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Fine root dynamics along an elevational gradient in tropical Amazonian and Andean forests

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[1]   The key role of tropical forest belowground carbon stocks and fluxes is well recognised as one of the main components of the terrestrial ecosystem carbon cycle. This study presents the first detailed investigation of spatial and temporal patterns of fine root stocks and fluxes in tropical forests along an elevational gradient, ranging from the Peruvian Andes (3020 m) to lowland Amazonia (194 m), with mean annual temperatures of 11.8°C to 26.4 °C and annual rainfall values of 1900 to 1560 mm yr^{-1}, respectively. Specifically, we analyse abiotic parameters controlling fine root dynamics, fine root growth characteristics, and seasonality of net primary productivity along the elevation gradient. Root and soil carbon stocks were measured by means of soil cores, and fine root productivity was recorded using rhizotron chambers and ingrowth cores. We find that mean annual fine root below ground net primary productivity in the montane forests (0–30 cm depth) ranged between 4.27±0.56 Mg C ha^{-1} yr^{-1} (1855 m) and 1.72±0.87 Mg C ha^{-1} yr^{-1} (3020 m). These values include a correction for finest roots (<0.6 mm diameter), which we suspect are under sampled, resulting in an underestimation of fine roots by up to 31% in current ingrowth core counting methods. We investigate the spatial and seasonal variation of fine root dynamics using soil depth profiles and an analysis of seasonal amplitude along the elevation gradient. We report a stronger seasonality of NPP_{FineRoot} within the cloud immersion zone, most likely synchronised to seasonality of solar radiation. Finally, we provide the first insights into root growth characteristics along a tropical elevation transect: fine root area and fine root length increase significantly in the montane cloud forest. These insights into belowground carbon dynamics of tropical lowland and montane forests have significant implications for our understanding of the global tropical forest carbon cycle.

1.   Introduction

[2]   The key role of tropical forest belowground carbon (C) stocks and fluxes is well recognised as one of the main components of the terrestrial ecosystem carbon cycle. The lowland Amazonian rainforest alone holds 24 Pg C in its top 30 cm soil surface [*Batjes et al.*, 2005], estimated as 21 % to 29 % of the total carbon stock of the Amazon rainforest [*Houghton*, 2000; *Malhi*, 2005]. To understand tropical forest ecosystem function, it is valuable to record information about soil C stocks and spatial and temporal patterns of fine root net primary productivity, biomass and

residence time (i.e., fine root dynamics). However, we are only beginning to understand fine root C dynamics of tropical montane forests (TMFs). While considerable work has been undertaken on the assessment of the main aboveground components of *NPP* for many forest ecosystems [*Clark et al.*, 2001; *Malhi et al.*, 2011], the quantification of belowground *NPP* is still in its early years and our understanding of ecosystem-level productivity is limited. To date, studies from only three elevational transects have provided data on fine root dynamics along TMF elevational gradients, in Borneo [*Kitayama and Aiba*, 2002], in the Ecuadorian Andes [*Leuschner et al.*, 2007], and in the Peruvian Andes [*Girardin et al.*, 2010]. All studies found evidence of an increase in fine root biomass with increasing elevation. *Girardin et al.* [2010] reported 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 below the cloud base. These authors also report a decrease in mean annual fine root productivity and increase in residence time with increasing elevation. On the other hand, *Roderstein et al.* [2005] found that fine root productivity increased

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threefold with elevation in the Ecuadorian Andes. At the same site, *Graefe et al.* [2008a] found that fine roots in the lower-most (1000 m) and upper-most (3020 m) stands had lower residence time than midelevation stands. These studies point to the importance of quantifying C residence time to understand the C cycle of a terrestrial ecosystem [*Lal*, 2006; Galbraith et al., in review].

[3] The present study builds upon a previous study by *Girardin et al.* [2010] in which we report an increase in root biomass (1.50 to 4.95 $\pm$ 0.62 Mg C ha^{-1}) and residence time (1.04 to 3.78 years), and a decrease in $NPP_{FineRoots}$ (4.80 $\pm$ 0.57 to 1.31$\pm$0.23 Mg C ha^{-1} yr^{-1}) with increasing elevation (194 to 3020 m). Here, we dissect the spatial and seasonal patterns of fine root carbon stocks, productivity and residence time to explore the abiotic controls of below ground carbon dynamics. Specifically, we address the following questions: (1) What are the spatial and seasonal patterns of soil C stocks, fine root C stocks, *NPP* and residence time along the elevational gradient? (2) What are the key abiotic drivers of fine root dynamics? (3) How do fine root growth characteristics (fine root specific length and fine root specific area) vary with elevation?

2. Materials and Methods

2.1. Site Description

2.1.1. Site History

[4] Since 2003, the Andes Biodiversity Ecosystems Research Group (ABERG, andesresearch.org) has operated a number of permanent hectare plots in the Kosñipata Valley in S.E. Peru [*Malhi et al.*, 2010]: eight along the Trocha Union ridge-top trail (1855–3500 m asl), two at the Estación Biologica de Wayqecha (2825–3025 m asl) and two at San Pedro (1500–1750 m asl) where the valley enters the Madre de Dios region of Peru. Henceforth, we refer to these plots as the Kosñipata elevational transect. Partial carbon cycle data from the elevational transect have been reported in previous papers: soil carbon stocks in *Zimmermann et al.* [2009, 2010], forest aboveground and belowground productivity in *Girardin et al.* [2010], leaf physiology in *van der Weg et al.* [2011], modeling studies in *Marthews et al.* [2012], and stem respiration in *Robertson et al.* [2010]. *Girardin et al.* [2010] reported change in total biomass, mean annual *NPP* and *NPP* allocation between aboveground and below-ground components in nine forest sites along the gradient. In terms of belowground *NPP*, these authors observed a decline in fine root *NPP* with elevation, although the proportion of *NPP* allocated to aboveground and belowground components showed no net trend along the elevation gradient. The present paper builds on this previous work by providing the first comprehensive description of the seasonal and spatial variation of fine root *NPP*, residence time and root growth characteristics along the Kosñipata elevation transect.

2.1.2. Site Characteristics

[5] The six experimental sites were located on the eastern slope of the Andes, in the Kosñipata valley, Province of Paucartambo, Department of Cusco, Peru (3025 m elevation, lat 13° 11′ 24″ S long 71° 35′ 13″ W to 1855 m elevation, lat 13° 4′ 16″ S long 17° 33′ 18″ W). One additional site (Tono) located in a neighbouring valley near the base of the Kosñipata valley was established at 1000 m elevation (lat 12° 57′ 33″ S long 71° 33′ 57″ W). A further two sites

were established and monitored according to the same protocol in the Tambopata reserve, Peru (210 m elevation, lat 12° 50′ 11″S long 69° 16′ 45″ W and 194 m elevation, lat 12° 49′ 48″ S long 69° 16′ 16″ W). *NPP* data from these lowland sites were presented in *Aragão et al.* [2009]. Permanent plots of 1 ha projected area were established along the elevational gradient, extending from lowland forest (<800 m), through premontane (800–1200 m), lower montane (1200–2200 m) and upper montane forest (2200–3400 m). Plots between 1500 m and 3020 m undergo frequent periods of immersion in clouds, and have structural features of cloud forest (short stature, gnarled trunks and branches, dense compact crowns, small tough leaves (sclerophyll), more soil organic matter as altitude increases). All plots were selected in areas with relatively homogeneous stand structure, geological substrate and topography, and with minimal signs of human interference. All have closed canopies without any large gaps. As the geological substrate and topographic position can have a significant impact on montane forest dynamics, all the montane plots along the main transect were established along a ridge-top with the same substrate (Palaeozoic shales-slates, except the plots at 1500 m and 1855 m, which sits on a granite intrusion) and soil type (humus-rich fine argillaceous soils). Soil C, nitrogen (N) and phosphorus (P) stocks are highest in the 1500–3000 m band (an order of magnitude higher than in the lowland forests, Quesada (personal communication, 10/11/2012)), where there is a build up of a thick layer of humic material (typically 20–30 cm thick) above a carbon-rich A horizon (Table 1). A further description of the sites is provided in *Girardin et al.* [2010].

