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

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Keywords:	tropical montane forest, belowground biomass, root production, wood increment, root/shoot ratio
Abstract:	<p>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 20fold. Coarse and large root biomass increased slightly, fine root biomass 4fold, 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</p>

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	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.

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3 1 **Elevation effects on the carbon budget of tropical mountain forests (S**
4 **Ecuador): The role of the belowground compartment**

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8 4 **Running title:** Elevation effects on forest carbon cycling
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34 22 **Keywords:** aboveground biomass, belowground biomass, fine root production, net
35 primary production, root/shoot ratio, SOC, tropical montane forest, wood increment
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601 **ABSTRACT**

2 Carbon storage and sequestration in tropical mountain forests and their dependence on
3 elevation and temperature are not well understood. In an altitudinal transect study in the
4 South Ecuadorian Andes, we tested the hypotheses that (i) aboveground net primary
5 production (ANPP) decreases continuously with elevation due to decreasing
6 temperatures, whereas (ii) belowground productivity (BNPP) remains constant or even
7 increases with elevation due to a shift from light to nutrient limitation of tree growth. In
8 five tropical mountain forests between 1050 and 3060 m a.s.l., we investigated all major
9 above- and belowground biomass and productivity components, and the stocks of soil
10 organic carbon (SOC). Leaf biomass, stemwood mass and total aboveground biomass
11 (AGB) decreased by 50 to 70%, ANPP by about 70% between 1050 and 3060 m, while
12 stem wood production decreased 20fold. Coarse and large root biomass increased
13 slightly, fine root biomass 4fold, while fine root production (minirhizotron study)
14 roughly doubled between 1050 and 3060 m. The total tree biomass (above- and
15 belowground) decreased from about 320 to 175 Mg dry mass ha⁻¹, total NPP from ca.
16 13.0 to 8.2 Mg ha⁻¹ yr⁻¹. The belowground/aboveground ratio of biomass and
17 productivity increased with elevation indicating a shift from light to nutrient limitation
18 of tree growth. We propose that, with increasing elevation, an increasing nitrogen
19 limitation combined with decreasing temperatures causes a large reduction in stand leaf
20 area resulting in a substantial reduction of canopy carbon gain toward the alpine tree
21 line. We conclude that the marked decrease in tree height, AGB and ANPP with
22 elevation in these mountain forests is caused by both a belowground shift of C
23 allocation and a reduction in C source strength, while a temperature-induced reduction
24 in C sink strength (lowered meristematic activity) seems to be of secondary importance.

1 INTRODUCTION

2 Tropical rainforests occupy only some 12% of the terrestrial surface but contain about
3 55% of the biomass (Grace & Meir 2009). An accurate characterization of carbon stores
4 and net primary production in tropical forests will be fundamental for realistic global
5 and regional C budgets and for predicting how these will be affected by the changing
6 climate. Not only forest conversion, but also changes in temperature, [CO₂] and rainfall
7 may significantly affect the C sequestration potential of tropical forests (Grace *et al.*
8 1995).

9 There is no simple approach for obtaining information on the possible future response
10 of tropical old-growth rainforests to the expected changes in temperature, rainfall and
11 atmospheric [CO₂]. Field manipulation studies may help to investigate forest responses
12 to altered rainfall and [CO₂] (e.g. da Costa *et al.* 2010), but they are hardly practicable
13 for studying long-term effects of elevated temperature on tropical forests. One source of
14 indirect information can be transect studies along latitudinal or altitudinal temperature
15 gradients, or meta-analyses of comprehensive data bases on forest ecosystem
16 functioning in different climates. Even though most gradient studies are suffering from
17 the fact that one or more environmental factors covary with the target variable, valuable
18 insights into the temperature dependence of productivity and carbon cycling in forests
19 have been achieved by comparing C pools and fluxes in forests differing in mean
20 temperature (e.g. Clark *et al.* 2001; Luysaert *et al.* 2007).

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

28 Clark *et al.* (2001) synthesized the available data on the biomass and productivity of
29 tropical forests based on published data for 39 forest sites. While numerous studies have
30 measured aboveground biomass, stem wood increment and fine litterfall, only very
31 limited or no data exist on other aboveground NPP components such as leaf herbivory,
32 organic leachates or the release of VOCs. More critical, however, is the scarcity of
33 information on belowground biomass and belowground NPP (BNPP). The biomass of

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1 coarse and large roots (i.e. roots > 2 mm in diameter) was measured at very few sites
2 only and typically by excavating a few trees or digging a few monoliths (Clark et al.
3 2001). The data base is more comprehensive for fine root biomass (< 2 mm in diameter)
4 with 32 and 19 investigated tropical forest sites listed in the reviews of Vogt et al.
5 (1996) and Jackson et al. (1996). A recent data compilation by Finér et al. (in press)
6 contains fine root biomass data from 83 tropical forest stands, mostly from lowland
7 sites. For Amazonian forests, Houghton *et al.* (2001) report a mean root biomass value
8 of 21% (range 13-26%) of aboveground live tree biomass.

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

17 In this study along a 2000-m elevation transect in South Ecuador, we collected a
18 unique dataset on above- and belowground biomass fractions and related carbon pools,
19 SOC, and above- and belowground productivity of five mountain forest stands situated
20 at elevations between 1000 and 3000 m a.s.l. The main focus is on root biomass and
21 root productivity, the fractions with largest uncertainties.

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

32 MATERIAL AND METHODS

33 *Study sites*

1 We installed five permanent forest plots between 1050 m and 3060 m a.s.l. at a
2 maximum distance to each other of 30 km in the South Ecuadorian provinces of
3 Zamora-Chinchipe and Loja. The lowermost stands #1 and 2 are within the Podocarpus
4 National Park at pre-montane elevation close to the park entrance at Bombuscaro, south
5 of the provincial capital Zamora (#1: S 04°06'54'', W 78°58'20''; #2: S04° 06'42'', W
6 78°58'20''). Stands #3 and 4 (montane elevation) are located in the adjacent Reserva
7 Biológica San Francisco (#3: S 03°58'35'', W 79°04'55''; #4: S 03°59'19'', W
8 79°04'55''). Stand #5 is a stunted upper montane forest located in the Cajanuma area of
9 the national park (S 04°06'771'', W 79°10'58''). Patches of treeless alpine paramo
10 vegetation are found about 200 m upslope of this stand (Fig.1).

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

22 The extremely high need of labour for quantifying the root biomass and production
23 did not allow to study more than five stands in the transect. To cope with the problems
24 that arise from the lack of repetition at the stand level and in order to place our results in
25 a broader pan-tropical context, we completed our study with a meta-analysis of
26 altitudinal transect studies in tropical mountain forests.

