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Phenotypic plasticity of seedlings of five tropical tree species in response to different light and nutrient availability

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Abstract: There is an ongoing debate to which extent the phenotypic plasticity is associated with the shade-tolerance of species along a broad environmental gradient. Seedlings of five species of varying shade tolerance were grown under each of the four combinations of high and low light or nutrient availabilities in shade houses. Leaf, fine root and whole-plant traits were measured to evaluate the phenotypic plasticity in seedlings of five species in response to light and nutrition gradients. Generally, leaf nitrogen and phosphorus concentrations, specific leaf area (SLA), leaf area ratio, specific fine-root length and surface area (SRL, SRSA), leaf mass ratio, and relative growth rate decreased, whereas total root mass ratio increased with increasing shade tolerance of species, indicating light-demanding species had higher ability to capture above- and below-ground resources and thus had higher growth rate than shade-tolerant species. Light was a more important limiting factor than soil nutrients for the five studied species; and the light responsiveness at different nutrient availability for most morphological variables was similar among different species. In response to light and nutrient gradients, the mean plasticity index of all variables measured did not differ significantly among the five species, indicating that the species with contrasting shade tolerance have similar plasticity. There were significantly positive correlations in leaf area (mass) and fine-root surface area (mass) for each species along light and nutrient gradients. Moreover, there were significant correlations between leaf and fine-root nitrogen and phosphorus concentrations, leaf area and fine-root surface area, SLA and SRL or SRSA across all species and treatments. Our result thus provided an evidence of a common leaf and root traits syndrome linking traits to effects on plant and ecosystem process.

Key words: Morphological traits, phenotypic plasticity, pioneers, shade tolerance.

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Introduction

In tropical forests, spatio-temporal variation in above- (light) and below-ground (nutrient and water) resources within plant communities affect regeneration, composition, dynamics and lead to the evolution of a variety of plant strategies (Choudhury *et al*. 2014; Schulze and Chapin 1987). Light is the most limiting factor for plant growth and survival in the forest understorey, but nutrients can be limiting as well, especially in high light (Bazzaz and Wayne 1994; Fetcher *et al.* 1996;

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Paz 2003). The capacity to acquire above- and below-ground resources is associated with total leaf area and root length/surface, respectively. Generally, compared to shade-tolerant species, light-demanding species are associated with higher leaf area per unit plant dry mass (leaf area ratio, LAR) and higher specific fine-root length and surface area (SRL, SRSA), which enable the tree to acquire more resources and thus possesses inherently fast growth rates (Cai *et al.* 2009; Kitajima 1994; Paz 2003; Poorter 2001; Reich *et al.* 1998). Moreover, plant resource acquisition may be enhanced through morphological and physiological adjustments (phenotype plasticity) in these traits in response to environmental gradients (Callaway *et al.* 2003; Holdaway *et al.* 2011; Negreiros *et al.* 2014). For example, plants usually enhance their light capture capacity in low light by a plastic increase in LAR (Cai *et al.* 2005, 2007; Reich *et al.* 1998); and low nutrient supply results in an increased SRL and SRSA (Craine *et al.* 2001; Holdaway *et al.* 2011), with pioneers having a strong plastic response to light and nutrient enrichment than shade-tolerant species (Fetcher *et al.* 1996; Paz 2003). Because of the obvious impossibility for a plant to allocate a given unit biomass simultaneously both in its leaves and roots, there is a functional trade-off balance between leaves and fine roots (Withington *et al.* 2006). It has been reported that within a site unique strong relationships existed among root and leaf traits (Tjoelker *et al.* 2005; O'Grady *et al.* 2006; Holdaway *et al.* 2011). Even though the availability of resources can influence root functional traits and their relationship with leaf traits (Craine *et al.* 2001), how the relationship between leaf and root traits changes across environmental gradients is uncertain (Hajek *et al.* 2013).

It is commonly assumed that species with high phenotypic plasticity have a growth advantage over, and thus outcompete species with low phenotypic plasticity under heterogeneous conditions (Valladares *et al.* 2006). Pioneer species that regenerate in forest gaps and open areas were hypothesized to have a higher plasticity than shade tolerant species, because they grow in a more variable environment (Bazzaz 1979). However, up to date there is little consensus about this hypothesis. Some studies find indeed a higher plasticity for pioneer species (Bazzaz and Wayne 1994; Portsmuth and Niinemets 2007; Sánchez-Gómez *et al.* 2006; Strauss-Debenedetti and Bazzaz 1996; Valladares *et al.* 2000; Paz 2003), whereas other studies find that pioneers have a similar (Coste *et al.* 2010; Ellis *et al.* 2000; Kitajima, 1994; Markesteijn *et al.* 2007; Rozendaal *et al.* 2006) or even lower plasticity in comparison with shade-tolerant species (Popma *et al.* 1992). Moreover, in temperate forest, mid-successional species were found to have greater phenotypic plasticity than either early or late succession species (Neuner and Bannister 1995), which was suggested to be an adaptation to a broad range of ecosystem conditions. In this study, we determined the relationships between the ability to acquire above- and below-ground resour-ces and species' shade tolerance, and evaluated phenotypic plasticity in seedlings of five tropical tree species with contrasting shade tolerance in response to different levels of light and nutrient availability. Firstly, we expected that light-demanding species would have a higher growth rate, due to their higher ability to capture above- and below-ground resources attributed to their leaf and fine-root traits than shade-tolerant species. Moreover, we tested whether above- and below-ground (i.e. leaf and fine-root) traits exhibit structural and functional convergence along an environmental gradient both within and between species. Secondly, we expected that the mean phenotypic plasticity of all measured variables would be consistent with species' shade tolerance response to different light and nutrient availa-bility, i.e. light-demanding species would have higher plasticity than the shade-tolerant species.

