

Effects of light and nutrients on seedlings of tropical *Bauhinia* lianas and trees

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Summary Lianas differ from trees in many life history characteristics, and we predicted that they are phenotypically more responsive to environmental variation than trees. We analyzed responsiveness to light and nutrient availability of five *Bauhinia* species (three lianas and two trees). Seedlings were grown in a shade house in two light regimes (5 and 25% of full sunlight) and two nutrient supply regimes (field soil and N fertilization equivalent to 100 kg ha⁻¹), and important growth-related physiological and morphological plant parameters were measured. Light availability affected most of the measured variables, whereas N addition had only weak effects. In the four light-demanding species (two lianas and two trees), relative plant biomass growth rate increased and specific leaf area (SLA) decreased with increased light availability, whereas a shade-tolerant liana did not respond. Leaf N concentration and light-saturated photosynthetic rate per unit leaf area increased in response to increased irradiance or soil N in the light-demanding tree species and the shade-tolerant liana, but not in the two light-demanding lianas. The light-demanding lianas also had higher SLA and leaf mass ratio, resulting in a higher leaf area ratio (LAR) in high light, whereas the light-demanding trees did not. Across all treatments, mean plasticity indices of physiological and morphological traits, and all traits combined were similar among the studied species. Plasticity was higher in response to light than to N, indicating that light is the main factor controlling seedling responses of the studied species. Although lianas and trees did not differ in mean plasticity in response to light and N, the light-demanding lianas were phenotypically less plastic in LAR and in photosynthetic rates and biomass allocation than the trees. Light and N interacted in their effects on most physiological variables, but the consequences for relative growth rate differed little among species. We conclude that, contrary to our predictions, lianas were no more responsive to variation in light and N availability than trees.

Keywords: biomass allocation, phenotypic plasticity, photosynthesis, relative growth rate, shade tolerance.

Introduction

In tropical rain forests, there are marked spatial and temporal gradients in light, nutrient and water availability (Poorter 2005, John et al. 2007). Light is the most limiting factor for plant growth and survival in the forest understory, but nutrients can be limiting as well, especially at high irradiances (Veenendaal et al. 1996, Coomes and Grubb 2000). Yet, light and nutrient availability are often negatively associated along the gap–understory gradient (Bazzaz and Wayne 1994, Fownes and Harrington 2004).

Plant performance may be enhanced through morphological and physiological adjustments to the environment (Niinemets and Valladares 2004, Mittler 2006). Phenotypic adjustments to light and nutrients range from physiological changes in PSII quantum yield at the leaf level (Percy and Sims 1994, Cai et al. 2005) to changes in allocation and morphology at the whole-plant level (Poorter and Nagel 2000, Poorter 2005, Cai et al. 2007a). For example, shade-tolerant species increase their capacity for light capture when light availability is low through increased biomass allocation to leaves, whereas light-demanding plants maximize carbon gain and minimize photoinhibition when light availability is high through an increase in photosynthetic capacity (Percy and Sims 1994, Poorter 2005). Pioneer species show a greater response to additional nutrients than shade-tolerant species (Huante et al. 1995, Fetcher et al. 1996). Phenotype plasticity is thought to differ predictably among species and functional groups; light-demanding species were hypothesized to have a higher plasticity than shade-tolerant species because they grow in a more variable environment (Bazzaz 1979). There is no general consensus about this hypothesis; some studies show a greater phenotypic plasticity in pioneer species (Bazzaz and Wayne 1994, Portsmouth and Niinemets 2007), whereas other studies show that pioneer species have a similar (Sims and Percy 1992, Rozendaal et al. 2006, Markesteijn et al. 2007) or even lower (Popma et al. 1992) phenotypic plasticity than shade-tolerant species.

