Nutrient limitation in rainforests and cloud forests along a 3,000-m elevation gradient in the Peruvian Andes

8 authors, including:

Some of the authors of this publication are also working on these related projects:

Project   Interactions Between Climate, Forests, and Land Use in the Amazon Basin Modeling and Mitigating Large Scale Savannization View project

Project   Markedly divergent estimates of Amazon forest carbon density from ground plots and satellites View project

ECOSYSTEM ECOLOGY - ORIGINAL RESEARCH

Nutrient limitation in rainforests and cloud forests along a 3,000-m elevation gradient in the Peruvian Andes

Joshua B. Fisher · Yadvinder Malhi · Israel Cuba Torres · Daniel B. Metcalfe ·
Martine J. van de Weg · Patrick Meir · Javier E. Silva-Espejo · Walter Huaraca Huasco

Abstract We report results from a large-scale nutrient fertilization experiment along a "megadiverse" (154 unique species were included in the study) 3,000-m elevation transect in the Peruvian Andes and adjacent lowland Amazonia. Our objectives were to test if nitrogen (N) and phosphorus (P) limitation shift along this elevation gradient, and to determine how an alleviation of nutrient limitation would manifest in ecosystem changes. Tree height decreased with increasing elevation, but leaf area index (LAI) and diameter at breast height (DBH) did not vary with elevation. Leaf N:P decreased with increasing elevation (from 24 at 200 m to 11 at 3,000 m), suggesting increased N limitation and decreased P limitation with increasing elevation. After 4 years of fertilization (N, P, N + P), plots at the lowland site (200 m) fertilized with N + P showed greater relative growth rates in DBH than did the control plots; no significant differences were evident at the 1,000 m site, and plots fertilized with N at the highest elevation sites (1,500, 3,000 m) showed greater relative growth rates in DBH than did the control plots, again suggesting increased N constraint with elevation. Across elevations in general N fertilization led to an increase in microbial respiration, while P and N + P addition led to an increase in root respiration and corresponding decrease in hyphal respiration. There was no significant canopy response (LAI, leaf nutrients) to fertilization, suggesting that photosynthetic capacity was not N or P limited in these ecosystems. In sum, our study significantly advances ecological understanding of nutrient cycling and ecosystem response in a region where our collective knowledge and data are sparse: we demonstrate N limitation in high elevation tropical montane forests, N and P co-limitation in lowland Amazonia, and a nutrient limitation response manifested not in canopy changes, but rather in stem and belowground changes.

Keywords Fertilization · Forest · Montane · Nitrogen · Phosphorus · Tropical

J. B. Fisher · Y. Malhi
Environmental Change Institute, School of Geography
and the Environment, Oxford University, South Parks Road,
Oxford OX1 3QY, UK

Present Address:
J. B. Fisher (✉)
Jet Propulsion Laboratory, California Institute of Technology,
4800 Oak Grove Drive, Pasadena, CA 91109, USA
e-mail: joshbfisher@gmail.com

I. C. Torres · J. E. Silva-Espejo · W. H. Huasco
Department of Biology, Universidad San Antonio
Abad del Cusco, Cusco, Peru

D. B. Metcalfe
Department of Forest Ecology and Management, Swedish
University of Agricultural Sciences, Skogmarksgränd,
90660 Umeå, Sweden

M. J. van de Weg
Amsterdam Global Change Institute, Vrije Universiteit, De
Boelenlaan 1085, 1081 HV Amsterdam, The Netherlands

P. Meir
School of Geosciences, University of Edinburgh, Drummond
Street, Edinburgh EH8 9XP, UK

Introduction

Both nitrogen (N) and phosphorus (P) limit net primary productivity (NPP) in most terrestrial ecosystems globally (Elser et al. 2007; Vitousek and Howarth 1991), but P may be more limiting than N in lowland Amazonia (Aragão et al. 2009; Benner et al. 2010; Meir et al. 2001; Quesada et al. 2009a, b; Vitousek 1984; Vitousek and Sanford 1986). Natural P limitation in lowland Amazonia results from leaching of highly weathered soils, as well as chemical processes that immobilize P within the soils, whereas N limitation is relatively lower due to high rates of plant turnover and decomposition as well as abundant N fixers (Hedin et al. 2009; Vitousek et al. 2010).

Tropical montane forests such as those in the adjacent Andes, however, may experience less P limitation than the lowland tropical forests. Andean soils are generally much younger, and thus less weathered, than lowland Amazonian soils (Garzione et al. 2008). Conversely, because Andean ecosystems are relatively young, they may be N limited because N accumulates in ecosystems over time. Furthermore, these montane ecosystems turnover frequently because of landslides and erosion (Blodgett and Isacks 2007; Bussmann et al. 2008; Lozano et al. 2005; Wilcke et al. 2003) and have slower decomposition and mineralization rates due to lower temperatures (Kirschbaum 1995; Salinas et al. 2011), also limiting N availability. These patterns are presumed to follow the prevailing hypothesis for tropical montane ecosystems: moving up-slope decreases P limitation but increases N limitation, and vice versa down-slope; mid-elevation forests may be co-limited by both nutrients (Aerts and Chapin 2000; Benner et al. 2010; Davidson and Howarth 2007; Güsewell 2004; Tanner et al. 1998; Vitousek 1984; Vitousek and Farrington 1997).

N limitation in the Andes might be mitigated by two processes, however: (1) atmospheric N deposition from Amazonian biomass burning (Aragão et al. 2007, 2008; Boy et al. 2008; Fabian et al. 2005; Galloway et al. 2004; Hietz et al. 2011; van de Weg et al. 2009); and (2) increased decomposition and nutrient mineralization rates from rising temperatures with climate change (Malhi and Wright 2004; Pastor and Post 1988; Peterjohn et al. 1994; Salinas et al. 2011; Vuille and Bradley 2000; Zimmermann et al. 2010a). Therefore, it may well be that Andean forests are only marginally P or N limited if, in fact, both nutrients are in sufficient supply due to new soils providing P, and atmospheric deposition and increased mineralization providing N (Fisher et al. 2012). NPP could instead be primarily constrained less by N or P supply, but more by other environmental variables such as temperature, light and/or moisture, or other nutrients (Chapin et al. 1986). However, we do not know if this is the case, as, until recently, there

have been no extensive measurements or manipulation experiments linking productivity to nutrient supply in the Andes (Wullaert et al. 2010). Here, we present results from an investigation of nutrient limitation in the Peruvian Andes from one of the largest tropical forest elevation gradients ever studied.

Our objectives were to determine if N and/or P limits the productivity of Andean forests, and if there is an elevation gradient in N and/or P limitation. To assess the coupling between the nutrients regime and ecosystem productivity, we conducted a large-scale factorial fertilization experiment at four sites along a 3,000-m elevation transect in the Peruvian Andes and adjacent lowland Amazonia (200, 1,000, 1,500, 3,000 m). Our aim was to eliminate N or P limitation and observe the forest response. We hypothesized that we would observe an elevation gradient in N and P limitation following the prevailing hypothesis for nutrient limitation in tropical montane ecosystems.

The hypothesis that N limitation will increase and P limitation will decrease while ascending tropical elevation gradients has not been rigorously tested, and there exist several viable alternatives. How a plant allocates nutrient resources depends on a variety of interacting factors such as life strategy, species traits, competition, disturbance, and other limiting elements (Chapin et al. 1986; Eckstein et al. 1999; Grime 1977). Additional nutrients could alter any, all or none of the following physiological and ecosystem responses: leaf nutrient content, leaf biomass, leaf area, leaf quantity, leaf and plant lifespan, retranslocation rates, wood accumulation, tree height, photosynthetic and respiration rates, root biomass and productivity, mycorrhizal activity, soil respiration, and abundance of insects and fauna (Aerts 1996; Auerbach and Strong 1981; Brix 1971; Chapin et al. 1990; Field and Mooney 1986; Johnson et al. 1994; Johnson 1993; Meyer and Root 1996; Ryan and Yoder 1997; Shaver 1981; Wilson and Tilman 1993). Limitation by temperature, light and moisture could minimize the effects of nutrient addition, even if the ecosystems are nutrient limited (Chapin et al. 1986).

To address possible ecosystem responses to fertilization, we monitored not only the nutrients themselves in the soils and leaves along the gradient but also key aspects of major biomass changes in the leaves, wood and soil. Specifically, we measured: (1) canopy response (i.e., leaf area index or LAI); (2) woody accumulation or tree growth (i.e., increment change in diameter at breast height or DBH); and (3) soil respiration partitioning between microbes, roots, fungal hyphae, and litter. We repeated our measurements across an elevation transect, which allowed us to control for some of the climatic variables. We asked how or if these ecosystem components changed with fertilization and with elevation. Specifically, we asked how an alleviation of nutrient limitation might manifest in changes to canopy

Table 1 Site characteristics

	Tambopata	Tono	San Pedro	Wayqecha
Elevation (m)	200	1,000	1,500	3,000
Mean annual temperature (°C)	26.4	20.7	18.8	12.5
Mean annual precipitation (mm)	2,730	3,087	5,302	1,706
Slope (%)	0	8	27	28
Aspect	–	W	W	E
Geological substrate	Pleistocene alluvial terrace	Alluvial terrace	Granite	Paleozoic shales–slates
Soil pH	3.9	3.8	4.0	4.1
Dominant plant families	*Myristicaceae, Fabaceae*	*Rubiaceae, Fabaceae, Moraceae*	*Lauraceae, Rubiaceae, Melastomataceae*	*Cunoniaceae, Clusiaceae*
Longitude	−69.2967	−71.5327	−71.5370	−71.5870
Latitude	−12.8387	−12.9475	−13.0492	−13.1903

For consistency with related papers, it is noted that the long-term 1-ha plot at Wayqecha is 25 m upslope from the fertilization experiment (i.e. at 3,025 m)

(e.g., adjustments to foliar stoichiometry, LAI) versus stem growth versus belowground respiration (e.g., decrease fungal respiration associated with symbioses).