27 In the study region on the eastern slopes of the Andes, precipitation shows a principal
28 increase with elevation from 1050 m to 3060 m (P. Emck and M. Richter, unpublished
29 data). The soil types change along the gradient due to changes in climate, bedrock type
30 and hydrology (Table 1). The mineral topsoil is moderately to highly acidic with
31 pH(CaCl₂) values between 2.9 and 3.9, while the organic top layers have higher pH
32 values and base saturations (Iost 2007). The transect is characterized by a general, but
33 not continuous, increase in organic layer thickness with elevation. The availability of N

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3 1 in the densely rooted uppermost organic horizons markedly decreased between 1050
4 2 and 3060 m as is evidenced by decreasing gross N mineralization rates and extractable
5 3 concentrations of inorganic N [N_{inorg}], but increasing C/N ratios of the organic material
6 4 (Iost 2007; Table 1). Such a trend is absent, or even reversed, in the mineral topsoil.
7 5 However, gross N mineralization rate and [N_{inorg}] were by a magnitude higher in the
8 6 organic top layers than in the mineral soil.

9 7 Along the 2000-m elevation transect, a characteristic change in tree species
10 8 composition takes place. Only canopy trees belonging to the family of Melastomataceae
11 9 occurred at all elevations; another five plant families were present at least in four of the
12 10 five stands. Most other families showed clear preferences for the pre-montane, montane
13 11 or upper montane belt (J. Homeier, pers. comm.).
14 12

15 13 ***Estimation of aboveground biomass and production***

16 14 The forest structure and tree biometric data were investigated in samples of 80 trees
17 15 per stand that reached at least the lower canopy, without defining a minimum diameter
18 16 at breast height (DBH, at 1.3 m). These 80 trees covered an area of 827 m² in stand #1,
19 17 and of 360, 343, 290 and 96 m² (in horizontal projection) in the stands #2, 3, 4 and 5,
20 18 respectively, reflecting the increase in stem density (from 968 to 8317 ha⁻¹) with
21 19 elevation. The smallest DBH of canopy trees was 5 cm at 1050 m and 3 cm at 3060 m.
22 20 Along the transect from 1000 to 3000 m, mean DBH decreased to about 40%, canopy
23 21 height to about 30%, and leaf area index (LAI) to about 35% of its value at 1000 m
24 22 (Table 1). For more details on stand structure see Moser *et al.* (2008).
25 23

26 24 Total aboveground tree biomass was estimated with allometric equations for the 80
27 25 canopy trees per stand based on measured DBH, tree height and wood specific gravity.
28 26 We ignored understorey trees and shrubs, and standing or lying dead trunks (see Wilcke
29 27 *et al.* 2005) since understorey biomass in mature tropical moist forests may typically
30 28 comprise less than 3% of aboveground biomass (Brown 1997).
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32 30 We used the pan-tropical allometric equation of Chave *et al.* (2005) for wet tropical
33 31 forests. This equation estimates the total aboveground tree biomass including leaves,
34 32 twigs, branches, bark and boles, and bases on data of 2410 harvested trees from all over
35 33 the tropics.
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37 35 We tested the applicability of this allometric equation to our stands in small samples
38 36 of three recently wind-thrown tree individuals per each stand, which were analyzed for
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1 stem length, DBH, wood volume and wood specific gravity. The biomass figures were
2 sufficiently close to the predictions of the Chave equation which calculates the total
3 aboveground live biomass of a tree from:

$$(1) \quad AGB_{tree} = \exp(-2.557 + 0.940 \ln(\sigma D^2 H))$$

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

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

24 We assumed that leaf growth and leaf abscission occurred at similar rates in the study
25 year, i.e. that leaf biomass in May 2003 and in May 2004 were equal. This would imply
26 that annual leaf litter production equalled annual leaf biomass production.

27 Leaf lifespan was recorded by establishing leaf survivorship curves for leaf
28 populations on 10-15 trees per stand that were selected randomly in the plots. In all
29 cases, small individuals (1.5 to 5 m high) of canopy tree species were selected since
30 continuous access to the upper canopy of large trees could not be provided. In the stands
31 #1 to 4, these trees were part of the understorey or lower canopy strata, whereas they
32 formed the uppermost canopy layer in stand #5. In May 2003, 24 twigs were marked in
33 the 10-15 trees of each plot resulting in 254-666 leaves observed per stand. Every three

1 to six weeks, the number of young, mature and dead leaves per marked twig was
2 counted. We registered the survivorship of all leaves of the first census until the last leaf
3 was shed. In the stands #3-5, the average lifespan of many leaves exceeded the
4 observation period of 19 months. In these cases, the average leaf lifespan in the leaf
5 population was obtained from linear extrapolation of the survivorship curves. Stand leaf
6 biomass (in Mg ha^{-1}) was then calculated from equation (2):

$$(2) \quad B_1 = M_1 \times D_1$$

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

15 Stem growth was measured with 80 dendrometer tapes (UMS, Ibbenbüren, Germany;
16 resolution 0.1 mm) per stand that were read every six weeks starting in May 2003.
17 Annual stem wood production was calculated as the difference in wood biomass in May
18 2003 and in May 2004.

19 20 **Measurement of root biomass and estimation of root production**

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

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

1 investigation of a smaller number of soil cores to 60-80 cm depth had shown that at
2 | least 75% of the profile total of tree fine root biomass was contained in the organic
3 layers and the mineral soil to 30 cm depth. Consequently, the fine root densities in the
4 subsoil were very low. In this study, only the profile totals of fine root biomass from the
5 organic layers and the mineral soil to 30 cm depth are considered.

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

12 Fine root production (P_{FR}) was estimated from minirhizotron observation of fine root
13 birth, growth and death in the five stands; this technique was found to give more reliable
14 data on P_{FR} than other methods (Graefe *et al.* 2008a, Moser *et al.* in press). In June
15 2005, we installed 10 transparent minirhizotron tubes with an external diameter of 70
16 mm at random positions in each of the five stands. They were placed vertically to the
17 soil surface and installed to a depth of ca. 40 cm wherever possible.

18 In this study, only the uppermost 10 cm of the tube in the organic layers or mineral
19 topsoil were analyzed for fine root dynamics, because the very high stone content of the
20 mineral soil in the lowermost stand did not allow a deeper penetration of the tubes into
21 the soil at several measuring locations. For monitoring root growth, a root scanner
22 system (CI-600 Root Growth Monitoring System, CID Inc., USA) was inserted into the
23 tubes at monthly intervals from June 2005 to January 2007. However, only data from
24 November 2005 onwards were considered in the analysis in order to minimize errors in
25 root production estimation caused by disturbance effects during tube installation. The
26 images were analyzed for changes in fine root length using the software WinRHIZO
27 Tron (Régent, Quebec, Canada). Relative increases and relative losses in root length
28 (unit: $\text{cm cm}^{-1} \text{ mo}^{-1}$) were calculated by relating root length increase or root length loss
29 between two observation dates to the root length visible at the previous measuring date
30 (Graefe *et al.* 2008a). By relating this data to 12 months, we estimated the annual root
31 length production of the visible fine root population in the rhizotron tubes (Nadelhoffer
32 2000). By means of the root productivity in the uppermost 10 cm of the soil and the

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3 1 standing biomass of the organic layers and the mineral topsoil (0-30 cm) we estimated
4 2 the fine root production in the soil profile (P_{FR}).