Light and nutrients can affect plant growth and plasticity interactively (Denslow et al. 1990, Latham 1992, Portsmouth and Niinemets 2007). These interactive effects can alter species competitive potential at different resource availabilities, and therefore they can have important consequences for the coexistence of species and the evolution of adaptive strategies (Grubb et al. 1996, Poorter 2005). Lianas (woody climbers), for example, an important component in tropical forests (Schnitzer and Bongers 2002), differ from tree species in growth strategies and biomass allocation patterns (Putz and Mooney 1991, Cai et al. 2007b). Lianas are generally considered to be light-demanding, because their abundance increases with forest disturbance and light availability (Putz 1984, Schnitzer et al. 2000). During ontogenetic development, lianas experience temporal and spatial heterogeneity in solar irradiance (Ray 1990, Teramura et al. 1991, Selaya et al. 2007) and show high phenotypic plasticity in response to changes in light availability (Salzer et al. 2006). We might, therefore, expect lianas to show greater morphological changes in response to light than trees, because species with high carbon gain and high growth rates can more easily realize costly morphological changes (Popma and Bongers 1991). Moreover, some experiments revealed that lianas generally colonize nutrient-rich soil patches quickly and show a high response to nutrition addition (Balfour and Bond 1993), although this pattern is not always clear (Balfour and Bond 1993, DeWalt and Chave 2004, Macía et al. 2007). To our knowledge, no experiments have been done on the interactive effects of light and nutrients on lianas.

In this study, we compared phenotypic leaf- and plant-level responses of five coexisting *Bauhinia* species to light and nitrogen availability. Species from one genus were selected for comparison based on their phylogenetic relatedness and life forms (lianas versus trees), an important condition for inference in comparative studies (Felsenstein 1985). Our objectives were to determine: (1) whether lianas and trees show differences in their physiological and morphological responses to light and nutrient availability; and (2) whether lianas differ from trees in the plasticity of their phenotypic response to light and nutrient availability. We predicted that liana species have more flexible traits and are thus better adapted to light and nutrient gradients compared with their tree congeners and that this flexibility accounts for their success in variable environments.

Materials and methods

Study site and plant species

The study was conducted in Xishuangbanna (21°09′–22°33′ N, 99°58′–101°50′ E), SW China. Mean annual temperature in Xishuangbanna is 21.4 °C. Mean annual rainfall is 1539 mm, 85% of which occurs in the rainy season (May–October), with heavy fog partially compensating for the reduced rainfall during the dry season (November–April). We selected five species of *Bauhinia* (three lianas and two trees). *Bauhinia claviflora* L. Chen and *B. tenuiflora* Watt ex C.B. Clarke are

light-demanding liana species that are abundant in large canopy gaps. *Bauhinia aurea* Levl. is an extremely shade-tolerant liana and is found in the shaded understory. *Bauhinia purpurea* Linn. and *B. monandra* Kurz are both light-demanding tree species and are more abundant in canopy gaps than in the understory (Cai et al. 2007b).

Experimental design

Seedlings were collected from Xishuangbanna Botanical Garden and a nearby nursery during May 2004, transplanted to 20 × 30 cm pots containing topsoil from the nearby forest and placed in a shade house. After 5–6 weeks, bud expansion started and 4–6 seedlings per species (mean dry biomass ranged from 3.8 to 11 g) were harvested. 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 treatment (25% of full sunlight, 6.97 mol m⁻² day⁻¹, typical of a large canopy gap) and low-light treatment (5% of full sunlight, 1.37 mol m⁻² day⁻¹, typical of a small gap formed by a single falling tree) were created by placing layers of neutral-density screen on a steel frame. Light availability in the shade house (photosynthetic photon flux, PPF) was measured with LI-190SA quantum sensors connected to an LI-1400 data logger (Li-Cor) over four sunny days. The low-nitrogen (N) treatment consisted of untreated forest topsoil, and the high-N treatment consisted of bi-monthly applications of ammonium nitrate solution to the forest topsoil to raise the soil N concentration to 100 kg N ha⁻¹. All plants were watered on days without rain to maintain the soil near field capacity. Lianas were supported with dry bamboo shoots. All lianas started to climb halfway through the experiment. At the end of the experiment (about 6 months after the initial harvest), physiological measurements were made on one leaf per plant from 3–4 plants per treatment combination. Morphological and biomass measurements were made on 5–7 plants per species per treatment.

