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Nutrient resorption is associated with leaf vein density and growth performance of dipterocarp tree species

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Summary

1. Nutrient resorption is important for the nutrient budget of plants, but little is known about which plant traits mediate nutrient resorption, how resorption efficiency is associated with other leaf traits and whether nutrient resorption has an impact on plant growth.

2. In this study, 17 dipterocarp tree species were compared in a common garden experiment. N and P resorption efficiencies were regressed against suites of traits associated with phloem transport capacity (i.e. leaf vein density; D_{vein}), leaf nutrient conservation traits (e.g. leaf mass per area; LMA) and species growth rate.

3. Across the dipterocarp species studied, N resorption efficiency (percentage N resorbed) was positively correlated with D_{vein} and leaf thickness. N resorption efficiency was also correlated with D_{vein} after considering phylogenetic effects. N resorption proficiency (N remaining in senesced leaves) was negatively correlated with D_{vein}, LMA, leaf thickness and palisade and spongy mesophyll thickness. Senesced-leaf N concentration was still negatively correlated with LMA and leaf thickness after considering phylogenetic effects.

4. N resorption efficiency was positively correlated with both height and diameter growth rates. After considering phylogenetic effect, N resorption efficiency was marginally correlated with diameter growth rate. Green-leaf N concentration was positively correlated with height growth rate after considering phylogenetic effect.

5. P resorption efficiency and proficiency were not related to any of the leaf morphological and anatomical traits, or to species growth rates.

6. *Synthesis.* These results indicate that higher phloem transport capacity of the dipterocarp species is positively correlated with greater N resorption efficiency and that N resorption proficiency is closely linked with leaf nutrient conservation traits. Growth rates of the dipterocarps are more likely governed by photosynthetic rates associated with green-leaf N concentration than N resorption rates per se. Although P is generally deficient in tropical soils, it appears that N rather than P availability is the key limiting factor for the growth of the dipterocarp species.

Key-words: common garden, ecophysiology, nutrient resorption efficiency, nutrient resorption proficiency, phloem transport capacity, tropical rain forest trees

Introduction

Nutrient economy is an important determinant of plant performance. Resorption is a process by which nutrients are translocated from the senescing leaves to the storage organs or growing tissues. This activity can contribute substantially to the nitrogen (N) and phosphorus (P) annually used by plants (Ryan & Bormann 1982). Conserving these nutrients makes a species less dependent on its current capacity for nutrient uptake (Aerts 1996; Eckstein, Karlsson & Weih 1999). Therefore, knowledge of resorption patterns and their determinants is essential for understanding its influence on plant fitness and ecosystem nutrient cycling.

Despite the pivotal role of nutrient resorption in the nutrient economy of plants and ecosystems, we know surprisingly little about (i) which plant traits mediate nutrient resorption, (ii) how resorption efficiency is associated with other leaf traits,

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and (iii) whether nutrient resorption has an impact on plant growth performance. To obtain insight into the mechanisms underlying nutrient resorption, most global, comparative studies have evaluated leaf chemistry and stoichiometry of green and senesced leaves. These studies have shown that nutrient concentrations of senesced leaves are positively correlated with those of green leaves (Kobe, Lepczyk & Iyer 2005; Vergutz *et al.* 2012; Liu *et al.* 2014) and that the efficiency of nutrient resorption decreases somewhat with increasing nutrient concentration in green leaves (Aerts 1996; Kobe, Lepczyk & Iyer 2005) and in the soils (Reed *et al.* 2012; Hayes *et al.* 2014; Mayor, Wright & Turner 2014; Tang *et al.* 2014; Vourlitis *et al.* 2014). At first sight, this provides evidence that species from nutrient-poor habitats (with low leaf nutrient concentrations) recycle their nutrients more efficiently, with the important caveat that species were sampled from soils differing widely in fertility, thus confounding species adaptation with acclimation (Kobe, Lepczyk & Iyer 2005). Hence, by using common garden approach to standardize plant growth environments, one may assess whether plant differences in nutrient resorption are attributable to inherited adaptive responses (Monson 1996).

Few studies have looked at the actual mechanisms of nutrient resorption, and what other leaf traits could be involved in this process. Previous studies have shown that nutrient resorption efficiency may be related to the ability of phloem transport (Chapin & Kredowski 1983; Chapin & Moilanen 1991). Phloem is the major path for transporting N and P from senescing leaves to other plant tissues. The amount of nutrients that can be transported is, therefore, partly determined by the amount of phloem tissue. Having a high leaf vein density (i.e. total vein length per area) implies a large phloem transport capacity (Sack *et al.* 2012). Vein density is therefore an easy-to-measure and promising proxy of phloem transport capacity and nutrient resorption ability, but to date, no studies have evaluated whether vein density is linked to nutrient resorption.