5 3 For two reasons we assume that the P_{FR} figure for the uppermost stand (3060 m)
6 4 derived from the minirhizotron data is an overestimate (Moser *et al.*, in press).
7 5 Consequently, we replaced these values by a lower production figure that was
8 6 calculated by extrapolating the P_{FR} data of the stands #1-4 to 3060 m. The first reason is
9 7 that root growth and death events observed in the minirhizotron tubes in the uppermost
10 8 10 cm of the soil profile may not be representative for the root mass in the entire soil
11 9 profile, in particular in the very thick, acidic and moist organic soils at 3060 m. Second,
12 10 P_{FR} could be overestimated at 3060 m because fine root growth is slower in lower
13 11 temperatures at higher elevations with the consequence that fine root initiation and
14 12 death in high-elevation forests require longer periods for reaching a steady state at the
15 13 tube surfaces than in low-elevation forests (Graefe *et al.* 2008b). Thus, slow-growing
16 14 roots at 3060 m could still have been in the recovery phase after the disturbance by the
17 15 tube installation. As a consequence, all subsequent calculations were conducted with the
18 16 extrapolated (conservative) fine root production ($4.7 \text{ Mg ha}^{-1} \text{ yr}^{-1}$) and total BNPP
19 17 values ($5.1 \text{ Mg ha}^{-1} \text{ yr}^{-1}$) for the 3060 m stand.

20 18 Coarse root production was measured with 20 dendrometer tapes per stand, mounted
21 19 on superficially growing coarse and large roots at diameters in the range 20-300 mm.
22 20 The tapes were read every six weeks, starting in May 2003. From diameter increment,
23 21 we calculated the relative volume increment of each measured coarse root segment.
24 22 Based on the coarse root biomass data obtained in the soil pits, stand totals of coarse
25 23 root production were calculated (for details see Soethe *et al.* 2006a, b).

26 24 For expressing the biomass stocks and productivity components in terms of carbon,
27 25 we analyzed the C concentration in sub-samples of all biomass fractions using a CN
28 26 auto-analyzer (Vario EL III, elementar, Hanau, Germany) at the University of Göttingen
29 27 (live fine and coarse roots, stem wood, fine root and leaf litter: $n = 20$, leaves: $n = 10-20$
30 28 per stand).

31 29

32 30 ***Measurement of soil organic carbon pools***

33 31 Eighteen soil cores were extracted at random positions in each stand in April 2004; the
34 32 organic layer horizons were sampled using a 20 cm × 20 cm wooden frame. The two
35 33 organic layer horizons separated during soil sampling were designated as Oi (recently

1 shed litter) and OeOa (strongly decomposed material with no visible structure). The
2 latter horizon consisted of small aggregates of humic substances and a high density of
3 fine root mass. Mineral soil was sampled to a depth of 30 cm below the transition zone
4 from the organic OeOa to the mineral topsoil. At the majority of coring locations, the
5 bedrock was reached at this depth. The samples were taken with a soil auger of 10 cm in
6 diameter. For each horizon and stand, six composite samples were assembled from three
7 individual samples each. These composite samples were subject for further analysis.
8 During soil sampling organic layer thickness was determined at each sampling point.
9 The samples were transported in polyethylene (PE) bags to the laboratory of the ECSF
10 and weighed for the determination of soil dry mass. The soil was then homogenized by
11 hand, which involved cutting of the litter layer in approximately 1 cm × 1 cm pieces.
12 Stones, coarse woody debris and roots were removed carefully. Subsequently, the
13 samples were transported to Germany via airplane within one week and immediately
14 processed in the laboratories of the Institute for Soil Science and Site Ecology of
15 Dresden University of Technology. During transport the samples were cooled to
16 approximately 10 °C and care was taken that the temperature of the samples did not rise
17 above the average temperature at the location of origin. We did not freeze the soil
18 material because we expected that such a treatment would affect the soil microbial
19 community of tropical soils more severely than cooling for several days would do.
20 Due to the nature of the bedrocks and the low pH of the mineral soil, the soils were free
21 of carbonate. Thus, all carbon in the soil is organic C (SOC). For the determination of
22 SOC an aliquot of each sample was dried (40 °C mineral soil; 60 °C organic layers) and
23 milled (vibratory disc mill RS 100, Retsch, Germany). Organic layer samples were
24 milled at 700 rpm for 45 s and mineral soil samples at 1400 rpm for 60 s. After milling,
25 the samples were dried again overnight at 40 °C. The amount of carbon was determined
26 by a thermal conductivity sensor after complete dry combustion at 1150 °C (CNS-
27 Analyzer vario EL III, elementar, Hanau, Germany). The stocks of SOC were expressed
28 in kg ha⁻¹ per horizon and as profile totals (organic layers plus mineral soil to 30 cm
29 depth).

30 The salt-extractable inorganic nitrogen concentration [N_{inorg}] was analysed in KCl-
31 extracts of the organic layers and the mineral soil horizons twice in 2004. 10 g of
32 mineral soil or 5 g of organic layer material were suspended in 100 ml 0.1 M KCl-
33 solution and shaken for two hours (180 rpm). The concentrations of nitrate and

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1 ammonium N were determined photometrically with a continuous flow autoanalyzer
2 (Skalar Analytik GmbH, Germany). Nitrite was not considered separately but was
3 included in the nitrate fraction.

