

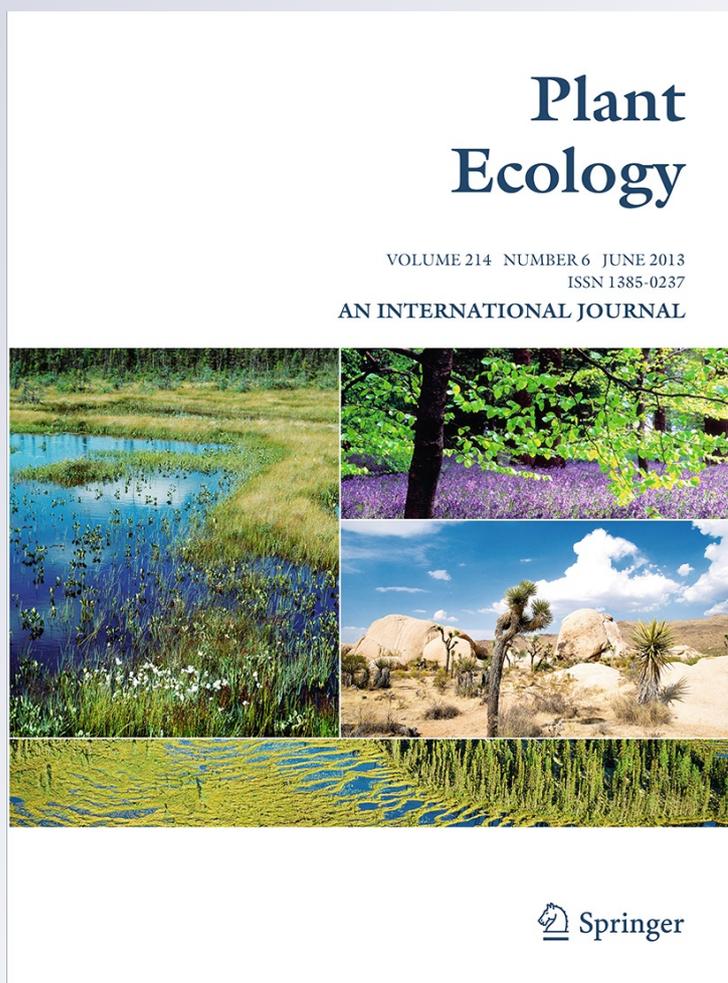
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Fine root dynamics in relation to nutrients in oligotrophic Bornean rain forest soils

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Abstract The fine roots of plants are key structures enabling soil resource acquisition, yet our understanding of their dynamics and the factors governing them is still underdeveloped, especially in tropical forests. We evaluated whether Bornean tree communities on soils with contrasting resource availability display different soil resource uptake strategies, based on their fine root properties and dynamics, and related responses of fine roots to the availability of multiple nutrients. Using root cores and ingrowth cores, we quantified variation in community-level fine root properties (biomass, length, and area) and their growth rates, biomass turnover rate, and specific root length (SRL) between clay and sandy loam soils, on which tree community composition differs dramatically. We found that standing fine root biomass and biomass, length, and area growth were higher in sandy loam, the soil type that is better-drained, coarser-textured, and less fertile for most nutrients. In clay SRL was significantly greater, and turnover tended

to be faster, than in sandy loam. Across both soils, greater supplies of K^+ , NH_4^+ , and PO_4^{3-} were associated with greater standing biomass and growth rates of fine roots, suggesting foraging for these nutrients. Our data support the hypothesis that the sandy loam tree community achieves fine root absorptive area through faster growth and greater investment on a mass basis, whereas trees on clay achieve a similar standing absorptive area through slower growth of less-dense fine root tissues. Furthermore, our results suggest colimitation by multiple nutrients, which may enhance tree species coexistence through increased dimensionality of soil-resource niches.

Keywords Fine root growth rate · Fine root biomass · Malaysia · Soil nutrient supply rate · Tropical forest

Introduction

As the principal structures involved in water and nutrient acquisition, fine roots influence tree growth and survival, and, hence, forest community structure (Bloom et al. 1985). Fine roots also play critical roles in biogeochemical processes and primary production (Nadelhoffer and Raich 1992; Silver et al. 2005). Therefore, an ability to make predictions about fine root dynamics and the factors governing them is fundamental to understanding plant-soil interactions and their community- and ecosystem-level consequences (Wardle 2002).

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Resource acquisition from soils is mediated by both physiological and morphological characteristics of roots. However, plant functional traits related to root morphology and biomass allocation to roots, are considered to be key determinants of uptake in soils typical of natural forests (Aerts 1999; Aerts and Chapin 2000). Given the biomass that an individual allocates to roots, how this biomass is distributed may vary depending on characteristics such as the growth (production) rate, longevity, and tissue density of roots (Robinson 1994; Ostonen et al. 2007; Hodge 2009). These root characteristics vary in relation to both environmental resource-availability and the species' ecological strategy (e.g., stress tolerance versus exploitative competitive ability; Bloom et al. 1985; Eissenstat and Yanai 1997; Kozłowski and Pallardy 2002), and together they determine the standing biomass of roots at the forest-stand scale.

Deficits in water and nutrients generally promote increased belowground investment (Bloom et al. 1985; Kozłowski and Pallardy 2002; Hodge 2009), which can increase the surface area of fine roots for nutrient absorption. Greater standing biomass and biomass growth of fine roots are associated with lower soil moisture and nutrient availabilities, particularly for nitrogen and phosphorus (Ostertag 2001; Yavitt and Wright 2001; Lima et al. 2010), although recent evidence also suggests a key role for base cations (Tripler et al. 2006; Yavitt et al. 2011) and potential colimitation by multiple nutrients (Wright et al. 2011). However, the availabilities of above- and belowground resources often vary in opposition to each other in forests, as light levels below the canopy are generally lower on moister, more fertile compared to resource-limited soil types (Coomes and Grubb 2000; Russo et al. 2012), likely due to complex feedbacks associated with reduced allocation to roots versus to shoots and increased competition for light (Tilman 1988; Aerts 1999; Coomes et al. 2009).

