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Nutrient limitation in rainforests and cloud forests along a 3000 m elevation gradient in the Peruvian Andes

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Abstract

Nitrogen (N) limits net primary productivity in most terrestrial ecosystems globally, but phosphorus (P) is more limiting in many lowland tropical forests such as those in Amazonia. However, tropical montane soils such as those of the Andes may be less P limited than the lowlands. Here we report results from a large-scale fertilization experiment (N, N+P, P) along a 3000 m elevation transect in the Peruvian Andes and adjacent lowland Amazonia. Our objectives were to present ecosystem–nutrients data for a region that is underrepresented in global ecosystem–nutrients analyses, to determine if N and/or P limit the productivity of these Andean and Amazonian forests and to identify if there is an elevation gradient in nutrient limitation. We measured leaf and soil nutrients, leaf area index (LAI), diameter at breast height (DBH) and soil respiration partitioning between microbes, roots, mycorrhizae and litter. Leaf N:P decreased with increasing elevation, crossing 15 at mid-elevation (between 1000–1500 m), suggesting increased P limitation and decreased N limitation with increasing elevation. DBH and tree height decreased with increasing elevation, but LAI did not vary with elevation or fertilization. The DBH response to P fertilization increased with elevation and vice versa for N fertilization. Root respiration decreased (and mycorrhizal respiration increased) with the DBH increases due potentially to a shift in carbon allocation from roots to wood rather than an overall growth increase to nutrient amendment. This study provides the first large-scale study of nutrient dynamics, limitation and response to fertilization in rain and cloud forests in the Peruvian Andes and Amazon.

Key words: fertilization; montane; nitrogen; phosphorus.

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Introduction

Nitrogen (N) limits net primary productivity in most terrestrial ecosystems globally (Vitousek & Howarth 1991), but phosphorus (P) tends to be more limiting than N in lowland Amazonia (Aragão *et al.* 2009; Quesada *et al.* 2009a; Quesada *et al.* 2009b; Vitousek 1984; Vitousek & Sanford 1986). P limitation in 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.

The adjacent tropical montane forests in the Andes, however, may experience less P limitation than the Amazon. Andean soils are generally 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 needs to accumulate in an ecosystem over time. Furthermore, these montane ecosystems turnover frequently from landslides and erosion (Blodgett & 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). 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 & Chapin III 2000; Davidson & Howarth 2007; Güsewell 2004; Tanner *et al.* 1998; Vitousek 1984; Vitousek & Farrington 1997).

Nonetheless, N limitation in the Andes might be mitigated by two processes: 1) atmospheric N deposition from Amazonian biomass burning (Aragão *et al.* 2008; Aragão *et al.* 2007; Boy *et al.* 2008; Fabian *et al.* 2005); and, 2) increased decomposition and nutrient mineralization rates from rising temperatures with climate change (Malhi & Wright 2004; Pastor

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& Post 1988; Peterjohn *et al.* 1994; Vuille & Bradley 2000). Therefore, it may well be that Andean forests are neither P nor N limited if, in fact, both nutrients are in abundant supply due to new soils providing P, and atmospheric deposition and increased mineralization providing N. Productivity could instead be primarily limited not by N or P, but by other environmental variables such as temperature, light and/or moisture, or other nutrients (Chapin III *et al.* 1986). However, we do not actually know if this is the case, as there have been no extensive measurements linking productivity to nutrient limitation in the Andes until recently. Here we present results from an investigation of nutrient limitation in the Peruvian Andes.

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 3000 m elevation transect in the Peruvian Andes and adjacent lowland Amazon (200 m, 1000 m, 1500 m, 3000 m). Our aim was to eliminate any N or P limitation and observe the forest response. We expected to observe an elevation gradient in N and P limitation following the prevailing hypothesis for nutrient limitation in tropical montane ecosystems.

It is difficult to predict exactly how such "megadiverse" ecosystems as those in the Andes might respond to fertilization. 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 III *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,

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mycorrhizal activity, soil respiration and abundance of insects and fauna (Aerts 1996; Auerbach & Strong 1981; Brix 1971; Chapin III *et al.* 1990; Field & Mooney 1986; Johnson *et al.* 1994; Johnson 1993; Meyer & Root 1996; Ryan & Yoder 1997; Shaver 1981; Wilson & Tilman 1993). Limitation due to temperature, light and moisture could minimize the effects of nutrient addition, even if the ecosystems are nutrient limited (Chapin III *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 we also measured key aspects of major biomass changes in the leaves, wood and soil. Specifically, we measured: (i) canopy response (i.e., leaf area index or LAI); (ii) woody accumulation or tree growth (i.e., increment change in diameter at breast height or DBH); and, (iii) soil respiration partitioning between microbes, roots, mycorrhizae and litter; due to financial limitations, we were unable to measure litterfall rates and fine root growth. We asked how these ecosystem components changed with fertilization and with elevation.

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Materials and Methods

Study Sites

We conducted a fertilization experiment adjacent to four long-term monitoring sites along the eastern flank of the SE Peruvian Andes and adjacent Amazonian lowlands (Fig. 1). The long-term monitoring sites were established in 2003 as 100 x 100 m plots located at elevations of 200 m (Tambopata), 1000 m (Tono), 1500 m (San Pedro) and 3000 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 1500 m and 3000 m sites were situated in the Kosñipata Valley (13°S, 70°W); they both represent cloud forests, with the 1500 m site at the base of the clouds. The 1000 m site was situated just outside the valley in the sub-montane transition zone between the Andean mountains and the Amazonian lowlands. The 200 m site was located further down river from the other sites in lowland Amazonia.

Across all sites the mean annual temperature ranged from 12.5ºC – 26.4°C, and mean annual precipitation ranged from 1706 – 3087 mm, with peak precipitation near the base of the mountain range (Table 1) (Girardin *et al.* 2010). Soils were alluvial terraces (200 m and 1000 m) and Paleozoic shales/slates (1500 m and 3000 m). All sites had very acidic soils and there were no significant differences in soil pH (~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* (1000 m); *Lauraceae*, *Rubiaceae* and *Melastomataceae* (1500 m); and, *Cunoniaceae* and *Clusiaceae* (3000 m). A total of 637 trees were included (351 fertilized, 286 control) in the experiment. 41% (73) of the 180 trees at the 200 m site were unique species; 42% (68) of the 165 trees at the 1000 m site were unique

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species; 53% (71) of the 135 trees at the 1500 m site were unique species; and, 25% (37) of the 157 trees at the 3000 m site were unique species.

The fertilization experiment was established in 2007, adjacent and down-slope of the long-term monitoring plots as 10 x 110 m transects along three sides of each long-term 100 x 100 m plot (Fig. 2). Within each transect were eleven 10 x 10 m sub-plots, two of which were fertilized (dissolved in solution) every three months (Jan, Apr, Jul, Oct) starting in Oct 2007 with N (0.5 kg urea/10 m^2), two with P (0.25 kg triple superphosphate/10 m^2), two with both N and P (same amounts as alone) and six controls separated each fertilized sub-plot (see, for example, Tanner *et al.* 1992; Tanner *et al.* 1990). The long-term monitoring plots also served as controls. Each sub-plot contained approximately 5 trees that were fertilized and measured (i.e., if there were more than 5 in a sub-plot, then not every tree was fertilized and measured). Litter at the base of each tree was cleared, fertilizer was applied and worked into the soil by foot, and the litter was returned to reduce runoff and provide the fertilizer closer to the roots. Minimal leaching or outgassing was reported in a similar experimental design fertilization experiment in the Ecuadorian Andes (Wullaert *et al.* 2010). 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 2009. 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 two-fold replication in time as well as three-fold replication in space at each site.

Measurements

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Soil and leaves were collected for nutrients analysis in October 2008. Soils were collected in each 10 x 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 3000 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. Soils were weighed to calculate soil bulk density. One transect per site was used for pH measurements for the soil organic layer only. Leaves were cut fresh from three canopy heights (top, middle, bottom) for trees (n=77) from all fertilized plots and 60% of the control plots (Table S1). 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; 2) we kept individual trees separate, but still aggregated canopy heights, for ~20 trees per site.

Soil and leaf samples were analysed 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 on a Kjeldahl machine (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. Standard quality control samples were run every 20 samples.

Dendrometers measured with a caliper were fitted to each numbered and tagged tree with a diameter at breast height (DBH, 1.3 m) greater than 10 cm. For trees with DBH less than 10 cm

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a DBH tape was used. 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 trees were generally avoided, as were palms and tree ferns, which do not exhibit extended DBH growth. DBH measurements were recorded every three months beginning in April 2007, which was six months before the initial fertilization began. The DBH distribution for each site and the tree height (measured from a laser altimeter) to DBH relationship are shown in Fig. 3a,b.

Skyward-pointing (perpendicular to level) hemispherical photos with three different exposures were taken at the centre of each sub-plot in October 2009. Photos were taken at dawn under dry weather. Photos were processed for leaf area index (LAI) calculation using Can-Eye v5.0 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 their website (http://147.100.66.194/can_eye/). This method may 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 centre of each 10 m^2 sub-plot (both fertilized and control) in October 2009 using an infrared gas analyser (EGM-4 and SRC-1 chamber, PP Systems, Hitchin, UK). An experimental design was set up to partition the contributions from

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surface organic litter, roots, mycorrhizae 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 ($R_{litter}+R_{roots}+R_{mycorrhizae}+R_{microbes}$); 2) a surface core with litter removed ($R_{roots}+R_{mycorrhizae}+R_{microbes}$); 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 ectomyccorhizal hyphae but excluded roots (Langley *et al.* 2006) and litter removed ($R_{mycorrhizae}+R_{microbes}$); and, 4) a deep core that excluded both roots and mycorrhizae, and litter removed ($R_{microbes}$). The cores were installed three 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 measurements were taken per core.

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 using ANOVA and one-tailed t tests were: 1) soil N declined with elevation; 2) soil P increased with elevation; 3) soil N:P declined with elevation (and crossed 15 at mid-elevation: Aerts & Chapin III 2000; Güsewell 2004; Koerselman & Meuleman 1996; Tessier & Raynal 2003); 4) soil N and/or P were greater in the fertilized sub-plots than in the control sub-plots. We provide

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summaries of canopy height (n=108) differences in leaf nutrients as well as individual tree (n=77) data in the supplementary information.

DBH measurements were recorded every ~3 months. Measurements from 11 trees were removed from analyses as outliers because of unrealistic/inconsistent growth patterns. To assess the main DBH response due to fertilization, we used data from the sub-plots fertilized starting in the first year and all controls, and calculated the difference in DBH from the average of Oct 08 and Jan 09 minus the average of Oct 07 and Jan 08. This allowed for initial dendrometer settling from Apr 07, and gave a full year response with an average over the dry (Oct) and wet (Jan) seasons. To assess the temporal control, we compared the growth in the sub-plots fertilized in year 1 (Oct 07 – Oct 08) as a percentage of the growth rate of the controls to the growth in the sub-plots fertilized in year 2 (Oct 08 – Oct 09) as a percentage of the growth rate of the controls in that year. Hypotheses tested using ANOVA and one-tailed t tests were: 1) mean DBH decreased with elevation; 2) DBH growth rates were significantly 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 t tests were: 1) LAI decreased with elevation; 2) LAI was significantly greater in fertilized sub-plots than in control sub-plots.

