Species-specific responses of foliar nutrients to long-term nitrogen and phosphorus additions in a lowland tropical forest

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Summary

1. The concentration, stoichiometry and resorption of nitrogen (N) and phosphorus (P) in plant leaves are often used as proxies of the availability of these growth-limiting nutrients, but the responses of these metrics to changes in nutrient availability remain largely untested for tropical forest trees.

2. We evaluated changes in N and P concentrations, N/P ratios and resorption for four common tree species after 13 years of factorial N and P additions in a lowland tropical forest in Panama.

3. Chronic P addition increased foliar P concentrations, decreased P resorption proficiency and decreased N/P ratios in three locally common eudicot tree species (*Alseis blackiana, Heisteria concinna, Tetragastris panamensis*). The increase in foliar P involved similar proportional increases in organic and inorganic P in two species and a disproportionately large increase in inorganic P in *A. blackiana*.

4. Nitrogen addition did not alter foliar N concentrations in any species, but did decrease N resorption proficiency in *H. concinna*.

5. A fourth species, the palm *Oenocarpus mapora*, demonstrated remarkably static foliar nutrient concentrations, responding only with a marginal decrease in P resorption proficiency under N plus P co-addition.

6. *Synthesis.* Collectively, these results suggest that adjustment of N/P ratios can be expected in eudicots exposed to elevated P, but foliar N appears to already be at optimal levels in these lowland rain forest tree species. The complexity of species-specific responses to altered nutrient availability highlights the difficulty in predicting future responses of tropical forest trees to a changing world.

Key-words: gigante fertilization experiment, luxury consumption, plant–soil interactions, resorption, stoichiometry

Introduction

The capacity of tropical forests to mitigate increasing atmospheric CO_2 concentrations through accelerated growth will depend in part upon their ability to meet increasing demand for growth-limiting mineral nutrients (Wright 2012; Cernusak *et al.* 2013; Reich & Hobbie 2013). Nutrient limitation of tree productivity is typically defined as an increase in some aspect of net primary productivity (stem growth, root growth, reproductive output, litterfall) following fertilization (Chapin, Vitousek & Vancleve 1986; Vitousek & Howarth 1991). However, only a handful of fertilization studies have been conducted in lowland tropical forests (Cleveland *et al.* 2011).

Nutrient limitation is therefore often inferred from measurements of foliar nutrients, including leaf-level nitrogen-to-phosphorus (N/P) ratios, resorption proficiency (the amount of nutrient remaining in senesced leaves) and resorption efficiency (ratio of nutrients resorbed relative to green leaf concentrations) (Field *et al.* 1992; Killingbeck 1996).

Foliar N/P ratios have been used to assess relative N or P limitation in agricultural systems (Vitousek & Howarth 1991) and in wild plants (Tessier & Raynal 2003; Güsewell 2004; Ågren 2008). In tropical forests, meta-analyses have confirmed that tropical forest trees have the highest foliar N/P values globally (Reich & Oleksyn 2004; Yuan & Chen 2009), which is assumed to reflect a greater degree of P limitation compared to temperate and boreal forests (Vitousek & Sanford 1986; McGroddy, Daufresne & Hedin 2004; Townsend *et al.* 2007). Changes in foliar or litterfall N/P ratios have also been used to detect changes in nutrient

limitation in relatively mature tropical forests (Davidson *et al.* 2007) and in temperate forests subjected to anthropogenic N deposition (Koerselman & Meuleman 1996; Hurd, Brach & Raynal 1998).

Uncertainty concerning the flexibility of foliar N/P ratios suggests that their response to changes in soil nutrient availability might be limited (Sterner & Elser 2002; Sistla & Schimel 2012). For instance, variability in the N/P ratios of individual species might be constrained phylogenetically, while locally adapted genotypes might also limit plasticity in foliar N/P ratios (Tessier & Raynal 2003; Elser *et al.* 2010; Ostertag 2010). Foliar N/P ratios might also be driven more by variation in P availability, irrespective of N availability, because plants store N mainly as structural amino acids and proteins (Chapin, Schulze & Mooney 1990), whereas P is also stored as relatively labile non-structural inorganic forms in leaf cytoplasm and vacuoles (Bieleski 1973). It is believed that N storage increases the risk of herbivory (Fine, Mesones & Coley 2004), although P and potassium (K) addition, but not N, increased leaf herbivory in the Gigante Fertilization Experiment (Santiago *et al.* 2012). In addition, a foliar N/P response to altered N and P availability is not necessarily expected if plant growth is limited by light, water or other mineral nutrients (Aerts & Chapin 2000; Wright, Reich & Westoby 2001; Townsend *et al.* 2011).

