Above- and below-ground litter production in three tropical montane forests in southern Ecuador

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(Accepted 28th January 2005)

Abstract: Litter production from above-ground (leaves, twigs, fruits, flowers) and below-ground (roots) plant organs is an important component of the cycling of carbon and nutrients in forests. Tropical montane forests possess comparatively large quantities of fine-root biomass, suggesting that litter production by dying fine roots may represent a major component of total litter production. In a comparative study in three tropical montane forests of southern Ecuador at 1890, 2380 and 3060 m elevation, we measured leaf-fall by litter trapping and fine-root litter production by sequential soil coring and fine-root biomass and necromass analysis for about 1 y with the objectives (1) to quantify annual above- and below-ground litter production, and (2) to investigate elevational differences in litter production. Leaf litter mass decreased to less than a third (862 to 263 g m⁻² y⁻¹) with increasing elevation (1890 m to 3060 m), whereas fine-root litter production increased by a factor of about four (506 to 2084 g m⁻² y⁻¹). Thus, the ratio of leaf to fine-root litter shifted by an order of magnitude in favour of fine-root litter production between 1890 to 3060 m. Fine-root litter production was not synchronized with leaf litterfall and was seasonal only at 3060 m with mortality peaks in the drier and the wetter periods. We conclude that dying fine roots represent a very important fraction of total litterfall in tropical montane forests that can exceed the quantity of leaf litter. At 3060 m, the largest part of the organic material on top of the soil must originate from dying fine roots but not from fallen leaves.

Key Words: Elevation, fine-root biomass, fine-root necromass, leaf litterfall, sequential soil coring

INTRODUCTION

Plant litter originates from two primary sources: (1) above-ground plant organs including leaves, stems and reproductive organs and (2) below-ground organs, i.e. roots. The latter include long-lived coarse (diameter > 2 mm) roots, which typically contribute only small quantities of litter, and fine roots (< 2 mm) with a high turnover rate. Root sampling led to the conclusion that fine root production and turnover contributes from 33–67% to the annual net primary production in temperate forests (Grier et al. 1981, Jackson et al. 1997, Santantonio & Grace 1987). If valid in a more general sense, these results suggest a key role for fine-root litter production in the cycling of carbon and nutrients in forest soils. Dying and decomposing fine roots could be as important, or even more important, than leaf litter as a source of organic matter in forest soils.

In most tropical forest litterfall studies, only above-ground litter has been sampled (Medina & Cuevas 1989, Vogt et al. 1986). Fine-root biomass has been analysed in quite a number of tropical lowland and montane forests (e.g. Cairns et al. 1997, Sanford & Cuevas 1996, Vogt et al. 1996), whereas fine-root production and turnover data are scarce. We are aware of only a single study which compared synchronously measured above-ground and below-ground litterfall in a tropical forest stand (Sanford & Cuevas 1996). In tropical montane forests, that often possess large quantities of fine-root biomass (Hertel et al. 2003), neither the total (above-ground and below-ground) litter production nor the relative importance of the root litter fraction are known.

As part of a more comprehensive investigation on carbon cycling in tropical montane forests, this study has two objectives: (1) the quantification of both above-ground and below-ground components of litter production and (2) the investigation of elevational changes in litter production. The measurements were conducted in three mid- to upper montane forests in
the Andes of southern Ecuador with a humid climate throughout the year.

METHODS

Study sites

We selected three forest stands at 1890–3060 m elevation south-east of Loja in the southern Ecuadorian Andes at a maximum distance of 30 km from each other (Figure 1 and Table 1). The study area is located on the northern and north-western fringes of Podocarpus National Park on the eastern Andes slope. Stands 1 and 2 are in the vicinity of Estacion Scientifica San Francisco (ECSF) south of the road from Loja to Zamora. Stand 3 is located in the Cajanuma area near the north-western entrance of Podocarpus National Park south of Loja. The sites are situated on moderately steep slopes (27–31°) facing north-east to north-west. Plot selection was done on the basis of a detailed structural and floristic survey of the montane forests of the region which indicated several floristically defined forest communities along the slope (Homeier 2004). The root study plots (20 × 20 m) were established in representative sections of three forest stands at 1890, 2450 and 3060 m elevation. The plots were selected in areas with a more or less homogeneous stand structure and little or no signs of human influence. The stands had closed canopies without any large gaps on the study plots.

