

Chapter 10

The Carbon Balance of Tropical Mountain Forests Along an Altitudinal Transect

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10.1 Introduction

The storage and sequestration of carbon is one of the most important ecosystem services provided by forests. Although tropical forests cover only about 12 % of the land surface of the earth, it is estimated that they account for about 25 % of the world's biomass carbon and contribute c. 40 % of terrestrial net primary production (Cleveland et al. 2011; Townsend et al. 2011). Consequently, tropical forests play

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an outstanding role in the global C cycle and a solid understanding of the C pools and fluxes with carbon assimilation, net primary production and decomposition in this biome is of paramount importance for predicting changes in the earth's climate and to adopt suitable mitigation strategies for reducing global warming (Grace and Meir 2009).

In the last two decades, our knowledge about the tropical forest carbon cycle has considerably increased due to several large-scale biomass inventories and growth analyses in neotropical and paleotropical forest plot networks (e.g. Malhi et al. 2004; Slik et al. 2010) and the application of the eddy covariance technique on towers for measuring ecosystem-level CO₂ fluxes in tropical old-growth forests (Grace et al. 1995). One prominent result is that, in the past two decades, intact tropical lowland forests apparently represented CO₂ sinks in moist years (overview in Malhi 2010), while they often were CO₂ sources in dry years (Davidson et al. 2012). Another surprising outcome of global carbon flux data bases is that the net primary production (NPP) of forest ecosystems appears to be independent from mean annual temperature (MAT) in regions with MAT > 10 °C, i.e. in tropical and subtropical climates (Luysaert et al. 2007). This view is challenged by an earlier compilation of data from tropical moist forests along elevation transects by Raich et al. (2006) who reported a mean increase in aboveground NPP (ANPP) by 0.66 Mg C ha⁻¹ year⁻¹ per K temperature increase. However, these authors provided no data on belowground NPP (root production) but gave only an indirect estimate of belowground C allocation from data on litter fall and soil respiration. The C transfer to the roots increased with increasing MAT as well, indicating an increase in total NPP with higher temperatures. However, without more reliable data on root production, this conclusion must remain vague. Another surprising outcome of the data compilation by Luysaert et al. (2007) is the lacking precipitation dependence of NPP above a threshold of about 1,500 mm year⁻¹ indicating that neither temperature nor precipitation should be important controls of NPP in tropical moist forests. However, the scatter in the data of this analysis was large and total NPP (above- and belowground) consists of a number of components, which are difficult to measure, often are estimated and thus are likely to introduce a considerable bias in the calculation of gross primary production (GPP), NPP and net ecosystem production (NEP) in tropical forests. So far, only very few studies have attempted to measure all relevant C stores and C fluxes in tropical forests completely or near-completely which leaves a considerable uncertainty in current data analyses and syntheses with respect to the tropical forest carbon cycle (Clark et al. 2001).

The situation is even less satisfying for tropical mountain forests, which once covered the mountains of the tropics from about 1,000 to more than 4,000 m elevation and that have been found to store considerable C amounts in biomass and soil (e.g. Kitayama and Aiba 2002; Benner et al. 2010). Due to their poor accessibility and the often steep slopes in rugged terrain, carbon inventories and the measurement of C fluxes is often more difficult than in tropical lowland forests. For example, using eddy covariance technique is rarely an option in tropical mountain forests. However, these forests are not only important in the cycles of C and water (McJannet et al. 2010) and are havens of a unique biodiversity (Gentry 2001;

Bruijnzeel et al. 2010), they also offer the rare opportunity to examine the C cycle of tropical forests along well-defined temperature gradients (Girardin et al. 2010), which may help to understand the temperature dependence of forest NPP (Malhi 2012; Malhi et al. 2010) and to test the more recent conclusions on the apparent temperature insensitivity of tropical forest productivity drawn from global data surveys (Luyssaert et al. 2007).

This contribution summarises extensive field work in pristine tropical pre-montane to upper montane forests conducted over the past 10 years in an altitudinal transect from 1,000 to 3,000 m a.s.l. on the eastern slope of the southern Ecuadorian Andes. For the first time, it was attempted to measure all major C pools and C fluxes in a set of forest plots at different elevations, including the C pools in above- and belowground biomass, and the fluxes associated with photosynthesis, stem wood growth, leaf and fine litter production, fine and coarse root production, and autotrophic (tree) and soil respiration by applying up-to-date ecophysiological techniques in a considerable number of plots and tree species under field conditions.

The main aims of the study were (1) to analyse altitudinal changes in forest above- and belowground biomass and forest structure using a large number of plots (59), (2) to close gaps in our knowledge on rarely studied components of the C cycle in tropical forests (in particular root production, autotrophic respiration and photosynthesis) and (3) to search for altitudinal trends in GPP, NPP, NEP and respiration components, which could give hints on their temperature dependence.

This chapter compiles a wealth of data on C cycle components that have been published or are being prepared for publication (see references list), in order to reach at a comprehensive synthesis on the C balance of the forests between 1,000 and 3,000 m elevation.

10.2 Materials and Methods

10.2.1 *Climate, Geology and Vegetation of the Study Region*

The study region close to the equator on the eastern slope of the Andes has a humid tropical montane climate with MAT ranging between 19 °C at 1,000 m and 9 °C at 3,000 m a.s.l. (Bendix et al. 2008; Emck 2007, see Table 10.1). The soils along the slope are generally acidic with increasing amounts of humus material on top of the soil towards higher elevations (Moser et al. 2011, see also Wolf et al. 2011). The availability of N in the densely rooted uppermost organic layer markedly decreases along the transect as is shown by large reductions in gross N mineralisation rate and in the amount of KCl-extractable inorganic N in the organic layers from 1,050 to 3,060 m indicating a slowing down of decomposition with increasing elevation. The species-rich premontane to upper montane forest communities are described in detail in Homeier et al. (2008) and Chap. 8. All stands are located in protected forest sections with a representative stand structure and no marked signs of human impact or recent natural disturbance.

Table 10.1 Location and climatic, edaphic and stand structural characteristics of the five intensive study plots (adopted from Moser et al. 2011)

Plot 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.]	1,050	1,540	1,890	2,380	3,060
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 year ⁻¹]	c. 2,230	c. 2,300	c. 1,950	c. 5,000	c. 4,500
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 (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]	3.9	3.9	3.5	3.3	2.9
Soil C/N [Oi horizon, g g ⁻¹]	22	29	28	46	63
KCl-extract. N _{inorg.} : Oi layer [μg g ⁻¹]	1,180 (329–2,238)	219 (76–953)	234 (34–574)	17 (12–209)	6 (4–19)
KCl-extract. N _{inorg.} : 0–10 cm min. soil [μg g ⁻¹]	45 (43–69)	19 (14–27)	73 (35–78)	26 (11–44)	38 (19–46)
Pool of KCl-extract. N _{inorg.} in org. layers [g N m ⁻²]	2.9	2.5	3.3	3.1	1.1
Gross N mineralisation: Oi layer [μg g ⁻¹ day ⁻¹]	159 (80–213)	n.d.	115 (107–120)	n.d.	23 (0–32)
Gross N mineralisation: 0–10 cm min. soil [μg g ⁻¹ day ⁻¹]	0 (<0–48)	n.d.	8 (3–13)	n.d.	13 (9–17)
Stem density (>5 cm DBH) [ha ⁻¹]	968	2,167	2,245	2,512	5,613
Canopy height [m]	31.8	21.7	18.9	12.0	9.0

Mean annual air temperature and relative air humidity 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/Oi) after Iost (2007); rainfall data after P. Emck & M. Richter and own measurements (3-year means, unpublished); KCl-extractable inorganic N measured in April 2004 by Iost (2007), (median and range), gross N mineralisation according to the ¹⁵N isotopic pool dilution approach (three plots only), the pool of KCl-extract. N in the organic layers is a rough estimate derived from N_{inorg.} concentrations and humus mass; data on forest structure were measured for 80 trees per plot (after Moser et al. 2008)

10.2.2 Study Plots

In the transect of about 30-km length and 2,000-m elevation distance, a set of 59 study plots of 20 m × 20 m size was identified in a stratified random selection procedure. Three plots served for the very intensive carbon cycle measurement programme (all C fluxes including photosynthesis and respiration measurements; plots # 1, 3 and 5), five for the spatially more extended intensive measurement program (net primary production including root production; plots # 1, 2, 3, 4 and 5) and 54 additional plots for the analysis of the spatial variability of selected biomass and productivity parameters in the rugged landscape (“matrix plots”). Each 18 of the 54 matrix plots were located at 1,000, 2,000 and 3,000 m elevation with each six plots being assigned to upper slope, mid-slope and lower slope positions to cover the variable topography of the rugged terrain. The intensive study plots # 1–5 (“core plots”) were located on mid-slope positions. The biomass and soil C pools were inventoried in all plots. All stands were selected randomly in closed stands without larger gaps (>2 m) that met the above-mentioned criteria of elevation and slope position.