Foliar nutrient resorption, a mechanism by which plants can recycle nutrients internally, also varies with latitude. Tropical trees have lower N resorption and greater P resorption than temperate and boreal trees (Yuan & Chen 2009). However, there is marked variability in foliar nutrient resorption within plant communities (Hättenschwiler *et al.* 2008), particularly for P (Inagaki *et al.* 2011; Reed *et al.* 2012). This reflects the wide range in P availability and taxonomic diversity in tropical forests (Townsend *et al.* 2007; Vitousek *et al.* 2010; Alvarez-Clare, Mack & Brooks 2013) and genetic constraints on leaf P resorption proficiency (reviewed in McGroddy, Daufresne & Hedin 2004). As for total N concentration, leaf N resorption seems considerably less flexible than P resorption (McGroddy, Daufresne & Hedin 2004; Yuan & Chen 2009), perhaps because leaf N concentrations are more related to taxonomic lineage than local soil fertility (Townsend *et al.* 2007; Fyllas *et al.* 2009). In contrast, P resorption proficiency ranges from 0 to 90% (Aerts 1996; Killingbeck 1996; Kobe, Lepczyk & Iyer 2005) and usually increases where soil P availability decreases (Kobe, Lepczyk & Iyer 2005; Richardson, Allen & Doherty 2008; Hidaka & Kitayama 2011; Lambers *et al.* 2011). Taken together, these findings suggest that resorption efficiency and proficiency are greater where nutrients are most limiting and that there is greater flexibility in resorption of foliar P compared to foliar N.

Although patterns of leaf stoichiometry and resorption have been compared globally (Aerts 1996; Ågren 2008), data on tropical trees remain scarce and experimental evidence rarer still (McGroddy, Daufresne & Hedin 2004; Ostertag 2010; Reed *et al.* 2012). There is a particularly strong need to examine how mature tropical trees respond to experimentally altered soil fertility, given the complexity of nutrient limitation found in tropical forests (Cleveland *et al.* 2011; Townsend *et al.* 2011; Wright *et al.* 2011; Wurzburger *et al.* 2012), the uncertainty regarding their capacity to adjust to future environmental perturbation (Reed *et al.* 2012; Sistla & Schimel 2012; Wright 2012), and the variable relationships between resorption dynamics and fertilization (Aerts 1996; Vitousek 1998). Further, relatively few studies have examined whether individual foliar P fractions (i.e. inorganic vs. organic P) are more or less responsive to changes in soil nutrient availability than total P (Ostertag 2010; Hidaka & Kitayama 2011).

Here, we report foliar nutrient concentrations, resorption proficiency and resorption efficiency in four species of tropical trees growing in a long-term factorial N and P fertilization experiment in a mature lowland tropical rain forest. We predicted that all the four of the locally common tree species would exhibit (i) greater foliar accumulation of total P compared to N following addition of the respective nutrients, due to a physiological limitation to N storage in leaves; (ii) greater accumulation of inorganic P (P_i) relative to organic P (P_o) following P addition, because orthophosphate storage in vacuoles enables greater resorption during leaf senescence (Thomas, Montagu & Conroy 2006; Turnbull, Warren & Adams 2007); (iii) decreased resorption efficiency of both N and P under respective nutrient addition, because both nutrients influence an aspect of productivity (i.e. N influenced stem growth, whereas P increased litterfall) in the fertilization experiment (Wright *et al.* 2011); (iv) greater N resorption proficiency and decreased P resorption proficiency in response to P addition due to induction of greater relative N demand and a relaxation of P demands; and (v) greater P resorption proficiency and decreased N resorption proficiency in response to N addition, due to induction of greater relative P demand and a relaxation of N demand.

Materials and methods

THE GIGANTE FERTILIZATION EXPERIMENT

The Gigante Fertilization Experiment began in 1998 and is the longest running fertilization experiment in lowland tropical rain forest. In 1997, 36 40×40 m plots were established within a 38.4-ha plot (9°06′31″ N, 79°50′37″ W) of mature (>200 years old) secondary rain forest where all the canopy trees (>20 cm DBH) are mapped and identified to species (Yavitt *et al.* 2009; Wright *et al.* 2011). The site has a 7% slope, a mean annual temperature of 26 °C and a mean annual precipitation of *c.* 2600 mm year^{-1} with a pronounced dry season from December to April (Windsor 1990). We sampled a subset of the fertilization treatments, using 16 plots comprised of four replicate factorial combinations of N and P arrayed as blocks from high to low elevation. Nutrients are applied four times per year during the rainy season as 125 kg N ha^{-1} year^{-1} as urea [$(NH_2)_2CO$], 50 kg P ha^{-1} year^{-1} as triple superphosphate [Ca$(H_2PO_4)_2H_2O$] or both N and P together in the same amounts as the individual treatments. Nitrogen and P addition are equal to 69% and 470% of annual inputs from fine litterfall at a nearby (3 km) site (Yavitt, Wright & Wieder 2004). The relatively large annual P addition was chosen to offset P occlusion in the strongly P-fixing

soils of the Gigante experiment (Wright *et al.* 2011; Schreeg, Mack & Turner 2013a). Details regarding the significant increases in extractable soil nitrate and phosphate resulting from respective N and P addition are detailed elsewhere (Yavitt *et al.* 2009; Mirabello *et al.* 2013; Turner *et al.* 2013). Briefly, seasonally averaged nitrate concentrations were found to be roughly double in plots receiving N, whereas phosphate was roughly 30 times greater in plots receiving P (overall treatment effects, Turner *et al.* 2013). Based on the measured increases in available N and P, we assume that the treatments increased the availability of the respective nutrients despite differences in application rates and ion mobility.