Nutrient resorption rates could be an integral part of plants' strategy to deal with a shortage of nutrients. N and P concentrations in senesced leaves have been found to decline with leaf traits that confer well-protected and robust leaves such as leaf mass per area (LMA) and leaf toughness (Wright & Westoby 2003; Bakker, Carreño-Rocabado & Poorter 2011), and therefore with leaf life span (Wright & Westoby 2003). An enhanced nutrient resorption would prolong the nutrient residence time in the plants and hence overall plant nutrient use efficiency (Berendse & Aerts 1987; Escudero *et al.* 1992). This suggests that nutrient resorption rates should be closely related to the leaf economics spectrum and its components (Wright *et al.* 2004). Nevertheless, recent studies have shown that nutrient resorption and plant economics spectrum are largely uncoupled, probably because resorption processes are affected in counteracting ways by multiple physiological traits associated with leaf carbon and nutrient economics, each with their own adaptation strategies under evolutionary selection (Freschet *et al.* 2010).

It has been postulated that increased nutrient resorption can increase plant fitness, especially in nutrient-poor environments (Gloser 2005; Marty, Lamaze & Pornon 2009). May & Killingbeck (1992) demonstrated with a defoliation experiment that avoidance of resorption can reduce plant growth. Bausenwein, Millard & Raven (2001) found that resorbed N from old leaves contributes 70–82% for two temperate grasses to the total N used for spring growth. Growth of the evergreen *Rhododendron ferrugineum* depends on resorbed N, which almost completely uncouples its N requirement from root uptake (Lamaze, Pasche & Pornon 2003). However, some studies showed that plant growth was not related to nutrient resorption (e.g. Eckstein, Karlsson & Weih 1998; Pasche, Pornon & Lamaze 2002). Overall, further evidence is needed to evaluate whether nutrient resorption matters at all for plant growth.

Although N and P resorption efficiencies respond in a very similar way to the factors mentioned above, they show strikingly different patterns across the latitudinal gradient. In general, N limitation is stronger in the temperate zone, whereas P limitation is stronger in the tropics where the soils are older and more strongly weathered. Consequently, N:P resorption ratios increase with latitude (Reich & Oleksyn 2004; Yuan & Chen 2009; Reed *et al.* 2012; but see Vergutz *et al.* 2012), with N:P resorption ratios being < 1 in the tropics, indicating that a higher proportion of P is resorbed than N in highly weathered tropical soils. This also suggests that interspecific variation in growth of tropical trees could be more strongly related to P resorption efficiency than to N resorption efficiency.

Here, we compared the nutrient resorption of 17 dipterocarp tree species grown for > 12 years in a common garden experiment on nutrient-poor tropical soils. N and P resorption efficiencies were regressed against a suite of traits associated with phloem transport capacity (e.g. leaf vein density), the leaf economics spectrum (e.g. LMA) and species growth performance (i.e. height and diameter growth rates). We tested the following hypotheses: (i) nutrient resorption efficiency is positively related to the phloem transport capacity, as indicated by a high leaf vein density, (ii) nutrient resorption efficiency is positively associated with leaf nutrient conservation traits (such as high LMA, leaf thickness) that enhance leaf life span and nutrient residence time in the plants, (iii) nutrient resorption efficiency is positively related to plant growth, and (iv) given that these species are adapted to highly weathered tropical soils, more P will be resorbed than N, and P resorption efficiency will be associated with interspecific variation in plant growth.

Materials and methods

STUDY SITE AND SPECIES

This study was conducted in a dipterocarp plantation at Xishuangbanna Tropical Botanical Garden (21°41′N, 101°25′E; elevation 570 m) in southern Yunnan Province, China. The garden is surrounded by a tributary of the upper Mekong River. Mean annual temperature is 21.7 °C, and mean annual precipitation is 1560 mm, with 80% of precipitation occurring in the rainy season (May to October). A distinct dry period (with < 77 mm/mo) occurs from November to April. The soil in this plantation is sandy alluvium with pH being 4.49, total N and P being 0.875 and 0.329 mg g^{-1}, available N and P being 80.9 and 2.64 mg kg^{-1}, respectively, within a 0–20 cm profile. This soil is relatively deficient in N, but very deficient in P based on classification standard of soil fertility across China (National Soil Survey Office 1992).