5 *Statistical analyses*

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

22 **RESULTS**

23 *Altitudinal trends in tree biomass and productivity*

24 Total above- and belowground tree biomass decreased from 317 to 174 Mg dry mass
25 ha^{-1} (or 154 to 87 Mg C ha^{-1}) between 1050 and 3060 m elevation, showing the
26 minimum at 2380 m a.s.l., where stem density was markedly smaller than in the
27 uppermost stand while mean tree height was relatively low. Aboveground live biomass
28 (AGB) decreased to about 60% of its value at 1050 m between 1050 and 1890 m
29 elevation and showed a further reduction to 40% in the uppermost stand at 3060 m
30 (Table 2). The stand total of tree leaf biomass increased with elevation in the lower part
31 of the transect from 6.8 (1050 m) to 9.7 Mg ha^{-1} (1890 m), but showed a sharp decrease
32 higher upslope to 3.6 Mg ha^{-1} at 3060 m. In contrast to AGB, belowground tree biomass
33 (BGB) nearly doubled between 1050 and 3060 m (32 to 63 Mg ha^{-1}), being more or less

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3 1 invariant between 1050 and 2380 m and showing a large increase toward the uppermost
4 2 stand at 3060 m. While coarse and large root biomass (all roots > 2mm in diameter)
5 3 remained constant between 1050 and 2380 m and increased only higher upslope, fine
6 4 root biomass ($d < 2$ mm) showed a more or less continuous increase from 2.7 Mg ha^{-1}
7 5 (1050 m) to 10.8 Mg ha^{-1} (3060 m). The proportion of leaf biomass in total biomass
8 6 remained unchanged between 1050 and 3060 m (2%), while fine root biomass
9 7 contributed by less than 1% at 1050 m and increased to about 6% at 3060 m. Total root
10 8 biomass (fine and coarse) accounted for roughly 10% of total biomass at 1050 m
11 9 (equivalent to a root/shoot biomass ratio of only 0.11), while roots contributed by about
12 10 35% to total biomass at 3060 m, yielding a R/S ratio > 0.5 .

13 11 The production of leaf biomass was by far the most important single component of
14 12 aboveground productivity (ANPP) in all five forest stands, contributing by 50 to 65% to
15 13 ANPP. Only 5 to 25% of ANPP referred to wood growth which reached annual rates of
16 14 2.8 to $0.1 \text{ Mg dry mass ha}^{-1} \text{ yr}^{-1}$ or 1.4 to $< 0.1 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ in the stands (Table 2).
17 15 Wood increment showed a steeper elevational decrease from 1050 to 3060 m (to about
18 16 5% of the value at 1050 m) than leaf production (reduction to about 35%). Moreover,
19 17 broken and abscised twigs and non-tree litter components (such as fallen epiphytes)
20 18 represented a larger carbon sink in the two uppermost stands (2380 and 3060 m) than
21 19 stem wood production. While wood production showed a more or less continuous
22 20 decrease from 1050 to 3060 m, leaf production remained stable up to 1890 m, but
23 21 dropped markedly higher upslope between 1890 and 3060 m.

24 22 Similar to root biomass, root productivity deviated in its vertical pattern from that of
25 23 ANPP. Coarse and large root increment as estimated from dendrometer readings and
26 24 root biomass excavations showed a substantial variation among the five stands but
27 25 revealed no significant trend with elevation. However, the highest coarse root
28 26 productivity was recorded in the stands at 3060 m and 1540 m elevation where the wind
29 27 exposure is higher than in the other three stands. Fine root production (P_{FR}) as estimated
30 28 from minirhizotron observations and root coring data was roughly 10 times larger than
31 29 coarse root production and showed a significant increase from 1050 m ($2.3 \text{ Mg ha}^{-1} \text{ yr}^{-1}$)
32 30 to 3060 m ($9.4 \text{ Mg ha}^{-1} \text{ yr}^{-1}$). Adding coarse and fine root production data gave total
33 31 belowground productivity (BNPP) figures in the range of 2.5 to $4.0 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ for the
34 32 stands #1-4, but a much higher productivity ($> 10 \text{ Mg ha}^{-1} \text{ yr}^{-1}$) for the uppermost stand.
35 33 When considering the more plausible conservative P_{FR} estimate for the 3060 m stand

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(4.4 Mg ha⁻¹ yr⁻¹, see Material and Methods section), BNPP was estimated at 5.3 Mg ha⁻¹ 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 Mg dry mass ha⁻¹ yr⁻¹ or 6.1 – 6.6 Mg C ha⁻¹ yr⁻¹) were calculated. A significantly smaller NPP total was found only for stand #4 at 2380 m (7.9 Mg dry mass ha⁻¹ yr⁻¹) and stand #5 at 3060 m, if the conservative P_{FR} value is used (8.2 Mg ha⁻¹ 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, non-tree litter), all aboveground biomass 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 non-linear 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 soil organic carbon

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

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3 1 #1) and 204 Mg ha⁻¹ (stand #5) with no trend between 1050 and 2380 m and a very high
4 2 value close to the alpine timberline at 3060 m.
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9 **DISCUSSION**

10 *Elevational changes in biomass and soil carbon stocks*

11 Our study is the first to investigate synchronously all major aboveground and
12 belowground biomass and production components in a long altitudinal transect in
13 tropical mountain forests. Other transect studies in tropical mountains (Hawaii: Raich *et al.*
14 1997; Sabah, Malaysia: Kitayama & Aiba 2002; Puerto Rico: Weaver & Murphy
15 1990, Wang *et al.* 2003; Sulawesi, Indonesia: Culmsee *et al.* 2010) were less complete,
16 17 in most cases focusing only on aboveground compartments and often covering shorter
18 altitudinal distances. Root biomass was only investigated in the transects on Mt.
19 Kinabalu in Sabah and recently in the Peruvian Andes (Girardin *et al.*, in press).
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22 According to figure 2A, aboveground live biomass (AGB) tended to decrease with
23 elevation in all cited longer tropical mountain transects. The decrease was, however, not
24 always continuous with elevation, which may result from a marked tree species turnover
25 along the slope (as in Ecuador) or due to inadequate sampling of the local topographic
26 27 variability. Due to the large scatter in the biomass data of the seven transects, the pooled
28 data of the meta-analysis showed no significant AGB decrease between 500 and 3000 m
29 a.s.l.
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32 One striking result of the Ecuador transect study is the more than fourfold increase in
33 standing fine root biomass from 1050 to 3060 m elevation. The few existing data on
34 root biomass in tropical mountain forests also indicate that fine root biomass does
35 increase, and not decrease, with elevation, which contrasts with the altitudinal patterns
36 found for AGB (Leuschner *et al.* 2007). A positive altitudinal trend in root biomass was
37 also reported from the transect studies by Kitayama & Aiba (2002) on the slopes of Mt.
38 Kinabalu and by Girardin *et al.* (2010, in press) in the Peruvian Andes. A compilation of
39 literature data of root biomass in tropical forest stands at different altitudes also supports
40 this finding (Hertel & Leuschner 2010).
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43 The Ecuadorian transect is also the first to provide detailed information on altitudinal
44 trends in coarse and large root biomass, and total root biomass. Clearly, our coarse root
45 data are doubtlessly underestimated in particular in the case of the lowermost stands
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3 1 where stem densities are lower, because the data base on excavations in soil pits at a
4 2 minimum stem distance of 1 m. We expect that the coarse and large root biomass
5 3 directly under the stems is greater than at larger stem distance. Consequently, the stand
6 4 averages of coarse and large root biomass should be higher than measured, particularly
7 5 in the stands # 1-3. Our data and those of Soethe et al. (2006a, b) indicate that trees
8 6 develop greater amounts of coarse and large root biomass at sites with elevated wind
9 7 exposure, where a good anchorage is important.