LEAF AND LITTERFALL SAMPLING

We collected canopy foliage and fresh litterfall from up to three individuals of four locally common tree species that occurred in replicate across most of the 16 plots (13 plots had at least one individual of each species, and three plots were missing one of the four species). The four species included a medium-sized canopy tree *Alseis blackiana* (Rubiaceae)*,* a medium-sized subcanopy tree *Heisteria concinna* (Erythropalaceae)*,* a large canopy tree *Tetragastris panamensis* (Burseraceae) and a medium-sized, multistemmed, subcanopy palm, *Oenocarpus mapora* (Arecaceae). Fully sun exposed canopy leaves were obtained from up to three healthy individuals of the eudicots in March 2011 using steel ammunition fired from the forest floor. Each tree was represented by a composite of 5–10 healthy canopy leaves representing a range of ages and relatively devoid of excessive phyllospheric growth. Freshly senesced leaf litterfall from the eudicot species was collected between November 2010 and March 2011 using 1-m²-mesh litter traps located under up to three individuals of each species in each plot. The traps were emptied every 2 weeks, dried at 60 °C for 48 h and composited by species in each plot. For the *O. mapora* palm, both fresh and senesced leaflets were cut from a minimum of three separate ramets from three mature individuals (genets) in April 2011 with an extendable pole cutter. Leaflets were composited by tree (fresh) or plot (senesced).

Total foliar and litter P was determined by combustion (1 h at 550 °C) and dissolution of the ash in 10 mL of 1 M H_2SO_4 shaken for 16 h. Inorganic 'weak-acid' foliar P_i was extracted by shaking 0.2 g of leaf tissue for 30 min in 10 mL of 0.25 M H_2SO_4. Organic P was calculated as the difference between total P and P_i. All digests were filtered through glass fibre (GF/A) filters, and phosphate was determined by automated colorimetry on a Lachat QuikChem 8500 (Hach Ltd., Loveland, CO, USA). The efficiency of leaf nutrient resorption was calculated as ((leaf [mg g^{-1}]–litter [mg g^{-1}])/leaf [mg g^{-1}]) × 100 (Killingbeck 1996). Because it has been established that leaf mass loss resulting from carbon resorption during senescence can lead to substantial underestimates of nutrient resorption (van Heerwaarden, Toet & Aerts 2003), we adjusted litterfall nutrient concentrations by the 21.6% average mass loss estimates for deciduous angiosperms derived from a global meta-analysis of 86 studies in 31 countries. Although each of the four tree species in the Gigante Fertilization Experiment may have unique mass loss rates, the global correction is derived from 159 (N) and 177 (P) samples from tropical trees (Vergutz *et al.* 2012), suggesting it is a robust estimate.

STATISTICAL ANALYSES

We analysed leaf nutrient concentrations using mixed effect models and the lmer function in the package lme4 version 0.999999-0 (Bates, Maechler & Bolker 2012) in R version 2.15. We treated *Plot* as a random effect and the N and P fertilizer treatments as fixed effects. Significance was assessed using posterior distributions of Markov chain Monte Carlo parameters based on 10 000 iterations calculated with the pvals.fnc function in the languageR package version 1.4 (Baayen 2011). Because this method is conservative with respect to sample size, it is the least controversial method for testing hypotheses in mixed effect models (Baayan, Davidson & Bates 2008). Leaf litterfall elemental concentrations, which lacked within-plot replication, were analysed using linear models with *Block* included as a fixed effect as fitting random effects with fewer than five levels is not recommended (Bolker *et al.* 2009).

Results

ELEMENTAL RESPONSE OF GREEN AND SENESCED LEAVES TO N AND P ADDITION

Green and senesced leaf N concentrations (mg g^{-1}; hereafter [N]) exhibited consistent species rankings that were unaltered by nutrient addition, with *A. blackiana > H. concinna > O. mapora > T. panamensis* (Fig. 1a). The ranking of leaf litter [N] among species remained unchanged by fertilization, although the resorption proficiency of N decreased in *H. concinna* following both N and P addition (Fig. 2a). Foliar [N] was significantly correlated with senesced leaf litter [N] in two of the four tree species; *A. blackiana* ($R^2 = 0.47$, $P = 0.013$, $n = 12$) and *H. concinna* ($R^2 = 0.18, P = 0.011, n = 15$).