The three sites represent typical vegetation types of mid- to upper montane rain forest of the southern Ecuadorian Andes. Stand 1 is 19 m in maximum height and consists mainly of trees of the genera *Graffenrieda* and *Miconia* (Melastomataceae), *Schefflera* (Araliaceae) and *Prumnopitys* (Podocarpaceae). Important tree genera of stand 2 are *Clusia* (Clusiaceae), *Schefflera* (Araliaceae), various genera of Melastomataceae and *Podocarpus* (Podocarpaceae). This site has a maximum height of 12 m. Stand 3 is a typical ‘elfin forest’ with very crooked stem forms and a maximum stand height of only 9 m. Notable tree genera are *Clusia* (Clusiaceae), *Weinmannia* (Cunoniaceae), *Ilex* (Aquifoliaceae) and *Hedyosmum* (Chloranthaceae) (Homeier 2004). Stand 3 is situated close to the timberline which occurs at a relatively low elevation in the Loja/Zamora region. Patches of alpine paramo are found about 200 m upslope of stand 3.

The soils of the three sites developed on metamorphic shale, quartzite or sandstone bedrock and are nutrient-poor. They are classified as Inceptisols (USA classification) or Humic Cambisols (FAO taxonomy). On top of the mineral soil, thick organic layers exist (300 mm depth at 1890 m, 430 mm at 3060 m). The pH value of the mineral soil (0–30 cm) decreases with elevation from 3.8 (stand 1) to 3.3 and 3.2 (stands 2 and 3) whereas the C/N ratio increases (16 to 25, N. Soethe, unpublished). We found an increase in the quantity of organic material on top of the soil by a factor of 2.5 between 1890 and 3060 m asl.

**Table 1.** Location and characteristics of the study sites. Mean temperature and humidity were measured at 1.5 m height inside the stands (means of the period March–August 2003, data by G. Moser, unpublished); rainfall data are extrapolated from measurements in gaps at 1950, 2680 and 3170 m (P. Emck, unpublished).


<table>
<thead>
<tr>
<th>Stand no.</th>
<th>Location</th>
<th>Elevation (m asl)</th>
<th>Slope (°)</th>
<th>Mean air temperature (°C)</th>
<th>Mean air humidity (%)</th>
<th>Rainfall (mm y⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>S03°58' W79°04'</td>
<td>1892</td>
<td>31</td>
<td>14.9</td>
<td>93.7</td>
<td>1950</td>
</tr>
<tr>
<td>2</td>
<td>S03°59' W79°04'</td>
<td>2380</td>
<td>28</td>
<td>12.3</td>
<td>95.4</td>
<td>5000</td>
</tr>
<tr>
<td>3</td>
<td>S04°06' W79°10'</td>
<td>3059</td>
<td>27</td>
<td>8.6</td>
<td>94.3</td>
<td>4500</td>
</tr>
</tbody>
</table>

Microclimate and soil moisture measurements

Rainfall and temperature data were obtained from P. Emck (University of Erlangen, unpubl. data) who operated rain gauges and climate stations during the period of August 2001 to February 2003 in gaps at 1950, 2680 and 2900 m elevation upslope of the ECSF, and at 3170 m in the Cajanuma area. These data were used to estimate rainfall at the study sites by interpolation. Additionally, temperature stations at 1.5 m above the forest floor recorded air temperature and air humidity.
inside stands 1, 2 and 3 from March 2003 to August 2003 (Table 2). The study period 2001–2003 did not include a marked El Nino year.

Measurements of soil water content (θ) were done gravimetrically by extracting 10 soil samples per site every sixth week using a soil corer (55 mm diameter) and a randomized sampling design. The samples were separated into organic and mineral soil (0–20 cm); the thickness of the uncompressed organic horizon was measured separately to allow calculation of the volumetric water content. Samples were transferred in plastic bags to the ECSF laboratory, where the water content was measured by weighing before and after drying (70 °C, 48 h).

Above-ground litter sampling

Above-ground litter was collected in the field every 6 wk from November 2001 to October 2002. Due to the remote location of the three plots, sampling took place during four consecutive days following 15 October 2001, 26 November, 16 January 2002, 23 February, 14 April, 29 May, 9 July and 13 August. Twelve litter traps (40 × 40 cm) were placed in each plot using a random-block design. The collected litter was transferred to the laboratory and separated into leaves, fruits, twigs and epiphytes. In this paper, only the leaf fraction results are reported. The leaf fraction included small organic particles (< 5 mm (bud scales etc.) which were not separated from the leaves. Dry mass was determined at 60 °C (4 d). The leaf mass sampled in a period was normalized to monthly litterfall rates. The litterfall values are underestimates because a certain degree of decomposition may have occurred during the 6-wk sampling intervals. Moreover, part of the leaf fraction probably decomposes in the canopy and does not reach the ground.