10 8 The carbon stocks in live tree biomass (above- and belowground) decreased from 154
11 9 (1050 m) to 87 Mg C ha⁻¹ (3060 m) in the Ecuadorian transect, while the total C pool (C
12 10 stocks in biomass and soil) showed no significant elevational trend (range: 188 - 291
13 11 Mg C ha⁻¹). Remarkably, the largest ecosystem C pool was detected in the uppermost
14 12 stand (3060 m) close to the alpine tree line. Given that Amazonian lowland forests store
15 13 on average about 210 Mg C ha⁻¹ in biomass (above- and belowground, Malhi et al.
16 14 2006) and 98 Mg C ha⁻¹ in the soil (0-1 m, Batjes & Dijkshoorn 1999), our data indicate
17 15 that neotropical high-elevation forests can also contain substantial amounts of C in
18 16 biomass and soil despite a relatively small tree size. Inventories in other tropical
19 17 mountain forests are needed to confirm this assumption.

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21 19 *Elevational change in primary production*

22 20 Our study provides data not only on fine, coarse and large root biomass, but also on
23 21 root productivity using up-to-date approaches of fine root growth measurement. Thus,
24 22 we were able to analyze changes in total NPP (above- and belowground) with elevation,
25 23 instead of focusing on aboveground productivity only, which must lead to wrong
26 24 conclusions.

27 25 Stem wood increment showed a continuous and steep decline with elevation in this
28 26 transect which exceeded the reduction in annual leaf biomass production and canopy
29 27 fine litter fall. The data of seven other transect studies in the meta-analysis support these
30 28 altitudinal trends in stem wood and leaf production (Fig. 2B and 2C). While the absolute
31 29 ANPP figures for a certain elevation differed more than fivefold among the sites due to
32 30 floristic, climatic and edaphic differences between the study regions, leaf production
33 31 was much less variable across this pan-tropical data set. Carbon allocation to leaves
34 32 must be a C sink of higher priority than stem wood growth in tropical mountain trees,
35 33 because it is needed to maintain a sufficiently large leaf area.

1 The elevational decrease in ANPP components contrasts with belowground
2 productivity which may consume similar or larger amounts of carbohydrates than wood
3 production in the Ecuadorian transect. At least in the two uppermost stands, a neglect of
4 root production would have led to unrealistic conclusions on the productivity of the
5 forests. When considering only the four stands between 1050 and 2380 m, we found
6 based on the minirhizotron approach a significant increase in P_{FR} with elevation (from
7 2.3 to 3.7 Mg ha⁻¹ yr⁻¹). By including the much higher production value for the
8 uppermost stand at 3060 m (9.4 Mg ha⁻¹ yr⁻¹), even an exponential increase in P_{FR} with
9 altitude appears. For several reasons, however, we assumed that the figure of 9.4 Mg ha⁻¹
10 yr⁻¹ for the uppermost stand represents an overestimation of root productivity and we
11 consequently used a more conservative P_{FR} value for this stand by extrapolating the
12 linear trend of the four lowermost stands to 3060 m (see Material and Methods section).
13 This reduced fine root production estimate for the uppermost stand (4.4 Mg ha⁻¹ yr⁻¹)
14 appears much more plausible than the original high value, given that canopy carbon
15 gain decreases by at least 50% from 1050 to 3060 m (Moser *et al.* 2007).

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

27 Adding the aboveground and belowground production figures allows to estimate stand
28 net primary production (NPP) and the related sequestration of carbon. NPP as the
29 difference between canopy carbon gain and total plant respiration was approximated
30 here by adding all biomass increment terms that were measured in the study. Based on
31 the most likely estimate of fine root production, our data indicate only minor or no
32 change in NPP from 1050 to 1890 m (13.1 - 12.4 Mg dry mass ha⁻¹ yr⁻¹), but a marked

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1 productivity decrease from 1890 to 3060 m (to about 8.2 Mg ha⁻¹ yr⁻¹), yielding a
2 reduction in NPP by about 40% between 1050 and 3060 m.

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

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

11 A more or less continuous decrease of tree height with elevation is perhaps the most
12 obvious structural change occurring in our 2000-m altitudinal transect. In many other
13 mountain forests, tropical and temperate, tree size tends to decrease with altitude more
14 or less continuously, and not abruptly, toward the alpine tree line (Liebermann *et al.*
15 1996; Raich *et al.* 1997; Aiba & Kitayama 1999; Pollmann & Hildebrand 2005; Shi *et*
16 *al.* 2008). This indicates that wood production is increasingly limited by environmental
17 constraints or assimilate shortage when approaching the uppermost limit of tree growth.
18 Bruijnzeel & Veneklaas (1998) proposed various environmental factors that could be
19 responsible for a growth reduction of tropical trees at higher elevations, among them (1)
20 reduced leaf temperatures and their effects on carbon gain, (2) periodic water shortage,
21 (3) temporal soil hypoxia resulting in reduced root activity, (4) nutrient shortage and/or
22 nutrient uptake limitation, (5) high concentrations of phenolic substances in the soil, (6)
23 high doses of UV-b radiation, and (7) exposure to strong winds. In the following, we
24 focus on factors directly or indirectly related to the acquisition and investment of carbon
25 for tree growth.

26 The NPP decrease along mountain slopes, as observed in this study, could have
27 different reasons: (i) a reduction in C source strength, i.e. decreased canopy carbon gain
28 at higher elevations, (ii) increased C consumption by plant respiration, and (iii) reduced
29 C sink strength, i.e. environmentally-induced reductions in tree growth at higher
30 elevations despite sufficient carbohydrate supply. Canopy carbon gain undoubtedly
31 decreases markedly with elevation in this transect, simply because the LAI at 3060 m
32 reaches only 40% of the stand leaf area at 1050 m. We estimate that the annual canopy
33 assimilation must decline by at least 50% between 1050 and 3060 m because light-

1 saturated net photosynthesis rate (leaf-area basis) does not change significantly along
2 the 2000-m elevation distance (B. Wittig, pers. comm.).

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

10 Whether sink limitation of growth, i.e. reduced meristematic activity of high-elevation
11 trees, is responsible for the reduction in NPP, may ultimately be decided only on the
12 basis of physiological studies in the laboratory. Indirect evidence from the Ecuador
13 transect seems to indicate that stem wood cambial activity is reduced with elevation
14 independently of carbohydrate supply because stem wood increment decreased much
15 more rapidly between 1050 and 3060 m (to 5% of its value at 1050 m) than did the leaf
16 area index as an estimator of canopy carbon gain (to about 35%). However, we also
17 observed a marked increase, perhaps a doubling, of fine root production from 1050 to
18 3060 m elevation which contradicts the assumption that the C sink caused by tree
19 meristematic activity is reduced from low to high elevation due to the temperature
20 reduction from 19 to 9 °C. The minirhizotron observations showed that the fine roots
21 grew indeed more slowly at higher elevation, but turned over as rapidly as at 1050 m
22 due to a reduced longevity (see Table 5). More important, the fine root system of the
23 stand at 3060 m was four times larger than that at 1050 m, resulting in a larger C sink
24 strength at higher than at lower elevations (Graefe *et al.* 2008b). It is not very likely that
25 stem wood growth is reduced due to environmental limitation of meristematic activity
26 but fine root growth of the same tree is not.