Materials and methods

Study sites

We conducted a nutrient fertilization experiment adjacent to four long-term monitoring sites along the eastern flank of the SE Peruvian Andes and adjacent Amazonian lowlands (Table 1, Supplemental Fig. 1). The long-term monitoring sites were established in 2003 as 100 × 100 m plots located at elevations of 200 m (Tambopata), 1,000 m (Tono), 1,500 m (San Pedro), and 3,000 m (Wayqecha). The sites were established to assess biodiversity patterns, elevation species range shifts and productivity in an elevation gradient with minimal horizontal distance between sites (e.g., similar atmospheric influences) and minimal vertical distance within sites for mature forests. The 1,500 and 3,000 m sites are situated in the Kosñipata Valley (13°S, 70°W); they both represent cloud forests, with the 1,500 m site at the base of the clouds and the 3,000 m site near the tree line. The 1,000 m site is situated in an adjacent valley in the sub-montane transition zone between the Andean mountains and the Amazonian lowlands. The 200 m site is located on a Pleistocene floodplain terrace much further down river from the other sites in the Tambopata valley in lowland Amazonia.

Across all sites, the mean annual temperature ranged from 12.5 to 26.4 °C, and mean annual precipitation ranged from 1,706 to 5,300 mm, with peak precipitation near the base of the mountain range (Table 1) (Girardin et al. 2010; Huaraca Huasco et al. 2012). The 200 and 1,000 m sites are situated on alluvial terraces, the 1,500 m site on a shallow soil (60 cm depth) with a thick organic layer and overlying granite bedrock, and the 3,000 m site on a shallow soil (50 cm depth) with a thick organic layer overlying Paleozoic shales/slates (Zimmermann et al. 2010b, 2012). All sites have very acidic soils and there were no significant differences in soil pH ($\sim$4.0) across sites or with fertilization treatment. The dominant (number of stems) plant families in the fertilization experiment were: *Myristicaceae* and *Fabaceae* (200 m); *Rubiaceae*, *Fabaceae* and *Moraceae* (1,000 m); *Lauraceae*, *Rubiaceae* and *Melastomataceae* (1,500 m); and, *Cunoniaceae* and *Clusiaceae* (3,000 m). A total of 637 trees were included (351 fertilized, 286 control) in the experiment. Of the 180 trees at the 200 m site, 41 % (73) were of species unique to that site, and this applied to 42 % (68) of the 165 trees at the 1,000 m site, 53 % (71) of the 135 trees at the 1,500 m site, and 25 % (37) of the 157 trees at the 3,000 m site.

The fertilization experiment was established in 2007, adjacent and down-slope of the long-term monitoring plots as 10 × 110-m transects along three sides of each long-term 100 × 100 m plot following previous experimental designs in tropical montane forests (Tanner et al. 1990, 1998) (Supplemental Fig. 2). Within each transect were eleven 10 × 10 m sub-plots, two of which were fertilized (dissolved in solution) every 3 months (January, April, July, October) starting in October 2007 with N (0.5 kg urea/100 m^2; 46 % N concentration), two with P (0.25 kg triple superphosphate/100 m^2; 20 % P, 50 % P_2O_5 concentration), two with both N and P (same amounts as alone), while six controls separated each fertilized sub-plot

(following, for example, Tanner et al. 1990, 1992). Each sub-plot contained ~5 trees that were fertilized and measured (if there were more than 5 in a sub-plot, then not every tree was measured). Litter at the base of each tree was cleared, fertilizer was applied at the base of each tree (rather than uniformly across the full area of the 100 m² sub-plots), and worked into the soil by foot, and the litter was returned; this action was designed to reduce runoff of the fertilizer. Litter disturbance was simulated in control plots, but water was not added as we determined the water added was negligible given how wet the forests already were (in addition to the logistical difficulty with carrying extra water to the remote field sites). Although we were unable to measure all leaching and gaseous loss components, Wullaert et al. (2010) report minimal leaching or gaseous loss in a similar experimental design fertilization experiment in the Ecuadorian Andes, suggesting nearly complete uptake (>90 %) of fertilizer by the local ecosystem. Of those fertilized sub-plots within each transect, half began fertilization in the first year and the other half in the second year. All sub-plots continued to receive fertilization through 2011. This temporal stagger was designed as a temporal control: the response of nutrient addition after the first year for the first group should be similar to that after the second year for the second group, after accounting for the background rate of growth. Therefore, this experimental design enabled twofold replication in time as well as threefold replication in space at each site.

Measurements

Soil and leaves were collected for nutrients analysis from a subset of the total trees in October 2008. Our intention was to collect samples for nutrient analysis each year, but mid-project funding restrictions limited this particular analysis to 2008 alone; this also limited the possibility of litterfall and fine root growth measurements. Soils were collected in each 10 × 10 m sub-plot (both fertilized and control) with a soil corer. We sampled the entire depth of the organic layer for each site, the entire depth of the mineral layer for the 3,000 m site, and half the depth of the mineral layer for the other sites (see Table 1). Organic and mineral layers were separated. The organic layer soil was used primarily for analysis as per findings from an Ecuadorian elevation transect indicating the importance of the organic layer for tree growth (Unger et al. 2010; Wilcke et al. 2008). Soils were analyzed to calculate soil bulk density (stones removed). One transect per site was used for pH measurements for the soil organic layer only. Leaves were cut fresh from three vertical canopy height positions (top, middle, bottom) for trees ($n = 77$) from all fertilized plots and 60 % of the control plots. The leaves were then combined for an aggregate sub-plot canopy sample. Some

leaves were reserved for more detailed analyses: (1) we kept the canopy heights separated, but aggregated per sub-plot, for one transect (only half the controls) per site; and (2) we kept individual trees separate, but still aggregated canopy heights, for ~20 trees per site.

Soil and leaf samples were analyzed for nutrients content at A & L Western Agricultural Laboratories, Modesto, CA, USA. Soil pH was determined from a deionized water-based saturated paste extract. Total soil N (organic N, NH_3 and NH_4^+) was determined by measuring total Kjeldahl N (Distillation Unit 100; Fisher Scientific). Total soil P was determined from nitric/hydrochloric acid digestion by method AOAC 957.02/SW846-60101B. Leaf nutrients were determined from nitric/hydrochloric acid digestion prepared using a modified MARS microwave oven (http://www.CEM.com), and analysis by inductively coupled plasma spectrometry. All other procedures followed the North American Proficiency Testing Program standards (http://www.naptprogram.org). Standard quality control samples were run every 20 samples.

Dendrometers measured with a caliper were fitted to each numbered and tagged tree with a DBH (1.3 m) >10 cm. A DBH tape was used for trees with DBH <10 cm. Dendrometers were made from high-tension polyester strapping, springs and clamps, and crosschecked with a DBH tape for every measurement. Precision was reported to 0.01 cm. Moss, roots, lianas, and other debris were separated from the bark of each tree at the point of measurement. A painted mark on each tree indicated the exact location for repeat measurements and to ensure that dendrometers had not been moved between measurements. Many trees grew at angles away from the steep slopes—the point of measurement was 1.3 m from the up-slope base of the tree along its length. Split-bole trees were generally avoided, as were palms and tree ferns, which do not exhibit extended DBH growth. DBH measurements were recorded every 3 months beginning in April 2007, which was 6 months before the initial fertilization began, through August 2011. The DBH distribution for each site and the tree height (measured from a laser altimeter) to DBH relationship are shown in Fig. 1a and b.