Total [P] in canopy leaves increased following P addition in all but the *O. mapora* palm (Fig. 1b). Canopy leaf [P] was appreciably lower in the +N+P relative to the +P treatment in *A. blackiana* and *T. panamensis*, although the magnitude of the difference was not large enough to cause significant interactive effects (Fig. 1b). The increased [P] of canopy leaves contributed to an overall decrease in the resorption proficiency of these trees, although the differences were significant only for two species-by-treatment combinations: *H. concinna* in the +P treatment and *O. mapora* in the +N+P treatment (Fig. 2b).

Partitioning of canopy leaf P into two fractions, the weak-acid extractable P_i and remaining P_o fraction, allowed us to examine whether [P_i] increased disproportionally more in response to P addition. Foliar [P_i] and [P_o] increased by similar amounts following P addition in all but the *O. mapora* palm (Fig. 3). As a result, the proportion of P_i comprising total [P] was significantly greater in only one species-by-treatment combination, *A. blackiana* in the +P treatment (Fig. 3). The lack of a corresponding increase in the +N+P treatment led to a marginally significant N×P interaction in leaf [P_i] from *A. blackiana* as well (Fig. 3).

As a result of green leaf P accumulation following P addition, significant declines in leaf N/P ratios were also observed in the eudicot species and marginally so in *O. mapora* in the +N+P treatment only (Fig. 1c). Under control conditions canopy leaves from *A. blackiana* and *H. concinna* had similarly high N/P ratios (31), suggesting greater relative P limitation than the lower N/P ratios in *T. panamensis* and *O. mapora* (23 and 19, respectively; Fig. 1c). All were >16, the level broadly considered to reflect P limitation (Reich & Oleksyn
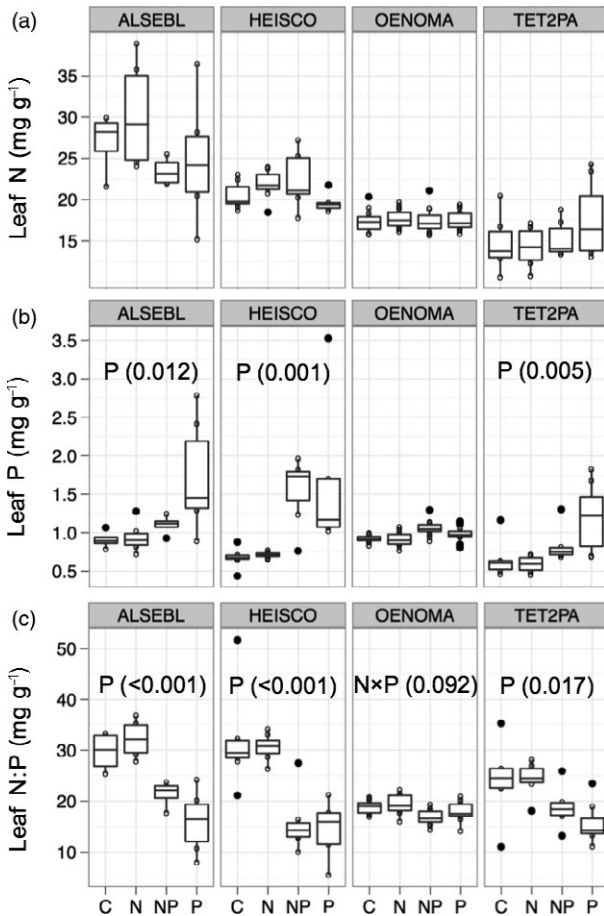
Fig. 1. Canopy leaf elemental concentrations (mg g^{-1}) from four common tree species in the Gigante Fertilization Experiment following 13 years of fertilization with nitrogen (N), phosphorus (P) or both (NP). Panel a shows leaf N, panel b shows leaf P, and panel c shows leaf N/P ratios. ALSEBL = *Alseis blackiana*, HEISCO = *Heisteria concinna*, OENOMA = *Oenocarpus mapora*, TET2PA = *Tetragastris panamensis*. Letters (N, P or N×P) indicate significant overall N and P effects or an N×P interaction effect followed by Monte Carlo Markov chain-based *P*-values (P_{MCMC}).
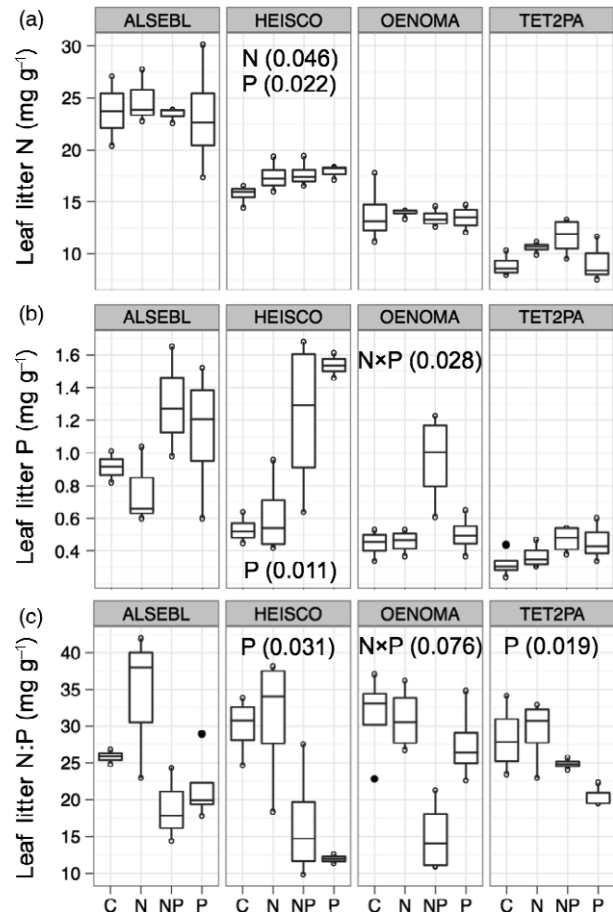