### Table 2. Annual rates of leaf and fine-root litter production in the mineral soil (min. soil) and the organic layer (org. layer) at the sites 1, 2 and 3 in g m⁻² y⁻¹. Leaf litter: November 2001–October 2002, root litter: October 2001–August 2002, data extrapolated to 12 mo total = mineral soil plus organic layer. Significant differences between the stands are indicated by different letters. Given are means ± SE.

<table>
<thead>
<tr>
<th>Stand</th>
<th>Elevation (m asl)</th>
<th>Annual leaf litter production</th>
<th>Annual root litter production</th>
</tr>
</thead>
<tbody>
<tr>
<td>no.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>1890</td>
<td>862 ± 85ab</td>
<td>506 ± 45a (total)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>393 ± 77a (org. layer)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>113 ± 14b (min. soil)</td>
</tr>
<tr>
<td>2</td>
<td>2380</td>
<td>433 ± 33b</td>
<td>1226 ± 149b (total)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>694 ± 201a (org. layer)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>533 ± 97b (min. soil)</td>
</tr>
<tr>
<td>3</td>
<td>3060</td>
<td>263 ± 44b</td>
<td>2084 ± 177c (total)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>922 ± 125b (org. layer)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>1162 ± 228b (min. soil)</td>
</tr>
</tbody>
</table>

### Fine-root analysis

Biomass and turnover of tree fine roots were investigated by sequential soil coring in the organic layer and in the top 20 cm of the mineral soil. Earlier investigation showed that the soil profiles were rather shallow at all sites except for stand 1, not exceeding 30–40 cm in depth. Fine-root density decreased rapidly with soil depth from the organic horizon (2.6–4.6 kg m⁻³ of root biomass) to the 20–30 cm horizon (0.15–0.66 kg m⁻³, C. Bertsch, unpubl. data). Thus, up to 80% or more of the profile total of fine-root biomass occurred in the organic layer and in the top 20 cm of the mineral soil. Twenty sampling locations were selected with a random-block design in each plot. From October 2001 to August 2002, one soil sample per sampling location was collected with a 33-mm-diameter steel corer at 6-wk intervals on the above-mentioned eight sampling dates. This procedure allowed a statistical analysis of the data (n = 20). The extracted soil cores were separated into organic and mineral soil horizons, transferred to plastic bags, and transported to the ECSF laboratory where the stored (4 °C) samples were processed within 30 d. In total, 960 root samples were analysed.

In the laboratory, root samples were soaked in water and separated from soil residues using a 0.25-mm-mesh sieve. Long root fractions (> 10 mm length) were extracted by hand. Only fine roots (i.e. roots with diameter < 2 mm) were subject to further analysis. Live root biomass and dead root particles (necromass) were distinguished under a stereomicroscope by colour, root elasticity and the degree of cohesion of cortex, periderm and stele. A dark cortex and stele, or a white, but non-turgid cortex and stele, or the complete loss of the stele and cortex with only the periderm being present, were used as indicators of root death (Persson 1978). All tree roots (including tree fern roots), but not herbaceous roots, were analysed. Six of the 20 soil samples per horizon were subjected to a detailed analysis of fine-root necromass particles < 10 mm length according to a method described by van Praag et al. (1988) and modified by Hertel & Leuschner (2002). Following the manual extraction of the necromass > 10 mm length, the residue of the sample was evenly spread on a piece of filter paper (730 cm²) with a grid of 36 squares. Six of the squares were randomly selected and analysed under the microscope for even the smallest dead fine-root fragments. These decaying root particles represent the main necromass fraction (Bauhus & Bartsch 1996, Hertel 1999). Root biomass and necromass were dried at 60 °C (48 h) and weighed. The mass of small dead rootlets in the six squares was extrapolated to the entire sample using a relationship between small, dead root fragments and large, dead roots (> 10 mm length) that was established in other sub-samples.
We calculated fine-root litter production from seasonal changes in fine-root biomass (B) and necromass (N) in a given soil horizon which allows estimation of fine-root mortality. We used the decision matrix of McClaugherty et al. (1982), Fairley & Alexander (1985) and Santantonio & Grace (1987) to estimate fine-root mortality M (i.e. the production of fine-root necromass) in all 6-wk sampling intervals of the 10-mo study period. According to the decision matrix, M equals \( \Delta N \) if both \( \Delta B \) and \( \Delta N \) are positive; if both \( \Delta B \) and \( \Delta N \) are negative, M is equal to the amount of \( \Delta B \); if \( \Delta B \) is positive and \( \Delta N \) is negative, M is zero. Finally, if \( \Delta B \) is negative and \( \Delta N \) is positive, M equals \( \Delta N \) if \( \Delta N > \Delta B \) or \( \Delta B \) if \( \Delta N < \Delta B \). This calculation was conducted separately for all 20 sampling locations per site and for each 6-wk sampling interval.

