

# Net primary productivity allocation and cycling of carbon along a tropical forest elevational transect in the Peruvian Andes

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## Abstract

The net primary productivity, carbon (C) stocks and turnover rates (i.e. C dynamics) of tropical forests are an important aspect of the global C cycle. These variables have been investigated in lowland tropical forests, but they have rarely been studied in tropical montane forests (TMFs). This study examines spatial patterns of above- and belowground C dynamics along a transect ranging from lowland Amazonia to the high Andes in SE Peru. Fine root biomass values increased from 1.50 Mg C ha<sup>-1</sup> at 194 m to 4.95 ± 0.62 Mg C ha<sup>-1</sup> at 3020 m, reaching a maximum of 6.83 ± 1.13 Mg C ha<sup>-1</sup> at the 2020 m elevation site. Aboveground biomass values decreased from 123.50 Mg C ha<sup>-1</sup> at 194 m to 47.03 Mg C ha<sup>-1</sup> at 3020 m. Mean annual belowground productivity was highest in the most fertile lowland plots (7.40 ± 1.00 Mg C ha<sup>-1</sup> yr<sup>-1</sup>) and ranged between 3.43 ± 0.73 and 1.48 ± 0.40 Mg C ha<sup>-1</sup> yr<sup>-1</sup> in the premontane and montane plots. Mean annual aboveground productivity was estimated to vary between 9.50 ± 1.08 Mg C ha<sup>-1</sup> yr<sup>-1</sup> (210 m) and 2.59 ± 0.40 Mg C ha<sup>-1</sup> yr<sup>-1</sup> (2020 m), with consistently lower values observed in the cloud immersion zone of the montane forest. Fine root C residence time increased from 0.31 years in lowland Amazonia to 3.78 ± 0.81 years at 3020 m and stem C residence time remained constant along the elevational transect, with a mean of 54 ± 4 years. The ratio of fine root biomass to stem biomass increased significantly with increasing elevation, whereas the allocation of net primary productivity above- and belowground remained approximately constant at all elevations. Although net primary productivity declined in the TMF, the partitioning of productivity between the ecosystem subcomponents remained the same in lowland, premontane and montane forests.

**Keywords:** Amazon basin, Andes, carbon, carbon stocks, ecophysiology, elevational gradient, net primary productivity, residence time, soil water content, temperature, tropical montane forests

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## Introduction

The important role of the Amazonian lowland forest in global biogeochemical cycles, and in particular the global carbon (C) cycle, is widely recognized (Intergovernmental Panel on Climate Change, 2007). However, the C cycle of tropical montane forests (TMFs) is only starting to be explored. In the Amazon basin, the montane forests of the Andes extend from the lowlands up to 3000–4000 m a.s.l. In addition to their intrinsic interest, studies of the ecosystem functioning of montane forests provide an opportunity to explore how environmental variables (particularly temperature and soil moisture) affect ecosystem functions, whilst keep-

ing seasonal factors constant. In particular, there is no dormant winter or drought season that complicates interpretation of latitudinal gradients. In this paper, we explore the production, allocation and turnover of C along an elevation gradient in the Peruvian Amazon and Andes.

A number of studies have reported on variation of aboveground biomass with elevation in TMFs in Borneo, Ecuador, Puerto Rico, Venezuela, New Guinea, Panama and Hawaii (Kitayama & Mueller Dombois, 1994; Delaney *et al.*, 1997; Leuschner *et al.*, 2007). These consistently report a decline in aboveground biomass with increasing elevation as a key characteristic of TMFs. There have been far fewer studies of belowground biomass. Observations of fine root C stocks in Southern Ecuador and in Borneo show an increase in fine root C stocks with increasing elevation (Kitayama

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& Aiba, 2002; Leuschner *et al.*, 2007). Based on these previous findings, we would expect to observe a shift in the partitioning of C standing stocks from above- to belowground as elevation increases.

Net primary productivity (NPP) is defined as the amount of C incorporated into new organic matter produced by a plant of ecosystem in a specified time interval. The components of NPP include the production of stems, branches, leaves, flowers, fruit, coarse and fine roots, volatile organic compounds and root exudates. Although there is a long record of tropical forest aboveground net primary productivity (NPP<sub>AG</sub>) measurement studies in the ecological literature, only a handful of studies focus on TMFs (reviewed in Clark *et al.*, 2001a, b). Studies in the Jamaican Blue Mountain, the Luquillo Mountains in Puerto Rico, Mount Kinabalu in Borneo and the Ecuadorian Andes consistently reported a decline in NPP<sub>AG</sub> with increasing elevation. Whereas its cause is still poorly understood, this is reported as one of the most fundamental features of TMFs. The quantification of below ground net primary productivity (NPP<sub>BG</sub>) is still in its early years and our understanding of total ecosystem-level productivity is very limited. To date, only one study in South Ecuadorian montane forests published NPP<sub>BG</sub> estimates along an elevational transect (Roderstein *et al.*, 2005) but did not report parallel measurements of NPP<sub>AG</sub> (see, however, new results reported by G. Moser, C. Leuschner, D. Hertel, S. Graefe & S. Iost, unpublished results, this issue). The study found that fine root production, NPP<sub>FineRoot</sub> increases with increasing elevation.

The mean residence time of C in biomass can be estimated by dividing each C pool's standing stocks by the NPP of that pool. Only a few studies have estimated stem C turnover rates or residence times in tropical forests (Malhi *et al.*, 1999, 2006); none of these were carried out on TMFs. Similarly, very few studies have been conducted on C turnover rates of fine roots in tropical forests (Cuevas & Medina, 1988; Herbert & Fownes, 1999; Ostertag, 2001), with only one study of an elevational transect (Graefe *et al.*, 2008).

Raich *et al.* (1997) measured aboveground productivity and soil respiration in three Hawaiian rainforests, but to date there have been no complete analyses of NPP and its allocation along a tropical elevation transect. Here, we present the first reported analysis of total directly measured NPP and its allocation along a large vertical gradient in the tropics. We also describe changes in total biomass and its distribution between above- and belowground components in nine tropical forests sites along an elevational transect in the Peruvian Andes. In addition, we provide an examination of overall changes in ecosystem C dynamics across the elevational transect. To this end, we analyse standing stocks, production rates

and residence time of aboveground (stems, canopy) and belowground (roots) vegetation components. Specifically, we test the following hypotheses:

- (1) There is no change in total C stocks with elevation, but there is a shift in relative stock of C from above- to belowground (Leuschner *et al.*, 2007).
- (2) Total NPP declines with elevation, but the proportion of NPP allocated to above- and belowground components stays fixed along the elevation gradient.
- (3) The NPP allocation patterns on the elevation transect are the same as those observed for lowland Amazonian forests (Aragão *et al.*, 2009; Malhi *et al.*, 2009).
- (4) NPP decline can largely be explained by decreasing temperature as elevation increases.

## Materials and methods

### Site characteristics

The study region is the focus of the interdisciplinary Andes Biodiversity and Ecosystem Research Group (ABERG, <http://darwin.winston.wfu.edu/andes/>). Nine permanent tree sampling plots of 1 ha each were established along an elevational gradient ranging from 194 to 3025 m elevation, extending from lowland forest (<800 m), through premontane (800–1200 m), lower montane (1200–2200 m) and upper montane forest (2200–3400 m). Of these, six experimental sites were established at elevations from 3020 to 1500 m on the eastern slope of the Andes, in the Kosñipata valley, Province of Paucartambo, Department of Cusco, Southern Peruvian Andes. One site was established at 1000 m in an adjacent valley (Tono valley). A further two lowland Amazonian sites were established and monitored according to the same protocol in the Tambopata reserve, Tambopata Province, Department of Madre de Dios, Peru, approximately 244 km east of the main transect. Data from these two lowland sites were published in Araújo *et al.* (2009). Site descriptions are provided in Table 1. The transect ranging from the high Andes to lowland Amazonian sites (nine plots in total) is hereafter referred to as the Kosñipata transect. Plots established from 1855 to 3020 m are located on a ridge adjacent to an ancient Inca path referred to as the Trocha Union. As the path is fairly inaccessible and carved on difficult terrain, it is rarely used. As the geological substrate and topographic position can have a significant bearing on montane forest dynamics (Takyu *et al.*, 2002), all the montane plots along the Trocha Union were established along a ridge-top with the same substrate (Palaeozoic shaleslates), with the exception of the 1855 m plot (situated on a granite batholith). Plots at 1000 m and below are situated on clay-rich sediments formed from alluvial deposition (though all are now above river flood levels). All plots along the elevational transect were selected in areas with relatively homogeneous stand structure, geological substrate and topography and with no sign of significant recent human influence. All have closed canopies without any large gaps. Soil C, nitrogen and phosphorus stocks in the top 50 cm are highest

Table 1 Summary of site characteristics

Site Name	Wayqecha	Trocha Union III	Trocha Union IV	Trocha Union VII	Trocha Union VIII	San Pedro	Tono	Tambopata III	Tambopata IV
Site Code	WAY	TU3	TU4	TU7	TU8	SPD	TON	TAM 3	TAM4
Latitude	13°11'24"	13°6'34"	13°6'30"	13°4'24"	13°4'16"	13°2'56"	12°57'33"	12°50'11"	12°49'48"
Longitude	71°35'13"	71°35'59"	71°35'21"	71°33'30"	71°33'18"	71°32'13"	71°33'57"	69°16'45"	69°16'16"
Elevation (m)	3025	3020	2720	2020	1855	1500	1000	210	194
Aspect	E	W	W	W	W	W	W	-	-
Mean annual air temperature (°C)	12.5 ± 0.05	11.8 ± 0.01	13.5 ± 0.01	17.4 ± 0.02	18.0 ± 0.01	18.8 ± 0.02	20.7 ± 0.02	26.4	26.4
Annual precipitation (mm yr <sup>-1</sup> )	1706	1776	2318	1827	2472	2631	3087	2730	2730
Soil organic layer depth (cm)	20.2	42.2	43.63	35.34	26.28	10.55	4.65	1.5	1.5
Dominant families	<i>Weinmannia</i> ; <i>Clusia</i> ; <i>Hesperomeles</i>	<i>Clusiaceae</i> ; <i>Cunoniaceae</i>	<i>Cunoniaceae</i> ; <i>Lauraceae</i>	<i>Clusiaceae</i> ; <i>Alzateaceae</i>	<i>Clethraceae</i> ; <i>Myrtaceae</i> ; <i>Clusiaceae</i>	<i>Euphorbiaceae</i> ; <i>Fabaceae</i> ; <i>Lauraceae</i>	<i>Moraceae</i> ; <i>Fabaceae</i> ; <i>Rubiaceae</i>	<i>Bixaceae</i> ; <i>Moraceae</i> ; <i>Fabaceae</i>	<i>Lecythidaceae</i>

in the 2000–3025 m band, where there is a build-up of a thick layer of humic material (typically 20–30 cm thick) above C-rich topsoil (C. A. J. Girardin, L. E. O. C. Aragão, Y. Malhi, W. Huaraca Huasco, D. Metcalfe & J. E. Silvae, unpublished results). The base of the cloud zone is located at 1500–1800 m, and the cloud forest zone extends to the tree line at approximately 3400 m, above which puna grasslands dominate.