Greater belowground absorptive surface area can be achieved with faster growth rates or longer longevity of fine roots, which together determine the turnover rate. If nutrients are depleted quickly in the rhizosphere or nutrient supply rates are variable in space and time, then faster fine root turnover would enable a more dynamic response to changing nutrient availability (Hodge 2009). Fine roots with higher specific root length (SRL, root length per unit mass), enable greater absorptive area per unit biomass

invested, potentially enabling faster turnover rates if higher SRL is associated with faster growth or shorter longevity of fine roots (Aerts and Chapin 2000; Ostonen et al. 2007; Metcalfe et al. 2008). Trees growing on resource-depleted soils are predicted to have lower SRL and longer-lived roots than those on soils with greater resource availability (Chapin et al. 1993). If so, then, given the faster growth rates expected to enhance resource uptake, standing fine root biomass should be greater on resource-poor compared to resource-rich soils, although standing fine root length, area, and turnover may not differ. Alternatively, trees growing on depleted soils may facilitate resource acquisition through increased SRL, and potentially decreased longevity, of fine roots, which may lead to no differences in standing biomass, but greater standing length, area, and turnover of fine roots on resource-poor versus resource-rich soil types.

Our objectives were to evaluate whether tropical tree communities growing on soils with contrasting resource availability have different soil resource uptake strategies, as indicated by their fine root properties and dynamics, and to quantify the responses of fine roots to the availability of multiple soil nutrients. Specifically, we contrasted stand-level properties (biomass, length, area, and SRL) and growth and turnover rates of fine roots between clay and sandy loam soils underlying mixed dipterocarp forest in Borneo. The clay is finer-textured, shallower, derived from shale, and poorly drained, but with greater availability of most nutrients, both total and exchangeable, than sandy loam, which is coarser, deeper, sandstone-derived, well-drained, and more nutrient-depleted (Table 1; Baillie et al. 2006). Tree species' composition of each soil type varies significantly and is dominated by soil specialists (Fig. 1; Lee et al. 2002b; Davies et al. 2005), which differ in trunk diameter growth and mortality rates (Russo et al. 2005) and leaf and wood functional traits (Russo et al. 2010; Katabuchi et al. 2012; SE Russo, unpub. data). Although the overlying tree community clearly responds to the difference in resource availability of these contrasting soils (Fig. 1), we sought to move beyond the dichotomy of resource-rich versus poor soil types (*sensu* Ostertag 2001) and therefore quantified covariation of fine root properties and their growth rates with supply rates of nutrients to identify limiting nutrients and the potential for nutrient colimitation. We predicted that

Table 1 Properties of sandy loam and clay soil types underlying mixed dipterocarp forest at Lambir Hills National Park, Borneo

Soil property	Sandy loam	Clay
Soil texture		
% Sand*	67.4	39.4
% Silt*	19.5	35.4
% Clay*	13.1	25.2
Bulk density (g/cm ³)*	0.83	0.95
Soil chemistry		
% Organic C*	1.90	1.49
% N	0.14	0.14
C:N*	14.2	10.6
Exch. P (mg/kg)	2.52	2.30
Exch. Ca (mg/kg)*	10.8	61.0
Exch. Mg (mg/kg)*	21.5	67.1
Exch. K (mg/kg)	37.0	47.8
Total P (mg/kg)*	83	151
Total Ca (mg/kg)*	19	65
Total Mg (mg/kg)*	546	1398
Total K (mg/kg)*	2342	7481

Mean values for each property are from Palmiotto (1998) based on 42 sandy loam and 36 clay samples (0–15 cm depth)

Exch. exchangeable

* Properties with statistically significant differences between soil types

(1) the growth rates of fine root biomass, length, and area would be greater in sandy loam, compared with clay, due to its reduced nutrient and water availabilities, (2) fine roots in sandy loam would have lower SRL and slower turnover rate, in parallel to the greater wood densities, lower specific leaf areas, and longer leaf lifespans of sandy loam specialists (Katabuchi et al. 2012; SE Russo, unpub. data), (3) as a result of predictions one and two, standing fine root biomass would be greater in sandy loam than clay, (4) due to foraging for nutrients, biomass, length, and area growth of fine roots would be greater in locations with larger nutrient supply rates, and (5) that inorganic phosphorus would be the most important limiting nutrient, as is widely true of tropical soils (Vitousek and Sanford 1986; Tanner et al. 1998). Given the difficulties associated with estimating net primary production and turnover rates of fine roots, our focus was on comparisons between soil types in relation to nutrient supply rates.

Methods

Study site

This study was conducted at Lambir Hills National Park (4°11' N, 114°01' E), a 6800 ha lowland mixed dipterocarp forest reserve in Northwest Borneo in Sarawak, Malaysia. The climate is aseasonal with an average of >100 mm of rainfall per month, totaling ca. 3000 mm of rainfall annually (Watson 1985). The soil structure and geomorphology at Lambir have been previously described (Baillie et al. 2006; Tan et al. 2009) and are classified as typic and inceptic hapludults and dystrodepts. They range from poorly drained, relatively nutrient-rich, fine-textured shale-derived clay soils with little surface humus to highly drained, nutrient-poor, coarse-textured, sandstone-derived sandy loam soils with up to 10 cm of surface humus (Table 1). The sandy loam soil is deeper, with saprolite at 80–220 cm versus 50–150 cm in clay, and no visible traces of podsolization (Baillie et al. 2006). It is also better-drained and has significantly lower volumetric water content throughout the year compared to clay (Russo et al. 2010). Understorey light levels are lower on clay, relative to sandy loam (Russo et al. 2012).

Root cores

We used root cores and ingrowth cores (Raich et al. 1994; Vogt et al. 1998) to estimate standing fine root and fine root growth parameters at the forest stand scale in sandy loam and clay. Fourteen plots in clay and sandy loam were located at randomly selected 20 m by 20 m coordinates (but with little incline) in the 52 ha forest research plot at Lambir (Lee et al. 2002a). Portions of some plots were destroyed by foraging wild pigs, reducing sample sizes (root core plots: $n = 11$ in each soil type; ingrowth core plots: $n = 13$ in clay and $n = 11$ in sandy loam). We estimated (1) standing fine root properties (biomass, length, and area) using root cores ($n = 4$ cores per plot) and (2) growth rates in these root properties using ingrowth cores ($n = 6$ – 14 cores per plot). Root ingrowth cores were placed at 1 m intervals along a 15 m transect within the plot, and the cores for standing root properties were sampled haphazardly within 5 m of the ingrowth core transect.