We report soil respiration as the proportional contribution to total respiration from each individual component. Hypotheses tested using ANOVA and one-tailed t tests were: 1) Litter, roots, mycorrhizae and/or microbial contribution to soil respiration were significantly different in

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the fertilized sub-plots than in the control sub-plots; 2) there was a significant difference in soil respiration components with fertilization and with elevation.

We report results for sub-plots with at least 2 trees in the *Fabaceae* family, which is potentially N-fixing, though the trees were not tested to determine if they were actively fixing N. There were a total of 32 trees in the *Fabaceae* family (8 at 1500 m, 5 at 1000 m, 20 at 200 m). At 1000 m 2 were in a 1st year P fertilized plot. At 200 m, 2 were in a 1st year P fertilized plot, 2 were in a 2nd year P fertilized plot, and 2 were in a control plot. There were no more than one in any plot at 1500 m.

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Results

Soil Nutrients

Soil N decreased with elevation from 200 m to 1500 m, but increased at 3000 m to concentrations similar to that at 200 m (Fig. 4a). Soil N after fertilization was not significantly greater than in the controls at $p<0.05$ (Table 2). The mean soil N in all treatments was greater than that in the controls at the lowest elevation sites (200 m and 1000 m). There were no significant trends with elevation for soil P, though mean soil P increased with elevation from 1000 m to 3000 m (Fig. 4b). Soil P was greatest at 200 m. Soil P was greatest for all sites with the N+P treatment. Soil N and P were generally lower in plots with *Fabaceae*.

There were no significant elevation trends for soil N:P (Fig. 4c). 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 3000 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 as well (Table 3). Soil N was greater in the organic layer than in the mineral layer for the lower elevation sites (200 and 1000 m), but this trend was reversed for the higher elevation sites (1500 m and 3000 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 decreased with elevation, and was always greater in the mineral layer than in the organic layer.

Leaf Nutrients

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Mean leaf N increased slightly from 200 m to 1500 m, but decreased sharply at 3000 m (Fig. 4d). The increase is more pronounced when normalized by soil N (not shown). This pattern was the inverse of that for soil N. Leaf N was not significantly greater after fertilization than in the controls. Leaf P significantly increased from 200 m to 1500 m for the control sub-plots, but decreased at 3000 m, though still greater than that at 1000 m (Fig. 4e). 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 1000 m and with N+P at 1500 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 plots with *Fabaceae*.

Leaf N:P significantly decreased with elevation for all sites from 200 m to 3000 m (Fig. 4f). Leaf N:P was significantly less than that from the controls for N addition at 200 m and P addition at 1000 m. The 200 m site with N addition was also the outlier to the general pattern that mean leaf N:P was generally greater for N addition, then N+P addition, then P addition. Leaf N:P at the lower elevation sites (200 m and 1000 m) was significantly greater than 15, suggesting potential P limitation, and was significantly less than 15 at the higher elevation sites (1500 m and 3000 m), suggesting potential N limitation (Aerts & Chapin III 2000; Güsewell 2004; Koerselman & Meuleman 1996; Tessier & Raynal 2003). The N:P ratio tended to be similar between the two temporally staggered fertilization groups, except in the 1000 m site, where the N:P ratio was less in the year 1 fertilized group than in the year 2 fertilized group.

We provide leaf N, P and N:P partitioned by canopy height (top, middle, bottom) as supplementary information (Fig. S1a,b,c; the means are equivalent to Fig. 4d,e,f). There were generally few significant differences between canopy heights and leaf nutrients. At the highest

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elevation sites (1500 m and 3000 m) leaf N in the top canopy was generally greater than or equal to that in 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 (1500 m and 3000 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 m and 1000 m) than in the higher elevation sites (1500 m and 3000 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 as supplementary information (Table S2). LAI for the fertilized sub-plots was not significantly greater than that of the control sub-plots (data not shown).

DBH

In contradiction with what would be expected from leaf stoichiometry, we found an inverse relationship in woody growth response to fertilization treatment with elevation. The DBH response was greatest at 3000 m with P fertilization, decreasing with decreasing elevation, and vice versa for N fertilization (Fig. 5). This pattern was consistent primarily for the sites in the Kosñipata Valley. At 1000 m (i.e., the base of the valley), DBH with N fertilization was greater than that in the control sub-plots. The mid-elevation 1500 m site responded minimally to all treatments, though slightly greater on average (not significant) with the N+P treatment. At 3000 m, the DBH response with P fertilization was greater than that in the control sub-plots. DBH in general decreased with elevation (i.e., Fig. 2a,b). There were no significant differences in plots with *Fabaceae*.

Another test for the response to fertilization was if the response pattern in the first year for the sub-plots fertilized in the first year was the same as that in the second year for the sub-

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plots fertilized in the second year (Fig. 5). Although the response in the second year group was generally less than that of the first year group (except for the 1000 m site), the response pattern was nearly identical, but with one exception. This exception was for the P fertilized plots in the second year group, which exhibited almost no response to P fertilization, and which contradicts the large response to P fertilization from the first year group. Upon further inspection, we found a sample bias in these trees: they were on average 1 m shorter than the other trees in the experiment. Thus, it may be that for these trees light limitation may have suppressed growth rates more than did nutrient limitation. Nonetheless, the similar response patterns for all other sub-plots and sites indicate a more robust pattern in fertilization response with elevation.

Soil Respiration

Soil respiration for the control sub-plots was divided approximately into three equal sources: 1) litter, 2) roots and mycorrhizae, and 3) microbes (Figs 6 and S2). Litter respiration contribution was relatively constant across sites, though increased marginally with elevation (29-37%). Microbial respiration contribution (31-34%) was similar for all but the 1000 m site, where the contribution was half that of the other sites (16%). Root respiration contribution was 21% at 3000 m and 1500 m, and 51% and 39% at 1000 m and 200 m, respectively. Mycorrhizal respiration contribution was the lowest of the four components at 10% and 13% at 3000 m and 1500 m, respectively, and negligible at 1000 m and 200 m.

For the sub-plots fertilized in year 1 litter respiration contribution was relatively constant (12-28%) across sites for the fertilized plots, though generally less than that from the controls. Root contribution was large at 1500 m and 1000 m. There were no clear trends in mycorrhizal contribution with elevation or fertilization treatment. Microbial contribution followed a similar

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pattern across sites with that from the controls. For the sub-plots fertilized in year 1 the respiration from the roots was inversely proportional to that from the mycorrhizae (r^2=0.67, $p<0.05$)—i.e., when the contribution from mycorrhizae decreased, the contribution from the roots increased, and vice versa.

There were some large differences in soil respiration partitioning between the sub-plots fertilized in year 1 and those fertilized in year 2. The litter contribution generally decreased from year 1 fertilized sub-plots to year 2 fertilized sub-plots for all treatments between groups due to an increased contribution from roots and mycorrhizae. The mycorrhizal contribution increased where the DBH response was greatest for the respective sites and fertilization treatments: at 3000 m with P fertilization, at 1000 m with N fertilization, and at 200 m site N+P fertilization. At 1500 m site, where there was marginal response to fertilization, the mycorrhizal contribution decreased, and the root contribution increased for N+P.

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. The mean litter contribution was generally less in the fertilized sub-plots than in the control sub-plots, though not significantly different. The mean root contribution was greatest at 1500 m and least at 200 m for all treatments. Root contribution was significantly greater than that from the controls for N+P at 1500 m. Mycorrhizal contribution was significantly greater than that from the controls for N at 3000 m. Mean microbial contribution was greater than that from the controls for N at all sites and greatest at 200 m for all treatments. Microbial contribution was significantly greater than that from the controls for N at 3000 m and 200 m, for N+P at 200 m, and less than the controls for P at 1500 m.

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Discussion

Elevation and Fertilization

Soil N decreased and soil P increased with elevation for three out of four sites (prevailing hypothesis partially supported). Leaf N increased very slightly and leaf P increased strongly with elevation from 200 m to 1000 m and 1500 m, but thereafter both leaf N and P decreased at 3000 m (prevailing hypothesis inconclusive). The leaf N and P result is counter to that found by 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 tropical montane forests, but in agreement with observations from Kitayama and Aiba (2002) from Borneo. For direct comparison in a separate study, van de Weg *et al.* (2009) found the same values for leaf N at our sites (controls only), but they included measurements at 1750 m, 2300 m and 3500 m that together showed a modest decrease in leaf N with elevation, but no altitudinal relationship with N per leaf area. Likewise, they found the same values for leaf P at our 200 m and 1000 m sites, but less than at our 1500 m and 3000 m sites. Leaf P increased with elevation on a per leaf area basis in their study.

The clearest trend from our results and perhaps the measurement of most direct connection to nutrient limitation was the steady and significant decrease in leaf N:P ratio with elevation, particularly with the "optimal" value of 15 (more on this below) crossed at mid-elevation (prevailing hypothesis supported). van de Weg *et al.* (2009) found similar values at all but the 1500 m site, where they had larger leaf N:P—and greater than 15—but the same general decrease in leaf N:P with elevation.

Tree height and DBH decreased with increasing elevation, but LAI did not vary with elevation, which is in agreement with Tanner (1980) and Lieberman *et al.* (1996). The DBH response to P fertilization increased with elevation, and the DBH response to N fertilization

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decreased with elevation for three out of four sites (prevailing hypothesis unsupported). 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).

The least response was in litter contribution to soil respiration, leaf N, LAI and DBH (Table 2). We might expect that there should be no response in litter contribution, particularly if leaf N and LAI did not change. The most response was in the microbial and mycorrhizal contributions, followed by leaf N:P, leaf P, root contribution, soil N:P and soil N. We might expect that the non-litter belowground components would respond to fertilization much more quickly than would the aboveground (i.e., DBH) components because belowground growth changes on faster time scales than does aboveground growth (e.g., fine roots versus wood). Leaf N:P was largely affected by changes in leaf P, and soil N:P was largely affected by changes in soil N. Generally, the number of significant responses between treatments was similar.

Nutrient Limitation

Generally, an optimal soil and leaf N:P ratio is between 14–16 (Aerts & Chapin III 2000; Koerselman & Meuleman 1996; Tessier & Raynal 2003). Anything less than that may tend to be N limited, more than that P limited, and in between N+P co-limited. Güsewell (2004) broadens that range of co-limitation to 10–20. The clearest trend in our results was the decrease in leaf N:P with elevation across the 14–16 threshold at mid-elevation, which supports the prevailing hypothesis of nutrient limitation for tropical montane forests (Fig. 4f). However, the inverse response of DBH increment growth—increased response to P fertilization and decreased response to N fertilization with elevation—is seemingly in contradiction with the stoichiometric

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results. How could sites that are supposedly N limited respond primarily to P fertilization, and sites that are supposedly P limited respond primarily to N fertilization? Is "nutrient limitation" from leaf stoichiometry equivalent to "nutrient limitation" from growth response?