It is important to note that all C pool and C flux data presented here refer to the projected horizontal area, i.e. the original data were corrected for slope angle.

10.2.3 Methods for Determining Biomass and Soil C Pools and Components of Productivity

Table 10.2 lists the principal methods used to measure the above- and belowground biomass stocks and their C pools and the productivity components. For further details, see the publications listed in this table. A few details are given below for the photosynthesis measurements and the calculation of carbon gain.

A stand-level estimate of gross photosynthesis was obtained from measured A_{\max} , leaf dark respiration and the Leaf Area Index (LAI) and incident global radiation data of the stands (Table 10.2). Because most of the canopy leaves are not exposed to full sunlight in dense tropical forests, we followed Mercado et al. (2006) who calculated the fraction of shaded leaves to account for 70–85 % of total leaf area in a mature tropical lowland forest in Brazil with an LAI of 5.7. For the dense stands at 1,050 and 1,890 m, we assumed that only 20 % of the leaf area is exposed to more or less full sunlight, while 80 % were assumed to be shade leaves. In the elfin forest at 3,060 m with a much smaller LAI, in contrast, we estimated that half of the leaves were sun leaves. We reduced the measured sun-canopy A_{\max} figures by 35 % following Strauss-Debenedetti and Bazzaz (1996) and used these values to extrapolate to the assimilation of the shade canopy. To account for the effect of light limitation, we assumed that sun and shade leaves operated with light saturation during the sunshine hours but reached only $0.3 \times A_{\max}$ in the remaining overcast or rainy hours (model 1). In a second approach (model 2), we assumed that

Table 10.2 Approaches and measuring conditions for investigating the biomass and productivity parameters in the 5 (3) intensive study plots (INT) and the 54 matrix plots (MAT)

Parameter measured	Plot type	Methods and measuring conditions	Replicates per plot	References
Live biomass				
Trunk and branch biomass	INT	Allometric equation (DHB, height, wood density) of Chave et al. (2005)	80 trees >10 cm DBH	Moser et al. (2008, 2011)
Trunk and branch biomass	MAT	Allometric equation (DHB, height, wood density) of Chave et al. (2005)	All trees ≥ 5 cm DBH in 0.04 ha-plots	
Liana biomass	MAT	Allometric equations (DHB), average of Lü et al. (2009), Schnitzer et al. (2006) and Sierra et al. (2007)	All liana stems ≥ 1 cm DBH in 0.04 ha-plots	
Biomass of epiphytes and ground vegetation	None	Literature data from tropical forests with similar structure (see Table 10.7)	None	Werner et al. (2012), Sierra et al. (2007), Gibbon et al. (2010), Vieira et al. (2011)
Standing leaf biomass	INT	Annual leaf litter production \times mean leaf lifespan	12 litter traps, 254–666 marked leaves	Moser et al. (2007)
Leaf area index (1)	INT	LAI-2000 Plant Canopy Analyzer (Li-Cor)	Taken at 10 random locations	Moser et al. (2007)
Leaf area index (2)	INT	Leaf litter production + mean leaf lifespan + mean SLA	Data from 12 litter traps	Moser et al. (2007)
Fine root biomass (<2 mm in diameter)	INT	Soil coring to 30 cm depth (diameter: 3.5 cm); live/dead separation under microscope	20 locations per plot	Moser et al. (2010), Hertel and Leuschner (2002)
Coarse and large root biomass (>2 mm–30 cm in diameter)	INT	Excavation to 50 cm, live/dead separation; root stumps not covered	12–16 soil pits	Soethe et al. (2007)
Productivity				
Stem wood increment	INT	Dendrometer tapes (D1, UMS, Munich) read monthly	80 trees >10 cm DBH	Moser et al. (2011)
Stem wood increment	MAT	Repeated annual DBH measurements	All trees >10 cm in 0.04 ha-plot	

(continued)

Table 10.2 (continued)

Parameter measured	Plot type	Methods and measuring conditions	Replicates per plot	References
Leaf litter fall	INT	Litter traps (0.25 m ²) sampled every 3–6 weeks	12, randomly placed	Moser et al. (2007), Moser et al. (2011)
Leaf litter fall	MAT	Litter traps (0.36 m ²) sampled every 2–4 weeks	6, randomly placed	
Leaf lifespan	INT	Leaf survivorship curves of 10–15 understorey trees	254–666 leaves per plot	Moser et al. (2007)
Fine root production	INT	Minirhizotron observation to 40 cm depth, CI-600 root growth scanner (Washington, USA)	10 tubes per plot	Graefe et al. (2008a, b), Moser et al. (2010)
Coarse and large root growth	INT	Dendrometer tapes (D1, UMS) on roots >3 cm and <32 cm diameter, read every 3 months	20 root segments	Soethe et al. (2007)
Gross photosynthesis (trees)	INT	LI-6400 (Li-Cor), A_{\max} at ambient T and [CO ₂] of light-exposed leaves, 4–20 m tall trees (lower sun canopy), light response curves (see Table 10.3)	10–15 species per plot (62 species in total), each 3 leaves on 1 tree per species	Wittich et al. (2012), Zach (2008)
Leaf dark respiration (trees)	INT	LI-6400, sun-exposed leaves, 2–5 min acclimation to darkness, shade leaf respiration: Veneklaas and Poorter (1998)	10–15 species per plot (40 species in total), 1 tree per species	Wittich et al. (2012)
Stem and coarse root respiration	INT	6-chamber respiration system ANARESY 2 (Walz, Germany), LI-7000 analyser, branch respiration estimated	13–16 species (stem respiration) and 4–8 coarse roots per plot	Zach et al. (2008, 2010)
Soil respiration	INT	Closed chamber method (EGM-4 IRGA, PP systems, UK), correction for root decomposition	16 per plot, root trenching for estimating root respiration	Iost (2007)
Soil organic carbon	MAT	Organic layer + mineral soil to 50 cm depth, corrected for bulk density	Soil pits in close vicinity of the plots (1,000 m: 14, 2,000 m: 16 and 3,000 m: 12)	

For further details see the publications listed
DHB diameter at breast height, *SLA* specific leaf area

Table 10.3 Parameters characterising the radiation climate and photosynthetic capacity in the canopies of the plots # 1, 3 and 5 and estimated annual gross photosynthesis according to two different models (photosynthesis data after Wittich et al. unpubl. radiation data from Emck 2007)

Plot no.	1	3	5
Elevation [m]	1,050	1,890	3,060
LAI (litter production + leaf lifespan + SLA)	6.0	5.7	2.2
LAI (LAI-2000 measurement)	5.1	3.9	2.9
Proportion of LAI in sun canopy (estim.) [%]	20	20	50
Proportion of LAI in shade canopy (estim.) [%]	80	80	50
Mean global radiation ^a [W m^{-2}]	285 ^b	348	360
Mean PPFD ^{a,c} [$\mu\text{mol photons m}^{-2} \text{s}^{-1}$]	610 ^b	740	765
Sunshine duration [% of daytime period]	18	27	30
A_{max} of sun leaves [$\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$]	6.9 (± 0.6)	8.6 (± 0.5)	5.3 (± 0.7)
Light compensation point of sun leaves [$\mu\text{mol photons m}^{-2} \text{s}^{-1}$]	601	696	620
A_{max} of shade leaves (estimate) ^d [$\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$]	c. 4.5	c. 5.9	c. 3.7
Leaf dark respiration in daylight hours ^e [$\text{Mg C ha}^{-1} \text{year}^{-1}$]	5.6	4.0	3.5
Gross photosynthesis (annual total)—Model 1 ^f [$\text{Mg C ha}^{-1} \text{year}^{-1}$]	26.0	27.2	16.0
Gross photosynthesis (annual total)—Model 2 ^g [$\text{Mg C ha}^{-1} \text{year}^{-1}$]	26.0	23.7	12.5