For standing fine root properties, we removed a 3 cm diameter and 10 cm deep (70.69 cm³) core of

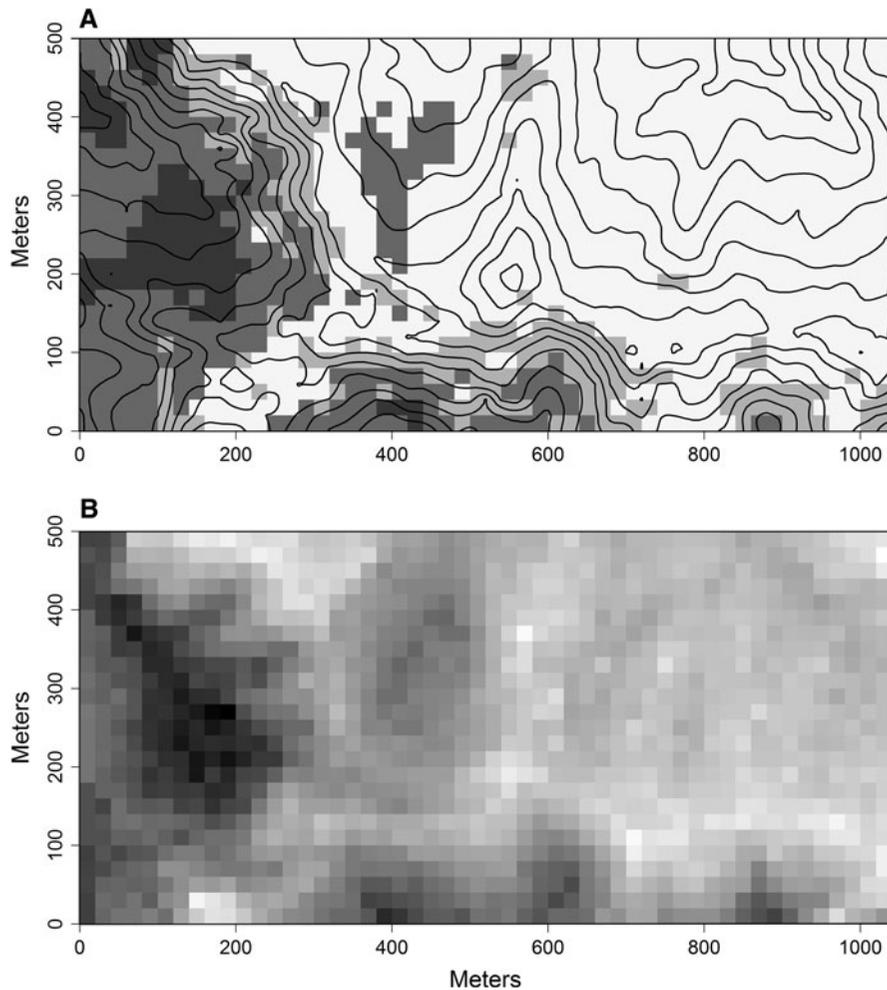


Fig. 1 **a** Four soil types (sandy loam, *white*; loam, *light gray*; fine loam, *gray*; clay, *dark gray*) along an edaphic gradient underlying mixed dipterocarp forest in Borneo, as defined by Davies et al. (2005). Sandy loam and clay represent the extremes of the edaphic gradient and were the focus of this study. **b** Variation in tree species composition closely mirroring the edaphic gradient in **a**. The first component of a non-metric multi-dimensional scaling (NMDS; Legendre and Legendre

1998) analysis is plotted, with colors scaled to the value of the component. NMDS was performed with the 2004 census data from the Lambir Center for Tropical Forest Science plot using all trees alive at the time of the census. Bray-Curtis dissimilarity indices were estimated between pairs of 20 × 20 m quadrats, and NMDS was performed based on the matrix of dissimilarity indices using the *vegan* package (Oksanen et al. 2011) in the statistical package, R (R Core Development Team 2011)

soil, and for ingrowth cores, we removed a 5 cm diameter and 10 cm deep core (196.35 cm³) of soil, after first removing the litter layer. Each ingrowth core was placed in a plastic bowl, and roots were removed by hand with forceps for 20 min. The root-free soil was repacked into the original location to a similar bulk density. After 6–8 month, cores 3 cm in diameter and 10 cm deep, centered on the ingrowth core location, were extracted. A 6–7 month period was used to ensure adequate time for roots to grow to the core–edge and to measure fine root growth within the

core (Vogt et al. 1998). This is a longer period than employed in some ingrowth core studies in the tropics (e.g., Cuevas and Medina 1988). However, in slower-growing forests colonization of cores can take 6–12 months (Vogt et al. 1998), and aboveground trunk diameter growth of trees at Lambir is slower than in many tropical forests (Condit et al. 2006). We recognize that there could have been root death and un-accounted for root turnover, and so our root growth estimates are likely minimum values. We lack information on the phenology of fine root growth at

Lambir. However, Lambir is an ever-wet forest (no month with rainfall < 100 mm), and both soil types experience the same rainfall regime, as they occur less than several hundred meters from each other (Fig. 1). The August–March study period spans both drier and wetter times of year (Palmiotto 1998), and thus our study period encompasses when fine root growth would have likely occurred. Although widely used, the ingrowth core method has limitations, including assuming that growth into a homogenized, root-free medium is a good estimate of the growth that would naturally occur in a more competitive, non-homogenized region (Vogt et al. 1998) and that root death during the incubation period is minimal (Majdi et al. 2005). To mitigate such effects, we used the same soil as was removed from that location to repack the ingrowth core, and, as much as possible, we repacked the soil to match the bulk density of the surrounding soil and prevent discontinuities between the repacked and surrounding soil. Our methods were guided by the goal of our study, which was to infer differences in the fine root growth rates between soil types and with respect to nutrient supplies, not to estimate annual production of fine roots. Our within-plot replication for ingrowth cores was substantially larger than for cores to estimate standing properties, which should reduce the effect of variation between cores on these inferences.

Harvested cores were soaked in water; then the mixture was poured through a series of sieves with a mesh size of ca. 1 mm. Live roots (as judged by visual inspection) <2 mm in diameter were removed from fragmented organic matter and other debris for 15 min by hand with forceps and a dissecting microscope at 10× magnification. Fifteen minutes was sufficient for sorting even from cores with the greatest amount of biomass. A digital image of the fresh roots from each core was created using a scanner (CanoScan LiDE 100, Canon Ltd.; 600 dots per inch). Images were analyzed using WinRhizo software (v. 5A Regent Instruments) to estimate total fine root length and surface area (area) in each core. Fine roots were dried at 60° C for >72 h and weighed. Biomass, length, and area of fine roots in each core were estimated as the total dry mass (mg), fresh length (mm), and fresh area (mm²) of roots, respectively. To estimate growth rates, root properties were quantified in each ingrowth core then divided by the fractional number of months the core was in the field. Thus, these mean monthly

estimates of fine root growth average over any variation in growth occurring during this time. Root parameters were expressed as a root density (per cm³ soil volume). Specific root length (SRL, m/g) was estimated separately for both standing biomass cores and ingrowth cores as the total fresh length/total dry mass of fine roots in a core.