Materials and methods

Study species and experimental design

We selected seedlings of five tree species, which are common in the Xishuangbanna forest reserve and differed in shade tolerance. *Barringtonia macrostachya* (Jack) Kurz is a slow-growing middle-canopy species with very large seed (seed mass: 23 g per dry seed), abundant in shaded understorey. *Pterospermum acerifolium* Willd. is an upper-canopy species that is found in both shaded understorey and canopy gaps (Lan *et al.* 2011). *Cleistanthus sumatranus* (Miq.) Muell.-Arg. is a non-pioneer light-demander, typically found in high-light calcareous areas. *Macaranga denticulata* (Bl.) Muell-Arg. is a fast-growing, long-lived pioneer, and *Trema orientalis* (L.) Blume is a fast-growing, short-lived pioneer with a maximum age of about 30 y (Vázquez-Yanes 1998). According to their distribution and plot observations, which are consistent with the literature categorization (Vázquez-Yanes 1998; Lan *et al.* 2011), species' shade tolerance was qualitatively ranked as follows: *B. macrostachya* > *P. acerifolium* > *C. sumatranus* > *M. denticulata* > *T. orientalis*.

The experiment was conducted in shade houses in Xishuangbanna Tropical Botanical Garden (21° 6' N, 101° 5' E, 600 m asl), Chinese Academy of Science, Yunnan, South-West China. Seedlings of *T. orientalis* were collected from a nearby tropical forest and seedlings of other four studied species were collected from nursery of Xishuangbanna Tropical Botanical Garden during August 2006, in the middle of the rainy season; and 40 - 60 seedlings with similar size for each species were planted in pottery pots (25 L in volume) in a shade house with 20 % full sunlight for acclimation (Weinig and Delph 2001). The mean height of seedlings of the five species ranged from 12.7 to 20.6 cm. The seedlings were grown in pots with substrates consisting of forest surface soil fully mixed up with river sand by 1:2 in volume. The forest soil was used to provide a substrate with a natural composition of macro- and micro-nutrients. The river sand improves the texture leading to adequate drainage, and facilitated harvests of the whole root system, including fine roots. After 4 - 5 weeks, bud expansion started and 4 - 6 seedlings per species were harvested for the measurement of their initial biomass. The remaining seedlings were randomly assigned to one of four treatments: high or low light combined with high or low nitrogen availability. The high-light (20 % of full sunlight, typical of a large canopy gap) and low-light treatments (4 % of full sunlight, typical of a small gap formed by a single fallen tree) were created using layers of neutral-density screen on a steel frame. Light availability in the shade house (photosynthetic photon flux, PPF) was measured using LI-190SA quantum sensors over four sunny days and the relative light intensity was calculated. The low- and high-nutrition treatment consisted of applications of 15 and 25 g of slow-release, compound fertilizer with N:P:K ratio at 1:1:1, respectively. This level was chosen because the interaction of higher soil temperature and moisture may increase nutrition several-fold in large gaps (Denslow *et al.* 1998). The fertilizer was dissolved as 0.5 % solution in weight for irrigating the plants every week and lasted for four months. All pots were watered to maintain the soil near field capacity on days without rain and were rotated at a 20-d interval to avoid rooting into ground and to minimize possible effects of position in the shade house. Weeds were removed regularly and insecticides were used when necessary. At the end of the experiment (after approx. 5 months), the nutrient measurements of leaves and fine roots were made for four or five plants per species per treatment. Morphological and biomass measurements were made for six to seven plants per species for each treatment.

Measurements

At the end of the experiment, plants were washed free of soil particles with tap water with all root systems intact and were separated into leaves, stems, coarse root (diameter > 2 mm) and fine root (diameter < 2 mm). Subsamples of leaf and fine-root were scanned on a desktop scanner. The acquired images were analyzed for leaf area, root length and average diameter, using DT-SCAN image analysis software (Delta-T Devices, Cambridge, UK) at 400 dots per inch. All samples were dried at 70 °C to a constant mass and then weighed. Specific leaf area (SLA), leaf area ratio (LAR), leaf mass ratio (LMR), stem mass ratio (SMR) and root mass ratio (RMR), and specific fine-root length (SRL) were then calculated. Relative biomass growth rate (RGR) was calculated as: RGR = (ln (final plant biomass at harvest)- ln (initial plant biomass))/time.

We assumed fine roots to be cylindrically shaped and the surface area of the cylinder was calculated as the surface area of the fine root (neglecting the area of the ends of the cylinder). Specific fine-root surface area (SRSA) was calculated. The total leaf and fine-root nitrogen concentration (N_{mass}) was measured by semi-micro Kjeldahl analysis using a wet digestion procedure; total leaf and fine-root phosphorus concentration (P_{mass}) was measured by atomic absorption spectrophotometry.

Statistical analyses

For each variable, data were analyzed with a three-way ANOVA, with species, light and nutrition as main fixed factors followed by a Tukey HSD post hoc test for species. Prior to analysis, data were checked for normality and homogeneity of variance, and were $\log_{10}$– transformed when necessary to satisfy the assumption of ANOVA. Because of the strong controls of plant size on allocation and foliage morphology and physiology (Poorter 2001), we analysed the influence of whole-plant dry mass on statistical models using covariance analyses. Pearson correlation analyses were

Table 1. Summary of the species, light and nutrition effects on physiological, morphological and growth traits in seedlings of five species with contrasting shade tolerance; the *P*-values of three-way ANOVA. Abbreviations: N_{mass}, nitrogen concentration; P_{mass}, phosphorus concentration; LAR, leaf area ratio; SLA, specific leaf area; SRL, specific fine-root length; SRSA, specific fine-root surface area; LMR, leaf mass ratio; SMR, stem mass ratio; RMR, root mass ratio; RGR, relative growth rate.

