**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 stocks and turnover rates (i.e. carbon dynamics) of tropical forests are an important aspect of the global carbon cycle. These variables have been investigated in lowland tropical forests, but they have rarely been studied in tropical montane forests. This study examines spatial patterns of above- and below-ground carbon dynamics along a transect ranging from lowland Amazonia to the high Andes in S.E. Peru. Fine root biomass values increased from 1.50 Mg C ha ⁻¹ at 194m to 4.95±0.62 Mg C ha ⁻¹ at 3020 m, reaching a maximum of 6.83±1.13 Mg C ha ⁻¹ at the 2020 m elevation site. Above-ground biomass values decreased from 123.50 Mg C ha ⁻¹ at 194 m to 47.03 Mg C ha ⁻¹ at 3020 m. Mean annual below-ground productivity was highest in the most fertile lowland plots (7.40±1.00 Mg C ha ⁻¹ yr ⁻¹) and ranged between 3.43±0.73 Mg C ha ⁻¹ yr ⁻¹ and 1.48±0.40 Mg C ha ⁻¹ yr ⁻¹ in the pre-montane and montane plots. Mean annual above-ground productivity was estimated to vary between 9.50±1.08 Mg C ha ⁻¹ yr ⁻¹ (210 m) and

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	2.59±0.40 Mg C ha ⁻¹ yr ⁻¹ (2020 m), with consistently lower values observed in the cloud immersion zone of the montane forest. Fine root carbon residence time increased from 0.31 years in lowland Amazonia to 3.78±0.81 years at 3020 m and stem carbon 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 below-ground remained approximately constant at all elevations. Although net primary productivity declined in the tropical montane forest, the partitioning of productivity between the ecosystem sub-components remained the same in lowland, pre-montane and montane forests.

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

Running title: Net primary productivity from Andes to Amazon.

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

Abstract

The net primary productivity, carbon stocks and turnover rates (*i.e.* carbon dynamics) of tropical forests are an important aspect of the global carbon cycle. These variables have been investigated in lowland tropical forests, but they have rarely been studied in

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30 37 constant along the elevational transect, with a mean of 54±4 years. The ratio of fine
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40 42 sub-components remained the same in lowland, pre-montane and montane forests.
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52 Introduction

55 The important role of the Amazonian lowland forest in global biogeochemical cycles,
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57 46 and in particular the global carbon cycle, is widely recognised (IPCC, 2007).
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59 47 However, the carbon cycle of tropical montane forests (TMFs) is only starting to be
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3 48 explored. In the Amazon basin, the montane forests of the Andes extend from the
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5 49 lowlands up to 3000 – 4000 m a.s.l. In addition to their intrinsic interest, studies of the
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8 50 ecosystem functioning of montane forests provide an opportunity to explore how
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10 51 environmental variables (particularly temperature and soil moisture) affect ecosystem
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12 52 functions, whilst keeping seasonal factors constant. In particular, there is no dormant
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14 53 winter or drought season that complicates interpretation of latitudinal gradients. In
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16 54 this paper, we explore the production, allocation, and turnover of carbon along an
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18 55 elevation gradient in the Peruvian Amazon and Andes.
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25 57 A number of studies have reported on variation of above-ground biomass with
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27 58 elevation in TMFs in Borneo, Ecuador, Puerto Rico, Venezuela, New Guinea, Panama
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29 59 and Hawaii (Kitayama *et al.*, 1994, Delaney *et al.*, 1997, Leuschner *et al.*, 2007).
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31 60 These consistently report a decline in above-ground biomass with increasing elevation
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33 61 as a key characteristic of TMFs. There have been far fewer studies of below-ground
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35 62 biomass. Observations of fine root carbon stocks in Southern Ecuador and in Borneo
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37 63 show an increase in fine root carbon stocks with increasing elevation (Kitayama *et al.*,
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39 64 2002, Leuschner *et al.*, 2007). Based on these previous findings, we would expect to
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41 65 observe a shift in the partitioning of carbon standing stocks from above- to below-
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51 68 Net primary productivity (NPP) is defined as the amount of carbon incorporated into
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53 69 new organic matter produced by a plant of ecosystem in a specified time interval. The
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55 70 components of NPP include the production of stems, branches, leaves, flowers, fruit,
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57 71 coarse and fine roots, volatile organic compounds, and root exudates. Although there
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59 72 is a long record of tropical forest above-ground net primary productivity (NPP_{AG})
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73 measurement studies in the ecological literature, only a handful of studies focus on
74 TMFs (reviewed in Clark *et al.*, 2001). Studies in the Jamaican Blue Mountain, the
75 Luquillo Mountains in Puerto Rico, Mount Kinabalu in Borneo, and the Ecuadorian
76 Andes consistently reported a decline in NPP_{AG} with increasing elevation. Whereas its
77 cause is still poorly understood, this is reported as one of the most fundamental
78 features of tropical montane forests. The quantification of below ground net primary
79 productivity (NPP_{BG}) is still in its early years and our understanding of total
80 ecosystem-level productivity is very limited. To date, only one study in South
81 Ecuadorian montane forests published NPP_{BG} estimates along an elevational transect
82 (Roderstein *et al.*, 2005) but did not report parallel measurements of NPP_{AG} (see,
83 however, new results reported by Moser *et al.*, this volume). The study found that fine
84 root production, $NPP_{FineRoot}$, increases with increasing elevation.
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86 The mean residence time of carbon in biomass can be estimated by dividing each
87 carbon pool's standing stocks by the NPP of that pool. Only a few studies have
88 estimated stem carbon turnover rates or residence times in tropical forests (Malhi *et*
89 *al.*, 1999, 2006); none of these were carried out on TMFs. Similarly, very few studies
90 have been conducted on carbon turnover rates of fine roots in tropical forests (Cuevas
91 *et al.*, 1988, Herbert *et al.*, 1999, Ostertag, 2001), with only one study of an
92 elevational transect (Graefe *et al.*, 2008).
93
94 Raich *et al.* (1997) measured above-ground productivity and soil respiration in three
95 Hawaiian rainforests, but to date there have been no complete analyses of NPP and its
96 allocation along a tropical elevation transect. Here, we present the first reported
97 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-ground and below-ground 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 carbon dynamics across the elevational transect. To this end, we analyse standing stocks, production rates, and residence time of above-ground (stems, canopy) and below-ground (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 carbon from above- to below-ground (Leuschner *et al.*, 2007).

(2) Total NPP declines with elevation, but the proportion of NPP allocated to above- and below-ground 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, darwin.winston.wfu.edu/andes/). Nine permanent tree sampling plots of 1 ha each were established along an elevational gradient ranging from 194 m to 3025 m elevation, extending from lowland forest (< 800 m), through pre-montane (800 - 1200 m), lower montane (1200 - 2200 m) and upper montane forest (2200 - 3400 m). Of these, six experimental sites were

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established at elevations from 3020 m 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 Aragão *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 m 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 shales-slates), 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 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 carbon- rich topsoil (C.A.J. Girardin, submitted). The base of the cloud zone is located at 1500 - 1800 m, and the

146 cloud forest zone extends to the tree line at approximately 3400 m, above which *puna*
147 grasslands dominate.