Nutrient supply rates

We quantified nutrient supply rates using anion and cation exchange resins, which are considered good indicators of nutrient supply rates to plant roots (Robertson et al. 1999). Three grams (dry mass) of ion exchange resins (DOWEX 50w × 8–100 and DOWEX 1 × 8–100 (Cl⁻), Sigma Aldrich) were placed in bags made of nylon stocking material. Supply rates of inorganic phosphate (PO₄⁻³), base cations (calcium, Ca²⁺; potassium, K⁺; magnesium, Mg²⁺), and ammonium (NH₄⁺) and nitrate (NO₃⁻) were quantified with bags containing anion, cation, and a mixture of anion/cation resins, respectively. Anion resin bags were shaken in 0.5 M NaHCO₃ baths then rinsed with distilled, de-ionized (DI) water to exchange Cl⁻ with HCO₃⁻; other resin bags were washed with 0.5 M NaCl to exchange H⁺ for Na⁺ (Lajtha 1988). Three sets of resin bags (one bag per bag type in a set) were buried in soil 10 cm deep in each plot (*n* = 39 and 33 per bag type for clay and sandy loam, respectively). Sets of resin bags were buried >5 m from each other at haphazard locations within 5 m of the transect along which root cores were placed, avoiding areas disturbed from foraging wild pigs and fallen or uprooted trees. After 5 week, bags were removed, rinsed with DI water; resins were extracted by shaking overnight in an extractant solution (PO₄⁻³:0.5 M HCl; Ca²⁺, K⁺, and Mg²⁺:2 M HCl; NH₄⁺ and NO₃⁻:1 M KCl) (Robertson et al. 1999). Phosphate, ammonium, and nitrate concentrations were determined by colorimetry (Ecosystem Analysis Laboratory, University of Nebraska, USA; Lachat Quick Chem 8500; Lachat instruments). Concentrations of cations were determined using Inductively Coupled Plasma Emission Spectroscopy (Agriculture Diagnostic Laboratory, University of Arkansas, USA; ARCOS EOP; SPECTRO Analytical Instruments, Inc.). Supply rates were expressed as nutrient concentration in the solution per dry mass of resin per month burial time.

Statistical analysis

Differences between soil types (clay or sandy loam) in nutrient supply rates were tested with Student's *t*-tests, using plot-level mean rates and assuming unequal variances. Pairwise relationships between nutrient supply rates across plots were estimated using Pearson correlation tests. Estimates of fine root biomass turnover rate (month^{-1}) were calculated according to Gill and Jackson (2000) using a commonly used model (Dahlman and Kucera 1965), as mean fine root biomass growth per month divided by the maximum fine root biomass for each plot. Differences between soil types were tested separately for each response variable (standing fine root properties, their growth rates, biomass turnover rate, and SRL) using a linear mixed-effects model with a normal error distribution using the *nlme* package (Pinheiro et al. 2012), with soil type as a fixed effect and a random effect for core nested within plot. Variation across plots in the response variables due to soil type and nutrient supply rate were tested separately for each nutrient and root parameter using plot-level mean values in linear fixed-effects models. Analyses were performed in the statistical package, *R* v. 2.14.0 (R Core Development Team 2011). Square-root or logarithmic transformations were used when necessary to improve normality.

Results

Soil-related differences in nutrient supply rates

Clay and sandy loam soils differed significantly in the supply rates of most nutrients in the upper 10 cm of soil (Fig. 2). Clay provided significantly greater supply rates of NO_3^- ($t = 6.806$, $df = 18.9$, $p < 0.001$), Ca^{2+} ($t = 3.006$, $df = 16.0$, $p = 0.008$), and Mg^{2+} ($t = 3.496$, $df = 20.2$, $p = 0.002$), but not of NH_4^+ ($t = -1.595$, $df = 19.1$, $p = 0.127$), nor K^+ ($t = -1.752$, $df = 18.3$, $p = 0.097$), which showed no significant differences between soil types. The supply rate of PO_4^{3-} was greater in sandy loam than clay ($t = -4.222$, $df = 17.0$, $p < 0.001$). Average supply rates in plots of some, but not all, nutrients were correlated with each other across