2.2. Climate

[6] Solar radiation, photosynthetically active radiation (PAR), air temperature, relative humidity and precipitation time series were collected from automatic weather stations (AWS) located in the valley near the 3025 m, 1500 m and 1000 m plots. At each ingrowth core and rhizotron collection session, soil temperature was recorded at a soil depth of 10 cm using a Testo 926 thermometer and Testo penetration probe T260 (Testo Ltd, Hampshire, U.K.) and volumetric soil water content (SWC) was recorded over a soil depth of 0–30 cm using a water content reflectometer CS616 probe and a Hydrosense data logger (Campbell Scientific, Loughborough, U.K.). Information on climate data collection and analysis is provided in more detail in *Girardin et al.* [2010].

[7] SWC data were directly calibrated for the highly organic soils of tropical montane forests [*Zegelin*, 1989; *Heimovaara*, 1993] by determining the linear relation between SWC estimated with the CS616 probe and a Hydro-sense data logger and SWC estimated using a gravimetric method. Soil samples from three plots (at 3025 m, 1500 m, and 1000 m) were collected in the field, brought to the lab and saturated with water. They were then left to dry in open air for several days, their SWC and weight were estimated at regular intervals using the Hydrosense data logger and a precision balance over the first 48 h. Finally, the samples were oven dried at 100 °C to constant mass (no free water). The gravimetric water content of each sample was estimated using the equation ((mass-dry mass)$\times$100)/mass. The linear equation obtained from regressing SWC measured using the Hydrosense data logger with SWC derived from the gravimetric method was used to calibrate the SWC dataset.

Table 1. Summary of Site Characteristics

Site Code	Wayqecha WAY	Trocha Union III TU3	Trocha Union IV TU4	Trocha Union VII TU7	Trocha Union VIII TU8	San Pedro SPD	Tono TON	Tambopata III TAM3	Tambopata IV TAM4
Latitude	13° 11' 24" S	13° 6' 34" S	13° 6' 30" S	13° 4' 24" S	13° 4' 16" S	13°2'56" S	12° 57' 33" S	12° 50' 11" S	12° 49' 48" S
Longitude	71° 35' 13" W	71° 35' 59" W	71° 35' 21" W	71° 33' 30" W	71° 33' 18" W	71°32'13" W	71° 33' 57" W	69° 16' 45" W	69° 16' 16" W
Elevation (m)	3025	3020	2720	2020	1855	1500	1000	210	194
Aspect	E	W	W	W	W	W	W	-	-
Slope (%)	28	12	n/a	18	31	27	8	n/a	n/a
Soil profile OL:ML (cm)	20:4	42:11	43:9	35:27	26:26	10:45	5:42	2:30	2:30
Mean annual air temp. (°C)	12.5 ± 0.05	11.8 ± 0.01	13.5 ± 0.01	17.4 ± 0.02	18.03 ± 0.01	18.8 ± 0.02	20.7 ± 0.02	26.4	26.4
Mean annual soil temp. (°C)	11.5 ± 0.02	10.4 ± 0.01	11.9 ± 0.01	16.1 ± 0.02	17.4 ± 0.02	19.1 ± 0.03	20.7 ± 0.02	23.9 ± 0.02	24.5 ± 0.18
Annual precipitation (mm yr^{-1})	1560*	1776	2318	1827	2472	5302*	3087	1900[a]	1900[a]
Soil C content (%)	n/a	n/a	30.1	n/a	18.8	10.7	n/a	1.1	0.8
Soil N content (mg/kg)	15420	n/a	n/a	n/a	n/a	8648	9470	9230	n/a
Soil P content (mg/kg)	1154	n/a	n/a	n/a	n/a	727	628	760	n/a
Soil pH	4.1	2.7	3.02	2.92	3.43	4.0	3.7	3.9	n/a
Geological substrate	Paleozoic shales-slates	Paleozoic shales-slates	Paleozoic shales-slates	Paleozoic shales-slates	Granite batholith	Granite batholith	Alluvial terrace	Pleistocene alluvial terrace	Holocene alluvial terrace

[a]Mean annual precipitation data were updated with values from *Girardin et al.* [2013], *Huaraca Huasco et al.* [2013], *Malhi et al.* [2013].

Data from other plots were calibrated using the equation from the closest calibration equation available. One rain gauge was placed above the canopy in each plot and precipitation was collected approximately biweekly by measuring the level of water (mm) collected. Annual rainfall was estimated by adding all rainfall values collected over a year.

2.3. Measurement of Fine Root Productivity

[8] We utilised two approaches to estimate fine root productivity: rhizotrons and soil ingrowth cores. A detailed description of the methodologies described here is provided in *Marthews et al.* [2012].

2.3.1. Rhizotrons

[9] The net primary productivity of fine roots ($NPP_{FineRoot}$) was estimated using root observation pits (screen rhizotrons), a method for measuring surface root growth (≤30 cm depth, 35 cm wide) in tropical field sites, allowing more regular readings than in-growth cores (monthly as opposed to three-monthly) [*Burke and Raynal*, 1994; *Metcalfe et al.*, 2008; *Girardin et al.*, 2010]. Three rhizotrons were installed at the end of the dry season in areas characterising the topographic variation of each site (November 2006). Monthly root growth was recorded from the rhizotrons over 23 months. Root increments were recorded 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 = red, 2–3 mm = blue, <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 and equations (1 and 2) described by *Bernier and Robitaille* [2004]. This method uses information on the number and root diameter of roots touching the rhizotron screen at each data collection session. These values permit us to calculate the total cross sectional surface area of the roots intersecting the rhizotron screen at each session (XSr, mm^2) from root radius (r, mm) using the following equation:

$$XSr = \left(\pi^2 \sum r^2 / \sqrt{2} \right) \tag{1}$$

[10] Root production ($NPP_{FineRoot}$, Mg ha^{-1}) was estimated for each data collection session using the following equation:

$$NPP_{FineRoot} = 2 \times 10^4 \times D_r(1\text{-}F_c \times XS_r \times ((sin\,\alpha \times cos\,\gamma)/W) \tag{2}$$

where 10^4 converts g mm^{-2} into Mg ha^{-1}, D_r is the density of the root tissue obtained by dividing the root volume by the root mass recorded from the ingrowth core data, F_c is the soil coarse fraction (the fraction of soil composed of particles >2 mm; usually = 0 in forest soils), α is the angle of the rhizotron observation screen relative to the ground (for a rhizotron inserted vertically, should = 90°), γ is the ground angle relative to the horizontal (i.e., on a 1 in 10 slope put = atan(1/10) = 5.7°), and W is the width of the rhizotron screen (mm). Finally, the multiplication factor of 2 is used because roots can only intersect with the rhizotron screen from behind (i.e., it is assumed that if there was not

an empty space in front of the rhizotron screen to allow for measurement and observation then an equal amount of roots would intersect from behind as well as from the front). For this same reason, roots which branched after contact with the rhizotron observation screen were not counted as new roots at the point of branching [*Marthews et al.*, 2012].

2.3.2. Root Ingrowth Cores

[11] Fine root productivity was also quantified in all plots using the ingrowth core (IC) technique [*Vogt et al.*, 1998; *Steingrobe et al.*, 2000; *Hendricks et al.*, 2006], following the methodology described in *Metcalfe et al.* [2007]. These are cores (mesh cages 12 cm diameter, installed to 30 cm depth) of root-free soil in which roots were allowed to grow over a set period of time (3 months), providing estimates of fine root production per unit area and time (Mg ha^{-1} yr^{-1}). Nine ingrowth cores were installed in the plots in May 2007, in close proximity to rhizotrons. Soil cores were extracted and soil layers were separated into organic layer (OL) and mineral layer (ML) to avoid mixing the nutrient rich organic soil with the mineral soil. Fine roots were manually removed every three months using a method which corrects for underestimation of fine root biomass [*Metcalfe et al.*, 2008]. Root-free soil was then replaced in each ingrowth core, keeping the same bulk density of the undisturbed soil. Sampled fine roots were rinsed in water to remove soil particles, scanned as greyscale images at 600 dpi resolutions, oven dried at 70°C in the lab until constant mass and weighed. Monthly NPP_{FineRoot} was estimated from the quantity of fine root mass produced in the three months' interval since the last collection, allowing us to estimate annually averaged fine root growth. We sampled roots <5 mm diameter, separated into fine roots (<2 mm) and coarse roots (2–5 mm). In ecological literature, fine roots are conventionally defined as roots <2 mm diameter and coarse roots include all roots above 2 mm diameter [*Cornelissen et al.*, 2003; *Graefe et al.*, 2008a; *Metcalfe et al.*, 2008; *Aragão et al.*, 2009; *Marthews et al.*, 2012]. For the purpose of this paper, IC coarse roots are defined as roots 2–5 mm in diameter, as ingrowth cores capture root growth data up to 5 mm. The scanned images were analyzed using commercially available software (WinRHIZO Pro version 2003b, Regent Instruments, Canada), to calculate fine root length and surface area, according to the methodology described in *Metcalfe et al.* [2008]. Finally, organic layer depth and mass were also measured to 30 cm depth at 25 points for each elevation (five at 2020 m), using a 12 cm diameter manual soil corer.