Factor	Leaf N_{mass}	Fine-root N_{mass}	Leaf P_{mass}	Fine-root P_{mass}	SLA	LAR	SRL	SRSA	LMR	SMR	RMR	RGR
Species (S)	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Light (L)	<0.001	<0.001	<0.001	0.035	0.034	<0.001	<0.001	0.001	0.024	0.650	0.314	<0.001
Nutrition (N)	<0.001	<0.001	<0.001	0.012	0.033	0.658	0.649	0.648	0.080	0.231	0.549	0.025
S × L	<0.001	<0.001	<0.001	<0.001	0.028	0.045	<0.001	0.710	0.035	0.049	0.212	<0.001
S × N	<0.001	0.016	<0.001	<0.001	0.001	0.010	0.839	0.393	0.044	0.126	0.126	<0.001
L × N	<0.001	0.440	<0.001	0.001	0.983	0.535	0.466	0.087	0.387	0.455	0.095	0.006
S × L × N	<0.001	<0.001	<0.001	<0.001	0.829	0.320	0.446	0.626	0.906	0.080	0.082	0.065

used to correlate the leaf and fine-root traits within and among species across all treatments. Plant dry mass was included as an additional explanatory variable to rule out the possibility that the correlations between leaf and fine-root traits resulted from overall differences in seedling size. We therefore used partial correlation coefficients between leaf and fine-root traits, controlling for the influence of plant biomass.

We calculated a plasticity index (PI) for each measured trait of each species, following Valladares *et al.* (2006). The index ranges from zero to one and is the difference between the maximum and minimum mean value of a trait among treatments divided by the maximum value. We used two approaches to test for differences in plasticity among species: (i) interaction terms (species × light, species × nutrient, species × light × nutrient) for a given trait in the three-way ANOVA analysis; (ii) the differences for the mean PI value of all variables were evaluated by a one-way ANOVA among species. Statistical analyses were performed using SPSS 13.0 (SPSS Inc., Chicago).

Results

Responses of leaf and fine-root nutrient concentrations to light and nutrient availability

Nitrogen and phosphorus concentrations of leaf and fine-root (N_{mass} and P_{mass}) differed significantly among the five studied species in all the treatments (Table 1, Fig. 1). With increasing shade tolerance, leaf N_{mass} and P_{mass} generally decreased, but not for fine-root N_{mass} and P_{mass}. There was a significant species × light × nutrient interaction for nutrient concentrations, indicating that the five species differed greatly in those variables when both light and nutrients are in abundant supply. Furthermore, all the paired interactions of these treatments (i.e. species × light, species × nutrient, nutrient × light) were significant. The differences in response of leaf and fine-root P_{mass} to light at different nutrient availability were indicated by the significant nutrient supply × light interaction (Table 1).

Responses of leaf, fine-root and whole-plant traits to light and nutrient availability

All morphological traits differed significantly among the five studied species. In general, with increasing shade tolerance, LAR, SRL, SRSA, LMR, and RGR of species decreased, whereas RMR increased across light and nutrient treatments (Fig. 2). Light had significant effects on most morphological traits, whereas nutrients had significant effects on only a few morphological traits (Table 1). On average, SLA, LAR, SRL, SRSA and SMR decreased, whereas LMR and RGR increased with increase in irradiance; SLA, LAR, LMR and RGR increased, whereas SRL, SRSA and SMR decreased with the increase in nutrition (Fig. 2). To further analyse interspecific variation in growth rate, RGR was related to some of its underlying components. RGR was significantly correlated with LAR, SRL and LMR, but not with SLA (Fig. 3). The positive correlation between SRL and RGR indicates that this root characteristic is important for plant productivity.

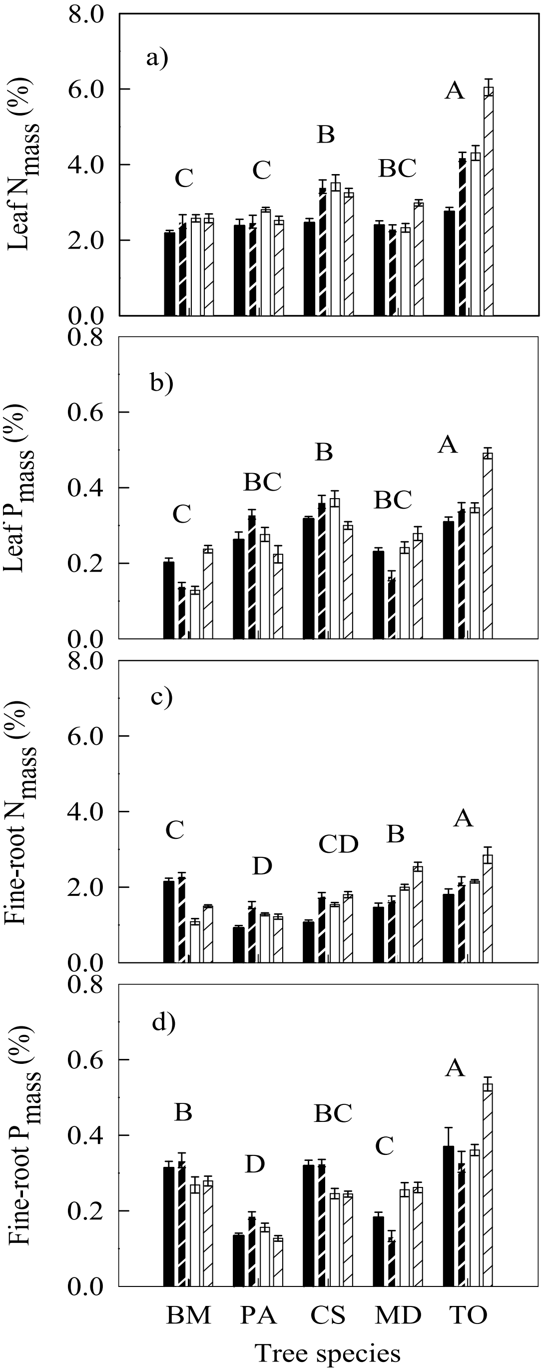

Fig. 1. The nitrogen and phosphorus concentrations of leaves and fine roots in seedlings for each species and treatment (mean ± SE, n = 4 - 5). Open and closed bars represent effects of light intensity (20 % and 4 % of full sunlight, respectively). Hatched bars represent effects of high nutrition addition. Significant differences (at $P < 0.05$) among the species across all treatments are indicated by different letters. Abbreviations of variables and species codes are as defined in Table 1 and 2, respectively.