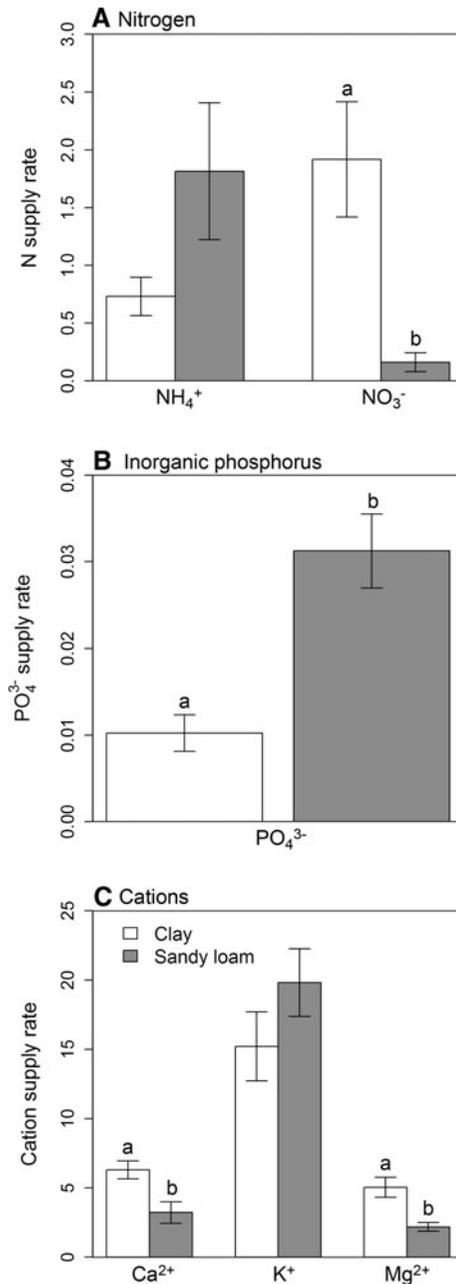


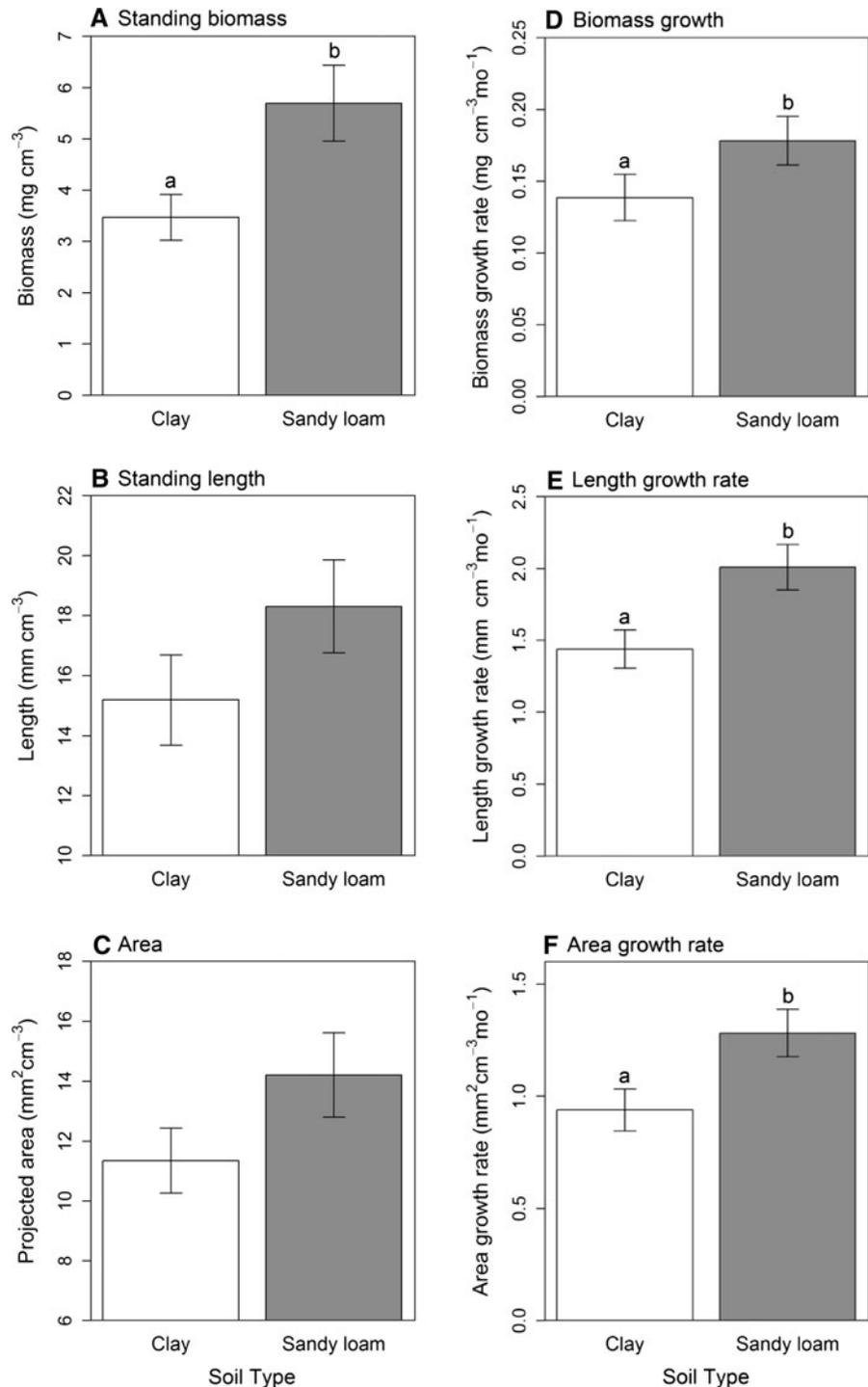
Fig. 2 Differences between clay and sandy loam soils underlying Bornean rain forest in their nutrient supply rates (mg/L extractant/g resin/mo): **a** ammonium (NH_4^+) and nitrate (NO_3^-), **b** inorganic phosphorus (PO_4^{3-}), **c** potassium (K^+), calcium (Ca^{2+}), and magnesium (Mg^{2+}). Across-plot means and standard errors are shown ($n = 13$ and 11 plots for clay and sandy loam, respectively). Different letters indicate statistically significant differences ($p < 0.05$)

soil types (Table S1). Supply rates of NO_3^- were significantly correlated with those of Ca^{2+} , Mg^{2+} , and PO_4^{3-} . Supply rates of K^+ and PO_4^{3-} and of Ca^{2+} and Mg^{2+} were significantly correlated with each other.

Soil-related differences in root parameters

Clay and sandy loam soils differed in some standing fine root parameters (Fig. 3a–c). Standing root biomass was

Fig. 3 Standing fine root properties (a–c) and their growth rates (d–f) in clay and sandy loam soils underlying Bornean rain forest: (a, d) biomass, (b, e) length, (c, f) projected area. All parameters are reported per cm^3 soil. Across-plot means and standard errors are shown ($n = 11$ plots per soil type for standing parameters; $n = 13$ and 11 plots for clay and sandy loam, respectively, for growth parameters). Different letters indicate statistically significant differences ($p < 0.05$)



significantly greater in sandy loam than clay ($F_{1,20} = 6.905, p = 0.016$; Fig. 3a). Root length and area tended to be higher in sandy loam, but the differences between soil types were not significant (length: $F_{1,20} = 2.167, p = 0.157$; area: $F_{1,20} = 2.443, p = 0.134$; Fig. 3b–c). Growth rates in root biomass, length, and area were faster in sandy loam than clay (biomass: $F_{1,22} = 4.766, p = 0.040$; length: $F_{1,22} = 8.231, p = 0.009$; area: $F_{1,22} = 6.428, p = 0.019$; Fig. 3d–f).