Fig. 2. Senesced leaf litterfall elemental concentrations (i.e. resorption proficiency) from four common tree species in the Gigante Fertilization Experiment following 13 years of fertilization with nitrogen (N), phosphorus (P) or both (NP). Panel a shows leaf litter N, panel b shows leaf litter P, and panel c shows leaf litter N/P ratios. ALSEBL = *Alseis blackiana*, HEISCO = *Heisteria concinna*, OENOMA = *Oenocarpus mapora*, TET2PA = *Tetragastris panamensis*. Letters (N, P or N×P) indicate significant overall N and P effects or an N×P interaction effect followed by linear model *P*-values.

2004; Townsend *et al.* 2007). Following P addition, the higher *A. blackiana* and *H. concinna* N/P ratios decreased by 37% and 50% to 19 and 15, respectively. The lower values for *T. panamensis* and *O. mapora* decreased less by 28% and 5% to 16 and 18, respectively (Fig. 1c).

The N/P ratios of senesced leaves responded to P addition in a similar manner as canopy foliage, with parallel declines observed in the eudicots, and a marginally significant effect for the palm leaflets ($P = 0.076$; Fig. 2c). The general N/P declines were only significant for *H. concinna* and *T. panamensis* ($P = 0.031, 0.019$, respectively).

Correlations between average canopy leaf N/P ratios and bulked leaf litter N/P ratios indicate that leaf litter N/P values are not a reliable predictor of canopy leaf N/P across treatments, because the strength, intercept, and slope of the relationships varied appreciably by species (*A. blackiana*: $litter_{N/P} = 10.91 + 0.56 \times leaf_{N/P}$, $R^2 = 0.26$, $P = 0.09$, $n = 12$; *H. concinna*: $litter_{N/P} = 0.94 + 0.96 \times leaf_{N/P}$, $R^2 = 0.63$, $P = 0.0007$, $n = 14$; *O. mapora*: $litter_{N/P} = -28.67 + 3.03 \times leaf_{N/P}$,

$R^2 = 0.29$, $P = 0.03$, $n = 16$; and, *T. panamensis*: $litter_{N/P} = 11.96 + 0.70 \times leaf_{N/P}$, $R^2 = 0.47$, $P = 0.005$, $n = 15$).