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

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1 50%, respectively). Nevertheless, co-limitation of tree growth by reduced C source
2 strength cannot be excluded.

3 Increasing C source limitation at higher elevation in the Ecuadorian mountain forests
4 is mostly a consequence of a reduction in leaf area, and not of reduced photosynthetic
5 activity. From foliar nutrient concentrations and soil chemical data, we conclude that a
6 combined effect of increasing N limitation and decreasing temperatures with increasing
7 elevation must primarily be responsible for this marked leaf area reduction. A large
8 reduction in the mass-specific gross N mineralization rate in the organic topsoil
9 measured by the ^{15}N pool dilution approach was found to be associated with a marked
10 increase in the C/N ratio (from 22 to 63 g g^{-1}) of the organic top layer, and a 20-fold
11 decrease in the concentration of KCl-extractable inorganic N between 1050 and 3060 m
12 (Iost 2007). While N availability decreased markedly with elevation on a soil mass
13 basis, a much slighter decrease, or perhaps no change, was detected when N
14 mineralization was related to ground area because the depth of the organic layers
15 increased. Thus, the root systems of the high-elevation forests face a greatly reduced N
16 supply density (N release per soil volume) which may require the build-up of a more
17 extended and costly root system to maintain nutrient uptake. This could explain the
18 extraordinarily high amount of fine root biomass in these soils.

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

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3 1 toward higher elevations. This is support for the assumption that N limitation is the
4 2 primary cause of the marked leaf area and NPP reduction with elevation in this transect.

5 3 Increasing N limitation with elevation should also be the cause of the tremendous C
6 4 allocation shift from above- to belowground organs observed in our transect. Following
7 5 the resource balance hypothesis formulated by Bloom *et al.* (1985), this shift is best
8 6 explained by a growing importance of limiting soil resources with increasing elevation.
9 7 Increasing C and nutrient allocation to roots may represent a compensatory measure of
10 8 the trees to cope with increasing growth limitation by nutrient shortage with elevation,
11 9 and in the case of the coarse and large root system, by the growing need for stable
12 10 anchorage due to high wind loads. Interestingly, Duivenvoorden and Lips (1995)
13 11 observed a similarly large shift of C allocation to roots in Amazonian lowland forests as
14 12 nutrient availability decreased. Girardin *et al.* (2010, in press) reported a more than
15 13 threefold increase in fine root biomass between 200 and 3000 m elevation in a Peruvian
16 14 altitudinal transect. In contrast, they observed a decrease, and not an increase, in fine
17 15 root production with elevation. Additional transect studies investigating the C balance
18 16 of tropical mountain forests are needed to draw more general conclusions on altitudinal
19 17 trends in belowground productivity.

20 18 Yet, we cannot rule out that other factors such as increasing soil moisture and more
21 19 frequent soil hypoxia are also contributing to the observed reduction in LAI and the
22 20 increase in R/S ratio with elevation, since LAI and R/S showed a close relation to those
23 21 factors as well. Multi-factorial growth experiments with tropical trees are needed to
24 22 disentangle the physiological effects of those environmental factors that change in
25 23 concert along tropical mountain slopes.

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27 25 We conclude that carbon budgets of tropical mountain forests, that ignore root
28 26 biomass and root productivity, will lead to wrong conclusions on the size and altitudinal
29 27 change of C storage and C sequestration in these ecosystems. High-elevation forests in
30 28 south Ecuador contain relatively large C stocks in biomass and soil despite their low
31 29 stunted stature, which is a consequence of large SOC pools and a high root biomass.
32 30 Aboveground and belowground biomass and productivity show opposite altitudinal
33 31 trends indicating a shift from predominant light to nutrient (N) limitation of tree growth
34 32 with increasing elevation. The large reduction in stand leaf area with elevation is most
35 33 likely a consequence of a more pronounced N limitation at higher elevations. We

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3 1 propose that reductions in leaf area and associated canopy carbon gain caused by N
4 2 limitation, i.e. a C source limitation of tree growth, are more likely causes of the
5 3 reduction in aboveground tree size and biomass with altitude in south Ecuador than is C
6 4 sink limitation. Transect studies in other tropical mountains have to confirm whether
7 5 these results are of more general validity.
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14
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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/Of1) and soil organic carbon (SOC; organic layers and 0-30 cm of mineral soil) after Iost (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 Iost (2007, median and range), gross N mineralization according to ¹⁵N isotopic pool dilution approach (3 sites only), the pool of KCl-extract. 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	S 04°06'54" W 78°58'02"	S 04°06'42" W 78°58'20"	S 03°58'35" W 79°04'65"	S 03°59'19" W 79°04'55"	S 04°06'71" W 79°10'58"
Elevation (m a.s.l.)	1050	1540	1890	2380	3060
Inclination (°)	26	10	31	28	27
Air temperature (°C)	19.4	17.5	15.7	13.2	9.4
(min-max)	(11.5-30.2)	(11.2-26.7)	(7.9-29.4)	(7.0-25.1)	(3.1-18.8)
Rainfall (mm yr ⁻¹)	c. 2230	c. 2300	c. 1950	c. 5000	c. 4500
Relative air humidity (%)	88.7	88.9	90.8	93.3	93.5
(min-max)	(15.5-100)	(31.7-100)	(15.7-100)	(34.0-100)	(28.6-100)
Bedrock types	Leuco- and hornblende, granodiorites	Leuco- and hornblende, granodiorites	Black phyllites, quartzite, metasiltstone, metasandstone	Black phyllites, quartzite, metasiltstone, metasandstone	Black phyllites, quartzite, metasiltstone, metasandstone
Soil types	Alumic Acrisol	Alumic Acrisol	Gleyic Cambisol	Gleyic Cambisol	Podzol
Organic layer thickness (mm)	48	243	305	214	435
Soil moisture (vol.%)	29.7	30.3	35.4	44.7	49.1
(min-max)	(15.3-38.5)	(20.4-43.5)	(27.4-44.7)	(35.7-48.7)	(39.5-59.5)
Soil pH (CaCl ₂)	3.94	3.90	3.52	3.26	2.86
SOC: organic layers	11.1	50.5	36.5	47.8	75.1