Root biomass turnover rates tended to be faster in clay than sandy loam (mean \pm one standard error: 0.030 ± 0.006 and $0.022 \pm 0.004 \text{ month}^{-1}$, respectively), although this difference was not statistically significant ($F_{1,20} = 1.173, p = 0.292$). Tissues of fine roots in clay from standing root cores were significantly less dense than in sandy loam, as indicated by the greater SRL in clay ($F_{1,20} = 7.908, p = 0.011$; Fig. 4a); however, there was no significant between-soil difference in SRL of fine roots from ingrowth cores ($F_{1,22} = 0.082, p = 0.777$; Fig. 4b).

Variation in root parameters with nutrient supply rates

In models testing the relationships of standing fine root biomass, length, and area with nutrient supply rates,

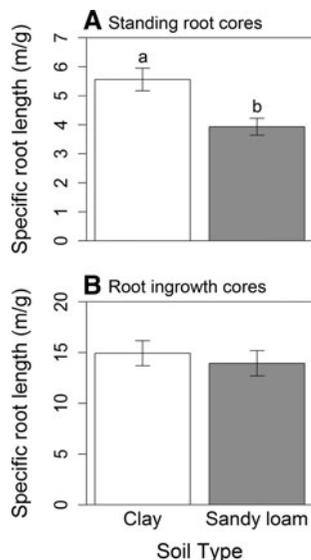


Fig. 4 Specific length (m/g) of fine roots in clay and sandy loam soils underlying Bornean rain forest: **a** root cores ($n = 11$ plots per soil type) and **b** root ingrowth cores ($n = 13$ and 11 plots for clay and sandy loam, respectively). Across-plot means and standard errors are shown. Different letters indicate statistically significant differences ($p < 0.05$)

there were no significant interactions between any nutrient supply rate and soil type. Based on models including only main effects, some nutrient supply rates showed significant variation with root parameters (Table S2). Standing root biomass increased significantly with the supply rate of PO_4^{3-} (Fig. 5). With increasing K^+ supply rate, standing root biomass, length, and area increased significantly (Fig. 6; Table S2).

In models testing the relationships of growth rates in fine root biomass, length, and area with nutrient supply rates, there were no significant interactions between any nutrient supply rate and soil type. Growth rates in root biomass, length, and area increased with greater supply rates of NH_4^+ and PO_4^{3-} , but relationships were not always statistically significant (Table S3). Growth in root biomass was significantly faster with greater supply rates of PO_4^{3-} (Fig. 7a), but there were no statistically significant relationships with any other nutrient supply rate (Table S3). Growth in root length was significantly faster in plots with greater PO_4^{3-} supply rates (Fig. 7b), with marginally non-significant increases in length growth associated with greater supply rates of NH_4^+ and K^+ (Table S3). Growth rates in root area were significantly faster in plots with greater supply rates of PO_4^{3-} and NH_4^+ (Figs. 7c, S1). The faster growth rates in root area associated with greater supply rates of K^+ showed a marginally non-significant relationship (Table S3). Greater supply rates of Mg^{2+} were associated with significant reductions in growth rates of root length and area (Fig. S2).

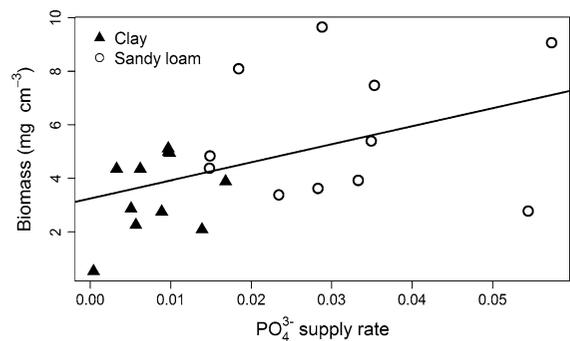


Fig. 5 Fine root biomass (g cm^{-3} soil) versus PO_4^{3-} supply rate ($\text{mg P/L extract/g resin/month}$) in clay and sandy loam soils underlying Bornean rain forest. The line is the least-squares regression line based on a statistically significant relationship with supply rate in a linear model (Table S2). Triangles and circles are mean values for clay and sandy loam plots, respectively ($n = 11$ plots per soil type)

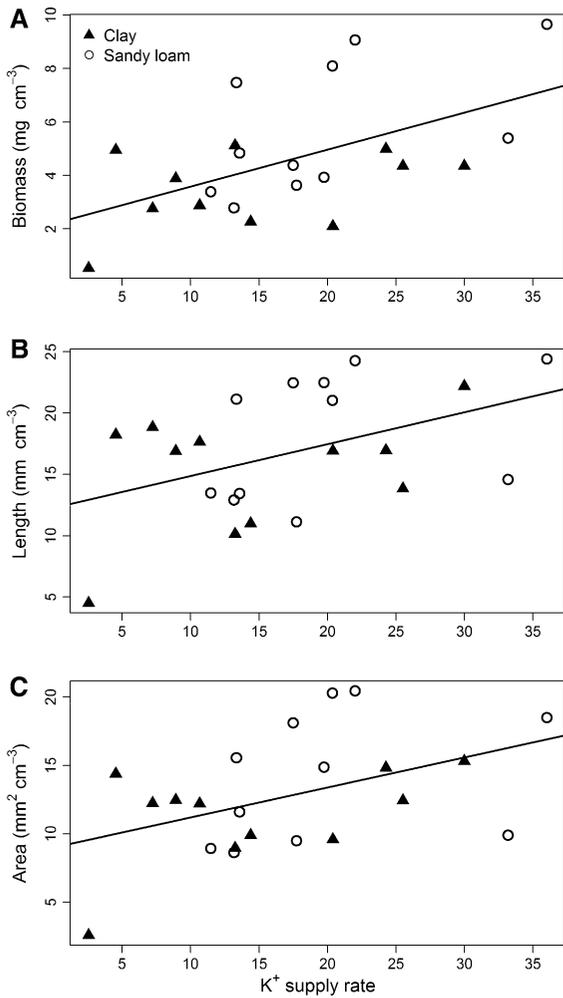


Fig. 6 Fine root **a** biomass, **b** length, and **c** area versus soil K^+ supply rate (mg K/L extract/g resin/month) in clay and sandy loam soils underlying Bornean rain forest. Root parameters are reported per cm^3 soil. The *line* is the least-squares regression line based on a statistically significant relationship with supply rate in a linear model (Table S2). *Triangles* and *circles* are mean values for clay and sandy loam plots, respectively ($n = 11$ plots per soil type)