Photosynthesis, nitrogen concentration and carbon isotope measurements

Light-saturated net CO₂ assimilation was measured at ambient CO₂ concentration (about 400 ppm) and temperature (25–27 °C) with a portable infrared gas analyzer in open-system mode (LI-6400, Li-Cor). Photosynthetic photon flux was set at 1000–1500 μmol m⁻² s⁻¹ with the built-in LED-B light source. Light-response curves showed that this was sufficient to saturate photosynthesis in all species and under all treatments (results not shown). Measurements were made on fully expanded, healthy leaves. Chlorophyll fluorescence was measured with a portable fluorescence system (FMS-2.02, Hansatech, King's Lynn, U.K.) and used to assay for photo-inhibition. Minimal (F_o) and maximal (F_m) fluorescence yields were measured on leaves after maintaining them in the dark for about 15 min. Variable fluorescence (F_v) was calculated as the difference between maximal and minimal fluorescence. The dark-adapted photochemical efficiency of PSII (F_v/F_m) was measured before dawn (0630 h) and in the middle

of the day (1400 h). Diurnal photoinhibition ($\%F_v/F_m$) was calculated as:

$$\%F_v/F_m = \left(1 - \frac{F_v/F_m|_{1400\text{h}}}{F_v/F_m|_{0630\text{h}}}\right) 100$$

After the photosynthetic measurements, leaves were collected and analyzed for N concentration, $\delta^{13}\text{C}$ isotope ratio and biomass. The $\delta^{13}\text{C}$ isotope ratio provides an integrated estimate of the ratio of photosynthesis to conductance and therefore can be used as an index of intrinsic water-use efficiency (Farquhar and Richards 1984). Leaves were ground to a fine powder for elemental analyses of $\delta^{13}\text{C}$ and N concentration. The $\delta^{13}\text{C}$ isotope ratio for leaves from all species but *B. aurea* was measured in 2 mg subsamples with a Thermo Finnigan MAT stable isotope mass spectrometer (Bremen, Germany) at the Stable Isotope Laboratory at the Institute of Botany of the Chinese Academy of Sciences. Foliar N concentration (N_m , %) was measured by semi-micro Kjeldahl analysis using a wet digestion procedure. Intrinsic photosynthetic N-use efficiency (PNUE, $\mu\text{mol CO}_2 \text{ mol}^{-1} \text{ N s}^{-1}$) was determined as light-saturated photosynthetic rate based on mass (A_m) divided by N_m .

Plant growth and biomass

At harvest, plants were separated into leaves, stems and roots. Leaf areas were determined with a Li-Cor leaf area meter (LI-3000A). Roots were washed in tap water. All tissues were dried to constant mass at 70 °C for 48 h. Specific leaf area (SLA, $\text{cm}^2 \text{ g}^{-1}$), leaf area to plant mass ratio (LAR, $\text{cm}^2 \text{ g}^{-1}$), leaf mass ratio (LMR), stem mass ratio (SMR) and root mass ratio (RMR) were calculated. Relative biomass growth rate (RGR) was calculated as: $\text{RGR} = (\ln(\text{final plant mass at harvest}) - \ln(\text{initial plant mass}))/\text{time}$.

Statistical analysis

To compare plasticity among leaf and whole-plant traits, e.g., physiological versus morphological traits, we calculated a plasticity index (PI_v) 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. Plasticity to environmental heterogeneity in general was calculated based on the highest and lowest parameter values found in the four treatment combinations. For the calculation of the plasticity to irradiance, we used the mean trait value at low and high light by pooling both N treatments. For plasticity to nutrients, we used the mean trait value at low and high N by pooling both light treatments. In addition, a mean plasticity index was calculated for each species by averaging the 12 variables.

For each morphological and physiological variable in each species, data were analyzed by three-way ANOVA, with species, light and nutrient as main fixed factors. Effects of light and nutrients on each variable within each species were assessed by a two-way ANOVA. Before analysis, data were checked for normality and homogeneity of variables, and were

\log_{10} or square-root transformed when necessary to satisfy the assumption of ANOVA. Pearson correlation analyses were used to correlate the maximum observed RGR across all treatments (RGR_{max}) with the plasticity indices.