2.4. Soil and Fine Root Carbon Stocks

[12] Fine root biomass in the organic layer and mineral layer and mass of the soil organic layer were measured using the first ingrowth cores sampled in May 2007 at 0–30 cm depth. We estimated soil mineral layer carbon stocks by sampling the mineral layer to 30 cm soil depth in two subplots per plot and scaling up to 1 ha. As rhizotron data do not directly provide root biomass values, we could not estimate biomass and residence time for each 10 cm depth. However, data from the ingrowth cores provided $NPP_{\text{Fine-Root}}$ and biomass values for the soil organic layer. These values permitted us to estimate residence time in the organic layer and mineral layer at most elevations (Table 2).

2.5. Analytical Techniques

[13] We describe the spatial and temporal variations of soil and fine root C stocks, NPP_{FineRoot}, and fine root C turnover along the Kosñipata elevational gradient. All sampling variance is summarised as the standard error (SE) of the mean. Linear regression analyses were conducted to identify significant effects of elevation, soil temperature, soil water content (SWC), rainfall, and depth of soil organic matter (SOM) on mean annual rate of $NPP_{\text{FineRoots}}$.

[14] We explored the sensitivity of seasonal variation of NPP_{FineRoot} to environmental conditions by determining the sensitivity coefficients of linear regressions between $NPP_{\text{Fine-Root}}$ and soil temperature and plotting these sensitivity coefficients against mean annual soil temperature at each point [*Chatterjee and Hadi*, 2008]. The same approach was carried out for examining the sensitivity of NPP_{FineRoot} to SWC. A univariate analysis of variance (ANOVA) was used to evaluate differences between NPP_{FineRoot} rates at each elevation above 1855 m. All statistical analyses were performed with Matlab statistical packages (MATLAB 7.0.4).

3. Results

3.1. Climate

[15] Mean annual air temperatures over the study period ranged from 26.4 °C (194 m) to 11.8 °C (3000 m). Precipitation decreased from ~1900 mm yr^{-1} in the lowlands to ~1560 mm yr^{-1} at the driest high altitude site (Table 1, Figure 1a). However, this change in precipitation was not monotonic, with the highest rainfall values 5302 mm yr^{-1} recorded near the base of the mountain range (1000–1500 m), where

Table 2. Fine Root (<2 mm) Carbon Turnover Rates in the Organic Layer (OL) and Mineral Layer (ML) Along the Elevational Gradient at Depths Provided in Table 1[a]

Elevation (m.a.s.l)	Organic Layer			Mineral Layer			Total Soil Sampled		
	Fine Root Biomass (MgC ha^{-1})	Residence Time (years)	SE	Fine Root Biomass (Mg C ha^{-1})	Residence Time (years)	SE	Fine Root Biomass (MgC ha^{-1})	Residence Time (years)	SE
3020	4.95	3.78	0.81	-	-		4.95	3.78	0.81
2720	3.77	2.94	0.78	0.28	0.81	1.03	4.05	2.49	0.59
2020	4.97	4.39	1.04	1.87	2.80	0.92	6.83	3.80	0.72
1855	4.24	2.47	0.39	2.31	1.49	0.55	6.54	2.01	0.40
1000	1.48	1.54	0.45	1.15	0.79	0.49	2.62	1.09	0.32
210	-	-	-	-	-	-	2.70	1.13	-
194	-	-	-	-	-	-	1.75	1.04	-

[a]SE denotes the standard error of the mean (estimated according to *Malhi et al.* [2009]).
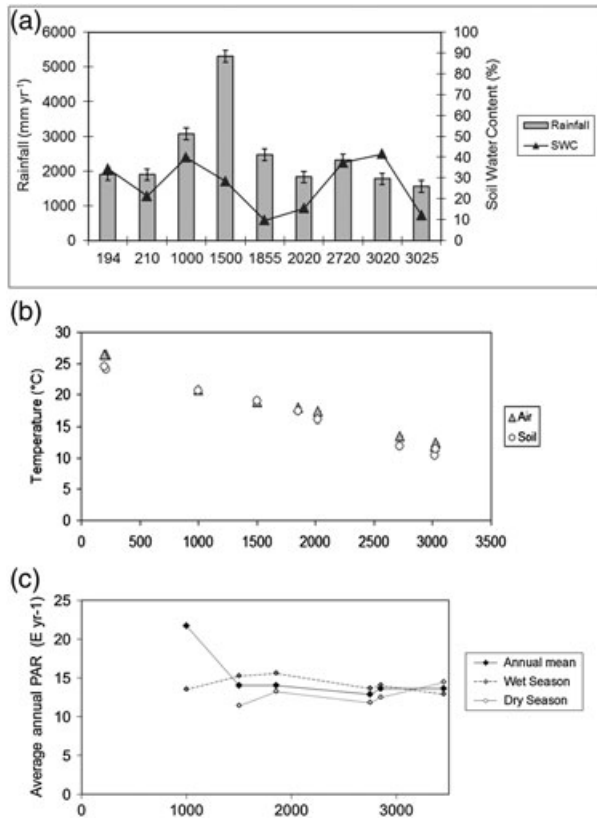
Figure 1. Elevation gradients of (a) rainfall (error bars are minimum and maximum values) and soil water content (SWC), (b) mean annual temperature and soil temperature, (c) photosynthetically active radiation (PAR). Mean annual temperature (slope = -0.0049 °C m^{-1}, r^2 = 0.99, p < 10^{-7}), and soil temperature (circles, slope = -0.0047 °C m^{-1}, r^2=0.99, p < 10^{-7}) are linearly regressed against elevation. PAR values are monthly averages (μE) from June 2007 to July 2008, but data are not available for every month.

orographic uplift of moist Amazonian air results in very high precipitation rates. There was a close association between elevation and temperature (r^2 = 0.99, P < 0.0001), implying a lapse rate of soil temperature of 4.79 °C km^{-1}, and a lapse rate of air temperature of 4.94 °C km^{-1} within the Kosñipata valley (Figure 1b). Mean annual PAR (Figure 1c) was highest in the lowland sites. PAR and soil water content (SWC) did not show a clear and consistent change with elevation (Figures 1a and 1c). This may be explained by micro site effects which reflect site slope, aspect and/or geomorphology rather than elevation [Killeen et al., 2007; Moser et al., 2008]. Rainfall showed strong seasonal patterns along the elevational gradient, with highest rainfall values typically recorded between December and March. Soil temperature and SWC displayed some seasonality at every elevation. The driest months (austral winter, May–July) had lowest soil temperatures, whilst the wettest months (austral summer) displayed highest soil temperatures. Nevertheless, high elevation sites showed little evidence of seasonality in SWC, soil and air temperature. The seasonal variation of these environmental variables becomes more pronounced as elevation decreases. Cloud base is lowest in the austral winter and rises in the austral summer. Relative humidity (RH) at the

sites within the cloud immersion zone is highest in austral winter owing to an increased frequency of cloud immersion, but then reduces to a minimum in September as cloud base height increases before the onset of the wet season. On a diurnal basis, cloud base height decreases from morning to afternoon as a result of moist upslope flow from the lowlands [Halladay et al., 2012]. Hence in the austral winter these plots are frequently immersed in cloud, with a larger degree of immersion in the higher plots.

