with this conclusion, nutrient concentrations in fine roots (Table 3) and foliar nitrogen concentrations of trees were substantially lower at high (11.3 mg g^{-1} at 3000 m) in comparison with low altitudes (21.7 mg g^{-1} at 1900 m). Furthermore, stem concentrations of non-structural carbohydrates were generally high and similar at 1900 m (90–166 mg g^{-1}) and 3000 m (81–149 mg g^{-1}). Thus, there was no evidence for a deficiency in C supply at high altitude.

The proportion of coarse roots to fine roots was higher at 2400 and 3000 m in comparison to 1900 m (Table 1). This was associated with a significant increase in coarse-root biomass and an increase of coarse root to shoot ratios from 0.11:1 at 1900 m to 0.33:1 at 2400 m and 0.48:1 at 3000 m. Cordero (1999) as well as Henry & Thomas (2002) observed that in tree saplings and annual species, root to shoot ratios were increased by exposure to wind. Since tree anchorage is mainly provided by coarse roots (Robinson *et al.* 2003) increased allocation to coarse root biomass may be an indication of increased mechanical stress. In comparison to lower altitudes, mechanical stress at 3000 m was increased by high wind speeds and hampered deep rooting, possibly as a result of oxygen deficiency and shallow mineral soils (Soethe *et al.* 2006a, b). Potential root soil plates were always shallow at this altitude and coarse root systems exhibited a large range of traits that were supposed to improve anchorage, such as marked root system asymmetry and stilt roots (Soethe *et al.* 2006a). There is evidence that increased below-ground biomass at high altitudes is at least partly a response to increased mechanical stress.

Contribution of soil and plant biomass to C sequestration

Soil C stocks at 2400 m (Table 7) were slightly higher than the average of tropical forests (12 300 g m^{-2}) given in the review of Malhi *et al.* (1999). Soil C stocks at 3000 m even exceeded average C stocks in boreal forests (34 300 g m^{-2}; Mahli *et al.* 1999), emphasizing the high potential for C sequestration of tropical montane forest soils. However, no consistent impact of altitude on soil C stocks became apparent.

The contribution of biomass C to total C stocks (soil plus biomass) varied between 18% at 3000 m and 35% at 2400 m (Table 7). This is somewhat lower than in a tropical montane forest in New Guinea (29–41%) reported by Edwards & Grubb (1977). In a global comparison, the C distribution between plant biomass and soil at least at 1900 m and 3000 m was more similar to C distribution in boreal forests where most C (about 84%) is stored in soil organic matter than to C distribution in tropical lowland forests, where about half the C is stored in biomass (Dixon *et al.* 1994, Malhi *et al.* 1999). However, no consistent effect of altitude on carbon stocks in the plant biomass or the contribution of plant biomass C to total C (soil plus biomass) became apparent.

Carbon stocks in the root biomass increased with increasing altitude (Table 6). At 3000 m root C stocks were about three times higher than those reported by Silver *et al.* (2000) for lowland tropical forests. Furthermore, the contribution of roots to total plant C stocks continuously increased with increasing altitude. However, irrespective of altitude, the contribution of roots to total C sequestration in the forest ecosystem was small (Table 7).

The impact of altitude on nutrient stocks in roots

Fine-root biomass as well as stocks of N, P and Mg stored in fine-root biomass were similar to a tropical lowland forest (Klinge 1975; biomass: 1613, N: 13.7, P: 0.24, Mg: 0.86 g m^{-2}) whereas stocks of K and Ca in fine roots (Table 6) were several times higher than in the tropical lowland forest (Klinge 1975; K: 0.6 g m^{-2}, Ca: 0.5 g m^{-2}). In contrast to the significantly increased fine-root biomass at high in comparison to low altitudes, nutrient stocks in fine roots showed no consistent pattern of change with increasing altitude. This was due to a decrease in the concentrations of N, S, P, K and Mg in fine roots with increasing altitude (Table 3), counteracting the increase in nutrient stocks by increasing biomass. In general, nutrient concentrations in roots $\leq$ 5 mm in diameter lay within the range of those reported by Priess *et al.* (1999) for two submontane tropical forest stands and one cloud forest stand in Venezuela and one montane rain forest stand in New Guinea (N: 7.4–14.1, P: 0.33–0.50, K: 2.4–5.0, Ca: 1.1–7.3, Mg: 1.3–6.1 mg g^{-1}). As an exception, concentrations of P at 1900 m markedly exceeded these ranges.

Decreasing root N concentration with increasing altitude was also detected in different grass species growing in New Zealand between 45 and 1205 m (Craine & Lee 2003). The authors suggested that the decrease in N concentrations with increasing altitude could be attributed to a decrease in nutrient availability. Accordingly, Ostertag & Hobbie (1999) observed lower P concentrations in fine roots at a P-deficient site than at a site with sufficient P supply in a tropical montane forest in Hawaii. Our own unpublished data showing a consistent pattern of decreasing foliar nutrient concentrations with increasing altitude also suggest that the decrease in nutrient concentrations in root tissue with increasing altitude was mainly caused by nutrient deficiency.

In contrast to nutrient stocks in fine-root biomass, estimated nutrient stocks in total root biomass followed the increase in root biomass with increasing altitude (Table 6). This was due to the absence of an impact of altitude on nutrient concentrations in coarse roots of *G. emarginata*. The calculation of nutrient stocks in coarse root biomass at all altitudes with average nutrient concentrations from 1900 m and 2400 m seems justified

because in this root pool concentrations of all elements except Ca were not dependent on altitude. However, for Ca this procedure may lead to a slight overestimation of stocks at 1900 m and to a slight underestimation at higher altitude, because the significant increase in Ca concentrations with increasing altitude is not considered.

The impact of environmental conditions on nutrient concentrations in coarse roots is poorly understood. Differences in the impact of altitude on nutrient concentrations in fine- and coarse-root biomass in the present study may either be caused by the differences in the methodological approaches or may indicate that nutrient concentrations in coarse-root biomass are less sensitive to changes of environmental conditions than nutrient concentrations in fine roots.

The contribution of fine- and coarse-root biomass to element storage in total root biomass varied considerably between nutrients (Table 6). Considerable proportions (33.3–72.7%) of total root N, S and P were stored in fine-root biomass < 2 mm in diameter, but only small proportions of Ca (between 5.3 and 9.3%). This implies that in the present study large proportions of root N, S and P were included in short-term nutrient cycling, i.e. these nutrients were returned to the soil within a few years, whereas most Ca in roots was immobilized in the long term.

CONCLUSIONS

Higher root biomass at higher than at lower altitudes reflected the increased allocation of biomass to the root system, presumably as a response to decreased nutrient availability in soil and high mechanical stress affecting trees growing at high altitudes. Higher C and nutrient stocks in coarse roots at higher than at lower altitudes suggest that the importance of this root fraction for long-term nutrient accumulation is increased at high altitudes. Due to the response of nutrient concentrations in fine roots to the change of environmental conditions such as soil nutrient availability along the altitudinal gradient, nutrient stocks in this root fraction did not follow the marked increase of root biomass with increasing altitude. Root biomass of this tropical montane forest may contribute significantly to short-term nutrient cycling by fine-root turnover. However, the contribution of root biomass to C sequestration within this forest is rather low.

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