^aMean of daytime hours

^bMeteorological station El Libano at 1,970 m above plot # 1

^cEstimated by assuming that 1 mol photons is equivalent to 0.235 J and 50 % of incident global radiation is in the PhAR range

^dAssuming an A_{max} reduction by 35 % relative to the sun leaves according to empirical data of Strauss-Debeneditii and Bazzaz (1996)

^eBased on R_D means

^fAssuming photosynthesis at light saturation during sunshine hours and a mean rate of $0.3 \times A_{\text{max}}$ during overcast periods in all three stands

^gAssuming photosynthesis at light saturation during sunshine hours and at mean rates of 0.3, 0.2 or $0.1 \times A_{\text{max}}$ during overcast periods in the 1,050, 1,890 and 3,060 m stands, respectively

photosynthesis is, in addition to light limitation, temporarily reduced by unfavourable temperatures at higher elevations and thus set the reduction factor to 0.3 , 0.2 or $0.1 \times A_{\text{max}}$ in the stands at 1,050, 1,890 and 3,060 m, respectively. We added the measured leaf dark respiration to the sum of CO_2 net assimilation (12 h day^{-1} , 365 days) for obtaining annual gross photosynthesis (see Table 10.3). Clearly, the calculated daily and annual sums of carbon influx into the forest stands are only rough estimates, but they may be useful for characterising the altitudinal trend because two influential variables used for upscaling (A_{max} and LAI) were measured with quite a large effort.

To account for differences in dark respiration (R_D) of sun and shade leaves, we used the proportional difference in R_D measured by Veneklaas and Poorter (1998) in tropical tree seedlings grown either under high ($1,000 \mu\text{mol photons m}^{-2} \text{s}^{-1}$) or low light ($100 \mu\text{mol photons m}^{-2} \text{s}^{-1}$, 53 % lower). In an attempt to calculate

annual totals of foliage dark respiration, we assumed that nighttime leaf respiration (R_N) is roughly equal to the measured daytime respiration rates (R_D). Such a rough approximation may be justified because, in these forests, temperatures at night are typically 5–7 K lower than the daytime temperatures when the R_D measurements were conducted. On the other hand, R_D may be only 50 % or less of R_N at equal temperatures due to re-fixation of CO_2 (Evans et al. 2004).

We did not measure branch and twig wood respiration (R_B) but added a term of the same size of wood respiration, thereby accounting for the observation that stem and branch wood respiration in forests may be equally large (e.g., Ryan et al. 1995). Cavaleri et al. (2006) found wood elements < 10 cm in diameter to account for 70 % of the total wood CO_2 efflux in various plant functional groups (trees, lianas and palms) in a tropical lowland forest indicating that our assumed figure may even underestimate reality.

10.3 Results and Discussion

10.3.1 Carbon in Biomass and Soil

Data on C pools in biomass (above- and belowground) and soil organic matter are compiled for the five intensive study plots in Tables 10.4 and 10.5. In addition, Table 10.6 presents means, standard errors and ranges of aboveground biomass (and wood and litter production) for the 54 matrix plots at 1,000, 2,000 and 3,000 m elevation. The matrix plot data may help to place the results from the intensive plots in a broader context and to extrapolate from the plot to the landscape level. In the synthetic Table 10.7, data from the intensive plots and the matrix plots are combined to generate an as accurate as possible estimate of the carbon stored in all relevant biomass and soil fractions of South Ecuadorian pre-montane (~1,000 m a.s.l.), montane (~2,000 m) and upper montane forests (~3,000 m).

Accordingly, total aboveground C (AGC) markedly decreases from 1,000 to 3,000 m (from 128 to 70 Mg C ha⁻¹), while belowground C (BGC) seems to remain invariant with elevation or shows a slight increase (from 242 to 270 Mg C ha⁻¹; tree stumps are not included in these figures). With 190–240 Mg C ha⁻¹, the soil organic carbon (SOC) pool (determined to a mineral soil depth of 50 cm plus organic layer; Iost 2007) was much larger at all three elevations than SOC pools reported from lowland forests: For the 0–100 cm profile, roughly 100 Mg C ha⁻¹ are a typical estimate for tropical soils (mainly under forest) in Central Africa (82–84 Mg C ha⁻¹; Batjes 2008), Amazonia (98 Mg C ha⁻¹, Batjes and Dijkshoorn 1999; 103 Mg C ha⁻¹, De Moraes et al. 1995) and Southeast Asia (102–124 Mg C ha⁻¹, Chen et al. 2005; 55 Mg C ha⁻¹, Yonekura et al. 2010). Given that our figures cover only the 0–50 cm profile, the montane forests in South Ecuador stored more than twice the SOC amount than lowland forest soils.

Table 10.4 Above- (AGB) and belowground biomass (BGB) and above- (ANPP) and belowground production fractions (BNPP) of the core study plots # 1–5 (after Moser et al. 2011)

Plot no.	Dry mass					Carbon				
	1	2	3	4	5	1	2	3	4	5
Elevation [m a.s.l.]	1,050	1,540	1,890	2,380	3,060	1,050	1,540	1,890	2,380	3,060
Biomass [Mg DM ha ⁻¹]	Biomass [Mg C ha ⁻¹]									
Tree leaves	5.9	6.8	6.6	6.9	4.8	2.9	3.5	3.4	3.5	2.4
Stem and branch wood	278.3	159.5	163.2	94.6	108.6	134.7	77.4	79.2	45.1	51.7
Total AGB	284.1	166.3	169.8	101.5	113.4	137.6	80.8	82.5	48.6	54.1
Coarse roots	29.4	30.7	19.9	32.9	51.9	14.2	14.9	9.7	15.7	24.7
Fine roots ^a	2.7	5.6	6.2	6.3	10.8	1.2	2.7	2.8	3.0	5.4
Total BGB	32.1	36.3	26.1	39.2	62.8	15.5	17.6	12.5	18.7	33.1
Total tree biomass	316.2	202.7	195.9	140.7	176.1	153.1	98.4	95.0	67.3	87.3
Production [Mg DM ha ⁻¹ year ⁻¹]	Production [Mg C ha ⁻¹ year ⁻¹]									
Tree leaves	5.05	5.06	4.96	2.64	1.79	2.54	2.57	2.51	1.34	0.92
Reproductive 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
Epiphyte biomass	0.28	0.58	0.25	0.25	0.21	0.14	0.29	0.13	0.13	0.11
Bamboo biomass	0.00	0.00	1.55	0.12	0.20	0.00	0.00	0.78	0.06	0.10
Other fine litter compon.	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 and branch wood	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 ^b	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 ^b	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^b	13.05	12.84	12.41	7.85	12.96 (8.15)	6.40	6.34	6.08	3.85	6.56 (4.10)

The plots # 1, 3 and 5 are the intensive C flux study plots

^aData for the plots # 3, 4 and 5 after Leuschner et al. (2007)

^bFor plot # 5, extrapolated fine root production estimates are given in brackets

Table 10.5 Estimates of stand leaf biomass and leaf area index (LAI) for the five core study plots as obtained with each two different approaches (see text; from Moser et al. 2007)

Approach	Plot no.				
	1	2	3	4	5
Elevation [m]	1,050	1,540	1,890	2,380	3,060
Stand leaf biomass [Mg C ha ⁻¹]	3.4 (±0.2) ^a	4.1 (±0.02) ^b	5.0 (±0.4) ^{b*}	2.6 (±0.2) ^{c*}	1.8 (±0.2) ^d
Leaf litter production + leaf lifespan LAI2000 + SLA data	2.9 (±0.06) ^a	3.5 (±0.03) ^b	3.3 (±0.1) ^b	3.5 (±0.09) ^b	2.4 (±0.2) ^a
Leaf area index	6.0 (±0.4) ^a	5.4 (±0.4) ^a	5.7 (±0.5) ^{a*}	2.8 (±0.2) ^{b*}	2.2 (±0.2) ^c
Leaf litter production + leaf lifespan + SLA LAI-2000	5.1 (±0.1) ^a	4.6 (±0.1) ^b	3.9 (±0.2) ^c	3.6 (±0.1) ^c	2.9 (±0.3) ^d

Different letters indicate significant differences between the plots, *significant differences between the two approaches (one-way ANOVA, Tukey HSD test at $p < 0.05$)

Table 10.6 Some parameters characterising stand structure and productivity of the 54 matrix plots at the three elevations (18 plots per elevation level each)