*Weather.* Weather patterns along the elevational gradient are described in a companion paper in this issue (C. A. J. Girardin, L. E. O. C. Aragão, Y. Malhi, W. Huaraca Huasco, D. Metcalfe & J. E. Silvae, unpublished results). Mean annual air temperatures over the study period ranged from 26.4 °C (194 m) to 11.8 °C (3000 m). There was a close association between elevation and temperature ( $r^2 = 0.99$ ,  $P < 10^{-4}$ ), implying a vertical lapse rate of soil temperature of 4.79 °C km<sup>-1</sup>, and a lapse rate of air temperature of 4.94 °C km<sup>-1</sup>. Over the measurement period (August 2007–August 2008), precipitation showed a humped relationship with elevation, with our recorded highest values (3086–2746 mm yr<sup>-1</sup>) near the base of the mountain range (1000–1500 m). Light incidence and soil water content (SWC) showed no clear relationships with elevation. There may be microsite effects along the elevational gradient, which reflect the geomorphological situation rather than the influence of elevation *per se* (Moser *et al.*, 2008). This is illustrated by the variation of rainfall patterns between the two forest sites under investigation at 3000 m: the plot located on a slope (3025 m) was, on average, drier and received higher annual light incidence than that located on the Trocha Union ridge (3020 m). Nonetheless, within the cloud immersion zone, SWC is typically above 25% throughout the year, because of limited evapotranspiration and fog deposition.

#### Aboveground C stocks and fluxes

We determined wood productivity using multiple censuses of the forest plots. Tree censuses were carried out in our plots in 2003 and 2007 to determine the growth rate of existing surviving trees and the rate of recruitment of new trees. Mortality was estimated for each site by calculating the biomass of trees that were measured in 2003 and dead in 2007. Only trees >10 cm diameter at breast height (DBH) were included in the census. These measurements were subsequently converted into estimates of coarse wood productivity using allometric equations for moist forest stands that relate tree diameter to biomass (Chave *et al.*, 2005). Two equations were explored in order to determine the importance of including tree height in biomass estimates of montane forest trees:

$$AGB = \rho \times (\rho \times (DBH^2) \times H)0.94 \quad (1)$$

$$AGB = \rho \times \exp(-1.499 + 2.1481 \times \ln(DBH) + 0.207 \times (\ln(DBH))^2 - 0.0281 \times (\ln(DBH))^3), \quad (2)$$

where AGB is aboveground biomass in kg m<sup>-2</sup>,  $\rho$  is density of the wood obtained from (Chave *et al.*, 2006), DBH (cm), and  $H$  is height (m). Both were derived from the same pan-tropical dataset, however (2) only incorporates diameter information and so is applicable for data sets where height information is

not available. As we had some height data from each plot, Eqn (1) was used for the subsequent analysis. It includes census data on DBH, a single measurement of tree height and species-specific values for wood density. Tree height was available for approximately 125 trees in each plot. Where tree height was not available for particular trees, it was estimated by fitting an exponential model to existing height and diameter at breast height data for trees at that elevation. To convert biomass values into C, we assumed that dry stem biomass is 50% C (Chave *et al.*, 2005).

We calculated annual aboveground woody biomass productivity,  $NPP_{\text{stem}}$ , from full plot census data from 2003 and 2007. This was calculated using the allometric equations of Chave *et al.* (2005), including estimates for height, as described above. The biomass of new recruits measured at the second census was then added.

To determine seasonal variation in  $NPP_{\text{stem}}$ , we used 3-monthly dendrometer band measurements on approximately 200 randomly selected trees per plot from August 2007 to January 2009. Dendrometer measurements were converted into 3-month biomass increments for each tree. To scale from the dendrometer trees to the full plot, we grouped the tree species by genus. From the full census data we determined the annual NPP of each genus  $g$ , and what fraction of the annual NPP of each genus was captured by dendrometers,  $f_g$ . The 3-monthly whole-plot NPP of each genus was then estimated by dividing the dendrometer-measured 3-month NPP of that genus by  $f_g$ . These whole plot estimates of NPP for each genus were then summed over genus to obtain a total plot NPP.

Given that some species of tree ferns and palms can grow vertically without increasing in girth, hence measuring their increase in diameter at breast height over time is futile, we included tree ferns and palms as recruits in our NPP estimates and in our stem biomass estimates, as described in Malhi *et al.* (2004), but did not estimate growth rates over time. The proportion of tree ferns in the plots ranged from 2.5% (1000 and 3020 m) to 21% (2020 m), peaking between 1855 and 2720 m. Palm proportion varied from 0% (3100 m) up to 27% one plot in the Tambopata lowlands. There were no tree ferns at the lowland sites, and no palms above 1500 m elevation.

Canopy productivity was estimated by collecting litterfall in 0.25 m<sup>2</sup> litter traps (PVC tubes and 1 mm mesh nylon screen, 25 ha<sup>-1</sup>) set up 1 m above the ground. Litterfall was collected bi-weekly to minimize loss by decomposition, split into different components, oven dried at 80 °C and weighed. Components of litterfall include leaves; reproductive organs (fruits and flowers); twigs (up to 2 cm girth, including bark); epiphytes and bromeliads (all parts combined); and fine debris (unidentifiable particles that pass through 2 mm mesh). In the present analysis, we refer to the sum of leaves, twigs, reproductive organs, epiphytes, bromeliads and unidentified material as canopy productivity.

#### *Belowground C stocks and fluxes*

Soil and root C stocks were estimated using soil cores only (these soil cores were sampled during the installation of ingrowth cores), while root production was estimated using

two independent approaches, rhizotrons and soil ingrowth cores. The comparison of these two approaches gives us some metric of confidence in these results. A detailed description of the methodologies described here is presented in Metcalfe *et al.* (2008a). For an in depth review and critique of these methods refer to Vogt *et al.* (1998) and Hendricks *et al.* (2006).

*Rhizotrons.*  $NPP_{\text{BG}}$  was determined using rhizotron root observation chambers (Burke & Raynal, 1994). These observation chambers were framed on three sides using lumber or metal. The fourth side was a 6 mm thick pane of Perspex 40 cm deep, 0 cm being the surface of the organic top layer, and 35 cm wide. Lowland sites with thin organic layers (OL) had their observation chambers mostly in mineral soils, while at highland sites with thick OL, the chambers mostly observed root growth in the OL and not in the mineral soil (Table 1). The rhizotron measurements began 2 months after installation, once we could observe the roots growing rapidly against the observation chamber, to let the roots recover from the initial disturbance resulting from severing the roots during the installation of rhizotrons. Three rhizotrons were installed at sites chosen to encompass the topographic variation in each plot, in November 2006, at the end of the dry season. Monthly root growth was recorded from the rhizotrons over 23 months. Each month, root increments were recorded at each session by tracing over visible roots with permanent markers on transparent A4 acetate sheets placed over the glass face. Information on root diameter class was recorded through colour coding (< 1 mm = black, 1–2 mm = blue, 2–3 mm = red, < 4 mm = green) and the dates of root appearance and disappearance were recorded by numbering each root increment traced. Root intersections with the rhizotron screens were counted on each sheet and converted to biomass production per unit ground area using the method described in Bernier & Robitaille (2004). In this method, the number of roots contacting the rhizotron screen at each time-step, together with root diameter, is used to calculate the total cross-sectional surface area of intersecting roots using the equations presented by Bernier & Robitaille (2004). As roots can only intersect with the rhizotron screen from one side, the resulting value was doubled, assuming that if there was not an empty space behind the rhizotron screen, an equal amount of roots would contact the rhizotron screen from the other side.

*Root ingrowth cores.*  $NPP_{\text{BG}}$  was also quantified in all plots using the ingrowth core technique (Vogt *et al.*, 1998; Steingrobe *et al.*, 2000; Hendricks *et al.*, 2006), following the methodology described in Metcalfe *et al.* (2008b). These are cores of root-free soil surrounded by mesh bags in which roots were allowed to grow over a set period of time (3 months), providing estimates of root production per unit area and time (Mg ha<sup>-1</sup> yr<sup>-1</sup>). Nine ingrowth cores were installed in the plots in May 2007, three of which were in close proximity to rhizotrons. Soil cores were extracted and soil layers were separated into O-horizon OL and A- and B-horizon mineral layer (ML). Fine roots were manually removed every 3 months using a method which corrects for underestimation of fine root biomass. Roots were manually extracted from soil cores during 10 min time

intervals, over a period of 40 min. The curve of cumulative extraction over time was used to predict root extraction beyond 40 min (Metcalf *et al.*, 2007). This method only accounts for live fine roots, as the 3-monthly sample period was much lower than the turnover time of the roots. Root-free soil was then replaced in each ingrowth core, maintaining the horizon layering of the undisturbed soil. Sampled roots were rinsed in water to remove soil particles, oven dried at 70 °C in the lab until constant mass, weighed and scanned as greyscale images at 600 dpi resolution. Fine root biomass and mass of the soil OL were measured using the first soil cores sampled in May 2007. NPP<sub>BG</sub> was estimated from the quantity of root mass produced in the 3-month interval since the last collection. Fine and coarse roots were defined as <2 mm and >2 mm in diameter, respectively. The scanned images were analysed using commercially available software (WINRHIZO PRO version 2003b, Regent Instruments, Ottawa, Canada), to calculate root length and surface area, according to the methodology described by Metcalfe *et al.* (2008a,b). Finally, OL depth and root mass within the OL were also measured using soil cores in August 2008 at 25 points for each elevation (only five at 2000 m). As it is very difficult to discern between biomass and necromass of fine roots, fine root biomass are likely to be overestimated.

### NPP calculations

NPP of an ecosystem can be defined as the total biomass of autotrophs produced in a specified time interval (Roy *et al.*, 2001). Total productivity (NPP<sub>Total</sub>) can be divided into belowground (NPP<sub>BG</sub>) and aboveground (NPP<sub>AG</sub>) production of C per unit time. Aboveground NPP consists of stem production (NPP<sub>Stem</sub>), canopy production (NPP<sub>Canopy</sub>), branch turnover (NPP<sub>Branch</sub>) and volatile organic compound production (NPP<sub>VOC</sub>).

$$\text{NPP}_{\text{AG}} = \text{NPP}_{\text{Stem}} + \text{NPP}_{\text{Canopy}} + \text{NPP}_{\text{Branch}} + \text{NPP}_{\text{VOC}}. \quad (3)$$

We obtained stem (NPP<sub>Stem</sub>) and leaf (NPP<sub>Canopy</sub>) production values through direct measurement. NPP<sub>Canopy</sub> consist of leaves, small branches, flowers and fruit. As we did not directly measure branch production in this study, it is scaled from NPP<sub>Stem</sub> using the ratio (0.4) of NPP<sub>Branch</sub>:NPP<sub>Stem</sub> estimated from published values in lowland Amazonian plots (Aragão *et al.*, 2009). NPP<sub>VOC</sub> is the emission of volatile organic C from the vegetation. VOC flux appears to be a very small component of the C cycle of tropical forests (Malhi *et al.*, 2009) and is not quantified in this study.