RESORPTION EFFICIENCY RESPONSE TO N AND P ADDITION

In control plots, *O. mapora* was the least efficient in N and P resorption and *T. panamensis* the most efficient (Fig. 4). Chronic nutrient additions had little effect on nutrient resorption efficiencies. Leaf N resorption efficiency declined significantly (10% on average) in *H. concinna* following P addition ($P = 0.005$, $n = 7$), which led to a significant N×P interaction ($P = 0.008$) because N co-addition eliminated the P effect on N resorption efficiency. The P resorption efficiency of *A. blackiana* increased slightly in the +N treatments ($P = 0.065$, $n = 4$) and increased even more (50% on average) under +N+P co-addition resulting in a significant N×P interaction (Fig. 4). In contrast, the marginally signifi-
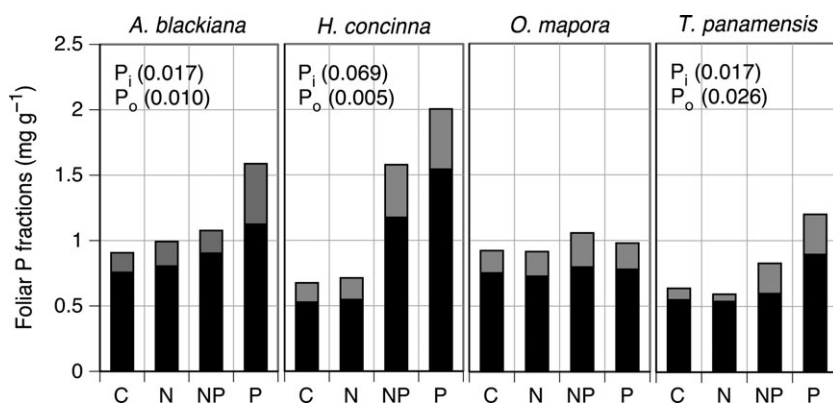
Fig. 3. Significance tests for +N or +P fertilization effects for foliar concentrations of inorganic and organic P following 13 years of fertilization with nitrogen (N), phosphorus (P) or both (NP). Weak-acid extractable inorganic foliar P (P_i) as grey bars stacked on organic foliar P (P_o) in black. Letters (P_i or P_o) above bars indicate significant overall P addition effects for inorganic and organic P, respectively, followed by Monte Carlo Markov chain-based P-values (P_{MCMC}).
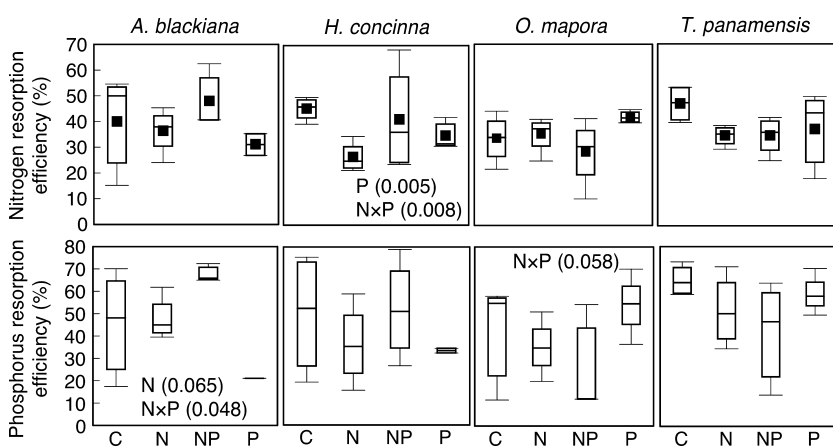

Fig. 4. Average mass loss-corrected nutrient resorption efficiencies for four tropical tree species following 13 years of fertilization with nitrogen (N), phosphorus (P) or both (NP). Letters (N, P or N×P) indicate significant overall N, P or N×P interaction effects followed by linear model P-values.

cant N×P interaction ($P = 0.058$) in *O. mapora* was caused by a small reduction in P resorption efficiency under nutrient co-addition. Despite expectations based on previously described patterns (Kobe, Lepczyk & Iyer 2005), there were no relationships between initial leaf [N] or [P] and the mass-corrected resorption efficiencies of those elements across species and treatments. The stoichiometric ratios among N/P resorption efficiencies were also compared with a recent meta-analysis of tropical species (Reed *et al.* 2012); however, no overall N or P fertilization effects were observed.

Discussion

FOLIAR N, P AND N/P

Chronic N addition did not significantly alter canopy foliar [N] in the species examined here. The non-significant 9.6% increase averaged across species is similar to increases in leaf tissue [N] observed previously at our site. For instance, the magnitude of increase relative to control plots was similar to the 11% average increase observed across five seedling species after 2 years of N fertilization in the Gigante Fertilization Experiment, three of which were the eudicots included in this study (Santiago *et al.* 2012). In addition, a similar magnitude increase in [N] was also observed on nearby Barro Colorado Island, where canopy leaves sampled in 2007 were 11.5% greater than herbarium collections dating from the 1960s, an increase attributed to increasing regional anthropogenic N deposition in recent decades

(Hietz *et al.* 2011). These small and relatively uniform increases in leaf [N] support the idea that tropical trees are at the high end of the global leaf [N] spectrum and do not appreciably accumulate (i.e. *c.* 10% increase) N following fertilization (Aerts 1996; Harrington, Fownes & Vitousek 2001; Ostertag 2010), perhaps due to fundamental limits on photosynthetic gains (Reich 2012) balanced with greater risks of herbivory (Andersen *et al.* 2010). Given that our focal taxa exhibited a broad range in green and senesced foliar [N], our results appear to be generalizable across a broad range of tropical tree species. The largest species, *T. panamensis*, exhibited senesced foliar N concentrations at the lower end of the global spectrum (Fyllas *et al.* 2009), indicating this species in particular exhibits high N use proficiency.