148 *Weather*

149 Weather patterns along the elevational gradient are described in a companion paper in
150 this issue (C.A.J. Girardin *et al.*, submitted). Mean annual air temperatures over the
151 study period ranged from 26.4 °C (194 m) to 11.8 °C (3000 m). There was a close
152 association between elevation and temperature ($r^2=0.99$, $P<10^{-4}$), implying a vertical
153 lapse rate of soil temperature of 4.79 °C km⁻¹, and a lapse rate of air temperature of
154 4.94 °C km⁻¹. Over the measurement period (Aug 2007 – Aug 2008), precipitation
155 showed a humped relationship with elevation, with our recorded highest values (3086
156 - 2746 mm yr⁻¹) near the base of the mountain range (1000 - 1500 m). Light incidence
157 and soil water content (SWC) showed no clear relationships with elevation. There
158 may be microsite effects along the elevational gradient, which reflect the
159 geomorphological situation rather than the influence of elevation per se (Moser *et al.*,
160 2008). This is illustrated by the variation of rainfall patterns between the two forest
161 sites under investigation at 3000 m: the plot located on a slope (3025 m) was, on
162 average, drier and received higher annual light incidence than that located on the
163 Trocha Union ridge (3020 m). Nonetheless, within the cloud immersion zone, SWC is
164 typically above 25% throughout the year, because of limited evapotranspiration and
165 fog deposition

167 *Above-ground carbon stocks and fluxes*

168 We determined wood productivity using multiple censuses of the forest plots. Tree
169 censuses were carried out in our plots in 2003 and 2007 to determine the growth rate

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3 170 of existing surviving trees and the rate of recruitment of new trees. Mortality was
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6 171 estimated for each site by calculating the biomass of trees that were measured in 2003
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8 172 and dead in 2007. Only trees >10cm diameter at breast height (dbh) were included in
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10 173 the census. These measurements were subsequently converted into estimates of coarse
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12 174 wood productivity using allometric equations for moist forest stands that relate tree
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14 175 diameter to biomass (Chave *et al.*, 2005). Two equations were explored in order to
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16 176 determine the importance of including tree height in biomass estimates of montane
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18 177 forest trees:
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24 179 $AGB=0.0776*(\rho * (DBH^2) * H)^{0.94}$ (1)
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27 180 $AGB=\rho * \exp(-1.499+2.1481*\ln(DBH) +0.207*(\ln(DBH))^2 -0.0281*(\ln(DBH))^3)$ (2)
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32 182 Where AGB is above-ground biomass in kg m⁻², ρ is density of the wood obtained
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34 183 from (Chave *et al.*, 2006), DBH is diameter at breast height in cm, and H is height in
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36 184 m. Both were derived from the same pan-tropical dataset, however (2) only
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38 185 incorporates diameter information and so is applicable for data sets where height
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40 186 information is not available. As we had some height data from each plot, equation (1)
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42 187 was used for the subsequent analysis. It includes census data on diameter at breast
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44 188 height, a single measurement of tree height and species specific values for wood
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46 189 density. Tree height was available for approximately 125 trees in each plot. Where
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48 190 tree height was not available for particular trees, it was estimated by fitting an
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50 191 exponential model to existing height and diameter at breast height data for trees at that
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52 192 elevation. To convert biomass values into carbon, we assumed that dry stem biomass
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54 193 is 50% C (Chave *et al.*, 2005).
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4 195 We calculated annual above-ground woody biomass productivity, NPP_{Stem} , from full
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6 196 plot census data from 2003 and 2007. This was calculated using the allometric
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8 197 equations of Chave et al (2005), including estimates for height, as described above.
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10 198 The biomass of new recruits measured at the second census was then added.
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14 200 To determine seasonal variation in NPP_{Stem} , we employed three-monthly dendrometer
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16 201 band measurements on approximately 200 randomly selected trees per plot from
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18 202 August 2007 to January 2009. Dendrometer measurements were converted into three-
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20 203 month biomass increments for each tree. To scale from the dendrometer trees to the
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22 204 full plot, we grouped the tree species by genus. From the full census data we
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24 205 determined the annual NPP of each genus g , and what fraction of the annual NPP of
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26 206 each genus was captured by dendrometers, f_g . The three-monthly whole-plot NPP of
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28 207 each genus was then estimated by dividing the dendrometer-measured three-month
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30 208 NPP of that genus by f_g . These whole plot estimates of NPP for each genus were then
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32 209 summed over genus to obtain a total plot NPP.
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40 211 Given that some species of tree ferns and palms can grow vertically without
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42 212 increasing in girth, hence measuring their increase in diameter at breast height over
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44 213 time is futile, we included tree ferns and palms as recruits in our NPP estimates and in
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46 214 our stem biomass estimates, as described in Malhi *et al.* (2004), but did not estimate
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48 215 growth rates over time. The proportion of tree ferns in the plots ranged from 2.5%
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50 216 (1000 m and 3020 m) to 21% (2020 m), peaking between 1855 m and 2720 m. Palm
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52 217 proportion varied from 0% (3100 m) up to 27% one plot in the Tambopata lowlands.
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56 218 There were no tree ferns at the lowland sites, and no palms above 1500 m elevation
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3 220 Canopy productivity was estimated by collecting litterfall in 0.25 m² litter traps (PVC
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5 221 tubes and 1 mm mesh nylon screen, 25 per hectare) set up 1 m above the ground.
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7 222 Litterfall was collected bi-weekly to minimise loss by decomposition, split into
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9 223 different components, oven dried at 80 °C and weighed. Components of litterfall
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11 224 include leaves; reproductive organs (fruits and flowers); twigs (up to 2 cm girth,
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13 225 including bark); epiphytes and bromeliads (all parts combined); and fine debris
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15 226 (unidentifiable particles that pass through 2 mm mesh). In the present analysis, we
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17 227 refer to the sum of leaves, twigs, reproductive organs, epiphytes, bromeliads and
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19 228 unidentified material as canopy productivity.
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28 230 ***Below ground carbon stocks and fluxes***

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31 231 Soil and root C stocks were estimated using soil cores only (these soil cores were
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33 232 sampled during the installation of ingrowth cores), while root production was
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35 233 estimated using two independent approaches, rhizotrons and soil ingrowth cores. The
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37 234 comparison of these two approaches gives us some metric of confidence in these
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39 235 results. A detailed description of the methodologies described here is presented in
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41 236 Metcalfe *et al.* (2008a). For an in depth review and critique of these methods refer to
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43 237 Vogt *et al.* (1998) and Hendricks *et al.* (2006).
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50 239 ***Rhizotrons***

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52 240 NPP_{BG} was determined using rhizotron root observation chambers (Burke *et al.*,
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54 241 1994). These observation chambers were framed on three sides using lumber or metal.
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56 242 The fourth side was a 6 mm thick pane of Perspex 40 cm deep, 0 cm being the surface
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58 243 of the organic top layer, and 35 cm wide. Lowland sites with thin organic layers had
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60 244 their observation chambers mostly in mineral soils, while at highland sites with thick

organic layers, the chambers mostly observed root growth in the organic layers and not in the mineral soil (Table 1). The rhizotron measurements began two 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.