Zenith-pointing hemispherical photos with three different exposures were taken at the center of each sub-plot in October 2009 alone. Photos were taken at dawn without the solar disc visible, and under dry, and where possible, cloudy weather (i.e., when the diffuse radiation fraction is large). Photos were processed for LAI calculation using Can-Eye v.5.0 software. The software's algorithm is based on the measurement of gap fraction, which depends on light transmittance through the canopy considering the vegetation elements as opaque. Further details on the theory and algorithms can be found on the Can-Eye website (https://www4.paca.infra.fr/can-eye). This method may
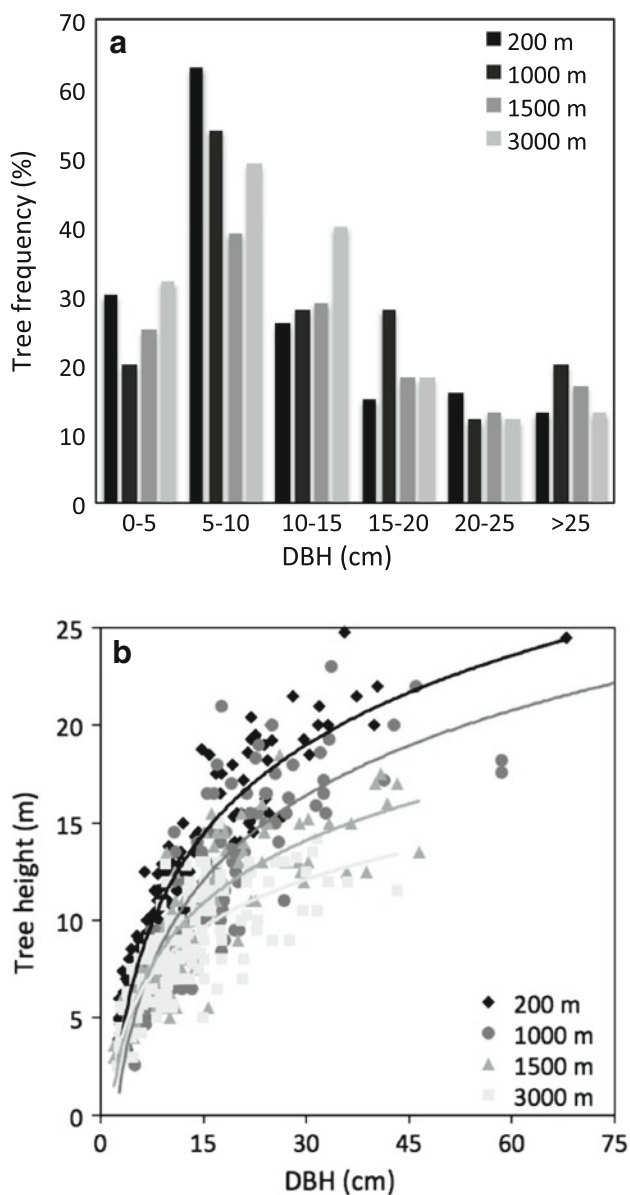
Fig. 1 Average tree diameter at breast height (DBH) for each site (200, 1,000, 1,500, 3,000 m): **a** frequency distribution, and **b** as a function of tree height. The regression equations for tree height (*y*) versus DBH (*x*) are: $y = 6.60LN(x) - 3.44$ at 200 m ($r^2 = 0.89$); $y = 6.29LN(x) - 5.00$ at 1,000 m ($r^2 = 0.81$); $y = 4.63LN(x) - 1.66$ at 1,500 m ($r^2 = 0.78$); $y = 3.53LN(x) + 0.08$ at 3,000 m ($r^2 = 0.67$)

provide larger LAI values than from a spherical densiometer so the relative change in LAI is more useful here than are the absolute values.

Soil CO_2 respiration was measured at the center of each 10×10 m sub-plot (both fertilized and control) in October 2009 alone using an infrared gas analyzer (EGM-4 and SRC-1 chamber; PP Systems, Hitchin, UK). An experimental design was set up to partition the contributions from surface organic litter, roots, fungal hyphae and soil microbes (Heinemeyer et al. 2007). Four soil cores were installed in

each sub-plot for the partitioning: (1) a surface core that integrated all components for total respiration ($R_{litter} + R_{roots} + R_{hyphae} + R_{microbes}$); (2) a surface core with litter removed ($R_{roots} + R_{hyphae} + R_{microbes}$); (3) a deep core (40 cm) with fine 41 μm gauge nylon mesh covering cut out windows in the core that permitted the in-growth of fungal hyphae but excluded roots (Langley et al. 2006) and litter removed ($R_{hyphae} + R_{microbes}$); and (4) a deep core that excluded both roots and fungal hyphae, and litter removed ($R_{microbes}$). Fungal hyphae may derive from both mycorrhizal and saprotrophic fungi. The cores were installed at the center of each sub-plot 3 months prior to the first measurements. Roots were manually removed from soil within the deep cores; disturbance was accounted for with a sub-set of cores used to disturb the soil in the same manner as the root removal procedure, but without actually removing roots. Soil moisture and temperature were measured inside and outside each core with each measurement. The contribution of each soil component was calculated from simple arithmetic differences between cores (e.g., $R_{litter} = R_{core\ 1} - R_{core\ 2}$). Ten soil respiration measurements were taken per core. Control plot data were normalized to fertilization plot measurements. Belowground components at the sites are addressed in greater detail in other papers (Huaraca Huasco et al. 2012; Silva-Espejo et al. 2012).

Data analysis

We report total soil N and P from the organic ($n = 108$) and mineral ($n = 36$) layers separately for all sites and fertilization treatments, and most control sub-plots (3 of 5 per transect for cost reduction). For leaf nutrients, we report sub-plot averages and standard errors aggregated for fertilization treatment and control sub-plots within each site ($n = 132$). Hypotheses tested for soil N and P, and leaf N and P, using ANOVA and one-tailed *t* tests were: (1) soil N or leaf N declined with elevation; (2) soil P or leaf P increased with elevation; (3) soil N:P or leaf N:P declined with elevation (Aerts and Chapin 2000; Güsewell 2004; Koerselman and Meuleman 1996; Tessier and Raynal 2003); and (4) soil N and/or P or leaf N and/or P were greater in the fertilized sub-plots than in the control sub-plots. Although one-tailed *t* tests generally provide less statistical significance than do two-tailed *t* tests, we selected the former to adhere stringently to our hypotheses. That is, we were looking for specific directional change, rather than any change. We provide summaries of vertical canopy height position ($n = 108$) differences in leaf nutrients as well as individual tree ($n = 77$) data.

To assess the DBH response due to fertilization, and account for potential size class differences (though we also conduct a separate size class analysis), we calculate the relative growth rate (RGR):

$$RGR = \frac{\ln DBH_i - \ln DBH_j}{dt} \quad (1)$$

where the time (t) difference is between August 2011 (i) and October 2007 (j). We did not include the April 2007 measurement to allow for dendrometer settling. Hypotheses tested using ANOVA and one-tailed t tests were: (1) mean DBH decreased with elevation; and (2) DBH growth rates were greater in fertilized sub-plots than in control sub-plots.

For LAI, we calculated the proportional difference in LAI between the sub-plots fertilized in year 1 with those fertilized in year 2. The expectation was that the LAI of the former would be greater than that of the latter. Hypotheses tested using ANOVA and one-tailed significance t tests were: (1) LAI decreased with elevation; and (2) LAI was greater in fertilized sub-plots than in control sub-plots.

We report soil respiration as both the absolute CO_2 flux and the proportional contribution to total respiration from each individual component. Hypotheses tested using ANOVA and one-tailed significance t tests were: (1) litter, roots, fungal hyphae and/or microbial contribution to soil respiration were different in the fertilized sub-plots than in the control sub-plots; and (2) there was a difference in soil respiration components with fertilization and with elevation.

We note results for sub-plots with at least two trees in the *Fabaceae* family, which is potentially N-fixing, though the trees were not tested to determine if they were actively fixing N. Outside of *Fabaceae*, there were no other known potential N-fixers (e.g., no *Alnus*, which is a common N-fixer in the area). There were a total of 32 trees in the *Fabaceae* family (8 at 1,500 m, 5 at 1,000 m, 20 at 200 m). At 1,000 m, 2 were in a first-year P fertilized plot. At 200 m, two were in a first-year P fertilized plot, two were in a second-year P fertilized plot, and two were in a control plot. There was no more than one in any plot at 1,500 m.

Results

Soil nutrients

Soil N decreased with elevation across both control and fertilized plots from 200 to 1,500 m, but increased at 3,000 m to concentrations similar to that at 200 m (Fig. 2a). The mean soil N in all treatments was not significantly ($p > 0.05$) greater than that in the controls at the lowest elevation sites (200 and 1,000 m). Soil P was greatest at 200 m, with a non-significant ($p > 0.05$) increase in mean soil P with elevation from 1,000 to 3,000 m (Fig. 2b). Soil P was greatest for all sites with the N + P treatment. Soil N and P were generally lower in all plots with *Fabaceae*.

There were no significant elevation trends for soil N:P by mass (Fig. 2c). Mean soil N:P was generally greatest with N addition. Soil N:P was significantly less than that of the controls for N + P fertilization at the 3,000 m site ($p < 0.05$). There were no significant differences in soil N, P and N:P between the temporally staggered fertilization groups.

Nutrients data were collected for a sub-set of samples in the mineral layer (Table 2). Soil N was greater in the organic layer than in the mineral layer for the lower elevation sites (200 and 1,000 m), but this trend was reversed for the higher elevation sites (1,500 and 3,000 m). There was no elevation trend with soil P; it was generally somewhat higher in the organic layer than in the mineral layer. Subsequently, the soil N:P ratio followed the pattern of soil N—greater in the organic layer in the lower elevation sites, and greater in the mineral layer in the higher elevation sites. Soil bulk density (mass/volume) decreased with elevation, and was always greater in the mineral layer than in the organic layer (see, also, Zimmermann et al. 2012).