The literature is divided on how nutrient limitation is defined (Güsewell 2004). Most fertilization studies link growth response in DBH and/or LAI to nutrient limitation to the fertilized element (e.g., Adamek *et al.* 2009; Harrington *et al.* 2001; Herbert & Fownes 1995; Kitayama & Aiba 2002; Moser *et al.* 2007; Nomura & Kikuzawa 2003; Tanner *et al.* 1992; Tanner *et al.* 1990; Vitousek *et al.* 1993; Weaver & Murphy 1990). One problem with leaf stoichiometry is that the "optimal" value of ~15 in fact varies widely among individual species (e.g., Aerts & Chapin III 2000; Güsewell 2004; Koerselman & Meuleman 1996). This is due in part because N and P use efficiencies also vary widely (Aerts 1990; Aerts & Chapin III 2000; Berendse & Aerts 1987; Vitousek 1982). However, one problem with growth response is that a given plant might be nutrient limited, but light, moisture and/or temperature may be more limiting to growth than nutrients so additional nutrients may not increase the growth of that plant (Aerts & Chapin III 2000; Chapin III *et al.* 1986). Wullaert *et al.* (2010) also show an inconclusive growth response to fertilization at a ~2070 m elevation site in the Ecuadorian Andes (1300 km NW from our sites).

Another major problem with growth response is that with DBH and LAI we are not directly measuring net primary productivity nor whole plant growth rates, but carbon allocation. Two trees could have the same photosynthetic and productivity rates, but tree A could allocate more carbon to woody growth and tree B to root growth. With a measurement of DBH alone it would appear that tree A is more "productive". In the same vein, adding nutrients to a tree might result in an increase in DBH increment rates, which would seemingly indicate nutrient limitation.

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However, it may be a potential carbon allocation shift—e.g., less carbon allocation to roots if fewer roots are needed to find nutrients, and the carbon that would have otherwise been allocated to roots instead goes to woody growth (Aerts *et al.* 1991; Aerts & Chapin III 2000; Gower & Vitousek 1989; Nomura & Kikuzawa 2003; Ostertag 2001; Röderstein *et al.* 2005).

Although we did not measure root growth directly with response to fertilization, we did measure root respiration and its response to fertilization. Furthermore, we measured mycorrhizal respiration concurrently with root respiration. Respiration from roots was inversely proportional to that from the mycorrhizae (Fig. 7). In other words, when root respiration increased, mycorrhizal respiration decreased, and vice versa. This pattern was well distributed across all sites. Thus, to separate nutrient limitation from carbon allocation, we would expect that there would be no decrease in root respiration with DBH increases.

Mycorrhizal contribution to soil respiration was largest at 3000 m with P fertilization. This was also where the largest increase in DBH occurred (Fig. 5). Mycorrhizal contribution was second largest at 1000 m with N fertilization. This was where the second largest increase in DBH occurred. The third largest contribution was at 200 m with N+P fertilization. This was where the third largest increase in DBH occurred. For all but the 1500 m site, mycorrhizal respiration contribution correlated well (r^2=0.90, $p<0.05$) with DBH growth increases in fertilized plots. Therefore, we cannot conclusively say that the greatest DBH responses were related to nutrient limitation, but they may be more indicative of potential carbon allocation shifts.

The 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 would be to obtain nutrients from

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mycorrhizae (Fisher *et al.* 2010; Smith *et al.* 2009). Roots would still be useful for water and stability, but water was not limiting at our sites, and slopes were steep only at the 1500 m and 3000 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) or leaves (i.e., LAI). LAI in our study was relatively insensitive to nutrient perturbation. Results from van de Weg *et al.* (in press) point to a poor fit between leaf N and photosynthetic parameters (V_{max}, J_{max}) and constant leaf N per leaf area with elevation suggesting that temperature and light, rather than nutrients, limit productivity. The newly available carbon as seen from DBH growth increases in the fertilization experiment is therefore likely not from increased productivity, but may be potentially from a shift in allocation from root to wood carbon, aiding structural support.

This does not fully explain why at all of our sites except 1500 m, mycorrhizal contribution increased and root contribution decreased when the *non*-limiting nutrient was applied. In agreement, Falkengren-Grerup (1995) and Flückiger and Braun (1998) found that high N supply in P-deficient plants reduced root allocation (e.g., 1000 m). This is because N is used to increase the mobilization of P through phosphatase production (Johnson *et al.* 1999; Treseder & Vitousek 2001). Nonetheless, although mycorrhizae transport both N and P, mycorrhizae are much more efficient and symbiotically used in the transport of P (Marschner & Dell 1994). It is possible that at a P non-limited site (3000 m) mycorrhizae are more active in general. Our results show that across all treatments mycorrhizal contribution was largest at 3000 m. The addition of P to this site possibly served to enhance mycorrhizal activity from fungal species already well-positioned to take advantage of P. Regardless, these hypotheses were untested, and further study is required to disprove them.

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One site did not follow the mycorrhizae–DBH relationship: the mid-elevation 1500 m site. The fourth and fifth largest increases in DBH, though small (not significantly greater than the DBH growth in the control sub-plots), occurred at 1500 m with N+P and P fertilization, respectively. Yet, mycorrhizal contribution at 1500 m was minimal, and these DBH increases corresponded to the largest and second largest contribution of roots to soil respiration for all the sites and treatments. Thus, both DBH and root respiration increased with N+P fertilization at 1500 m. Also, leaf P significantly increased with N+P fertilization in the first year fertilized group at 1500 m. According to the prevailing hypothesis of nutrient limitation for tropical montane forests, mid-elevation would be N and P co-limited (Aerts & Chapin III 2000; Davidson & Howarth 2007; Güsewell 2004; Tanner *et al.* 1998; Vitousek 1984; Vitousek & Farrington 1997; Wullaert *et al.* 2010), which was consistent with our results.

Conclusions

We presented here the first large scale study of nutrient dynamics and limitation in rain and cloud forests along a 3000 m elevation transect in the Peruvian Andes and Amazonia. 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 & Wright 2004; Pastor & Post 1988; Peterjohn *et al.* 1994; Salinas *et al.* 2011; Vuille & Bradley 2000), biomass burning in Amazonia leading to downwind deposition (Aragão *et al.* 2008; Aragão *et al.* 2007; Boy *et al.* 2008; Fabian *et al.*

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2005) and shifts and migration in tree communities (Feeley & 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).

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Draft for Review

References

ADAMEK, M., CORRE, M. D. & HÖLSCHER, D. 2009. Early effect of elevated nitrogen input on above-ground net primary production of a lower montane rain forest, Panama. *Journal of Tropical Ecology* 25:637-647.

AERTS, R. 1990. Nutrient use efficiency in evergreen and deciduous species from heathlands. *Oecologia* 84:391-397.

AERTS, R. 1996. Nutrient resorption from senescing leaves of perennials: Are there general patterns? *Journal of Ecology* 84(4):597-608.

AERTS, R., BOOT, R. G. A. & VAN DER AART, P. J. M. 1991. The relation between above- and belowground biomass allocation patterns and competitive ability. *Oecologia* 87(4):551-559.

AERTS, R. & CHAPIN III, F. S. 2000. The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. *Advances in Ecological Research* 30:1-67.

ARAGÃO, L. E. O. C., MALHI, Y., BARBIER, N., LIMA, A., SHIMABUKURO, Y., ANDERSON, L. & SAATCHI, S. 2008. Interactions between rainfall, deforestation and fires during recent years in the Brazilian Amazonia. *Philosophical Transactions of the Royal Society of London Series B* 363(1498):1779-1785.

ARAGÃO, L. E. O. C., MALHI, Y., METCALFE, D. B., SILVA-ESPEJO, J. E., JIMÉNEZ, E., NAVARRETE, D., ALMEIDA, S., COSTA, A. C. L., SALINAS, N., PHILLIPS, O. L., ANDERSON, L. O., BAKER, T. R., GONCALVEZ, P. H., HUAMÁN-OVALLE, J., MAMANI-SOLÓRZANO, M., MEIR, P., MONTEAGUDO, A., PEÑUELA, M. C., PRIETO, A., QUESADA, C. A., ROZAS-DÁVILA, A., RUDAS, A., SILVA JUNIOR, J. A. & VÁSQUEZ, R. 2009. Above- and below-ground net primary productivity across ten Amazonian forests on contrasting soils. *Biogeosciences Discuss.* 6(1):2441-2488.

ARAGÃO, L. E. O. C., MALHI, Y., ROMAN-CUESTA, R. M., SAATCHI, S., ANDERSON, L. O. & SHIMABUKURO, Y. E. 2007. Spatial patterns and fire response of recent Amazonian droughts. *Geophysical Research Letters* 34(L07701):1-5.

AUERBACH, M. J. & STRONG, D. R. 1981. Nutritional ecology of *Heliconia* herbivores: Experiments with plant fertilization and alternative hosts. *Ecological Monographs* 51(1):63-84.

BERENDSE, F. & AERTS, R. 1987. Nitrogen-ese-efficiency: a biologically meaningful definition? *Functional Ecology* 1(3):293-296.

BLODGETT, T. A. & ISACKS, B. L. 2007. Landslide erosion rate in the Eastern Cordillera of Northern Bolivia. *Earth Interactions* 11(19):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. *Global Biogeochemical Cycles* 22(GB4011):1-16.

BRIX, H. 1971. Effects of nitrogen fertilization on photosynthesis and respiration in Douglas-Fir. *Forest Science* 17(4):407-414.

BUSSMANN, R. W., WILCKE, W. & RICHTER, M. 2008. Landslides as important disturbance regimes - Causes and regeneration. Pp. 319-330 in Beck, W., Bendix, J., Kottke, I., Makeschin, F. & Mosandl, R. (eds.). *Gradients in a Tropical Mountain Ecosystem of ecuador*. Springer, Berlin. 319-330 pp.

CHAPIN III, F. S., SCHULZE, E.-D. & MOONEY, H. A. 1990. The ecology and economics of storage in plants. *Annu. Rev. Ecol. Syst.* 21:423-447.

Draft For Review

Draft For Review

CHAPIN III, F. S., VITOUSEK, P. M. & CLEVE, K. V. 1986. The nature of nutrient limitation in plant communities. *The American Naturalist* 127(1):48-58.

DAVIDSON, E. A. & HOWARTH, R. W. 2007. Nutrients in synergy. *Nature* 449:1000-1001.

ECKSTEIN, R. L., KARLSSON, P. S. & WEIH, M. 1999. Leaf life span and nutrient resorption as determinants of plant nutrient conservation in temperate-arctic regions. *New Phytologist* 143(1):177-189.

FABIAN, P., KOHLPAINTNER, M. & ROLLENBECK, R. 2005. Biomass burning in the Amazon-Fertilizer for the mountaineous rain forest in Ecuador. *Environmental Science and Pollution Research* 12(5):290-296.

FALKENGREN-GRERUP, U. 1995. Interspecies differences in the preference of ammonium and nitrate in vascular plants. *Oecologia* 102(3):305-311.

FEELEY, K. J. & SILMAN, M. R. 2010. Biotic attrition from tropical forests correcting for truncated temperature niches. *Global Change Biology* 16:1830-1836.

FIELD, C. B. & MOONEY, H. A. 1986. The photosynthesis-nitrogen relationship in wild plants. Pp. 25-55 in Givnish, T. J. (ed.). *On the Economy of Plant Form and Function*. Cambridge University Press, Cambridge, England. 25-55 pp.