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267 *Root ingrowth cores*

268 NPP_{BG} was also quantified in all plots using the ingrowth core technique (Vogt *et al.*,
269 1998, Steingrobe *et al.*, 2000, Hendricks *et al.*, 2006), following the methodology

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3 270 described in Metcalfe *et al.* (2008b). These are cores of root-free soil surrounded by
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5 271 mesh bags in which roots were allowed to grow over a set period of time (three
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8 272 months), providing estimates of root production per unit area and time ($\text{Mg ha}^{-1} \text{ yr}^{-1}$).
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10 273 Nine ingrowth cores were installed in the plots in May 2007, three of which were in
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12 274 close proximity to rhizotrons. Soil cores were extracted and soil layers were separated
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14 275 into O-horizon organic layer (OL) and A- and B-horizon mineral layer (ML). Fine
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16 276 roots were manually removed every three months using a method which corrects for
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18 277 underestimation of fine root biomass. Roots were manually extracted from soil cores
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20 278 during 10 min time intervals, over a period of 40 min. The curve of cumulative
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22 279 extraction over time was used to predict root extraction beyond 40 min (Metcalfe *et*
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24 280 *al.*, 2007). This method only accounts for live fine roots, as the three-monthly sample
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26 281 period was much lower than the turnover time of the roots. Root-free soil was then
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28 282 replaced in each ingrowth core, maintaining the horizon layering of the undisturbed
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30 283 soil. Sampled roots were rinsed in water to remove soil particles, oven dried at 70°C
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32 284 in the lab until constant mass, weighed and scanned as greyscale images at 600 dpi
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34 285 resolution. Fine root biomass and mass of the soil OL were measured using the first
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36 286 soil cores sampled in May 2007. NPP_{BG} was estimated from the quantity of root mass
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38 287 produced in the three month interval since the last collection. Fine and coarse roots
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40 288 were defined as <2 mm and >2 mm in diameter, respectively. The scanned images
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42 289 were analyzed using commercially available software (WinRHIZO Pro version 2003
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44 290 b, Regent Instruments, Canada), to calculate root length and surface area, according to
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46 291 the methodology described by Metcalfe *et al.* (2008). Finally, OL depth and root mass
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48 292 within the OL were also measured using soil cores in August 2008 at 25 points for
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50 293 each elevation (only five at 2000 m). As it is very difficult to discern between biomass
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52 294 and necromass of fine roots, fine root biomass are likely to be overestimated.
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295 *Net Primary Productivity calculations*

296 Net primary productivity (NPP) of an ecosystem can be defined as the total biomass
 297 of autotrophs produced in a specified time interval (Roy *et al.*, 2001). Total
 298 productivity (NPP_{Total}) can be divided into below-ground (NPP_{BG}) and above-ground
 299 (NPP_{AG}) production of carbon per unit time. Above-ground NPP consists of stem
 300 production (NPP_{Stem}), canopy production (NPP_{Canopy}), branch turnover (NPP_{Branch}) and
 301 volatile organic compound production (NPP_{VOC}).

$$303 \quad NPP_{AG} = NPP_{Stem} + NPP_{Canopy} + NPP_{Branch} + NPP_{VOC} \quad (3)$$

305 We obtained stem (NPP_{Stem}) and leaf (NPP_{Canopy}) production values through direct
 306 measurement. NPP_{Canopy} consist of leaves, small branches, flowers and fruit. As we
 307 did not directly measure branch production in this study, it is scaled from NPP_{Stem}
 308 using the ratio (0.4) of $NPP_{Branch}:NPP_{Stem}$ estimated from published values in lowland
 309 Amazonian plots (Aragão *et al.*, 2009). NPP_{VOC} is the emission of volatile organic
 310 carbon from the vegetation. VOC flux appears to be a very small component of the
 311 carbon cycle of tropical forests (Malhi *et al.*, 2009) and is not quantified in this study.

313 NPP_{BG} consists of fine ($NPP_{FineRoot}$) and coarse root ($NPP_{CoarseRoot}$) production (Clark
 314 *et al.*, 2001a), and exudate production.

$$316 \quad NPP_{BG} = NPP_{FineRoot} + NPP_{CoarseRoot} + NPP_{Exudate} \quad (4)$$

318 Whereas we estimated $NPP_{FineRoot}$ directly, $NPP_{CoarseRoot}$ presents a methodological
 319 challenge and is very difficult to estimate directly. Hence $NPP_{CoarseRoot}$ was estimated

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as a fraction of NPP_{Stem} , following the method proposed by Malhi *et al.* (2009):
 $NPP_{CoarseRoot}=0.21(\pm0.03)*NPP_{Stem}$ where 0.21 ± 0.03 is the mean ratio of below-ground stocks to above-ground 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 ± 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_{BG} 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.*, 2001 b).

Analytical techniques

We used these data to describe the spatial variations of above- and below-ground 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, d.f. = 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, 2009).

Results

Carbon stocks

Estimates of carbon 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 employ it here to explore the importance of directly accounting for height. Equation (2) assumes a fixed polynomial relationship between $\ln(H)$ and $\ln(DBH)$ 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 equation (2) would result in a systematic overestimation of biomass by $52\pm 10\%$ at higher elevations. Fig. 1a demonstrates the importance of including height estimates into stem carbon stocks calculations in TMFs, as height is the dominant factor dictating a decline in above-ground carbon stocks with increasing elevation. Fig. 1a includes published data 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 equation (2). We observed a significant decrease in stem biomass with increasing elevation with equation (1) ($r^2=0.80$, $P<0.0005$, $n=17$).

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Fig. 1b indicates a step change in fine root biomass in the soil organic layer at the base of the cloud immersion zone. Fine root carbon stocks increased from 1.50 Mg C ha⁻¹ at 194 m to 6.54±0.54 Mg C ha⁻¹ at 1855 m, and thereafter no significant changes in root carbon 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.

Net Primary Productivity

The patterns of NPP components along the elevational gradient are shown in Fig. 2 and 3. NPP_{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 pre-montane and montane forests: lowland values (16.9±1.48 Mg C ha⁻¹ yr⁻¹ at 210 m and 13.6±1.25 Mg C ha⁻¹ yr⁻¹ at 194 m, Aragão *et al.* 2009) were significantly higher than values recorded in the Andes (7.07±0.98 Mg C ha⁻¹ yr⁻¹ at 1000 m to 4.11±0.26 Mg C ha⁻¹ 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 NPP_{Total} are significantly lower than NPP_{Total} from even the least fertile soils in central Amazonia.

NPP_{Stem} ranged between 0.79±0.08 (1855 - 2020 m) and 2.80±0.24 Mg C ha⁻¹ yr⁻¹ (210 m), with a change in regime between lowland Amazonian forests and pre-montane to montane forests. Likewise, we recorded a significant decline in NPP_{Canopy} with increasing elevation (slope=-0.001, r²=0.74, P=0.002, n=9) (Fig. 3a). Hence,

393 NPP_{AG} decreased with elevation (slope = -0.001, $r^2=0.69$, $P=0.005$, $n=9$). These linear
 394 relationships provide indications on the overall tendency of the trends we observed,
 395 however, rather than a steady linear decline, there appears to be a fairly rapid decline
 396 in NPP_{AG} with elevation until the base of the cloud immersion zone (around 1500 m),
 397 and then no trend in NPP_{AG} with elevation within the cloud zone all the way up to the
 398 tree line. There appears to be two distinct regimes, one below the clouds where NPP
 399 declines with elevation, and one within the cloud zone where NPP does not change
 400 with elevation. Average NPP_{AG} was estimated at 3.53 ± 0.38 Mg C ha⁻¹ yr⁻¹ ($n=7$) in
 401 the TMF and 8.87 ± 0.63 Mg C ha⁻¹ yr⁻¹ ($n=2$) in the lowland Amazonian plots.