Leaf nutrients

Mean leaf N increased slightly across both control and fertilized plots from 200 to 1,500 m, but decreased at 3,000 m (Fig. 2d). This pattern was the inverse of that for soil N (Fig. 2a). Hence, the leaf N to soil N ratio increased significantly with elevation (not shown). Leaf N was not significantly greater after fertilization than in the controls. Leaf P significantly increased from 200 to 1,500 m for the control sub-plots, but decreased at 3,000 m, though still greater than that at the two lower elevation sites (Fig. 2e). The increase is more pronounced when normalized by soil P (not shown). Leaf P was not significantly greater after fertilization than in the controls, except with P at 1,000 m and with N + P at 1,500 m for the year 1 fertilized group only. On average, leaf N and P tended to be greater in the plots fertilized in year 1 relative to the plots fertilized in year 2, but not significantly so. There were no consistent trends in leaf N and P for any plots with *Fabaceae*.

Leaf N:P significantly decreased with elevation for all sites (Leaf N:P = $-0.005 \times$ Elevation (m) + 23.18; $p < 0.05$, $r^2 = 0.80$), from 24 at 200 m to 11 at 3,000 m (Fig. 2f). Leaf N:P was significantly less than that from the controls for N addition at 200 m and P addition at 1,000 m. The 200 m site with N addition was also the outlier to the general pattern that mean leaf N:P was generally greatest for N addition, lower for N + P addition, and lowest for P addition. We show for comparison a shaded bar generally where N and P limitation may be present for the leaf N:P ratios given other findings in the literature, though none of those studies represent the same ecosystems as those in our
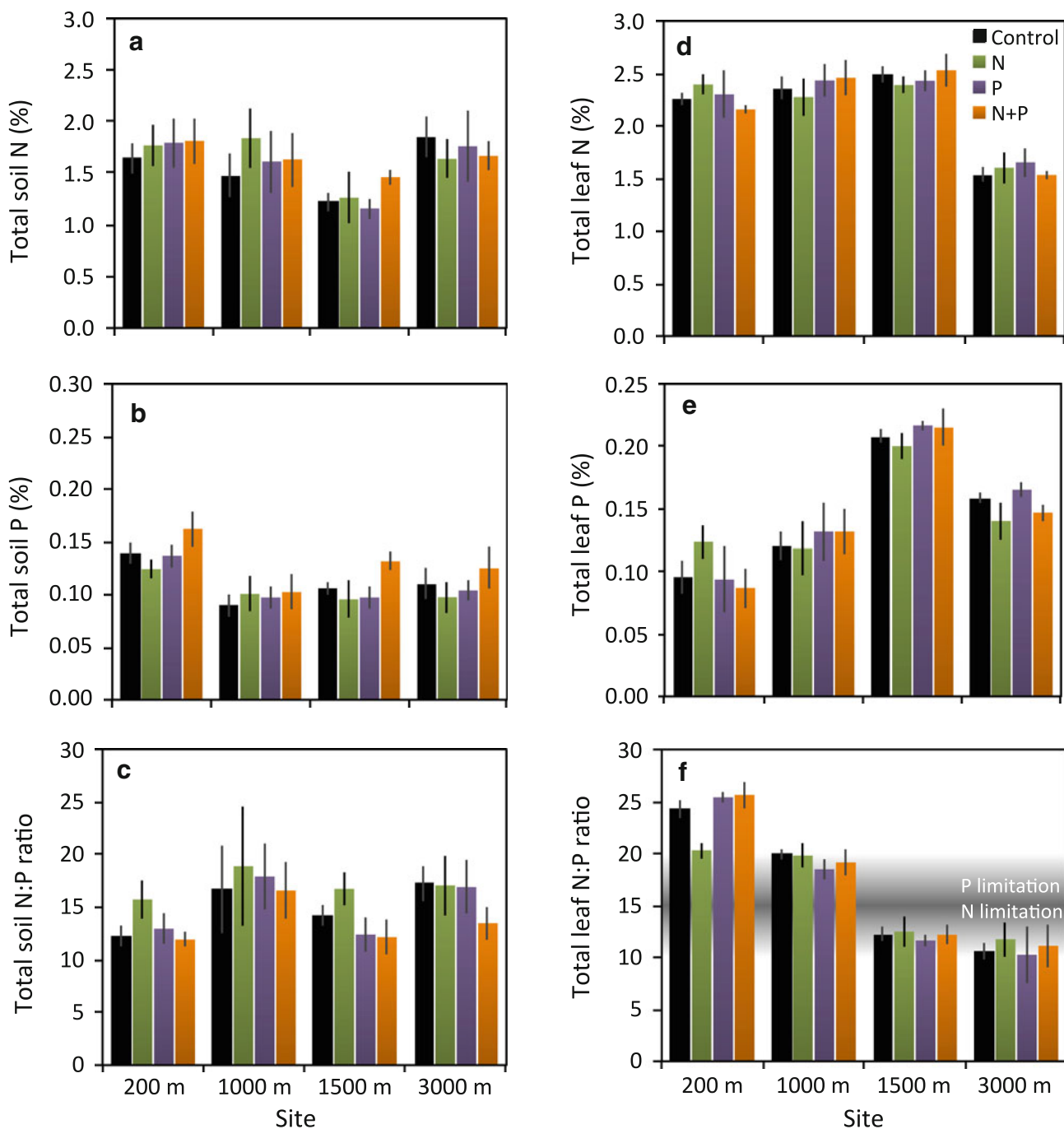
Fig. 2 Total organic soil (**a**) and leaf (**b**) nitrogen (N), total soil (**c**) and leaf (**d**) phosphorus (P), and total soil (**e**) and leaf (**f**) N:P ratio in 2008 after 1 year of fertilization (N: 6 kg urea/site; P: 3 kg triple superphosphate/site; N + P: 6 kg urea/site + 3 kg triple superphosphate/site). Soil concentrations are for the organic layer. Data are shown for all four sites (200, 1,000, 1,500 and 3,000 m) and all four treatments (control, N, P, N + P) as mean ± SE (color figure online)

study (Aerts and Chapin 2000; Güsewell 2004; Koerselman and Meuleman 1996; Tessier and Raynal 2003). The N:P ratio tended to be similar between the two temporally staggered fertilization groups, except in the 1,000 m site, where the N:P ratio was less in the year 1 fertilized group than in the year 2 fertilized group.

We analyzed leaf N, P and N:P partitioned by vertical canopy height position (top, middle, bottom), but there were generally few significant differences between canopy heights and leaf nutrients (Supplemental Fig. 3). At the highest elevation sites (1,500 and 3,000 m), leaf N in the top canopy was generally greater than or equal to that in

Table 2 Soil properties (totals) for control plots at the four elevation sites

	200 m	1,000 m	1,500 m	3,000 m
Soil N (%; organic)	1.74	1.62	1.27	1.74
Soil N (%; mineral)	0.49	0.34	1.49	2.09
Soil P (%; organic)	0.14	0.10	0.11	0.11
Soil P (%; mineral)	0.11	0.06	0.08	0.07
Soil N:P (organic)	12:1	17:1	12:1	16:1
Soil N:P (mineral)	5:1	6:1	19:1	32:1

the bottom canopy, but this trend reversed at the lowest elevation site (200 m). Leaf P, however, was generally lowest in the upper canopy for the higher elevation sites (1,500 and 3,000 m). Leaf N:P was greatest in the upper canopy for the higher elevation sites. There was greater variation in leaf N at the lower elevation sites (200 and 1,000 m) than in the higher elevation sites (1,500 and 3,000 m); the opposite was true for leaf P. We also provide individual tree data (leaf NPK, DBH, tree height, family, genera, species, and fertilization treatment) for 77 trees across all sites (Supplemental Table 1). LAI for the fertilized sub-plots was not significantly greater than that of the control sub-plots (data not shown).

DBH

DBH RGR varied with fertilizer treatment and elevation, as well as tree size class and treatment temporal stagger, with most differences not statistically significant at $p < 0.05$, though many differences were evident at $p < 0.20$, which we note as observed and not significant (Fig. 3a–d).

At the 200 m site, the DBH RGR was significantly ($p = 0.05$) greater in the N + P treatment than the control plots (with the removal of one outlier tree, otherwise $p = 0.07$) (Fig. 3a). No significant differences with fertilization were found partitioned by size class (Fig. 3b–d), though medium size trees (10–20 cm DBH) had larger DBH RGR with N and N + P than control, though p values were not <0.05 (i.e., $p = 0.13$ and 0.12, respectively).

There were no statistically significant differences between any fertilized plots and the control plots at the 1,000 m site for all data and size classes combined. However, DBH RGR for N + P plots was significantly ($p < 0.05$) greater than that for the controls for the year 2 treatment alone. Small trees (<10 cm) with N + P addition and big trees (>20 cm) with N or P addition showed greater DBH RGR against controls, though p values were not <0.05 (i.e., $p = 0.20$, 0.06, and 0.14, respectively).

At the 1,500 m site, DBH RGR was significantly greater with N addition than the control plots (with the removal of the four largest trees—DBH = 30, 30, 43 and 46 cm—

otherwise $p = 0.16$ for all trees). Medium sized trees (10–20 cm) were greater than control with N addition and large trees (>20 cm) were greater than control with N + P addition, though p values were not <0.05 (i.e. $p = 0.17$ and 0.09, respectively).

DBH RGR at the 3,000 m site was significantly ($p < 0.05$) greater than control for the N treatment. Partitioned by size class: (1) all treatments were greater than control (N: $p = 0.01$; P: $p = 0.18$; N + P: $p = 0.14$), with the largest and only significant difference in the N treatment, for <10 cm; (2) no significant differences for 10–20 cm (year 1 N treatment plots were greater than control at $p = 0.07$); (3) no significant differences for >20 cm.