In line with our predictions, chronic P addition increased P accumulation of canopy foliage in three of the four species examined. In contrast to our prediction that P_i, the more labile orthophosphate fraction, would accumulate relatively more than the predominantly structural organic fraction, we found that both P_i and P_o increased proportionally to one another in all but one species-by-treatment combination (*A. blackiana* in the +P treatment). Leaf P fractions are rarely determined on wild plants, but the scant available data are consistent with our results. Tropical trees growing along a P availability gradient on Mount Kinabalu, Borneo, exhibited consistent relative proportions of leaf [P_i] to total [P], despite mean foliar [P] ranging from 0.3 to 0.6 mg g^{-1} across sites (Hidaka & Kitayama 2011). In addition, 13 species on 'low' and 'high'

P Hawaiian soils did not vary in their relative concentrations of P_i and P_o following fertilization (Ostertag 2010). Inorganic P comprised 18–23% of total green leaf [P] in our study and 31–36% in the Hawaiian study (Ostertag 2010), while 'metabolic' P comprised 25% of total leaf [P] in the Bornean study (Hidaka & Kitayama 2011). Methodological differences among studies complicate direct comparisons of these percentages. However, there does seem to be a narrow range (*c.* 18–36%) over which tropical leaves can store P in labile inorganic fractions regardless of natural or experimentally induced variation in soil P availability. Given the lability of this fraction within plants, it is likely that seasonal variations in foliar [P] and N/P observed in tropical forest plants (Townsend *et al.* 2007; Fyllas *et al.* 2009) could largely be due to changes in the proportion of P_i.

In response to the increase in foliar [P], foliar N/P ratios decreased in the three eudicot species. These declines in foliar N/P ratios caused the typical tropical tree N/P ratios (*c.* 30) to decline towards those found in high-latitude, putatively N-limited plants (i.e. <14, Reich & Oleksyn 2004; Elser *et al.* 2010). Combined with simultaneous enriched soil nitrate $\delta^{15}N$ values following +N and +N+P addition (J. R. Mayor, S. J. Wright, E. A. G. Schuur, M. E. Brooks & B. L. Turner, unpublished manuscript), these findings further support a P-conserving and leaky N strategy in the Gigante forest. This agreement between foliar N/P and foliar $\delta^{15}N$ as indicators of N vs. P limitation was also reported for an epiphyte fertilization experiment, although for different reasons (Wanek & Zotz 2011). Enriched epiphyte $\delta^{15}N$ values in the latter study were attributed to decreased fractionation under P-limiting conditions rather than use of ^{15}N-enriched soil N sources resulting from the stimulation of denitrification under N addition in the Gigante Fertilization Experiment (Koehler *et al.* 2012). Regardless of the mechanism, there is a clear link between excess N availability, enriched foliar $\delta^{15}N$ values and high N/P ratios in tropical forests. Less clear is how to determine where critical N/P values indicate colimitation for individual species (Garrish *et al.* 2010) or when a switch from P limitation to N limitation occurs (Wanek & Zotz 2011).

The lack of foliar P accumulation by the *O. mapora* palm suggests that this species is (i) incapable of luxury consumption; (ii) is uniquely capable of down regulating P uptake; or (iii) that increased P uptake was allocated to greater production or stored elsewhere in the palm. Growth and tissue production by palms have shown both positive and equivocal responses to P addition in other tropical forests. For instance, *Socratea exorrhiza* increased foliar [P] by 17% and exhibited higher relative growth rates following addition of both N and P in Costa Rica (Alvarez-Clare, Mack & Brooks 2013). In contrast, *Bactris gasipaes* did not increase foliar [P] but did increase relative growth rates following P addition in an Amazonian agro-ecosystem (Ares *et al.* 2003). As palms are often conspicuous components of many tropical forests, there is good reason to include them in future attempts at community-level assessments of nutrient limitations to forest growth and allocation patterns of limiting nutrients.

RESORPTION PROFICIENCY

Nitrogen addition did not appreciably alter N resorption proficiency, with the exception of *H. concinna*. Litterfall [N] of *H. concinna* increased from 15.7 to 17.7 mg g^{-1} in both N and P treatments, indicating that nutrient resorption proficiency declined regardless of which element was added. The very low litterfall [N] in *T. panamensis* showed non-significant trends towards reduced proficiency under N addition. These results suggest that the previously observed 16% increase in the community average litterfall [N] collected from the +N plots during 1998–2007 (Fig. 2c in Corre *et al.* 2010) might be partially dependent on the contribution of similarly responsive species, including *H. concinna*, but do not reflect overall changes in N resorption across the entire community. Fertilization of a relatively P-rich lowland rain forest in Costa Rica also resulted in minor, but significant, increases (13%) in litterfall [N], but not canopy foliar [N], after 2.7 years of N addition (S. Alvarez-Claire & M. Mack, unpublished data). Combined, these results suggest that [N] is more responsive to N addition in the leaf litterfall than corresponding green foliage of some tropical tree species, but generally reflects the overall weak ability of tropical trees to alter N concentrations for reasons already discussed.

In line with our predictions, chronic P addition reduced P resorption proficiency in the three eudicot species, but the magnitude was only statistically significant in *H. concinna* generally and the palm under N and P co-addition. Also, similar to the increase in foliar [P], N/P ratios in senesced leaves decreased in the three eudicot species (significant in just two) and under N and P co-addition in the palm. Although significant, the moderate correlations between green and senesced foliar N/P ratios suggest that senesced litterfall is not an accurate proxy of canopy leaf N/P ratios without wider community sampling, given the variable relationships between foliar and litter N/P ratios observed among species.