FISHER, J. B., SITCH, S., MALHI, Y., FISHER, R. A., HUNTINGFORD, C. & TAN, S.-Y. 2010. Carbon cost of plant nitrogen acquisition: A mechanistic, globally-applicable model of plant nitrogen uptake and fixation. *Global Biogeochemical Cycles* 24(GB1014):doi:10.1029/2009GB003621.

FLÜCKIGER, W. & BRAUN, S. 1998. Nitrogen deposition in Swiss forests and its possible relevance for leaf nutrient status, parasite attacks and soil acidification. *Environmental Pollution* 102:69-76.

GARZIONE, C. N., HOKE, G. D., LIBARKIN, J. C., WITHERS, S., MACFADDEN, B., EILER, J., GHOSH, P. & MULCH, A. 2008. Rise of the Andes. *Science* 320(5881):1304-1307.

GIRARDIN, C. A. J., MALHI, Y., ARAGÃO, L. E. O. C., MAMANI, M., HUARACA HUASCO, W., DURAND, L., FEELEY, K. J., RAPP, J., SILVA-ESPEJO, J. E., SILMAN, M., SALINAS, N. & WHITTAKER, R. J. 2010. Net primary productivity allocation and cycling of carbon along a tropical forest elevational transect in the Peruvian Andes. *Global Change Biology* 16(12):3176-3192.

GOWER, S. T. & VITOUSEK, P. M. 1989. Effects of nutrient amendments on fine root biomass in a primary successional forest in Hawai'i. *Oecologia* 81(4):566-568.

GRIME, J. P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *The American Naturalist* 111(982):1169-1194.

GÜSEWELL, S. 2004. N:P ratios in terrestrial plants: variation and functional significance. *New Phytologist* 164:243-266.

HARRINGTON, R. A., FOWNES, J. H. & VITOUSEK, P. M. 2001. Production and resource use efficiencies in N- and P-limited tropical forests: a comparison of responses to long-term fertilization. *Ecosystems* 4(7):646-657.

HEINEMEYER, A., HARTLEY, I. P., EVANS, S. P., DE LA FUENTES, J. A. C. & INESON, P. 2007. Forest soil CO_2 flux: uncovering the contribution and environmental responses of ectomycorrhizas. *Global Change Biology* 13(8):1786-1797.

HERBERT, D. A. & FOWNES, J. H. 1995. Phosphorus limitation of forest leaf area and net primary production on a highly weathered soil. *Biogeochemistry* 29(3):223-235.

Draft For Review

Draft For Review

JOHNSON, D., GEISINGER, D., WALKER, R., NEWMAN, J., VOSE, J., ELLIOT, K. & BALL, T. 1994. Soil pCO_2, soil respiration, and root activity in CO_2-fumigated and nitrogen-fertilized ponderosa pine. *Plant and Soil* 165(1):129-138.

JOHNSON, D., LEAKE, J. R. & LEE, J. A. 1999. The effects of quantity and duration of simulated pollutant nitrogen deposition on root-surface phosphatase activities in calcareous and acid grasslands: a bioassay approach. *New Phytologist* 141:433-442.

JOHNSON, N. C. 1993. Can fertilization of soil select less mutualistic mycorrhizae? *Ecological Applications* 3(4):749-757.

KIRSCHBAUM, M. U. F. 1995. The temperature dependence of soil organic matter decomposition, and the effect of global warming on soil organic C storage. *Soil Biology and Biochemistry* 27(6):753-760.

KITAYAMA, K. & AIBA, S.-I. 2002. Ecosystem structure and productivity of tropical rain forests along altitudinal gradients with contrasting soil phosphorus pools on Mount Kinabalu, Borneo. *Journal of Ecology* 90(1):37-51.

KOERSELMAN, W. & MEULEMAN, A. F. M. 1996. The vegetation N:P ratio: a new tool to detect the nature of nutrient limitation. *Journal of Applied Ecology* 33(6):1441-1450.

LANGLEY, J. A., CHAPMAN, S. K. & HUNGATE, B. A. 2006. Ectomycorrhizal colonization slows root decomposition: the post-mortem fungal legacy. *Ecology Letters* 9:955-959.

LIEBERMAN, D., MILTON, L., PERALTA, R. & HARTSHORN, G. S. 1996. Tropical forest structure and composition on a large-scale altitudinal gradient in Costa Rica. *Journal of Ecology* 84(2):137-152.

LOZANO, P., BUSSMANN, R. W. & KÜPPERS, M. 2005. Landslides as ecosystem disturbance - their implications and importance in South Ecuador. *Lyonia* 8(1):61-65.

MALHI, Y. & WRIGHT, J. 2004. Spatial patterns and recent trends in the climate of tropical rainforest regions. *Philosophical Transactions of the Royal Society of London* 359(1443):311-329.

MARSCHNER, H. & DELL, B. 1994. Nutrient uptake in mycorrhizal symbiosis. *Plant and Soil* 159(1):89-102.

MEYER, G. A. & ROOT, R. B. 1996. Influence of feeding guild on insect response to host plant fertilization. *Ecological Entomology* 21:270-278.

MOSER, G., HERTEL, D. & LEUSCHNER, C. 2007. Altitudinal change in LAI and stand leaf biomass in tropical montane forests: a transect study in Ecuador and a pan-torpical meta-analysis. *Ecosystems* 10:924-935.

MYERS, N., MITTERMEIER, R. A., MITTERMEIER, C. G., DA FONSECA, G. A. B. & KENT, J. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403:853-858.

NOMURA, N. & KIKUZAWA, K. 2003. Productive phenology of tropical montane forests: Fertilization experiments along a moisture gradient. *Ecological Research* 18(5):573-586.

OSTERTAG, R. 2001. Effects of nitrogen and phosphorus availability on fine-root dynamics in Hawaiian montane forests. *Ecology* 82(2):485-499.

OSTLE, N. J., SMITH, P., FISHER, R. A., WOODWARD, F. I., FISHER, J. B., SMITH, J. U., GALBRAITH, D., LEVY, P., MEIR, P., MCNAMARA, N. P. & BARDGETT, R. D. 2009. Integrating plant-soil interactions into global carbon cycle models. *Journal of Ecology* 97:851-863.

PASTOR, J. & POST, W. M. 1988. Response of northern forests to CO_2-induced climate change. *Nature* 334:55-58.

Draft For Review

Draft For Review

PETERJOHN, W. T., MELILLO, J. M., STEUDLER, P. A., NEWKIRK, K. M., BOWLES, F. P. & ABER, J. D. 1994. Responses of trace gas fluxes and N availability to experimentally elevated soil temperatures. *Ecological Applications* 4:617-625.

QUESADA, C. A., LLOYD, J., ANDERSON, L. O., FYLLAS, N. M., SCHWARZ, M. & CZIMCZIK, C. I. 2009a. Soils of Amazonia with particular reference to the RAINFOR sites. *Biogeosciences Discuss.* 6:3851-3921.

QUESADA, C. A., LLOYD, J., SCHWARZ, M., BAKER, T. R., PHILLIPS, O. L., PATIÑO, S., CZIMCZIK, C., HODNETT, M. G., HERRERA, R., ARNETH, A., LLOYD, G., MALHI, Y., DEZZEO, N., LUIZÃO, F. J., SANTOS, A. J. B., SCHMERLER, J., ARROYO, L., SILVEIRA, M., PRIANTE FILHO, N., JIMENEZ, E. M., PAIVA, R., VIEIRA, I., NEILL, D. A., SILVA, N., PEÑUELA, M. C., MONTEAGUDO, A., VÁSQUEZ, R., PRIETO, A., RUDAS, A., ALMEIDA, S., HIGUCHI, N., LEZAMA, A. T., LÓPEZ-GONZÁLEZ, G., PEACOCK, J., FYLLAS, N. M., ALVAREZ DÁVILA, E., ERWIN, T., DI FIORE, A., CHAO, K. J., HONORIO, E., KILLEEN, T., PEÑA CRUZ, A., PITMAN, N., NÚÑEZ VARGAS, P., SALOMÃO, R., TERBORGH, J. & RAMÍREZ, H. 2009b. Regional and large-scale patterns in Amazon forest structure and function are mediated by variations in soil physical and chemical properties. *Biogeosciences Discuss.* 6(2):3993-4057.

RAICH, J. W., RUSSELL, A. E. & VITOUSEK, P. M. 1997. Primary productivity and ecosystem development along an elevational gradient on Mauna Loa, Hawai'i. *Ecology* 78(3):707-721.

RÖDERSTEIN, M., HERTEL, D. & LEUSCHNER, C. 2005. Above- and below-ground litter production in three tropical montane forests in southern Ecuador. *Journal of Tropical Ecology* 21(5):483-492.

RYAN, M. G. & YODER, B. J. 1997. Hydraulic limits to tree height and tree growth. *BioScience* 47(4):235-242.

SALINAS, N., MALHI, Y., MEIR, P., SILMAN, M., ROMAN CUESTA, R., HUAMAN, J., SALINAS, D., HUAMAN, V., GIBAJA, A., MAMANI, M. & FARFAN, F. 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 Phytologist* 189(4):967-977.

SHAVER, G. R. 1981. Mineral nutrition and leaf longevity in an evergreen shrub, *Ledum palustre* ssp. *decumbens*. *Oecologia* 49:362-365.

SMITH, F. A., GRACE, E. J. & SMITH, S. E. 2009. More than a carbon economy: nutrient trade and ecological sustainability in facultative arbuscular mycorrhizal symbioses. *New Phytologist* 182(2):347-358.

TANNER, E. V. J. 1980. Studies on the biomass and productivity in a series of montane rain forests in Jamaica. *Journal of Ecology* 68(2):573-588.

TANNER, E. V. J., KAPOS, V. & FRANCO, W. 1992. Nitrogen and phosphorus fertilization effects on Venezuelan montane forest trunk growth and litterfall. *Ecology* 73(1):78-86.

TANNER, E. V. J., KAPOS, V., FRESKOS, S., HEALEY, J. R. & THEOBALD, A. M. 1990. Nitrogen and phosphorus fertilization of Jamaican montane forest trees. *Journal of Tropical Ecology* 6(2):231-238.

TANNER, E. V. J., VITOUSEK, P. M. & CUEVAS, E. 1998. Experimental investigation of nutrient limitation of forest growth on wet tropical mountains. *Ecology* 79(1):10-22.

Draft For Review

Draft For Review

TESSIER, J. T. & RAYNAL, D. J. 2003. Use of nitrogen to phosphorus ratios in plant tissue as an indicator of nutrient limitation and nitrogen saturation. *Journal of Applied Ecology* 40(3):523-534.

TRESEDER, K. K. & VITOUSEK, P. M. 2001. Effects of soil nutrient availability on investment in acquisition of N and P in Hawaiian rain forests. *Ecology* 82(4):946-954.

VAN DE WEG, M. J., 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 Ecology & Diversity* 2(3):243-254.

VAN DE WEG, M. J., MEIR, P., GRACE, J. & DAMIÁN RAMOS, G. in press. Photosynthetic parameters, dark respiration and leaf traits in the canopy of a Peruvian tropical montane cloud forest. *Oecologia*.

VITOUSEK, P. 1982. Nutrient cycling and nutrient use efficiency. *The American Naturalist* 119(4):553-572.