For estimating annual root litter production, we applied the ‘minimum-maximum calculation’ approach which estimates root mortality from the significant difference between the lowest and highest total fine-root mass (bio- plus necromass) in the study period. The minimum-maximum calculation is only applicable in stands with a distinct seasonality in root biomass. This precondition was fulfilled in the study region. However, this calculation approach neglects synchronous events of fine-root production and death that may occur between the sampling dates. Thus, our annual fine-root litter production values may underestimate fine-root turnover. Nevertheless, comparative analysis showed that this calculation method is less susceptible to systematic errors than other root mass-based approaches such as the compartmental flow method (Sala et al. 1988).

Statistical analysis

Differences in soil water content, in leaf litterfall and in root parameters among the three stands, or between different sampling dates or the two soil horizons were analysed using a non-parametric analysis of variance (Kruskal–Wallis test) and a Mann–Whitney two-sample test (Wilcoxon U-test). For the leaf litter data with a Gaussian distribution according to the Shapiro & Wilk test, differences among stands were analysed with ANOVA and a parametric two-sample test after Scheffé. All calculations were done with SAS/STAT software (P < 0.05).

RESULTS

Thermal and hydrologic regimes

Mean air temperature inside the forest decreased from 14.9°C at 1890 m to 8.6°C at 3060 m reflecting a temperature lapse rate of about 5 K km\(^{-1}\) along the slope (Table 1). Temperature seasonality was low with the warmest month (November) exceeding the coldest month (August) in mean temperature by only 1.9–2.4 K. The mean air humidity inside the forest was high (94–95%) at all three elevations.

Annual rainfall increased with elevation from an estimated 1950 mm to about 5000 mm (2380 m) and 4500 mm (3060 m, period October 2001 to September 2002, Figure 1, data from P. Emck). There was only a slight seasonality in rainfall at the 1950 m weather station in the 2001–2002 measuring period: April to July were wetter than October to March with peak rainfall recorded in July 2002 (299 mm) and lowest precipitation measured in January 2002 (58 mm). At the 2680-m station, the difference between the wetter season (April–July) and the drier season (October–March) was much more pronounced. The rainfall in July 2002 (1198 mm) exceeded the precipitation in November 2001 more than sixfold (183 mm).

Water content in the organic layer showed a significant increase from stand 1 to stand 3 (annual means: 14.5, 25.0 and 30.0 vol.%, respectively, Figure 3a). A marked seasonality occurred only at the uppermost site with a particularly high organic layer water content in January and February 2002.

Soil water content in the mineral soil increased with elevation from stand 1 (mean = 23.3 vol.%) to stand 2 (mean = 33.7 vol.%, Figure 2b). The highest stand (3) had an intermediate mean water content in the mineral soil (27.0 vol.%). Seasonal variations in \( \theta \) were low in the mineral soil at 1890 and 3060 m but showed a peak in May 2002 at 2380 m.

Leaf litter production

Annual totals of leaf litter decreased with elevation (Table 2). Stand 1 produced twice as much leaf litter
as stand 2, and exceeded stand 3 by a factor of three (differences significant between stands 1 and 2, but not between 2 and 3). At 1890 m, leaf-fall showed a distinct seasonality in the 2001/2002 period with a marked peak in November in the drier season, and a second peak in June/July in the wetter season; both peaks differed significantly from the lows in the drier periods in March and September/October 2002 (Figure 4). Seasonality in litterfall was less pronounced at high elevations with no significant differences between the highest and lowest values of a season. Throughout the year, leaf litter of 20–40 g m⁻² mo⁻¹ were recorded in the stands 2 and 3. There was a tendency for higher litterfall in the wetter season (June and July). However, in contrast to stand 1, a second small peak was visible in the stands 2 and 3 at the end of the drier season (December to February).