When all species and treatments were pooled, there was consistent covariation in root and leaf traits across the environmental gradients (Fig. 4a-f). Leaf P_{mass} (N_{mass}) was positively correlated with fine-root P_{mass} (N_{mass}); and leaf mass (area) was positively correlated with fine-root mass (surface area), respectively. In addition, SLA was positively linearly correlated with SRL and SRSA.

Phenotypic plasticity among species and traits

The degree of light-dependent change in all traits except SRSA and RMR varied among species (significant species × light interaction). There were no significant species × light × nutrient interactions for morphological variables, indicating the light responsiveness at different nutrient availabilities was similar among different species (Table 1; Fig. 2). The plasticity index (PI) across all light and nutrient conditions varied from 0.035 to 0.544 and differed greatly among variables (Table 2). However, the mean plasticity of all traits com-bined did not differ significantly among the five studied species ($F_{4, 55} = 2.49$, $P > 0.05$). The degree of species' plasticity was dependent on the plant trait examined, and no one species was consis-tently the most or least flexible across the various traits. For example, *C. sumatranus* showed relatively higher plasticity in SRL but lower plasticity in LMR and SMR, whereas *M. denticulata* showed the reverse.

Discussion

Effects of light and nutrients and species difference

Light availability affected most measured variables, but the effects of nutrient addition were less pronounced, indicating that light may be a more important limiting factor than nutrition for tropical forest species (Cai *et al.* 2007, 2008; Graham *et al.* 2003; Lopez-Toledo *et al.* 2008). In general, plant responses to light or nutrient availability are directed to enhance the acquisition of resources that are in most limiting supply (Callaway *et al.* 2003). In low light, plants had a high LAR to enhance light capture, and plants had a high RMR in high light, exploring more water and nutrients (Poorter and Nagel 2000). Similarly, at low nutrient availability plants had a high SRL and SRSA to capture more nutrients, whereas at high nutrient availability they had a high SLA and LAR to capture light more efficiently per unit biomass and thus enhance growth (Poorter and

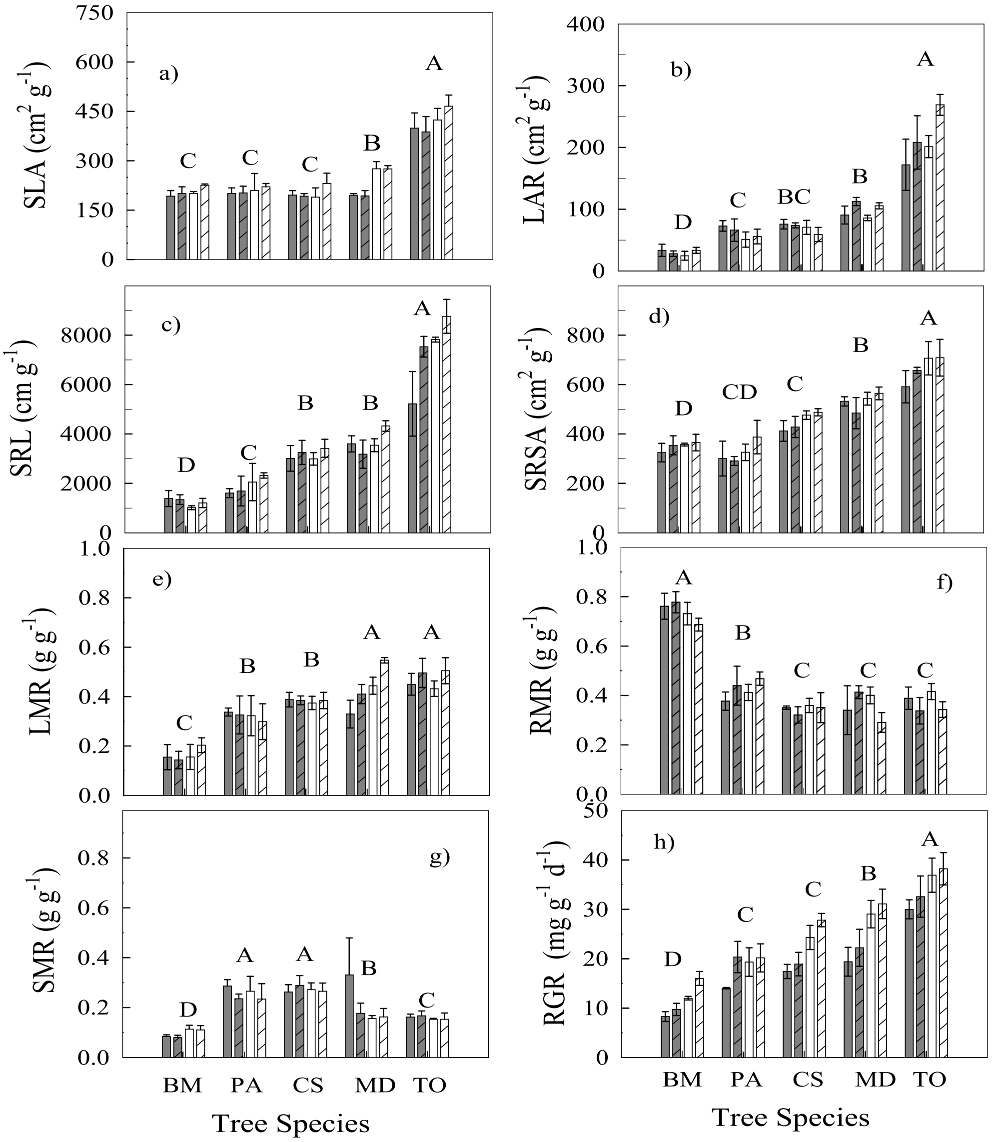

Fig. 2. The morphological traits of leaves, fine roots and whole plants in seedlings for each species and treatments (mean ± SE, n = 6 - 7). Open and closed bars represent effects of light intensity (20 % and 4 % of full sunlight, respectively). Hatched bars represent effects of high nutrient addition. Significant differences (at $P <$ 0.05) among the species across all treatments are indicated by different letters. Abbreviations of variables and species codes are as defined in Table 1 and 2, respectively.

