

Elevation effects on the carbon budget of tropical mountain forests (S Ecuador): the role of the belowground compartment

GERALD MOSER*†, CHRISTOPH LEUSCHNER*, DIETRICH HERTEL*, SOPHIE GRAEFE*‡, NATHALIE SOETHE§ and SUSANNE IOST¶

*Plant Ecology, Albrecht von Haller Institute for Plant Sciences, University of Göttingen, Untere Karspüle 2, 37073 Göttingen, Germany, †Plant Ecology, University of Giessen, Heinrich-Buff-Ring 26-29, 35392 Giessen, Germany, ‡International Center for Tropical Agriculture, Recta Cali Palmira, km 17 Cali, Colombia, §Botany and Landscape Ecology, University of Greifswald, Grimmer Str. 88, 17487 Greifswald, Germany, ¶Institute for World Forestry, Johann Heinrich von Thünen-Institut (vTI), Federal Research Institute for Rural Areas, Forestry and Fisheries, Leuschnerstr. 91, D-21031 Hamburg, Germany

Abstract

Carbon storage and sequestration in tropical mountain forests and their dependence on elevation and temperature are not well understood. In an altitudinal transect study in the South Ecuadorian Andes, we tested the hypotheses that (i) aboveground net primary production (ANPP) decreases continuously with elevation due to decreasing temperatures, whereas (ii) belowground productivity (BNPP) remains constant or even increases with elevation due to a shift from light to nutrient limitation of tree growth. In five tropical mountain forests between 1050 and 3060 m a.s.l., we investigated all major above- and belowground biomass and productivity components, and the stocks of soil organic carbon (SOC). Leaf biomass, stemwood mass and total aboveground biomass (AGB) decreased by 50% to 70%, ANPP by about 70% between 1050 and 3060 m, while stem wood production decreased 20-fold. Coarse and large root biomass increased slightly, fine root biomass fourfold, while fine root production (minirhizotron study) roughly doubled between 1050 and 3060 m. The total tree biomass (above- and belowground) decreased from about 320 to 175 Mg dry mass ha⁻¹, total NPP from ca. 13.0 to 8.2 Mg ha⁻¹ yr⁻¹. The belowground/aboveground ratio of biomass and productivity increased with elevation indicating a shift from light to nutrient limitation of tree growth. We propose that, with increasing elevation, an increasing nitrogen limitation combined with decreasing temperatures causes a large reduction in stand leaf area resulting in a substantial reduction of canopy carbon gain toward the alpine tree line. We conclude that the marked decrease in tree height, AGB and ANPP with elevation in these mountain forests is caused by both a belowground shift of C allocation and a reduction in C source strength, while a temperature-induced reduction in C sink strength (lowered meristematic activity) seems to be of secondary importance.

Keywords: aboveground biomass, belowground biomass, fine root production, net primary production, root/shoot ratio, SOC, tropical montane forest, wood increment

Received 25 November 2009 and accepted 14 October 2010

Introduction

Tropical rainforests occupy only some 12% of the terrestrial surface but contain about 55% of the biomass (Grace & Meir 2009). An accurate characterization of carbon stores and net primary production (NPP) in tropical forests will be fundamental for realistic global and regional C budgets and for predicting how these will be affected by the changing climate. Not only forest conversion, but also changes in temperature, [CO₂] and

rainfall may significantly affect the C sequestration potential of tropical forests (Grace *et al.*, 1995).

There is no simple approach for obtaining information on the possible future response of tropical old-growth rainforests to the expected changes in temperature, rainfall and atmospheric [CO₂]. Field manipulation studies may help to investigate forest responses to altered rainfall and [CO₂] (e.g. da Costa *et al.*, 2010), but they are hardly practicable for studying long-term effects of elevated temperature on tropical forests. One source of indirect information can be transect studies along latitudinal or altitudinal temperature gradients, or meta-analyses of comprehensive data bases on forest ecosystem functioning in different climates. Even

Correspondence: Christoph Leuschner, tel. + 49 551 395718, fax + 49 551 395701, e-mail: cleusch@gwdg.de

though most gradient studies are suffering from the fact that one or more environmental factors covary with the target variable, valuable insights into the temperature dependence of productivity and carbon cycling in forests have been achieved by comparing C pools and fluxes in forests differing in mean temperature (e.g. Clark *et al.*, 2001a,b; Luyssaert *et al.*, 2007).

The majority of studies assessing C pools and C sequestration in tropical moist forests have been conducted in lowland forests (e.g. Clark *et al.*, 2003; Feeley *et al.*, 2007), while the C stores of tropical mountain forests are less well known. The decrease in tree size with elevation indicates a reduction of the biomass C pool towards higher altitudes, whereas reduced decomposition rates may cause higher amounts of soil organic carbon (SOC) in tropical montane and upper montane forests as compared with lowland stands (e.g. Grubb *et al.*, 1963; Tanner 1981; Schawe *et al.*, 2007).

Clark *et al.* (2001a,b) synthesized the available data on the biomass and productivity of tropical forests based on published data for 39 forest sites. While numerous studies have measured aboveground biomass (AGB), stem wood increment and fine litterfall, only very limited or no data exist on other aboveground NPP (ANPP) components such as leaf herbivory, organic leachates or the release of VOCs. More critical, however, is the scarcity of information on belowground biomass and belowground NPP (BNPP). The biomass of coarse and large roots (i.e. roots >2 mm in diameter) was measured at very few sites only and typically by excavating a few trees or digging a few monoliths (Clark *et al.*, 2001a,b). The data base is more comprehensive for fine root biomass (<2 mm in diameter) with 32 and 19 investigated tropical forest sites listed in the reviews of Vogt *et al.* (1996) and Jackson *et al.* (1996). A recent data compilation by Finér *et al.* (2011) contains fine root biomass data from 83 tropical forest stands, mostly from lowland sites. For Amazonian forests, Houghton *et al.* (2001) report a mean root biomass value of 21% (range 13–26%) of aboveground live tree biomass.

Only a small number of studies attempted to quantify fine root production (e.g. Espeleta & Clark 2007; Metcalfe *et al.*, 2008), but often with inadequate methods. Empirical data on the coarse root increment of tropical forests are virtually lacking. Clark *et al.* (2001a,b) proposed a range for the BNPP of tropical forests of 20–120% of ANPP, which demonstrates the importance of BNPP in productivity estimates. Such wide ranges in estimated root production reflect the fact that our knowledge on BNPP in tropical forests is very limited causing large uncertainties about carbon balance and C turnover in these forests.

In this study along a 2000-m elevation transect in South Ecuador, we collected a unique dataset on above-

and belowground biomass fractions and related carbon pools, SOC, and above- and belowground productivity of five mountain forest stands situated at elevations between 1000 and 3000 m a.s.l. The main focus is on root biomass and root productivity, the fractions with largest uncertainties.

Based on earlier work in the area (Leuschner *et al.*, 2007; Moser *et al.*, 2007; Graefe *et al.*, 2008a, b), we hypothesized that (i) ANPP decreases continuously with elevation driven by the more or less constant temperature decrease, whereas (ii) belowground NPP remains constant or increases with altitude, reflecting a change in resource limitation from predominant light limitation at low elevations to an increasing nutrient limitation at high elevations. Several other environmental parameters were also measured along this transect for identifying putative underlying causes of elevational change in biomass and productivity.

Material and methods

Study sites

We installed five permanent forest plots between 1050 and 3060 m a.s.l. at a maximum distance to each other of 30 km in the South Ecuadorian provinces of Zamora-Chinchipe and Loja. The lowermost stands #1 and 2 are within the Podocarpus National Park at pre-montane elevation close to the park entrance at Bombuscaro, south of the provincial capital Zamora (#1: 04°06'54"S, 78°58'20"W; #2: 04°06'42"S, 78°58'20"W). Stands #3 and 4 (montane elevation) are located in the adjacent Reserva Biológica San Francisco (#3: 03°58'35"S, 79°04'55"W; #4: 03°59'19"S, 79°04'55"W). Stand #5 is a stunted upper montane forest located in the Cajanuma area of the national park (04°06'771"S, 79°10'58"W). Patches of treeless alpine paramo vegetation are found about 200 m upslope of this stand (Fig. 1).

The stands are situated on moderately steep slopes facing northeast to northwest, except for stand #2 (10° inclination, Table 1). Study plots of 400 m² size were selected in forest areas with no or only minimal signs of human influence (as indicated by charcoal, stumps, or the presence of light-demanding pioneer trees). We used the floristic and physiognomic classification system of Balslev & Øllgaard (2002) to select forest patches that were representative for the forest vegetation of the respective elevation. Parts of the stand without larger canopy gaps and unaffected by topsoil disturbance due to animal activity were selected for study. Since pedological investigations in Ecuadorian mountain forests had revealed that the soil properties can vary significantly even over short distances, we chose a relatively small plot size of 20 m × 20 m. Large plots may thus include stands of considerable structural heterogeneity.

The extremely high need of labour for quantifying the root biomass and production did not allow to study more than five stands in the transect. To cope with the problems that arise

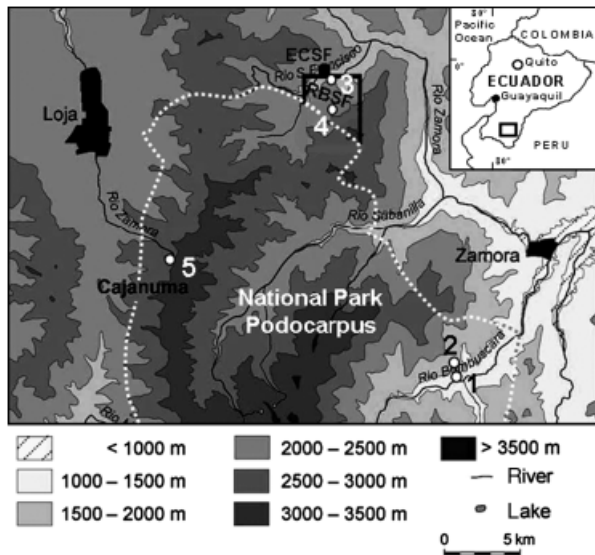


Fig. 1 Topographic map of the study area with its location in the south of Ecuador, position of the study sites #1–5, the “Estación Científica San Francisco” (ECSF) and its protected “Reserva Biológica San Francisco” RBSF, showing altitudinal belts from <1000 to >3500 m.a.s.l. The dotted line indicates the border of Podocarpus National Park, in black the province capitals Loja and Zamora.

from the lack of repetition at the stand level and in order to place our results in a broader pan-tropical context, we completed our study with a meta-analysis of altitudinal transect studies in tropical mountain forests.