NPP<sub>BG</sub> consists of fine (NPP<sub>FineRoot</sub>) and coarse root (NPP<sub>CoarseRoot</sub>) production (Clark *et al.*, 2001a), and exudate production.

$$\text{NPP}_{\text{BG}} = \text{NPP}_{\text{FineRoot}} + \text{NPP}_{\text{CoarseRoot}} + \text{NPP}_{\text{Exudate}}. \quad (4)$$

Whereas we estimated NPP<sub>FineRoot</sub> directly, NPP<sub>CoarseRoot</sub> presents a methodological challenge and is very difficult to estimate directly. Hence, NPP<sub>CoarseRoot</sub> was estimated as a fraction of NPP<sub>Stem</sub>, following the method proposed by Malhi *et al.* (2009):  $\text{NPP}_{\text{CoarseRoot}} = 0.21 (\pm 0.03) \times \text{NPP}_{\text{Stem}}$  where  $0.21 \pm 0.03$  is the mean ratio of belowground stocks to aboveground stocks reported across lowland tropical forests. This may result in underestimation of production, as the NPP of

smaller roots is likely to exceed that of large structural roots. For the TMFs, we chose to use the same ratio with a higher uncertainty ( $0.21 \pm 0.10$ ); on wind or erosion prone sites it is likely that trees invest more in coarse root anchoring, but on the other hand on shallow montane soils they are not able to have a large root core or deep roots.

Exudates and export to mycorrhizae are not measured in this study, resulting in an underestimation of the NPP<sub>BG</sub> values presented in this study to our knowledge. This component has never been explicitly measured in any tropical forest, it has been found to account for 3–15% of NPP in temperate forests (Vogt *et al.*, 1982; Bekku *et al.*, 1997; Clark *et al.*, 2001b).

### Analytical techniques

We used these data to describe the spatial variations of above- and belowground C stocks, NPP and turnover rates along the Kosñipata transect. All uncertainty estimates are given as the standard error of the mean. The statistical significance of correlation coefficients was based on a two tailed approach,  $df = n - 2$ ,  $P < 0.05$ . Linear regression analyses were conducted to identify significant elevational trends in ecosystem allocation to different NPP components and the relationships between components. All statistical analyses were performed with the R version 2.9.0 statistical package (Chambers, 2008).

## Results

### C stocks

Estimates of C stocks are presented in Table 2. We calculated stem biomass using two of the moist forest stand equations presented by Chave *et al.* (2005), as described above. Equation (1) requires measurements of tree height,  $H$ . Equation (2) does not account for height, and we use it here to explore the importance of directly accounting for height. Equation (2) assumes a fixed polynomial relationship between  $\ln(H)$  and  $\ln(\text{DBH})$  derived for lowland tropical forests. It would only be valid if the tree form, as expressed by the relationship between diameter and height, did not vary with elevation. Hence the comparison of these two equations gives us some indication of the importance of variation in tree form with elevation in determining forest biomass. Our data show that the allometric form of trees in our sites varies with elevation: trees at high elevation have less stature for the same DBH, i.e. tree form becomes gradually more squat and stunted with increasing elevation. Hence, using Eqn (2) would result in a systematic overestimation of biomass by  $52 \pm 10\%$  at higher elevations. Figure 1a demonstrates the importance of including height estimates into stem C stocks calculations in TMFs, as height is the dominant factor dictating a decline in aboveground C stocks with increasing elevation. Figure 1a includes published data

**Table 2** Synthesis of carbon stocks estimates

Plot	Elevation (m)	C stock <sub>Soil</sub> (ML)	C stock <sub>Soil</sub> (OL)	C stock <sub>FineRoots</sub>	C stock <sub>CoarseRoots</sub>	C stock <sub>BG</sub>	C stock <sub>Stem</sub>
WAY	3025	2.45	59.6 ± 5.00				64.9
TU3	3020	1.42	68.8 ± 4.47	4.95 ± 0.62	9.88 ± 0.54	14.8 ± 0.82	47.0
TU4	2720	3.97	63.6 ± 4.37	4.05 ± 0.56	13.8 ± 0.78	17.9 ± 0.96	65.9
TU7	2020	8.35	52.1 ± 10.7	6.83 ± 1.13	8.11 ± 1.47	14.9 ± 1.85	38.6
TU8	1855	10.5	58.3 ± 8.45	6.54 ± 0.54	11.7 ± 0.87	18.2 ± 1.03	55.6
SPD	1500	15.7	27.6 ± 1.93		21.6		102.8
TON	1000	5.69	8.45 ± 0.92	2.62 ± 0.29	16.7 ± 0.54	19.3 ± 0.61	79.5
TAM05	210			2.31	31.5	33.8	123.5
TAM06	194	11.9	3.55	1.50	31.5	33.0	118.5

All values are in  $\text{Mg C ha}^{-1}$ .  $\text{Bm}_{\text{CoarseRoots}}$  were estimated as described in the text (Malhi *et al.*, 2009). All other values were directly measured as described in the text.  $\text{Bm}_{\text{Stem}}$  were calculated as the sum of all stem stocks of trees > 10 cm diameter.

Bm, biomass; ML, mineral layer; OL, organic layer; BG, below ground.

from nine plots in lowland Amazonia (two of which are the lowland plots from this transect), for which biomass was estimated using the same methodology and Eqn (2). We observed a significant decrease in stem biomass with increasing elevation with Eqn (1) ( $r^2 = 0.80$ ,  $P < 0.0005$ ,  $n = 17$ ).

Figure 1b indicates a step change in fine root biomass in the soil OL at the base of the cloud immersion zone. Fine root C stocks increased from  $1.50 \text{ Mg C ha}^{-1}$  at 194 m to  $6.54 \pm 0.54 \text{ Mg C ha}^{-1}$  at 1855 m, and thereafter no significant changes in root C stocks were observed within the cloud immersion zone. Coarse root biomass was calculated as a fixed fraction of stem biomass, and thus we presumed coarse root biomass to follow a similar pattern to stem biomass and decrease with elevation. Fine root to stem biomass ratio increased with elevation, from 0.02 at 194 m to 0.11 at 3020 m.

### NPP

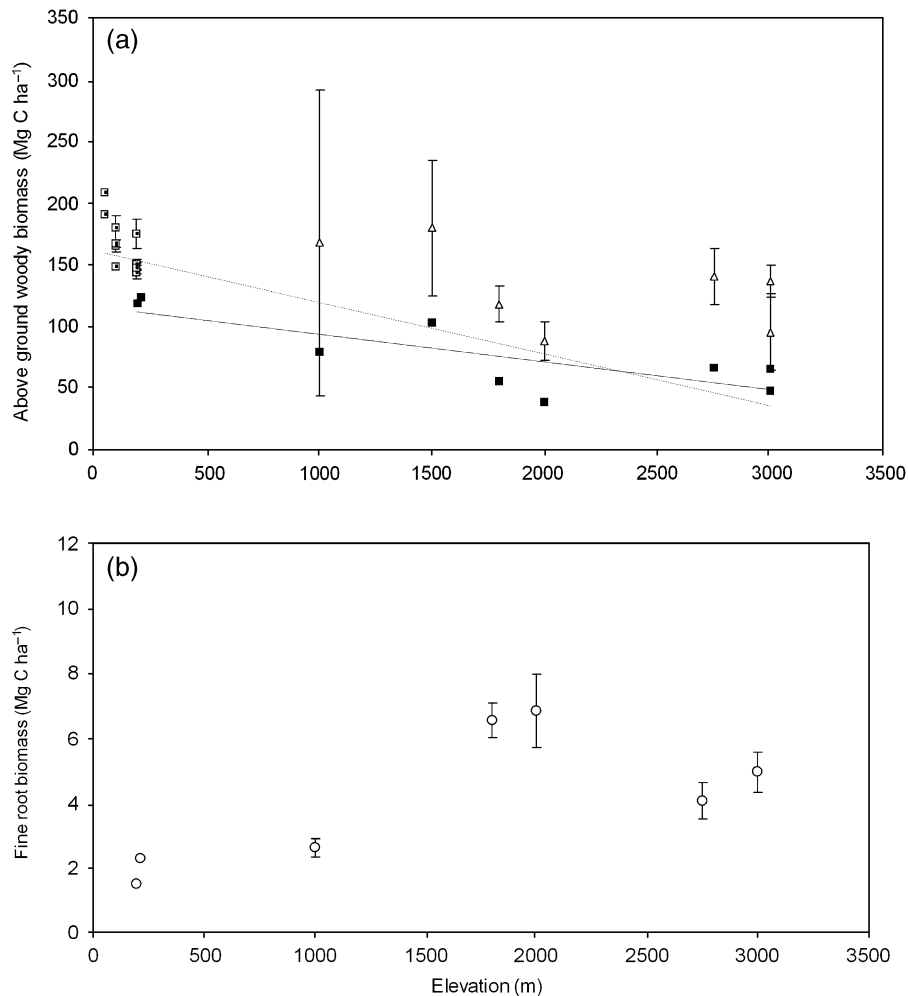
The patterns of NPP components along the elevational gradient are shown in Figs 2 and 3.  $\text{NPP}_{\text{Total}}$  estimated in nine plots along the elevational transect did not decline monotonically with increasing elevation. However, we observed a change in regime in the premontane and montane forests: lowland values ( $16.9 \pm 1.48 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$  at 210 m and  $13.6 \pm 1.25 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$  at 194 m, Aragão *et al.*, 2009) were significantly higher than values recorded in the Andes ( $7.07 \pm 0.98 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$  at 1000 m to  $4.11 \pm 0.26 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$  at 3020 m). This relationship is particularly apparent in Fig. 2, in which values from central Amazonia reported by Malhi *et al.* (2009) and Aragão *et al.* (2009) are also included. Here, TMF values of  $\text{NPP}_{\text{Total}}$  are significantly lower than  $\text{NPP}_{\text{Total}}$  from even the least fertile soils in central Amazonia.

$\text{NPP}_{\text{Stem}}$  ranged between  $0.79 \pm 0.08$  (1855–2020 m) and  $2.80 \pm 0.24 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$  (210 m), with a change

in regime between lowland Amazonian forests and premontane to montane forests. Likewise, we recorded a significant decline in  $\text{NPP}_{\text{Canopy}}$  with increasing elevation (slope =  $-0.001$ ,  $r^2 = 0.74$ ,  $P = 0.002$ ,  $n = 9$ ) (Fig. 3a). Hence,  $\text{NPP}_{\text{AG}}$  decreased with elevation (slope =  $-0.001$ ,  $r^2 = 0.69$ ,  $P = 0.005$ ,  $n = 9$ ). These linear relationships provide indications on the overall tendency of the trends we observed, however, rather than a steady linear decline, there appears to be a fairly rapid decline in  $\text{NPP}_{\text{AG}}$  with elevation until the base of the cloud immersion zone (around 1500 m), and then no trend in  $\text{NPP}_{\text{AG}}$  with elevation within the cloud zone all the way up to the tree line. There appears to be two distinct regimes, one below the clouds where NPP declines with elevation, and one within the cloud zone where NPP does not change with elevation. Average  $\text{NPP}_{\text{AG}}$  was estimated at  $3.53 \pm 0.38 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$  ( $n = 7$ ) in the TMF and  $8.87 \pm 0.63 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$  ( $n = 2$ ) in the lowland Amazonian plots.