Nagel 2000). We did not find significant light × nutrition interactions on most measured traits, which are consistent with previous studies (Portsmuth and Niinemets 2007; Cai *et al.* 2008). Perhaps plant morphological responses at the whole-plant level need more time to respond to the interactions of resources (Cai *et al.* 2008).

In line with our first prediction, it seemed that there was a relationship between above- and below-ground resources acquisition ability and the shade tolerance of species. Although the trend was not tightly followed, in general, leaf N_{mass} and P_{mass}, SLA, LAR, SRL, SRSA and LMR increased, whereas the RMR decreased across treatments with the decrease in shade tolerance among the five studied species. These patterns of leaf and fine-root traits in the present study contributed to effective strategy for maximizing above- and

Table 2. Phenotypic plasticity indices (PI = (max - min)/max) of 12 variables of five species in response to light and nutrition gradients. Means of total variables were not significantly different among the five studied species (*P* > 0.05, ANOVA). Abbreviations of variables are as defined in Table 1. Species codes: BM, *Barringtonia macrostachya*; PA, *Pterospermum acerifolium*; CS, *Cleistanthus sumatranus*; MD, *Macaranga denticulata*; TO, *Trema orientalis.*

Species code	Leaf trait			Fine-root trait				Whole-plant trait					Mean
	Leaf N_{mass}	Leaf P_{mass}	SLA	Fine-root N_{mass}	Fine-root P_{mass}	SRL	SRSA	LAR	LMR	SMR	RMR	RGR	
BM	0.153	0.459	0.265	0.53	0.196	0.266	0.208	0.263	0.296	0.297	0.116	0.155	0.267
PA	0.154	0.321	0.231	0.403	0.323	0.304	0.26	0.302	0.115	0.183	0.195	0.187	0.248
CS	0.302	0.191	0.207	0.412	0.251	0.21	0.217	0.22	0.035	0.092	0.107	0.204	0.211
MD	0.221	0.401	0.300	0.428	0.492	0.158	0.09	0.236	0.398	0.249	0.296	0.387	0.305
TO	0.544	0.371	0.263	0.371	0.385	0.491	0.163	0.361	0.145	0.083	0.187	0.450	0.318

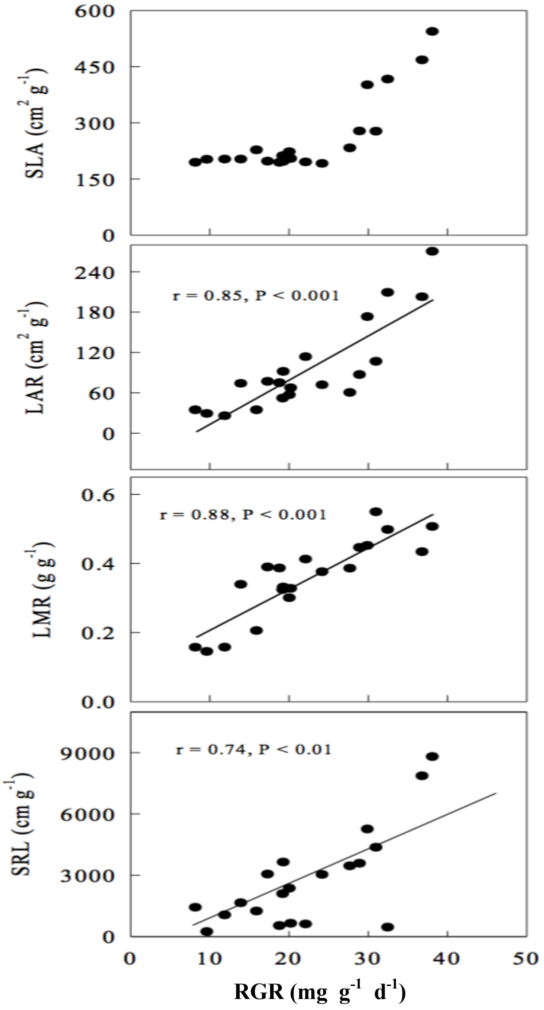

Fig. 3. Relationships between relative growth rate (RGR) and specific leaf area (SLA), leaf area ratio (LAR), leaf mass ratio (LMR) and specific fine-root length (SRL) for five studied species across different light and nutrition gradients.

below-ground resource capture (light, water and nutrients) for light-demanding species, which consequently had higher potential growth rates (i.e., RGR) than shade-tolerant species (this study; Cai *et al.* 2009; Coll *et al.* 2008; Comas and Eissenstat 2004; Paz 2003; Poorter and Rozendaal 2008). The increase in LMR, SLA and LAR of young seedlings with the decrease of shade tolerance in our study is consistent with the results from temperate and tropical angiosperms (Kitajima 1994; Reich *et al.* 1998; Walters and Reich 1996; but see temperate gymnosperms reviewed by Valladares and Niinemets 2008). This pattern has been suggested that plant's survival in shade (e.g. shade tolerance) is strongly related to plant resistance to biotic and abiotic stress (stress tolerant hypothesis; Kitajima 1994; Valladares and Niinemets 2008; Walters and Reich 1996). However, under natural conditions, some studies have found that pioneers can have considerably lower LMR values than shade-tolerant species (Selaya *et al.* 2007; Selaya and Anten 2010). The explanation could be that in natural conditions where plants experience spectral shading, pioneers tend to show a great response to the close proximity of neighbours by increasing mass investment to stem elongation (Gilbert *et al.* 2001). Another possible factor responsible for the low LMR of pioneers might be the strong leaf turnover to support leaf production in pioneers (Selaya *et al.* 2007). In general, fine-root nutrient concentrations did not increase with the decrease in shade tolerance across treatments among the five species, probably because fine-root physiology can vary sharply with fine-root age and root branch order, and the relationship between age and physiology can also vary between species (Comas and Eissenstat 2004).