Elevation [m]	1,000 (1,020–1270)	2,000 (1,910–2,090)	3,000 (2,800–2,900)
Stem density (DBH \geq 5 cm) [ha ⁻¹]	1,707 \pm 111 ^a (1,327–1,884)	2,486 \pm 196 ^b (1,915–2,973)	2,804 \pm 320 ^b (1,949–3,663)
Tree basal area (DBH \geq 5 cm) [m ² ha ⁻¹]	46 \pm 6 (31–56)	48 \pm 4 (43–56)	41 \pm 2 (34–47)
Stem and branch wood biomass (DBH \geq 5 cm) [Mg C ha ⁻¹]	109 \pm 9 ^a (84–121)	104 \pm 13 ^a (70–113)	60 \pm 4 ^b (49–66)
Stem and branch wood biomass increment (DBH \geq 10 cm) [Mg C ha ⁻¹ year ⁻¹]	1.6 \pm 0.1 ^a (1.1–2.1)	1.3 \pm 0.2 ^a (0.7–1.6)	0.7 \pm 0.1 ^b (0.5–0.9)
Leaf litter production [Mg C ha ⁻¹ year ⁻¹]	2.9 \pm 0.2 ^a (2.6–3.2)	3.4 \pm 0.2 ^b (2.8–4.0)	1.9 \pm 0.1 ^c (1.7–2.0)

The labels 1,000, 2,000 and 3,000 m stand for the elevation ranges indicated below. Given are means \pm standard errors and the range of second to third quartile. C concentrations for wood biomass and leaf litter were taken from Table 10.4. Different letters indicate significant differences among elevations (one-way ANOVA, Tukey HSD test at $p \geq 0.05$)

DHB diameter at breast height

Assuming Amazonian lowland forests to store on average about 160 Mg C ha⁻¹ in aboveground biomass (Malhi et al. 2006) and adding a root biomass estimate by assuming a root:shoot ratio of 0.235 for tropical moist forests (Mokany et al. 2006) plus 100 Mg C ha⁻¹ for the SOC pool, an ecosystem C pool of about 300 Mg C ha⁻¹ is obtained for lowland forests, which is less than the estimate of 319–369 Mg C ha⁻¹ for the pre-montane to upper montane forests in Ecuador. It may well be that certain other tropical mountain forests contain even larger ecosystem C pools than those reported here since Raich et al. (2006) found SOC pools up to >400 Mg C ha⁻¹ (0–100 cm, excluding surface litter), which is more than that found in the Ecuadorian mountain forests. However, lower SOC figures have also been reported (e.g. 118 Mg C ha⁻¹ in Peruvian treeline forests, Zimmermann et al. 2010). One likely reason for high belowground/aboveground ratios in C storage in tropical mountain forests is low N (and perhaps P) availability in many montane and upper montane forests (Moser et al. 2011, Chap. 23). Thus, we conclude that the tropical mountain forests of this study represent similarly important, or even more important, carbon stores than tropical lowland forests despite the markedly smaller wood biomass at higher elevations.

10.3.2 Carbon Fluxes

Our estimates of gross primary production (GPP, i.e. NPP + R_{aut} , Table 10.8: lines 38 and 39) ranged between 25.5 and 14.1 Mg C ha⁻¹ year⁻¹ for the stands at 1,050 and 1,890 m, respectively, which is markedly lower than the GPP mean given by

Table 10.7 Carbon pools [Mg C ha^{-1}] in biomass and soil in forests at 1,000, 2,000 and 3,000 m elevation. Values in parentheses (lines 3, 5 and 6) are estimates

Elevation [m]	1,000	2,000	3,000
Leaves ^a	2.9	3.4	2.4
Stem and branch wood ^b	109	104	61
Epiphytes ^c	(2.5)	2.1	(1.5)
Lianas	2.5	1.7	0.4
Ground vegetation ^{d,e,f}	(0.3) ^d	1.5 ^f	(2.7) ^e
Coarse woody debris ^{d,e,g,h}	(2.7–19.1) ^{d,g}	4.3 ^h	(1.8) ^e
Coarse roots ^a	14.2	9.7	24.7
Fine roots ^a	1.8	2.8	5.4
SOC ^{b,i}	226	191	241
Total	370.1	319.5	339.9
Total aboveground (AGC)	128.1 (35 %)	117.0 (37 %)	69.8 (21 %)
Total belowground (BGC)	242 (65 %)	203.5 (63 %)	270.1 (79 %)
C in biomass	133.2 (36 %)	125.2 (39 %)	98.1 (29 %)

^aIntensive study plots # 1, 3 and 5

^bMatrix plots; DBH \geq 5 cm, means of $n = 18$ plots each

^cWerner et al. (2012): data from Puerto Rico (pre-montane forest, 930–1,015 m a.s.l.), from the San Francisco (S Ecuador) study site (lower montane forest, 2,050–2,150 m a.s.l.) and from Costa Rica (upper montane forest, 2,900 m a.s.l.), carbon fraction in dry epiphyte biomass was estimated to be 0.45

^dSierra et al. (2007), data from Colombia (pre-montane forest, ~1,000 m a.s.l.): CWD > 2 cm diameter, ground vegetation included herbs and all woody plants with DBH < 1 cm

^eGibbon et al. (2010), data from Peru (upper montane forest, >3,000 m a.s.l.): CWD > 10 cm diameter, ground vegetations included shrubs and bamboo

^fNo data available, figures estimated

^gVieira et al. (2011): data from Brazil (montane Atlantic forest, 1,027–1,070 m a.s.l.): CWD > 2 cm diameter

^hWilcke et al. (2005): data from the San Francisco study site (S Ecuador, lower montane forest, 1,900–2,180 m a.s.l.): CWD > 10 cm diameter

ⁱMineral soil 0–50 cm depth plus organic layer

Luyssaert et al. (2007) for tropical humid evergreen forests at low elevations ($35.51 \pm 1.60 \text{ Mg C ha}^{-1} \text{ year}^{-1}$, $n = 6$); our GPP figures are closer to the means given by these authors for temperate evergreen and deciduous forests (17.62 and $13.75 \text{ Mg C ha}^{-1} \text{ year}^{-1}$). The annual total of gross photosynthesis (30.4 – $32.0 \text{ Mg C ha}^{-1} \text{ year}^{-1}$) calculated by Malhi et al. (1999, 2012) for an Amazonian lowland forest is also considerably larger than the GPP value of our pre-montane and montane forests. One explanation for the comparatively low calculated gross primary production in the Ecuadorian mountain forests is that our NPP figure is an underestimate because it does not include all relevant components such as herbivory and root exudation. However, a probably equally important cause is the lower temperature in pre-montane and montane elevation (19 and 16 °C compared to 23 – 24 °C in the lowlands), which must result in a smaller GPP than in lowland forests due to lower autotrophic respiration rates. According to the data compilation of Luyssaert et al. (2007), tropical moist forests at low elevations have a mean autotrophic respiration rate of

Table 10.8 Summary table of C fluxes [$\text{Mg C ha}^{-1} \text{ year}^{-1}$] in the three intensive study plots # 1, 3 and 5