The Dipterocarpaceae is one of the most important tree families both ecologically and commercially in Asian tropical forests (Ashton 1964; Whitmore 1984). Since the 1980s, seeds of about 40 dipterocarp species have been collected from Southeastern Asia, including southern China, and germinated at the Botanical Garden. One-year-old seedlings of each of the dipterocarps have been planted in monocultures at a density of about 1100 trees per ha, with the whole plantation covering an area of 7 ha. We selected 17 dipterocarp species (Table S1 in Supplementary Information; see Zhang & Cao 2009 for sites where these species were collected) for the current study. These species belong to six genera: *Anisoptera* (one species), *Dipterocarpus* (five species), *Hopea* (four species), *Parashorea* (one species), *Shorea* (three species) and *Vatica* (three species). Among these, only *D. tuberculatus* is deciduous, having a leafless period of 1.5 months (February to March). All of our examined species are deep-rooted emergent or canopy species from primary forests. At the time of measurement, the sampled trees were 12–24 years old, 9–29 m tall and 10.5–47.8 cm in diameter at breast height (DBH; 1.3 m).

LEAF SAMPLING

Green leaves were sampled in the rainy season (July–August 2010) to evaluate their nutrient concentrations, anatomy and morphology. For nutrient measurements, at least five leaves per plant were collected for three to five plants of each species. To eliminate the effect of variation in light on leaf anatomy, morphology and physiology, only current-season, fully expanded, light-exposed outer canopy leaves were gathered.

Senesced leaves are those in which an abscission layer has formed at the base of the petiole, preventing further nutrient withdrawal. These leaves are easily identified because their overall colour (often yellow) differs from that of live, green leaves and can become detached by gently flicking the branch or leaf, those without an abscission layer cannot be removed in this way. Nutrient resorption is often accompanied by carbon resorption and leaf shrinkage (see van Heerwaarden, Toet & Aerts 2003; Vergutz *et al.* 2012). To minimize the effect of leaf mass loss on the estimate of nutrient resorption efficiency, senesced leaves were collected directly from the plants rather than from the litter layer during the following dry season (November 2010–April 2011). At each collection time, several leaves were gathered from three to five individual plants and pooled for nutrient analysis. On average, three to five pooled collections of senesced leaves were made for each species. It was impossible to collect the same amount of leaves from a standard number of individuals (as had been done with the green-leaf samples) because the number of senesced leaves, where present, varied among species. However, by pooling across several individuals, we tried to obtain a reliable estimate of nutrient concentrations that would be comparable to the estimates made for green-leaf nutrients.

NUTRIENT RESORPTION AND STOICHIOMETRY

Both green-leaf and senesced-leaf samples were dried and pulverized to pass a 60-mesh sieve (0.25 mm diameter). Leaf samples were digested with H_2SO_4, and their N concentrations were determined with an auto Kjeldahl unit (K370; BÜCHI Labortechnik AG, Flawil, Switzerland). Other samples were digested with concentrated HNO_3–$HClO_4$, and their foliar P concentrations were analysed with an inductively coupled plasma atomic-emission spectrometer (IRIS Advantage-ER; Thermo Jarrell Ash Corporation, Franklin, MA, USA). The concentrations of N and P in green and senesced leaves were used to calculate nutrient resorption efficiencies (Killingbeck 1996). Nitrogen resorption efficiency (NRE) was calculated as:

$$\text{NRE}\ (\%) = [(N_{gr} - N_{sen})/N_{gr}] \times 100$$

where N_{gr} and N_{sen} are the concentrations of N measured from mature green leaves and senesced leaves, respectively. Similar calculations were made for P, using values for P concentrations of green (P_{gr}) and senesced leaves (P_{sen}) to compute P resorption efficiency (PRE).

Nutrient resorption can also be described in terms of proficiency. N and P resorption proficiencies were defined as N and P concentrations in senesced leaves, respectively (cf. Killingbeck 1996).

LEAF ANATOMY AND MORPHOLOGY

Leaf vein density (D_{vein}) was measured from paradermal sections prepared by removing the upper epidermis and palisade mesophyll from whole leaves with a sharp, double-sided razor. The remaining leaf sections were boiled in a 5% NaOH aqueous solution for *ca.* 30 min, bleached in sodium hypochlorite, stained with 1% toluidine blue, mounted on slides and observed under a Leica DM2500 microscope (Leica Microsystems Vertrieb GmbH, Wetzlar, Germany). Leaf vein density was measured using IMAGEJ (http://rsbweb.nih.gov/ij/) from digital photomicrographs of the paradermal sections (5× or 10× magnification). To assess D_{vein}, three fields (0.63–2.54 mm^2) were monitored of each section from the middle part of each leaf. We measured D_{vein} on three to five leaves per each of three to five trees for each species.

Green leaves were harvested from five trees per species during the rainy season and sealed in plastic bags. Their anatomy and morphology were examined in the laboratory. Hand-cut transverse sections were taken from middle-lamina sections, avoiding the midribs. The thicknesses of the lamina and palisade and spongy mesophylls were measured with the Leica DM2500 microscope. The value for each leaf was averaged from five fields of the same laminar section.