In the study region on the eastern slopes of the Andes, precipitation shows a principal increase with elevation from 1050 to 3060 m (P. Emck and M. Richter, unpublished data). The soil types change along the gradient due to changes in climate, bedrock type and hydrology (Table 1). The mineral topsoil is moderately to highly acidic with pH(CaCl₂) values between 2.9 and 3.9, while the organic top layers have higher pH values and base saturations (Iost 2007). The transect is characterized by a general, but not continuous, increase in organic layer thickness with elevation. The availability of N in the densely rooted uppermost organic horizons markedly decreased between 1050 and 3060 m as is evidenced by decreasing gross N mineralization rates and extractable concentrations of inorganic N [N_{inorg}], but increasing C/N ratios of the organic material (Iost 2007; Table 1). Such a trend is absent, or even reversed, in the mineral topsoil. However, gross N mineralization rate and [N_{inorg}] were by a magnitude higher in the organic top layers than in the mineral soil.

Along the 2000-m elevation transect, a characteristic change in tree species composition takes place. Only canopy trees belonging to the family of Melastomataceae occurred at all elevations; another five plant families were present at least in four of the five stands. Most other families showed clear preferences for the pre-montane, montane or upper montane belt (J. Homeier, personal communication).

Estimation of AGB and production

The forest structure and tree biometric data were investigated in samples of 80 trees per stand that reached at least the lower canopy, without defining a minimum diameter at breast height (DBH, at 1.3 m). These 80 trees covered an area of 827 m² in stand #1, and of 360, 343, 290 and 96 m² (in horizontal projection) in the stands #2, 3, 4 and 5, respectively, reflecting the increase in stem density (from 968 to 8317 ha⁻¹) with elevation. The smallest DBH of canopy trees was 5 cm at 1050 m and 3 cm at 3060 m. Along the transect from 1000 to 3000 m, mean DBH decreased to about 40%, canopy height to about 30%, and leaf area index (LAI) to about 35% of its value at 1000 m (Table 1). For more details on stand structure see Moser *et al.* (2008).

Total aboveground tree biomass was estimated with allometric equations for the 80 canopy trees per stand based on measured DBH, tree height and wood specific gravity. We ignored understorey trees and shrubs, and standing or lying dead trunks (see Wilcke *et al.*, 2005) since understorey biomass in mature tropical moist forests may typically comprise <3% of AGB (Brown 1997).

We used the pan-tropical allometric equation of Chave *et al.* (2005) for wet tropical forests. This equation estimates the total aboveground tree biomass including leaves, twigs, branches, bark and boles, and bases on data of 2410 harvested trees from all over the tropics.

We tested the applicability of this allometric equation to our stands in small samples of three recently wind-thrown tree individuals per each stand, which were analysed for stem length, DBH, wood volume and wood specific gravity. The biomass figures were sufficiently close to the predictions of the Chave equation which calculates the total aboveground live biomass (AGB) of a tree from:

$$AGB_{tree} = \exp(-2.557 + 0.940 \ln(\sigma D^2 H)),$$

where AGB_{tree} is the single-tree AGB (kg per tree), D is DBH (cm), H is tree height (m) and σ is wood specific gravity (g cm⁻³), the latter being measured in a subsample of 20 trees per plot by stem wood coring. We used stand-level means of wood density for the remaining 60 trees because we found for σ a coefficient of variation among the species of a stand of only 15–20%. Total AGB of the stand was calculated as the sum of the 80 trees of a plot. To obtain wood biomass (trunks, branches, twigs), stand leaf biomass (B_l) was determined independently and subtracted from AGB.

Stand leaf biomass was calculated from the measurement of annual leaf litter production. Twelve litter buckets per stand equipped with 50 cm × 50 cm gauze sheets of 1 mm-mesh width were positioned randomly in the 400 m² plots. During the 1-year measuring period, the litter was collected every 3 weeks in the stands #1 and 2, where decomposition rates were high, and every 6 weeks in the three other stands, starting on May 26, 2003. For estimating B_l , only the tree leaf fraction was considered. The small fractions of epiphyte leaves, leaves of understorey plants (including bamboo), reproductive organs (flowers and fruits), twigs and the residual litter were determined separately; they were included in the fine litter total.

We assumed that leaf growth and leaf abscission occurred at similar rates in the study year, i.e. that leaf biomass in May

Table 1 Location and stand characteristics of the five study sites in South Ecuador: Mean annual air temperature and relative air humidity were measured at 1.5 m height inside the stands, soil moisture in 10 cm depth of the mineral soil; given are annual means, minimum and maximum (in brackets) for the period April 2003–March 2004; bedrock types after Litherland *et al.* (1994); soil classification (FAO system), pH(CaCl₂) of the mineral topsoil (0–30 cm), C/N ratio of the organic layer (L/Oft) and soil organic carbon (SOC); organic layers and 0–30 cm of mineral soil) after Lost (2007); rainfall data are extrapolated from own measurements in a gap at approximately 1050 m (measuring period Mai 2003–Mai 2004), and from measurements in gaps at 1950, 2680 and 3170 m done by P. Emck & M. Richter (3-year means, unpublished); data on forest structure, as mean diameter in breast height (DBH), stem density, basal area and canopy height were measured for 80 trees per plot (Moser *et al.*, 2008); KCl-extractable inorganic N measured in April 2004 by Lost (2007, median and range), gross N mineralization according to ¹⁵N isotopic pool dilution approach (3 sites only), the pool of KCl-extractable N in the org. layers is a rough estimate derived from N_{inorg} concentrations and humus mass; LAI derived from annual leaf litter fall, specific leaf area (SLA) and leaf lifespan (Moser *et al.*, 2007)

Stand no.	1	2	3	4	5
Coordinates	04°06'54"S 78°58'02"W	04°06'42"S 78°58'20"W	03°58'35"S 79°04'65"W	03°59'19"S 79°04'55"W	04°06'71"S 79°10'58"W
Elevation (m a.s.l.)	1050	1540	1890	2380	3060
Inclination (°)	26	10	31	28	27
Air temperature (°C) (min–max)	19.4 (11.5–30.2)	17.5 (11.2–26.7)	15.7 (7.9–29.4)	13.2 (7.0–25.1)	9.4 (3.1–18.8)
Rainfall (mm yr ⁻¹)	ca. 2230	ca. 2300	ca. 1950	ca. 5000	ca. 4500
Relative air humidity (%) (min–max)	88.7 (15.5–100)	88.9 (31.7–100)	90.8 (15.7–100)	93.3 (34.0–100)	93.5 (28.6–100)
Bedrock types	Leuco- and hornblende, granodiorites	Leuco- and hornblende, granodiorites	Black phyllites, quartzite, metasilstone, metasandstone	Black phyllites, quartzite, metasilstone, metasandstone	Black phyllites, quartzite, metasilstone, metasandstone
Soil types	Alumic Acrisol	Alumic Acrisol	Gleyic Cambisol	Gleyic Cambisol	Podzol
Organic layer thickness (mm)	48	243	305	214	435
Soil moisture (vol.%) (min–max)	29.7 (15.3–38.5)	30.3 (20.4–43.5)	35.4 (27.4–44.7)	44.7 (35.7–48.7)	49.1 (39.5–59.5)
Soil pH (CaCl ₂)	3.94	3.90	3.52	3.26	2.86
SOC: organic layers (Mg ha ⁻¹)	11.1	50.5	36.5	47.8	75.1
SOC: 0–30 cm mineral soil (Mg ha ⁻¹)	95.3	61.2	123.4	73.6	128.4
SOC: profile total (Mg ha ⁻¹) (± 1 SE)	106 (± 7)	112 (± 16)	160 (± 17)	121 (± 16)	204 (± 27)
Soil C/N (Oi horizon, g g ⁻¹)	22	29	28	46	63
KCl-extract. inorganic N: Oi layer (µg g ⁻¹) (min–max)	1180 (329–2238)	219 (76–953)	234 (34–574)	17 (12–209)	6 (4–19)
KCl-extract. inorganic N: 0–10 cm min. soil (µg g ⁻¹) (min–max)	45 (43–69)	19 (14–27)	73 (35–78)	26 (11–44)	38 (19–46)
Gross N mineralization: Oi layer (µg g ⁻¹ day ⁻¹) (min–max)	159 (80–213)	nd	115 (107–120)	nd	23 (0–32)
Gross N mineralization: 0–10 cm min. soil (µg g ⁻¹ day ⁻¹) (min–max)	0 (< 0–48)	nd	8 (3–13)	nd	13 (9–17)
Pool of KCl-extract. N _{inorg} in org. layers (g N m ⁻²)	2.9	2.5	3.3	3.1	1.1
Mean DBH (cm)	17.3	11.5	12.2	9.8	7.2
Stem density (ha ⁻¹)	968	2222	2333	2753	8317
Basal area (m ² ha ⁻¹)	33.6	27.5	36.9	27.2	42.2
Canopy height (m)	31.8	21.7	18.9	12.0	9.0
LAI (m ² m ⁻²)	6.0	5.4	5.7	2.8	2.2

2003 and in May 2004 were equal. This would imply that annual leaf litter production equalled annual leaf biomass production.

Leaf lifespan was recorded by establishing leaf survivorship curves for leaf populations on 10–15 trees per stand that were selected randomly in the plots. In all cases, small individuals (1.5–5 m high) of canopy tree species were selected since continuous access to the upper canopy of large trees could not be provided. In the stands #1–4, these trees were part of the understorey or lower canopy strata, whereas they formed the uppermost canopy layer in stand #5. In May 2003, 24 twigs were marked in the 10–15 trees of each plot resulting in 254–666 leaves observed per stand. Every 3–6 weeks, the number of young, mature and dead leaves per marked twig was counted. We registered the survivorship of all leaves of the first census until the last leaf was shed. In the stands #3–5, the average lifespan of many leaves exceeded the observation period of 19 months. In these cases, the average leaf lifespan in the leaf population was obtained from linear extrapolation of the survivorship curves. Stand leaf biomass (in Mg ha^{-1}) was then calculated from equation (2):

$$B_1 = M_1 \times D_1$$

with M_1 being the annual leaf litter production (in $\text{Mg ha}^{-1} \text{yr}^{-1}$) and D_1 the average leaf lifespan (in yr). The specific leaf area (SLA) and leaf N content per leaf area or leaf dry mass were measured in six representative sun canopy leaf samples of each of the five stands. Stand LAI was calculated by multiplying B_1 with the stand mean of SLA (Table 1; Moser *et al.*, 2007).

Stem growth was measured with 80 dendrometer tapes (UMS, Ibbenbüren, Germany; resolution 0.1 mm) per stand that were read every 6 weeks starting in May 2003. Annual stem wood production was calculated as the difference in wood biomass in May 2003 and in May 2004.