VITOUSEK, P. M. 1984. Litterfall, nutrient cycling, and nutrient limitation in tropical forests. *Ecology* 65(1):285-298.

VITOUSEK, P. M. & FARRINGTON, H. 1997. Nutrient limitation and soil development: Experimental test of a biogeochemical theory. *Biogeochemistry* 37:63-75.

VITOUSEK, P. M. & HOWARTH, R. W. 1991. Nitrogen limitation on land and in the sea: How can it occur? *Biogeochemistry* 13:87-115.

VITOUSEK, P. M. & SANFORD, R. L. 1986. Nutrient cycling in moist tropical forest. *Annual Review of Ecology and Systematics* 17(1):137-167.

VITOUSEK, P. M., WALKER, L. R., WHITEAKER, L. D. & MATSON, P. A. 1993. Nutrient limitations to plant growth during primary succession in Hawaii Volcanoes National Park. *Biogeochemistry* 23(3):195-215.

VUILLE, M. & BRADLEY, R. S. 2000. Mean annual temperature trends and their vertical structure in the tropical Andes. *Geophysical Research Letters* 27(23):3885-3888.

WEAVER, P. L. & MURPHY, P. G. 1990. Forest structure and productivity in Puerto Rico's Luquillo Mountains. *Biotropica* 22(1):69-82.

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.

WILSON, S. D. & TILMAN, D. 1993. Plant competition and resource availability in response to disturbance and fertilization. *Ecology* 74(2):599-611.

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. *Forest Ecology and Management* 260(9):1434-1445.

Draft For Review

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Tables and Figures

Table 1. Site characteristics. 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., 3025 m).

	Tambopata	Tono	San Pedro	Wayqecha
Elevation (m)	200	1000	1500	3000
Mean Annual Temperature (°C)	26.4	20.7	18.8	12.5
Mean Annual Precipitation (mm)	2730	3087	2631	1706
Slope (%)	0	8	27	28
Aspect	-	W	W	E
Geological Substrate	Pleistocene alluvial terrace	Alluvial terrace	Paleozoic shales-slates	Paleozoic shales-slates
Soil Profile OL:ML (cm)	2:30	5:42	10:45	20:4
Soil pH	3.9	3.8	4.0	4.1
Dominant Plant Families	*Myristicaceae; Fabaceae*	*Rubiaceae; Fabaceae; Moraceae*	*Lauraceae; Rubiaceae; Melastomatacea*	*Cunoniaceae; Clusiaceae*
Longitude	-69.2967	-71.5327	-71.5370	-71.5870
Latitude	-12.8387	-12.9475	-13.0492	-13.1903

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Table 2. Summary of measurements that increased (decreases included for soil and leaf N:P ratios and soil respiration) significantly (p-values shown for <0.20, in bold for <0.05) with fertilization (nitrogen, nitrogen+phosphorus, phosphorus) versus control sub-plots.

		Year 1 Group			Year 2 Group			Year 1+2		
Measurement	**Site**	**N**	**N+P**	**P**	**N**	**N+P**	**P**	**N**	**N+P**	**P**
Soil N	200 m		0.12	0.09						
	1000 m		0.08		0.19		0.06	0.11	0.09	0.17
	1500 m									
	3000 m									
Soil P	200 m								0.19	
	1000 m								0.12	0.12
	1500 m		0.09						0.11	
	3000 m									
Soil N:P	200 m				0.10			0.17		
	1000 m									0.13
	1500 m									
	3000 m	0.08	**0.02**		0.16	**0.03**			**0.00**	
Leaf N	200 m	0.08								
	1000 m	0.12								
	1500 m									
	3000 m									
Leaf P	200 m	0.15				0.20		0.06	0.17	
	1000 m		0.19	0.12			0.09			**0.04**
	1500 m		**0.00**							
	3000 m									
Leaf N:P	200 m	0.16			0.08			**0.03**		
	1000 m		0.16	0.06			0.15			**0.05**
	1500 m						0.14			
	3000 m	0.10						0.15		
DBH	200 m									
	1000 m	0.18				0.15				
	1500 m									
	3000 m			0.18						
LAI	200 m						0.17			
	1000 m									
	1500 m									
	3000 m			0.16						0.15
Litter Rs contribution	200 m									
	1000 m									
	1500 m		0.11						0.18	
	3000 m									
Root Rs contribution	200 m	0.07	0.07	0.16					0.17	0.07
	1000 m						0.12			
	1500 m		**0.04**	0.07	**0.05**					
	3000 m									
Mycorrhizal Rs contribution	200 m	0.20	0.07	0.16			0.19	**0.02**	0.06	0.06
	1000 m	0.08	0.09		0.10		**0.05**	**0.00**	**0.00**	0.17
	1500 m			0.11	0.13					
	3000 m			**0.05**	0.18					
Microbial Rs contribution	200 m	**0.05**	**0.04**					**0.02**	**0.03**	**0.01**
	1000 m			0.17	0.08			**0.00**	**0.01**	0.17
	1500 m	0.10	0.10	**0.02**	**0.01**			0.08	**0.00**	**0.02**
	3000 m	**0.01**								0.20

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732 **Table 3. Soil properties for control plots at the four elevation sites.**

	200 m	1000 m	1500 m	3000 m
Soil N (organic:mineral)	3.5:1	4.8:1	0.85:1	0.83:1
Soil P (organic:mineral)	1.3:1	1.6:1	1.3:1	1.7:1
Soil N:P (organic:mineral)	2.0:1	3.0:1	0.74:1	0.50:1
Soil bulk density ($g \cdot cm^{-3}$; organic)	1.71	0.64	0.53	0.10
Soil bulk density ($g \cdot cm^{-3}$; mineral)	2.22	1.46	0.69	0.87

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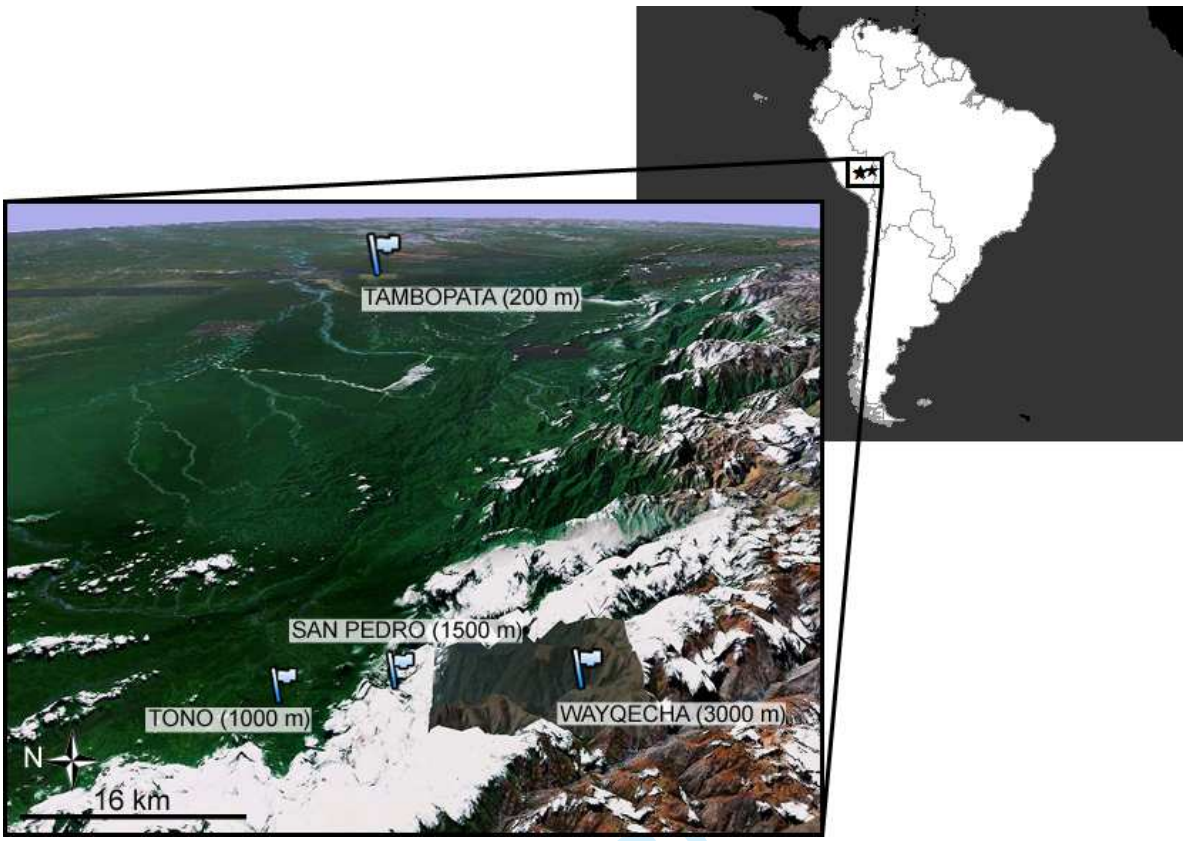

Fig. 1. Study sites with inset from Google Earth. Clouds (not snow) cover much of the mountains in the image.

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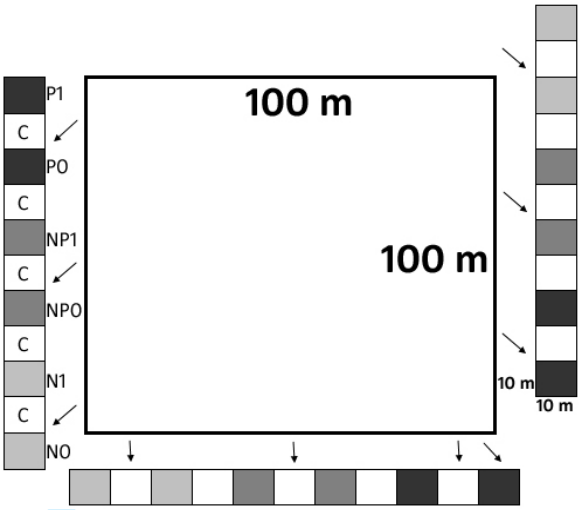

Fig. 2. The experimental set up for the fertilization experiment (shown here at the 1500 m site for example). The long-term 100 x 100 m plot is surrounded on three sides by 10 x 110 m transects consisting of 10 x 10 m sub-plots. Within each transect, two sub-plots were fertilized with N, two with P, two with both N and P, and six controls separated each fertilized sub-plot. Of those fertilized sub-plots within each transect, half began fertilization in the first year (N0, NP0, P0) and the other half in the second year (N1, NP1, P1).