402
 403 A change in regime of NPP_{BG} was observed around 1000 m, with a decrease in
 404 production and with the lowest values recorded within the cloud immersion zone,
 405 between 1.96 ± 0.18 and 1.48 ± 0.40 Mg C ha⁻¹ yr⁻¹. NPP_{FineRoot} followed a similar
 406 pattern, with values decreasing from 6.80 ± 1.0 Mg C ha⁻¹ yr⁻¹ in the lowlands (210 m)
 407 to 1.23 ± 0.40 Mg C ha⁻¹ yr⁻¹ in the upper TMF (Fig. 3c). NPP_{FineRoot} represented the
 408 largest proportion of below-ground productivity, ranging between 83% and 92% of
 409 NPP_{BG}. NPP_{CoarseRoot} (Fig. 2) was estimated as a fixed fraction of above-ground
 410 production stem biomass ($21 \pm 10\%$). As a result, we estimated a decrease in
 411 NPP_{CoarseRoot} in the TMF, from 0.60 ± 0.09 (194 m) to 0.21 ± 0.04 (3020 m) Mg C ha⁻¹
 412 yr⁻¹.

413
 414 Measurements of NPP and respiration fluxes are presented in Table 3. An analysis of
 415 the patterns of NPP_{Total} partitioning into above- and below-ground components
 416 demonstrated that the ratio of NPP_{BG} to NPP_{AG} (Fig. 4) shows high site-to-site
 417 variation (between 0.2 and 1.2) but no evidence of any overall trend with elevation.

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418 The mean value of the ratio is 0.69 ± 0.44 . A significant exception was the forest at
419 1855 m, where we observed a high NPP_{BG} driven by high fine root productivity. To
420 a small extent, this lack of trend in above- and below-ground partitioning is forced by
421 the fact we set $NPP_{CoarseRoot}$ as a fixed fraction of NPP_{Stem} . However, this effect is
422 relatively small, because $NPP_{CoarseRoot}$ is a relatively small component of NPP_{BG} (5-
423 17%), and NPP_{Stem} is a relatively small component of NPP_{AG} (~34%).
424
425 The ratio of each NPP component to NPP_{Total} showed no significant trends with
426 elevation (Fig. 5). On average, below the cloud base, 18 ± 5 % of NPP_{Total} is allocated
427 to stems, 34 ± 29 % to canopy and 37 ± 15 % to fine roots (n=3). Above the cloud base,
428 21 ± 7 % of NPP_{Total} is allocated to above-ground woody biomass, 32 ± 7 % to canopy
429 and 37 ± 15 % to fine roots (n=6). Fig. 6 shows the relationships between NPP_{AG}
430 ($y = 0.58 \pm 0.05 * x$, n=9) and NPP_{BG} ($y = 0.39 \pm 0.05 * x$, n=9) with NPP_{Total} in the
431 Kosñipata transect, with regressions forced through the origin. These variables are not
432 independent and thus the correlation statistics are not meaningful, but the regression
433 slopes are meaningful. Across the elevational transect, the regression suggests that
434 NPP_{AG} and NPP_{BG} are 58 ± 5 % and 39 ± 5 % of NPP_{Total} . The slopes of the relationships
435 were remarkably similar for (i) the nine plots from the Kosñipata transect only, (ii) the
436 lowland Amazonian plots from Aragão *et al.* (2009) only, and (iii) both data sets
437 combined. We found a significant relationship between NPP_{Canopy} and NPP_{Stem} (Fig. 7)
438 when we included all plots of the Kosñipata transect as well as when we included
439 montane forests.
440
441 Regressions of the components of NPP against environmental parameters are
442 presented in Table 4. There are particularly strong correlations between annual mean

air temperature and $\text{NPP}_{\text{Canopy}}$ and $\text{NPP}_{\text{FineRoot}}$, and weaker correlations with stem productivity. Overall 78% ($P < 0.005$) of the variance in $\text{NPP}_{\text{Total}}$ 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 carbon residence time with increasing elevation (Table 5, Fig. 8a). In the Kosñipata transect, the mean stem C residence time was 54 ± 4 years ($n=9$). However, as fine root biomass increased with elevation and $\text{NPP}_{\text{FineRoot}}$ was lower in TMFs than in most lowland forest plots, fine root carbon residence time (Table 5, Fig. 8b) increased significantly with increasing elevation ($r^2=0.80$, $P=0.006$, $n=7$) from 0.31 ± 0.61 years (194 m) to 3.78 ± 0.81 years (3020 m).

Discussion

We have presented data on C stocks, productivity, allocation and residence time of seven Andean montane and pre-montane 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 above-ground biomass and productivity are the main contributors of total C stocks and NPP at all elevations. Overall, $\text{NPP}_{\text{Total}}$ was lower in the pre-montane and montane forests than in lowland Amazonia. This

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pattern was driven by a decline in above- and below-ground NPP in pre-montane and montane forests, with lower values recorded within the cloud immersion zone.

No change in total carbon stocks with elevation

A decline in above-ground biomass with increasing elevation in altitudinal transects is a common feature of TMFs. Our results corroborate previous findings by showing a significant decline in above-ground 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 above-ground carbon stocks in TMF ecosystems. In terms of below-ground carbon 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 pre-montane and lowland plots. Further, the soil organic matter C stocks increase significantly with elevation. Hence, if we include increases in the soil carbon stock pool and fine root carbon stocks in our estimates of below-ground carbon 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 carbon from above- to below-ground.*

Net primary productivity

Total NPP declines with elevation

NPP_{Total} was lower in the pre-montane and montane forests than in lowland Amazonia. In a study on nine lowland Amazonian forest plots, Aragão *et al.* (2009)

491 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
 492 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.
 493 All components of $\text{NPP}_{\text{Total}}$ measured for this study ($\text{NPP}_{\text{Canopy}}$, NPP_{Stem} and
 494 $\text{NPP}_{\text{FineRoots}}$) were significantly lower in TMF plots compared to the two lowland
 495 Amazonian plots of this transect. Further, we found evidence of a change in regime of
 496 NPP_{AG} rates in the cloud forest zone, where NPP_{AG} rates are lower than in most
 497 lowland Amazonian plots (Fig. 2). This decline is driven by above- and below-ground
 498 NPP allocation. Stem and canopy productivity are both significantly lower in the pre-
 499 montane and montane forests than in lowland Amazonia, confirming previous
 500 published observations of NPP_{AG} along elevational transects from Hawaii (Raich *et al.*,
 501 1997, Herbert *et al.*, 1999, Schuur *et al.*, 2001) and Borneo (Kitayama *et al.*,
 502 2002) and of $\text{NPP}_{\text{Canopy}}$ from Jamaica (Tanner *et al.*, 1999), Puerto Rico (Waide *et al.*,
 503 1998), and Ecuador (Roderstein *et al.*, 2005). These authors used $\text{NPP}_{\text{Canopy}}$ as a proxy
 504 of NPP_{AG} . Similarly, Malhi *et al.* (2009) and Aragão *et al.* (2009) found that in
 505 lowland Amazonian forests, canopy productivity appears to be a good proxy for
 506 NPP_{AG} . Our results confirm that this relationship holds in montane forests (Fig. 7).
 507 Further, the number of plots we established along the transect allowed us to observe a
 508 change in regime in NPP_{AG} between lowland forest and montane forest for the first
 509 time in an elevational transect.
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 511 Studies that attempt to quantify NPP_{BG} in tropical montane forests are more limited in
 512 number. To date, only one study determined NPP_{BG} , in South Ecuador (Roderstein *et al.*
 513 *et al.*, 2005), and a second is being proposed for this site in (C.A.J. Girardin, in prep).
 514 Roderstein *et al.* (2005) found that, along a transect of three plots in the Ecuadorian
 515 Andes (1050 - 3060 m), $\text{NPP}_{\text{Canopy}}$ declined, whereas $\text{NPP}_{\text{FineRoot}}$ increased threefold,