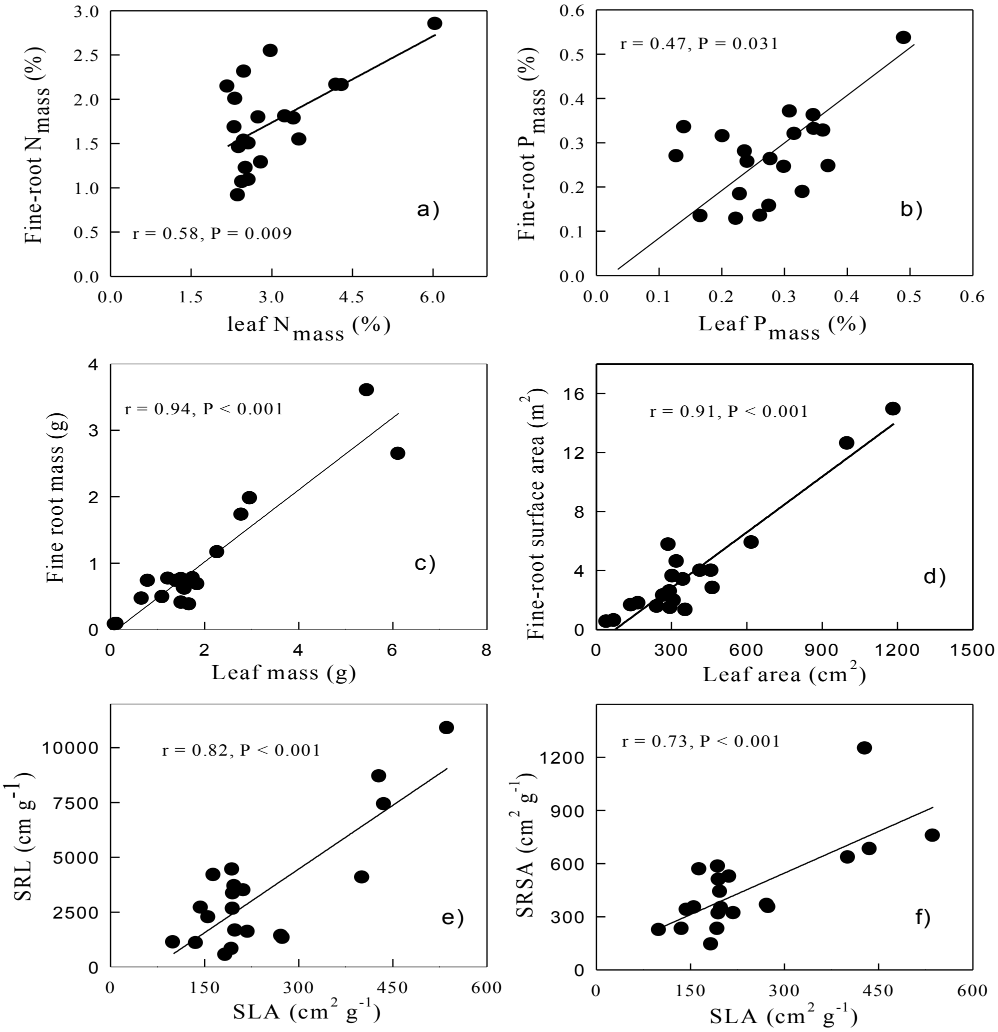

Fig. 4. Relationships between leaf and fine-root traits across species and treatments. Abbreviations of variables are as defined in Table 1.

Moreover, we found there were strong relationships between leaf and fine roots in structure, nutrient concentration and biomass allocation across species and treatments, suggesting a close coupling between above- and below-ground resource capture even over an environmental gradient (Holdaway *et al.* 2011; O'Grady *et al.* 2006). The leaf and fine-root relationship presented in this study provides support for a functional trade-off between above- and below-ground production (Hajek *et al.* 2013; O'Grady *et al.* 2006; Tjoelker *et al.* 2005; Withington *et al.* 2006).

Phenotypic plasticity

It was proposed that phenotypic plasticity of shade-tolerant species is generally lower than that of light-demanding species, although differences do not hold constant at each level of biological organization (leaf to whole plant) (Valladares and Niinemets 2008). In response to light and nutrient gradients, little evidence was found for the occurrence of an inter-specific variability of plasticity among our studied species irrespective of shade tolerance. This pattern contrasted with our second prediction and other results (Paz 2003; Portsmuth and Niinemets 2007; Sánchez-Gómez *et al.* 2006; Strauss-Debenedetti and Bazzaz 1996; Valladares *et al.* 2000). It was hypothesized that pioneers are more plastic than shade-tolerant species assuming that the environment of the former is more variable than that of the later (Bazzaz 1979; Strauss-Debenedetti and Bazzaz 1996). In contrast, shade-tolerant species may actually be more plastic than pioneers because they need to grow in a succession of shaded understory and gaps to reach the canopy (Pearcy 1987); and it is possible for pioneers not to show high plasticity because they always grow in high light and do not survive deep shade (Popma *et al.* 1992). Moreover, in a study of tropical tree species growing on Barro Colorado Island, Panama, individual leaves of shade-tolerant and light-demanding species experienced an equally wide range of light environments through the year; and thus no evidence was found for higher plasticity of pioneer compared with shade-tolerant species (Ellis *et al.* 2000). There are, nevertheless, several points that need be considered for the debate on variable plasticity among species and hence on the adaptive significance of plasticity. These contradictory results may partly be explained by the fact that: (1) in many studies only a few species have been evaluated (Cai *et al.* 2008; Portsmuth and Niinemets 2007; Sánchez-Gómez *et al.* 2006), and (2) it must be noted that conclusions on the role of phenotypic plasticity in shade tolerance crucially depend on the different suite of traits considered; and the shade tolerance of species is associated with a wide range of traits along the hierarchy from leaf to whole plant (Valladares and Niinemets 2008). One possible explanation for the similar plasticity of species with different shade tolerance is that they are more flexible in morphological traits but low flexible in physiological traits, and *vice versa* (Cai *et al.* 2008; Portsmuth and Niinemets 2007). (3) Plasticity is subject to large ontogenetic changes during the plant's life cycle (Markesteijn *et al.* 2007; Valladares and Niinemets 2008). Pioneers in the seedling stage are likely more plastic, whereas in the adult stage shade-tolerant species are more plastic (Grubb 1998). (4) Plasticity in response to one factor (e.g. light) can be affected by another factor (e.g. water and nutrient availability); and plasticity responded differently to different factors. For example, plasticity was higher in response to increased irradiance than in response to nutrient addition (this study; Cai *et al.* 2008; Portsmuth and Niinemets 2007).