Measurement of root biomass and estimation of root production

The biomass of coarse and large roots (all roots >2 mm in diameter) was determined in 12–16 soil pits (40 cm \times 40 cm) per stand that were dug to 60 cm soil depth. The position of the pits was chosen randomly in the stands for obtaining stand-level estimates of root biomass in the larger root diameter classes. Minimum stem distance was 1 m to stay outside the reach of root buttresses and adventitious roots. Consequently, our stand-level averages are most likely underestimates of coarse and large root biomass (termed 'coarse roots' hereafter) because the root stocks of the trees were not excavated. The root mass (biomass and necromass) in the soil pits was extracted in steps of 10 cm-thick soil layers in the organic layer and the mineral soil. In the laboratory, all coarse roots were washed and dried at 70 °C to constant dry mass.

For analysing the bio- and necromass of roots <2 mm in diameter (fine roots) in the five stands, soil coring was conducted from March to May 2003 in soil profiles of 30 cm depth (organic layers and mineral soil, $n = 20$ per stand). A preliminary investigation of a smaller number of soil cores to 60–

80 cm depth had shown that at least 75% of the profile total of tree fine root biomass were contained in the organic layers and the mineral soil to 30 cm depth. Consequently, the fine root densities in the subsoil were very low. In this study, only the profile totals of fine root biomass from the organic layers and the mineral soil to 30 cm depth are considered.

Root sampling was conducted with a 33 mm wide and 50 mm long steel corer. The soil material was stored at 4 °C in the laboratory of the Estación Científica San Francisco, where processing took place within 30 days. Fine root biomass and necromass were separated under a microscope according to the procedure described by Leuschner *et al.* (2001). In this paper, only fine root biomass will be considered. For details on fine root necromass and root decomposition see Moser *et al.* (2010).

Fine root production (P_{FR}) was estimated from minirhizotron observation of fine root birth, growth and death in the five stands; this technique was found to give more reliable data on P_{FR} than other methods (Graefe *et al.*, 2008a; Moser *et al.*, 2010). In June 2005, we installed 10 transparent minirhizotron tubes with an external diameter of 70 mm at random positions in each of the five stands. They were placed vertically to the soil surface and installed to a depth of ca. 40 cm wherever possible.

In this study, only the uppermost 10 cm of the tube in the organic layers or mineral topsoil were analysed for fine root dynamics, because the very high stone content of the mineral soil in the lowermost stand did not allow a deeper penetration of the tubes into the soil at several measuring locations. For monitoring root growth, a root scanner system (CI-600 Root Growth Monitoring System, CID Inc., Camas, WA, USA) was inserted into the tubes at monthly intervals from June 2005 to January 2007. However, only data from November 2005 onwards were considered in the analysis in order to minimize errors in root production estimation caused by disturbance effects during tube installation. The images were analysed for changes in fine root length using the software WinRHIZO Tron (Régent, Quebec, Canada). Relative increases and relative losses in root length (unit: $\text{cm cm}^{-1} \text{month}^{-1}$) were calculated by relating root length increase or root length loss between two observation dates to the root length visible at the previous measuring date (Graefe *et al.*, 2008a). By relating this data to 12 months, we estimated the annual root length production of the visible fine root population in the rhizotron tubes (Nadelhoffer 2000). By means of the root productivity in the uppermost 10 cm of the soil and the standing biomass of the organic layers and the mineral topsoil (0–30 cm) we estimated the fine root production in the soil profile (P_{FR}).

For two reasons we assume that the P_{FR} figure for the uppermost stand (3060 m) derived from the minirhizotron data is an overestimate (Moser *et al.*, 2010). Consequently, we replaced these values by a lower production figure that was calculated by extrapolating the P_{FR} data of the stands #1–4 to 3060 m. The first reason is that root growth and death events observed in the minirhizotron tubes in the uppermost 10 cm of the soil profile may not be representative for the root mass in the entire soil profile, in particular in the very thick, acidic and moist organic soils at 3060 m. Second, P_{FR} could be overestimated at 3060 m because fine root growth is slower in lower temperatures at higher elevations with the consequence

that fine root initiation and death in high-elevation forests require longer periods for reaching a steady state at the tube surfaces than in low-elevation forests (Graefe *et al.*, 2008b). Thus, slow-growing roots at 3060 m could still have been in the recovery phase after the disturbance by the tube installation. As a consequence, all subsequent calculations were conducted with the extrapolated (conservative) fine root production ($4.7 \text{ Mg ha}^{-1} \text{ yr}^{-1}$) and total BNPP values ($5.1 \text{ Mg ha}^{-1} \text{ yr}^{-1}$) for the 3060 m stand.

Coarse root production was measured with 20 dendrometer tapes per stand, mounted on superficially growing coarse and large roots at diameters in the range 20–300 mm. The tapes were read every 6 weeks, starting in May 2003. From diameter increment, we calculated the relative volume increment of each measured coarse root segment. Based on the coarse root biomass data obtained in the soil pits, stand totals of coarse root production were calculated (for details see Soethe *et al.*, 2006a, b).

For expressing the biomass stocks and productivity components in terms of carbon, we analysed the C concentration in subsamples of all biomass fractions using a CN auto-analyzer (Vario EL III, Elementar, Hanau, Germany) at the University of Göttingen (live fine and coarse roots, stem wood, fine root and leaf litter: $n = 20$, leaves: $n = 10\text{--}20$ per stand).

Measurement of SOC pools

Eighteen soil cores were extracted at random positions in each stand in April 2004; the organic layer horizons were sampled using a $20 \text{ cm} \times 20 \text{ cm}$ wooden frame. The two organic layer horizons separated during soil sampling were designated as Oi (recently shed litter) and OeOa (strongly decomposed material with no visible structure). The latter horizon consisted of small aggregates of humic substances and a high density of fine root mass. Mineral soil was sampled to a depth of 30 cm below the transition zone from the organic OeOa to the mineral topsoil. At the majority of coring locations, the bedrock was reached at this depth. The samples were taken with a soil auger of 10 cm in diameter. For each horizon and stand, six composite samples were assembled from three individual samples each. These composite samples were subject for further analysis. During soil sampling organic layer thickness was determined at each sampling point. The samples were transported in polyethylene bags to the laboratory of the Estación Científica San Francisco (ECSF) and weighed for the determination of soil dry mass. The soil was then homogenized by hand, which involved cutting of the litter layer in approximately $1 \text{ cm} \times 1 \text{ cm}$ pieces. Stones, coarse woody debris and roots were removed carefully. Subsequently, the samples were transported to Germany via airplane within 1 week and immediately processed in the laboratories of the Institute for Soil Science and Site Ecology of Dresden University of Technology. During transport the samples were cooled to approximately 10°C and care was taken that the temperature of the samples did not rise above the average temperature at the location of origin. We did not freeze the soil material because we expected that such a treatment would affect the soil microbial community of tropical soils more severely than cooling for several days would do.

Owing to the nature of the bedrocks and the low pH of the mineral soil, the soils were free of carbonate. Thus, all carbon in the soil is organic C (SOC). For the determination of SOC an aliquot of each sample was dried (40°C mineral soil; 60°C organic layers) and milled (vibratory disc mill RS 100, Retsch, Germany). Organic layer samples were milled at 700 rpm for 45 s and mineral soil samples at 1400 rpm for 60 s. After milling, the samples were dried again overnight at 40°C . The amount of carbon was determined by a thermal conductivity sensor after complete dry combustion at 1150°C (CNS-Analyzer vario EL III, Elementar). The stocks of SOC were expressed in kg ha^{-1} per horizon and as profile totals (organic layers plus mineral soil to 30 cm depth).

The salt-extractable inorganic nitrogen concentration [N_{inorg}] was analysed in KCl-extracts of the organic layers and the mineral soil horizons twice in 2004. Ten grams of mineral soil or 5 g of organic layer material were suspended in 100 mL 0.1 M KCl-solution and shaken for 2 h (180 rpm). The concentrations of nitrate and ammonium N were determined photometrically with a continuous flow autoanalyzer (Skalar Analytik GmbH, Germany). Nitrite was not considered separately but was included in the nitrate fraction.

Statistical analyses

Most of the aggregate data presented in this study refer to stand level data of C pools and fluxes in a single forest stand per elevation. To cope with the problem of lacking repetition on the stand level, we additionally conducted a meta-analysis of altitudinal transect studies in tropical forests and analysed this data set in a similar way as the Ecuadorian transect data. Linear and simple nonlinear regression analyses were applied to identify significant effects of elevation, mean air temperature, annual precipitation, soil moisture, proton concentration of the mineral soil, and C/N ratio of the organic layers on various biomass and production fractions. Additional regression analyses were performed to search for significant correlations of these environmental factors with elevation. All calculations were done using XACT software (SciLab, Hamburg, Germany, version 8.0). For certain biomass and production fractions, differences between the five stands were analysed with a nonparametric analysis of variance (Kruskal–Wallis test) and a subsequent Mann–Whitney two-sample test (*U*-test) using the package SAS, version 8.2 (SAS Institute, Cary, NC, USA).

Results

Altitudinal trends in tree biomass and productivity

Total above- and belowground tree biomass decreased from 317 to $174 \text{ Mg dry mass ha}^{-1}$ (or $154\text{--}87 \text{ Mg C ha}^{-1}$) between 1050 and 3060 m elevation, showing the minimum at 2380 m a.s.l., where stem density was markedly smaller than in the uppermost stand while mean tree height was relatively low. AGB decreased to about 60% of its value at 1050 m between 1050 and 1890 m elevation and showed a further reduction to 40% in the

uppermost stand at 3060 m (Table 2). The stand total of tree leaf biomass increased with elevation in the lower part of the transect from 6.8 (1050 m) to 9.7 Mg ha⁻¹ (1890 m), but showed a sharp decrease higher upslope to 3.6 Mg ha⁻¹ at 3060 m. In contrast to AGB, belowground tree biomass (BGB) nearly doubled between 1050 and 3060 m (32–63 Mg ha⁻¹), being more or less invariant between 1050 and 2380 m and showing a large increase toward the uppermost stand at 3060 m. While coarse and large root biomass (all roots >2 mm in diameter) remained constant between 1050 and 2380 m and increased only higher upslope, fine root biomass ($d < 2$ mm) showed a more or less continuous increase from 2.7 Mg ha⁻¹ (1050 m) to 10.8 Mg ha⁻¹ (3060 m). The proportion of leaf biomass in total biomass remained unchanged between 1050 and 3060 m (2%), while fine root biomass contributed by <1% at 1050 m and increased to about 6% at 3060 m. Total root biomass (fine and coarse) accounted for roughly 10% of total biomass at 1050 m (equivalent to a root/shoot biomass ratio of only 0.11), while roots contributed by about 35% to total biomass at 3060 m, yielding a R/S ratio >0.5.