We attempted to analyze the DBH RGR differences by species (e.g., Townsend et al. 2007), though statistical power was low due to the sheer number of species. Accumulating at the family level, statistical power was still low with 55 families, though the prevailing qualitative pattern that emerged was that there were few noticeable differences among families, except for *Urticaceae* and *Vochysiaceae*, both of which responded to P addition much more than the RGR of their controls, with the response by *Urticaceae* being one of the greatest of all the families studied (Supplemental Fig. 4). Still, only 13 families were represented across all four treatments. In *Myristicaceae*, *Myrsinaceae*, and *Rubiaceae*, for example, the DBH RGR was lowest for the controls, next greater for the N treatment, followed by the P treatment, and the greatest for the N + P treatment.

Soil respiration

Soil respiration was relatively evenly distributed among litter, microbes, roots, and fungal hyphae, though hyphal respiration was typically the lowest of the four (Fig. 4a–d). R_{litter} was generally consistent across elevation, and the largest at the higher elevation sites where a response to P or N + P was also evident. R_{roots} was also relatively consistent across elevation with some increase with P addition at 1,000 m, and overall less in the fertilization plots relative to the control plots. R_{hyphae} showed no elevation trends and was greater with the N and P treatments than with the N + P treatment or control plots. R_{hyphae} and R_{root} contribution were inversely correlated with each other ($p < 0.05$; $r^2 = 0.56$) (Fig. 5). $R_{microbes}$ was generally greatest at the low and high elevation sites, and least at the mid-elevation sites, and showed no major responses to fertilization.

To test our hypotheses of soil respiration partitioning response to fertilization, we focus on the sub-plots that received fertilization in year 1 because they have been fertilized longer than the sub-plots fertilized beginning in year 2 (Supplemental Fig. 5). The mean litter contribution was not significantly less in the fertilized sub-plots than in the control
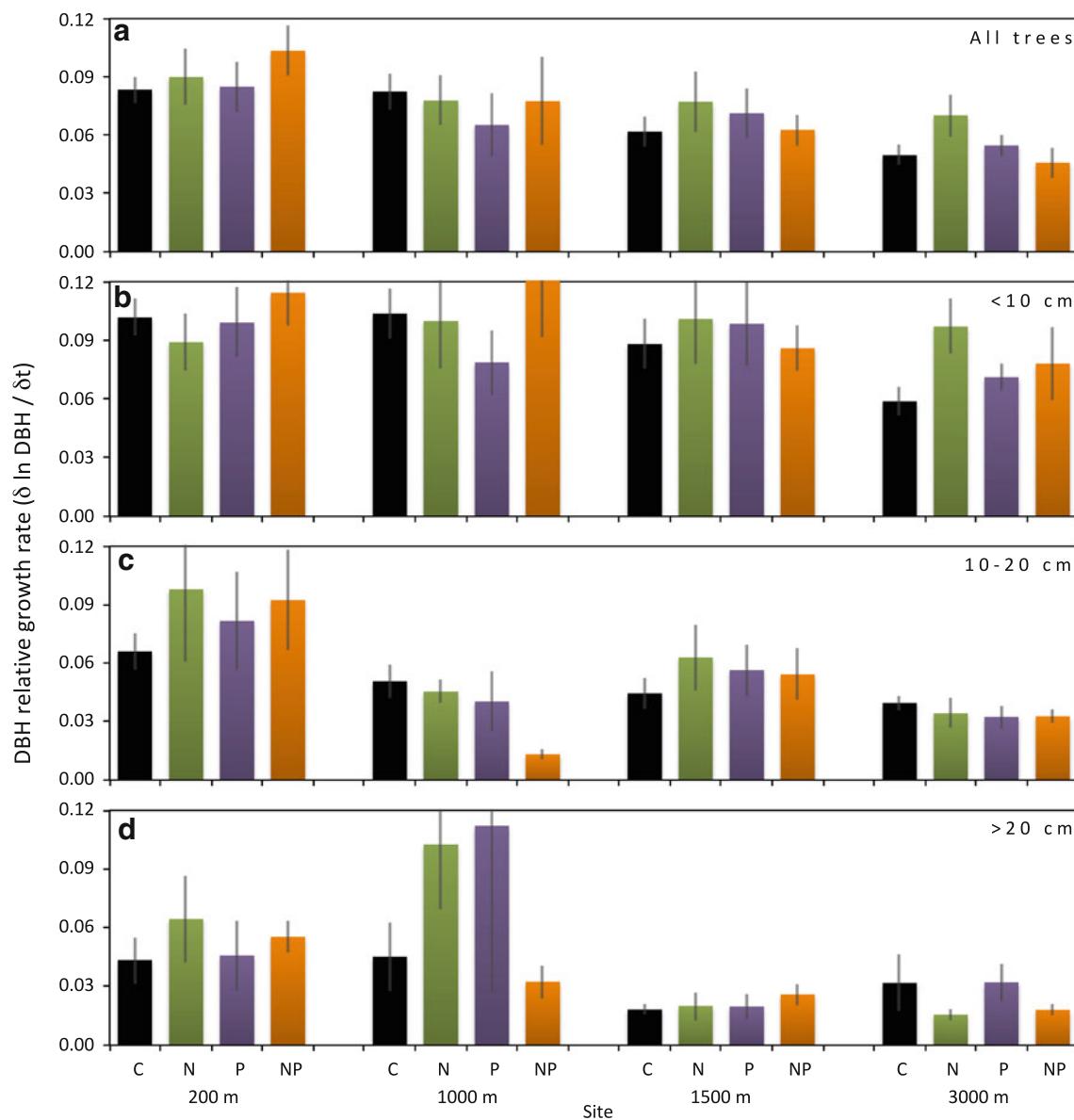
Fig. 3 The relative growth rate in diameter at breast height (DBH) for each treatment (control, nitrogen, phosphorus, nitrogen + phosphorus) for **a** all trees; **b** trees <10 cm DBH; **c** trees between 10 and 20 cm DBH; and, **d** trees >20 cm DBH

sub-plots. The mean root contribution was greatest at 1,500 m and least at 200 m for all treatments. Root contribution was significantly greater than that from the controls for N + P at 1,500 m. The contribution from fungal hyphae was significantly greater than that from the controls for N at 3,000 m. Microbial contribution was significantly greater than that from the controls for N at 3,000 and 200 m, for N + P at 200 m, and less than the controls for P at 1,500 m.

Discussion

Many of our results support the prevailing hypothesis for nutrient limitation with elevation in the tropical montane forests of the Peruvian Andes and Amazonia: N limitation increases with elevation, while P limitation decreases with elevation. Our foliar N:P ratio data show a clear decrease with elevation, starting with 24 at 200 m and moving towards 11 at 3,000 m. These values compare to leaf N:P ratios from a similar elevation transect in the Ecuadorian Andes, where Soethe et al. (2008) measured values of 11 at 2,400 m (compare to 12 by our regression for that elevation in Peru) and 8 at 3,000 m. Studies in other types of ecosystems have demonstrated that an "optimal" ratio is between 14 and 16 (Aerts and Chapin 2000; Koerselman and Meuleman 1996; Tessier and Raynal 2003), with N limitation more evident when the ratio is less than that and P limitation more evident when the ratio is greater than
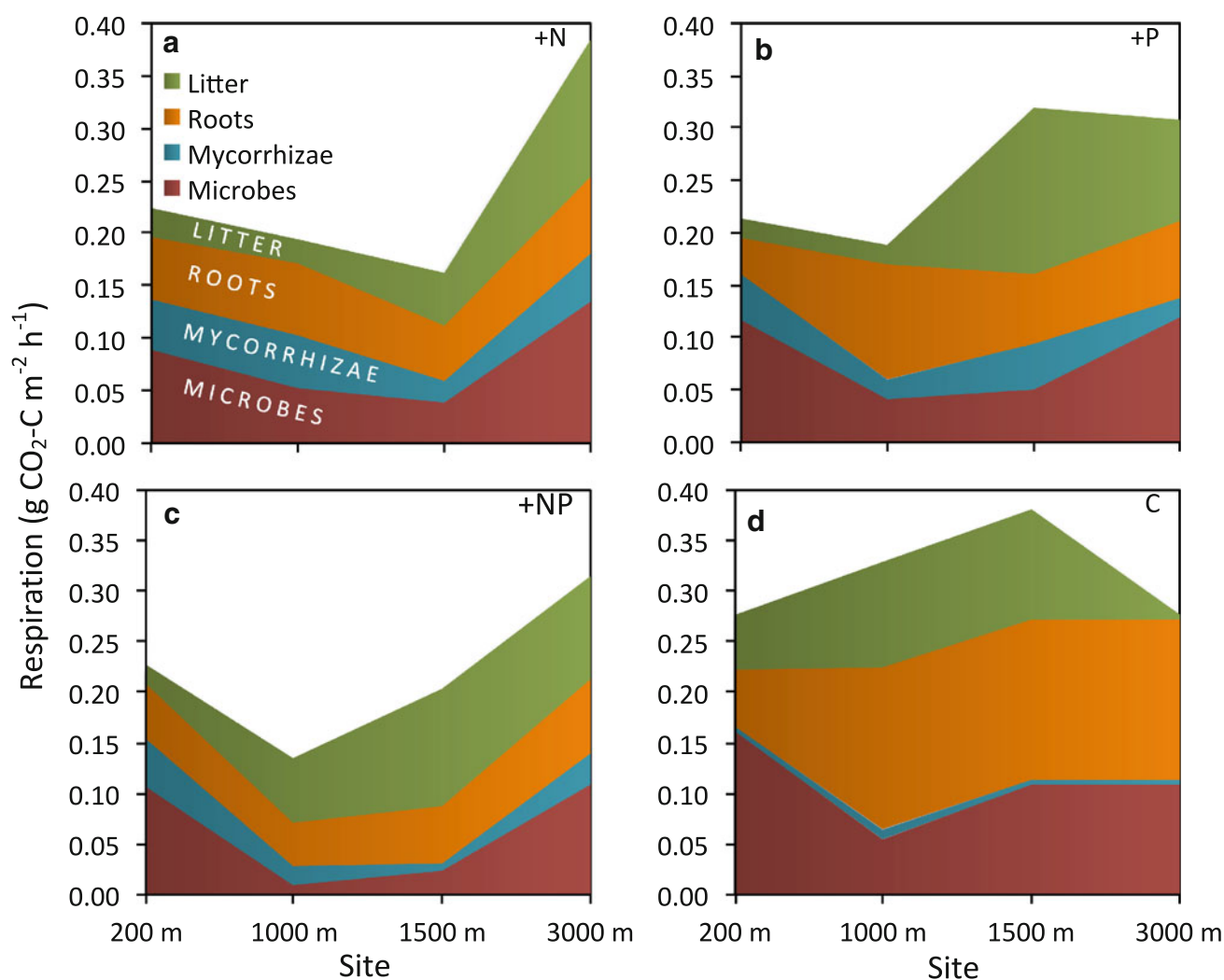
Fig. 4 Respiration from litter, roots, fungal hyphae, and microbes across the four sites (200, 1,000, 1,500, 3,000 m) and for the three fertilization treatments (nitrogen, phosphorus, nitrogen + phosphorus) and control. Data are for 2009