3.2. Belowground C Stocks

[16] Whereas soil carbon stocks in the organic layer (O-horizon) increased linearly with elevation (Figure 2a, r^2 = 0.92, P < 0.001), we observed a transition in soil organic layer depth (Figure 2b) and fine root C stocks (Figure 3) at the base of the cloud immersion zone (1500–1800 m). The depth of the soil organic layer varied between 2.5±0.3 cm at 194 m and 43±3 cm at 2720 m (Figure 2b), remaining constant within the cloud immersion zone. Soil organic layer C stocks increased significantly with increasing elevation from 2.3 Mg C ha^{-1} at 194 m [Zimmermann et al., 2009] to 84.2±5.5 Mg C ha^{-1} at 3025 m (slope = 0.03, r^2 = 0.93, P < 0.0005, n = 8).

[17] Fine root C stock (Figure 3) was calculated using dry weight biomass data, assuming fine root C stock is 50% of
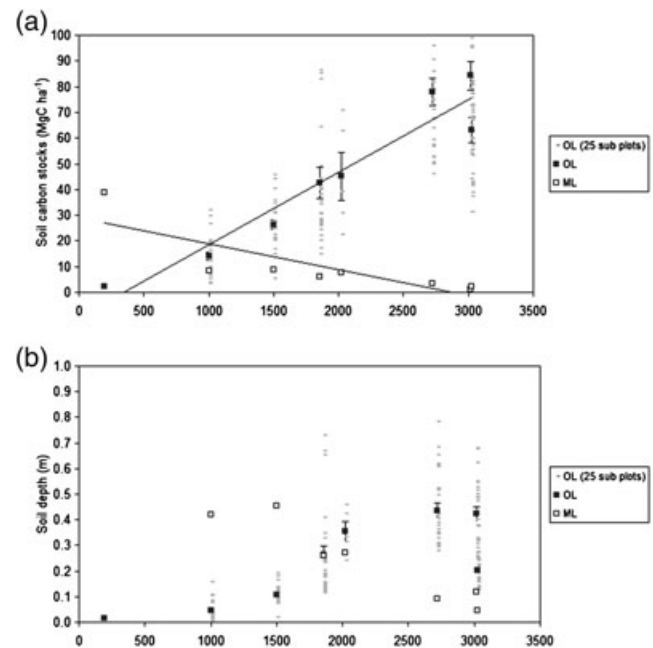
Figure 2. Variation with elevation of (a) soil C stock and (b) soil depth. (a) Soil C stock is provided for the soil organic layer (OL, closed squares, slope of linear regression=0.027 Mg C ha^{-1} m^{-1}, r^2 = 0.92, p < 0.001, n = 8) and mineral layer (ML, open squares) up to maximum sampled depths (1 m or less). (b) Soil depth OL (closed squares) and ML (open squares) are provided for each plot along the elevation gradient. The estimated base of the cloud zone is indicated by lines. Soil OL carbon and depth values were estimated as an average of 25 points at each elevation (grey dashes), soil ML carbon values were estimated as the average of two samples per plot. Soil ML depth in the lowland plots was estimated to be 2.5 m [Quesada, 2008].
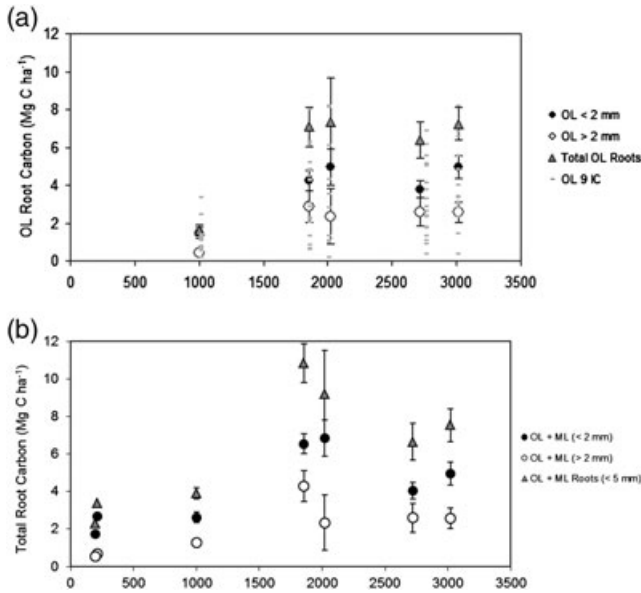
Figure 3. Root C stock in the (a) soil organic layer (OL), and (b) top 0–30 cm of soil (OL and ML). Data represent nine individual soil cores (grey dashes), total ingrowth core root carbon stock (<5 mm, closed triangles), fine roots (<2 mm, closed circles) and fine roots (>2 mm, open circles) against elevation (m). Root carbon values were obtained from nine soil cores sampled in May 2007 at each elevation. Root carbon stock was assumed to be 50% of dry biomass.

fine root mass. In the top 30 cm of soil, *Girardin et al.* [2010] reported a step change in root C stock in the organic layer at high elevations as fine root (<2 mm) carbon stocks increased from 2.62 ± 0.29 Mg C ha^{-1} at 1000 m to 6.54 ± 0.54 Mg C ha^{-1} at 1855 m. An analysis of variance on fine roots in the organic layer (Figure 3a, ANOVA: F = 0.16, P = 0.959) demonstrated that no significant change in fine root C stock occurred above 1855 m.*Zimmermann et al.* [2009] recorded that the average soil C concentrations in the top 30 cm of the soil (including O and A horizons) increased from 5.68 % C at 210 m (predominantly A horizon) to 47.4 % C at 3025 m (purely O horizon), mainly because of the increased depth of the organic layer. This increase in soil organic layer mass and fine root mass along the elevational transect resulted in a significant increase in soil organic layer C stocks at mid to high elevations.

[18] The thickness of the mineral layer (A and B horizons) in the top 400 cm decreased from approximately 250–300 cm [*Quesada et al.*, 2011] in the lowland plots to 4.5 cm at 3025 m elevation (soil depth is defined here as depth to rock or saprolite contact). Figure 2a shows a linear decrease in mineral layer soil carbon stocks with increasing elevation (slope = -0.011, r^2 = 0.69, P < 0.005, n = 8). As we only recorded fine root mass up to 30 cm depth, we only report the pattern of fine root C stocks in the mineral layer along the elevational gradient up to 30 cm total soil depth (Figure 3b). However, the characteristic step change consistently observed at the estimated base of the cloud zone (1500–1800 m) was also recorded for fine root C stocks in the mineral layer (Figure 3b). At all elevations, fine roots (<2 mm) dominated the total IC root C stock (<5 mm), representing 59% to 68% of total organic layer fine root C stock in the high elevation plots and increasing up to 91% in the lower montane forest plot (1000 m).

3.3. Fine Root Production

#### 3.3.1. $NPP_{FineRoot}$ Along the Elevational Gradient
[19] Comparing our estimates of *NPP* from data gathered using ingrowth cores [from *Girardin et al.*, 2010] and rhizotrons showed consistency between the two methods (Table 3, Figure 4, ANOVA: F = 0.53, P = 0.904). Whereas $NPP_{FineRoot}$ values calculated from ingrowth cores ranged between 7.60 ± 0.90 and 2.20 ± 0.40 Mg C ha^{-1} yr^{-1} in lowland Amazonia [*Nadelhoffer and Raich*, 1992; *Silver et al.*, 2000; *Metcalfe et al.*, 2008; *Aragão et al.*, 2009], values ranged between 1.31 ± 0.23 (3020 m) and 3.26 ± 0.59 (1855 m) Mg C ha^{-1} yr^{-1} in our montane sites (this study). We only report on fine root productivity values for 0–30 cm depth, as this study investigates root growth seasonality and it is uncertain that the seasonality of root growth at deeper layers would be identical. Studies from lowland Amazonian rainforests indicate that the top 30 cm depth includes 69–73% of total roots [*Jackson et al.*, 1998; *Quesada et al.*, 2011; Galbraith et al.*, in review].