The production of leaf biomass was by far the most important single component of aboveground produc-

tivity (ANPP) in all five forest stands, contributing by 50% to 65% to ANPP. Only 5% to 25% of ANPP referred to wood growth which reached annual rates of 2.8–0.1 Mg dry mass ha⁻¹ yr⁻¹ or 1.4 to <0.1 Mg C ha⁻¹ yr⁻¹ in the stands (Table 2). Wood increment showed a steeper elevational decrease from 1050 to 3060 m (to about 5% of the value at 1050 m) than leaf production (reduction to about 35%). Moreover, broken and abscised twigs and nontree litter components (such as fallen epiphytes) represented a larger carbon sink in the two uppermost stands (2380 and 3060 m) than stem wood production. While wood production showed a more or less continuous decrease from 1050 to 3060 m, leaf production remained stable up to 1890 m, but dropped markedly higher upslope between 1890 and 3060 m.

Similar to root biomass, root productivity deviated in its vertical pattern from that of ANPP. Coarse and large root increment as estimated from dendrometer readings and root biomass excavations showed a substantial variation among the five stands but revealed no significant trend with elevation. However, the highest coarse root productivity was recorded in the stands at 3060 and 1540 m elevation where the wind exposure is higher than

Table 2 Above- (AGB) and belowground biomass (BGB) and above- (ANPP) and belowground production fractions (BNPP) of the five study plots

Stand no.	Dry mass					Carbon				
	1	2	3	4	5	1	2	3	4	5
Elevation (m a.s.l.)	1050	1540	1890	2380	3060	1050	1540	1890	2380	3060
Biomass (Mg ha ⁻¹)										
Tree leaves	6.82	7.99	9.74	5.25	3.64	3.43	4.05	4.92	2.66	1.87
Stem wood	278.25	159.50	163.21	94.57	108.56	134.67	77.35	79.15	45.11	51.67
Total AGB	285.07	167.49	172.95	99.82	112.20	138.10	81.40	84.07	47.77	53.54
Coarse roots	29.44	30.72	19.90	32.92	51.93	14.24	14.89	9.65	15.70	24.72
Fine roots*	2.66	5.62	6.18	6.29	10.84	1.23	2.66	2.81	3.03	5.42
Total BGB	32.10	36.34	26.08	39.21	62.77	15.47	17.55	12.46	18.73	33.14
Total Tree Biomass	317.17	203.83	199.03	145.03	174.97	153.57	98.95	96.53	66.50	86.68
Production (Mg ha ⁻¹ yr ⁻¹)										
Tree leaves	5.05	5.06	4.96	2.64	1.79	2.54	2.57	2.51	1.34	0.92
Reprod. organs	0.91	0.43	0.36	0.11	0.07	0.45	0.21	0.18	0.05	0.03
Twigs	1.13	0.93	0.88	0.39	0.39	0.55	0.45	0.43	0.19	0.19
Epiphytes	0.28	0.58	0.25	0.25	0.21	0.14	0.29	0.13	0.13	0.11
Bamboo	0.00	0.00	1.55	0.12	0.20	0.00	0.00	0.78	0.06	0.10
Other components	0.41	0.34	0.34	0.14	0.04	0.21	0.17	0.17	0.07	0.02
Total fine litter	7.78	7.34	8.34	3.65	2.70	3.89	3.69	4.20	1.84	1.37
Stem wood incre-ment	2.82	1.58	0.87	0.22	0.14	1.37	0.77	0.42	0.11	0.07
Total ANPP	10.60	8.92	9.21	3.87	2.84	5.26	4.46	4.62	1.95	1.44
Coarse roots	0.17	0.79	0.23	0.23	0.89	0.08	0.38	0.11	0.11	0.42
Fine roots†	2.28	3.16	2.97	3.72	9.40 (4.42)	1.06	1.50	1.35	1.79	4.70 (2.21)
Total BNPP†	2.45	3.95	3.20	3.95	10.29 (5.31)	1.14	1.88	1.46	1.90	5.12 (2.66)
Total NPP†	13.05	12.84	12.41	7.85	12.96 (8.15)	6.40	6.34	6.08	3.85	6.56 (4.10)

*Data for the stands at 1890–3060 m after Leuschner *et al.* (2007),

†For the stand at 3060 m extrapolated fine root production estimates are given in brackets.

in the other three stands. P_{FR} as estimated from minirhizotron observations and root coring data was roughly 10 times larger than coarse root production and showed a significant increase from 1050 m ($2.3 \text{ Mg ha}^{-1} \text{ yr}^{-1}$) to 3060 m ($9.4 \text{ Mg ha}^{-1} \text{ yr}^{-1}$). Adding coarse and fine root production data gave total belowground productivity (BNPP) figures in the range of 2.5 to $4.0 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ for the stands #1–4, but a much higher productivity ($> 10 \text{ Mg ha}^{-1} \text{ yr}^{-1}$) for the uppermost stand. When considering the more plausible conservative P_{FR} estimate for the 3060 m stand ($4.4 \text{ Mg ha}^{-1} \text{ yr}^{-1}$, see 'Material and methods' section), BNPP was estimated at $5.3 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ in the uppermost stand which is still higher than at the four lower elevations.

Total NPP as the sum of ANPP and BNPP showed no trend over the 2000-m elevation distance: for the stands at 1050, 1540, 1890 and 3060 m, very similar figures (12.4 – $13.1 \text{ Mg dry mass ha}^{-1} \text{ yr}^{-1}$ or 6.1 – $6.6 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$) were calculated. A significantly smaller NPP total was found only for stand #4 at 2380 m ($7.9 \text{ Mg dry mass ha}^{-1} \text{ yr}^{-1}$) and stand #5 at 3060 m, if the conservative P_{FR} value is used ($8.2 \text{ Mg ha}^{-1} \text{ yr}^{-1}$). The marked decrease in ANPP along the slope, which is mainly caused by a reduction in wood and leaf production, was at least partly compensated by a higher fine and coarse root production at higher elevations.

Possible factors underlying the elevation effect on biomass and productivity

With a few exceptions (leaf biomass, nontree litter), all AGB and production components showed a significant negative correlation with elevation, while this relationship was positive for fine root biomass and fine root productivity, either in a linear or a nonlinear way (Table 3). However, most of the investigated climatological and edaphic factors were tightly correlated among each other, except for precipitation with a close relation only to soil moisture, VPD and soil C/N ratio (Table 4). The covariation among elevation, mean temperature, mean VPD and soil C/N ratio was particularly strong. Consequently, the biomass and productivity components investigated showed a similarly close relation to soil C/N ratio, temperature and VPD as to elevation. Moreover, most of the biomass and production parameters revealed an even tighter association with the C/N ratio of the organic Oi horizon than to elevation or temperature. In contrast, the weakest correlation was detected between biomass or productivity and precipitation (Table 3).

Stocks of SOC

The carbon stocks in the organic layers ranged between 11 Mg C ha^{-1} at 1050 m and 75 Mg ha^{-1} at 3060 m and

reflected the general increase in organic layer depth with increasing altitude (Table 1). In the 0–30 cm horizon of the mineral soil, the SOC pools varied between 61 and 128 Mg C ha^{-1} with no significant elevational trend visible. The total C stocks of organic layers and mineral soil varied between 106 Mg C ha^{-1} (stand #1) and 204 Mg ha^{-1} (stand #5) with no trend between 1050 and 2380 m and a very high value close to the alpine timberline at 3060 m.

Discussion

Elevational changes in biomass and soil carbon stocks

Our study is the first to investigate synchronously all major aboveground and belowground biomass and production components in a long altitudinal transect in tropical mountain forests. Other transect studies in tropical mountains (Hawaii: Raich *et al.*, 1997; Sabah, Malaysia: Kitayama & Aiba, 2002; Puerto Rico: Weaver & Murphy, 1990; Wang *et al.*, 2003; Sulawesi, Indonesia: Culmsee *et al.*, 2010) were less complete, in most cases focusing only on aboveground compartments and often covering shorter altitudinal distances. Root biomass was only investigated in the transects on Mt. Kinabalu in Sabah and recently in the Peruvian Andes (Girardin *et al.*, 2010).

According to Fig. 2a, AGB tended to decrease with elevation in all cited longer tropical mountain transects. The decrease was, however, not always continuous with elevation, which may result from a marked tree species turnover along the slope (as in Ecuador) or due to inadequate sampling of the local topographic variability. Owing to the large scatter in the biomass data of the seven transects, the pooled data of the meta-analysis showed no significant AGB decrease between 500 and 3000 m a.s.l.

One striking result of the Ecuador transect study is the more than fourfold increase in standing fine root biomass from 1050 to 3060 m elevation. The few existing data on root biomass in tropical mountain forests also indicate that fine root biomass does increase, and not decrease, with elevation, which contrasts with the altitudinal patterns found for AGB (Leuschner *et al.*, 2007). A positive altitudinal trend in root biomass was also reported from the transect studies by Kitayama & Aiba (2002) on the slopes of Mt. Kinabalu and by Girardin *et al.* (2010) in the Peruvian Andes. A compilation of literature data of root biomass in tropical forest stands at different altitudes also supports this finding (Hertel & Leuschner, 2010).