that; however, other data have broadened that range to 10–20 (Güsewell 2004) or have found it to be unconstrained (Townsend et al. 2007). Our leaf N:P data cross these thresholds mid-elevation—at 1,500 m, we measured values of 12 (the linear regression would predict 16). Working at many of our sites, van de Weg et al. (2009) found similar values at all but the 1,500 m site, where they had larger leaf N:P but the same general decrease in leaf N:P with elevation. It is not readily evident, however, that any one particular value or range of values mark the crossover point between N and P limitation, with most of our sites falling within the co-limitation range of 10–20 reported by Güsewell (2004).

The fertilization experimental results also support the prevailing hypothesis. The greatest DBH RGR response was with N addition at the highest elevation site, indicating that growth was N limited at high elevation. This response was still prevalent, though weaker with some N + P effect

for large trees at the 1,500 m site. Some evidence for co-limitation was found at 1,000 m for small trees (N + P response) and large trees (N, P response). The lowest elevation site exhibited the greatest DBH response with the N + P addition, indicating co-limitation. While a response from fertilization with elevation was not observed at all sites, this response (or lack thereof) is not entirely unexpected given the megadiverse and highly complex nature of these ecosystems (Wullaert et al. 2010). However, we did indeed find critical components of the gradient—that is, strong N and P co-limitation at the low elevation site and strong N limitation at the highest elevation site—and these results should not be overlooked in light of results that do not necessarily fit the paradigm.

With the lowland site, we may consider comparing this site alone with other lowland tropical sites, especially throughout Amazonia. Typically, lowland Amazonia has been considered P limited, rather than N and P co-limited,
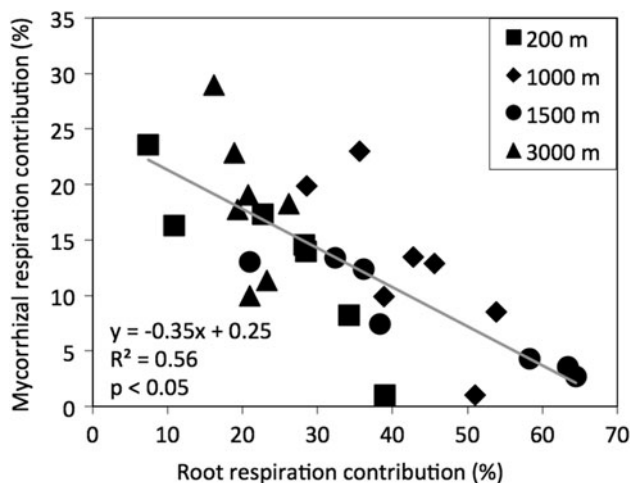
Fig. 5 Root contribution (%) to soil respiration versus hyphal contribution (%) to soil respiration for all fertilization treatments (nitrogen, phosphorus, nitrogen + phosphorus) and controls and all sites (200, 1,000, 1,500, 3,000 m)

though it is understood that there is a general P availability gradient from east to west, increasing in Western Amazonia (Aragão et al. 2009; Benner et al. 2010; Meir et al. 2001; Quesada et al. 2009a, b; Vitousek 1984; Vitousek and Sanford 1986). The high fertility of Western Amazonia is related to the exposure of Miocene lacustrine/marine sediments, and also by floodplain deposition by rivers with high sediment loads originating in the Andes (Higgins et al. 2011). However, recent literature points to co-limitation in the lowland tropics (Wright et al. 2011). The tropical forest carbon–nutrients dynamic has notably large implications for considerations of a variety of global changes and feedbacks. Our data suggest lowland co-limitation, and if other sites like ours are common then we will need to revise our understanding of nutrient limitation in lowland forests, though a spatially stratified sampling is needed to document the extent of P versus co-limitation. While further study is still needed, we have contributed a substantial dataset to the very sparse data currently available, thus making a sizeable advancement to our collective knowledge on the subject.

The RGR fertilization observations and the foliar N:P data are consistent with each other. Both data suggest N limitation at high elevation: low foliar N:P and high RGR response to N fertilization at 3,000 m. The foliar N:P data suggest a progression away from N limitation moving downslope, and the fertilization observations show significant N and P co-limitation at our lowest elevation site. However, we found no significant differences in foliar N:P after fertilization, which is indicative of either that more time is needed to detect a change in foliar nutrient concentration relative to DBH change (though our experiment went beyond leaf lifespan), or that this is a resource

allocation strategy for these species to concentrate new nutrients into stem biomass rather than leaves. Support for the latter argument comes from van de Weg et al. (2012), who showed that at the 3,000 m site leaf N and photosynthetic parameters (V_{max}, J_{max}) had a significant but poor fit. That is, when photosynthetic capacity is not much constrained by foliar N concentration, the extra N from fertilization is more likely to be allocated to stem growth, for example, than to the photosynthetic apparatus. Further, Fyllas et al. (2009) and McGroddy et al. (2004) also suggest that taxonomic affiliation in Amazonia may constrain foliar N much more strongly than foliar P. Given this, foliar N:P response may not be the best response parameter with which to measure the effects of fertilization. In addition, we also found no changes in LAI with fertilization. Therefore, the response of increased RGR after fertilization is not a consequence of increased carbon uptake capacity of the canopy (either through greater photosynthetic capacity per leaf or investment in more leaves), which is in agreement with Tanner (1980) and Lieberman et al. (1996). Instead, fertilization enabled a greater RGR for stem biomass.

We have thus far argued against a canopy response component from fertilization, and demonstrated a stem biomass response based on our aboveground data. For the belowground response, we document significant shifts in respiration partitioning with fertilization. Addition of N was associated with an increase in microbial respiration, which is opposite to widespread results in temperate forest ecosystems, though in agreement with studies that found increased decomposition with N addition in genera producing easily degradable leaf litter (Janssens et al. 2010). The respiration contribution from litter increased slightly with increasing elevation, and that from roots generally decreased with increasing elevation for the control plots only, which is consistent with rhizotron results from Girardin et al. (2010) and respiration measurements from Zimmermann et al. (2009a) at some of our sites. Addition of P and N + P was associated with a decline in hyphal respiration and a corresponding rise in root respiration.

The shifting balance between more or less root versus mycorrhizal respiration is not surprising from the standpoint of an individual tree. If symbiotic mycorrhizae can provide nutrients at less of a carbon cost to the plant than would be the carbon cost of building and maintaining new roots, then the optimal carbon economic allocation may be to obtain nutrients from mycorrhizae, all else equal (Fisher et al. 2010; Smith et al. 2009). Mycorrhizal hyphae are well adapted for uptake of soil nutrients, particularly P, and promote plant growth under nutrient-limiting conditions (Plassard and Dell 2010). Roots would still be useful for water and stability, but water was not limiting at our sites, and slopes were steep only at the 1,500 and 3,000 m sites.

Less carbon allocation to roots, and hence more of an active role of mycorrhizae in this symbiosis, means that more carbon can be allocated elsewhere, such as to wood (i.e., DBH) for height gain. Hence, this study lends support to the notion that mycorrhizal symbioses in tropical forests constitute an important strategy for plants coping with severe P limitation. Our results further indicate that this symbiosis is relatively flexible, and can be altered quickly if, for example, nutrient availability increases. We note, however, that the hyphal respiration recorded in this study likely includes contributions from saprotrophic fungi. Further work is required to identify the relative abundance and importance of different fungal types in this ecosystem.