3.3.2. Abiotic Parameters Controlling $NPP_{FineRoot}$
[20] In our elevational gradient, fine root productivity was positively correlated with soil (slope = 0.29, r^2 = 0.66, P < 0.05, n = 9) and air (slope = 0.30, r^2 = 0.77, P < 0.005, n = 9) temperature, poorly correlated with rainfall (slope = 0.002, r^2 = 0.28, P < 0.5, n = 9), and not correlated with soil water content. $NPP_{FineRoot}$ was significantly seasonal at all elevations, with higher production rates during the wet season at ~3000 m, and higher production rates in the dry season at all other elevations (Table 4).

Table 3. Fine root (< 2mm) Net Primary Productivity (*NPP*, Mg C ha^{-1} yr^{-1}) Estimated Using Ingrowth Cores and Rhizotrons, Specific Fine Root Length (SFRL, km kg^{-1}) and Specific Fine Root Area (SFRA, m^2 kg^{-1})

Elevation (m a.s.l.)	Ingrowth core $NPP_{FineRoot}$ (Mg C ha^{-1} yr^{-1})		SE	Rhizotron $NPP_{FineRoot}$ (Mg C ha^{-1} yr^{-1})		SE	SFRL (km kg^{-1})		SE	SFRA (m^2 kg^{-1})		SE
3025	2.08	±	0.52	4.25	±	1.15	23.18	±	3.64	44.04	±	6.21
3020	1.31	±	0.23	2.80	±	0.48	28.70	±	3.52	57.55	±	5.92
2720	1.62	±	0.31	2.17	±	0.29	39.79	±	6.09	71.39	±	9.70
2020	1.80	±	0.17	2.42	±	0.64	31.29	±	3.20	58.07	±	6.26
1855	3.26	±	0.59	2.99	±	0.61	35.31	±	2.98	65.86	±	5.55
1500	1.70	±	0.13	3.62	±	0.72	36.67	±	4.57	76.20	±	9.30
1000	2.42	±	0.65	2.42	±	0.57	20.30	±	1.37	49.28	±	3.24
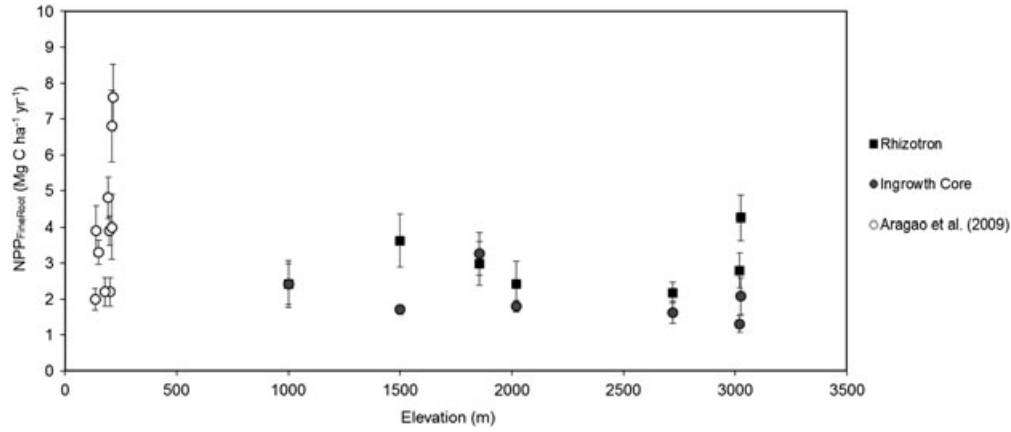
Figure 4. Fine root net primary productivity ($NPP_{FineRoot}$) using rhizotrons and ingrowth cores. $NPP_{FineRoot}$ calculated from rhizotrons (closed squares, n=3) and ingrowth cores (closed circles, n=9). The figure also presents results from *Aragão et al.* [2009] in lowland Amazonia (open circles). Error bars are SE of the mean.

3.3.3. $NPP_{FineRoot}$ per Diameter Class

[21] We plotted fine root productivity against root diameter class, as determined by scanning root samples from the ingrowth cores. We observed a peak in fine root productivity in the 0.5–0.6 mm diameter class (0.28 ± 0.028 Mg ha^{-1} yr^{-1}). From 0.6 to 2 mm, $NPP_{FineRoot}$ decreased linearly with increasing fine root diameter class (slope = -0.09, r^2 = 0.47, P < 0.005, n = 15). This pattern was consistently recorded at all elevations (Figure 5).

3.3.4. Fine Root Growth Characteristics

[22] Figure 6 provides values of fine and coarse root characteristics (length and surface area production) along the elevational gradient. Fine root length growth rate (Figure 6a) in the surface 0-30 cm of soil was estimated to vary between 9.6 (1855 m) and 4.1 km m^{-2} yr^{-1} (1000 m). In the montane forest, fine root surface area growth (Figure 6b) was estimated at 9–17 m^{-2} m^{-2} yr^{-1} above 1000 m and 2.4–3.6 m^2 m^{-2} yr^{-1} in lowland Amazonia. Annual fine and coarse root length and surface area production showed no significant change with elevation at mid- to high elevations.

[23] The mean specific fine root length (SFRL, Figure 6c) values estimated in our premontane to montane sites were five times higher (mean of 31 ± 3 m root g^{-1} root, n = 7) than those obtained by *Metcalfe et al.* [2008] in lowland Amazonia (mean of 6 ± 0.5 km root kg root^{-1}, n = 4). Similarly, our estimates of mean specific fine root area (SFRA, Figure 6d)

in the pre-montane to montane sites (60 ± 4 m^2 kg^{-1}, n = 7) were almost twice as high as those obtained in lowland Amazonia (19 ± 2 m^2 kg^{-1}, n = 4). These first estimates of SFRL and SFRA in TMFs indicate a shift in SFRL and SFRA patterns from lowlands to montane forests. However, neither parameter changed significantly with elevation above 1000 m (ANOVA: P = 0.97, F = 0.15).

3.4. Fine Root C Residence Time

3.4.1. Fine Root C Residence Time Along the Elevation Gradient

[24] The residence time of carbon, i.e., the average time carbon resides in a pool under steady state conditions, is determined as the time between fixation in photosynthates and return to the atmosphere by respiration or chemical transformation into volatile organic compounds, exudates and CH$_4$ [*Lal*, 2006]. Carbon residence time was estimated for fine roots using the fraction of standing fine root biomass to $NPP_{FineRoot}$ obtained from ingrowth core sampling (Table 2) [*Girardin et al.*, 2010]. When we considered the top 30 cm of soil only (organic layer and mineral layer), we observed a significant increase in fine root residence time (slope = 0.012, r^2 = 0.80, P = 0.006, n = 7) with increasing elevation, from 1.04 years (194 m) to 3.78 ± 0.81 years (3020 m). The residence time values for lowland sites (194 and 210 m)

Table 4. Metric of Seasonality of $NPP_{FineRoot}$[a]

| Elevation (m a.s.l.)	Wet Season (Mg C ha^{-1} yr^{-1})	SE	Dry Season (Mg C ha^{-1} yr^{-1})	SE	Difference (Mg C ha^{-1} yr^{-1})	SE	% Difference	SE
3025[b]	2.16	0.60	1.80	0.60	0.36	0.85	17	40
3020[b]	2.11	0.34	1.77	0.15	0.34	0.37	16	18
2720[b]	1.21	0.39	3.30	0.26	-2.09	0.47	-173	-68
2020[b]	1.77	0.31	1.90	0.35	-0.13	0.46	-8	-26
1855[b]	2.23	0.85	3.17	0.73	-0.94	1.12	-42	-53
1500[b]	0.68	0.05	2.60	1.34	-1.92	1.34	-282	-198
1000[b]	2.36	0.24	2.48	0.76	-0.11	0.80	-5	-34