The Ecuadorian transect is also the first to provide detailed information on altitudinal trends in coarse and large root biomass, and total root biomass. Clearly, our

Table 3 Results of regression analyses relating various biomass and production fractions to elevation and six climatic and edaphic variables

Dependent	Elevation		Temperature		VPD		Precipitation		Soil moisture		Proton concentration		C/N ratio	
	r^2_{adj}	P	r^2_{adj}	P	r^2_{adj}	P	r^2_{adj}	P	r^2_{adj}	P	r^2_{adj}	P	r^2_{adj}	P
Biomass														
Leaves	–	0.25 0.112	0.31 0.096	0.31 0.097	–	–	0.65 0.031	–	0.44 0.068	–	0.49 0.058	–	0.59 0.040	–
AG wood	–	0.81 0.045 *	0.86 0.032 *	0.61 0.037	–	–	0.38 0.081	–	0.50 0.055	–	0.18 0.133	–	0.98 0.003 *	–
AGB	–	0.85 0.036 *	0.82 0.034 *	0.63 0.033	–	–	0.41 0.073	–	0.53 0.050	–	0.21 0.124	–	0.99 0.002 *	–
Coarse roots		0.13 0.149	–	0.01 0.191	–	–	0.14 0.145	–	0.12 0.153	–	0.48 0.059	–	0.46 0.064	–
Fine roots		0.87 0.006	0.86 0.007	0.63 0.033	–	–	0.16 0.140	–	0.61 0.036	–	0.80 0.012	–	0.77 0.015	–
BGB		0.58 0.040	–	0.64 0.032	–	–	0.57 0.043	–	0.82 0.043	–	0.78 0.014	–	0.87 0.006	–
Total biomass	–	0.88 0.025 *	0.88 0.027 *	0.69 0.080	–	–	0.24 0.114	–	0.36 0.085	–	0.83 0.040 *	–	0.93 0.014 *	–
Production														
Leaves	–	0.79 0.013	0.83 0.009	0.87 0.006	–	–	0.85 0.007	–	0.93 0.002	–	0.77 0.015	–	0.93 0.002	–
Reproductive organs	–	0.97 0.006	0.95 0.009 *	0.82 0.043 *	–	–	0.39 0.078	–	0.60 0.108 *	–	0.55 0.119 *	–	0.97 0.006 *	–
Twigs	–	0.84 0.008	0.82 0.010	0.93 0.002	–	–	0.84 0.009	–	0.91 0.003	–	0.54 0.048	–	0.93 0.015 *	–
Wood	–	0.98 0.003	0.99 0.002 *	0.95 0.009 *	–	–	0.37 0.081	–	0.80 0.049 *	–	0.08 0.060 *	–	0.85 0.035 *	–
Tree ANPP	–	0.93 0.002	0.92 0.003	0.97 0.001	–	–	0.74 0.019	–	0.95 0.001	–	0.87 0.030 *	–	0.95 0.009 *	–
Nontree litter	–	–0.19 0.293	–0.15 0.272	–0.16 0.276	–	–	0.30 0.100	–	–0.08 0.230	–	–0.02 0.206	–	0.10 0.158	–
Total ANPP	–	0.85 0.007	0.86 0.007	0.90 0.004	–	–	0.86 0.007	–	0.92 0.003	–	0.69 0.026	–	0.92 0.003	–
Coarse roots		0.07 0.168	0.07 0.168	–0.16 0.274	–	–	–0.24 0.331	–	–0.14 0.236	–	0.19 0.129	–	0.18 0.132	–
Fine roots*		0.92 0.003	–	0.79 0.013	–	–	0.54 0.049	–	0.78 0.014	–	0.73 0.019	–	0.91 0.003	–
Total BNPP*		0.74 0.018	–	0.51 0.052	–	–	0.30 0.099	–	0.52 0.052	–	0.65 0.030	–	0.79 0.013	–
Total NPP*	–	0.71 0.023	0.72 0.021	0.87 0.006	–	–	0.95 0.001	–	0.90 0.004	–	0.52 0.514	–	0.77 0.15	–
LAI	–	0.80 0.013	0.81 0.011	0.86 0.007	–	–	0.90 0.004	–	0.90 0.004	–	0.68 0.026	–	0.91 0.003	–
BNPP/ANPP*		0.86 0.007	–	0.98 0.004 *	–	–	0.55 0.047	–	0.98 0.004 *	–	0.96 0.001	–	0.98 <0.001	–
N pool in leaf biomass	–	0.54 0.048	0.58 0.041	0.64 0.032	–	–	0.92 0.002	–	0.73 0.020	–	0.56 0.045	–	0.79 0.014	–

Elevation in m a.s.l., mean air temperature in °C, vapour pressure deficit VPD in h Pa, annual precipitation in mm yr^{–1}, soil moisture in vol.%, proton concentration of mineral soil derived from pH value, C/N ratio of the organic Oi layer. Significant relations are printed in bold ($P = 0.05$), negative relationships are indicated by –, nonlinear relationships are marked with *.

*Regression analyses were calculated considering the extrapolated fine root production value for the 3060 m stand.

Table 4 Results of correlation analyses between six environmental variables and elevation in the five Ecuadorian study plots (Pearson correlation coefficient *r* and *P*)

													Proton concentration		
	Elevation			Temperature			VPD		Precipitation			Soil moisture			
	<i>r</i>	<i>P</i>		<i>r</i>	<i>P</i>		<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>		<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>
Temperature	+	1.00	<0.001												
VPD	−	0.97	0.002	+	0.97	0.002									
Precipitation	+	0.80	0.053	−	0.80	0.051	−	0.88	0.025						
Soil moisture	+	0.97	0.003	−	0.97	0.002	−	0.99	<0.001	+	0.90	0.019			
Proton concentration	+	0.93	0.011	−	0.95	0.006	−	0.88	0.023	+	0.72	0.083	+	0.91	0.015
C/N ratio	+	0.96	0.004	−	0.97	0.002	−	0.94	0.008	+	0.86	0.030	+	0.96	0.005
													+	0.96	0.004

Elevation in m.a.s.l., mean air temperature in °C, VPD in hPa, annual precipitation in mm yr^{–1}, soil moisture in vol.%, proton concentration (pH) of the upper mineral soil in mol L^{–1}, C/N ratio of the organic Oi layer in g g^{–1}. Significant relationships are printed in bold (*P* < 0.05), negative relationships are indicated by –, positive by +.

coarse root data are doubtlessly underestimated in particular in the case of the lowermost stands where stem densities are lower, because the data base on excavations in soil pits at a minimum stem distance of 1 m. We expect that the coarse and large root biomass directly under the stems is greater than at larger stem distance. Consequently, the stand averages of coarse and large root biomass should be higher than measured, particularly in the stands # 1–3. Our data and those of Soethe *et al.* (2006a,b) indicate that trees develop greater amounts of coarse and large root biomass at sites with elevated wind exposure, where a good anchorage is important.

The carbon stocks in live tree biomass (above- and belowground) decreased from 154 (1050 m) to 87 Mg C ha^{–1} (3060 m) in the Ecuadorian transect, while the total C pool (C stocks in biomass and soil) showed no significant elevational trend (range: 188–291 Mg C ha^{–1}). Remarkably, the largest ecosystem C pool was detected in the uppermost stand (3060 m) close to the alpine tree line. Given that Amazonian lowland forests store on average about 210 Mg C ha^{–1} in biomass (above- and belowground, Malhi *et al.*, 2006) and 98 Mg C ha^{–1} in the soil (0–1 m, Batjes & Dijkshoorn, 1999), our data indicate that neotropical high-elevation forests can also contain substantial amounts of C in biomass and soil despite a relatively small tree size. Inventories in other tropical mountain forests are needed to confirm this assumption.

Elevational change in primary production

Our study provides data not only on fine, coarse and large root biomass, but also on root productivity using up-to-date approaches of fine root growth measurement. Thus, we were able to analyse changes in total NPP (above- and belowground) with elevation, instead

of focusing on aboveground productivity only, which must lead to wrong conclusions.

Stem wood increment showed a continuous and steep decline with elevation in this transect which exceeded the reduction in annual leaf biomass production and canopy fine litter fall. The data of seven other transect studies in the meta-analysis support these altitudinal trends in stem wood and leaf production (Fig. 2b and c, Fig. 3). While the absolute ANPP figures for a certain elevation differed more than fivefold among the sites due to floristic, climatic and edaphic differences between the study regions, leaf production was much less variable across this pan-tropical data set. Carbon allocation to leaves must be a C sink of higher priority than stem wood growth in tropical mountain forest trees, because it is needed to maintain a sufficiently large leaf area.

The elevational decrease in ANPP components contrasts with belowground productivity which may consume similar or larger amounts of carbohydrates than wood production in the Ecuadorian transect. At least in the two uppermost stands, a neglect of root production would have led to unrealistic conclusions on the productivity of the forests. When considering only the four stands between 1050 and 2380 m, we found based on the minirhizotron approach a significant increase in *P*_{FR} with elevation (from 2.3 to 3.7 Mg ha^{–1} yr^{–1}). By including the much higher production value for the uppermost stand at 3060 m (9.4 Mg ha^{–1} yr^{–1}), even an exponential increase in *P*_{FR} with altitude appears. For several reasons, however, we assumed that the figure of 9.4 Mg ha^{–1} yr^{–1} for the uppermost stand represents an overestimation of root productivity and we consequently used a more conservative *P*_{FR} value for this stand by extrapolating the linear trend of the four lowermost stands to 3060 m (see 'Material and methods' section). This reduced fine root production estimate for the uppermost stand (4.4 Mg ha^{–1} yr^{–1}) appears much