All evaluated species have simple leaves. Areas of three leaves were determined for each of three to five trees per species using a portable leaf area meter (LI-3000A; LI-COR, Lincoln, NE, USA) and then oven-dried at 80 °C for 48 h. The petiole was excluded from these measurements. Leaf mass per area (LMA) was calculated as leaf dry mass divided by leaf area; leaf density as LMA divided by leaf thickness.

GROWTH RATES

For 10 individuals per species, height from ground to tree top and DBH were measured with tapes with the help of a 18-m high crane mounted on a truck when necessary. Average rates of height growth (HGR) and diameter growth (DGR) were calculated by dividing height and DBH by tree age.

STATISTICAL ANALYSIS

All statistical analyses were performed using R statistical software (R Core Team 2013). Beforehand, all data were $\log_{10}$-transformed to satisfy the assumptions of normality and homoscedasticity.

Associations among 17 traits were analysed with a principal component analysis (PCA). Relationships of N and P resorption efficiencies with other leaf traits and growth rates were analysed using Pearson correlation analysis. Some studies have shown that plant age may affect nutrient resorption (e.g. Mediavilla *et al.* 2014; Wang *et al.* 2014). In this study, we found that age of the dipterocarps was not significantly correlated with N and P resorption efficiencies ($r = 0.23$, $P = 0.37$ and $r = -0.03$, $P = 0.92$ for NRE and PRE, respectively), indicating that age of the dipterocarps has no effect on their nutrient resorption.

Because phylogeny may influence the process of resorption (Killingbeck 1996), we conducted a phylogenetically independent contrast (PIC) analysis to test whether these phenotypic relationships are evolutionarily correlated (Felsenstein 1985). Phylogenetic affiliation among six genera (Fig. S1 in Supplementary Information) was constructed based on published DNA sequences (Gamage *et al.* 2003; Li, He & Xu 2004). Any polytomy, if present, within a genus was further resolved through a combination of DNA sequences and trait similarity. We tested phylogenetic signals using *K* statistics and a randomization test (Blomberg, Garland & Ives 2003). Our primary analysis showed that the traits evaluated here exhibited relatively high degrees of phylogenetic signals, with *K* values ranging from 0.38 for leaf density to 0.90 for palisade mesophyll thickness (Table S2), suggesting that traits tested here were less similar than that expected by a Brownian motion model of trait evolution due to adaptive evolution (Felsenstein 1985). Finally, pairwise PIC correlations were calculated with the 'PICANTE' package (Kembel *et al.* 2010), assuming uniform branch lengths.

Table 1. Traits examined in this study

Group/trait	Code	Unit	Mean (range)
Nutrient resorption			
N resorption efficiency	NRE	%	43 (23–63)
P resorption efficiency	PRE	%	53 (34–71)
Nutrient stoichiometry			
N concentration in green leaves	N_{gr}	mg g^{-1}	19.7 (16.2–26.8)
P concentration in green leaves	P_{gr}	mg g^{-1}	1.23 (0.95–1.66)
N/P ratio in green leaves	N/P_{gr}		16.3 (13.1–19.3)
N resorption proficiency	N_{sen}	mg g^{-1}	11.1 (6.0–15.5)
P resorption proficiency	P_{sen}	mg g^{-1}	0.58 (0.32–0.95)
N/P ratio in senesced leaves	N/P_{sen}		20.0 (12.5–25.6)
Leaf anatomy and morphology			
Vein density	D_{vein}	mm mm^{-2}	9.1 (5.6–14.2)
Leaf thickness	LT	μm	190 (123–299)
Palisade mesophyll thickness	PMT	μm	62 (35–103)
Spongy mesophyll thickness	SMT	μm	88 (29–149)
Ratio of palisade to spongy mesophyll thickness	RPS		0.80 (0.48–2.24)
Leaf mass per unit area	LMA	g m^{-2}	91 (52–163)
Leaf density	LD	kg m^{-3}	482 (343–734)
Growth			
Height growth rate	HGR	m year^{-1}	0.89 (0.49–1.39)
Diameter growth rate	DGR	cm year^{-1}	1.21 (0.70–1.99)