[a]This table presents fine root *NPP* during the wet season (December to March), dry season (May to July), the difference and percentage difference between the two seasons. SE is standard error of the mean. Data are Mg C ha^{-1} yr^{-1}.
[b]There was a significant difference between wet season and dry season $NPP_{FineRoot}$.
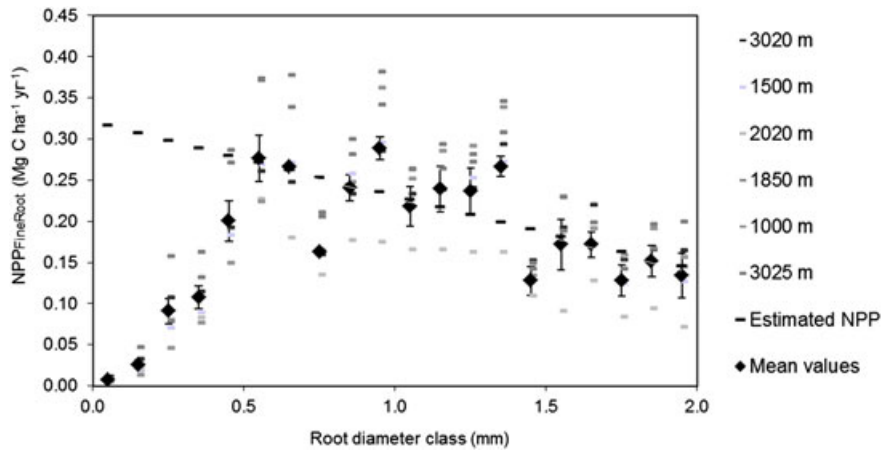
Figure 5. Fine root net primary productivity ($NPP_{FineRoot}$, Mg C ha^{-1} yr^{-1}) per diameter class (mm). Measured values (grey dashed), mean values (closed diamonds, SE of the mean, n=6) and expected values (black dashes), estimated from a linear regression of NPP against diameter classes >0.6 mm (y=-0.09 x+0.32; r^2=0.47; p=0.004; n=15).
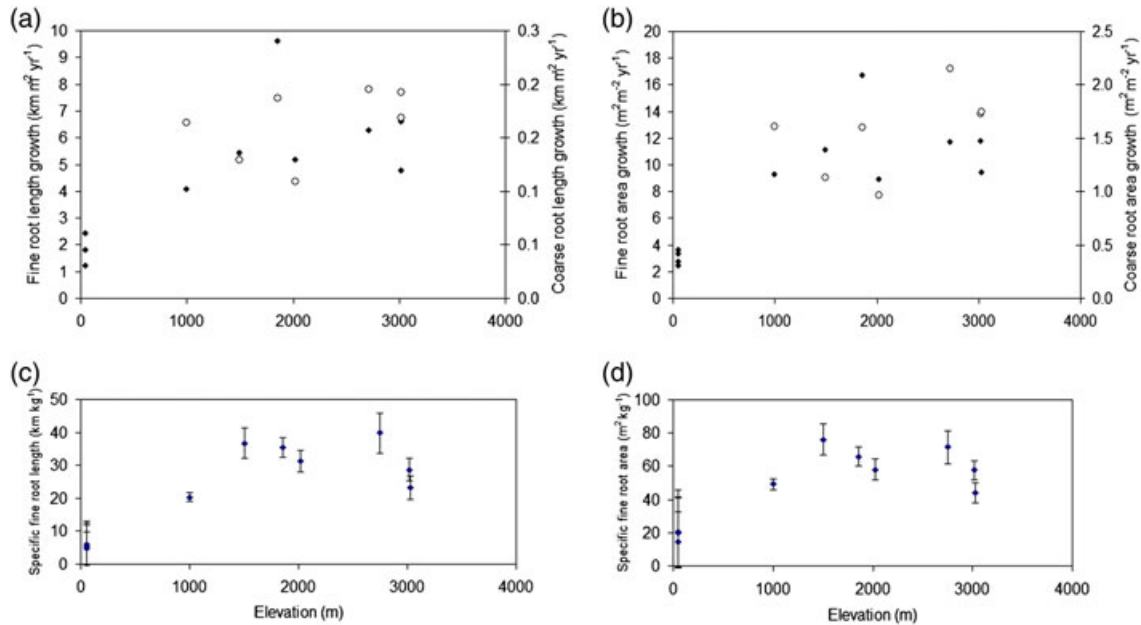
Figure 6. Root characteristics along the elevation gradient. (a) Root length growth (km root m^{-2} ground year^{-1}), (b) surface area growth (m^2 root m^{-2} ground area year^{-1}) of fine (<2 mm, closed circles, n=4) and coarse (> 2 mm, open circles, n=4) roots, (c) Specific fine root length (km kg^{-1}) and (d) specific fine root area (m^2 kg^{-1}).

were corrected for depth in this study, hence supersede values presented in *Girardin et al*. [2010].

3.4.2. Soil Profile of Fine Root Productivity and Residence Time

[25] Data gathered using rhizotrons permitted us to estimate $NPP_{FineRoot}$ distribution within the first 10, 20 and 30 cm of soil depth (Figure 7). We found a marked decrease in $NPP_{FineRoot}$ with increasing depth at all elevations. The first 10 cm of forest floor accounted for 35–48% of $NPP_{FineRoot}$. In addition, we report a significantly longer fine root residence time in the organic layer, compared to that of roots growing in the mineral layer (Table 2).

4. Discussion

4.1. Belowground C Stocks

[26] Several groups have reported fine root biomass values in TMFs of Hawaii [*Herbert and Fownes*, 1999]; Colombia [*Cavalier*, 1996; *Sierra et al*., 2007]; India [*Sundarapandian and Swamy*, 1996]; Costa Rica [*Maycock and Congdon*, 2000]; and Australia [*Vance and Nadkarni*, 1992]. However, only three groups have published information on belowground carbon stocks distribution along TMF *elevational* gradients. Studies from Borneo [*Kitayama and Aiba*, 2002], Southern Ecuador [*Roderstein et al*., 2005; *Moser et al*., 2008; *Graefe*
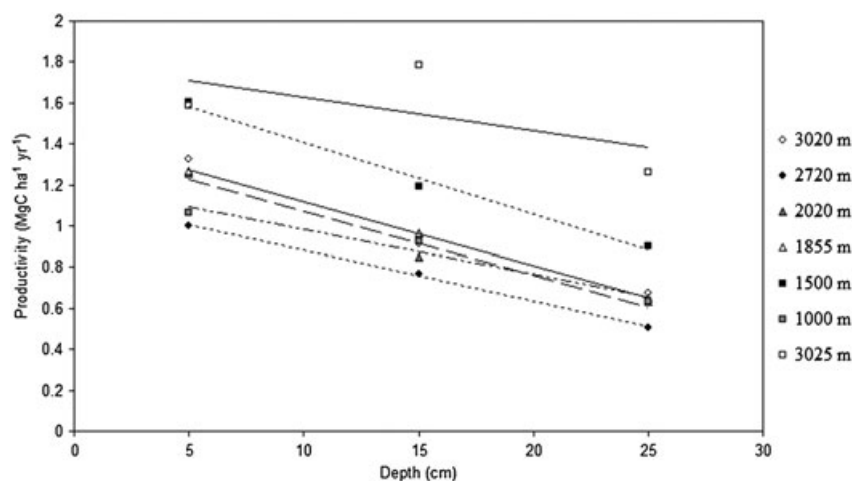
Figure 7. Soil profile of fine root (<2 mm) productivity (Mg C ha^{-1} yr^{-1}) for all elevations: 3020 m (open circles), 2720 m (closed circles), 2020 m (closed triangles), 1855 m (open triangles), 1500 m (black squares), 1000 m (grey squares), 3025 m (open square). Lines represent significant linear regressions at each elevation. SE of the mean typically <0.5 Mg C ha^{-1} yr^{-1}.

et al., 2008a], and the present transect [*Girardin et al.*, 2010] demonstrated that TMFs contain higher fine root biomass. In the Southern Ecuadorian Andes, fine root biomass increased from 2.68 to 11.27 Mg ha^{-1} from 1050 m to 3060 m elevation [*Leuschner et al.*, 2007; *Moser et al.*, 2008]. In two elevational transects from 700 to 3100 m on Mt. Kinabalu, Borneo, *Kitayama and Aiba* [2002] also found a marked increase in fine root biomass with elevation from 5.20 to 14.40 Mg ha^{-1}. *Girardin et al.* [2010] reported an increase in fine root biomass with increasing elevation. However, unlike the previous work, these authors also reported a step change in fine root stocks occurring at the base of the cloud zone.