A change in regime of  $\text{NPP}_{\text{BG}}$  was observed around 1000 m, with a decrease in production and with the lowest values recorded within the cloud immersion zone, between  $1.96 \pm 0.18$  and  $1.48 \pm 0.40 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ .  $\text{NPP}_{\text{FineRoot}}$  followed a similar pattern, with values decreasing from  $6.80 \pm 1.0 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$  in the lowlands (210 m) to  $1.23 \pm 0.40 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$  in the upper TMF (Fig. 3c).  $\text{NPP}_{\text{FineRoot}}$  represented the largest proportion of belowground productivity, ranging between 83% and 92% of  $\text{NPP}_{\text{BG}}$ .  $\text{NPP}_{\text{CoarseRoot}}$  (Fig. 2) was estimated as a fixed fraction of aboveground production stem biomass (21 ± 10%). As a result, we estimated a decrease in  $\text{NPP}_{\text{CoarseRoot}}$  in the TMF, from  $0.60 \pm 0.09$  (194 m) to  $0.21 \pm 0.04$  (3020 m)  $\text{Mg C ha}^{-1} \text{ yr}^{-1}$ .

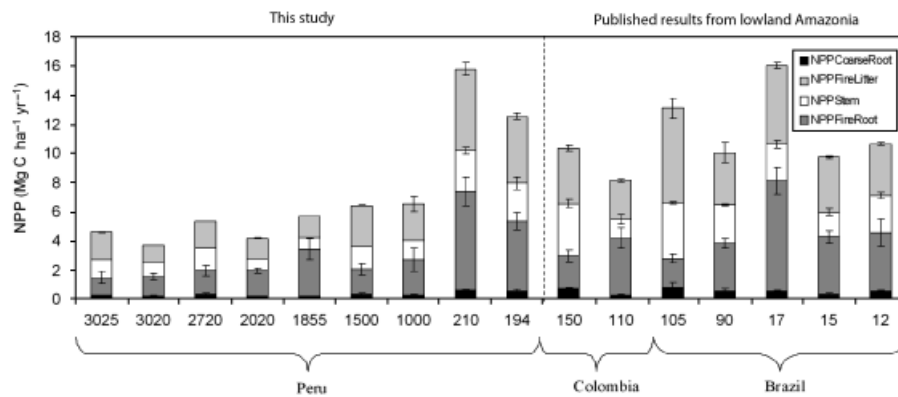
Measurements of NPP and respiration fluxes are presented in Table 3. An analysis of the patterns of  $\text{NPP}_{\text{Total}}$  partitioning into above- and belowground components demonstrated that the ratio of  $\text{NPP}_{\text{BG}}$  to



**Fig. 1** The variation with elevation of above- and belowground standing carbon stocks ( $\text{Mg C ha}^{-1}$ ): (a) stem biomass and (b) fine root biomass. Biomass estimated using a height and diameter based allometric equation (a, closed squares) showed a clear decrease in aboveground biomass with increasing elevation, both when data points from this study were combined with data presented in Aragão *et al.* (2009) (dotted line,  $y = -0.042x + 161.3$ ,  $r^2 = 0.76$ ,  $P < 10^{-4}$ ,  $n = 17$ ) and when we included the data points from the Kosñipata transect only (solid line,  $y = -0.023x + 116.5$ ,  $r^2 = 0.65$ ,  $P = 0.008$ ,  $n = 9$ ). Biomass estimated without including height data (a, open triangles) showed no change in aboveground biomass with elevation ( $y = -0.022x + 180.3$ ,  $r^2 = 0.26$ ,  $P = 0.24$ ,  $n = 7$ ). Stem biomass values for the lowlands (a, open squares) were obtained from Aragão *et al.* (2009). Root carbon stocks were from the top 30 cm of soil. Root carbon values were obtained from nine soil cores at each elevation (only five at 1000 m). Root carbon content was estimated at 50% as in Malhi *et al.* (2009). Error bars are SE of the mean. The estimated base of the cloud immersion zone is located at 1500–1800 m.

$\text{NPP}_{\text{AG}}$  (Fig. 4) shows high site-to-site variation (between 0.2 and 1.2) but no evidence of any overall trend with elevation. The mean value of the ratio is  $0.69 \pm 0.44$ . A significant exception was the forest at 1855 m, where we observed a high  $\text{NPP}_{\text{BG}}$  driven by high fine root productivity. To a small extent, this lack of trend in above- and belowground partitioning is forced by the fact we set  $\text{NPP}_{\text{CoarseRoot}}$  as a fixed fraction of  $\text{NPP}_{\text{Stem}}$ . However, this effect is relatively small, because  $\text{NPP}_{\text{CoarseRoot}}$  is a relatively small component of  $\text{NPP}_{\text{BG}}$  (5–17%), and  $\text{NPP}_{\text{Stem}}$  is a relatively small component of  $\text{NPP}_{\text{AG}}$  (~34%).

The ratio of each NPP component to  $\text{NPP}_{\text{Total}}$  showed no significant trends with elevation (Fig. 5). On average, below the cloud base,  $18 \pm 5\%$  of  $\text{NPP}_{\text{Total}}$  is allocated to stems,  $34 \pm 29\%$  to canopy and  $37 \pm 15\%$  to fine roots ( $n = 3$ ). Above the cloud base,  $21 \pm 7\%$  of  $\text{NPP}_{\text{Total}}$  is allocated to aboveground woody biomass,  $32 \pm 7\%$  to canopy and  $37 \pm 15\%$  to fine roots ( $n = 6$ ). Figure 6 shows the relationships between  $\text{NPP}_{\text{AG}}$  ( $y = 0.58 \pm 0.05x$ ,  $n = 9$ ) and  $\text{NPP}_{\text{BG}}$  ( $y = 0.39 \pm 0.05x$ ,  $n = 9$ ) with  $\text{NPP}_{\text{Total}}$  in the Kosñipata transect, with regressions forced through the origin. These variables are not independent and thus the correlation statistics



**Fig. 2** The net primary productivity (NPP) of the seven premontane and montane sites from this study compared with values from nine sites in lowland Amazonia. All values to the right of the dotted line, described as published results from lowland Amazonia, are presented in Aragão *et al.* (2009). Bars correspond to  $NPP_{Total}$  for each site, they combine  $NPP_{Canopy}$  (pale grey),  $NPP_{FineRoot}$  (dark grey),  $NPP_{Stem}$  (white) and  $NPP_{CoarseRoot}$  (black). Error bars are SE of the mean.

are not meaningful, but the regression slopes are meaningful. Across the elevational transect, the regression suggests that  $NPP_{AG}$  and  $NPP_{BC}$  are  $58 \pm 5\%$  and  $39 \pm 5\%$  of  $NPP_{Total}$ . The slopes of the relationships were remarkably similar for (i) the nine plots from the Kosñipata transect only, (ii) the lowland Amazonian plots from Aragão *et al.* (2009) only, and (iii) both data sets combined. We found a significant relationship between  $NPP_{Canopy}$  and  $NPP_{Stem}$  (Fig. 7) when we included all plots of the Kosñipata transect as well as when we included montane forests.

Regressions of the components of NPP against environmental parameters are presented in Table 4. There are particularly strong correlations between annual mean air temperature and  $NPP_{Canopy}$  and  $NPP_{FineRoot}$ , and weaker correlations with stem productivity. Overall 78% ( $P < 0.005$ ) of the variance in  $NPP_{Total}$  correlated with temperature. Rainfall directly is a weak predictor of NPP, though it may explain some of the residuals once temperature correlation is factored out.

### Residence time

A significant decrease in stem biomass with elevation coupled with a decrease in  $NPP_{Stem}$  resulted in no significant change in stem C residence time with increasing elevation (Table 5, Fig. 8a). In the Kosñipata transect, the mean stem C residence time was  $54 \pm 4$  years ( $n = 9$ ). However, as fine root biomass increased with elevation and  $NPP_{FineRoot}$  was lower in TMFs than in most lowland forest plots, fine root C residence time (Table 5, Fig. 8b) increased significantly with increasing elevation ( $r^2 = 0.80$ ,  $P = 0.006$ ,  $n = 7$ ) from  $0.31 \pm 0.61$  years (194 m) to  $3.78 \pm 0.81$  years (3020 m).

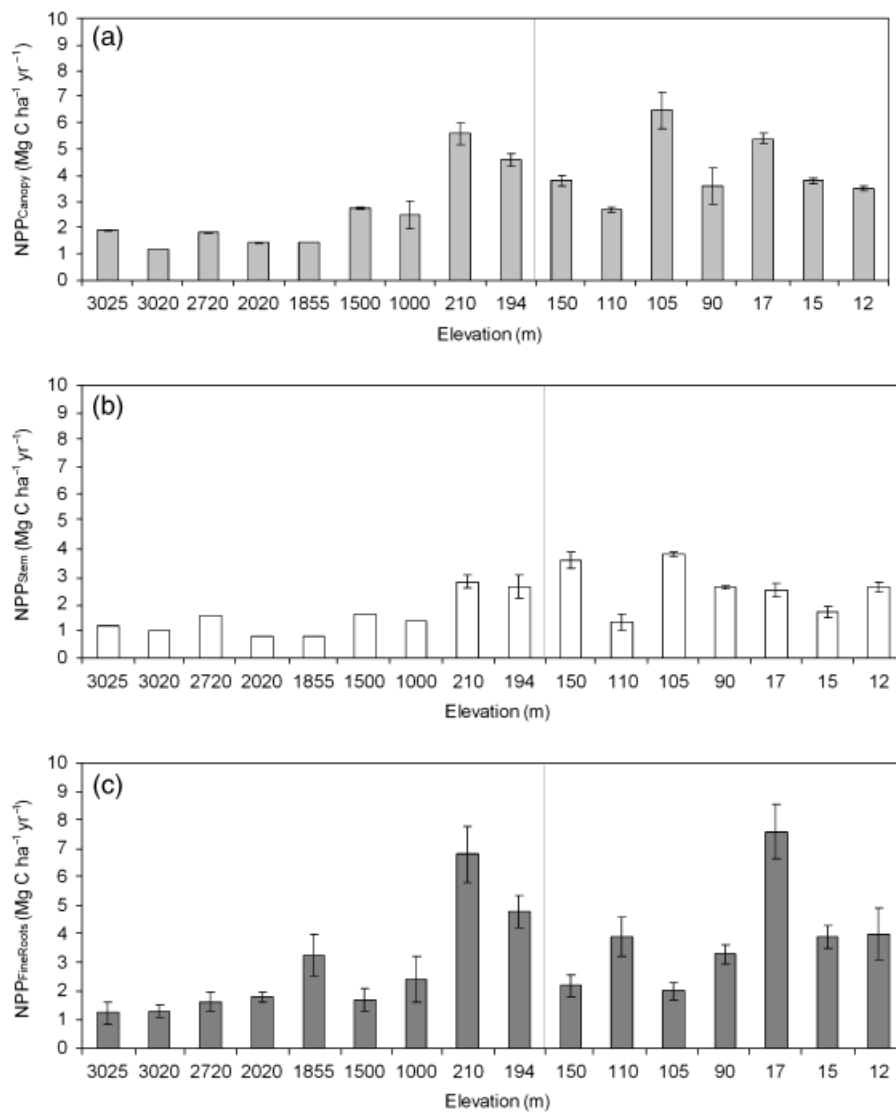
### Discussion

We have presented data on C stocks, productivity, allocation and residence time of seven Andean montane and premontane forests and two lowland Amazonian rainforest sites. In addition, we reviewed published data from nine lowland plots, two of which were the lowland plots of our elevation transect (Aragão *et al.*, 2009; Malhi *et al.*, 2009). Our results confirmed that aboveground biomass and productivity are the main contributors of total C stocks and NPP at all elevations. Overall,  $NPP_{Total}$  was lower in the premontane and montane forests than in lowland Amazonia. This pattern was driven by a decline in above- and belowground NPP in premontane and montane forests, with lower values recorded within the cloud immersion zone.