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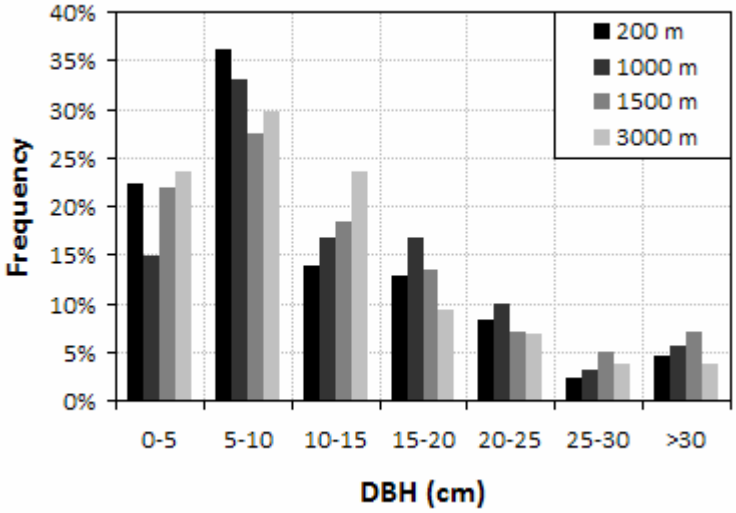
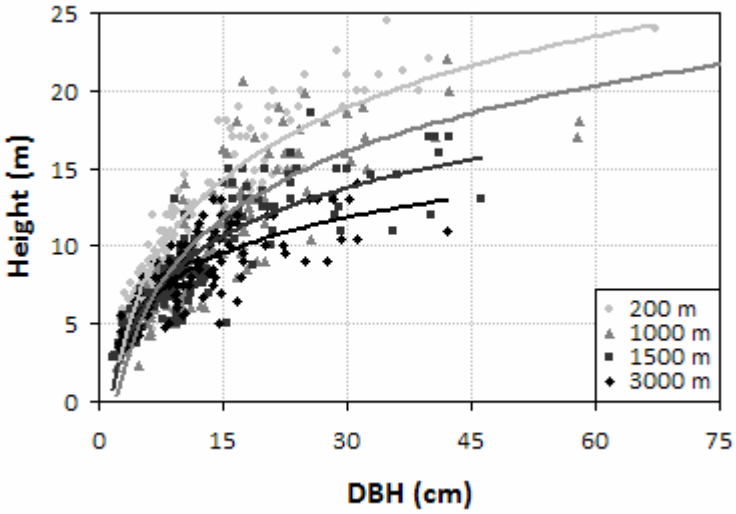


a)



b)

Fig. 3. Average tree diameter at breast height (DBH) for each site (200 m, 1000 m, 1500 m, 3000 m): a) frequency distribution, and b) as a function of tree height. The regression equations for tree height (y) versus DBH (x) are: y = 6.59LN(x) – 3.50 at 200 m (r^2 = 0.88); y = 6.11LN(x) – 4.70 at 1000 m (r^2 = 4.70); y = 4.48LN(x) – 1.48 at 1500 m (r^2 = 0.78); y = 3.31LN(x) + 0.57 at 3000 m (r^2 = 0.66).

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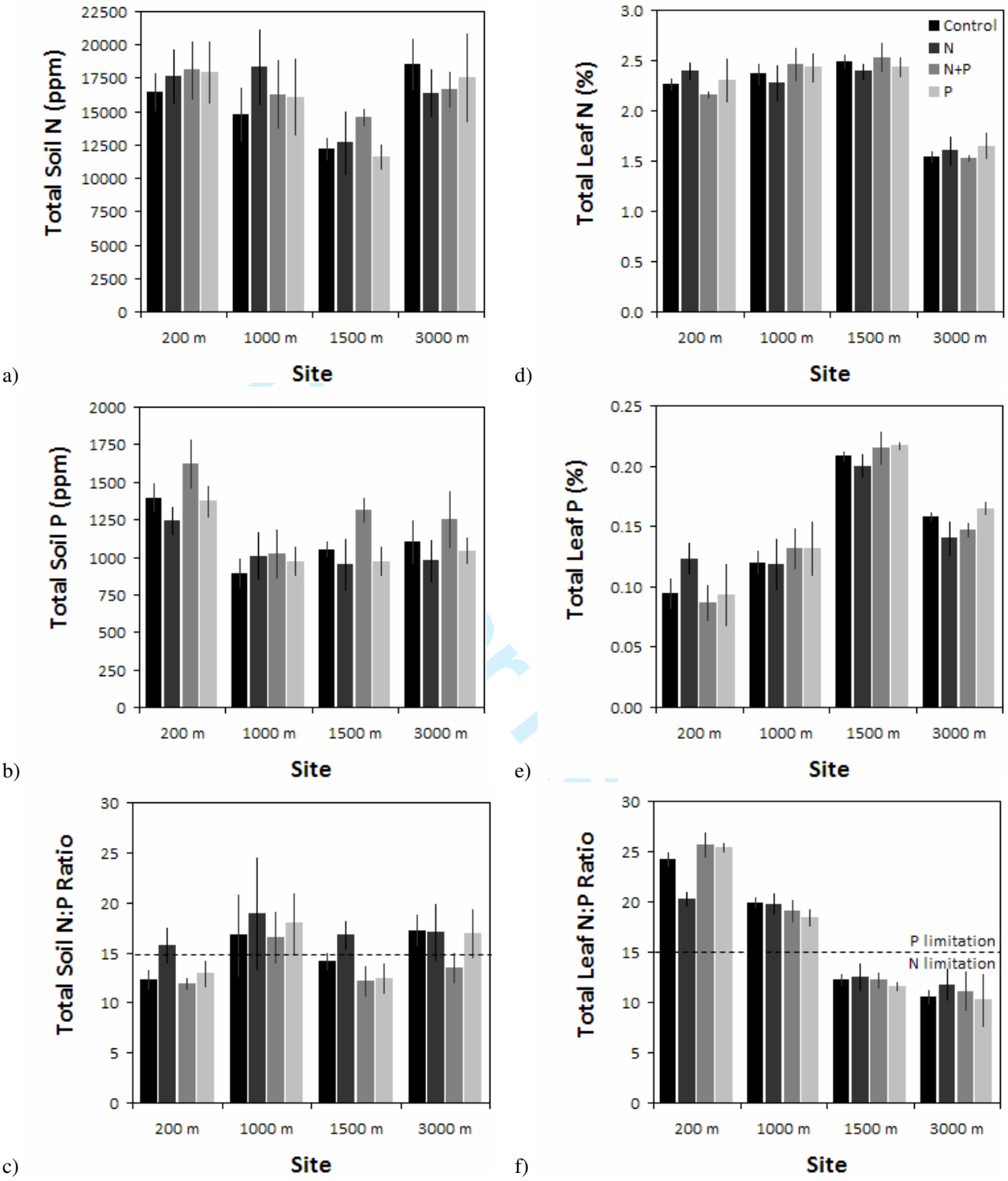

Fig. 4. Total soil (a) and leaf (b) nitrogen (N), total soil (c) and leaf (d) phosphorus (P), and total soil (e) and leaf (f) N:P ratio in 2008 after one year of fertilization (N: 6 kg urea/site; P: 3 kg triple superphosphate/site; N+P: 6 kg urea/site + 3 kg triple superphosphate/site). Data are shown for all four sites (200 m, 1000 m, 1500 m and 3000 m) and all four treatments (control, N, N+P, P) as mean ± SE. The dashed line in the leaf N:P ratio (and shown for comparison for soil N:P) shows the "optimal" N:P ratio (15) where values above the line suggest P limitation and values below suggest N limitation. Soil concentrations are for the organic layer.

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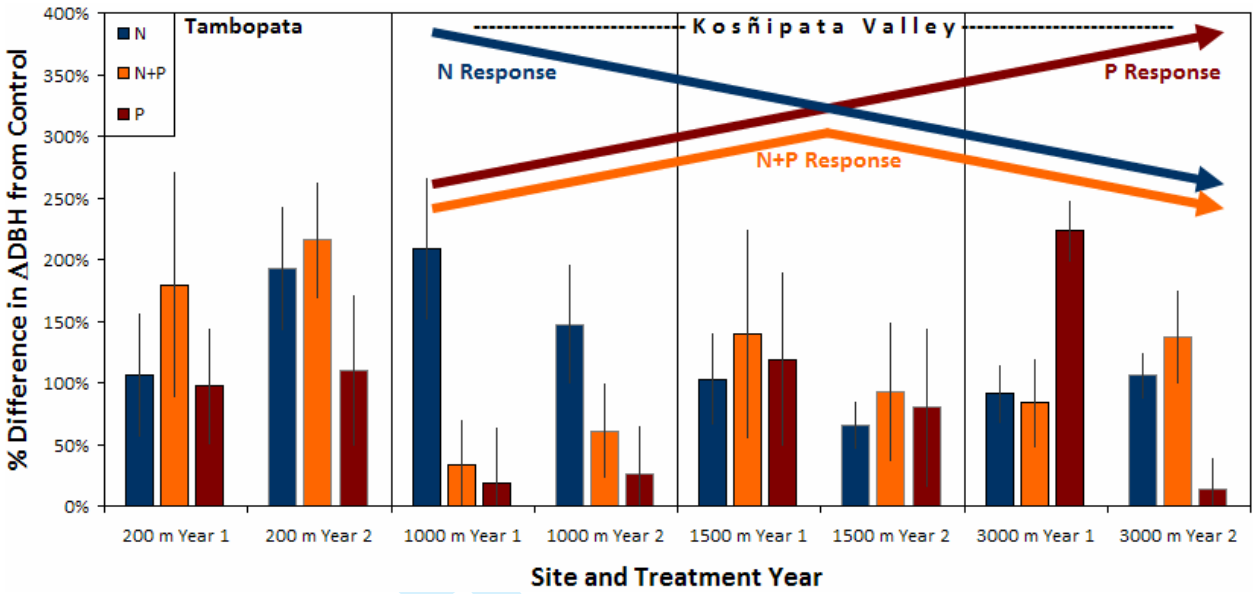

Fig. 5. The growth rate (Δ) in diameter at breast height (DBH) for each fertilization treatment (Nitrogen, Nitrogen+Phosphorus, and Phosphorus) as a percentage of the change in DBH for the control sub-plots. The 1000 m, 1500 m and 3000 m sites are all situated in the same valley, and they follow inverse gradients in N and P response with elevation. The first year change in DBH for the fertilized sub-plots as a percentage of that for the control sub-plots split into two groups: sub-plots fertilized in the first year, and sub-plots fertilized in the second year.