Patterns from our other response variables also emerged to support our main conclusions. Total soil N decreased with elevation, which supports the suggestion of N limitation with elevation. However, the decrease was only from 200 to 1,500 m. Similarly, soil P increased with elevation, suggesting decreasing P limitation with elevation, but again only for three sites (1,000–3,000 m), and soil P was high at 200 m. Still, total soil N and P are not necessarily directly indicative of plant-available soil N and P. Quesada et al. (2010) found that the same 200 m site had one of the largest total P, and P fractions, out of 71 sites analyzed throughout the Amazon Basin. The partial decrease in soil N with elevation is in (partial) agreement with decomposition results from Salinas et al. (2011), who showed that decomposition rates were strongly correlated with soil temperature. The partial increase in soil P and leaf P is in (partial) agreement with Hidaka and Kitayama (2011), who found that soil P availability and foliar P concentration were well correlated.

Likewise, leaf N and P showed trends with elevation for three of four sites, with the 3,000 m site breaking the trend. We found a marginal increase in total leaf N over the whole elevation transect, and a significant increase in leaf N with elevation from 200 to 1,500 m, though the trend disappeared at 3,000 m. This is primarily due to the large increase in leaf area with elevation, thereby increasing total leaf N. These findings are in contrast to Tanner et al. (1998) and Raich et al. (1997), who found that both leaf N and P decreased with increasing elevation across a range of neo-tropical montane forests. Work from van de Weg et al. (2009) also found similar leaf N and P values at our same sites, and they included additional measurements at 1,750, 2,300 and 3,500 m that showed no elevation trend with leaf N per leaf area, but an increase in leaf P per leaf area with elevation.

The observed ecosystem responses to temperature (through the altitudinal proxy) and fertilization in our study point to possible future responses with changing climate. Our global understanding of ecosystem–nutrients dynamics relies mostly on studies conducted in temperate regions, with very few in tropical regions, and even fewer in tropical

montane regions. The eastern flank of the tropical Andes mountains and adjacent lowland Amazonia is the most biologically diverse region of the planet, and this "megadiversity" is generally sustained on nutrient-poor soils (Myers et al. 2000). Given increasing temperatures leading to increasing decomposition and mineralization rates (Malhi and Wright 2004; Pastor and Post 1988; Peterjohn et al. 1994; Salinas et al. 2011; Vuille and Bradley 2000; Zimmermann et al. 2009b, 2010a), biomass burning in Amazonia leading to downwind deposition (Aragão et al. 2007, 2008; Boy et al. 2008; Fabian et al. 2005), and shifts and migration in tree communities (Feeley and Silman 2010), the Andean nutrient regime is almost certain to be changing and so too are its ecosystems. What we can expect from these ecosystem changes in response to the nutrient regime changes can be investigated with models (Fisher et al. 2010), observations, and experiments (Ostle et al. 2009). Nutrient availability in the Andes will likely increase with warming (Salinas et al. 2011), and our results suggest that the forest response will be in the form of increased RGR of stems and therefore aboveground biomass. We may also see an increase in microbial respiration, which would in turn decrease the soil C stocks. The changing nutrient regime may not alter canopy CO_2 uptake, however, as evident in the lack of canopy response to nutrient addition, though ecosystem carbon cycling will still be altered through changes in above and belowground C stocks and belowground C fluxes.

Conclusions

We have presented a large-scale study of nutrient dynamics and limitation in rain and cloud forests along a 3,000-m elevation transect in the Peruvian Andes and Amazonia. Our study captured some of the complexity of nutrient–productivity relationships in these ecosystems, and lays the foundation for further work. We showed a DBH response to fertilization (e.g., N limitation at high elevation, N + P co-limitation at low elevation), elevation trends in leaf N:P (e.g., steady decrease with elevation), and specific controls N and P have on ecosystem function and response. Our results contribute to the development of existing ecological theory for plant–soil dynamics in the tropics and soil development along elevation gradients.

References

Aerts R (1996) Nutrient resorption from senescing leaves of perennials: are there general patterns? J Ecol 84:597–608

Aerts R, Chapin FS III (2000) The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. Adv Ecol Res 30:1–67

Aragão LEOC, Malhi Y, Roman-Cuesta RM, Saatchi S, Anderson LO, Shimabukuro YE (2007) Spatial patterns and fire response of recent Amazonian droughts. Geophys Res Lett 34:1–5

Aragão LEOC et al (2008) Interactions between rainfall, deforestation and fires during recent years in the Brazilian Amazonia. Philos Trans R Soc Lond B 363:1779–1785

Aragão LEOC et al (2009) Above- and below-ground net primary productivity across ten Amazonian forests on contrasting soils. Biogeosci Discuss 6:2441–2488

Auerbach MJ, Strong DR (1981) Nutritional ecology of *Heliconia* herbivores: experiments with plant fertilization and alternative hosts. Ecol Monogr 51:63–84

Benner J, Vitousek PM, Ostertag R (2010) Nutrient cycling and nutrient limitation in tropical montane cloud forests. In: Bruijnzeel LA, Scatena FN, Hamilton LS (eds) Tropical montane cloud forests: science for conservation and management. Cambridge University Press, London

Blodgett TA, Isacks BL (2007) Landslide erosion rate in the Eastern Cordillera of Northern Bolivia. Earth Interact 11:1–30

Boy J, Rollenbeck R, Valarezo C, Wilcke W (2008) Amazonian biomass burning-derived acid and nutrient deposition in the north Andean montane forest of Ecuador. Glob Biogeochem Cycles 22:1–16

Brix H (1971) Effects of nitrogen fertilization on photosynthesis and respiration in Douglas-Fir. For Sci 17:407–414

Bussmann RW, Wilcke W, Richter M (2008) Landslides as important disturbance regimes—causes and regeneration. In: Beck W, Bendix J, Kottke I, Makeschin F, Mosandl R (eds) Gradients in a tropical mountain ecosystem of Ecuador, vol 198. Springer, Berlin, pp 319–330

Chapin FS III, Vitousek PM, Cleve KV (1986) The nature of nutrient limitation in plant communities. Am Nat 127:48–58

Chapin FS III, Schulze E-D, Mooney HA (1990) The ecology and economics of storage in plants. Annu Rev Ecol Syst 21:423–447

Davidson EA, Howarth RW (2007) Nutrients in synergy. Nature 449:1000–1001

Eckstein RL, Karlsson PS, Weih M (1999) Leaf life span and nutrient resorption as determinants of plant nutrient conservation in temperate–arctic regions. New Phytol 143:177–189

Elser JJ et al (2007) Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. Ecol Lett 10:1135–1142

Fabian P, Kohlpaintner M, Rollenbeck R (2005) Biomass burning in the Amazon-Fertilizer for the mountainous rain forest in Ecuador. Environ Sci Pollut Res 12:290–296

Feeley KJ, Silman MR (2010) Biotic attrition from tropical forests correcting for truncated temperature niches. Glob Change Biol 16:1830–1836

Field CB, Mooney HA (1986) The photosynthesis–nitrogen relationship in wild plants. In: Givnish TJ (ed) On the economy of plant form and function. Cambridge University Press, Cambridge, pp 25–55

Fisher JB, Sitch S, Malhi Y, Fisher RA, Huntingford C, Tan S-Y (2010) Carbon cost of plant nitrogen acquisition: a mechanistic, globally-applicable model of plant nitrogen uptake and fixation. Glob Biogeochem Cycles 24. doi:10.1029/2009GB003621

Fisher JB, Badgley G, Blyth E (2012) Global nutrient limitation in terrestrial vegetation. Glob Biogeochem Cycles 26:GB3007. doi:10.1029/2011GB004252

Fyllas NM et al (2009) Basin-wide variations in foliar properties of Amazonian forest: phylogeny, soils and climate. Biogeosciences 6:2677–2708

Galloway JN et al (2004) Nitrogen cycles: past, present, and future. Biogeochemistry 70:153–226

Garzione CN et al (2008) Rise of the Andes. Science 320:1304–1307

Girardin CAJ et al (2010) Net primary productivity allocation and cycling of carbon along a tropical forest elevational transect in the Peruvian Andes. Glob Change Biol 16:3176–3192

Grime JP (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. Am Nat 111:1169–1194

Güsewell S (2004) N:P ratios in terrestrial plants: variation and functional significance. New Phytol 164:243–266

Hedin LO, Brookshire ENJ, Menge DNL, Barron AR (2009) The nitrogen paradox in tropical forest ecosystems. Annu Rev Ecol Evol Syst 40:613–635

Heinemeyer A, Hartley IP, Evans SP, de la Fuentes JAC, Ineson P (2007) Forest soil CO_2 flux: uncovering the contribution and environmental responses of ectomycorrhizas. Glob Change Biol 13:1786–1797

Hidaka A, Kitayama K (2011) Allocation of foliar phosphorus fractions and leaf traits of tropical tree species in response to decreased soil phosphorus availability on Mount Kinabalu, Borneo. J Ecol 99:849–857

Hietz P, Turner BL, Wanek W, Richter A, Nock CA, Wright SJ (2011) Long-term change in the nitrogen cycle of tropical forests. Science 334:664–666