Results

Responses to light

The three-way ANOVA explained much of the variation in trait values, with a mean r^2 of 0.92 (range 0.81–0.99, Table 1). All traits were significantly affected by species. Light had a significant effect on all morphological and physiological variables except $\delta^{13}\text{C}$ and LAR (Table 1). With an increase in irradiance, the seedlings had, on average, a higher N_m and mass- and area-based photosynthetic rates, but lower PNUE. Compared with seedlings in the low-light treatment, seedlings in the high-light treatment had a higher LMR which, in combination with a lower SLA, resulted in a statistically similar LAR in high light and low light. Seedlings exposed to high irradiance had a higher RMR, lower SMR, and realized a higher RGR than seedlings exposed to low irradiance.

There were significant species \times light interactions for all traits (Table 1), implying that the responsiveness to light differed among species. Such interactions may indicate that species differ in the magnitude, significance or direction of the responses to light. For example, all species showed a significant increase in diurnal photoinhibition with an increase in irradiance, but the magnitude of increase was much greater in the shade-tolerant *B. aurea* compared with the four light-demanding species (Figure 1d). An increase in irradiance had a significantly positive effect on A_a and N_m in the two light-demanding tree species, but not in the two light-demanding lianas (Figures 1a and 1c). In contrast, the high-light treatment had a significant negative effect on LAR in the light-demanding lianas, but had no significant effect on LAR of the tree species. Species differed in the direction of response to light in one physiological trait (A_m) and four morphological traits (RMR, SMR, LMR and LAR) (Figures 1 and 2). For example, in response to higher irradiance, BA and BP increased in LMR, whereas BT and BC decreased in LMR (Figure 2a). There was a significant species \times light interaction for RGR (Table 1). All light-demanding species showed a significant increase in RGR with increased irradiance, whereas the shade-tolerant *B. aurea* did not (Figure 2f).

Responses to nutrients

Nutrients had a significant effect on seven of twelve measured traits (Table 1). With an increase in nutrient availability, the seedlings had a higher mean N_m , and hence, higher mean mass- and area-based photosynthetic rates (Table 1). At high nutrient availability, seedlings had a lower biomass fraction in roots (RMR) and higher biomass fraction in leaves (LMR) and, as a consequence, a higher LAR and RGR. A significant species \times nutrient interaction was found only for N_m and A_a , and a nearly significant interaction was found for LAR and $\%F_v/F_m$ (Table 1). The two light-demanding trees increased their A_a signif-

Table 1. Summary of the three-way ANOVA to evaluate the effects of species, light and nutrition on morphological and physiological traits and the mean value of each trait in different treatments. Abbreviations: A_a and A_m , light-saturated photosynthetic rate based on leaf area ($\mu\text{mol m}^{-2} \text{s}^{-1}$) and leaf mass ($\text{nmol g}^{-1} \text{s}^{-1}$), respectively; N_m , leaf nitrogen concentration (%); PNUE, photosynthetic nitrogen-use efficiency ($\mu\text{mol CO}_2 \text{mol}^{-1} \text{N s}^{-1}$); $\delta^{13}\text{C}$, carbon isotope ratio (‰); $\%F_v/F_m$, diurnal photoinhibition (%); LMR, leaf mass to plant mass ratio (%); SMR, stem mass to plant mass ratio (%); RMR, root mass to plant mass ratio (%); SLA, specific leaf area ($\text{cm}^2 \text{g}^{-1}$); LAR, leaf area to plant mass ratio ($\text{cm}^2 \text{g}^{-1}$); and RGR, relative growth rate ($\text{mg g}^{-1} \text{day}^{-1}$). Significant effects ($P < 0.05$) are shown in bold.