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revealing a clear belowground shift in carbon allocation with increasing elevation. We found that, along seven plots ranging from the high Andes to lower montane forests, $NPP_{FineRoot}$ remained constant within the cloud immersion zone (1855 m to 3025 m), with values below those reported in the least fertile soils of lowland Amazonia (Fig. 3c). Whereas we observed a decline in NPP_{Canopy} in TMFs compared to pre-montane and lowland sites, our results showed no evidence of a shift in allocation to $NPP_{FineRoots}$ as elevation increases. Instead, at our site, we found that productivity decreases proportionately above- and below-ground in TMFs, *supporting our hypothesis (2): total NPP declines with elevation, but the proportion of NPP allocated to above- and below-ground stays fixed.*

Net primary productivity 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_{BG} to NPP_{AG} 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 Aragón *et al.* (2009) between NPP_{AG} , NPP_{BG} and NPP_{Total} (i.e. a significant increase in both NPP_{AG} and NPP_{BG} with increasing NPP_{Total}) also applies to our TMF transect. Both studies found a similar sensitivity of above- and below-ground 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, Moser *et al.* (submitted; this volume) reported a

very different pattern of NPP allocation along an Ecuadorian elevational gradient, hence, generalising about the relationships between NPP components in tropical montane forests may still be premature.

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Nonetheless, in a review of above-ground 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, Aragão *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 Aragão et al. (2009) and Malhi et al. (2004).*

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559 *Factors controlling net primary productivity*

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In one of the most thorough appraisals of tropical forest NPP quantification of recent years, Clark *et al.* (2001) 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

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3 568 decreases at extremely high precipitation ($>3000 \text{ mm yr}^{-1}$), due to the indirect effects
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6 569 of excess moisture, such as low soil oxygen resulting in slow mineralisation rates and
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8 570 the loss of nutrients through leaching (Clark *et al.*, 2001b, Schuur, 2001). More
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10 571 recently, Malhi *et al.* (2004) concurred with these observations, and also reported that
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12 572 NPP_{Stem} varied substantially at the regional scale, and that a large part of this regional
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14 573 variation was due to soil type. Subsequently, Aragão *et al.* (2009) investigated the
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16 574 relationship between soil fertility and NPP in ten Amazonian forests on contrasting
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18 575 soil types, confirming the relationship between soil fertility (particularly phosphorus
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20 576 status) and productivity.
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27 578 Palm litter was not accounted for in the lowland plots, implying a further
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29 579 underestimation of $\text{NPP}_{\text{Canopy}}$ at 210 m and 194 m. Nonetheless, $\text{NPP}_{\text{Canopy}}$ was
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31 580 significantly lower in the cloud forest than in the pre-montane and lowland forests,
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33 581 showing evidence of a change of regime at the cloud base (Fig. 3a). Within the cloud
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35 582 immersion zone, $\text{NPP}_{\text{Canopy}}$ did not change significantly. The decrease in canopy
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37 583 production with increasing elevation may be largely explained by temperature
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39 584 ($r^2=0.76$, $P<0.005$, $n=9$), however, as temperature decreases linearly with elevation
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41 585 and $\text{NPP}_{\text{Canopy}}$ does not, this relationship may be a result of the indirect effects of
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43 586 temperature rather than the direct effects of temperature on plant physiology. Several
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45 587 authors have suggested that plants adjust their carbon allocation patterns in response
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47 588 to imbalances in resource availability (nutrients or water) (Bloom *et al.*, 1985, Litton
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49 589 *et al.*, 2007). Since SWC is typically above 25% in our plots, water shortage should
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51 590 not be limiting plant growth in any of our study sites. Nevertheless, water saturation
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53 591 in the soil may have prevented mineralization, reducing nutrient supply to the roots,
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55 592 as suggested by Leuschner *et al.* (2007).
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594 Our results indicate a strong correlation ($r^2=0.78$, $P<0.005$, $n=9$) between NPP_{Total} and
595 mean annual temperature, particularly so in the case of fine root ($r^2=0.77$, $P<0.005$,
596 $n=9$) and canopy productivity ($r^2=0.76$, $P<0.005$, $n=9$). Of course, correlation does not
597 necessarily indicate causation; further, linear regressions are not valid if there is a
598 sudden regime change at cloud base, as observed in this elevational gradient (Fig. 3).
599 The results of linear regressions are provided here to provide a summary statistic of
600 the overall trend observed along the elevational gradient, although we are cautious not
601 to over interpret them. Thus, over this extreme elevation gradient it is likely that
602 temperature plays an important role in influencing ecosystem function. This could be
603 through direct effects of temperature on plant physiology, or indirect effects via slow
604 decay and mineralization rates, which affect nutrient supply and canopy nitrogen and
605 leaf area index. Physiological studies at the 3025 m site in Wayquecha indicate no
606 decline in plant physiological capacity, but a decline in canopy leaf area and overall
607 canopy leaf nitrogen and N: P ratio (Fisher *et al.*, this issue). Hence the decline in
608 NPP components could be related to the observed decline in leaf nitrogen supply.
609 Finally, we observed a high rate of $NPP_{FineRoot}$ at 1855 m compared to other montane
610 forest sites, with values comparable to that of some lowland sites. Although this site is
611 located at the base of the cloud immersion zone, soil water content is lower at this site
612 than in other montane forest sites, as the soils are very steep and well drained in that
613 plot. It is also possible that the anomaly at 1855 m is driven secular trends, if long-
614 term warming is causing cloud base height to rise and the previous cloud base region
615 to dry. Although light incidence and rainfall patterns do not change significantly
616 within the cloud immersion zone, soil water content is uniformly high within the

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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 non-saturated soils, but no temperature sensitivity in the saturated soils. This may imply that the controlling factor is soil mineralisation 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.*

Carbon residence time

The discrepancy between above- versus below-ground allocation between biomass and NPP may be explained by differences in residence time of the carbon in above- and below-ground components. The stock of carbon in a particular carbon pool depends both on the rate of production of that pool and the mean residence time (or decomposition rate) of that pool. Carbon residence time differs for different pools of carbon in the ecosystem (Malhi *et al.*, 2009). Coarse wood has the longest residence time. Above-ground, stems have a carbon residence time of 42 to 71 years with insignificant lower residence times occurring at higher 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 to 100 years (Malhi *et al.*, 2006).

642 In contrast, the carbon residence times in below-ground components increase with
643 elevation from 4 months in the lowlands to almost 4 years at high elevations (Fig. 8).
644 Root residence time should be partly determined by the cost of root tissue
645 construction and maintenance, which is related to root C and N content (Gill &
646 Jackson 2000). There is evidence that low root tissue N content is linked with longer
647 residence time (Hendricks *et al.*, 1993; Gordon & Jackson 2000). Hence, water-
648 logged soils would contribute to longer residence time by slowing root mineral
649 uptake. Increasing soil acidity, as that found in the high elevation soils of the
650 Kosñipata transect, was also found to increase fine root residence time in temperate
651 forests (Jentschke *et al.*, 2001). In our study, decreasing temperatures explained 78%
652 of the variance in fine root residence time (slope=-0.24, $r^2=0.78$, $P<0.05$, $n=6$). This
653 long residence time explains the shift in C stocks from above- to below-ground as
654 elevation increases, despite the consistently slower productivity rates observed below-
655 ground.