	(Mg ha ⁻¹)					
	SOC: 0-30 cm mineral soil	95.3	61.2	123.4	73.6	128.4
	(Mg ha ⁻¹)					
	SOC: profile total	106 (± 7)	112 (± 16)	160 (± 17)	121 (± 16)	204 (± 27)
	(Mg ha ⁻¹) (±1 SE)					
	Soil C/N (Oi horizon, g g ⁻¹)	22	29	28	46	63
	KCl-extract. inorganic N:	1180	219	234	17	6
	Oi layer (µg g ⁻¹) (min-max)	(329–2238)	(76–953)	(34–574)	(12–209)	(4–19)
	KCl-extract. inorganic N:	45	19	73	26	38
	0-10 cm min. soil	(43–69)	(14–27)	(35–78)	(11–44)	(19–46)
	(µg g ⁻¹) (min-max)					
	Gross N mineralization:	159	n.d.	115	n.d.	23
	Oi layer (µg g ⁻¹ d ⁻¹)	(80–213)		(107–120)		(0–32)
	(min-max)					
	Gross N mineralization:	0	n.d.	8	n.d.	13
	0-10 cm min. soil	(<0–48)		(3–13)		(9–17)
	(µg g ⁻¹ d ⁻¹) (min-max)					
	Pool of KCl-extract. N _{inorg}	2.9	2.5	3.3	3.1	1.1
	in org. layers (g N m ⁻²)					
	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

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

¹Data for the stands at 1890-3060 m after Leuschner et al. (2007), ²for the stand at 3060 m extrapolated fine root production estimates are given in brackets.

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 ¹	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 increment	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	2.28	3.16	2.97	3.72	9.40	1.06	1.50	1.35	1.79	4.70
Total BNPP²	2.45	3.95	3.20	3.95	10.29	1.14	1.88	1.46	1.90	5.12
					(5.31)					(2.66)
Total NPP²	13.05	12.84	12.41	7.85	12.96	6.40	6.34	6.08	3.85	6.56
					(8.15)					(4.10)

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For Review Only

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

2 Elevation in m a.s.l., mean air temperature in °C, vapour pressure deficit VPD in hPa, annual precipitation in mm yr⁻¹, soil moisture in vol.%, proton concentration of
 3 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 -, non-
 4 linear relationships are marked with *. ¹Regression analyses were calculated considering the extrapolated fine root production value for the 3060 m stand

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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	-	0.59	0.040									
AG wood	-	0.81	0.045	*	0.86	0.032	*	0.61	0.037	-	0.38	0.081	-	0.50	0.055	-	0.98	0.003	*						
AGB	-	0.85	0.036	*	0.82	0.034	*	0.63	0.033	-	0.41	0.073	-	0.53	0.050	-	0.99	0.002	*						
Coarse roots		0.13	0.149	-	0.18	0.131	-	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		-	0.83	0.041	*		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	*			
Non-tree 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				

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3	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					
4	Fine roots ¹	0.92	0.003	-	0.90	0.004	-	0.79	0.013	0.54	0.049	0.78	0.014	0.73	0.019	0.91	0.003			
5	Total BNPP ¹	0.74	0.018	-	0.73	0.020	-	0.51	0.052	0.30	0.099	0.52	0.052	0.65	0.030	0.79	0.013			
6																				
7	Total NPP ¹	-	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
8																				
9	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
10	BNPP/ANPP ¹	0.86	0.007	-	0.90	0.004	-	0.98	0.004	0.55	0.047	0.98	0.004	0.96	0.001	0.98	<0.001			
11	N pool in leaf	-	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
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1 **Table 4:** Results of correlation analyses between six environmental variables and elevation in the five Ecuadorian
 2 study plots (Pearson correlation coefficient r and p).
 3 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
 4 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
 5 in bold ($p < 0.05$), negative relationships are indicated by -.

	Elevation		Temperature		VPD		Precipitation		Soil moisture		Proton concentration	
	r	p	r	p	r	p	r	p	r	p	r	p
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

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

2 AGB – aboveground biomass, ANPP – aboveground net primary production, BGB – belowground biomass,
 3 BNPP – belowground net primary production, n.d. – no data; ¹from Moser *et al.* (2007). ²from Graefe *et al.*
 4 (2008b). ³for the stand at 3060 m: extrapolated fine root production estimate from the trend line of stands 1 -
 5 4 in brackets.

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) ²	11.2	n.d.	15.3	n.d.	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 (%) ³	7.6	10.9	12.3	10.1	16.4
NPP per tree biomass (%) ³	4.1	6.3	6.2	5.4	7.4
					(8.5)
					(4.7)