### No change in total C stocks with elevation

A decline in aboveground biomass with increasing elevation in altitudinal transects is a common feature of TMFs. Our results corroborate previous findings by showing a significant decline in aboveground woody biomass with increasing altitude (Fig. 1). Further, Fig. 1 demonstrates that calculated stem biomass shows no significant trend with elevation when we do not include the decline in tree height in our allometric equation (Chave *et al.*, 2005). Hence, we can attribute this decline solely to a decrease in tree stature with increasing elevation, confirming the importance of measuring tree height when estimating aboveground C stocks in TMF ecosystems. In terms of belowground C allocation, we observed a step change in fine root biomass at the base of the cloud immersion zone, with consistently higher fine root biomass in the TMF than in the premontane and lowland plots. Further, the soil organic matter C stocks





**Fig. 3** Above- and belowground net primary productivity ( $\text{Mg C ha}^{-1} \text{ yr}^{-1}$ ) along the elevational gradient. (a)  $\text{NPP}_{\text{Canopy}}$  (pale grey), (b)  $\text{NPP}_{\text{FineRoot}}$  (dark grey) and (c)  $\text{NPP}_{\text{Stem}}$  (white). All values to the right of the vertical line are presented in Malhi *et al.* (2009) and Aragão *et al.* (2009). Error bars are SE of the mean.

increase significantly with elevation. Hence, if we include increases in the soil C stock pool and fine root C stocks in our estimates of belowground C stocks, these results are consistent with our first hypothesis: there is no significant change in total C stock with elevation, but there is a shift in relative stock of C from above- to belowground.

### NPP

**Total NPP declines with elevation.**  $\text{NPP}_{\text{Total}}$  was lower in the premontane and montane forests than in lowland Amazonia. In a study on nine lowland Amazonian forest plots, Aragão *et al.* (2009) estimated an average  $\text{NPP}_{\text{Total}}$  of  $12.6 \pm 2.5 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ . The present study

estimated a significantly lower average  $\text{NPP}_{\text{Total}}$  of  $5.68 \pm 0.44 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$  ( $n = 7$ ) in the TMFs. All components of  $\text{NPP}_{\text{Total}}$  measured for this study ( $\text{NPP}_{\text{Canopy}}$ ,  $\text{NPP}_{\text{Stem}}$  and  $\text{NPP}_{\text{FineRoots}}$ ) were significantly lower in TMF plots compared with the two lowland Amazonian plots of this transect. Further, we found evidence of a change in regime of  $\text{NPP}_{\text{AG}}$  rates in the cloud forest zone, where  $\text{NPP}_{\text{AG}}$  rates are lower than in most lowland Amazonian plots (Fig. 2). This decline is driven by above- and belowground NPP allocation. Stem and canopy productivity are both significantly lower in the premontane and montane forests than in lowland Amazonia, confirming previous published observations of  $\text{NPP}_{\text{AG}}$  along

**Table 3** Synthesis of net primary productivity (NPP) estimates

Plot	Elevation (m)	NPP <sub>FineRoots</sub>	NPP <sub>CoarseRoots</sub>	NPP <sub>BG</sub>	NPP <sub>Stem</sub>	NPP <sub>FineLitter</sub>	NPP <sub>Branch</sub>	NPP <sub>AG</sub>	NPP <sub>Total</sub>	R <sub>Soil</sub>	R <sub>Soilhet</sub>	R <sub>Roots</sub>
WAY	3025	1.23 ± 0.40	0.25 ± 0.04	1.48 ± 0.40	1.20 ± 0.12	1.92 ± 0.10	0.05	0.5 ± 0.5	3.60 ± 0.13	5.09 ± 0.42	11.63 ± 0.05	3.81 ± 0.64
TU3	3020	1.31 ± 0.23	0.21 ± 0.04	1.52 ± 0.23	1.00 ± 0.10	1.19 ± 0.05	0.04	0.4 ± 0.4	2.59 ± 0.11	4.11 ± 0.26	8.04 ± 0.02	3.05 ± 0.47
TU4	2720	1.63 ± 0.34	0.33 ± 0.04	1.96 ± 0.35	1.57 ± 0.16	1.83 ± 0.06	0.03	0.6 ± 0.6	4.03 ± 0.17	5.98 ± 0.39	10.67 ± 0.04	4.31 ± 0.74
TU7	2020	1.80 ± 0.18	0.16 ± 0.03	1.96 ± 0.18	0.79 ± 0.08	1.44 ± 0.06	0.04	0.3 ± 0.3	2.54 ± 0.09	4.50 ± 0.20	12.08 ± 0.09	3.66 ± 0.38
TU8	1855	3.26 ± 0.73	0.17 ± 0.03	3.43 ± 0.73	0.79 ± 0.08	1.44 ± 0.05	0.04	0.3 ± 0.3	2.55 ± 0.09	5.97 ± 0.73	10.46 ± 0.04	5.14 ± 0.80
SPD	1500	1.70 ± 0.40	0.34 ± 0.05	2.04 ± 0.41	1.62 ± 0.16	2.76 ± 0.13	0.05	0.6 ± 0.6	5.03 ± 0.18	7.06 ± 0.44	17.82 ± 0.06	5.34 ± 0.79
TON	1000	2.42 ± 0.81	0.28 ± 0.04	2.70 ± 0.81	1.34 ± 0.13	2.49 ± 2.02	0.81	0.5 ± 0.5	4.37 ± 0.55	7.07 ± 0.98	13.07 ± 0.05	5.64 ± 2.25
TAM05	210	6.80 ± 1.00	0.60 ± 0.10	7.40 ± 1.00	2.80 ± 0.24	5.60 ± 0.42	0.08	1.1 ± 1.1	9.50 ± 1.08	16.9 ± 1.48	14.38 ± 0.05	13.94 ± 1.58
TAM06	194	4.80 ± 0.57	0.60 ± 0.09	5.40 ± 0.58	2.60 ± 0.42	4.60 ± 0.24	0.05	1.0 ± 1.0	8.24 ± 1.11	13.6 ± 1.25	13.87 ± 0.10	10.87 ± 1.28

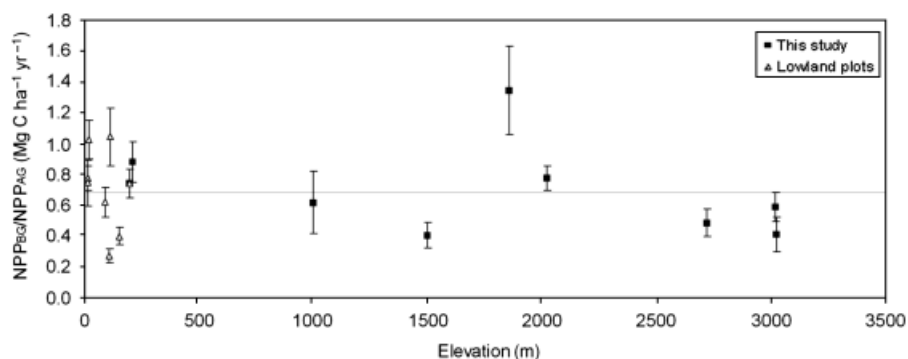
Error estimates are SE of the mean (value ± SE), SE was not available for NPP<sub>Stem</sub> as it is the sum of NPP<sub>Stem</sub> from each tree in the plot, hence, we assumed a SE of 10%, based on data available from lowland plots (Aragão *et al.*, 2009; Malhi *et al.*, 2009). Elevation is in meters; all other values are in Mg C ha<sup>-1</sup> yr<sup>-1</sup>. Values in bold were directly measured. NPP<sub>Branch</sub> data were obtained from Malhi *et al.* (2009). Other values were estimated as described in the text. AG, aboveground, BG, belowground.

elevational transects from Hawaii (Raich *et al.*, 1997; Herbert & Fownes, 1999; Schuur and Matson, 2001) and Borneo (Kitayama & Aiba, 2002) and of NPP<sub>Canopy</sub> from Jamaica (Tanner & Grubb, 1999), Puerto Rico (Waide *et al.*, 1998), and Ecuador (Roderstein *et al.*, 2005). These authors used NPP<sub>Canopy</sub> as a proxy of NPP<sub>AG</sub>. Similarly, Malhi *et al.* (2009) and Aragão *et al.* (2009) found that in lowland Amazonian forests, canopy productivity appears to be a good proxy for NPP<sub>AG</sub>. Our results confirm that this relationship holds in montane forests (Fig. 7). Further, the number of plots we established along the transect allowed us to observe a change in regime in NPP<sub>AG</sub> between lowland forest and montane forest for the first time in an elevational transect.

Studies that attempt to quantify NPP<sub>BG</sub> in TMFs are more limited in number. To date, only one study determined NPP<sub>BG</sub>, in South Ecuador (Roderstein *et al.*, 2005), and a second is being proposed for this site in (C. A. J. Girardin, L. E. O. C. Aragão, Y. Malhi, W. Huaraca Huasco, D. Metcalfe & J. E. Silvae, unpublished results). Roderstein *et al.* (2005) found that, along a transect of three plots in the Ecuadorian Andes (1050–3060 m), NPP<sub>Canopy</sub> declined, whereas NPP<sub>FineRoot</sub> increased three-fold, revealing a clear belowground shift in C allocation with increasing elevation. We found that, along seven plots ranging from the high Andes to lower montane forests, NPP<sub>FineRoot</sub> remained constant within the cloud immersion zone (1855–3025 m), with values below those reported in the least fertile soils of lowland Amazonia (Fig. 3c). Whereas we observed a decline in NPP<sub>Canopy</sub> in TMFs compared with premontane and lowland sites, our results showed no evidence of a shift in allocation to NPP<sub>FineRoots</sub> as elevation increases. Instead, at our site, we found that productivity decreases proportionately above- and belowground in TMFs, supporting our hypothesis (2): *total NPP declines with elevation, but the proportion of NPP allocated to above- and belowground stays fixed.*

*NPP allocation patterns on the elevation transect are the same as those observed in lowland Amazonia*

Aragão *et al.* (2009) found several significant relationships between the components of NPP. Here, we tested these relationships to determine if the patterns observed in lowland Amazonian forests hold in the Kosñipata montane forests. We found that the ratio of NPP<sub>BG</sub> to NPP<sub>AG</sub> did not change significantly along the elevational gradient (Fig. 4). The allocation of NPP to stems, canopy and fine roots did not change with elevation. Further, we established that the relationship found by Aragão *et al.* (2009) between NPP<sub>AG</sub>, NPP<sub>BG</sub> and NPP<sub>Total</sub> (i.e. a significant increase in both NPP<sub>AG</sub> and NPP<sub>BG</sub> with increasing NPP<sub>Total</sub>) also applies to our TMF transect. Both studies found a similar sensitivity of



**Fig. 4** Ratio of below- to aboveground net primary productivity ( $NPP_{BG}/NPP_{AG}$ ). Results from this study (closed squares) and published results from lowland Amazonia (Aragão *et al.*, 2009; Malhi *et al.*, 2009) are represented. Error bars are SE of the mean. The estimated base of the cloud immersion zone is located at 1500–1800 m.