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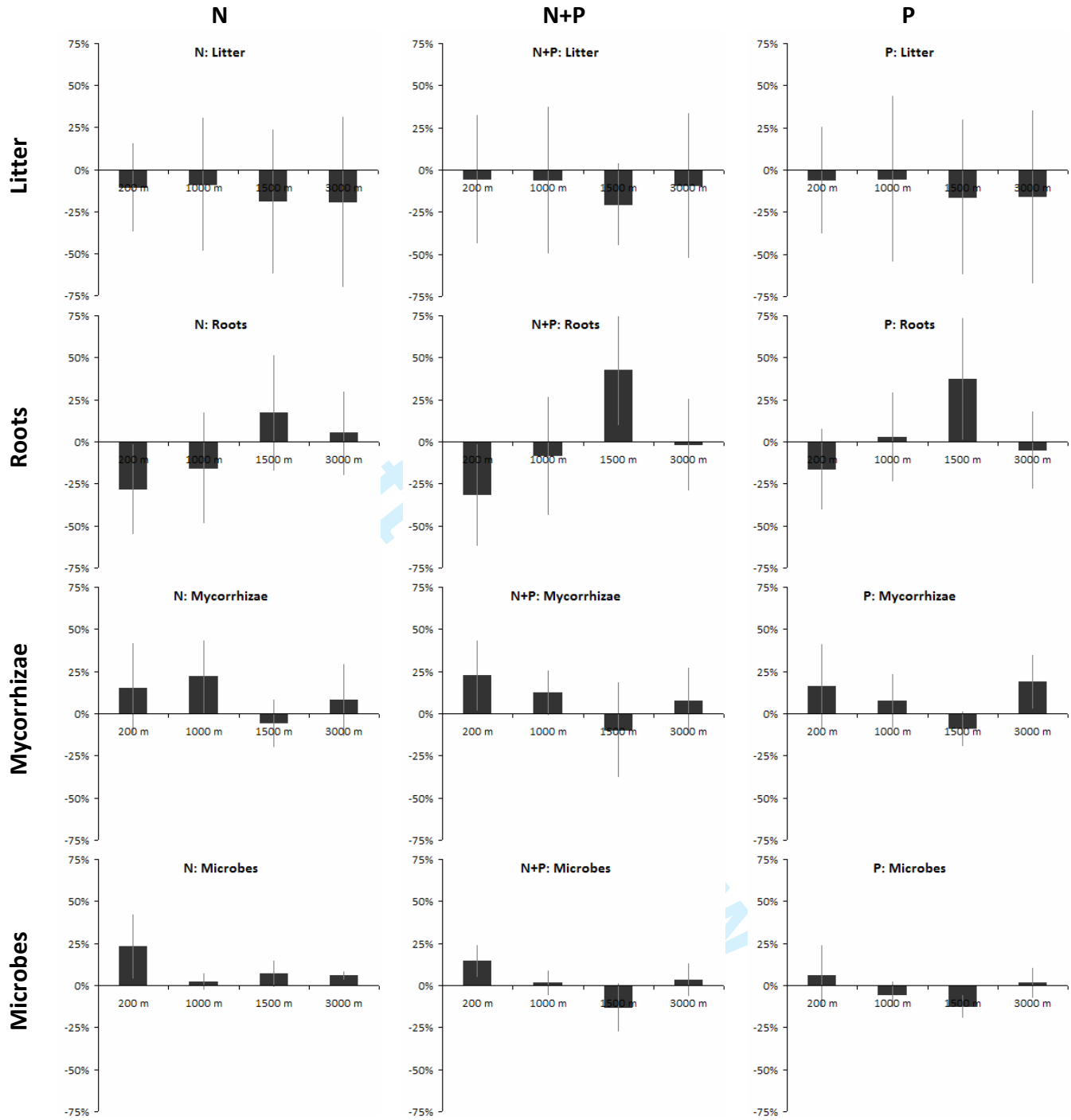

Fig. 6. The percent soil respiration contribution between litter, roots, mycorrhizae and soil microbes taken as that from the control sub-plots minus that from the fertilized (nitrogen, nitrogen+phosphorus, phosphorus) sub-plots after two years of fertilization given as mean ± SE scaled to percent of total error.

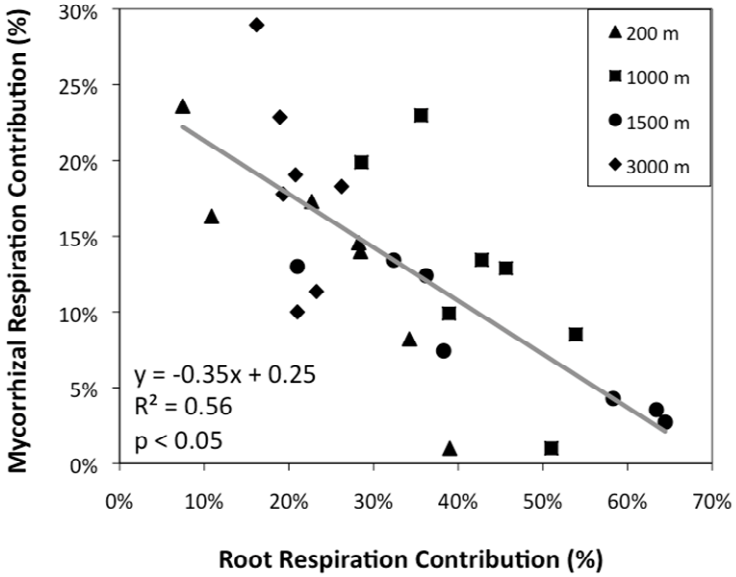

Fig. 7. Root contribution (%) to soil respiration versus mycorrhizal contribution (%) to soil respiration for all fertilization treatments (nitrogen, nitrogen+phosphorus, phosphorus) and controls and all sites (200 m, 1000 m, 1500 m, 3000 m).

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Supplementary Table and Figures

Table S1. Individual tree data for 77 trees across all four sites (WA=3000 m, SP=1500 m, TO=1000 m, TA=200 m). Fertilization treatments are given as N (N0), N+P (NP), P (P0) and control (C). DBH was measured in July 2009. Some data were missing or unknown.

Site	Tree #	Plot	Fert	Family	Genera	Species	DBH (cm)	Height (m)	Leaf N (%)	Leaf P (%)	Leaf K (%)
WA	51	7F	N0	CUNONIACEAE	Weinmannia	crassifolia	8.1	8.0	1.32	0.11	0.73
WA	52	7F	N0	CUNONIACEAE	Weinmannia	crassifolia	7.2	7.5	1.27	0.08	1.02
WA	53	7F	N0	CLUSIACEAE	Clusia	sp	14.4	8.0	1.51	0.12	0.61
WA	54	7F	N0	THEACEAE	Freziera	parva	16.6	11.5	1.86	0.13	0.79
WA	55	7F	N0	CLUSIACEAE	Clusia	sp	6.2	6.0	1.80	0.18	0.94
WA	32	9F	NP0	CUNONIACEAE	Weinmannia	bangii	10.6	10.0	1.85	0.19	0.83
WA	33	9F	NP0	CUNONIACEAE	Weinmannia	bangii	15.6	11.0	1.47	0.16	0.58
WA	34	9F	NP0	CUNONIACEAE	Weinmannia	crassifolia	14.8	12.0	1.19	0.12	0.41
WA	35	9F	NP0	CUNONIACEAE	Weinmannia	reticulata	3.2	4.5	1.95	0.17	0.99
WA	11	11F	P0	CLETHRACEAE	Clethra	sp	10.4	7.5	1.22	0.10	0.81
WA	12	11F	P0	CLUSIACEAE	Cusia	sp	21.4	12.0	1.31	0.38	1.00
WA	13	11F	P0	CLUSIACEAE	Clusia	sp	12.4	9.0	1.35	0.23	0.73
WA	14	11F	P0	CUNONIACEAE	Weinmannia	crassifolia	11.3	8.0	1.17	0.12	0.55
WA	15	11F	P0	CUNONIACEAE	Weinmannia	crassifolia	11.2	8.0	1.20	0.09	0.66
WA	36	8/9C	C	CUNONIACEAE	Weinmannia	bangii	12.2	11.0	1.49	0.12	0.61
WA	37	8/9C	C	MYRSINACEAE	Myrsine	coriacea	8.0	8.3	2.17	0.17	2.59
WA	38	8/9C	C	CUNONIACEAE	Weinmannia	crassifolia	12.7	12.0	1.18	0.10	0.90
WA	39	8/9C	C	CUNONIACEAE	Weinmannia	latifolia	9.8	10.0	1.68	0.11	1.25
WA	40	8/9C	C	ARALIACEAE	Oreopanax	microcephalus	4.7	7.0	2.60	0.28	2.10
SP	312	1F	N0	LAURACEAE	Endlicheria	griseo-sericea	8.9	9.2	1.90	0.26	0.62
SP	313	1F	N0	MELASTOMATACEAE	Miconia	sp	7.8	7.0	2.22	0.23	0.73
SP	314	1F	N0	EUPHORBIACEAE	Acalypha		5.5	6.0	2.39	0.36	1.01
SP	315	1F	N0	EUPHORBIACEAE	Hyeronima	alchorneiodes	42.8	17.0	2.24	0.20	0.63
SP	316	1F	N0	ROSACEAE	Prunus	herthae	4.9	5.1	2.14	0.22	1.25
SP	291	3F	NP0	ANNONACEAE	Guatteria	duodecima	8.9	8.8	2.23	0.13	0.73
SP	292	3F	NP0	SAPOTACEAE	Sarcaulus	sp	15.8	15.0	1.87	0.29	0.48
SP	293	3F	NP0	SAPOTACEAE	Sarcaulus	sp	17.4	15.0	1.74	0.18	0.33
SP	294	3F	NP0	FABACEAE	Inga		16.0	13.0	2.72	0.21	0.77
SP	295	3F	NP0	SAPINDACEAE	Paullinia		2.5	3.0	1.82	0.15	0.65
SP	271	5F	P0	ARECACEAE	Euterpe	sp	17.9	13.8	2.01	0.13	0.36
SP	273	5F	P0	FABACEAE	Inga	sp	20.5	12.5	3.15	0.16	0.64
SP	274	5F	P0	RUBIACEAE			5.0	5.0	3.00	0.16	0.91
SP	275	5F	P0	ACTINIDIACEAE	Saurauia	sp	15.8	11.3	2.10	0.20	1.70
SP	286	3/4C	C	PROTEACEAE			3.9	5.9	2.25	0.29	1.37
SP	287	3/4C	C	MONIMIACEAE	Mollinedia	sp	6.5	7.0	2.14	0.27	1.41
SP	288	3/4C	C	MORACEAE	Pseudolmedia	sp	17.1	12.3	2.45	0.18	1.44