Overall, we conclude that better above- and below-ground resource-foraging capacities allow the light-demanding species to outgrow the shade-tolerant species, but the seedlings of species with different shade tolerance have similar plasticity in response to light and nutrient gradients. The strong relationship between leaves and fine roots in structure and function across species emphasizes the importance of a concerted plastic response of plant characteristics as a means of maintaining balanced acquisition of above- and below-ground resources along the environmental gradients; and aiding in predicting plant and ecosystem response to in a changing environment (Holdaway *et al.* 2011).

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References

Bazzaz, F. A. & P. M. Wayne. 1994. Coping with environmental heterogeneity: the physiological ecology of tree seedling regeneration across the gap-understory continuum. pp. 349-390. *In*: M. M. Caldwell & R. W. Pearcy (eds.) *Exploitation of Environmental Heterogeneity by Plants: Ecophysiological Processes Above- and Belowground*. Academic Press, San Diego.

Bazzaz, F. A. 1979. The physiological ecology of plant succession. *Annual Review of Ecology and Systematics* **10**: 351-371.

Cai, Z. Q., Y. J. Chen & F. Bongers. 2007. Seasonal changes in photosynthesis and growth of *Zizyphus attopensis* seedlings in three contrasting microhabitats in a tropical seasonal rain forest. *Tree Physiology* **27**: 827-836.

Cai, Z. Q., L. Poorter, Q. Han & F. Bongers. 2008. Effects of light and nutrients on seedlings of tropical *Bauhinia* lianas and trees. *Tree Physiology* **28**: 1277-1285.

Cai, Z. Q., T. Rijkers & F. Bongers. 2005. Photosynthetic acclimation to light changes in tropical monsoon forest woody species differing in adult stature. *Tree Physiology* **25**: 1023-1031.

Cai, Z. Q., H. Wang, J. Yang & C. T. Cai. 2009. Growth, photosynthesis and root reserpine concentrations of two *Rauvolfia* species in response to a light gradient. *Industrial Crops and Products* **30**: 220-226.

Callaway, R. M., S. C. Penninge & C. L. Richards. 2003. Phenotypic plasticity and interactions among plants. *Ecology* **84**: 1115-1128.

Choudhury, B. I., M. L. Khan & A. K. Das. 2014. Seedling dynamics of the critically endangered tree legume *Gymnocladus assamicus* in northeast India. *Tropical Ecology* **55**: 375-384.

Coll, L., C. Potvin, C. Messier & S. Delagrange. 2008.

Root architecture and allocation patterns of eight native tropical species with different successional status used in open-grown mixed plantations in Panama. *Trees* **22**: 585-596.

Comas, L. H. & D. M. Eissenstat. 2004. Linking fine root traits to maximum potential growth rate among 11 mature temperate tree species. *Functional Ecology* **18**: 388-397.

Coste, S., J. Roggy, G. Sonnier & E. Dreyer. 2010. Similar irradiance-elicited plasticity of leaf traits in saplings of 12 tropical rainforest tree species with highly different leaf mass to area ratio. *Functional Plant Biology* **37**: 342-355.

Craine, J. M., J. Froehle, D. G. Tilman, D. A. Wedin & F. S. Chapin. 2001. The relationships among root and leaf traits of 76 grassland species and relative abundance along fertility and disturbance gradients. *Oikos* **93**: 274-285.

Denslow, J. S., A. M. Ellison & R. E. Sanford. 1998. Treefall gap size effects on above- and below-ground processes in a tropical wet forest. *Journal of Ecology* **86**: 597-609.

Ellis, A. R., S. P. Hubbell & C. Potvin. 2000. In situ field measurements of photosynthetic rates of tropical tree species: a test of the functional group hypothesis. *Canadian Journal of Botany* **78**: 1336-1347.

Fetcher, N., B. L. Haines, R. A. Cordero, D. J. Lodge, L. R. Walker, D. S. Fernandez & W. T. Lawrence. 1996. Response of tropical plants to nutrients and light on a landslide in Puerto Rico. *Journal of Ecology* **84**: 331-341.

Gilbert, I. R., P. G. Jarvis & H. Smith. 2001. Proximity signal and shade avoidance differences between early and late successional trees. *Nature* **411**: 792-795.

Graham, E. A., S. S. Mulkey, K. Kitajima, N. G. Phillips & S. J. Wright. 2003. Cloud cover limits net CO_2 uptake and growth of a rainforest tree during tropical rainy seasons. *Proceedings of the National Academy of Sciences, USA* **100**: 572-576.

Grubb, P. J. 1998. A reassessment of the strategies of plants which cope with shortage of resources. *Perspectives in Plant Ecology, Evolution and Systematics* **1**: 3-31.

Hajek, P., D. Hertel & C. Leuschner. 2013. Intraspecific variation in root and leaf traits and leaf-root trait linkages in eight aspen demes (*Populus tremula* and *P. tremuloides*). *Frontiers in Plant Science* **21**: 415.

Holdaway, R. J., S. J. Richardson, I. A. Dickie, D. A. Peltzer & D. A. Coomes. 2011. Species- and community-level patterns in fine root traits along a 120000-year soil chronosequence in temperate rain forest. *Journal of Ecology* **99**: 954-963.

Kitajima, K. 1994. Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance of 13 tropical trees. *Oecologia* **98**: 419-428.

Lan, G., H. Zhu & M. Cao. 2011. Tree species diversity of a 20-ha plot in a tropical seasonal rainforest in Xishuangbanna, southwest China. *Journal of Forestry Research* **17**: 432-439.