Higgins MA et al (2011) Geological control of floristic composition in Amazonian forests. J Biogeogr 38:2136–2149

Huaraca Huasco W et al (2012) Seasonal production, allocation and cycling of carbon in two mid-elevation tropical montane forest plots in the Peruvian Andes. Plant Ecol Divers (in press)

Janssens IA et al (2010) Reduction of forest soil respiration in response to nitrogen deposition. Nat Geosci 3:315–322

Johnson NC (1993) Can fertilization of soil select less mutualistic mycorrhizae? Ecol Appl 3:749–757

Johnson D et al (1994) Soil pCO_2, soil respiration, and root activity in CO_2-fumigated and nitrogen-fertilized ponderosa pine. Plant Soil 165:129–138

Kirschbaum MUF (1995) The temperature dependence of soil organic matter decomposition, and the effect of global warming on soil organic C storage. Soil Biol Biochem 27:753–760

Koerselman W, Meuleman AFM (1996) The vegetation N:P ratio: a new tool to detect the nature of nutrient limitation. J Appl Ecol 33:1441–1450

Langley JA, Chapman SK, Hungate BA (2006) Ectomycorrhizal colonization slows root decomposition: the post-mortem fungal legacy. Ecol Lett 9:955–959

Lieberman D, Milton L, Peralta R, Hartshorn GS (1996) Tropical forest structure and composition on a large-scale altitudinal gradient in Costa Rica. J Ecol 84:137–152

Lozano P, Bussmann RW, Küppers M (2005) Landslides as ecosystem disturbance—their implications and importance in South Ecuador. Lyonia 8:61–65

Malhi Y, Wright J (2004) Spatial patterns and recent trends in the climate of tropical rainforest regions. Philos Trans R Soc Lond B 359:311–329

McGroddy ME, Daufresne T, Hedin LO (2004) Scaling of C:N:P stoichiometry in forests worldwide: implications of terrestrial Redfield-type ratios. Ecology 85:2390–2401

Meir P, Grace J, Miranda AC (2001) Leaf respiration in two tropical rainforests: constraints on physiology by phosphorus, nitrogen and temperature. Funct Ecol 15:378–387

Meyer GA, Root RB (1996) Influence of feeding guild on insect response to host plant fertilization. Ecol Entomol 21:270–278

Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. Nature 403:853–858

Ostle NJ et al (2009) Integrating plant–soil interactions into global carbon cycle models. J Ecol 97:851–863

Pastor J, Post WM (1988) Response of northern forests to CO$_2$-induced climate change. Nature 334:55–58

Peterjohn WT, Melillo JM, Steudler PA, Newkirk KM, Bowles FP, Aber JD (1994) Responses of trace gas fluxes and N availability to experimentally elevated soil temperatures. Ecol Appl 4:617–625

Plassard C, Dell B (2010) Phosphorus nutrition of mycorrhizal trees. Tree Physiol 30:1129–1139

Quesada CA, Lloyd J, Anderson LO, Fyllas NM, Schwarz M, Czimczik CI (2009a) Soils of Amazonia with particular reference to the RAINFOR sites. Biogeosci Discuss 6:3851–3921

Quesada CA et al (2009b) Regional and large-scale patterns in Amazon forest structure and function are mediated by variations in soil physical and chemical properties. Biogeosci Discuss 6:3993–4057

Quesada CA et al (2010) Variations in chemical and physical properties of Amazon forest soils in relation to their genesis. Biogeosciences 7:1515–1541

Raich JW, Russell AE, Vitousek PM (1997) Primary productivity and ecosystem development along an elevational gradient on Mauna Loa, Hawai'i. Ecology 78:707–721

Ryan MG, Yoder BJ (1997) Hydraulic limits to tree height and tree growth. Bioscience 47:235–242

Salinas N et al (2011) The sensitivity of tropical leaf litter decomposition to temperature: results from a large-scale leaf translocation experiment along an elevation gradient in Peruvian forests. New Phytol 189:967–977

Shaver GR (1981) Mineral nutrition and leaf longevity in an evergreen shrub, Ledum palustre ssp. decumbens. Oecologia 49:362–365

Silva-Espejo JE et al (2012) Productivity and carbon allocation in a high elevation tropical mountain cloud forest of the Peruvian Andes. Plant Ecol Divers (in press)

Smith FA, Grace EJ, Smith SE (2009) More than a carbon economy: nutrient trade and ecological sustainability in facultative arbuscular mycorrhizal symbioses. New Phytol 182:347–358

Soethe N, Lehmann J, Engels C (2008) Nutrient availability at different altitudes in a tropical montane forest in Ecuador. J Trop Ecol 24:397–406

Tanner EVJ (1980) Studies on the biomass and productivity in a series of montane rain forests in Jamaica. J Ecol 68:573–588

Tanner EVJ, Kapos V, Freskos S, Healey JR, Theobald AM (1990) Nitrogen and phosphorus fertilization of Jamaican montane forest trees. J Trop Ecol 6:231–238

Tanner EVJ, Kapos V, Franco W (1992) Nitrogen and phosphorus fertilization effects on Venezuelan montane forest trunk growth and litterfall. Ecology 73:78–86

Tanner EVJ, Vitousek PM, Cuevas E (1998) Experimental investigation of nutrient limitation of forest growth on wet tropical mountains. Ecology 79:10–22

Tessier JT, Raynal DJ (2003) Use of nitrogen to phosphorus ratios in plant tissue as an indicator of nutrient limitation and nitrogen saturation. J Appl Ecol 40:523–534

Townsend AR, Cleveland CC, Asner GP, Bustamante MMC (2007) Controls over foliar N:P ratios in tropical rain forests. Ecology 88:107–118

Unger M, Leuschner C, Homeier J (2010) Variability of indices of macronutrient availability in soils at different spatial scales along an elevation transect in tropical moist forests (NE Ecuador). Plant Soil 336:443–458

van de Weg MJ, Meir P, Grace J, Atkin O (2009) Altitudinal variation in leaf mass per unit area, leaf tissue density and foliar nitrogen and phosphorus content along an Andes–Amazon gradient in Peru. Plant Ecol Divers 2:243–254

van de Weg MJ, Meir P, Grace J, Damián Ramos G (2012) Photosynthetic parameters, dark respiration and leaf traits in the canopy of a Peruvian tropical montane cloud forest. Oecologia 168:23–34

Vitousek PM (1984) Litterfall, nutrient cycling, and nutrient limitation in tropical forests. Ecology 65:285–298

Vitousek PM, Farrington H (1997) Nutrient limitation and soil development: experimental test of a biogeochemical theory. Biogeochemistry 37:63–75

Vitousek PM, Howarth RW (1991) Nitrogen limitation on land and in the sea: how can it occur? Biogeochemistry 13:87–115

Vitousek PM, Sanford RL (1986) Nutrient cycling in moist tropical forest. Annu Rev Ecol Syst 17:137–167

Vitousek PM, Porder S, Houlton BZ, Chadwick OA (2010) Terrestrial phosphorus limitation: mechanisms, implications, and nitrogen–phosphorus interactions. Ecol Appl 20:5–15

Vuille M, Bradley RS (2000) Mean annual temperature trends and their vertical structure in the tropical Andes. Geophys Res Lett 27:3885–3888

Wilcke W, Valladarez H, Stoyan R, Yasin S, Valarezo C, Zech W (2003) Soil properties on a chronosequence of landslides in montane rain forest, Ecuador. Catena 53:79–95

Wilcke W, Oelmann Y, Schmitt A, Valarezo C, Zech W, Homeier J (2008) Soil properties and tree growth along an altitudinal transect in Ecuadorian tropical montane forest. J Plant Nutr Soil Sci 171:220–230

Wilson SD, Tilman D (1993) Plant competition and resource availability in response to disturbance and fertilization. Ecology 74:599–611

Wright SJ et al (2011) Potassium, phosphorus, or nitrogen limit root allocation, tree growth, or litter production in a lowland tropical forest. Ecology 92:1616–1625

Wullaert H, Homeier J, Valarezo C, Wilcke W (2010) Response of the N and P cycles of an old-growth montane forest in Ecuador to experimental low-level N and P amendments. For Ecol Manag 260:1434–1445

Zimmermann M, Meir P, Bird M, Malhi Y, Ccahuana A (2009a) Litter contribution to diurnal and annual soil respiration in a tropical montane cloud forest. Soil Biol Biochem 41:1338–1340

Zimmermann M, Meir P, Bird MI, Malhi Y, Ccahuana AJQ (2009b) Climate dependence of heterotrophic soil respiration from a soil-translocation experiment along a 3000 m tropical forest altitudinal gradient. Eur J Soil Sci 60:895–906

Zimmermann M, Meir P, Bird MI, Malhi Y, Ccahuana AJQ (2010a) Temporal variation and climate dependence of soil respiration and its components along a 3000 m altitudinal tropical forest gradient. Glob Biogeochem Cycles 24:GB4012

Zimmermann M et al (2010b) No differences in soil carbon stocks across the tree line in the Peruvian Andes. Ecosystems 13:62–74

Zimmermann M, Leifeld J, Conen F, Bird M, Meir P (2012) Can composition and physical protection of soil organic matter explain soil respiration temperature sensitivity? Biogeochemistry 107:423–436