Fine-root litter production

The soil-coring study on fine-root live biomass and necromass in the three forest stands revealed two principal results. In both the organic layer and the mineral soil, the average fine-root biomass and necromass in the period October 2001–August 2002 increased significantly from 1890 to 3060 m asl (Figure 5, difference not significant between 1890 and 2380 m for the mineral soil). Significant seasonal fluctuations of biomass and necromass occurred at all three sites and in both horizons. They were more pronounced at the high-elevation stand 3 with a higher fine-root mass than in stands 1 and 2.

Fine-root litter production as calculated with the minimum-maximum method from the seasonal fluctuations in live root biomass and necromass was significantly higher at 3060 m than at 1890 or 2380 m (Table 2 and Figure 6). We obtained totals of 506, 1226 and 2084 g m⁻² y⁻¹ in the stands 1, 2 and 3, respectively. Thus, annual root litter production increased more than fourfold from 1890 to 3060 m.

At the highest stand, peaks of fine-root litter production occurred during the drier periods (November and February) and lows in the wetter period (June). In the mineral soil, these values differed significantly from each other (Figure 6). Fluctuations in other horizons and at other sites were not significant.

DISCUSSION

Quantity of above-ground litter

The annual above-ground leaf litterfall (263–862 g m⁻² y⁻¹) in the three stands was comparable to the range reported in 18 other tropical montane forests of the Americas and Asia (230–1259 g m⁻² y⁻¹ for stands at 1000–2900 m, Table 3). From this data compilation of 21 forest stands, we obtained a mean leaf
Figure 5. Seasonal courses of fine-root biomass (A and C) and necromass (B and D) in the organic layer and the mineral topsoil of the three study sites (mean and standard error, n = 20 soil cores per site and sampling date). Differences between the seasonal biomass or necromass maxima and minima were significant at all three sites for a given horizon.

litterfall of 538 g m\(^{-2}\) y\(^{-1}\) for tropical montane forests. Our comparison is based only on the leaf fraction and does not include other components such as twigs, fruits or epiphytes (Vitousek 1984, Wilcke et al. 2002). Since part of the litter is trapped in tree canopies and does not reach the soil, the data in Table 3 are underestimates of leaf litterfall and thus do not indicate total above-ground litterfall. However, if the focus is on tree litterfall as in this study, a comparison of total litterfall would be misleading because vascular and non-vascular epiphyte litter can make up more than 40% of total above-ground litterfall in tropical montane forests (Hölscher et al., in press). This fraction can vary with elevation and would mask elevational changes in tree litter.

### Quantity of root biomass and below-ground litter

Over the past 50 y, more than 50 studies on root biomass in tropical forests have been published (Sanford & Cuevas 1996). Most of these studies referred to lowland forests, and only few to tropical montane forests. Tropical moist forests (lowland and montane) seem to possess, on average, higher total root biomass (fine, coarse and large roots) than most other forest types, up to 5000 g m\(^{-2}\) of dry matter (Jackson et al. 1996). Data for fine-root biomass of tropical montane forests differ, with values ranging from only 150 g m\(^{-2}\) in Hawaii (Herbert & Fownes 1999) to 200–300 g m\(^{-2}\) in cloud forests of Colombia and India (Cavelier et al. 1996, Sundarapandian & Swamy 1996) and > 800 g m\(^{-2}\) in wet montane forests of Costa Rica and tropical Australia (Maycock & Congdon 2000, Vance & Nadkarni 1992). A particularly high fine-root biomass (> 1100 g m\(^{-2}\)) was found in upper montane oak forests of Costa Rica (Hertel et al. 2003). The large variation in fine-root biomass in these studies may partly reflect differences in species composition and environmental conditions of the forests. For example, the exceptionally high values reported by Hertel et al. (2003) for Costa Rica refer to ectomycorrhizal Quercus forests which could differ in fine-root biomass from other tropical montane forests with predominantly VA mycorrhizas as in our stands (Kottke et al. 2004). However, part of the variation is due to different methods used for fine-root extraction and different profile depths investigated.