657 ***Concluding remarks***

658 In summary, this study describes changes in total biomass and net primary
659 productivity (NPP) and their allocation between above-ground and below-ground
660 components in nine tropical forests sites along an elevational transect in the Peruvian
661 Andes. It found that (i) there is no change in total carbon stock with elevation, but
662 there is a shift in relative stock of carbon from above- to below-ground; (ii) total NPP
663 declines with elevation, but the proportion of NPP allocated to above-ground and
664 below-ground components stays fixed along the elevation gradient; (iii) NPP declines
665 linearly with elevation in lower forests, but is at a fairly constant low level within the
666 cloud forest zone. We conjecture that this pattern is driven by temperature limitation

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of mineralisation in the in lower forests, and by water-saturation inhibition of
mineralisation 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- versus belowground allocation between biomass and
NPP is explained by differences in residence time of the carbon in aboveground and
belowground components. Aboveground woody biomass components have a carbon
residence time of 42 to 71 with lower residence times occurring at higher elevations
as a result of high disturbance rates. In contrast, the carbon 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 (Malhi *et al.* 2009; Aragão et al 2009) probably represents the most comprehensive dataset to date on the carbon 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 $33\pm30\%$ of NPP_{Total} is allocated to canopy production, $20\pm8\%$ to above-ground woody production (and $61\pm21\%$ to above-ground NPP, including coarse root production). Below ground, $35\pm25\%$ of NPP_{Total} is allocated to fine root production, $4\pm2\%$ to coarse root production (and hence $39\pm25\%$ in total to below-ground 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**, 2759-2778.
- Bekku, Y, Kimura, M, Ikeda, H, *et al.* (1997) Carbon input from plants to soil through root exudation in *Digitaria adscendens* and *Ambrosia artemisiifolia*. *Ecological Research*, **12**, 305-312.
- Bernier, PY and 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 and Mooney, H (1985) Resource limitation in plants-an economic analogy. *Annual Review of Ecology and Systematics*, **16**.
- Burke, MK and Raynal, DJ (1994) Fine-root growth phenology, production, and turnover in a Northern hardwood forest ecosystem. *Plant and Soil*, **162**, 135-146.
- Chambers, JQ (2009) R project, in Laboratories, B, ed. Lucent Technologies.

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48
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55
56
57
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59
60

716 Chambers, JQ, Tribuzy, ES, Toledo, LC, *et al.* (2004) Respiration from a tropical
717 forest ecosystem: partitioning of sources and low carbon use efficiency. *Ecological*
718 *Applications*, 14, S72-S88.

719 Chave, J, Muller-Landau, HC, Baker, TR, *et al.* (2006) Regional and phylogenetic
720 variation of wood density across 2456 neotropical tree species, *Ecological*
721 *Applications*, 16(6), 2356-2367.

722 Chave, J, Andalo, C, Brown, S, *et al.* (2005) Tree allometry and improved estimation
723 of carbon stocks and balance in tropical forests. *Oecologia*, 145, 87-99.

724 Clark, DA, Brown, S, Kicklighter, DW, *et al.* (2001a) Measuring net primary
725 production in forests: Concepts and field methods. *Ecological Applications*, 11, 356-
726 370.

727 Clark, DA, Brown, S, Kicklighter, DW, *et al.* (2001b) Net primary production in
728 tropical forests: An evaluation and synthesis of existing field data. *Ecological*
729 *Applications*, 11, 371-384.

730 Cuevas, E and Medina, E (1988) Nutrient dynamics within Amazonian forests 2. Fine
731 root-growth, nutrient availability and leaf litter decomposition. *Oecologia*, 76, 222-
732 235.

733 Del Grosso, S, Parton, W, Stohlgren, T, *et al.* (2008) Global potential net primary
734 production predicted from vegetation class, precipitation, and temperature. *Ecology*,
735 89, 2117-2126.

736 Delaney, M, Brown, S, Lugo, AE, *et al.* (1997) The distribution of organic carbon in
737 major components of forests located in five life zones of Venezuela. *Journal of*
738 *Tropical Ecology*, 13, 697-708.

- 1
2
3 739 Gehring, C, Denich, M, Kanashiro, M, *et al.* (1999) Response of secondary vegetation
4
5 740 in Eastern Amazonia to relaxed nutrient availability constraints. *Biogeochemistry-US*,
6
7 741 45, 223-241.
8
9
10 742 Girardin, CAJ, Aragão LEOC, Malhi Y, Huaraca Huasco W, Metcalfe D,
11
12 743 Silvae JE (Submitted) Fine Root dynamics along an elevational gradient in tropical
13
14 744 Amazonian and Andean forests, *New Phytologist*.
15
16
17 745 Graefe, S, Hertel, D and Leuschner, C (2008) Estimating fine root turnover in tropical
18
19 746 forests along an elevational transect using Minirhizotrons. *Biotropica*, 40, 536–542.
20
21
22 747 Heimovaara, TJ (1993) Improved field probes for soil water content and electrical
23
24 748 conductivity measurements using time domain reflectometry *Water resource research*,
25
26 749 25, 2367-2376.
27
28
29 750 Hendricks, JJ, Hendrick, RL, Wilson, CA, *et al.* (2006) Assessing the patterns and
30
31 751 controls of fine root dynamics: an empirical test and methodological review. *Journal*
32
33 752 *of Ecology*, 94, 40–57.
34
35
36 753 Herbert, DA and Fownes, JH (1999) Forest productivity and efficiency of resource
37
38 754 use across a chronosequence of tropical montane soils. *Ecosystems*, 2, 242-254.
39
40
41 755 Intergovernmental Pannel on Climate Change (2007) *Climate Change 2007: The*
42
43 756 *Physical Science Basis. Contribution of Working Group I to the Fourth Assessment*
44
45 757 *Report of the IPCC, Cambridge, U.K., Cambridge University Press, 989.*
46
47
48 758 Kitayama, K and Aiba, SI (2002) Ecosystem structure and productivity of tropical
49
50 759 rain forests along altitudinal gradients with contrasting soil phosphorus pools on
51
52 760 Mount Kinabalu, Borneo. *Journal of Ecology*, 90, 37-51.
53
54
55 761 Kitayama, K and Mueller Dombois, D (1994) An altitudinal transect analysis of the
56
57 762 windward vegetation on haleakala, a Hawaiian island mountain: (2) Vegetation
58
59 763 zonation, *Phytocoenologia*, 24, 135-154.
60