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SP	289	3/4C	C	SABIACEAE	Meliosma	sp	28.8	12.0	1.52	0.10	0.72
SP	290	3/4C	C	ANNONACEAE	Annona	sp	10.5	7.5	2.20	0.12	0.79
TO	426	1F	N0	FABACEAE	Tachigali		13.0	8.7	2.40	0.14	0.90
TO	427	1F	N0	LAURACEAE			6.5	6.3	1.81	0.10	1.15
TO	428	1F	N0	EUPHORBIACEAE	Alchornea		15.5	11.1	3.07	0.24	1.22
TO	429	1F	N0	RUBIACEAE	Palicourea		6.0	5.0	2.96	0.15	1.68
TO	431	1F	N0	LAURACEAE	Ocotea		11.6	6.1	2.03	0.11	0.80
TO	406	3F	NP0	LACISTEMATACEAE	Lacistema		22.5	18.0	2.56	0.18	1.58
TO	407	3F	NP0	MYRISTICACEAE	Virola	mollissima	32.2	17.0	2.34	0.13	0.70
TO	408	3F	NP0	LECYTHIDACEAE	Eschweilera		9.1	6.0	2.11	0.09	0.72
TO	409	3F	NP0	MORACEAE	Pseudolmedia	macrophylla	23.9	16.0	2.39	0.12	1.04
TO	410	3F	NP0	RUBIACEAE	Elaeagia		6.0	4.3	2.04	0.08	1.50
TO	441	5F	P0	CHRYSOBALANACEAE	Licania		14.7	11.5	1.76	0.10	0.84
TO	442	5F	P0	RUBIACEAE	Elaeagia		17.9	8.5	1.90	0.08	0.59
TO	443	5F	P0	VOCHYSIACEAE	Vochysia	sp	31.0	15.5	1.76	0.09	0.68
TO	444	5F	P0	FLACOURTIACEAE			6.2	4.5	2.49	0.11	1.17
TO	445	5F	P0	RUBIACEAE			5.6	6.2	1.67	0.11	0.63
TO	401	3/4C	C	MYRISTICACEAE	Virola	calophylla	44.7	22.0	2.22	0.09	0.71
TO	402	3/4C	C	FLACOURTIACEAE	Carpotroche	longifolia	2.4	3.0	2.28	0.14	0.78
TO	403	3/4C	C	FABACEAE	Inga		20.7	13.0	3.47	0.15	0.82
TO	404	3/4C	C	MORACEAE	Brosimum	utile	5.5	6.0	2.10	0.11	0.99
TO	405	3/4C	C	FLACOURTIACEAE	Banara		3.8	5.6	2.27	0.10	0.67
TA	1	1F	N0	BURSERACEAE	Tetragastris	panamensis	21.1	14.5	1.76	0.08	0.80
TA	2	1F	N0	BIXACEAE	Bixa	arborea	18.5	13.5	3.00	0.13	1.05
TA	3	1F	N0	FABACEAE			6.4	8.3	3.22	0.14	0.82
TA	4	1F	N0	MORACEAE	Helicostylis	tomentosa	10.8	12.0	2.47	0.11	1.27
TA	5	1F	N0	MYRISTICACEAE	Virola		5.1	7.4	2.74	0.11	0.82
TA	21	3F	NP0	EUPHORBIACEAE	Conceveiba	guianensis	9.5	12.2	2.05	0.13	0.84
TA	22	3F	NP0	FABACEAE			16.6	15.8	1.83	0.07	0.55
TA	23	3F	NP0	LECYTHIDACEAE			10.7	11.0	4.34	0.18	0.73
TA	24	3F	NP0	MORACEAE	Helicostylis	tomentosa	8.9	11.0	2.90	0.10	1.28
TA	25	3F	NP0	BOMBACACEAE	Quararibea	witti	4.8	7.0	2.72	0.11	0.89
TA	41	5F	P0	MELIACEAE	Trichilia	sp	30.0	18.5	1.91	0.08	0.65
TA	42	5F	P0	MYRISTICACEAE	Iryanthera		6.5	4.6	1.95	0.10	0.83
TA	43	5F	P0	LAURACEAE			7.8	10.9	2.03	0.07	0.44
TA	44	5F	P0				3.2	4.2	2.92	0.13	1.02
TA	45	5F	P0	FABACEAE	Tachigalli	poliphylla	21.3	19.0	2.67	0.11	0.79
TA	27	3/4C	C				35.0	24.5	3.08	0.14	0.82
TA	28	3/4C	C	SIPARUNACEAE	Siparuna	decipiens	9.0	9.0	2.55	0.10	2.09
TA	29	3/4C	C	CLUSIACEAE	Calophyllum	brasiliensis	7.5	8.0	2.21	0.08	1.47
TA	30	3/4C	C	FABACEAE			6.0	8.0	1.78	0.07	0.74

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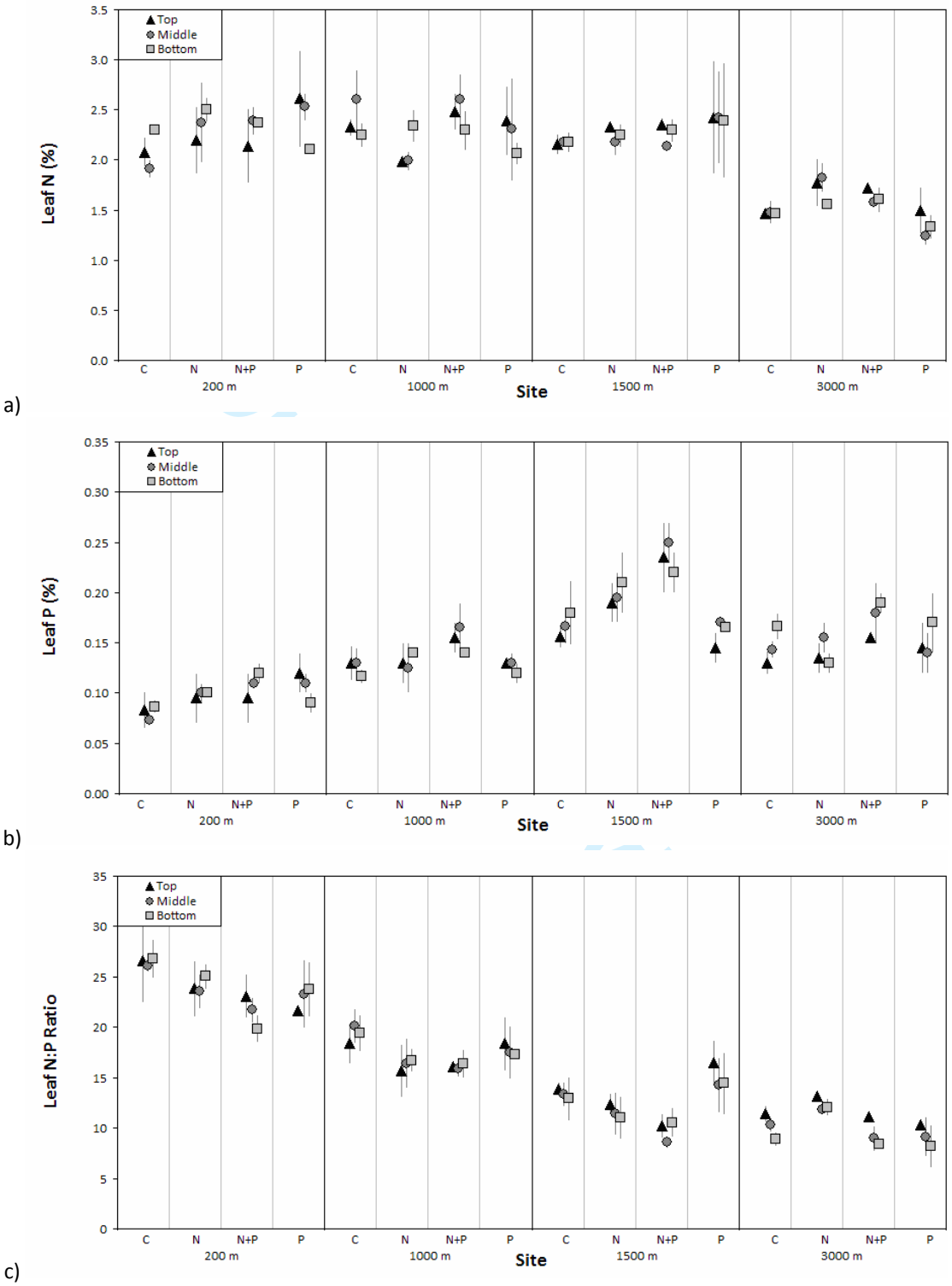

784 **Fig. S1. a) Leaf nitrogen (N), b) leaf phosphorus (P), and c) leaf N:P ratio from three**
785 **canopy heights (top, middle, and bottom) for all four sites (200 m, 1000 m, 1500 m, and**
786 **3000 m) and all four treatments (control, N, N+P, and P) in 2008 as mean ± SE.**

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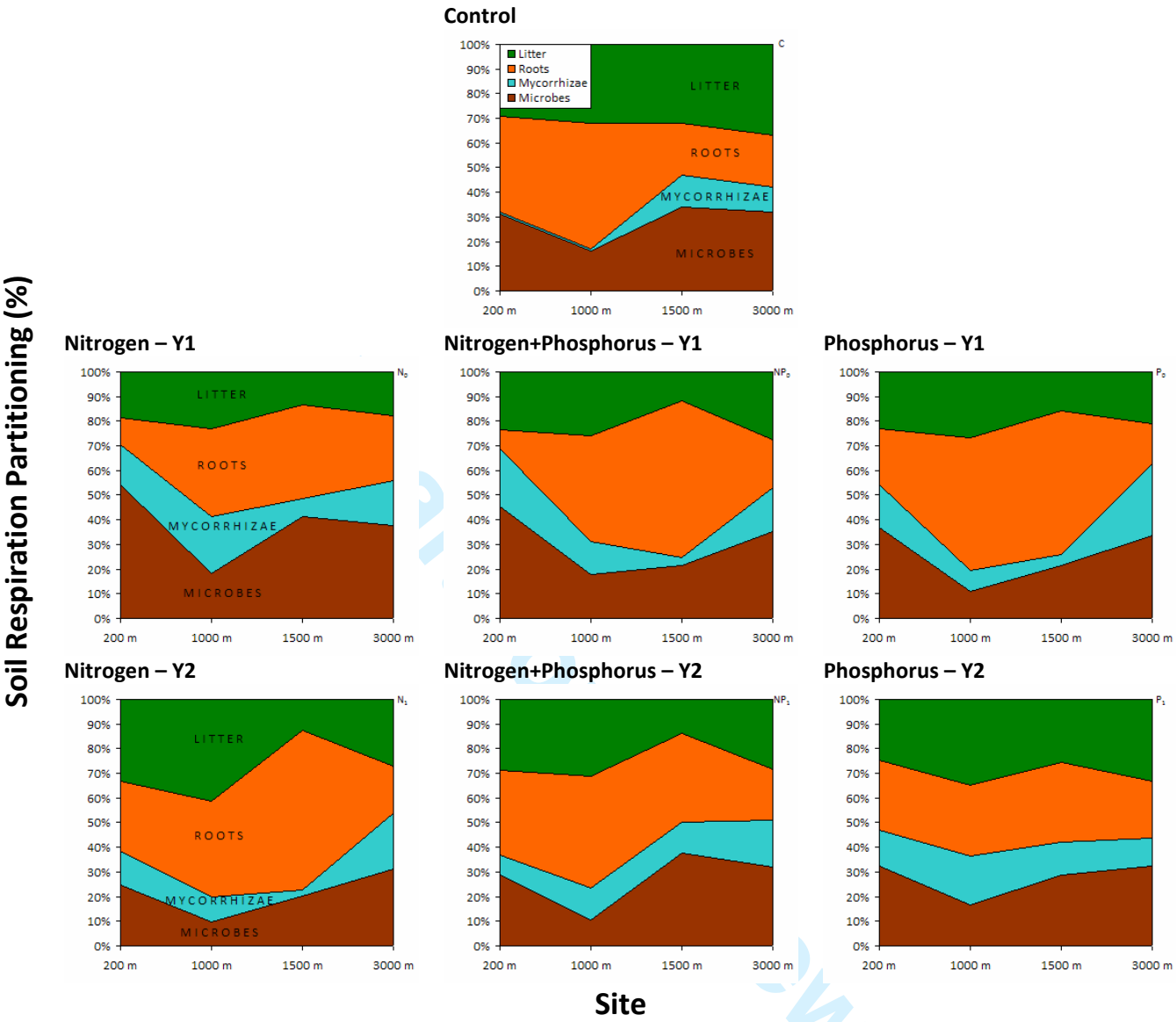

788 **Fig. S2. Soil respiration contribution for control and fertilized sub-plots from litter, roots,**
789 **mycorrhizae and microbes in 2009. The top three (Y1) panels are from the sub-plots that**
790 **received fertilization starting in the first year (2007), and the bottom three (Y2) panels are**
791 **from the sub-plots that received fertilization starting in the second year (2008).**