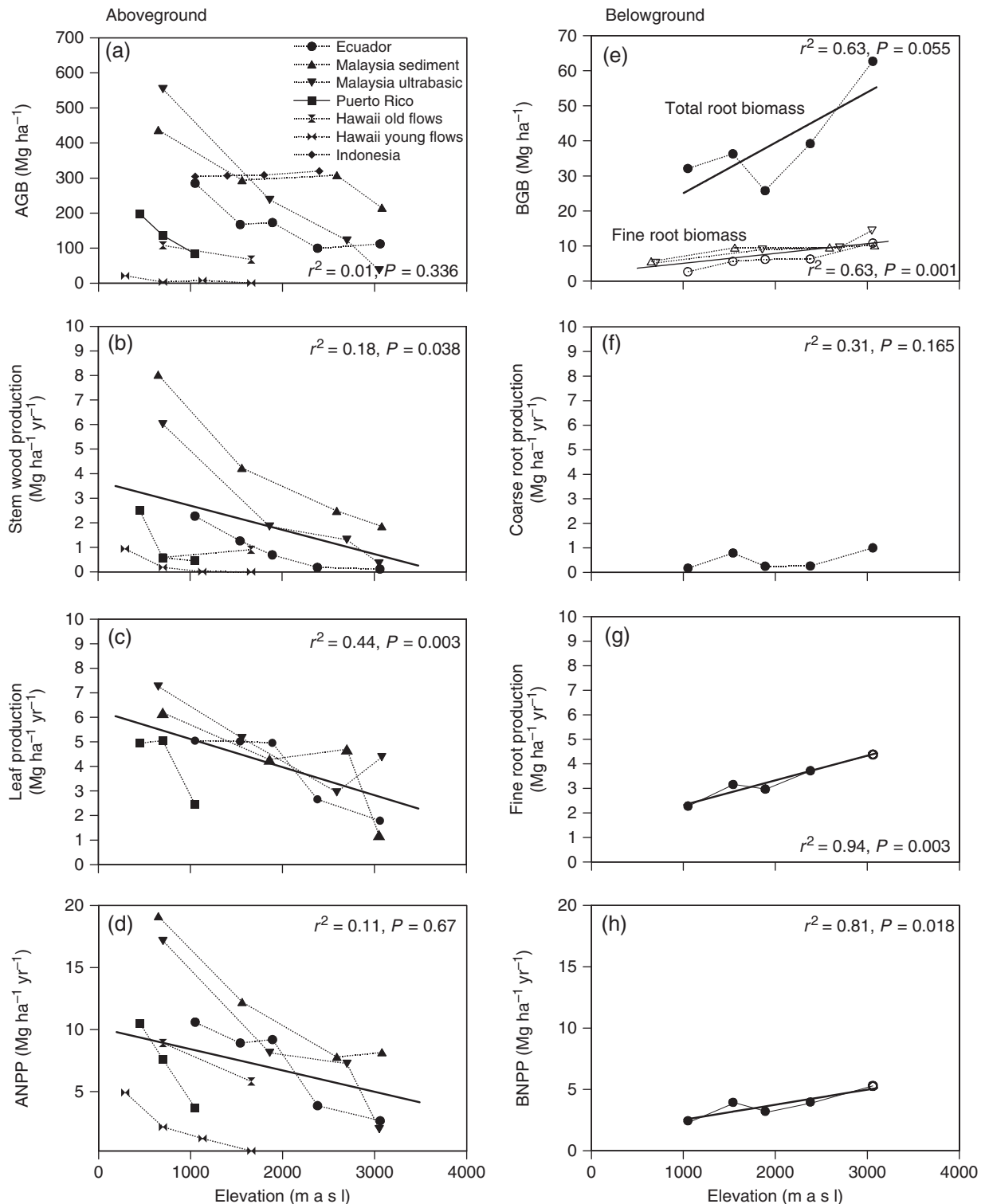


Fig. 2 Aboveground (a–d) and belowground (e–h) biomass and production fractions in their dependence on elevation in tropical mountain forests. Data compiled from a literature survey of pan-tropical mountain transect studies and several single plots. Data points from a given transect were connected with dotted lines for clarity. Bold lines indicate the regression lines of linear or simple non-linear regression analyses covering all transects. For belowground biomass (BGB), the regression analysis was conducted separately for data on total root and on fine root biomass. In the graphs (g) and (h), the fine root production at 3060 m in the Ecuador transect was estimated by extrapolating from the four lower stands. Ecuador – own data; Malaysia – Kitayama & Aiba (2002); Puerto Rico – Weaver & Murphy (1990) and Wang *et al.* (2003); Hawaii – Raich *et al.* (1997), Indonesia – Culmsee *et al.* (2010).

more plausible than the original high value, given that canopy carbon gain decreases by at least 50% from 1050 to 3060 m (Moser *et al.*, 2007).

Along the transect, fine root production correlated positively with elevation and with variables indicating poor nutrient availability (i.e. high soil acidity, high C/N ratio and high soil moisture). These factors are known to reduce fine root longevity (Eissenstat & Yanai, 1997; Eissenstat *et al.*, 2000) and thus could have increased fine root mortality in the soils at high elevations, thereby promoting fine root growth for compensating the root mass loss. Further, there is the possibility that fine root growth is stimulated in the high-elevation soils by the lowered mass-specific mineralization rates which reduce the N (and P) supply rates per soil volume, but which could promote the exploration of additional soil patches by root extension growth. Nutrient addition experiments are needed to clarify what factors are responsible for the high values of fine root biomass and productivity in the Ecuadorian upper montane forests.

Adding the aboveground and belowground production figures allows to estimate stand NPP and the related sequestration of carbon. NPP as the difference between canopy carbon gain and total plant respiration was approximated here by adding all biomass increment terms that were measured in the study. Based on the most likely estimate of fine root production, our data indicate only minor or no change in NPP from 1050 to 1890 m ($13.1\text{--}12.4\text{ Mg dry mass ha}^{-1}\text{ yr}^{-1}$), but a marked productivity decrease from 1890 to 3060 m (to about $8.2\text{ Mg ha}^{-1}\text{ yr}^{-1}$), yielding a reduction in NPP by about 40% between 1050 and 3060 m.

Despite great efforts to measure above- and belowground biomass and production as precisely as possible, we were not able to quantify all relevant plant-related carbon sinks. In particular, we ignored processes such as above- and belowground herbivory, rhizodeposition, C transfer to mycorrhizal hyphae, and emission of volatile organic compounds that, in most cases, have not yet been quantified in tropical forests (Clark *et al.*, 2001a,b).

Is tree growth limited by C sink or C source strength at high elevations?

A more or less continuous decrease of tree height with elevation is perhaps the most obvious structural change occurring in our 2000-m altitudinal transect. In many other mountain forests, tropical and temperate, tree size tends to decrease with altitude more or less continuously, and not abruptly, toward the alpine tree line (Lieberman *et al.*, 1996; Raich *et al.*, 1997; Aiba &

Kitayama, 1999; Pollmann & Hildebrand, 2005; Shi *et al.*, 2008). This indicates that wood production is increasingly limited by environmental constraints or assimilate shortage when approaching the uppermost limit of tree growth. Bruijnzeel & Veneklaas (1998) proposed various environmental factors that could be responsible for a growth reduction of tropical trees at higher elevations, among them (1) reduced leaf temperatures and their effects on carbon gain, (2) periodic water shortage, (3) temporal soil hypoxia resulting in reduced root activity, (4) nutrient shortage and/or nutrient uptake limitation, (5) high concentrations of phenolic substances in the soil, (6) high doses of UV-b radiation, and (7) exposure to strong winds. In the following, we focus on factors directly or indirectly related to the acquisition and investment of carbon for tree growth.

The NPP decrease along mountain slopes, as observed in this study, could have different reasons: (i) a reduction in C source strength, i.e. decreased canopy carbon gain at higher elevations, (ii) increased C consumption by plant respiration, and (iii) reduced C sink strength, i.e. environmentally-induced reductions in tree growth at higher elevations despite sufficient carbohydrate supply. Canopy carbon gain undoubtedly decreases markedly with elevation in this transect, simply because the LAI at 3060 m reaches only 40% of the stand leaf area at 1050 m. We estimate that the annual canopy assimilation must decline by at least 50% between 1050 and 3060 m because light-saturated net photosynthesis rate (leaf-area basis) does not change significantly along the 2000-m elevation distance (B. Wittig, personal communication).

Forest NPP could also decrease with elevation if plant respiration losses (relative to C gain) were increasing with elevation. This possibility can definitely be excluded. A rough extrapolation of stem wood and soil (and root) respiration measurements to the stand level indicates that wood respiration must have decreased at least to a quarter of its rate at 1050 m (Zach *et al.*, 2008). Soil (and included root) respiration declined even more rapidly than wood respiration (Iost *et al.*, 2008), leaving relatively more of the assimilated carbohydrates for NPP at 3060 m than at 1050 m.

Whether sink limitation of growth, i.e. reduced meristematic activity of high-elevation trees, is responsible for the reduction in NPP, may ultimately be decided only on the basis of physiological studies in the laboratory. Indirect evidence from the Ecuador transect seems to indicate that stem wood cambial activity is reduced with elevation independently of carbohydrate supply because stem wood increment decreased much more rapidly between 1050 and 3060 m (to 5% of its value at 1050 m) than did the LAI as an estimator of canopy

Table 5 Leaf and root traits, and various biomass and production ratios of the five forest stands

Stand no.	1	2	3	4	5
Elevation (m a.s.l.)	1050	1540	1890	2380	3060
Leaves					
Mean leaf longevity (months) ¹	16.2	19.1	23.6	23.7	24.5
N pool in leaf biomass (Mg ha ⁻¹)	0.21	0.21	0.25	0.09	0.07
Leaf N content/area (mmol m ⁻²)	0.024	0.026	0.025	0.025	0.025
Leaf N content/dry mass (mmol g ⁻¹)	2.18	1.86	1.82	1.26	1.39
C/N in leaf biomass (g g ⁻¹)	31.4	35.8	41.3	59.8	58.1
C/N in leaf litter (g g ⁻¹)	28.6	47.8	48.0	59.9	61.9
Roots					
Mean fine root longevity (months) [†]	11.2	nd	15.3	nd	8.4
N pool in root biomass (Mg ha ⁻¹)	0.053	0.091	0.053	0.055	0.059
C/N in fine root biomass (organic layers)	23.2	29.1	43.4	55.2	91.1
C/N in fine root litter (organic layers)	23.6	26.9	33.1	44.2	60.1
Ratios					
Fine root/leaf biomass ratio	0.39	0.70	0.63	1.20	2.98
Stem wood increment per wood mass (%)	1.0	1.0	0.5	0.2	0.1
Coarse root growth per coarse root biomass (%)	0.6	2.6	1.2	0.7	1.7
BGB/AGB ratio	0.11	0.22	0.15	0.39	0.56
ANPP per AGB (%)	3.7	5.3	5.3	3.9	2.5
BNPP per BGB (%) [‡]	7.6	10.9	12.3	10.1	16.4 (8.5)
NPP per tree biomass (%) [‡]	4.1	6.3	6.2	5.4	7.4 (4.7)

AGB – aboveground biomass, ANPP – aboveground net primary production, BGB – belowground biomass, BNPP – belowground net primary production, nd, no data;

*from Moser *et al.* (2007).

†from Graefe *et al.* (2008b).

‡For the stand at 3060 m: extrapolated fine root production estimate from the trend line of stands 1–4 in brackets.

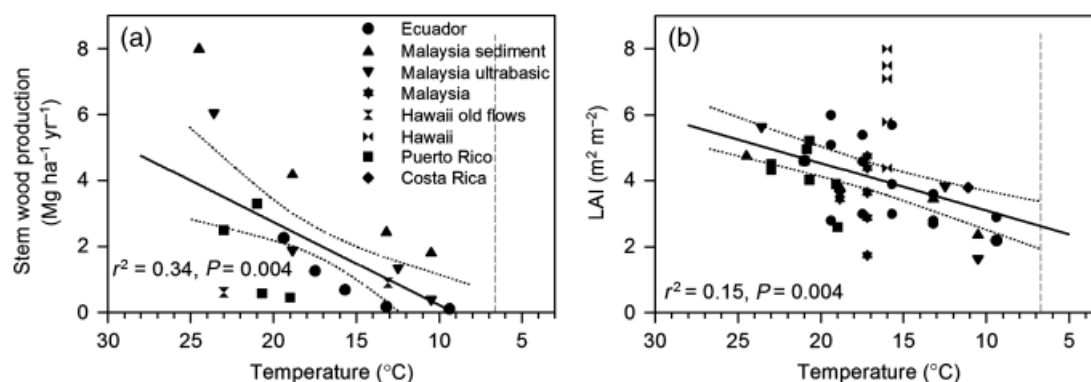


Fig. 3 Stem wood production (a) and LAI (b), and their dependence on annual mean air temperature in tropical mountain forests. Data compiled from a literature survey of pan-tropical mountain transect studies and several single plot studies. The vertical line indicates the elevation with an annual mean soil temperature of 6.7 °C proposed by Körner & Paulsen (2004) as the approximate position of the alpine tree line. Data sources: Ecuador – Moser *et al.* (2007); Malaysia – Kitayama & Aiba (2002), Takyu *et al.* (2003); Puerto Rico – Weaver & Murphy (1990) and Wang *et al.* (2003); Hawaii – Raich *et al.* (1997), Herbert & Fownes (1999); Costa Rica – Hölscher *et al.* (in press).