In models testing the relationships of root biomass turnover rate with nutrient supply rates, there were no significant interactions between any nutrient supply rate and soil type. Root biomass turnover rate varied significantly with the supply rates of K^+ , having decreased turnover with increasing supply (K^+ : $F_{1,19} = 7.957$, $p = 0.010$; Fig. S3a). The slower root turnover with increased K^+ supply rate was due to greater standing biomass of roots in plots with greater supplies of K^+ (Fig. 6a), which generates lower

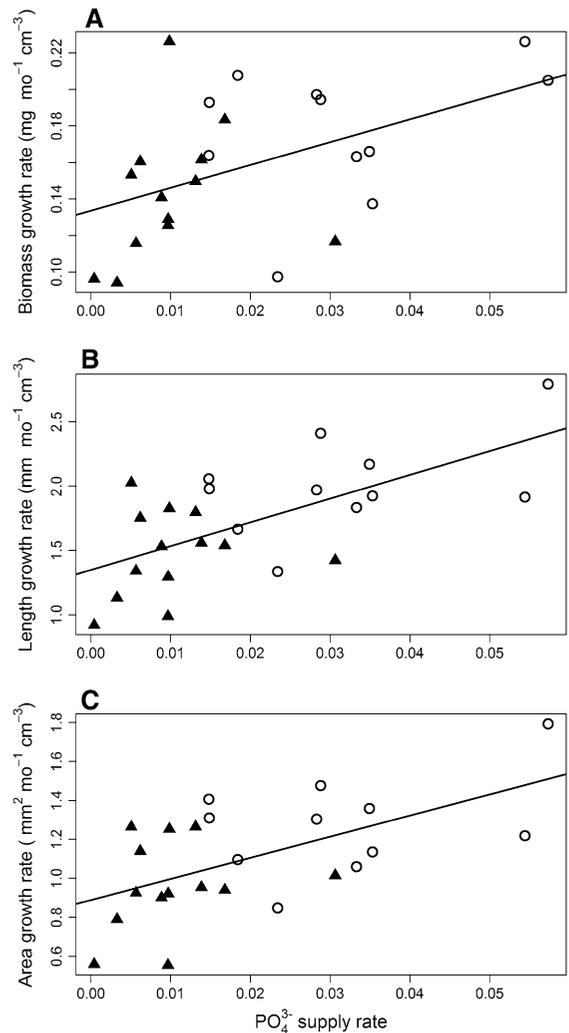


Fig. 7 Fine root **a** length and **b** area growth rates versus PO_4^{3-} supply rate (mg P/L extract/g resin/month) in clay and sandy loam soils underlying Bornean rain forest. Root parameters are reported per cm^3 soil. The *line* is the least-squares regression line based on a statistically significant relationship with supply rate in a linear model (Table S3). *Triangles* and *circles* are mean values for clay and sandy loam plots, respectively ($n = 13$ and 11 plots for clay and sandy loam, respectively)

turnover estimates. Biomass turnover and Mg^{2+} supply rate were also negatively correlated ($r = -0.44$, $df = 20$, $p = 0.042$; Fig. S3b), but in contrast to K^+ , the slower turnover was due to the significantly slower root growth rates associated with greater Mg^{2+} supply rate (Fig. S2). However, after accounting for soil type in a linear model, there was no significant relationship between turnover and Mg^{2+} ($F_{1,19} = 2.645$, $p = 0.120$). In this model, root turnover was

significantly faster in clay than sandy loam soil ($F_{1,19} = 7.032$, $p = 0.016$; Fig. S3b), which had lower Mg^{2+} supply rates (Fig. 2c).

Discussion

Soil-related differences in fine root properties: implications for resource acquisition strategies

In this Bornean rain forest, standing fine root properties and their growth rates varied strongly between soil types at the community-level. Most standing fine root and growth rate parameters were higher in sandy loam soil, which is considered the more resource-limited soil type (Baillie et al. 2006; Russo et al. 2010; Tan et al. 2009). Standing biomass of fine roots in clay was similar to published values for more fertile Panamanian soils (Wright et al. 2011), but in sandy loam, biomass was considerably higher. Consistent with our findings, fine root mass ratios of seedlings at Lambir were greater on sandy loam than clay (Palmiotto et al. 2004). Soils with lower resource availability are viewed as promoting investment in belowground organs, often resulting in greater standing biomass and faster growth rates of fine roots (Maycock and Congdon 2000; West et al. 2004; Espeleta and Clark 2007; Jimenez et al. 2009). The faster fine root growth rate in sandy loam than clay may reflect the reduced allocation to shoots and aboveground growth often found along gradients where competition shifts from light to soil resources (Tilman 1988; Palmiotto et al. 2004; Heineman et al. 2011; Poorter et al. 2012).

Compared with those on sandy loam, trees growing on clay had similar or significantly greater SRL, indicating that they achieved a greater absorptive area per unit tissue mass invested in fine roots. Similar differences in SRL have been found between clay and sandy soils in the Amazon (Metcalf et al. 2008). The difference we observed in SRL may explain why the standing biomass was significantly greater in sandy loam, but there was only a non-significant trend of greater standing length and area of fine roots. Our community-level data largely reflects soil specialists, as they dominate the basal area of their respective soil types. The lower SRL of fine roots in sandy loam is consistent with soil-related variation in traits of aboveground tissues, as sandy loam specialists have lower specific leaf area and higher wood density than

clay specialists (Katabuchi et al. 2012; SE Russo, unpub. data).

Our data support the hypothesis that trees growing on sandy loam and clay exhibit different ecological strategies of soil resource acquisition: trees on sandy loam achieve absorptive area through faster fine root growth and investing more in fine roots on a mass basis, whereas trees on clay achieve a similar standing absorptive area through slower growth of less-dense fine root tissues. An advantage of the higher-SRL strategy is that resource uptake can be increased while minimizing allocation of photosynthetically fixed carbon to roots (Eissenstat 2000). High-SRL roots may also be more dynamic, but whether trees on the two soils differ in turnover of fine roots is uncertain. Long life spans of fine roots are considered advantageous in soils with reduced nutrient and moisture availability because losses in tissue investment are limited, whereas faster turnover is viewed as beneficial in resource-rich, mesic soils (Eissenstat and Yanai 1997; Aerts and Chapin 2000; West et al. 2004). To the extent that above- and belowground functional traits of trees in this forest are coordinated (Ostertag 2001; Withington et al. 2006), trees on sandy loam should have longer-lived fine roots. We found weak evidence of faster turnover of fine roots in clay, but our growth and turnover rates may be underestimates, due to limitations of the ingrowth core method as described in the “Methods” Section.