Much less information exists on fine-root growth and root litter production in tropical montane forests. In an ingrowth-core study, Priess et al. (1999) reported very high production rates (>1000 g m\(^{-2}\) y\(^{-1}\)) in a submontane rain forest of Venezuela which are in the same order of magnitude as our root litter production data in the upper montane stand 2. In a submontane
Production in three tropical montane forests in southern Ecuador

Organic layer

Mineral soil (0-20 cm)

Figure 6. Seasonal course of fine-root litter production in organic layer and mineral topsoil of the three sites as calculated with the compartmental flow calculation (n = 20 soil cores per site and sampling date). The sampling periods had a length of about 6 wk.

The fine-root litter production rate. Accordingly, most of the organic material on top of the soil at higher elevations must originate from decaying tree fine roots, and not from leaf litter.

To our knowledge, the only study which measured fine-root litter production and leaf litterfall synchronously in a tropical forest is that of Sanford & Cuevas (1996) in a lowland moist forest in Costa Rica. They measured 763 and 1483 g m\(^{-2}\) y\(^{-1}\) of fine-root and leaf-litter production, respectively, at a nutrient-poor site, and 718 and 412 g m\(^{-2}\) y\(^{-1}\) at a fertile site. Thus, root litter far exceeded leaf litter with a leaf/root litter production ratio of about 0.5 in the infertile stand. In contrast, the ratio approached 1.7 in the fertile stand. Those results and ours are similar in that leaf/root litter ratios less than equality were obtained from tropical forests in environments with assumed soil resource limitation, i.e. nutrient-poor lowland forests and cool upper montane forests with putative nutrient limitation. In contrast, litter ratios greater than equality were observed in fertile lowland and moderately warm, lower montane forests where fine-root turnover apparently is much lower.

Seasonality in leaf and root litter production

Although our study region has a perhumid climate with only one or several relatively dry periods but no marked dry season, we observed a distinct litterfall peak in the relatively dry month November at the lowest site. According to Wright & Cornejo (1990) this peak could be explained by a combination of several environmental factors including a high evaporative demand in the dry season, associated stomatal closure and subsequent leaf overheating together with photoinhibition which may lead to leaf ageing and subsequent leaf shedding at the end of the drier season. However, our data show a second leaf-fall peak from May to July when the highest rainfall of the year occurred. This does not support a drought-related explanation. According to our observation, irregularly occurring strong valley winds may have contributed significantly to the observed seasonality at stand 1.

Fine-root production in tropical forests was found to be seasonal if extended dry periods occurred. Typically, an increase in fine-root growth was reported with the onset of the wet season, and a decrease in biomass during the dry season (Kummerow et al. 1990, Singh & Singh 1981, Srivastava et al. 1986). Kavanaugh & Kellman (1992) observed a fine-root growth peak with the onset of the wet season but a reduction in growth late in the wet season which was not related to soil moisture or soil nutrients. They speculated that carbohydrate reserves that accumulated in roots during the dry period were depleted in the early wet season. This shortage might have limited further root growth late in the wet season.
Table 3. Leaf litterfall in montane and upper montane tropical forests. If indicated in the sources, only data of leaf litter are considered.

<table>
<thead>
<tr>
<th>Country (site)</th>
<th>Elevation (m asl)</th>
<th>Leaf litterfall (g m(^{-2}) y(^{-1}))</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Puerto Rico</td>
<td>1000</td>
<td>245</td>
<td>Weaver et al. 1986</td>
</tr>
<tr>
<td>Costa Rica</td>
<td>1000</td>
<td>550</td>
<td>Heaney &amp; Proctor 1989</td>
</tr>
<tr>
<td>Malaysia</td>
<td>1310</td>
<td>570</td>
<td>Proctor et al. 1983</td>
</tr>
<tr>
<td>Costa Rica (Mor ridge)</td>
<td>1550</td>
<td>490</td>
<td>Tanner 1977</td>
</tr>
<tr>
<td>Jamaica (Mull ridge)</td>
<td>1550</td>
<td>530</td>
<td>Tanner 1977</td>
</tr>
<tr>
<td>Jamaica (gap)</td>
<td>1550</td>
<td>550</td>
<td>Tanner 1977</td>
</tr>
<tr>
<td>Jamaica (Mull humus)</td>
<td>1809</td>
<td>512</td>
<td>Hafkenscheid 2000</td>
</tr>
<tr>
<td>Jamaica (Mor humus)</td>
<td>1824</td>
<td>462</td>
<td>Hafkenscheid 2000</td>
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<tr>
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<td>1860</td>
<td>230</td>
<td>Proctor et al. 1983</td>
</tr>
<tr>
<td>Ecuador</td>
<td>1890</td>
<td>862</td>
<td>This study(^1)</td>
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<tr>
<td>Costa Rica</td>
<td>2000</td>
<td>480</td>
<td>Heaney &amp; Proctor 1989</td>
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<td>Venezuela</td>
<td>2300</td>
<td>338</td>
<td>Steinhardt 1979</td>
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<td>Ecuador</td>
<td>2380</td>
<td>433</td>
<td>This study(^1)</td>
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<td>Papua New Guinea</td>
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<td>620</td>
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<td>Ecuador</td>
<td>3060</td>
<td>263</td>
<td>This study(^1)</td>
</tr>
<tr>
<td>Mean</td>
<td></td>
<td>538</td>
<td></td>
</tr>
</tbody>
</table>