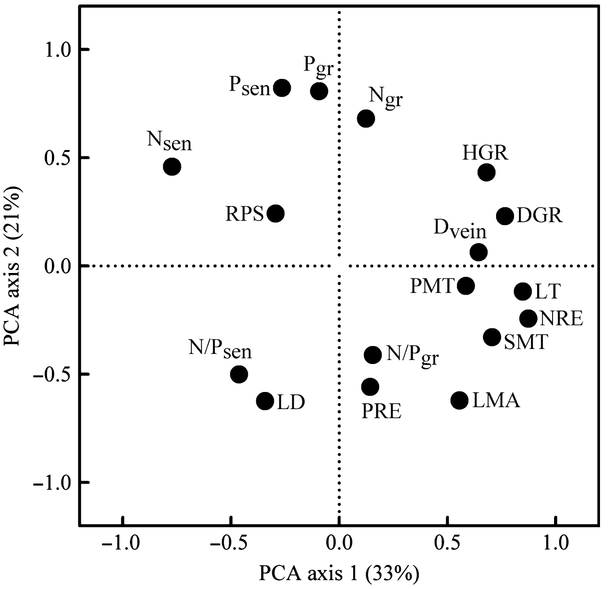

Fig. 1. Arrangement of 17 traits along the first 2 axes of principal component analysis (PCA) after Varimax rotation, with construction based on species trait values for 17 dipterocarp species. Values in parentheses on axis labels indicate percentage of variation explained. See Table 1 for trait codes.

Results

The 17 dipterocarp species showed wide variations in N and P resorption efficiencies and proficiencies (Table 1, Table S1). For example, NRE varied 2.7-fold among species (23–63%), PRE 2.1-fold (34–71%), N resorption proficiency (N_{sen}) 2.6-fold (6.0–15.5 mg g^{-1}) and P resorption proficiency (P_{sen}) 3.0-fold (0.32–0.95 mg g^{-1}). Leaf nutrient stoichiometry, anatomical and morphological traits, and growth rates also differed considerably among species (Table 1, Table S1). N_{sen}, N/P ratio in senesced leaves, palisade mesophyll thickness and ratio of palisade to spongy mesophyll thickness showed significant phylogenetic signals (Table S2).

We used principle component analysis (PCA) to analyse how nutrient resorption, anatomical traits and growth rates were associated (Fig. 1). The first PCA axis explained 33% of the total variation. At the left end are species with high N concentration and N:P ratio in senesced leaves, and at the right end are species with high NRE, leaf vein density, mesophyll thickness and height and diameter growth rates. The second axis explained 21% of the variation. At the top end are species with high P concentration in green and senesced leaves, and at the bottom end are species with high PRE.

N resorption was closely associated with phloem transport capacity and leaf nutrient conservation traits. For instance, NRE was positively correlated with leaf vein density (Fig. 2a), and leaf thickness (Fig. 2c). Using phylogenetically independent contrasts, NRE was still correlated with leaf vein density (Table 2). The N_{sen} was negatively correlated with leaf vein density (Fig. 3a), LMA (Fig. 3b), leaf thickness (Fig. 3c) and palisade and spongy mesophyll thicknesses (Table 2) across the dipterocarps studied. The relationships between N_{sen} and leaf thickness and LMA still held when the phylogeny was taken into consideration (Table 2). However,

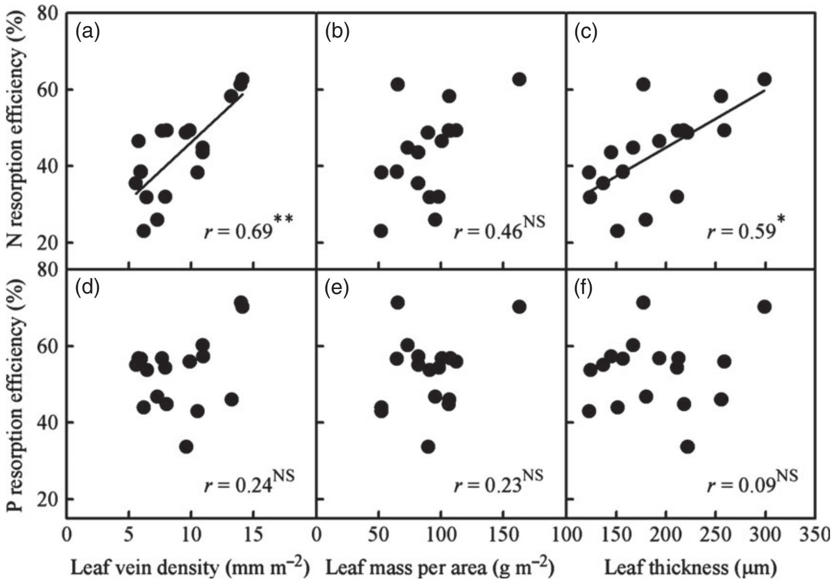

Fig. 2. Relationships of N and P resorption efficiencies with leaf vein density (a, d), leaf mass per unit area (b, e), leaf thickness (c, f) across 17 dipterocarp species. Coefficients of log–log correlations are given. $^{NS}P > 0.05$, $^{*}P < 0.05$, $^{**}P < 0.01$.