RESORPTION EFFICIENCY

We hypothesized that nutrient resorption efficiency would decline following addition of the respective nutrients. Furthermore, we hypothesized that N resorption efficiency would increase under P addition due to induced N limitation. These hypotheses were motivated by the expectation that single element resorption efficiencies would follow community-wide N or P conservation strategies (Vitousek 1998). Neither hypothesis was supported. Furthermore, P resorption efficiency in *H. concinna* declined under both N and P addition but not in +N+P plots (albeit not significantly under N addition). The unresponsive nutrient resorption patterns among the four locally common tree species, despite chronic nutrient addition, suggests that these species are able to maintain growth despite constraints on nutrient resorption (Sistla & Schimel 2012). It was particularly surprising that these plants were unable to increase P resorption following P addition, given the putatively P-limiting growth conditions

in many tropical forests (Vitousek 1984; Reed *et al.* 2012). Instead, it may be that the flexibility of leaf nutrient resorption is genetically constrained by adaptations to generally low-P conditions, a finding comparable to the genetic differences seen among *Metrosideros polymorpha* populations on high- and low-P soils in Hawaii (Harrington, Fownes & Vitousek 2001; Treseder & Vitousek 2001). Alternatively, flexibility in leaf P resorption could be a less important mechanism for P conservation than allocation towards reproductive output; a pattern recently described from *Pentaclethra macroloba* in La Selva National Park, Costa Rica (Tully *et al.* 2013).

Additional reasons for the absence of expected patterns in altered resorption efficiencies following P additions include the possibility that: (i) our sampling failed to capture seasonal or interannual variation in foliar [P] (Killingbeck 1996; Townsend *et al.* 2007); (ii) another unmeasured leaf trait, such as leaf mass area (Hidaka & Kitayama 2011) or leaf longevity (Reich, Ellsworth & Uhl 1995; Wright & Westoby 2003), is a more important mechanism by which these tropical trees retain nutrients; or (iii) actual P resorption efficiencies were substantially altered but strong (up to 35%) orthophosphate leaching from suspended litterfall traps (Schreeg, Mack & Turner 2013b) prevented detection in bi-weekly collections of litter.

FERTILIZATION EFFECTS ON N/P RATIOS IN RELATION TO PRODUCTIVITY

Linking leaf N/P ratios with demonstrated growth responses to fertilization is necessary to understand the efficacy of this proxy to indicate relative nutrient limitations. In the Gigante Fertilization Experiment, foliar N/P declined and fine litter production increased by 25% in response to P addition (Wright *et al.* 2011), but did not respond to N addition. Further, the addition of N and K reduced an otherwise forest-wide decline in trunk growth rates (stems of all species) (Wright *et al.* 2011), suggesting that (i) N can at least co-influence stem growth rates despite not influencing foliar N/P ratios and (ii) foliar nutrients may reflect only nutrients limiting leaf production as opposed to nutrients that limit wood production.

Examination of the three other P addition experiments in lowland tropical forests offers further support for a link between foliar nutrients and nutrient limitation to plant production. In Borneo, 1.8 years of P addition halved foliar N/P ratios and increased fine litterfall production by 25% (Mirmanto *et al.* 1999). In Cameroon, 2 years of P addition decreased foliar N/P, but not stem productivity or seedling establishment (Newbery *et al.* 2002). Lastly, in Costa Rica, 2.7 years of P addition did not alter foliar N/P, yet increased the growth of small stems (5–10 cm) (Alvarez-Clare, Mack & Brooks 2013). Thus, two of four studies detected a decline in foliar N/P and an increase in productivity following P addition, suggesting that long-term fertilization experiments are needed to reliably link foliar nutrients with nutrient limitations to plant productivity.

Conclusion

Tropical trees generally accumulate more P than N following nutrient addition and the relative proportions of P_i and P_o stored in leaves appear constrained. Declines in foliar N/P ratios among tropical tree species subjected to P addition, or low ratios of trees growing on relatively high-P soils, do not necessarily indicate relief or absence of P limitation, although results from two of four studies suggest that long-term experiments are necessary to detect such relationships. The responsiveness of leaf [P] in the three locally common eudicot species in the Gigante Fertilization Experiment, but not the palm, suggests that the palm species differs fundamentally in its allocation patterns. Although the 40–50% resorption efficiencies seen here are undoubtedly an important nutrient conserving mechanism, their general lack of response to chronic nutrient addition suggests phylogenetic constraints on this metric. The complexity of species-specific responses to altered nutrient availability suggests difficulty in predicting future responses of tropical forest trees to a changing world.

Acknowledgements

Data accessibility

Data available from the Dryad Digital Repository (Mayor, Wright & Turner 2013).

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