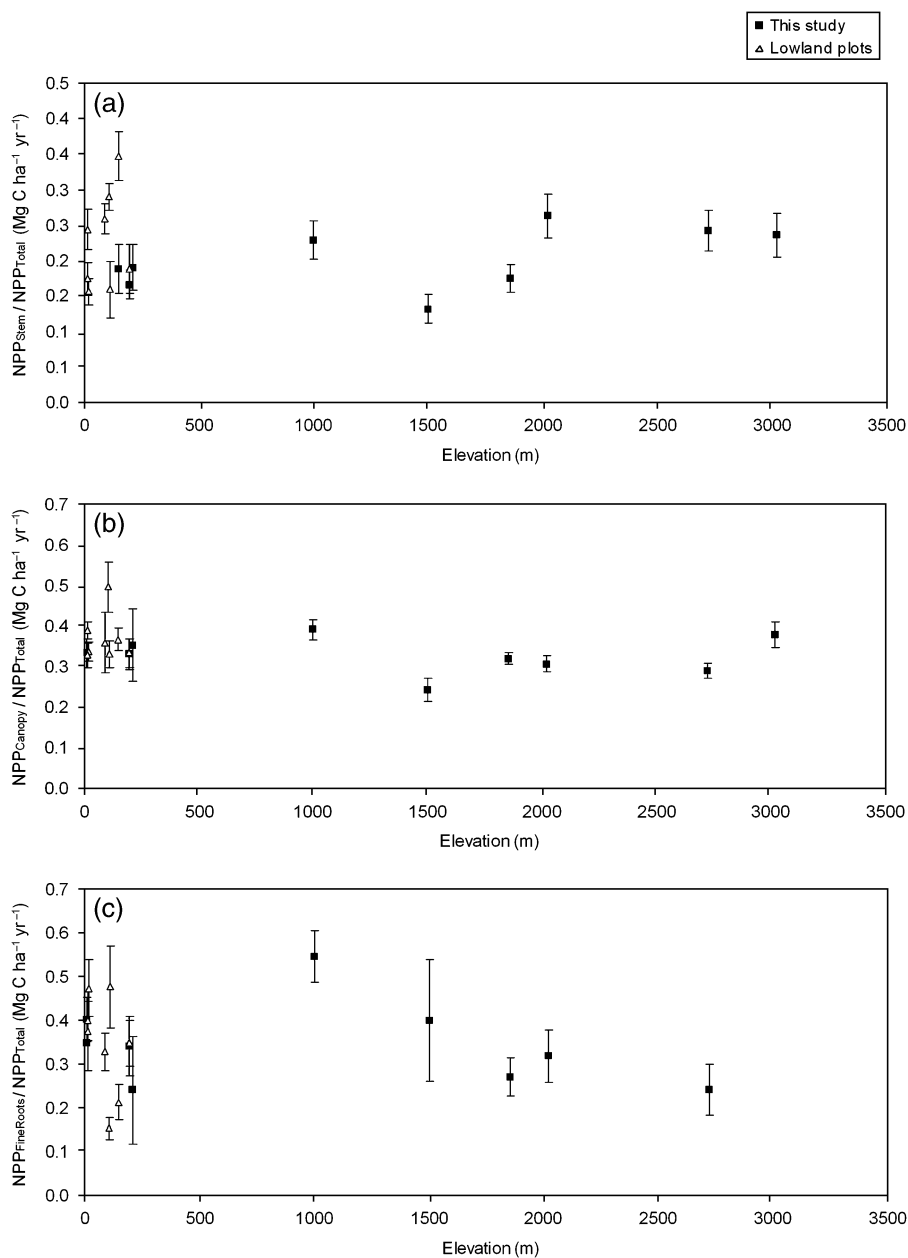
above- and belowground productivity to changes in  $NPP_{Total}$  (Fig. 6). These relationships confirm that, although the total productivity of forests is reduced in the mountains, the allocation patterns of NPP do not change with elevation in our elevation transect. However, G. Moser, C. Leuschner, D. Hertel, S. Graefe & S. Iost (unpublished results) reported a very different pattern of NPP allocation along an Ecuadorian elevational gradient, hence, generalizing about the relationships between NPP components in TMFs may still be premature.

Nonetheless, in a review of aboveground NPP in 104 Neotropical forest plots, Malhi *et al.* (2004) observed a constant partitioning between  $NPP_{Stem}$  and  $NPP_{Canopy}$  ( $NPP_{Stem} = 1.73 (\pm 0.09) \times NPP_{Canopy}$ ) when they combined their data with published results from (Clark *et al.*, 2001b). In a subsequent study, Araújo *et al.* (2009) found a significant relation between stem and canopy productivity ( $NPP_{Canopy} = 1.61 (\pm 0.07) \times NPP_{Stem}$ ,  $r^2 = 0.58$ ,  $P < 0.001$ ) when they combined their results to those presented in Malhi *et al.* (2004). The evidence from the Kosñipata elevational transect confirmed that this relationship holds in our TMF plots, providing further support that  $NPP_{Canopy}$  is a good proxy for  $NPP_{Total}$  in moist tropical forests (Fig. 7). These findings are consistent with hypothesis (3): *the TMF of the Kosñipata elevational gradient displays the same NPP allocation patterns as those observed in lowland Amazonian forests by Araújo *et al.* (2009) and Malhi *et al.* (2004).*

**Factors controlling NPP.** In one of the most thorough appraisals of tropical forest NPP quantification of recent years, Clark *et al.* (2001a,b) compiled data from 39 tropical forest sites and estimated total tropical forest NPP. Their estimates ranged between 3.1 and 21.7  $Mg C ha^{-1} yr^{-1}$ , confirming that our estimates of 4.11 (3020 m) to 7.07 (1000 m)  $Mg C ha^{-1} yr^{-1}$  in TMFs are situated in the lower range of lowland forest

estimates. Tropical forest NPP was found to be poorly correlated with mean annual temperature and with annual rainfall (Clark *et al.*, 2001b; Del Grosso *et al.*, 2008). Some authors found that NPP decreases at extremely high precipitation ( $> 3000 mm yr^{-1}$ ), due to the indirect effects of excess moisture, such as low soil oxygen resulting in slow mineralization rates and the loss of nutrients through leaching (Clark *et al.*, 2001b; Schuur *et al.*, 2001). More recently, Malhi *et al.* (2004) concurred with these observations, and also reported that  $NPP_{Stem}$  varied substantially at the regional scale, and that a large part of this regional variation was due to soil type. Subsequently, Araújo *et al.* (2009) investigated the relationship between soil fertility and NPP in ten Amazonian forests on contrasting soil types, confirming the relationship between soil fertility (particularly phosphorus status) and productivity.

Palm litter was not accounted for in the lowland plots, implying a further underestimation of  $NPP_{Canopy}$  at 210 m and 194 m. Nonetheless,  $NPP_{Canopy}$  was significantly lower in the cloud forest than in the premontane and lowland forests, showing evidence of a change of regime at the cloud base (Fig. 3a). Within the cloud immersion zone,  $NPP_{Canopy}$  did not change significantly. The decrease in canopy production with increasing elevation may be largely explained by temperature ( $r^2 = 0.76$ ,  $P < 0.005$ ,  $n = 9$ ), however, as temperature decreases linearly with elevation and  $NPP_{Canopy}$  does not, this relationship may be a result of the indirect effects of temperature rather than the direct effects of temperature on plant physiology. Several authors have suggested that plants adjust their C allocation patterns in response to imbalances in resource availability (nutrients or water) (Bloom *et al.*, 1985; Litton *et al.*, 2007). Since SWC is typically above 25% in our plots, water shortage should not be limiting plant growth in any of our study sites. Nevertheless, water saturation in the

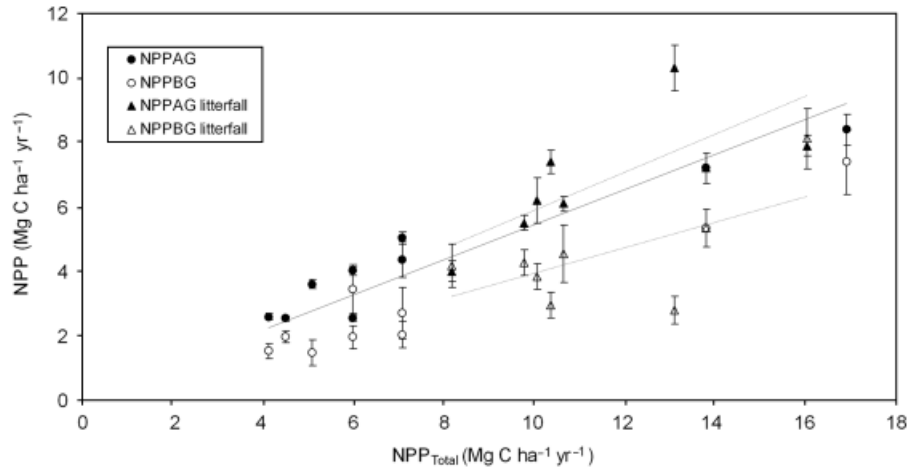


**Fig. 5** Partitioning of net primary productivity (NPP) components along the elevational gradient. (a)  $\text{NPP}_{\text{Stem}}/\text{NPP}_{\text{Total}}$ , (b)  $\text{NPP}_{\text{Canopy}}/\text{NPP}_{\text{Total}}$ , (c)  $\text{NPP}_{\text{FineRoots}}/\text{NPP}_{\text{Total}}$  ratios along the elevational gradient. Data from this study (closed squares) is compared with data presented in Aragão *et al.* (2009) (open triangles). Mean value represented by a solid horizontal line. Error bars are SE of the mean. The estimated base of the cloud immersion zone is located at 1500–1800 m.

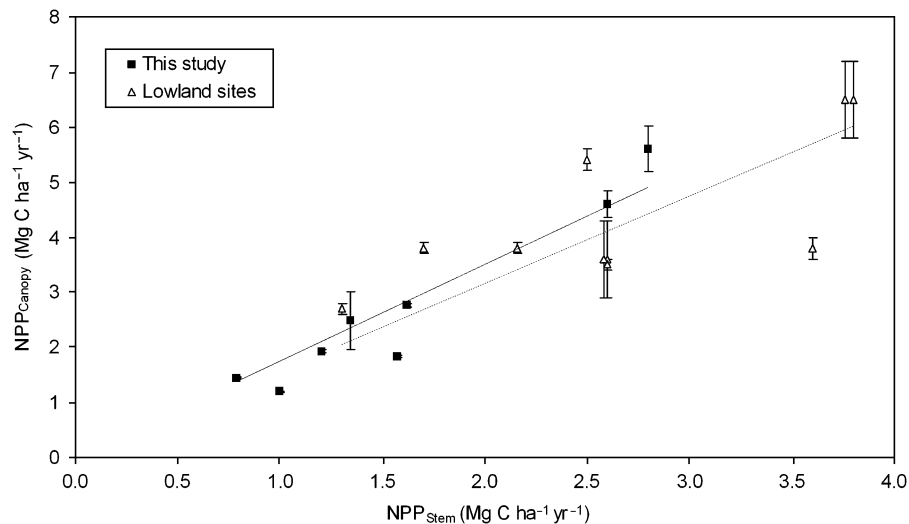
soil may have prevented mineralization, reducing nutrient supply to the roots, as suggested by Leuschner *et al.* (2007).