The observed alternative strategies of trees growing on these contrasting soils result from the combined effects of differences between soil specialists in their average fine root properties and dynamics and in the ability of individual trees to plastically alter fine root properties and dynamics in response to spatial and temporal variation in resources. For example, SRL varies with fine root diameter, as well as soil moisture and other exogenous factors (Ostonen et al. 2007; Metcalfe et al. 2008; Hodge 2009). Because our data represent a snapshot, we cannot address plasticity in fine root properties and dynamics, but it is likely to be an important, yet poorly understood, component defining the soil resource acquisition strategies of tree species.

Variation in root parameters with nutrient supply rates: implications for nutrient co-limitation

Although sandy loam is considered to be the more resource-limited soil type at this site, we did not find that

supply rates of all nutrients were uniformly lower in sandy loam: supply rates of some nutrients were higher in clay, as expected, yet others showed no significant differences between soil types, and inorganic P was in significantly greater supply in sandy loam, although the P supply rates on both soils were low. Furthermore, we found that standing fine root properties and growth rates varied in relation to the supply rates of several nutrients, which together with the complex patterns of nutrient supply, suggests that the often-cited dichotomy between fertile and infertile soils is likely more complicated (Baillie et al. 1987; Ostertag 2001).

Fine roots are known to proliferate into nutrient-rich soil regions, conferring local competitive advantages (Robinson et al. 1999). Despite substantial unexplained variation in standing fine root properties and their growth rates, these variables responded to nutrient supplies in similar ways across soil types, covarying significantly with PO_4^{3-} , K^+ , and NH_4^+ . Phosphorus is widely found to be the primary limiting nutrient in the weathered and leached soils typical of warm tropical regions (Vitousek and Sanford 1986; Burslem et al. 1994; Tanner et al. 1998), but our results indicate that K^+ availability is also likely to affect tree growth in this forest. To the extent that nutrient-correlated fine root growth is an indication of limitation, our results suggest that multiple colimiting resources (Harpole et al. 2011; Condit et al. 2013) affect tree growth.

Although experimental fertilization often causes increased tissue concentrations of phosphorus, seedlings do not always exhibit a growth response (Burslem et al. 1995; Mirmanto et al. 1999; Palmiotto et al. 2004; Wright et al. 2011), suggesting colimitation by multiple nutrients and that co-occurring species are not necessarily limited by the same nutrients (Cuevas and Medina 1988). The significant relationships we found for fine root standing biomass and growth rates with PO_4^{3-} supply were primarily driven by greater PO_4^{3-} supply in sandy loam. In the Amazon, consistent with our results, greater standing biomass and biomass production of fine roots were found in sandier soil with higher PO_4^{3-} supply rates compared to more clay-rich soil (Jimenez et al. 2009). Our results are also consistent with previous research at Lambir showing reserve phosphorus as a significant correlate of tree species' edaphic distributions (Baillie et al. 1987). Trees in the Dipterocarpaceae, the

dominant family in this forest, are known to form associations with ectomycorrhizal fungi (Moyersoen 2006; Peay et al. 2009), which is likely to play an important role in the responses of fine roots to phosphorus.

Potassium supply rates did not vary significantly between soil types, yet there was a clear signal of increased standing fine root biomass, length, and area with greater K^+ supply rate. Although K^+ is derived from rock, is an abundant ion in plant cells, and plays a key role in many plant metabolic and growth functions (Marschner 1995), it has not been emphasized as an important limiting nutrient in forests (Tripler et al. 2006). Our results are consistent with a stand-level fertilization experiment in a Panamanian forest showing soil K^+ to increase seedling height growth and affect seedling root:shoot allocation and fine root turnover (Wright et al. 2011; Yavitt et al. 2011; Santiago et al. 2012). Our findings also suggest that nitrogen may not be a key limiting nutrient in this forest, as the only significant relationships were weak and influenced by three plots with large NH_4^+ supply. Nitrogen may be important when simultaneously colimiting with phosphorus or potassium (Mirmanto et al. 1999; Wright et al. 2011; Santiago et al. 2012) or along successional gradients (Brearley 2011; Powers and Pérez-Aviles 2012).

Both soil types experience the same rainfall regime, but sandy loam is better-drained than clay and maintains lower volumetric water content throughout the year (Russo et al. 2010). In addition to greater nutrient supply rates, greater water availability is also often associated with faster fine root growth rates (Metcalf et al. 2008; Lima et al. 2010). It is therefore possible that, along with supplying more nutrients, the locations with faster fine root growth in our study may have also supplied greater moisture. We cannot rule out this possibility because we did not measure soil moisture during our study.

An unexpected finding was reduced fine root growth rates associated with greater Mg^{2+} supply. In sufficiently high concentrations, Mg^{2+} is known to inhibit root growth and is one of the metals responsible for toxicity of some ultramafic soils (Nagy and Proctor 1997). Our results suggest that locally high concentrations of soil Mg^{2+} may adversely affect tree growth, in accordance with previous work in Borneo demonstrating the importance of Mg^{2+} in determining forest composition (Baillie et al. 1987).

Conclusions

Our study of fine roots in contrasting soil types leads to several conclusions regarding the causes and consequences of variation in fine root dynamics in this Bornean rain forest. First, the tree communities on sandy loam and clay have different belowground resource acquisition strategies, defined in part by variation in SRL, growth rates, and turnover rates of fine roots. A more in-depth examination of these properties, especially turnover, and plasticity in them, is required to understand their relative importance in defining these alternative strategies. Insofar as our stand-level data reflect differences between tree species specializing on these soil types, we hypothesize that fine root properties and dynamics, and plasticity in them, are key components of the ecological strategies and resource economies that influence the distributions of tree species along the edaphic gradient in this Bornean forest. Second, we propose that multiple nutrients, rather than a single, dominant nutrient, may limit tree growth in this forest. Such nutrient co-limitation may act to maintain diversity by promoting coexistence of tree species through increased dimensionality of resource-based niches (Tilman 1982). Experimental tests of the synergistic effects of nutrients on fine root growth are required to further elucidate the range of possible fine root responses to multiple limiting nutrients, such as simultaneous or independent co-limitation (Harpole et al. 2011). Lastly, the observed variation in fine root properties and dynamics in relation to soil types and nutrient supply rates could significantly affect spatial and temporal patterns of carbon and nutrient dynamics in this forest.

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