Plot no.	1	3	5
Elevation [m]	1,050	1,890	3,060
Aboveground (AG)			
(1) Leaf area index [$\text{m}^2 \text{ m}^{-2}$] (LAI)	5.1	3.9	2.9
(2) Sun leaf A_{max} [$\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$] (A_{max})	6.9	8.6	5.3
(3) Estimate of annual gross photosynthesis ^{a,b}	26.0	23.7	12.5
(4) Production of stem and branch wood (P_{W})	1.37	0.42	0.07
(5) Production of tree leaves (P_{L})	2.54	2.51	0.92
(6) Production of reproductive organs (P_{Rep})	0.45	0.18	0.03
(7) Production of twigs (P_{Tw})	0.55	0.43	0.19
(8) Production of epiphyte biomass (P_{E})	0.14	0.13	0.11
(9) Production of bamboo biomass (P_{Ba})	0	0.78	0.10
(10) Other fine litter components (P_{oth})	0.21	0.17	0.02
(11) Total fine litter production (P_{FL})	3.89	4.20	1.37
(12) Dark respiration of tree foliage (R_{D})	5.60	3.96	3.38
(13) Respiration of reproductive organs (R_{Rep})	n.d.	n.d.	n.d.
(14) Respiration of branches and twigs ^c (R_{B})	1.86	1.20	0.43
(15) Respiration of stems (R_{W})	1.86	1.20	0.43
(16) Tree AG NPP (4) + (5) + (6) + (7) (ANPP _T)	4.91	3.54	1.21
(17) Total AG NPP (16) + (8) + (9) + (10) (ANPP _{tot})	5.26	4.62	1.44
(18) Total AG C efflux ^d (12) + (13) + (14) + (15)	9.32	6.36	4.24
(19) Total AG C consumption (17) + (18)	14.58	10.98	5.68
(20) C transfer to roots (39) – (17) – (18)	>10.90	>6.90	>3.52
Belowground (BG)			
(21) Production of fine roots (P_{FR})	1.06	1.35	2.21 ^e
(22) Production of coarse and large roots (P_{CR})	0.08	0.11	0.42
(23) Respiration of fine roots ^f (R_{FR})	5.36	1.44	0.30
(24) Respiration of coarse and large roots (R_{CR})	0.46	0.22	0.42
(25) Tree BG NPP ^g (21) + (22) (BNPP _T)	1.14	1.46	2.63
(26) Root respiration (23) + (24) (R_{R})	5.82	1.66	0.72
Soil			
(27) Total soil respiration (R_{soil})	13.03	9.32	3.83
(28) Heterotrophic respiration (27) – (26) (R_{het})	7.21	7.66	3.11
(29) Fine root litter production ^h (L_{FR})	1.06	1.35	2.21
(30) Coarse root litter production (L_{CR})	n.d.	n.d.	n.d.
(31) AG tree litter prod. (5) + (6) + (7) (L_{T})	3.54	3.12	1.14
(32) Non-tree fine litter (8) + (9) + (10) (L_{NT})	0.35	1.08	0.13
(33) SOM change (29) + (30) + (31) + (32) – (28) (ΔSOM)	–2.26	–2.11	+0.37
(34) Total autotrophic respiration (18) + (26) (R_{aut})	15.14	8.02	4.96
(35) Ecosystem respiration (28) + (34) (R_{eco})	22.35	15.68	8.07
(36) Tree NPP (16) + (25) (NPP _T)	6.05	5.00	3.84
(37) NPP (17) + (25) (NPP)	6.40	6.08	4.07
(38) GPP (37) + (34) (GPP)	>21.54	>14.10	>9.03
(39) GPP $\sim 1.14 \times R_{\text{eco}}$ ⁱ (GPP _{est})	25.48	17.88	9.20
(40) NEP ^j (38) – (35) (NEP)	–0.81	–1.58	0.96

(continued)

Table 10.8 (continued)

Plot no.	1	3	5
Elevation [m]	1,050	1,890	3,060
(41) Percent NPP of GPP_{est} (37)/(39) ⁱ	25	34	44
(42) Percent P_w of NPP_T (4)/(36)	23	8	2
(43) Percent root transfer of GPP_{est} (20)/(39)	>43	>39	>38

n.d. not determined

^aOnly trees, does not include epiphytes, lianas and understorey

^bOutput of model 2 assuming photosynthesis at light saturation during sunshine hours and at mean rates of 0.3, 0.2 or 0.1 $\times A_{max}$ during overcast periods in the 1,050, 1,890 and 3,060 m stands

^cAssumed to be equal to stem respiration

^dAboveground autotrophic respiration (only trees)

^eExtrapolated from the trend line over the plots # 1–4 (see Table 10.4)

^fSoil respiration in trenched plots corrected for root decomposition

^gC transfer to mycorrhiza and root exudation not considered

^hAssumed to equal fine root production

ⁱAssuming a R_{eco}/GPP ratio of 0.88 for tropical moist forests (Luuyssaert et al. 2007)

^jMinimum values due to the underestimation of NPP and GPP; NEP figures based on GPP_{est} are larger and in all plots positive

c. 23.2 Mg C ha⁻¹ year⁻¹, which is about 50 % larger than our R_{aut} estimate for the stand at 1,050 m with a 4–5 °C lower MAT. The significant temperature effect on gross primary production (GPP) is also visible in the much lower GPP value of the uppermost stand at 3,060 m, which apparently assimilated CO₂ at less than half the rate (c. 9.2 Mg C ha⁻¹ year⁻¹) than did the stand at 1,050 m.

We estimated the gross photosynthesis of the tree canopies in its annual total using the A_{max} , R_D and LAI data of the stands. Extrapolating photosynthesis and leaf respiration to the stand level is sensitive to variation in LAI and thus to the method used for leaf area measurement (Cavaleri et al. 2006). We preferred the optical LAI figures (LAI-2000 system) for calculation, because the values derived for the 1,890 and 3,060 m stands appeared to be more realistic than the biomass-related LAI data that require an estimate of mean leaf longevity. The LAI estimate of 5.1 for the 1,050-m stand agrees well with leaf area indices of 5–6 reported from tropical lowland forests (Malhi et al. 1999; Grace and Meir 2009), given that we found a LAI decrease by roughly 1 unit per km elevation increase along the transect (see also Moser et al. 2007 and Unger et al. 2013).

While the absolute amount of CO₂ assimilated by the tree canopies must remain relatively uncertain (estimated at 12.5–26.0 Mg C ha⁻¹ year⁻¹ in the three stands, Table 10.8: line 3), it is safe to conclude that gross photosynthesis is substantially reduced from 2,000 to 3,000 m elevation in this transect due to large decreases in LAI and photosynthetic capacity (Table 10.3).

We attempted to analyse the carbon balance of the three forests with a bottom-up approach, because it was not possible to conduct stand-level measurements of total CO₂ influx and efflux using eddy covariance or microclimatological gradient techniques in the mountainous terrain. This has the consequence that the upscaled growth and respiration figures cannot be checked against independent stand-level

data and certain fluxes calculated in this study must therefore be treated as rough estimates. For example, the GPP calculation is likely biased by errors in the upscaling process from organ-level respiration measurements to the stand level (Zach et al. 2010). Further, no empirical data exist for the respiration of branches and twigs, which may have higher CO₂ efflux rates than stems of the same diameter (Cavaleri et al. 2006; Robertson et al. 2010). Similarly, our “bottom-up” approach of calculating NPP faces a number of shortcomings; a major uncertainty is the fine root production figure especially of the uppermost plot (# 5), which may be an overestimate given the low root respiration rates measured in this stand (compare Moser et al. 2010). The direct observation of fine root growth and death by the minirhizotron technique in the 3,060 m stand may have included periods in which a steady state of root production and mortality had not yet been reached, thus resulting in the overestimation of root production. Furthermore, extrapolating root growth from the topsoil to lower horizons might introduce an additional error. However, most other studies on root production in tropical forests used even less reliable approaches such as the ingrowth core method or indirect estimates of fine root production (Raich et al. 2006), which similarly questions the accuracy of NPP and GPP figures that have been used for calculating biome means (e.g. the database in Luysaert et al. 2007). Similar to most other related investigations, we ignored a number of C consuming processes that are notoriously difficult to measure such as root exudation, C transfer to mycorrhizal hyphae, herbivory and the release of volatile organic compounds, which would increase our NPP figures.

A strength of our study is that the NPP, respiration and photosynthesis figures base on intensive measuring campaigns covering a large number of tree individuals and species, thus generating a more comprehensive data base than is typically available in carbon cycle studies in tropical forests. Moreover, the focus of this study was primarily on altitudinal trends in carbon cycle components and a relative comparison of the C balance of the stands. The data from the 54 additional matrix plots at 1,000, 2,000 and 3,000 m elevation are useful for validating altitudinal trends for a number of key carbon pool and flux parameters including aboveground biomass and wood production.

The data from the 54 matrix plots at variable slope positions show that the results from the three intensive study plots # 1, 3 and 5 give correct altitudinal trends for biomass and productivity along the transect (Table 10.6). However, the three plots are partly deviating from the landscape means of biomass and productivity as they appear from the matrix plots at 1,000, 2,000 and 3,000 m elevation. The stand # 1 possessed a higher than average wood biomass due to a relatively low number of stems, which had particularly large diameters. In contrast, the stands # 3 and 5 at 2,000 and 3,000 m had smaller than average wood biomasses and lower wood and leaf production figures, which is a consequence of a relatively low basal area in plot # 3 and a high density of small-diameter stems in plot # 5.