carbon gain (to about 35%). However, we also observed a marked increase, perhaps a doubling, of fine root production from 1050 to 3060 m elevation which contradicts the assumption that the C sink caused by tree meristematic activity is reduced from low to high eleva-

tion due to the temperature reduction from 19 to 9 °C (Fig. 4). The minirhizotron observations showed that the fine roots grew indeed more slowly at higher elevation, but turned over as rapidly as at 1050 m due to a reduced longevity (see Table 5). More important, the fine root

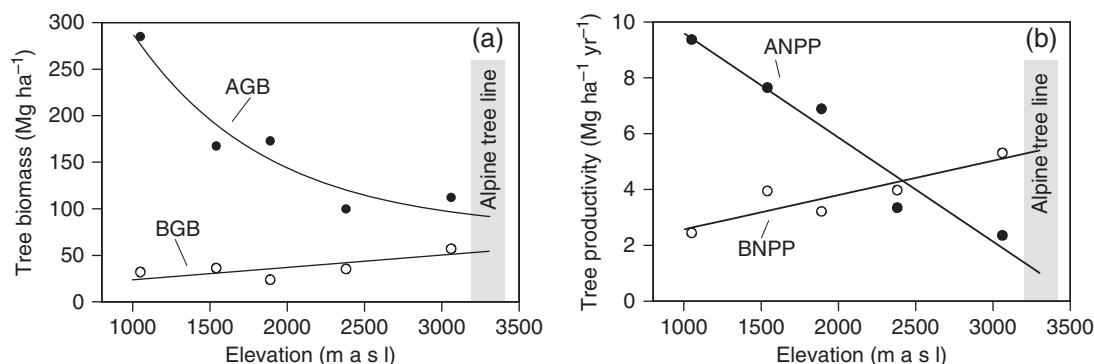


Fig. 4 Above- and belowground trend lines of tree biomass and productivity extrapolated toward the actual tree line. (a) The intersection point of the AGB and BGB curves coincides well with the position of the alpine tree line. (b) Regression lines of ANPP and BNPP in relation to the actual position of the alpine tree line at 3200–3400 m elevation.

system of the stand at 3060 m was four times larger than that at 1050 m, resulting in a larger C sink strength at higher than at lower elevations (Graefe *et al.*, 2008b). It is not very likely that stem wood growth is reduced due to environmental limitation of meristematic activity but fine root growth of the same tree is not.

We conclude that the reduction in NPP by roughly 40% between 1050 and 3060 m cannot primarily be attributed to a C sink limitation of tree growth. A much more plausible explanation is that C source limitation is the predominant cause, i.e. an elevational decrease in canopy carbon gain, which increasingly limits tree growth towards higher elevation, though at different intensities in the aboveground and belowground tree compartments. It is striking that estimated canopy C gain and NPP seem to decrease at roughly similar rates between 1050 and 3060 m (by about 40 and >50%, respectively). Nevertheless, co-limitation of tree growth by reduced C source strength cannot be excluded.

Increasing C source limitation at higher elevation in the Ecuadorian mountain forests is mostly a consequence of a reduction in leaf area, and not of reduced photosynthetic activity. From foliar nutrient concentrations and soil chemical data, we conclude that a combined effect of increasing N limitation and decreasing temperatures with increasing elevation must primarily be responsible for this marked leaf area reduction. A large reduction in the mass-specific gross N mineralization rate in the organic topsoil measured by the ¹⁵N pool dilution approach was found to be associated with a marked increase in the C/N ratio (from 22 to 63 g g⁻¹) of the organic top layer, and a 20-fold decrease in the concentration of KCl-extractable inorganic N between 1050 and 3060 m (Iost, 2007). While N availability decreased markedly with elevation on a soil mass basis, a much slighter decrease, or perhaps no change, was detected when N mineralization was related to ground

area because the depth of the organic layers increased. Thus, the root systems of the high-elevation forests face a greatly reduced N supply density (N release per soil volume) which may require the build-up of a more extended and costly root system to maintain nutrient uptake. This could explain the extraordinarily high amount of fine root biomass in these soils.

Nitrogen limitation of tree growth in general, and of leaf growth in particular, is further indicated by a considerable decrease of foliar N concentrations and SLA in upslope direction, and a concomitant increase in leaf longevity toward the uppermost stand (see Table 5). Smaller and thicker leaves with lower N concentration are a typical attribute of tropical trees at high elevations (Grubb & Tanner, 1976; Grubb, 1977). Besides N shortage, harsh environments with cold nights and high radiation intensities, as they occur in high-altitude environments, may also be the cause of leaves with high C/N ratios and low SLA. However, extreme climatic factors as a cause of the formation of durable, carbon-rich tree leaves could not explain why the trees at high elevations in Ecuador reduce their stand leaf area, instead of forming a larger number of smaller leaves adapted to the harsh environment, thereby compensating for the reduction in individual leaf size. Moreover, the N pool in stand leaf biomass decreased to about 33% between 1050 and 3060 m in this transect (see Table 5) indicating that the formation of new leaves and/or the process of leaf expansion are increasingly limited by N shortage toward higher elevations. This is support for the assumption that N limitation is the primary cause of the marked leaf area and NPP reduction with elevation in this transect.

Increasing N limitation with elevation should also be the cause of the tremendous C allocation shift from above- to belowground organs observed in our transect. Following the resource balance hypothesis formulated

by Bloom *et al.* (1985), this shift is best explained by a growing importance of limiting soil resources with increasing elevation. Increasing C and nutrient allocation to roots may represent a compensatory measure of the trees to cope with increasing growth limitation by nutrient shortage with elevation, and in the case of the coarse and large root system, by the growing need for stable anchorage due to high wind loads. Interestingly, Duivenvoorden & Lips (1995) observed a similarly large shift of C allocation to roots in Amazonian lowland forests as nutrient availability decreased. Girardin *et al.* (2010) reported a more than threefold increase in fine root biomass between 200 and 3000 m elevation in a Peruvian altitudinal transect. In contrast, they observed a decrease, and not an increase, in fine root production with elevation. Our results and those from other elevation transects in tropical mountains demonstrate that changes with altitude in forest carbon budgets reflect not only the change in climatic factors but also in nutrient availability. Additional transect studies investigating the C balance of tropical mountain forests are needed to draw more general conclusions on altitudinal trends in belowground productivity and their dependence on altitudinal change in climate and soil fertility.

Yet, we cannot rule out that other factors such as increasing soil moisture and more frequent soil hypoxia are also contributing to the observed reduction in LAI and the increase in R/S ratio with elevation, since LAI and R/S showed a close relation to those factors as well. Multi-factorial growth experiments with tropical trees are needed to disentangle the physiological effects of those environmental factors that change in concert along tropical mountain slopes.

We conclude that carbon budgets of tropical mountain forests, that ignore root biomass and root productivity, will lead to wrong conclusions on the size and altitudinal change of C storage and C sequestration in these ecosystems. High-elevation forests in south Ecuador contain relatively large C stocks in biomass and soil despite their low stunted stature, which is a consequence of large SOC pools and a high root biomass. Aboveground and belowground biomass and productivity show opposite altitudinal trends indicating a shift from predominant light to nutrient (N) limitation of tree growth with increasing elevation. The large reduction in stand leaf area with elevation is most likely a consequence of a more pronounced N limitation at higher elevations. We propose that reductions in leaf area and associated canopy carbon gain caused by N limitation, i.e. a C source limitation of tree growth, are more likely causes of the reduction in aboveground tree size and biomass with altitude in south Ecuador than is C sink limitation. Transect studies in other tropical mountains

have to confirm whether these results are of more general validity.

Acknowledgements

We thank Marina Röderstein, Jürgen Homeier, Bernhard Schuldt and Malte Unger, University of Göttingen, for data on fine root biomass and root C/N ratio in the uppermost three stands, tree species composition, foliar N content and photosynthetically active radiation and P. Emck & M. Richter, University of Erlangen, for precipitation data. We are grateful to the Fundación Científica San Francisco (Nature and Culture International) for the permission to work in the RBSF and ECSF, to the Ministerio del Ambiente in Quito for research permits and to the Deutsche Forschungsgemeinschaft (DFG) for financial funding within the Research Unit 402. Comments by four anonymous reviewers greatly improved the manuscript.

References

- Aiba S, Kitayama K (1999) Structure, composition and species diversity in an altitude-substrate matrix of rain forest tree communities on Mount Kinabalu, Borneo. *Plant Ecology*, **140**, 139–157.
- Balslev H, Øilgaard B (2002) Mapa de vegetación del sur de Ecuador. In: *Botánica Austroecuatorialiana - Estudios sobre los recursos vegetales en las provincias de el Oro, Loja y Zamora-Chinchi* (eds Aguirre ZM, Madsen JE, Cotton E, Balslev H), pp. 51–64. Ediciones ABYA YALA, Quito.
- Batjes NH, Dijkshoorn JA (1999) Carbon and nitrogen stocks in the soils of the Amazon region. *Geoderma*, **89**, 273–286.
- Bloom AJ, Chapin III FS, Mooney HA (1985) Resource limitation in plants – an economic analogy. *Annual Review of Ecology and Systematics*, **16**, 363–392.
- Brown S (1997) Estimating biomass and biomass change of tropical forests: a primer. *FAO Forestry Paper*, 134pp.
- Bruijnzeel LA, Veneklaas EJ (1998) Climatic conditions and tropical montane forest productivity: the fog has not lifted yet. *Ecology*, **79**, 3–9.
- Chave J, Andalo C, Brown S *et al.* (2005) Tree allometry and improved estimation of carbon stocks and balance in tropical forests. *Oecologia*, **145**, 87–99.
- Clark DA (2007) Detecting tropical forests' responses to global climatic and atmospheric change: current challenges and a way forward. *Biotropica*, **39**, 4–19.
- Clark DA, Brown S, Kicklighter DW, Chambers JQ, Thomlinson JR, Ni J (2001a) Measuring net primary production in forests: concepts and field methods. *Ecological Applications*, **11**, 356–370.
- Clark DA, Brown S, Kicklighter DW, Chambers JQ, Thomlinson JR, Ni J, Holland EA (2001b) Net primary production in tropical forests: an evaluation and synthesis of existing field data. *Ecological Applications*, **11**, 371–384.
- Clark DA, Piper SC, Keeling CD, Clark DB (2003) Tropical rain forest tree growth and atmospheric carbon dynamics linked to interannual temperature variation during 1984–2000. *Proceedings of the National Academy of Sciences of the United States of America*, **100**, 5852–5857.
- Culmsee H, Leuschner Ch, Moser G, Pitopang R (2010) Forest aboveground biomass along an altitudinal transect in Sulawesi, Indonesia, and the role of extra-tropical Fagaceae. *Journal of Biogeography*, **37**, 960–974.
- Duivenvoorden JF, Lips JM (1995) A land-ecological study of soils, vegetation, and plant diversity in Colombian Amazonia. The Tropenbos Foundation. Wageningen. *Tropenbos Series*, **12**, 1–437.
- Eissenstat DM, Wells CE, Yanai RD, Whitbeck JL (2000) Building roots in a changing environment: implications for root longevity. *New Phytologist*, **147**, 33–42.
- Eissenstat DM, Yanai RD (1997) The ecology of root lifespan. *Advances in Ecological Research*, **27**, 1–60.
- Espeleta K-F, Clark DA (2007) Multi-scale variation in fine-root biomass in a tropical rain forest: a seven year study. *Ecological Monographs*, **77**, 377–404.
- Feeley KJ, Wright SJ, Nur Supardi MN, Kassim AR, Davies SJ (2007) Decelerating growth in tropical forest trees. *Ecology Letters*, **10**, 461–469.
- Finér L, Ohashi M, Noguchi K, Hirano Y (2011) Factors causing variation in fine root biomass in forest ecosystems. *Forest Ecology and Management*, **261**, 265–277.
- Girardin CAJ, Malhi Y, Aragao LEOC *et al.* (2010) Net primary production and its allocation along a tropical forest elevational transect in the Peruvian Andes. *Global Change Biology*, **16**, 3176–3192.