\(^1\)Contains a small fraction of non-leaf fine litter < 5 mm.

In the Ecuadorian Andes, a distinct seasonality in fine-root biomass and necromass was only visible in the uppermost stand. At this site, we observed a relatively high root necromass in the drier period (November) as well as in the wetter season (June/July) as well. Increases in fine-root necromass coincided with peaks of fine-root litter production in these periods. It remains unclear whether partial anoxia after heavy rainfall (temporarily exceeding 1000 mm mo\(^{-1}\) at this site), a relatively dry period in November 2001, or other factors increased fine-root mortality in these two periods.

Litterfall and elevation

Our data showed a large elevational decrease in annual leaf litter mass with significant differences at least between the two lower stands. A reduced leaf-fall corresponded with decreases in maximum tree height, above-ground tree biomass and net primary production as estimated from stem diameter growth (Homeier 2004). Thus, in our transect, leaf litterfall decreased in parallel with plant productivity along the slope. In contrast, Kitayama & Aiba (2002) did not find a reduction in above-ground litterfall along an elevational transect from 700 to 3060 m on Mt. Kinabalu (Malaysia). Similarly, a meta-analysis of the leaf litter data from various tropical montane forests in Table 3 does not show a significant elevational change in leaf litterfall between 1000 and 3060 m asl (R\(^2\) = 0.32, P = 0.16). Thus, elevational patterns in leaf litterfall deserve more intensive study in tropical mountains.

Annual fine-root litter production significantly increased with elevation despite a decrease in temperature by 5 K km\(^{-1}\). To test the reliability of our root litter production measurements obtained by sequential coring and the minimum-maximum calculation, we additionally conducted an ingrowth-core study as an independent second method for assessing the growth potential of fine roots in situ. Based on 20 cores per stand exposed for 6 mo, we calculated a 9% increase in annual fine-root growth between 1890 and 3060 m (Röderstein, unpubl. data). These data can only give a very rough estimate of root litter production in the three stands, but they may indicate elevational trends. The elevational change found in the ingrowth cores was less than the increase obtained from the sequential coring data. However, both approaches independently indicated an elevational increase in fine-root growth. Kitayama & Aiba (2002) observed a doubling of fine-root biomass between 700 and 3060 m on Mt. Kinabalu which is in agreement with our root biomass data; however, they did not investigate fine-root production and root turnover.
We suggest that decreasing temperature along the slope affects decomposition and thus lowers nutrient availability at higher elevation. Trees respond by producing foliage with a higher degree of sclerophyll and by maintaining larger fine root systems. A larger total root surface area might compensate for reduced specific nutrient uptake rates of roots in nutrient-poor soils. It remains open whether the large stocks of root necromass found at high elevation result from reduced decomposition rates of dead roots, or are the consequence of higher root litter production rates. In theory, both processes could contribute to the large root necromass pools observed in our study. Direct observation of root longevity with mini-rhizotrons or other techniques is needed to answer this question.

ACKNOWLEDGEMENTS

We are very grateful to A. Martínez-Jervez and J. Homeier who conducted floristic inventories. We also thank P. Emck and M. Richter (University of Erlangen) for rainfall data, and N. Soethe (Berlin) for pH data. We gratefully acknowledge financial support supplied by DFG (German Science Foundation) through a grant to the Forschergruppe 402 (Funktionalität in einem tropischen Regenwald Südecuadors, subproject B7). We thank INEFAN for granting the research permit, and FondacionScientifica San Francisco for ongoing support at ECSF.

LITERATURE CITED