From the difference between GPP and the C consumption by aboveground tree organs (growth and respiration), we estimated a C transfer to the roots of c. 10.9–3.5 Mg C ha⁻¹ year⁻¹ for the stands # 1–5, which equals 43–38 % of GPP (lines 20 and 43 in Table 10.8). The order of magnitude agrees well with data

of Raich et al. (2006) on the estimated belowground C allocation in tropical evergreen forests growing at mean annual temperatures of $\sim 10\text{--}20\text{ }^{\circ}\text{C}$ (c. $1.8\text{--}10.0\text{ Mg C ha}^{-1}\text{ year}^{-1}$). Given that the estimated belowground transfers in Ecuador are minimum fluxes, the figures also are in accordance with the value (45 %) given by Malhi et al. (1999) for a tropical lowland forest. The estimated belowground C transfers in our three stands exceed the sum of measured root production and root respiration by 0.17 to $>3.5\text{ Mg C ha}^{-1}\text{ year}^{-1}$. Possible causes for this discrepancy are errors in the calculation of autotrophic respiration at the stand level and the existence of quantitatively important carbohydrate fluxes from the roots to the rhizosphere, which are not included in our calculation.

10.3.3 *Altitudinal Trends*

We found several changes in C cycle components with increasing elevation that may be direct effects of the temperature decrease or are caused by other factors that also change with altitude. GPP, NPP and NEP showed large and continuous decreases from $1,050\text{ m}$ ($19\text{ }^{\circ}\text{C}$) to $3,060\text{ m}$ ($9\text{ }^{\circ}\text{C}$); we calculated a GPP decrease by about $1.25\text{ Mg C ha}^{-1}\text{ year}^{-1}$ and an NPP decrease by about $0.23\text{ Mg C ha}^{-1}\text{ year}^{-1}$ per K temperature decrease. The NPP reduction was particularly large between $2,000$ and $3,000\text{ m}$, i.e., with a decrease in mean temperature from $16\text{ }^{\circ}\text{C}$ to $9\text{ }^{\circ}\text{C}$. In an altitudinal gradient in Peru, Girardin et al. (2010) found a relatively small NPP reduction between $1,000$ and $3,000\text{ m}$, but a drop to the half from 210 to $1,000\text{ m}$ elevation.

The results from tropical altitudinal transects indicate in general a positive relation between temperature and the NPP of tropical moist forests, thereby contradicting Luyssaert et al. (2007) who concluded that forest NPP does not increase at temperatures above $10\text{ }^{\circ}\text{C}$. However, their data from tropical forests showed a considerable scatter and included a few tropical seasonal forests with less than $1,500\text{ mm}$ rain per year. There is the possibility that a temperature effect on tropical forest NPP (above- and belowground) is only detectable in samples restricted to stands with defined moisture status as is the case in the moist mountain forests of this study. Moser et al. (2011) and Wittich et al. (2012) suggested that the main reason for the NPP decrease is N shortage at high elevations, which limits stand leaf area and A_{max} while reduced temperature should affect productivity mainly indirectly through a negative effect on N supply.

Marked decreases with elevation were also detected for autotrophic and heterotrophic respiration and all organ-specific respiration fluxes. While stem and root respiration on a tissue surface area basis decreased with elevation (see also Robertson et al. 2010), this was not the case with leaf dark respiration per leaf area, which remained invariant between $1,000$ and $3,000\text{ m}$; this is primarily a consequence of the large SLA decrease along the transect (Leuschner et al. unpubl.). The efflux of CO_2 from the soil (total soil respiration as the sum of root respiration and soil heterotrophic respiration) decreased to less than a third from

1,050 to 3,060 m in the intensive study plots and to the half in the 54 matrix plots. The upslope reduction in fine root respiration appeared to be even larger than the reduction in total soil respiration. Given the more than fourfold increase in standing fine root biomass between pre-montane and upper montane elevation, the decrease in fine root respiration implies that fine root relative growth rate and nutrient and water uptake must be much lower in the 3,060 m stand than under the higher temperatures at 1,050 m. It appears that the trees in the high-elevation elfin forest are maintaining a very large fine root system for compensating a low resource uptake and growth activity of their roots.

Leuschner et al. (2007), Hertel and Leuschner (2010) and Moser et al. (2011) reported a large shift in C allocation patterns from stem growth to root (mostly fine root) production in this transect between 1,050 and 3,060 m. Indeed, the proportion of stem growth in NPP dropped to a tenth of its value between 1,050 and 3,060 m, while the proportion of C invested in root production increased from 19 to 68 %. In the Peruvian elevation transect, the ratio of above- to belowground NPP stayed more or less constant between 210 and 3,000 m elevation (Girardin et al. 2010), which may point at different soil fertilities in the two Andean transects. A closer look with additional consideration of data on root respiration and relative belowground C transfer (lines 23, 24 and 20 of Table 10.8) shows no altitudinal trend in relative aboveground/belowground C allocation patterns in the Ecuadorian transect. Rather, a marked shift from root respiration to root biomass production occurred, i.e., from root metabolic activity to the production of root structures.

A large altitudinal decrease was also detected for the total amount of aboveground litter production, which reached at 3,060 m only a third of its low-elevation value (see Chap. 23) and was accompanied by a doubling of the amount of organic carbon stored in the organic layer and the mineral topsoil (0–30 cm). These opposing trends indicate a dramatic decrease in decomposition rate between 1,050 and 3,060 m elevation and consequently a rising mean carbon residence time in the soil with increasing altitude.

Our calculation of soil heterotrophic respiration shows that the C cycle in the soil appears not to be balanced; rather, it indicates a deficit of c. 2 Mg C ha⁻¹ year⁻¹ in the input/output balance of soil organic matter (SOM) for the 1,050 m and 1,890 m stands. If this statement is valid, substantial C losses from the belowground compartment are occurring in the pre-montane and lower montane stands and NEP should take a negative value as is indicated by our NEP estimates derived from the difference between GPP and R_{eco} . Whether this apparent imbalance is indeed caused by SOM losses over longer time spans and the stands at 1,050 and 1,890 m are in fact functioning as CO₂ sources in recent time, or whether the deficit is the result of erroneous estimates of heterotrophic respiration (possible overestimation) or of fine and coarse root mortality (possible underestimation), can only be answered by repeated sampling of the SOM pools over one or two decades.

We conclude that temperature is influencing mountain forest GPP and NPP both directly and indirectly. The most influential temperature effects are probably the altitudinal decline in stem and root respiration rates (but less in leaf respiration), which may be linked to reduced growth rates, and the reduction in heterotrophic

respiration in the soil, slowing down decomposition and mineralisation rates. Impaired N supply in the cold high-elevation forests seems to reduce annual carbon gain mainly through a restriction of leaf area expansion, which limits carbon gain.

10.4 Conclusions

Several results of this study are unexpected. First, the ecosystem C pool of the mountain forests was equally large, or even larger, than that of neotropical lowland forests, mainly due to the large C store in the soil. This finding highlights the outstanding role, tropical Andean mountain forests are playing with respect to C storage, an ecosystem service with increasing importance in the light of rising atmospheric carbon dioxide concentrations and temperatures (see Chap. 24). Second, total (above- and belowground) NPP decreased by about $0.23 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ per $^{\circ}\text{C}$ temperature decrease, which contradicts earlier assumptions that forest NPP is insensitive to temperature in tropical and subtropical regions. Marked decreases with elevation were also detected for the stand-level estimates of annual gross photosynthesis and autotrophic and heterotrophic respiration. While fine root production seems to increase with elevation, root respiration decreased, which indicates a marked shift from C investment in root metabolic activity to the production of root structures towards high elevations; we found no altitudinal trend in the relative aboveground/belowground C allocation patterns of the trees. We conclude that altitudinal gradient studies may represent a valuable tool for studying temperature effects on the functioning of tropical forests.