- Grace J, Lloyd J, McIntyre J *et al.* (1995) Carbon dioxide uptake by an undisturbed tropical rain forest in South-West Amazonia 1992–1993. *Science*, **270**, 778–780.
- Grace J, Meir P (2009) Tropical rain forests as old-growth forests. In: *Old-Growth Forests* (eds Wirth C, Gleixner G, Heimann M), pp. 391–408. Springer, Berlin, Heidelberg. *Ecological Studies*, 207.
- Graefe S, Hertel D, Leuschner Ch (2008a) Fine root dynamics along a 2,000-m elevation transect in South Ecuadorian mountain forests. *Plant and Soil*, **231**, 155–166.
- Graefe S, Hertel D, Leuschner Ch (2008b) Estimating fine root turnover in tropical forests along an elevational transect using minirhizotrons. *Biotropica*, **40**, 536–542.
- Grubb PJ (1977) Control of forest growth and distribution on wet tropical mountains with special reference to mineral nutrition. *Annual Reviews of Ecology and Systematics*, **8**, 567–601.
- Grubb PJ, Lloyd JR, Pennington TD, Whitmore TC (1963) A comparison of montane and lowland rain forest in Ecuador. I. The forest structure, physiognomy and floristics. *Journal of Ecology*, **51**, 567–601.
- Grubb PJ, Tanner EVJ (1976) The montane forests and soils of Jamaica: a reassessment. *Journal of the Arnold Arboretum*, **57**, 33–68.
- Hertel D, Leuschner Ch (2010) Fine root mass and fine root production in tropical moist forests as dependent on soil, climate and elevation. In: *Mountains in the Mist: Science for Conserving and Managing Tropical Montane Cloud Forests* (eds Bruijnzeel LA, Scatena FH, Hamilton LS), Cambridge University Press, Cambridge, in press.
- Herbert DA, Fownes JH (1999) Forest productivity and efficiency of resource use across a chronosequence of tropical montane soils. *Ecosystems*, **2**, 242–254.
- Hölscher D, Köhler L, Kapelle M, Leuschner Ch (in press) Ecology and use of old-growth and recovering montane oak forest in the Cordillera de Talamanca, Costa Rica. In: *Mountains in the mist: Science for conserving and managing tropical montane cloud forests* (eds Bruijnzeel LA, Scatena FH, Hamilton LS), Cambridge University Press, Cambridge.
- Houghton RA, Lawrence KT, Hackler JL *et al.* (2001) The spatial distribution of forest biomass in the Brazilian Amazon. *Global Change Biology*, **7**, 731–746.
- Iost S (2007) *Soil respiration, microbial respiration and mineralisation in soils of montane rainforests of Southern Ecuador: influence of altitude*. PhD thesis, Technical University of Dresden, Germany, 171 pp. Available at: <http://nbn-resolving.de/urn:nbn:de:bsz:14-ds-1201126765623-42870> (accessed 1 July 2010).
- Iost S, Makeschin F, Abiy M, Haubrich F (2008) Biotic soil activity. In: *Gradients in a tropical mountain ecosystem of Ecuador* (eds Beck E, Bendix J, Kottke I, Makeschin F, Mosandl R), pp. 217–227. Springer, Berlin. *Ecological Studies*, 198.
- Jackson RB, Canadell J, Ehleringer JR, Mooney HA, Sala OE, Schulze ED (1996) A global analysis of root distribution for terrestrial biomes. *Oecologia*, **108**, 389–411.
- Kitayama K, Aiba S-I (2002) Ecosystem structure and productivity of tropical rain forests along altitudinal gradients with contrasting soil phosphorus pools on Mount Kinabalu, Borneo. *Journal of Ecology*, **90**, 37–51.
- Körner C, Paulsen J (2004) A world-wide study of high altitude treeline temperatures. *Journal of Biogeography*, **31**, 713–732.
- Leuschner Ch, Hertel D, Coners H, Büttner V (2001) Root competition between beech and oak: a hypothesis. *Oecologia*, **126**, 276–284.
- Leuschner Ch, Moser G, Bertsch C, Röderstein M, Hertel D (2007) Large altitudinal increase in tree root/shoot ratio in tropical mountain forests of Ecuador. *Basic and Applied Ecology*, **8**, 219–230.
- Lieberman D, Lieberman M, Peralta R, Hartshorn GS (1996) Tropical forest structure and composition on a large-scale altitudinal gradient in Costa Rica. *Journal of Ecology*, **84**, 137–152.
- Litherland M, Aspden J, Jemielita R (1994) *The metamorphic belts of Ecuador. No. 11 in Overseas Memoir of the British Geological Survey*. British Geology Survey, Keyworth, UK.
- Da Costa ACL, Galbraith D, Almeida S *et al.* (2010) Effect of 7 yr of experimental drought on vegetation dynamics and biomass storage of an eastern Amazonian rainforest. *New Phytologist*, **187**, 579–591.
- Luyssaert S, Inglima I, Jungs M *et al.* (2007) CO₂ balance of boreal, temperate, and tropical forests derived from a global database. *Global Change Biology*, **13**, 2509–2537.
- Malhi Y, Wood D, Baker TR *et al.* (2006) The regional variation of aboveground live biomass in old-growth Amazonian forests. *Global Change Biology*, **12**, 1107–1138.
- Metcalfe D, Meir P, Williams M (2008) The effects of water availability on root growth and morphology in an Amazon rainforest. *Plant and Soil*, **311**, 189–199.
- Moser G, Hertel D, Leuschner Ch (2007) Altitudinal change in LAI and stand leaf biomass in tropical montane forests – a transect study in Ecuador and a pan-tropical meta-analysis. *Ecosystems*, **10**, 924–935.
- Moser G, Leuschner Ch, Röderstein M, Graefe S, Soethe N, Hertel D (2010) Biomass and productivity of fine and coarse roots in five tropical mountain forests along an altitudinal transect in South Ecuador. *Plant Ecology and Diversity*, **3**, 151–164.
- Moser G, Röderstein M, Soethe N, Hertel D, Leuschner Ch (2008) Altitudinal changes in stand structure and biomass allocation of tropical mountain forests in relation to microclimate and soil chemistry. In: *Gradients in a Tropical Mountain Ecosystem of Ecuador* (eds Beck E, Bendix J, Kottke I, Makeschin F, Mosandl R), pp. 229–242. Springer, Berlin. *Ecological Studies*, 198.
- Nadelhoffer KJ (2000) The potential effects of nitrogen deposition on fine-root production in forest ecosystems. *New Phytologist*, **147**, 131–139.
- Pollmann W, Hildebrand R (2005) Structure and the composition of species in timberline ecotones of the Southern Andes. In: *Mountain ecosystems – studies in treeline ecology* (eds Broll G, Keplin B), pp. 117–151. Springer, Berlin.
- Raich JW, Russel AE, Vitousek PM (1997) Primary productivity and ecosystem development along an elevational gradient on Mauna Loa, Hawai'i. *Ecology*, **78**, 707–721.
- Schawe M, Glatzel S, Gerold G (2007) Soil development along an altitudinal transect in a Bolivian tropical montane rainforest: Podzolization vs. hydromorphy. *Catena*, **69**, 83–90.
- Shi P, Körner C, Hoch G (2008) A test of the growth-limitation theory for alpine tree line formation in evergreen and deciduous taxa of the eastern Himalayas. *Functional Ecology*, **22**, 213–220.
- Soethe N, Lehmann J, Engels C (2006a) Root morphology and anchorage of six native tree species from a tropical montane forest and an elfin forest in Ecuador. *Plant and Soil*, **279**, 173–185.
- Soethe N, Lehmann J, Engels C (2006b) The vertical pattern of rooting and nutrient uptake at different altitudes of a south Ecuadorian montane forest. *Plant and Soil*, **286**, 287–299.
- Takay M, Aiba S-I, Kitayama K (2003) Changes in biomass, productivity and decomposition along topographical gradients under different geological conditions in tropical lower montane forests on Mount Kinabalu, Borneo. *Oecologia*, **134**, 397–404.
- Tanner EVJ (1981) The decomposition of leaf litter in Jamaican montane rain forests. *Journal of Ecology*, **69**, 263–273.
- Vogt KA, Vogt DJ, Palmiotto PA, Boon B, O'Hara J, Asbjornsen H (1996) Review of root dynamics in forest ecosystems grouped by climate, climatic forest type and species. *Plant Soil*, **187**, 159–219.
- Wang HQ, Hall CAS, Scatena FN, Fetcher N, Wu W (2003) Modelling the spatial and temporal variability in climate and primary productivity across the Luquillo Mountains, Puerto Rico. *Forest Ecology and Management*, **179**, 69–94.
- Weaver PL, Murphy PG (1990) Forest structure and productivity in Puerto-Rico Luquillo Mountains. *Biotropica*, **22**, 69–82.
- Wilcke W, Hess T, Bengel C, Homeier J, Valarezo E, Zech W (2005) Coarse woody debris in a montane forest in Ecuador: mass, C and nutrient stock, and turnover. *Forest Ecology and Management*, **205**, 139–147.
- Zach A, Horna V, Leuschner C (2008) Elevational change in woody tissue CO₂ efflux in a tropical mountain rain forest in southern Ecuador. *Tree Physiology*, **28**, 67–74.