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3 1 **Figure 1:** Topographic map of the study area with its location in the south of Ecuador, position of
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5 2 the study sites #1-5, the “Estación Científica San Francisco” (ECSF) and its protected “Reserva
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7 3 Biológica San Francisco” RBSF, showing altitudinal belts from <1000 to >3500 m a.s.l. The
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9 4 dotted line indicates the border of Podocarpus National Park, in black the province capitals Loja
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11 5 and Zamora.
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14 7 **Figure 2:** Aboveground (A - D) and belowground (E - H) biomass and production fractions in
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16 8 their dependence on elevation in tropical mountain forests. Data compiled from a literature survey
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18 9 of pan-tropical mountain transect studies and several single plots. Data points from a given
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20 10 transect were connected with dotted lines for clarity. Bold lines indicate the regression lines of
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22 11 linear or simple non-linear regression analyses covering all transects. For belowground biomass
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24 12 (BGB), the regression analysis was conducted separately for data on total root and on fine root
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26 13 biomass. In the graphs G and H, the fine root production at 3060 m in the Ecuador transect was
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28 14 estimated by extrapolating from the four lower stands. Ecuador – own data; Malaysia – Kitayama
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30 15 & Aiba (2002); Puerto Rico – Weaver & Murphy (1990) and Wang et al. (2003); Hawaii – Raich
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32 16 et al. (1997), Indonesia – Culmsee et al. (2010).
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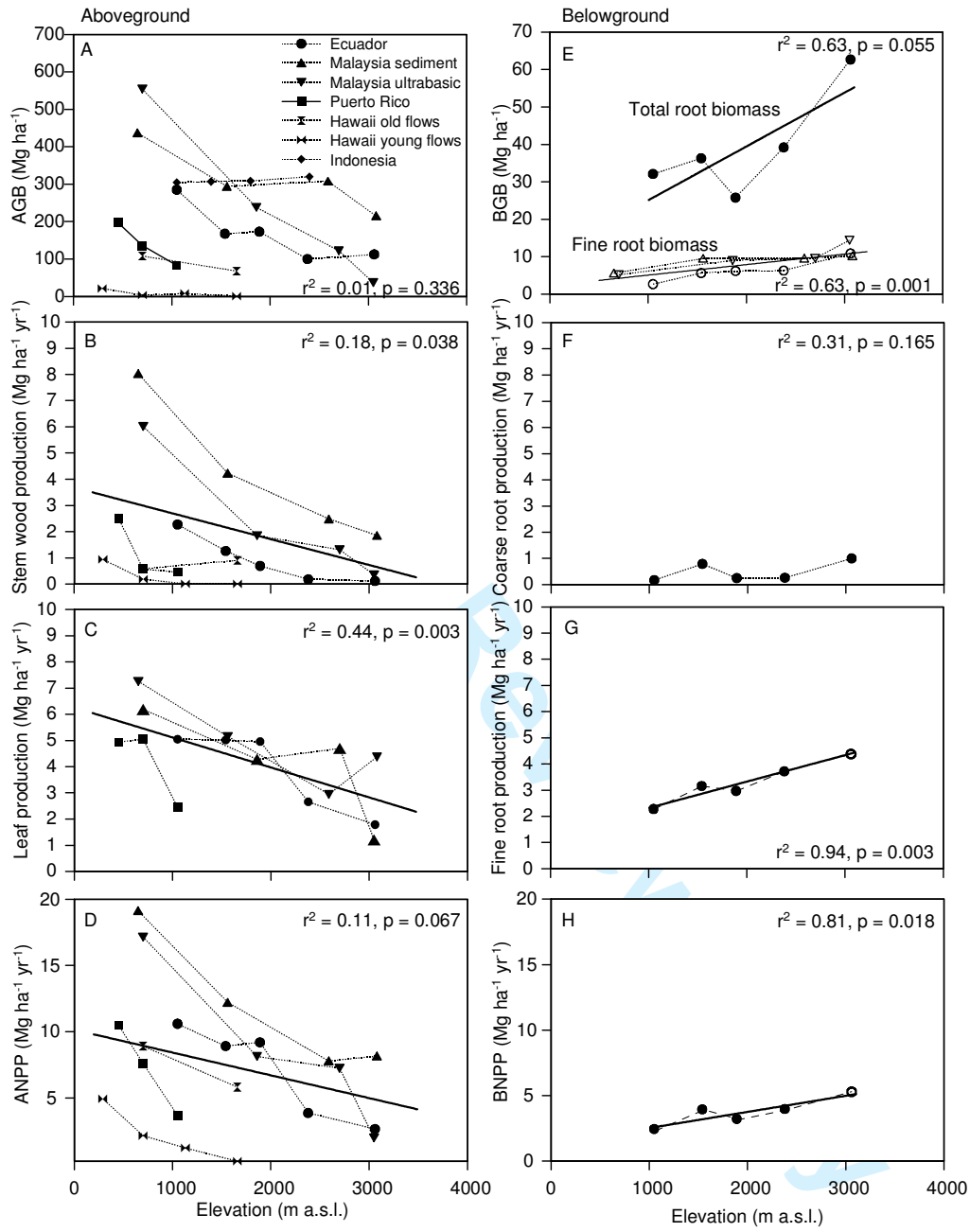
35 18 **Figure 3:** Stem wood production (A) and LAI (B), and their dependence on annual mean air
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37 19 temperature in tropical mountain forests. Data compiled from a literature survey of pan-tropical
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39 20 mountain transect studies and several single plot studies. The vertical line indicates the elevation
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41 21 with an annual mean soil temperature of 6.7°C proposed by Körner & Paulsen (2004) as the
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43 22 approximate position of the alpine tree line. Data sources: Ecuador – Moser et al. (2007); Malaysia
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45 23 – Kitayama & Aiba (2002), Takyu et al. (2003); Puerto Rico – Weaver & Murphy (1990) and
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47 24 Wang et al. (2003); Hawaii – Raich et al. (1997), Herbert & Fownes (1999); Costa Rica –
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49 25 Hölscher et al. (in press).
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3 1 **Figure 4:** Above- and belowground trend lines of tree biomass and productivity extrapolated
4 toward the actual tree line. A) The intersection point of the AGB and BGB curves coincides well
5 2
6 3 with the position of the alpine tree line. B) Regression lines of ANPP and BNPP in relation to the
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8 actual position of the alpine tree line at 3200-3400 m elevation.
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1 **Fig.2**

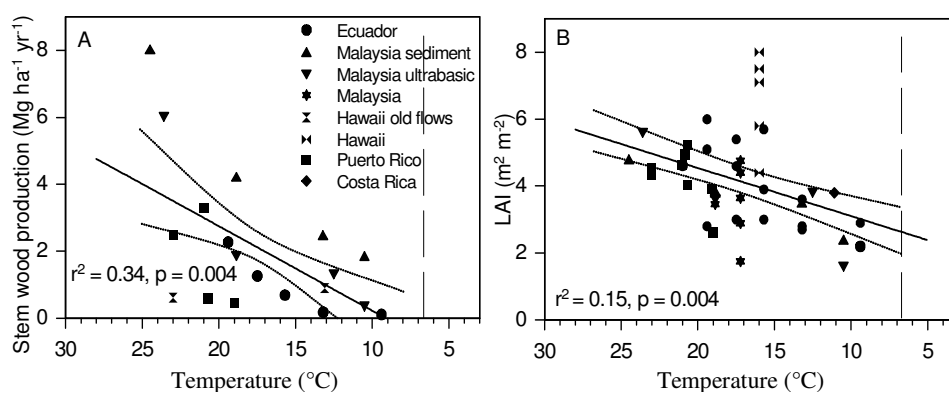
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1 **Fig. 3**

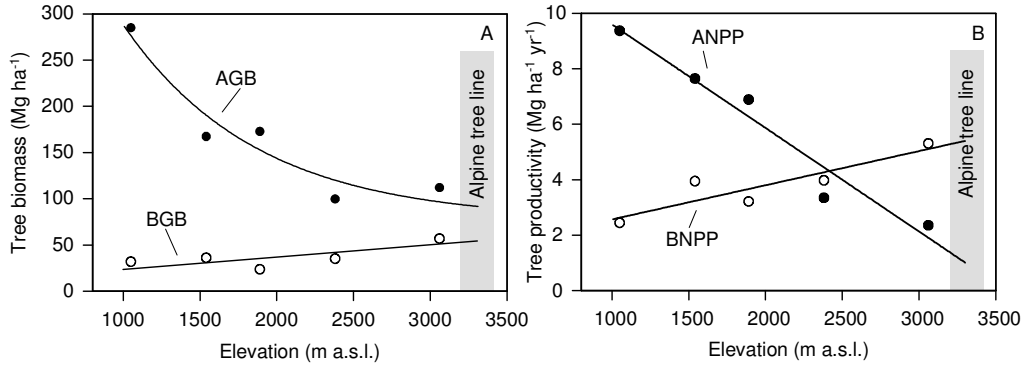


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1 **Fig. 4**



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