Our results indicate a strong correlation ( $r^2 = 0.78$ ,  $P < 0.005$ ,  $n = 9$ ) between  $\text{NPP}_{\text{Total}}$  and mean annual temperature, particularly so in the case of fine root ( $r^2 = 0.77$ ,  $P < 0.005$ ,  $n = 9$ ) and canopy productivity ( $r^2 = 0.76$ ,  $P < 0.005$ ,  $n = 9$ ). Of course, correlation does

not necessarily indicate causation; further, linear regressions are not valid if there is a sudden regime change at cloud base, as observed in this elevational gradient (Fig. 3). The results of linear regressions are provided here to provide a summary statistic of the overall trend observed along the elevational gradient, although we are cautious not to over interpret them. Thus, over this extreme elevation gradient it is likely that temperature



**Fig. 6** Above- (AG) and belowground (BG) net primary productivity (NPP) relationships with  $NPP_{Total}$ . The figure shows  $NPP_{AG}$  (closed triangles) and  $NPP_{BG}$  (open triangles) data from lowland Amazonian forests published by Aragão *et al.* (2009) as well as  $NPP_{AG}$  (closed circles) and  $NPP_{BG}$  (open circles) data from the Kosñipata transect. In both forests, a regression analysis with the intercept set to 0 showed a significant positive relationship between  $NPP_{AG}$ ,  $NPP_{BG}$  and  $NPP_{Total}$ . For the Kosñipata transect,  $NPP_{AG}$  (solid line,  $y = 0.58 \pm 0.025x$ ,  $r^2 = 0.94$ ,  $P < 10^{-4}$ ,  $n = 9$ ) and  $NPP_{BG}$  (solid line,  $y = 0.41 \pm 0.022x$ ,  $r^2 = 0.89$ ,  $P < 10^{-4}$ ,  $n = 9$ ). In lowland Amazonian forests,  $NPP_{AG}$  (dotted line,  $y = 0.61 \pm 0.035x$ ,  $r^2 = 0.52$ ,  $P < 0.04$ ,  $n = 8$ ) and  $NPP_{BG}$  (dotted line,  $y = 0.38 \pm 0.032x$ ,  $r^2 = 0.40$ ,  $P < 0.08$ ,  $n = 8$ ). For the combined dataset,  $NPP_{AG}$  ( $y = 0.54 \pm 0.026x$ ,  $r^2 = 0.89$ ,  $P < 0.0005$ ,  $n = 16$ ) and  $NPP_{BG}$  ( $y = 0.44 \pm 0.024x$ ,  $r^2 = 0.93$ ,  $P < 0.0005$ ,  $n = 16$ ). Error bars are SE of the mean.



**Fig. 7** Relationships between the two aboveground NPP components. We include values from the Kosñipata transect (closed squares,  $y = 1.73 \pm 0.23x$ ,  $r^2 = 0.90$ ,  $P < 0.0005$ ,  $n = 9$ ) and from lowland sites presented in Aragão *et al.* (2009) and Malhi *et al.* (2009) (open triangles,  $y = 1.58 \pm 0.36x$ ,  $r^2 = 0.44$ ,  $P < 0.05$ ,  $n = 11$ ). Error bars are SE of the mean.

plays an important role in influencing ecosystem function. This could be through direct effects of temperature on plant physiology, or indirect effects via slow decay and mineralization rates, which affect nutrient supply and canopy nitrogen and leaf area index. Physiological studies at the 3025 m site in Wayquecha indicate no decline in plant physiological capacity, but a decline in

canopy leaf area and overall canopy leaf nitrogen and N:P ratio (Fisher *et al.*, this issue). Hence the decline in NPP components could be related to the observed decline in leaf nitrogen supply. Finally, we observed a high rate of  $NPP_{FineRoot}$  at 1855 m compared with other montane forest sites, with values comparable to that of some lowland sites. Although this site is located at the

**Table 4** Statistical significance of net primary productivity (NPP) correlations with mean annual values of weather parameters along the Kosñipata elevational transect. Units of slope are in  $\text{Mg C ha}^{-1} \text{ yr}^{-1} \text{ } ^\circ\text{C}^{-1}$  for temperature correlations and  $\text{Mg C ha}^{-1} \text{ yr}^{-1} \text{ mm}^{-1}$  for rainfall correlations

Variable	NPP <sub>Total</sub>		NPP <sub>Stem</sub>		NPP <sub>Canopy</sub>		NPP <sub>AG</sub>		NPP <sub>FineRoot</sub>		NPP <sub>BG</sub>	
	Air temperature	Rainfall	Air temperature	Rainfall	Air temperature	Rainfall	Air temperature	Rainfall	Air temperature	Rainfall	Air temperature	Rainfall
Constant												
Slope	0.72	0.005	0.10	0.002	0.25	0.002	0.35	0.003	0.30	0.29	0.32	0.002
<i>P</i>	<0.005	<0.5	<0.05	<0.5	<0.005	<0.5	<0.005	<0.5	<0.005	<0.05	<0.005	<0.5
<i>r</i> <sup>2</sup>	0.78	0.33	0.59	0.35	0.77	0.35	0.72	0.34	0.77	0.66	0.78	0.28
<i>n</i>	9	9	9	9	9	9	9	9	9	9	9	9

**Table 5** Stem ( $\text{RT}_{\text{Stem}}$ ) and fine roots ( $\text{RT}_{\text{FineRoots}}$ ) residence time (years,  $\pm$  SE)

Elevation (m)	$\text{RT}_{\text{Stem}}$ (years)	$\text{RT}_{\text{FineRoots}}$ (years)
3025	$39 \pm 1.41$	
3020	$47 \pm 1.26$	$3.78 \pm 0.81$
2720	$42 \pm 1.48$	$2.49 \pm 0.63$
2020	$49 \pm 2.12$	$3.80 \pm 0.73$
1855	$71 \pm 1.91$	$2.01 \pm 0.48$
1500	$64 \pm 1.77$	
1000	$59 \pm 1.18$	$1.09 \pm 0.38$
210	$47 \pm 1.31$	$0.34 \pm 0.61$
194	$70 \pm 1.33$	$0.31 \pm 0.61$

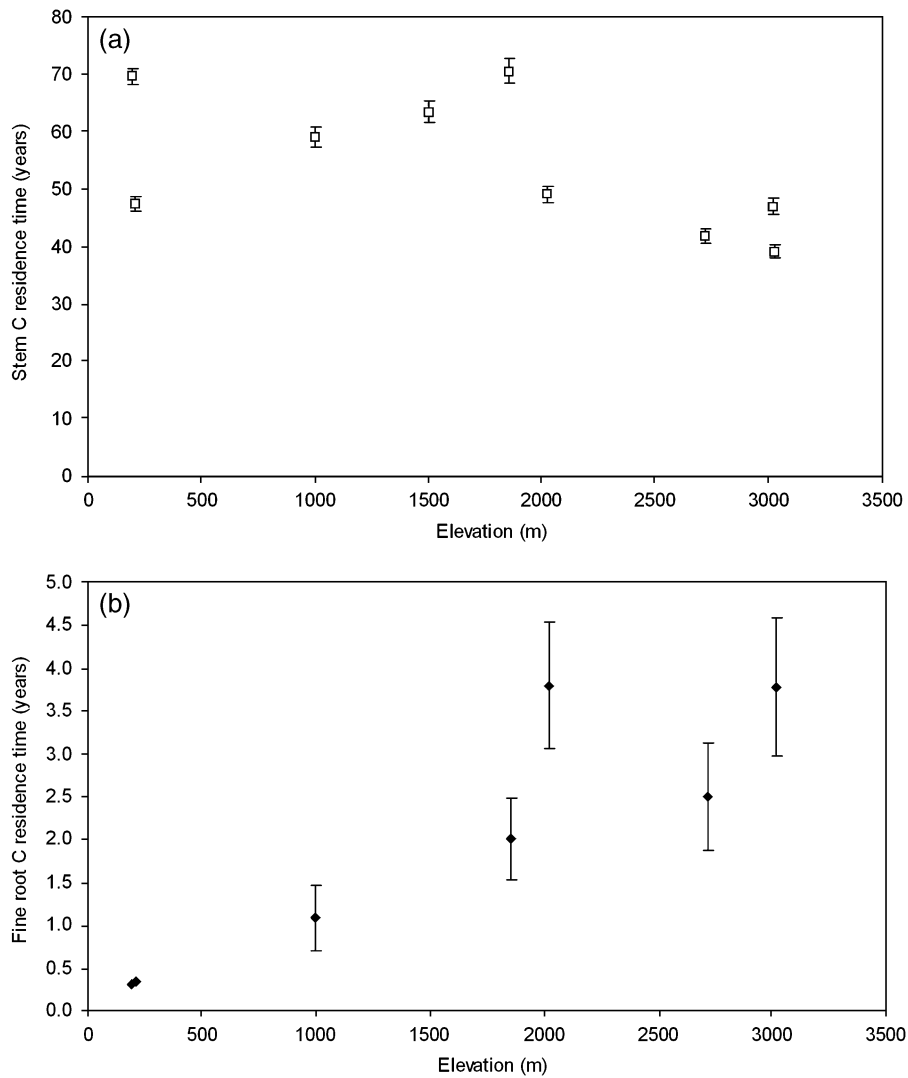
As we could not directly estimate SE of stem carbon stocks, we assumed a SE of 3% for  $\text{RT}_{\text{Stem}}$ , based on data available from lowland plots (Aragão *et al.*, 2009).

base of the cloud immersion zone, SWC is lower at this site than in other montane forest sites, as the soils are very steep and well drained in that plot. It is also possible that the anomaly at 1855 m is driven secular trends, if long-term warming is causing cloud base height to rise and the previous cloud base region to dry. Although light incidence and rainfall patterns do not change significantly within the cloud immersion zone, SWC is uniformly high within the cloud immersion zone (probably a consequence of droplet deposition and low transpiration rates) and decreases significantly below 1855 m.

There appears to be a temperature dependency of NPP in nonsaturated soils, but no temperature sensitivity in the saturated soils. This may imply that the controlling factor is soil mineralization rates, which are strongly influenced by temperature in the lower sites, but are restricted by soil saturation within the cloud zone. Hence our results only partly confirm our hypothesis (4): *NPP decline can largely be explained by decreasing temperature as elevation increases, albeit this relationship is likely to be an indirect one, via decay and mineralization rates.*

#### C residence time

The discrepancy between above- vs. belowground allocation between biomass and NPP may be explained by differences in residence time of the C in above- and belowground components. The stock of C in a particular C pool depends both on the rate of production of that pool and the mean residence time (or decomposition rate) of that pool. C residence time differs for different pools of C in the ecosystem (Malhi *et al.*, 2009). Coarse wood has the longest residence time. Aboveground, stems have a C residence time of 42–71 years with insignificant lower residence times occurring at higher



**Fig. 8** (a) Stem (b) and fine root carbon residence time (years) along the elevational gradient. Error bars are SE of the mean. The estimated base of the cloud immersion zone is located at 1500–1800 m.

elevations as a result of high disturbance caused by high wind exposure and steep slopes in the high elevation sites. In Amazonian forests, coarse wood (stems and branches) represent about 30% of  $NPP_{AG}$ , with a mean residence time of 50–100 years (Malhi *et al.*, 2006).