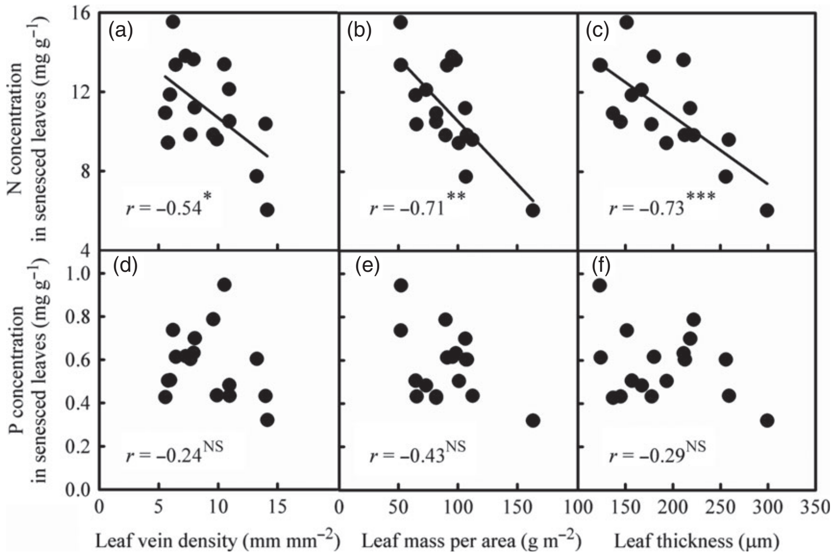

Fig. 3. Relationships of N and P concentrations in senesced leaves with leaf vein density (a, d), leaf mass per area (b, e) and leaf thickness (c, f) across 17 dipterocarp species. Coefficients of log–log correlations are given. $^{NS}P > 0.05$, $^{*}P < 0.05$, $^{**}P < 0.01$ $^{***}P < 0.001$.

P resorption efficiency and proficiency were not significantly correlated with any of the anatomical and morphological traits (Fig. 2d–f, Fig. 3d–f, Table 2).

Height and diameter growth rates were positively correlated with NRE (Fig. 4a,c), but not with PRE (Fig. 4b,d). When using phylogenetically independent contrasts, NRE was marginally correlated with diameter growth rate ($P = 0.09$, Table 2). However, height growth rate of the dipterocarps was positively correlated with green-leaf N concentration, both using regular cross-species correlations ($r = 0.50$, $P < 0.05$) and phylogenetically independent contrasts ($r = 0.56$, $P < 0.05$).

Discussion

IS NUTRIENT RESORPTION EFFICIENCY RELATED TO LEAF VEIN DENSITY?

We hypothesized that nutrient resorption would be positively related to the phloem transport capacity, as indicated by leaf vein density. We did find a strong positive association of N resorption efficiency (Fig. 2a) and a negative association of N resorption proficiency (Fig. 3a) with leaf vein density. We also found that N resorption proficiency was associated with leaf thickness (Table 2), which has shown to be positively correlated with leaf vein density (e.g. Sack & Frole 2006). All these correlations still held when phylogenetic effect was considered (Table 2). This is the first study to demonstrate that leaf venation architecture links to N resorption across a large pool of species, indicating that greater vein leaf density could contribute to stronger phloem transport capacity. Previous studies have shown that higher vein density corresponds to a greater capacity for water transport because the distance is reduced through which water travels outside the xylem (e.g. Sack & Frole 2006). P resorption efficiency and proficiency were not related to leaf vein density, for which we do not have a clear explanation, other than the possibility that P may not limit plant growth.

Table 2. Pearson and phylogenetically independent contrast correlations between nutrient resorption and leaf stoichiometry, anatomical and morphological traits, and growth rates across 17 dipterocarp species

		N_{gr}	P_{gr}	N/P_{gr}	N/P_{sen}	D_{vein}	LT	PMT	SMT	RPS	LMA	LD	HGR	DGR
NRE	Pearson correlation	0.16	–0.12	0.28	–0.33	**0.69****	**0.59***	0.47	0.39	–0.07	0.46	–0.09	**0.52***	**0.65****
	PIC correlation	0.26	–0.19	**0.52***	0.13	**0.67****	0.22	0.22	0.22	–0.15	0.17	0.01	0.30	0.44
PRE	Pearson correlation	0.07	–0.13	0.24	**0.64****	0.24	0.09	–0.06	0.19	–0.23	0.23	0.24	–0.03	0.09
	PIC correlation	0.09	–0.08	0.20	**0.81*****	0.26	0.03	–0.07	0.12	–0.20	0.19	0.22	–0.12	0.13
N_{sen}	Pearson correlation	0.35	0.43	–0.16	0.32	**–0.54***	**–0.73*****	**–0.50***	**–0.53***	0.17	**–0.71****	–0.10	–0.27	–0.40
	PIC correlation	0.44	**0.60***	–0.29	–0.07	–0.44	**–0.54***	–0.43	–0.47	0.31	**–0.54***	–0.17	0.01	–0.07
P_{sen}	Pearson correlation	0.28	**0.60***	–0.53	**–0.59***	–0.24	–0.29	–0.20	–0.34	0.19	–0.43	–0.28	0.08	–0.11
	PIC correlation	0.22	**0.55***	–0.46	**–0.74****	–0.23	–0.34	–0.15	–0.40	0.40	–0.44	–0.24	0.12	–0.14