1
2
3 764 Leuschner, C, Moser, G, Bertsch, C, *et al.* (2007) Large altitudinal increase in tree
4
5 765 root/shoot ratio in tropical mountain forests of Ecuador. *Basic and Applied Ecology*,
6
7 766 8, 219-230.
8
9
10 767 Litton, CM, Raich, JW and Ryan, MG (2007) Carbon allocation in forest ecosystems.
11
12 768 *Global Change Biology*, 13, 2089-2109.
13
14
15 769 Malhi, Y, Aragão, LEOC, Metcalfe, DB, *et al.* (2009) Comprehensive assessment of
16
17 770 carbon productivity, allocation and storage in three Amazonian forests. *Global*
18
19 771 *Change Biology*, 15, 1255 -1274.
20
21
22 772 Malhi, Y, Baker, TR, Phillips, OL, *et al.* (2004) The above-ground coarse wood
23
24 773 productivity of 104 Neotropical forest plots. *Global Change Biology*, 10, 563-591.
25
26
27 774 Malhi, Y, Baldocchi, DD and Jarvis, PG (1999) The carbon balance of tropical,
28
29 775 temperate and boreal forests. *Plant Cell and Environment*, 22, 715-740.
30
31
32 776 Malhi, Y, Wood D., Baker T.R., *et al.* (2006) The regional variation of aboveground
33
34 777 live biomass in old-growth Amazonian forests. *Global Change Biology*, 12, 1107-
35
36 778 1138.
37
38
39 779 Metcalfe, D, Meir P, Aragão LEOC, *et al.* (2008a) Sample sizes for estimating key
40
41 780 ecosystem characteristics in a tropical terra firme rainforest *Forest Ecology and*
42
43 781 *Management*, 255, 558-566.
44
45
46 782 Metcalfe, D, Meir, P, Aragão, LEOC, *et al.* (2008b) The effects of water availability
47
48 783 on root growth and morphology in an Amazon rainforest. *Plant and Soil*, 311, 189-
49
50 784 199.
51
52
53 785 Metcalfe, D, Williams, M, Aragão, LEOC, *et al.* (2007) A method for extracting plant
54
55 786 roots from soil which facilitates rapid sample processing without compromising
56
57 787 measurement accuracy. *New Phytologist*, 174, 697-703.
58
59
60

- 788 Moser, G, Röderstein, M, Soethe, N, *et al.* (2008) Altitudinal changes in stand
789 structure and biomass allocation of tropical mountain forests in relation to
790 microclimate and soil chemistry. *Ecological Studies*, 198, 229-242, Berlin Heidelberg,
791 Springer Verlag.
- 792 Moser, G, Leuschner, C, Hertel, D, Graefe, S, Iost, S (submitted, this issue) Elevation
793 effects on the carbon budget of tropical mountain forests (S Ecuador): The role of the
794 belowground compartment, *Global Change Biology*.
- 795 Nadelhoffer, K, Aber, J and Mellilo, J (1985) Fine roots, net primary production, and
796 soil nitrogen availability: A new hypothesis. *Ecology*, 66, 1377–1390.
- 797 Ostertag, R (2001) Effects of Nitrogen and phosphorous availability on fine root
798 dynamics in Hawaiian montane forests. *Ecology*, 82, 485-499.
- 799 Raich, JW and Nadelhoffer, KJ (1989) Belowground carbon allocation in forest
800 ecosystems: Global trends. *Ecology*, 70, 1346-1354.
- 801 Raich, JW, Russell, AE and Vitousek, PM (1997) Primary productivity and ecosystem
802 development along an elevational gradient on Mauna Loa, Hawai'i. *Ecology*, 78, 707-
803 721.
- 804 Roderstein, M, Hertel, D and Leuschner, C (2005) Above- and below-ground litter
805 production in three tropical montane forests in southern Ecuador. *Journal of Tropical*
806 *Ecology*, 21, 483-492.
- 807 Roy, R, Saugier, B and Mooney, HA (2001) *Terrestrial Global Productivity*,
808 Academic Press, 573.
- 809 Schuur, EAG (2003) Productivity and Global Climate Revisited: The Sensitivity of
810 Tropical Forest Growth to Precipitation. *Ecology*, 84, 1165-1170.

1
2
3 811 Schuur, EAG and Matson, PA (2001) Net primary productivity and nutrient cycling
4
5 812 across a mesic to wet precipitation gradient in Hawaiian montane forest. *Oecologia*,
6
7 813 128, 431-442.
8
9
10 814 Steingrobe, B, Schmid, H and Claassen, N (2000) The use of the ingrowth core
11
12 815 method for measuring root production of arable crops: influence of soil conditions
13
14 816 inside the ingrowth core on root growth. *Journal of Plant Nutrition and Soil Science*,
15
16 817 163, 617-622.
17
18
19 818 Takyu, M, Aiba, SI and Kitayama, K (2002) Effects of topography on tropical lower
20
21 819 montane forests under different geological conditions on Mount Kinabalu, Borneo.
22
23 820 *Plant Ecology*, 159, 35-49.
24
25
26 821 Tanner, EVJ and Grubb, PJ (1999) NPP tropical forest: John Crow Ridge, Jamaica,
27
28 822 1974-1978. Data set. , in ed. Oak Ridge National Laboratory Distributed Active
29
30 823 Archive Center, Oak Ridge, Tennessee, U.S.A.
31
32
33 824 Vogt, KA, Grier, CC, Meier, CE, *et al.* (1982) Mycorrhizal role in net primary
34
35 825 production and nutrient cycling in *Abies amabilis* ecosystems in western Washington.
36
37 826 *Ecology*, 63, 370-380.
38
39
40 827 Vogt, KA, Vogt, DJ and Bloomfield, J (1998) Analysis of some direct and indirect
41
42 828 methods for estimating root biomass and production of forests at an ecosystem level.
43
44 829 *Plant and Soil*, 200, 71-89.
45
46
47 830 Waide, RB, Zimmerman, JK and Scatena, FN (1998) Controls of primary
48
49 831 productivity: lessons from the Luquillo mountains in Puerto Rico. *Ecology*, 79, 31-37.
50
51 832 Zegelin, SJ (1989) Design of triple wire time domain reflectometry probes in practice
52
53 833 and theory. *Soil Science Society of America Journal*, 57.
54
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835 Tables and Figures

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837 **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
Site Code	WAY	TU3	TU4	TU7	TU8	SPD	TON	TAM 3
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"
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"
Elevation (m)	3025	3020	2720	2020	1855	1500	1000	210
Aspect	E	W	W	W	W	W	W	-
Mean annual air temp. (°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
Annual precipitation (mm yr ⁻¹)	1706	1776	2318	1827	2472	2631	3087	2730
Soil organic layer depth (cm)	20.20	42.20	43.63	35.34	26.28	10.55	4.65	1.50
Dominant Families	<i>Weinman- nia; Clusia; Hespero- meles</i>	<i>Clusiaceae; Cunoniceae</i>	<i>Cunoniceae; Lauraceae</i>	<i>Clusiaceae; Alzateaceae</i>	<i>Clethra- ceae; Myrtaceae; Clusiaceae</i>	<i>Euphorbi- aceae; Fabaceae; Lauraceae</i>	<i>MoraceaeFa baceae; Rubiceae</i>	<i>Bixaceae; Moraceae; Fabaceae</i>

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Table 2 Synthesis of carbon stocks estimates. All values are in Mg C ha⁻¹. Bm, biomass, ML, mineral layer, OL, organic layer, BG, below ground. Bm_{CoarseRoots} were estimated as described in the text (Malhi *et al.*, 2009). All other values were directly measured as described in the text. Bm_{Stem} were calculated as the sum of all stem stocks of trees >10cm diameter.

Plot	Elevation (m)	CStock _{Soil} (ML)	CStock _{Soil} (OL)	CStock _{FineRoots}		CStock _{CoarseRoots}		CStock _{BG}		CStock _{Stem}	
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				

Table 3 Synthesis of net primary productivity (NPP) estimates. Error estimates are SE of the mean (value $\pm$ SE), SE was not available for NPP_{Stem} as it is the sum of NPP_{Stem} 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⁻¹ yr⁻¹. AG, above-ground, BG, below ground. Values in bold were directly measured. NPP_{Branch} data were obtained from Malhi *et al.* (2009). Other values were estimated as described in the text.