In contrast, the C residence times in belowground components increase with elevation from 4 months in the lowlands to almost 4 years at high elevations (Fig. 8). Root residence time should be partly determined by the cost of root tissue construction and maintenance, which is related to root C and N content (Gill & Jackson 2000). There is evidence that low root tissue N content is linked with longer residence time (Gordon & Jackson 2000; Hendricks *et al.*, 2006). Hence, waterlogged soils would contribute to longer residence time by slowing root mineral uptake. Increasing soil acidity, as that

found in the high elevation soils of the Kosñipata transect, was also found to increase fine root residence time in temperate forests (Jentschke *et al.*, 2001). In our study, decreasing temperatures explained 78% of the variance in fine root residence time (slope =  $-0.24$ ,  $r^2 = 0.78$ ,  $P < 0.05$ ,  $n = 6$ ). This long residence time explains the shift in C stocks from above- to belowground as elevation increases, despite the consistently slower productivity rates observed belowground.

#### Concluding remarks

In summary, this study describes changes in total biomass and NPP and their allocation between above- and belowground components in nine tropical forests sites along an elevational transect in the Peruvian

Andes. It found that (i) there is no change in total C stock with elevation, but there is a shift in relative stock of C from above- to belowground; (ii) total NPP declines with elevation, but the proportion of NPP allocated to above- and belowground components stays fixed along the elevation gradient; (iii) NPP declines linearly with elevation in lower forests, but is at a fairly constant low level within the cloud forest zone. We conjecture that this pattern is driven by temperature limitation of mineralization in the in lower forests, and by water-saturation inhibition of mineralization in the cloud forest zone; and (iv) the NPP allocation patterns on the elevation transect are similar to those observed for lowland Amazonian forests. The discrepancy between above- vs. belowground allocation between biomass and NPP is explained by differences in residence time of the C in above- and belowground components. Aboveground woody biomass components have a C residence time of 42 to 71 with lower residence times occurring at higher elevations as a result of high disturbance rates. In contrast, the C residence times in belowground components increase with elevation from 4 months in the lowlands to almost 4 years at high elevations.

The work presented here and compiled from our other recent publications (Aragão *et al.*, 2009; Malhi *et al.*, 2009) probably represents the most comprehensive dataset to date on the C allocation of tropical forests (16 study plots in total). We have compiled enough data to propose an approximate 'rule of thumb' for the partitioning of NPP in Amazonian and Andean forests (and perhaps in other tropical forests). Our data suggest that approximately  $33 \pm 30\%$  of NPP<sub>Total</sub> is allocated to canopy production,  $20 \pm 8\%$  to aboveground woody production (and  $61 \pm 21\%$  to aboveground NPP, including coarse root production). Below ground,  $35 \pm 25\%$  of NPP<sub>Total</sub> is allocated to fine root production,  $4 \pm 2\%$  to coarse root production (and hence  $39 \pm 25\%$  in total to belowground NPP). This rule may of course be revised and refined as new data are collected; nevertheless it may be useful as it is for those attempting to model allocation of NPP, and in particular relate NPP to woody biomass construction.

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### References

- Aragão LEOC, Malhi Y, Metcalfe DB *et al.* (2009) Above- and below-ground net primary productivity across ten Amazonian forests on contrasting soils. *Biogeosciences*, **6**, 2441–2488.
- Bekku Y, Kimura M, Ikeda H, Koizumi H (1997) Carbon input from plants to soil through root exudation in *Digitaria adscendens* and *Ambrosia artemisiifolia*. *Ecological Research*, **12**, 305–312.
- Bernier PY, Robitaille G (2004) The plane intersect method for estimating fine root productivity of trees from minirhizotron images. *Plant Soil*, **265**, 165–173.
- Bloom A, Chapin FS III, Mooney H (1985) Resource limitation in plants—an economic analogy. *Annual Review of Ecology and Systematics*, **16**, 363–392.
- Burke MK, Raynal DJ (1994) Fine-root growth phenology, production, and turnover in a Northern hardwood forest ecosystem. *Plant and Soil*, **162**, 135–146.
- Chambers JM (2008) *Software for Data Analysis: Programming with R*. Springer, New York.
- Chave J, Andalo C, Brown S *et al.* (2005) Tree allometry and improved estimation of carbon stocks and balance in tropical forests. *Oecologia*, **145**, 87–99.
- Chave J, Muller-Landau HC, Baker TR *et al.* (2006) Regional and phylogenetic variation of wood density across 2456 neotropical tree species. *Ecological Applications*, **16**, 2356–2367.
- Clark DA, Brown S, Kicklighter DW, Chambers JQ, Thomlinson JR, Ni J (2001a) Measuring net primary production in forests: concepts and field methods. *Ecological Applications*, **11**, 356–370.
- Clark DA, Brown S, Kicklighter DW, Chambers JQ, Thomlinson JR, Ni J, Holland EA (2001b) Net primary production in tropical forests: an evaluation and synthesis of existing field data. *Ecological Applications*, **11**, 371–384.
- Cuevas E, Medina E (1988) Nutrient dynamics within Amazonian forests 2. Fine root-growth, nutrient availability and leaf litter decomposition. *Oecologia*, **76**, 222–235.
- Delaney M, Brown S, Lugo AE, TorresLezama A, Quintero NB (1997) The distribution of organic carbon in major components of forests located in five life zones of Venezuela. *Journal of Tropical Ecology*, **13**, 697–708.
- Del Grosso S, Parton W, Stohlgren T *et al.* (2008) Global potential net primary production predicted from vegetation class, precipitation, and temperature. *Ecology*, **89**, 2117–2126.
- Gill RA, Jackson RB (2000) Global patterns of root turnover for terrestrial ecosystems. *New Phytologist*, **147**, 13–31.
- Gordon WS, Jackson RB (2000) Nutrient concentrations in fine roots. *Ecology*, **81**, 275–280.
- Graefe S, Hertel D, Leuschner C (2008) Fine root dynamics along a 2,000 m elevation transect in South Ecuadorian mountain rainforests. *Plant and Soil*, **313**, 155–166.
- Hendricks JJ, Hendrick RL, Wilson CA, Mitchell RJ, Pecot SD, Guo D (2006) Assessing the patterns and controls of fine root dynamics: an empirical test and methodological review. *Journal of Ecology*, **94**, 40–57.
- Herbert DA, Fownes JH (1999) Forest productivity and efficiency of resource use across a chronosequence of tropical montane soils. *Ecosystems*, **2**, 242–254.
- Intergovernmental Panel on Climate Change. (2007) *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the IPCC*. Cambridge University Press, Cambridge, UK, 989pp.
- Jentschke G, Drexhage M, Fritz WH *et al.* (2001) Does soil acidity reduce subsoil rooting in 40-year-old Norway spruce (*Picea abies*)? *Plant Soil*, **237**, 91–108.
- Kitayama K, Aiba SI (2002) Ecosystem structure and productivity of tropical rain forests along altitudinal gradients with contrasting soil phosphorus pools on Mount Kinabalu, Borneo. *Journal of Ecology*, **90**, 37–51.
- Kitayama K, Mueller Dombois D (1994) An altitudinal transect analysis of the windward vegetation on Haleakala, a Hawaiian island mountain: (2) vegetation zonation. *Phytocoenologia*, **24**, 135–154.
- Leuschner C, Moser G, Bertsch C, Roderstein M, Hertel D (2007) Large altitudinal increase in tree root/shoot ratio in tropical mountain forests of Ecuador. *Basic and Applied Ecology*, **8**, 219–230.
- Litton CM, Raich JW, Ryan MG (2007) Carbon allocation in forest ecosystems. *Global Change Biology*, **13**, 2089–2109.



- Malhi Y, Aragão LEOC, Metcalfe DB *et al.* (2009) Comprehensive assessment of carbon productivity, allocation and storage in three Amazonian forests. *Global Change Biology*, **15**, 1255–1274.
- Malhi Y, Baker TR, Phillips OL *et al.* (2004) The above-ground coarse wood productivity of 104 Neotropical forest plots. *Global Change Biology*, **10**, 563–591.
- Malhi Y, Baldocchi DD, Jarvis PG (1999) The carbon balance of tropical, temperate and boreal forests. *Plant Cell and Environment*, **22**, 715–740.
- Malhi Y, Wood D, Baker TR, Wright J, Phillips OL, Cochrane T (2006) The regional variation of aboveground live biomass in old-growth Amazonian forests. *Global Change Biology*, **12**, 1107–1138.
- Metcalfe D, Meir P, Aragão LEOC *et al.* (2008a) Sample sizes for estimating key ecosystem characteristics in a tropical terra firme rainforest. *Forest Ecology and Management*, **255**, 558–566.
- Metcalfe D, Meir P, Aragão LEOC *et al.* (2008b) The effects of water availability on root growth and morphology in an Amazon rainforest. *Plant and Soil*, **311**, 189–199.
- Metcalfe D, Williams M, Aragão LEOC *et al.* (2007) A method for extracting plant roots from soil which facilitates rapid sample processing without compromising measurement accuracy. *New Phytologist*, **174**, 697–703.
- Moser G, Röderstein M, Soethe N *et al.* (2008) *Altitudinal Changes in Stand Structure and Biomass Allocation of Tropical Mountain Forests in Relation to Microclimate and Soil chemistry*. *Ecological Studies*, 198. Springer Verlag, Berlin, Heidelberg, pp. 229–242.
- Ostertag R (2001) Effects of Nitrogen and phosphorous availability on fine root dynamics in Hawaiian montane forests. *Ecology*, **82**, 485–499.
- Raich JW, Russell AE, Vitousek PM (1997) Primary productivity and ecosystem development along an elevational gradient on Mauna Loa, Hawai'i. *Ecology*, **78**, 707–721.
- Roderstein M, Hertel D, Leuschner C (2005) Above- and below-ground litter production in three tropical montane forests in southern Ecuador. *Journal of Tropical Ecology*, **21**, 483–492.
- Roy R, Saugier B, Mooney HA (2001) *Terrestrial Global Productivity*. Academic Press, New York, 573pp.
- Schuur EAG, Matson PA (2001) Net primary productivity and nutrient cycling across a mesic to wet precipitation gradient in Hawaiian montane forest. *Oecologia*, **128**, 431–442.
- Steingrobe B, Schmid H, Claassen N (2000) The use of the ingrowth core method for measuring root production of arable crops: influence of soil conditions inside the ingrowth core on root growth. *Journal of Plant Nutrition and Soil Science*, **163**, 617–622.
- Takyu M, Aiba SI, Kitayama K (2002) Effects of topography on tropical lower montane forests under different geological conditions on Mount Kinabalu, Borneo. *Plant Ecology*, **159**, 35–49.
- Tanner EVJ, Grubb PJ (1999) *NPP tropical forest: John Crow Ridge, Jamaica, 1974–1978*. Data set, Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, TN, USA.
- Vogt KA, Grier CC, Meier CE *et al.* (1982) Mycorrhizal role in net primary production and nutrient cycling in *Abies amabilis* ecosystems in western Washington. *Ecology*, **63**, 370–380.
- Vogt KA, Vogt DJ, Bloomfield J (1998) Analysis of some direct and indirect methods for estimating root biomass and production of forests at an ecosystem level. *Plant and Soil*, **200**, 71–89.
- Waide RB, Zimmerman JK, Scatena FN (1998) Controls of primary productivity: lessons from the Luquillo mountains in Puerto Rico. *Ecology*, **79**, 31–37.