References

- Batjes NH (2008) Mapping soil carbon stocks of Central Africa using SOTER. *Geoderma* 146:58–65
- Batjes NH, Dijkshoorn JA (1999) Carbon and nitrogen stocks in the soil of the Amazon region. *Geoderma* 89:273–286
- Bendix J, Rollenbeck R, Fabian P, Emck P (2008) Climate. In: Beck E, Bendix J, Kottke I, Makeschin F, Mosandl R (eds) Gradients in a tropical mountain ecosystem of Ecuador. Springer Verlag, Berlin, pp 63–74
- Benner J, Vitousek PM, Ostertag R (2010) Nutrient cycling and nutrient limitation in tropical montane cloud forests. In: Bruijnzeel LA, Scatena FN, Hamilton LS (eds) Tropical montane cloud forests: science for conservation and management. Cambridge University Press, Cambridge, pp 90–100
- Bruijnzeel LA, Kappelle M, Mulligan M, Scatena FN (2010) Tropical montane cloud forests: state of knowledge and sustainability perspectives in a changing world. In: Bruijnzeel LA, Scatena FN, Hamilton LS (eds) Tropical montane cloud forests: science for conservation and management. Cambridge University Press, Cambridge, pp 691–740
- Cavaleri MA, Oberbauer SF, Ryan MG (2006) Wood CO₂ efflux in a primary tropical rain forest. *Glob Change Biol* 12:2442–2458

- Chave J, Andalo C, Brown S, Cairns MA, Chambers JQ, Eamus D, Folster H, Fromard F, Higuchi N, Kira T, Lescure JP, Nelson BW, Ogawa H, Puig H, Riera B, Yamakura T (2005) Tree allometry and improved estimation of carbon stocks and balance in tropical forests. *Oecologia* 145:87–99
- Chen G-S, Yang Y-S, Xie J-S, Guo J-F, Gao R, Qian W (2005) Conversion of a natural broad leaved evergreen forest into pure plantation forests in a subtropical area: effects on carbon storage. *Ann For Sci* 62:659–668
- Clark DA, Brown S, Kicklighter DW, Chambers JQ, Thomlinson JR, Ni J (2001) Measuring net primary production in forests: concepts and field methods. *Ecol Appl* 11:356–370
- Cleveland CC, Townsend AR, Taylor P, Alvarez-Clare S, Bustamante MMC, Chuyong G, Dobrowski SZ, Grierson P, Harms KE, Houlton BZ, Marklein A, Parton W, Porder S, Reed SC, Sierra CA, Silver WL, Tanner EVJ, Wieder WR (2011) Relationships among net primary productivity, nutrients and climate in tropical rain forest: a pan-tropical analysis. *Ecol Lett* 14:939–947
- Davidson EA, de Araujo AC, Artaxo P, Balch JK, Brown IFC, Bustamante MM, Coe MT, DeFries RS, Keller M, Longo M, Munger JW, Schroeder W, Soares-Filho BS, Souza CM, Wofsy SC (2012) The Amazon basin in transition. *Nature* 481:321–328
- De Moraes JF, Cerri CC, Melillo JM, Kicklighter D, Neill C, Skole DL, Steudler PA (1995) Soil carbon stocks of the Brazilian Amazon Basin. *Soil Sci Soc Am J* 59:244–247
- Emck P (2007) A climatology of South Ecuador with special focus on the major Andean ridge as Atlantic-Pacific climate divide. PhD Thesis, University Erlangen, Germany
- Evans JR, Terashima I, Hanba Y, Loreto F (2004) Chloroplast to leaf. In: Smith WK, Vogelmann TC, Critchley C (eds) *Photosynthetic adaptation. Chloroplast to landscape. Ecological studies* 178. Springer, New York, pp 107–132
- Gentry AH (2001) Patrones de diversidad y composicion floristica en los bosques de las montanas neotropicales. In: Kappelle M, Brown AD (eds) *Bosques nublados del neotropico*. Editorial INBio, Santo Domingo de Heredia, Costa Rica, pp 85–123
- Gibbon A, Silman M, Malhi Y, Fisher J, Meir P, Zimmermann M, Dargie G, Farfan W, Garcia K (2010) Ecosystem carbon storage across the grassland–forest transition in the high Andes of Manu National Park, Peru. *Ecosystems* 13:1097–1111
- Girardin CAJ, Malhi Y, Aragao LEOC, Mamani M, Huasco WH, Durand L, Feeley KJ, Rapp J, Silva-Espejo JE, Silman M, Salinas N, Whittaker RJ (2010) Net primary productivity allocation and cycling of carbon along a tropical forest elevational transect in the Peruvian Andes. *Glob Change Biol* 16:3176–3192
- Grace J, Meir P (2009) Tropical rain forests as old-growth forests. In: Wirth C, Gleixner G, Heimann M (eds) *Old-growth forests. Function, fate and value. Ecological studies*, vol 207. Springer, Berlin, pp 391–408
- Grace J, Lloyd J, McIntyre J, Miranda A, Meir P, Miranda H, Moncrieff J, Massheder J, Wright I, Gash J (1995) Fluxes of carbon dioxide and water vapour over an undisturbed tropical forest in south-west Amazonia. *Glob Change Biol* 1:1–12
- Graefe S, Hertel D, Leuschner C (2008a) Estimating fine root turnover in tropical forests along an elevational transect using minirhizotrons. *Biotropica* 40:536–542
- Graefe S, Hertel D, Leuschner C (2008b) Fine root dynamics along a 2000-m elevation transect in South Ecuadorian mountain forests. *Plant Soil* 313:155–166
- Hertel D, Leuschner C (2002) A comparison of four different fine root production estimates with ecosystem carbon balance data in a *Fagus-Quercus* mixed forest. *Plant Soil* 239:237–251
- Hertel D, Leuschner C (2010) Fine root mass and fine root production in tropical moist forests as dependent on soil, climate, and elevation. In: Bruijnzeel LA, Scatena FN, Hamilton LS (eds) *Tropical montane cloud forests: science for conservation and management*. Cambridge University Press, Cambridge, pp 428–443
- Homeier J, Werner FA, Gradstein SR, Breckle S-W, Richter M (2008) Potential vegetation and floristic composition of Andean forests in South Ecuador, with a focus on the RBSF. In: Beck E, Bendix J, Kottke I, Makeschin F, Mosandl R (eds) *Gradients in a tropical mountain ecosystem of Ecuador. Ecological studies*, vol 198. Springer, Berlin, pp 87–100

- 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>
- 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. *J Ecol* 90:37–51
- Leuschner C, Moser G, Bertsch C, Röderstein M, Hertel D (2007) Large altitudinal increase in tree root/shoot ratio in tropical mountain forests of Ecuador. *Basic Appl Ecol* 8:219–230
- 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
- Lü X-T, Tang J-W, Feng Z-L, Li M-H (2009) Diversity and aboveground biomass of lianas in the tropical seasonal rain forests of Xishuangbanna, SW China. *Rev Biol Trop* 57(1–2):211–222
- Luyssaert S, Inglima I, Jung M, Richardson AD, Reichstein M, Papale D, Piao SL, Schulze ED, Wingate L, Matteucci G, Aragao L, Aubinet M, Beers C, Bernhoffer C, Black KG, Bonal D, Bonnefond JM, Chambers J, Ciais P, Cook B, Davis KJ, Dolman AJ, Gielen B, Goulden M, Grace J, Granier A, Grelle A, Griffis T, Grunwald T, Guidolotti G, Hanson PJ, Harding R, Hollinger DY, Hutrya LR, Kolar P, Kruijt B, Kutsch W, Lagergren F, Laurila T, Law BE, Le Maire G, Lindroth A, Loustau D, Malhi Y, Mateus J, Migliavacca M, Misson L, Montagnani L, Moncrieff J, Moors E, Munger JW, Nikinmaa E, Ollinger SV, Pita G, Rebmann C, Rouspard O, Saigusa N, Sanz MJ, Seufert G, Sierra C, Smith ML, Tang J, Valentini R, Vesala T, Janssens IA (2007) CO₂ balance of boreal, temperate, and tropical forests derived from a global database. *Glob Change Biol* 13:2509–2537
- Malhi Y (2010) The carbon balance of tropical forest regions, 1990–2005. *Curr Opin Environ Sustain* 2:237–244
- Malhi Y (2012) The productivity, metabolism and carbon cycle of tropical forest vegetation. *J Ecol* 100:65–75
- Malhi Y, Baldocchi DD, Jarvis PG (1999) The carbon balance of tropical, temperate and boreal forests. *Plant Cell Environ* 22:715–740
- Malhi Y, Baker TR, Phillips OL, Almeida S, Alvarez E, Arroyo L, Chave J, Czimczik CI, Di Fiore A, Higuchi N, Killeen TJ, Laurance SG, Laurance WF, Lewis SL, Montoya LMM, Monteagudo A, Neill DA, Nunez VP, Patino S, Pitman NCA, Quesada CA, Salomao R, Silva JNM, Torres LA, Vasquez MR, Terborgh J, Vinceti B, Lloyd J (2004) The above-ground coarse wood productivity of 104 Neotropical forest plots. *Glob Change Biol* 10:563–591
- Malhi Y, Wood D, Baker TR, Wright J, Phillips OL, Cochrane T, Meir P, Chave J, Almeida S, Arroyo L, Higuchi N, Killeen TJ, Laurance SG, Laurance WF, Lewis SL, Monteagudo A, Neill DA, Vargas PN, Pitman NCA, Quesada CA, Salomao R, Silva JNM, Lezama AT, Terborgh J, Martinez RV, Vinceti B (2006) The regional variation of aboveground live biomass in old-growth Amazonian forests. *Glob Change Biol* 12:1107–1138
- Malhi Y, Silman M, Salinas N, Bush M, Meir P, Saatchi S (2010) Introduction: elevation gradients in the tropics: laboratories for ecosystem ecology and global change research. *Glob Change Biol* 16:3171–3175
- McJannet DL, Wallace JS, Reddell P (2010) Comparative water budgets of a lower and an upper montane cloud forest in the Wet Tropics of northern Australia. In: Bruijnzeel LA, Scatena FN, Hamilton LS (eds) *Tropical montane cloud forests: science for conservation and management*. Cambridge University Press, Cambridge, pp 479–490
- Mercado L, Lloyd J, Carswell F, Malhi Y, Meir P, Nobre AD (2006) Modelling Amazonian forest eddy covariance data: a comparison of big leaf versus sun/shade models for the C-14 tower at Manaus. I. Canopy photosynthesis. *Acta Amazon* 36:69–82
- Mokany K, Raison RJ, Prokushkin AS (2006) Critical analysis of root:shoot ratios in terrestrial biomes. *Glob Change Biol* 12:84–96