[27] Figures 2 and 3 provide interesting insights on soil and fine root C stock trends along the Kosñipata transect. Several reasons for the substantial investment of carbon in the growth of a large fine root system in TMFs have been proposed. Unfavourable soil conditions [*Bruijnzeel and Veneklaas*, 1998; *Cavelier*, 1992], and slow mineralisation and nitrification rates of plant litter in relatively young soils resulting in low availability of N at high elevations [*Priess et al.*, 1999; *Soethe et al.*, 2008] may contribute to higher belowground carbon stocks at high elevations. In a global review of nutrient cycling in moist tropical forests, *Vitousek and Sanford*, 1986 and *Vitousek* [1998] found that upper montane forests cycle less N than lower montane forests. Conversely, we may expect to observe more P limitation in the younger, freshly weathered Andean soils than in lowland Amazonian soils [*Quesada et al.*, 2011; *Garzione et al.*, 2008; *Tanner et al.*, 1998]. More recently, *Fisher et al.* [2013] reported from leaf stochiometric data from the present elevation transect that N limitation increased and P limitation appeared to decrease with elevation, with colimitation at midelevation. Water shortage is unlikely to be a limiting factor for plant growth at tropical cloud forest elevations. However, whereas soil water content is not directly correlated to fine root carbon stocks, cooler temperatures, fog, and heavier rainfall interact to produce high soil water contents (up to 40%), inhibiting mineralisation and impeding fine root nutrient supply. These differences in soil conditions may explain the

change in belowground carbon stocks observed from lowlands to midelevations and the importance of cloud cover incidence for the step change observed at the base of the cloud zone. *Bloom et al.* [1985] suggest that plants respond to imbalances in resource availability (e.g., nutrients and/or water) by adjusting their carbon stocks so that the limitation for growth is equalized for all resources. *Raich* [1997] further suggested that there is a belowground shift in the partitioning of carbon as materials taken up by fine roots (water and nutrients) become more limiting to growth than those taken up by leaves (sunlight and CO_2). An increased investment in fine root material would facilitate nutrient foraging under low N supply, increasing plant growth and reproductive functions [*Vitousek and Sanford*, 1986; *Cuevas and Medina*, 1988; *Priess et al.*, 1999; *Aragão et al.*, 2009].

[28] Improved nutrient availability [*Soethe et al.*, 2006], C availability, aeration and more penetrable soil structures [*Metcalfe et al.*, 2002] concur to create a favourable environment for fine root growth in soil organic layers. Hence, fine root carbon stocks are greater in the soil organic matter. Further, soil organic matter depth increased significantly with elevation, with a step change at the base of the cloud zone (Figure 2b), contributing to the increase in fine root biomass. Recent data on fine root *NPP* and carbon stocks from a 1750 m plot in the present elevation transect corroborated with the data we present in this paper and confirmed the occurrence of a step change at the base of the cloud immersion zone [*Huaraca Huasco*, 2013], emphasizing the important role of cloud cover at that elevation. Ultimately, a decrease in temperature resulting in slower decomposition [*Takyu et al.*, 2003] rates and increased root longevity [*Graefe et al.*, 2008b] may explain the increase in belowground biomass observed above the cloud line. Nonetheless, we identified large spatial variation within the region. For instance, the replicated plots at approximately 3000 m indicated the spatial variation that we can expect to find at each elevation: soil organic layer depth on the mountain side (3025 m, 20.20±1.20 cm) was almost half of that found on the ridge top, (3020 m, 42.20±2.70 cm). The 3025 m stand was, on

average, drier, less cloud-prone and received higher annual solar radiation than the 3020 m stand.

4.2. Fine Root Production

4.2.1. $NPP_{FineRoot}$ Along the Elevational Gradient

[29] To date, only a few studies have been conducted on production and turnover of fine roots in tropical forests [*Cuevas and Medina*, 1988; *Ostertag*, 2001], and only two studies have measured $NPP_{FineRoot}$ in a TMF [*Roderstein et al.*, 2005; *Moser et al.*, 2011; *Girardin et al.*, 2010]. This lack of information reflects a serious limitation of previous studies on tropical montane forest productivity, which have assumed that aboveground *NPP* is a reasonable proxy of total productivity. *Roderstein et al.* [2005] challenged this assumption by reporting a threefold increase in fine root productivity coupled with a decline in aboveground productivity along a transect of three plots in the Ecuadorian Andes (1050–3060 m), revealing a clear belowground shift in carbon allocation with increasing elevation.

[30] In terms of fine root productivity, our results do not corroborate with those from the South Ecuadorian transect [*Roderstein et al.*, 2005; *Soethe et al.*, 2007], highlighting the danger of extrapolating findings from individual transects to the Andes or tropical montane forests in general. The present study found that $NPP_{FineRoot}$ of all premontane and montane forest sites was comparable to that found in the least fertile soils of lowland Amazonia (Tapajós and Manaus in Brazil, Amacayacu and Zafire in Colombia) [*Aragão et al.*, 2009], which may be explained by the low N uptake rates systematically found in TMF soils [*Vitousek et al.*, 1983; *Tanner*, 1985; *Kitayama et al.*, 2000; *Soethe \et al.*, 2008; *Fisher et al.*, 2013]. We observed a step change in productivity between most lowland and premontane plots at the base of the mountain (~1000 m) and no significant change in $NPP_{FineRoot}$ with elevation above 1000 m (ANOVA: F = 0.14, P = 0.99). If we concentrate our analysis on the plots located along our elevational gradient, from the Tambopata biosphere reserve to the Kosñipata valley, soil and air temperatures explained 66% and 77%, respectively, of the decline in $NPP_{FineRoot}$ in the TMF sites. However, the variation between our sites along the transect is no greater than the variation found between sites in lowland Amazonia on contrasting soils; soil properties are clearly an additional strong determinant of $NPP_{FineRoot}$ [*Malhi et al.*, 2009; *Aragão et al.*, 2009]. Finally, the lack of step-change in fine root production suggests that the step-change in carbon stocks is a direct result of the observed step-change in residence time, indicating that fine root carbon stocks increase in tropical montane forests as a result of an increase in residence time.

[31] In a review of methods used to estimate fine root production in forests, *Hertel and Leuschner* [2002] highlighted that no consensus existed on how best to measure fine root productivity in forests [*Majdi*, 1996; *Vogt et al.*, 1998]. Nonetheless, our estimates of *NPP* from data gathered using ingrowth cores and rhizotrons showed consistency between the two methods. This indicates the robustness of our findings, despite the use of different methods. Unlike rhizotrons, ingrowth cores entail substantial and continual disturbance of the soil as well as infrequent measurements. Conversely, rhizotrons are likely to result in an underestimation of fine root production after a few months as the rhizotron observation panel becomes saturated with fine roots. Some *NPP*

components and processes are difficult to measure directly and were not included in our estimates. These include C in exudates from roots and carbohydrates transferred to symbionts (e.g., mycorrhizae) and parasites. *Clark et al.* [2001] estimated that these elements can easily amount up to 20% of total *NPP* in tropical forests. For practical reasons, these terms are often incorporated into "root and rhizosphere" respiration, as they consist of labile carbon that is rapidly metabolised.

4.2.2. Seasonality of $NPP_{FineRoot}$

[32] We report significant seasonality of fine root productivity at all elevations. With the exception of the highest sites (~3000 m), root production increased during the austral winter (dry season) at all sites. *Huaraca Huasco et al.* [2013] and *Girardin et al.* [2013] observed a seasonal shift in allocation between wood and fine roots, indicating an optimal investment according to seasonal changes in resource availability over the annual cycle. Those authors identified solar radiation as a key factor controlling the seasonal above to belowground shift in allocation. We concur with those findings by reporting an increase in $NPP_{FineRoot}$ when solar radiation is at its lowest (dry season) at all elevations, except at the highest elevation plots where below ground-productivity is prioritised at the height of the austral summer.