Lopez-Toledo, L., M. Martinez, M. Breugel & F. J. Sterck. 2008. Soil and light effects on the sapling performance of the shade-tolerant species *Brosimum alicastrum* (Moraceae) in a Mexican tropical rain forest. *Journal of Tropical Ecology* **24**: 629-637.

Markesteijn, L., L. Poorter & F. Bongers. 2007. Light-dependent leaf trait variation in 43 tropical dry forest tree species. *American Journal of Botany* **94**: 515-525.

Neuner, G. & P. Bannister. 1995. Frost resistance and susceptibility to ice formation during natural hardening in relation to leaf anatomy in three evergreen tree species from New Zealand. *Tree Physiology* **15**: 371-377.

Negreiros, D., D. Esteves, G. Wilson Fernandes, R. L. L. Berbara, Y. Oki, V. Marcelo & C. Clarissa. 2014. Growth-survival tradeoff in the widespread tropical shrub *Baccharis dracunculifolia* (Asteraceae) in response to a nutrient gradient. *Tropical Ecology* **55**: 167-176.

O'Grady, A. P., D. Woeledge & M. Battaglia. 2006. Above- and below-ground relationships, with particular reference to fine roots, in a young *Eucalyptus globulus* (Labill.) stand in southern Tasmania. *Trees* **20**: 531-538.

Pearcy, R. W. 1987. Photosynthetic gas exchange responses of Australian tropical forest trees in canopy, gap, and understory micro-environments. *Functional Ecology* **1**: 169-178.

Poorter, H. & O. Nagel. 2000. The role of biomass allocation in the growth response of plants to different levels of light, CO_2, nutrients and water: a quantitative review. *Australian Journal of Plant Physiology* **27**: 595-607.

Poorter, L. 2001. Light-dependent changes in biomass allocation and their importance for growth of rain forest tree species. *Functional Ecology* **15**: 113-123.

Poorter, L. & D. M. A. Rozendaal. 2008. Leaf size and leaf display of 38 tropical tree species. *Oecologia* **158**: 35-46.

Popma, J., F. Bongers & M. J. A. Werger. 1992. Gap-dependence and leaf characteristics of trees in a tropical lowland rain forest in Mexico. *Oikos* **63**: 207-214.

Portsmuth, A. & Ü. Niinemets. 2007. Structural and physiological plasticity to light and nutrients in five temperate deciduous woody species of contrasting shade tolerance. *Functional Ecology* **21**: 61-77.

Paz, H. 2003. Root/shoot allocation and root architecture in seedlings: variation among forest sites, microhabitats, and ecological groups. *Biotropica* **35**: 318-332.

Reich, P. B., M. G. Tjoelker, M. B. Walters, D. W. Vanderklein & C. Buschena. 1998. Close association of RGR, leaf and root morphology, seed mass and shade tolerance in seedlings of nine boreal tree species grown in high and low light. *Functional Ecology* **12**: 327-338.

Rozendaal, D. M. A., V. H. Hurtado & L. Poorter. 2006. Plasticity in leaf traits of 38 tropical tree species in response to light; relationships with light demand and adult stature. *Functional Ecology* **20**: 207-216.

Sánchez-Gómez, D., F. Valladares & M. A. Zavala. 2006. Functional traits and plasticity underlying shade tolerance in seedlings of four Iberian forest tree species. *Tree Physiology* **26**: 1425-1433.

Schulze, E. D. & F. S. Chapin. 1987. Plant specialization to environments of different resource availability. pp. 120-148. *In*: E. D. Schulze & H. Zwoelfer (eds.) *Potentials and Limitations of Ecosystem Analysis*. Springer-Verlag, Berlin.

Selaya, N. G., N. P. R. Anten, M. Mathies, R. J. Oomen & M. J. A. Werger. 2007. Aboveground biomass investments and light interception of tropical forest trees early in succession. *Annals of Botany* **99**: 121-130.

Selaya, N. G. & N. P. R. Anten. 2010. Leaves of pioneer and later-successional trees have similar lifetime carbon gain in tropical secondary forest. *Ecology* **91**: 1102-1113.

Strauss-Debenedetti, S. & F. A. Bazzaz. 1996. Photosynthetic characteristics of tropical trees along successional gradients. pp. 162-186. *In*: S. S. Mulkey, R. L. Chazdon & A. P. Smith (eds.) *Tropical Forest Plant Ecophysiology*. Chapman & Hall, New York.

Tjoelker, M. G., J. M. Craine, D. Wedin, P. B. Reich & D. Tilman. 2005. Linking leaf and root trait syndromes among 39 grassland and savannah species. *New Phytologist* **167**: 493-508.

Valladares, F. & Ü. Niinemets. 2008. Shade tolerance, a key plant trait of complex nature and consequences. *Annual Review of Ecology, Evolution and Systematics* **39**: 237-257.

Valladares, F., S. J. Wright, E. Lasso, K. Kitajima & R. W. Pearcy. 2000. Plastic phenotypic response to light of 16 congeneric shrubs from a Panamanian rainforest. *Ecology* **81**: 1925-1936.

Valladares, F., D. Sanchez & M. A. Zavala. 2006. Quantitative estimation of phenotypic plasticity: Bridging the gap between the evolutionary concept and its ecological applications. *Journal of Ecology* **94**: 1103-1116.

Vázquez-Yanes, C. 1998. *Trema micrantha* (L.) Blume (Ulmaceae): a promising neotropical tree for site amelioration of deforested land. *Agroforestry Systems* **40**: 97-104.

Walters, M. B. & P. B. Reich. 1996. Are shade tolerance, survival, and growth linked? Low light and nitrogen effects on hardwood seedlings. *Ecology* **77**: 841-853.

Weinig, C. & L. F. Delph. 2001. Phenotypic plasticity early in life constrains developmental responses later. *Evolution* **55**: 930-936.

Withington, J. M., P. B. Reich, J. Oleksyn & D. M. Eissenstat. 2006. Comparisons of structure and life span in root and leaves among temperate tree. *Ecological Monographs* **76**: 381-397.

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