Data were $\log_{10}$-transformed prior to analysis. See Table 1 for trait codes and units of measure. Bold font indicates significant correlations. $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

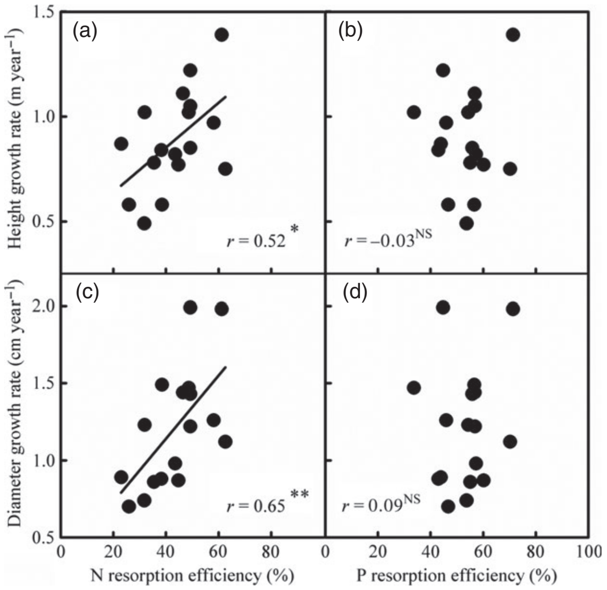

Fig. 4. Relationships of height and diameter growth rates with N (a, c) and P (b, d) resorption efficiencies across 17 dipterocarp species. Coefficients of log–log correlations are given. $^{NS}P > 0.05$, $^{*}P < 0.05$, $^{**}P < 0.01$.

IS NUTRIENT RESORPTION EFFICIENCY ASSOCIATED WITH LEAF NUTRIENT CONSERVATION TRAITS?

We hypothesized that efficient nutrient use (i.e. less nutrient remaining in senesced leaves) would be part of a leaf nutrient conservation trait syndrome. N resorption proficiency was negatively correlated with leaf nutrient conservation traits, that is LMA and leaf thickness, using regular cross-species correlations and phylogenetically independent contrasts (Fig. 3b,c, Table 2; cf. Wright & Westoby 2003 and Ozbucak *et al.* 2011; but see Freschet *et al.* 2010 and Wood, Lawrence & Wells 2011). Both LMA and leaf thickness are known to enhance leaf life span (Reich, Walters & Elsworth 1992; Kitajima *et al.* 2012) and hence nutrient residence time in the leaf. As most of leaf nitrogen is invested in Rubisco, this would allow for a longer photosynthetic revenue stream from the leaves (Schieving & Poorter 1999; Poorter *et al.* 2006). In combination with efficient nutrient recycling (i.e. high nutrient resorption rate), this would lead to higher nutrient residence time in the plant and increased plant nutrient use efficiency (Berendse & Aerts 1987; Escudero *et al.* 1992). Such high nutrient-use efficiency at the whole-plant level is thought to provide plants with a competitive advantage in nutrient-limited environments (Berendse & Aerts 1987). Thus, our results show that N resorption is coupled with the leaf economics spectrum and with a conservative resource-use strategy in these species (sensu Díaz *et al.* 2004).

IS NUTRIENT RESORPTION EFFICIENCY RELATED TO PLANT GROWTH?

We found nitrogen resorption efficiency was significantly and positively correlated with height and diameter growth rates across the dipterocarp species (Fig. 4a,c), with marginal positive correlation between N resorption efficiency and diameter growth rate using phylogenetically independent contrasts ($P = 0.09$, Table 2). This finding supports our hypothesis that nutrient resorption efficiency is positively associated with growth rate. Some studies have shown that foliar N resorption may provide a substantial fraction of the N used for plant growth (Ryan & Bormann 1982). For instance, Bausenwein, Millard & Raven (2001) found for two perennial grasses that resorbed N contributes a large proportion of the total N for the growth of new leaves and reproductive parts in early spring. Similarly, fast nitrogen resorption provides nearly all N required for spring growth of the evergreen *Rhododendron ferrugineum* (Lamaze, Pasche & Pornon 2003). In contrast, two other studies have shown that leaf nutrient resorption does not contribute to shoot growth, even in nutrient-poor soils (Eckstein, Karlsson & Weih 1998; Pasche, Pornon & Lamaze 2002). These results indicate that the contribution of nutrient resorption to plant growth may vary among plants. In our present and previous studies, N concentration in green leaves of the dipterocarps was significantly correlated with height and diameter growth rates (also see Zhang & Cao 2009). Green-leaf N concentration is still significantly correlated with height growth rate ($P < 0.05$), even after the phylogenetic effect was considered, indicating that growth rates of the dipterocarps are more likely a function of photosynthetic rates associated with green-leaf N concentration rather than N resorption itself.