Plot	Elevation (m)	NPP _{FineRoots}	NPP _{CoarseRoots}	NPP _{BG}	NPP _{Stem}	NPP _{FineLitter}	NPP _{Branch}	NPP _{AG}	NPP _{Total}
WAY	3025	1.23 $\pm$ 0.40	0.25 $\pm$ 0.04	1.48 $\pm$ 0.40	1.20 $\pm$ 0.12	1.92 $\pm$ 0.10	0.5 $\pm$ 0.5	3.60 $\pm$ 0.13	5.09 $\pm$ 0.42
TU3	3020	1.31 $\pm$ 0.23	0.21 $\pm$ 0.04	1.52 $\pm$ 0.23	1.00 $\pm$ 0.10	1.19 $\pm$ 0.05	0.4 $\pm$ 0.4	2.59 $\pm$ 0.11	4.11 $\pm$ 0.26
TU4	2720	1.63 $\pm$ 0.34	0.33 $\pm$ 0.04	1.96 $\pm$ 0.35	1.57 $\pm$ 0.16	1.83 $\pm$ 0.06	0.6 $\pm$ 0.6	4.03 $\pm$ 0.17	5.98 $\pm$ 0.39
TU7	2020	1.80 $\pm$ 0.18	0.16 $\pm$ 0.03	1.96 $\pm$ 0.18	0.79 $\pm$ 0.08	1.44 $\pm$ 0.06	0.3 $\pm$ 0.3	2.54 $\pm$ 0.09	4.50 $\pm$ 0.20
TU8	1855	3.26 $\pm$ 0.73	0.17 $\pm$ 0.03	3.43 $\pm$ 0.73	0.79 $\pm$ 0.08	1.44 $\pm$ 0.05	0.3 $\pm$ 0.3	2.55 $\pm$ 0.09	5.97 $\pm$ 0.73
SPD	1500	1.70 $\pm$ 0.40	0.34 $\pm$ 0.05	2.04 $\pm$ 0.41	1.62 $\pm$ 0.16	2.76 $\pm$ 0.13	0.6 $\pm$ 0.6	5.03 $\pm$ 0.18	7.06 $\pm$ 0.44
TON	1000	2.42 $\pm$ 0.81	0.28 $\pm$ 0.04	2.70 $\pm$ 0.81	1.34 $\pm$ 0.13	2.49 $\pm$ 2.02	0.5 $\pm$ 0.5	4.37 $\pm$ 0.55	7.07 $\pm$ 0.98
TAM05	210	6.80 $\pm$ 1.00	0.60 $\pm$ 0.10	7.40 $\pm$ 1.00	2.80 $\pm$ 0.24	5.60 $\pm$ 0.42	1.1 $\pm$ 1.1	9.50 $\pm$ 1.08	16.9 $\pm$ 1.48
TAM06	194	4.80 $\pm$ 0.57	0.60 $\pm$ 0.09	5.40 $\pm$ 0.58	2.60 $\pm$ 0.42	4.60 $\pm$ 0.24	1.0 $\pm$ 1.0	8.24 $\pm$ 1.11	13.6 $\pm$ 1.25

Table 4 Statistical significance of NPP correlations with mean annual values of weather parameters along the Kosñipata elevational transect. Units of slope are in Mg C ha⁻¹ yr⁻¹ °C⁻¹ for temperature correlations and Mg C ha⁻¹ yr⁻¹ mm⁻¹ for rainfall correlations.

Variable	NPP _{Total}		NPP _{Stem}		NPP _{Canopy}		NPP _{AG}		NPP _{FineRoot}		NPP _{BG}		NPP _{BG}	
Constant	Air	Rainfall	Air	Rainfall	Air	Rainfall	Air	Rainfall	Air	Soil	Air	Soil	Air	Rainfall
Slope	0.72	0.005	0.10	0.0008	0.25	0.002	0.35	0.003	0.30	0.29	0.002	0.32	0.31	0.002
P	< 0.005	< 0.5	< 0.05	< 0.5	< 0.005	< 0.5	< 0.005	< 0.5	< 0.005	< 0.05	< 0.5	< 0.005	< 0.05	< 0.5
r ²	0.78	0.33	0.59	0.3	0.77	0.35	0.72	0.34	0.77	0.66	0.28	0.78	0.67	0.29
n	9	9	9	9	9	9	9	9	9	9	9	9	9	9

Table 5 Stem (RT_{Stem}) and fine roots ($RT_{\text{FineRoots}}$) residence time (yrs, $\pm$ SE). As we could not directly estimate SE of stem carbon stocks, we assumed a SE of 3% for RT_{Stem} , based on data available from lowland plots (Aragão *et al.*, 2009).

Elevation (m)	RT_{Stem} (yrs)			$RT_{\text{FineRoots}}$ (yrs)		
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

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Figure Legends

Figure 1 The variation with elevation of above- and below-ground standing carbon stocks (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 above-ground biomass with increasing elevation, both when data points from this study were combined with data presented in Aragao *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 above-ground 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.

Figure 2 The net primary productivity (NPP) of the seven pre-montane and montane sites from this study compared to 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.

Figure 3 Above- and below-ground net primary productivity (Mg C ha⁻¹ yr⁻¹) along the elevational gradient. (a) NPP_{Canopy} (pale grey), (b) NPP_{FineRoot} (dark grey) and (c) NPP_{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.

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Figure 4 Ratio of below- to above-ground 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.

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Figure 5 Partitioning of net primary productivity (NPP) components along the elevational gradient. (a) NPP_{Stem}/NPP_{Total} , (b) NPP_{Canopy}/NPP_{Total} (c) $NPP_{FineRoot}/NPP_{Total}$ ratios along the elevational gradient. Data from this study (closed squares) is compared to 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.

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Figure 6 Above- (AG) and below-ground (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, $y = 0.58 \pm 0.025 x$, $r^2 = 0.94$, $P < 10^{-4}$, $n = 9$) and NPP_{BG} (solid line, $y = 0.41 \pm 0.022 x$, $r^2 = 0.89$, $P < 10^{-4}$, $n = 9$). In lowland Amazonian forests, NPP_{AG} (dotted line, $y = 0.61 \pm 0.035 x$, $r^2 = 0.52$, $P < 0.04$, $n = 8$) and NPP_{BG} (dotted line, $y = 0.38 \pm 0.032 x$, $r^2 = 0.40$, $P < 0.08$, $n = 8$). For the combined dataset, NPP_{AG}

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3 959 $(y=0.54\pm0.026x, r^2=0.89, P<0.0005, n=16)$ and $NPP_{BG} (y=0.44\pm0.024 x, r^2=0.93, P<0.0005,$
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6 960 $n=16)$. Error bars are SE of the mean.
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10 962 **Figure 7** Relationships between the two above-ground NPP components. We include values
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12 963 from the Kosñipata transect (closed squares, $y=1.73\pm0.23 x, r^2=0.90, P<0.0005, n=9)$ and from
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14 964 lowland sites presented in Aragão *et al.* (2009) and Malhi *et al.* (2009) (open triangles,
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16 965 $y=1.58\pm0.36 x, r^2=0.44, P<0.05, n=11)$. Error bars are SE of the mean.
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22 967 **Figure 8** (a) Stem (b) and fine root carbon residence time (years) along the elevational
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24 968 gradient. Error bars are SE of the mean. The estimated base of the cloud immersion zone is
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26 969 located at 1500 – 1800 m.
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Figures

Figure 1

Published results from lowland Amazonia

Brazil

Figure 3

Figure 4

Figure 5

Figure 6

Figure 7

Figure 8