4.2.3. $NPP_{FineRoot}$ Per Diameter Class

[33] When plotting $NPP_{FineRoot}$ against diameter class, we expected to see a decrease in *NPP* with increasing diameter class. Here, fine roots <0.6 mm displayed small $NPP_{FineRoot}$ values, peaking at 0.6 mm and decreasing linearly thereafter (Figure 5). The finest roots maximise surface area and are the most efficient roots for extracting water and nutrients from the soil, providing a greater uptake potential. Nonetheless, soil penetrability is often a decisive factor controlling root production and it is possible that a root diameter of 0.6 mm represents the optimum balance between root strength and uptake potential. This result could simply reflect a real pattern, demonstrating that fine roots in the 0.5–0.6 mm diameter class are the most productive. However, we suggest that the observed peak is in fact a result of a sampling bias. As there is no fundamental physiological constraint on producing minute fine roots as small as 0.025 mm in diameter [*Pallant et al.*, 1993], the most likely explanation is that we are observing a sampling bias, as sorting roots finer than 0.6 mm in the field is impractical. Further, it is possible that the rapid turnover rates of the finest roots [*Gill and Jackson*, 2000] lead us to underestimate their $NPP_{FineRoot}$ with three monthly sampling frequencies. Hence, we argue that the decline in $NPP_{FineRoot}$ recorded in roots <0.6 mm is likely to reflect mainly (1) an under sampling of finest roots and (2) the rapid turnover rates of roots finer than 0.6 mm. With this in mind, we used the relationship between root diameter class and $NPP_{FineRoot}$ to extrapolate the expected $NPP_{FineRoot}$ values for roots smaller than 0.6 mm and established that our estimates of fine root productivity were underestimated by an average of 31%. Fine roots (<2 mm) represent on average 87% of all roots collected from ingrowth cores (<5 mm). Thus, we estimated that fine roots (< 2 mm) are underestimated by approximately 31% if we do not account for undersampling of finest roots <0.6 mm diameter. By applying this correction, we obtain *NPP* values varying between 4.27 ± 0.56 Mg C ha^{-1} yr^{-1} (1855 m) and 1.72 ± 0.87 Mg C ha^{-1} yr^{-1} (3020 m). We suggest

that this is an additional methodological consideration to take into account when estimating fine root production from field sorting of root samples.

4.2.4. Fine Root Growth Characteristics

[34] The present study provides the first observations of fine root area growth, fine root length growth, specific fine root length (SFRL) and specific fine root area (SFRA) production in tropical montane forests. For most of the fine root characteristics described in this study, we

[35] found evidence of a step change occurring in the premontane forest. Fine root area growth, fine root length growth, SFRL and SFRA showed evidence of a change in regime, increasing substantially from lowland Amazonia (e.g., fine root area, 1.20–2.40 km m^{-2} yr^{-1}, *Metcalfe et al.* [2008]) to premontane and montane stands (4.06–9.58 km m^{-2} yr^{-1}) (Figure 6). Fine roots are longer and thinner in the TMF. Altering fine root morphology may provide an additional approach for plants to increase their nutrient uptake by ensuring close proximity between the root surface and low mobility nutrients (water is more readily available through osmosis than nutrients through diffusion and active transport) and increasing the volume of soil exploited per unit of biomass produced. These findings are consistent with the theory of resource allocation controlled by local soil conditions [*Bengough et al.*, 2006]. The change in root morphology from lowland to montane forests may also be explained by soil structure: cortical cells of roots grown in dense soil are generally shorter and fatter than those grown in loose soil [*Clark et al.*, 2003]. Finally, the effects of herbivory pressure on fine root growth characteristics remain largely unexplored as it is difficult to differentiate root mortality by herbivory and senescence [*Hunter*, 2008]. Studies carried out in controlled conditions on temperate species suggest a change in root anatomy with increasing herbivory pressure [*Huber et al.*, 2005], and studies on insects feeding on aboveground plant parts often demonstrate a decline in herbivory pressure with elevation [*Hodkinson*, 2005] but very little is known about equivalent patterns for soil herbivores. Thus, longer and thinner roots in the montane plots may also reflect a decrease in root herbivory along the elevation gradient, although this remains to be investigated.

4.2.5. Soil Profile of *NPP*$_{FineRoot}$ and C Residence Time

[36] Soil profiles of *NPP*$_{FineRoots}$ (Figure 7) demonstrated a decrease in *NPP*$_{FineRoots}$ with increasing depth. Belowground biomass decreased with depth at lower elevations and remained constant at mid to high elevations due to the increased depth of the soil organic layer (Figure 2b). A deeper organic layer at high elevations and increased fine root longevity result in increased fine root biomass values within the cloud zone, estimated at 1500 to 3500 m (Figure 2a). Nevertheless, the depth distribution of fine root biomass has been reported as an exponential reduction with increasing soil depth, and most of the variation of fine roots can be explained by the concentration of nitrogen in the soil [*Cavelier*, 1992; *Soethe et al.*, 2006]. We did not record this decrease, as the organic layer depth at high elevations reached up to 44 cm at high elevations and our 30 cm deep soil cores did not record fine root biomass of the mineral layer in most TMF sites. The observed decrease in *NPP*$_{FineRoots}$ with depth, combined with little change in biomass with soil depth at mid to high elevations suggested an increase in fine root residence time (the ratio of fine roots biomass to

NPP$_{FineRoots}$) with increasing soil depth. It is likely that cooler temperatures and lower nutrient availability of deeper soil layers contribute to increase fine root longevity [*Gill and Jackson*, 2000; *Graefe et al.*, 2008a].

4.3. Fine Root C Residence Time

[37] Data on patterns of fine root residence time in TMFs are limited to the South Ecuadorian transect [*Graefe et al.*, 2008a; *Graefe et al.*, 2008b] and the present site [*Girardin et al.*, 2010; this study]. These studies recorded an increase in fine root C residence time with increasing elevations, up to 3000 m. The present study's observations corroborate the findings of most studies comparing forest fine root residence time across latitudinal gradients: shorter fine root residence times were found at warmer mean annual temperatures [*Vogt et al.*, 1986; *Gill and Jackson*, 2000]. From our results, we estimate that soil temperature is the key driver of residence time, with a decline in mean residence time of 0.17 years (about 3 months) for each degree Celsius rise in air temperature (slope = -0.17, r^2 = 0.64, P < 0.05, n = 7). However, other factors that covary with temperature along this gradient may influence this relationship. A number of studies have found an increase in fine root residence time with decreasing nutrient (in particular N) availability [*Nadelhoffer et al.*, 1985; *Pregitzer et al.*, 1995; *Aragão et al.*, 2009]. Here, we assent that adverse soil mineral conditions result in a longer residence time of fine roots C. Further, *Godbold et al.* [2003] found that root longevity significantly decreased in highly acidic soils compared to less acidic soils in a temperate forest. As soil pH decreases significantly with increasing elevation along the elevational gradient, acidic soils may further explain an increase in fine root residence time. Thus, low temperatures, acidic soils, and low nutrient availability at high elevations are likely to be the dominant factors controlling fine root C residence time in TMF sites.

5. Conclusions

[38] This study presents the first detailed investigation of the spatial and seasonal patterns of fine root dynamics (C stocks, *NPP* and turnover rates), and changes in root growth characteristics along a tropical elevation transect. Building on previous results, we examine the change in fine root dynamics regime between lowland and montane forests. Ultimately, a decrease in temperature resulting in differences in soil mineral conditions, slower decomposition rates and increased root longevity may explain the increase in belowground biomass observed within the cloud immersion zone. We report a stronger seasonality of *NPP*$_{FineRoot}$ within the cloud immersion zone, most likely driven by seasonality of solar radiation. Remarkably, fine root area and fine root length growth increased substantially above 1000 m, suggesting that altering fine root growth characteristics may provide an additional approach for plants to increase nutrient uptake at higher elevations, reflect a change in soil structure, or decrease in root herbivory at higher elevations.

[39] Finally, we provide insights into the methodological approaches used to measure *NPP*$_{FineRoot}$. We hypothesise that the sharp decline in *NPP*$_{FineRoot}$ recorded in finest roots (<0.6 mm) indicates a sampling bias of ingrowth cores,

resulting in an underestimation of NPP$_{FineRoot}$ by up to 31% in conventional ingrowth core measurements.

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