- Moser G, Hertel D, Leuschner C (2007) Altitudinal change of leaf area and leaf mass in tropical mountain forests – a transect study in Ecuador and a pan-tropical meta-analysis. *Ecosystems* 10:24–935
- Moser G, Röderstein M, Soethe N, Hertel D, Leuschner C (2008) Altitudinal changes in stand structure and biomass allocation of tropical mountain forests in relation to microclimate and soil chemistry. In: Beck E, Bendix J, Kottke I, Makeschin F, Mosandl R (eds) *Gradients in a tropical mountain ecosystem of Ecuador*. Ecological studies, vol 198. Springer, Berlin, pp 229–242
- Moser G, Leuschner C, Röderstein M, Graefe S, Soethe N, Hertel D (2010) Biomass and productivity of fine and coarse roots in five tropical mountain forests stands along an altitudinal transect in southern Ecuador. *Plant Ecol Divers* 3:151–164
- Moser G, Leuschner C, Hertel D, Graefe S, Soethe N, Iost S (2011) Elevation effects on the carbon budget of tropical mountain forests (S Ecuador): the role of the belowground compartment. *Glob Change Biol* 17:2211–2226
- Raich JW, Russell AE, Kitayama K, Parton WJ, Vitousek PM (2006) Temperature influences carbon accumulation in moist tropical forests. *Ecology* 87:76–87
- Robertson AL, Malhi Y, Farfan-Amezquita F, Aragao LEOC, Espejo JES, Robertson MA (2010) Stem respiration in tropical forests along an elevation gradient in the Amazon and Andes. *Glob Change Biol* 16:3193–3204
- Ryan MG, Gower ST, Hubbard RM, Waring RH, Gholz HL, Cropper WP, Running SW (1995) Woody tissue maintenance respiration of four conifers in contrasting climates. *Oecologia* 101:133–140
- Schnitzer SA, DeWalt SJ, Chave J (2006) Censusing and measuring lianas: a quantitative comparison of the common methods. *Biotropica* 38(5):581–591
- Sierra CA, del Valle JI, Orrego SA, Moreno FH, Harmon ME, Zapata M, Colorado GJ, Herrera MA, Lara W, Restrepo DE, Berrouet LM, Loaiza LM, Benjumea JF (2007) Total carbon stocks in a tropical forest landscape of the Porcè region, Colombia. *For Ecol Manage* 243:299–306
- Slik JWF, Aiba S-I, Brearley FQ, Cannon CH, Forshed O, Kitayama K, Nagamasu H, Nilus R, Payne J, Paoli G, Poulsen AD, Raes N, Sheil D, Sidiyasa K, Suzuki E, van Valkenburg JLCH (2010) Environmental correlates of tree biomass, basal area, wood specific gravity and stem density gradients in Borneo's tropical forests. *Glob Ecol Biogeogr* 19:50–60
- Soethe N, Lehmann J, Engels C (2007) Carbon and nutrient stocks in roots of forests at different altitudes in the Ecuadorian Andes. *J Trop Ecol* 23:319–328
- Strauss-DeBenedetti S, Bazzaz F (1996) Photosynthetic characteristics of tropical trees along successional gradients. In: Mulkey SS, Chazdon RL, Smith AP (eds) *Tropical forest plant ecophysiology*. Chapman & Hall, New York, pp 162–186
- Townsend AR, Cleveland CC, Cory C et al (2011) Multi-element regulation of the tropical forest carbon cycle. *Front Ecol Environ* 9:9–17
- Unger M, Homeier J, Leuschner C (2013) Relationships among leaf area index, below-canopy light availability and tree diversity along a transect from tropical lowland to montane forests in NE Ecuador. *Trop Ecol* 54(1):33–45
- Veneklaas EJ, Poorter L (1998) Growth and carbon partitioning of tropical tree seedlings in contrasting light environments. In: Lambers H, Poorter H, van Vuuren MMI (eds) *Inherent variation in plant growth. Physiological mechanisms and ecological consequences*. Backhuys, Leiden, pp 337–361
- Vieira SA, Alves LF, Duarte-Neto PJ, Martins SC, Veiga LG, Scaranello MA, Picollo M, Camargo PB, do Carmo JB, Sousa Neto E, Santos FAM, Joly CA, Martinelli LA (2011) Stocks of carbon and nitrogen and partitioning between above- and belowground pools in the Brazilian coastal Atlantic Forest elevation range. *Ecol Evol* 1:421–434
- Werner FA, Homeier J, Oesker M, Boy J (2012) Epiphytic biomass of a tropical Andean forest varies with topography. *J Trop Ecol* 28:23–31

- Wilcke W, Hess T, Bengel C, Homeier J, Valarezo C, Zech W (2005) Coarse woody debris in a montane forest in Ecuador: mass, C and nutrient stock, and turnover. *For Ecol Manage* 205:139–147
- Wittich B, Horna V, Homeier J, Leuschner C (2012) Altitudinal change in the photosynthetic capacity of tropical trees: a case study from Ecuador and a pantropical literature analysis. *Ecosystems* 15:958–973
- Wolf K, Veldkamp E, Homeier J, Martinson GO (2011) Nitrogen availability links forest productivity, soil nitrous oxide and nitric oxide fluxes of a tropical montane forest in southern Ecuador. *Global Biogeochem Cycles* 25, GB4009
- Yonekura Y, Ohta S, Kiyono Y, Ahsa D, Morisada K, Tanaka N, Kanzaki M (2010) Changes in soil carbon stocks after deforestation and subsequent establishment of “Imperata” grassland in the Asian humid tropics. *Plant Soil* 329:495–507
- Zach A (2008) Carbon release from woody parts of trees along an elevation gradient in a tropical montane moist forest of southern Ecuador. PhD Thesis, University of Göttingen, Germany. 135 pp. Available at <http://webdoc.sub.gwdg.de/diss/2008/zach/>
- Zach A, Horna V, Leuschner C (2008) Elevational change in woody tissue CO₂ efflux in a tropical mountain rain forest in southern Ecuador. *Tree Physiol* 28:67–74
- Zach A, Horna V, Leuschner C (2010) Patterns of wood carbon dioxide efflux across a 2000-m elevation transect in an Andean moist forest. *Oecologia* 162:127–137
- Zimmermann M, Meir P, Silman MR, Fedders A, Gibbon A, Malhi Y, Urrego DH, Bush MB, Feeley KJ, Garcia KC, Dargie GC, Farfan WR, Goetz BP, Johnson WT, Kline KM, Modi AT, Rurau NMQ, Staudt BT, Zamora F (2010) No differences in soil carbon stocks across the tree line in the Peruvian Andes. *Ecosystems* 13:62–74