IS P A MORE LIMITING FACTOR THAN N?

We hypothesized that more P would be resorbed than N because P is stored in relatively labile forms (Bieleski 1973), whereas N is largely not (Chapin, Schulze & Mooney 1990). In our common garden experiment on nutrient-poor tropical soils, P resorption efficiency was indeed higher than N resorption (53% vs. 43%). These values are comparable to those for Amazonian rain forest trees growing on nutrient-poor soils (N resorption efficiency = 48%, Reich, Ellsworth & Uhl 1995; P resorption efficiency = 53%, Scott, Proctor & Thompson 1992) and close to the mean values found for terrestrial plants in China (N resorption efficiency = 46.9%, P resorption efficiency = 53.5%, Yuan & Chen 2009). By introducing the concept of resorption proficiency, Killingbeck (1996) considers plants to be highly proficient if they reduce the concentrations of N and P in senescing leaves to < 7 mg g^{-1} and 0.5 mg g^{-1}, respectively. Based on these categories, only two from 17 species studied (12%) were highly proficient with respect to N resorption, whereas seven species (41%) were highly proficient in P resorption. N:P ratio of senesced leaves is even higher than that of green leaves (20.0 vs. 16.3, Table 1), suggesting that more P is resorbed than N. Thus, it appears that conservation of P is relatively developed in our set of species. Such greater P conservation of the dipterocarps could be due to P being stored in labile fractions and/or due to low P availability in these soils.

Surprisingly, we found that P resorption of the dipterocarp species was not related to growth performance (Fig. 4b,d). We also found that P resorption was not associated with phloem transport capacity, as indicated by leaf vein density (Fig. 2d, Fig. 3d), and with leaf traits relating to the leaf economics spectrum, such as LMA and leaf thickness (Fig. 2e,f, Fig. 3e,f). Previous studies have shown that tropical plants can employ some adaptive strategies to cope with P deficiency, such as enhancing P acquisition by root and ectomycorrhizas (Lambers *et al.* 2008) and by P resorption before leaf abscission (e.g. Hidaka & Kitayama 2011). Exudation of organic acids by roots and rhizosphere micro-organisms can facilitate the solubilization of P bound to aluminium and iron oxides and enhance P uptake by dipterocarps from P-poor soils. The Dipterocarpaceae are often associated with ectomycorrhizas to acquire P from acidic soils (e.g. Fujii 2014). In Southeast Asia, the association with ectomycorrhizas is thought to be one of the reasons for the success of dipterocarps (Whitmore 1984). In the present study, we did not analyse P fractions recycled from senesced leaves. However, previous studies have shown that tropical plants can achieve high P resorption efficiency by withdrawing mainly metabolically labile inorganic P fractions prior to abscission (e.g. Ostertag 2010; Hidaka & Kitayama 2011; Mayor, Wright & Turner 2014) as inorganic P is more mobile in the vascular system of plants compared to organic P (Bloom, Chapin & Mooney 1985). N is mainly stored as structural amino acids and proteins (Chapin, Schulze & Mooney 1990). More energy may be required to hydrolyse these organic N-containing compounds, precluding the ability of plants to increase the proportion of N resorbed.

In summary, this study provides evidence that N resorption of the dipterocarp species is linked to leaf vein density, and that it is closely associated with leaf nutrient conservation traits such as leaf mass per area and leaf thickness. The significant correlations between growth rates and green-leaf N concentration and the marginally significant correlation between N resorption and diameter growth rate suggest that growth rates of the dipterocarps are most likely controlled by the green-leaf N concentration for photosynthesis. Although weathered tropical soils are P deficient, the growth rate of the dipterocarp species is mainly correlated with nitrogen and appears decoupled from presumedly limiting soil P availability.

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Data accessibility

All data are included in the article and the Supporting Information.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Phylogenetic tree of the 17 dipterocarp species studied.

Table S1. Species mean values for leaf nutrient resorption, other leaf traits, and growth rates.

Table S2. Phylogenetic signals for leaf nutrient resorption, other leaf traits, and growth rates.