Factor	Physiological variables						Morphological variables					
	A_a	A_m	N_m	PNUE	$\delta^{13}\text{C}$	$\%F_v/F_m$	LMR	SMR	RMR	SLA	LAR	RGR
Model r^2	0.994	0.959	0.976	0.812	0.876	0.845	0.845	0.895	0.967	0.952	0.968	0.976
Species	< 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	< 0.001	< 0.001	< 0.001	0.023	0.069	< 0.001	< 0.001	0.047	< 0.001	< 0.001	0.096	< 0.001
Nutrition	< 0.001	< 0.001	< 0.001	0.063	0.089	0.078	0.011	0.680	0.018	0.070	< 0.001	< 0.001
Species × Light	< 0.001	< 0.001	< 0.001	< 0.001	0.045	< 0.001	< 0.001	< 0.001	< 0.001	0.003	< 0.001	< 0.001
Species × Nutrition	< 0.001	0.184	0.017	0.071	0.065	0.052	0.435	0.169	0.633	0.537	0.063	0.116
Light × Nutrition	< 0.001	0.039	0.009	0.035	0.087	0.047	0.204	0.111	0.967	0.350	0.087	0.008
Species × Light × Nutrition	< 0.001	0.002	0.112	0.001	0.345	0.077	0.669	0.796	0.934	0.391	0.868	0.106
<i>Treatment means</i>												
Low light	4.20	139.81	3.07	47.31	-30.18	5.62	30.04	38.01	28.44	330.59	87.08	12.57
High light	5.70	149.34	3.57	42.85	-29.04	10.39	31.67	37.19	30.10	281.91	82.63	20.16
Low nutrient	4.73	138.92	3.24	44.14	-29.80	8.04	29.29	37.88	30.15	301.28	79.85	15.80
High nutrient	5.17	150.23	3.40	46.02	-29.42	7.96	32.43	37.32	28.39	311.23	89.86	16.93

icantly in response to increased nutrient availability, whereas the lianas did not (Figure 1a). Although BA and BP increased their N_m significantly in response to nutrient addition the other species did not (Figure 1c). The two light-demanding lianas increased their LAR in response to increased nutrient avail-

ability, whereas the other species did not (Figure 2d). There was no significant species × nutrient interaction for RGR (Table 1), indicating that all species showed a similar, modest, increase in RGR with an increase in nutrient availability (Figure 2f). There was a significant species × light × nutrient inter-

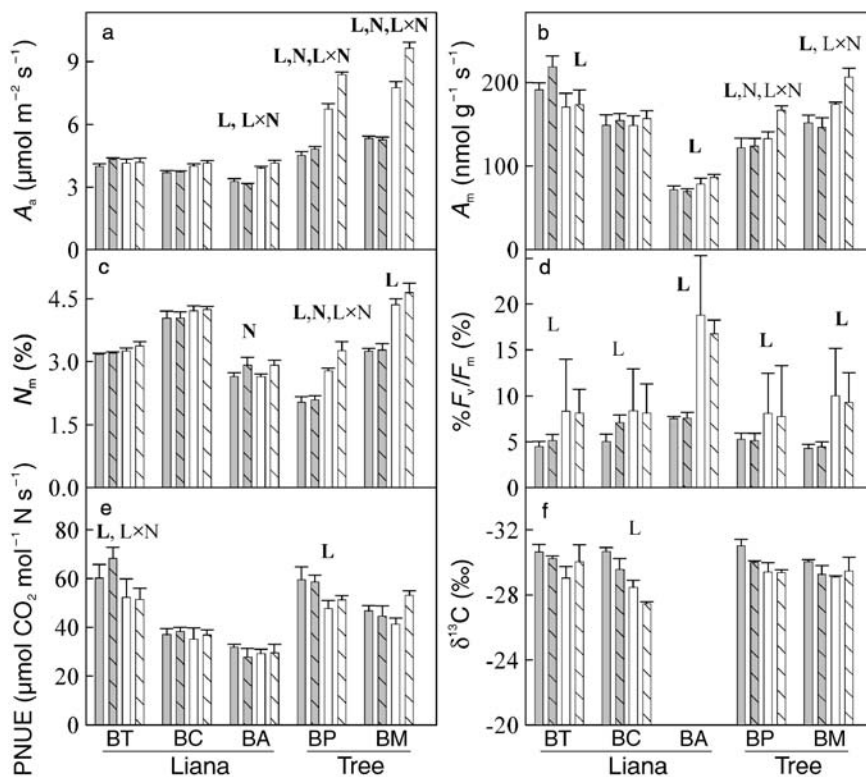


Figure 1. Mean values (\pm SD) of leaf traits for each species and treatment. Open and closed bars represent 25 and 5% of full sunlight, respectively. Hatched bars represent N fertilization. Significant treatment effects are indicated by L (light) and N (nitrogen) for each species ($P < 0.05$). Bold letters indicate $P < 0.01$. Species abbreviations: BT, *Bauhinia tenuiflora*; BC, *B. claviflora*; BA, *B. aurea*; BP, *B. purpurea*; and BM, *B. monandra*.

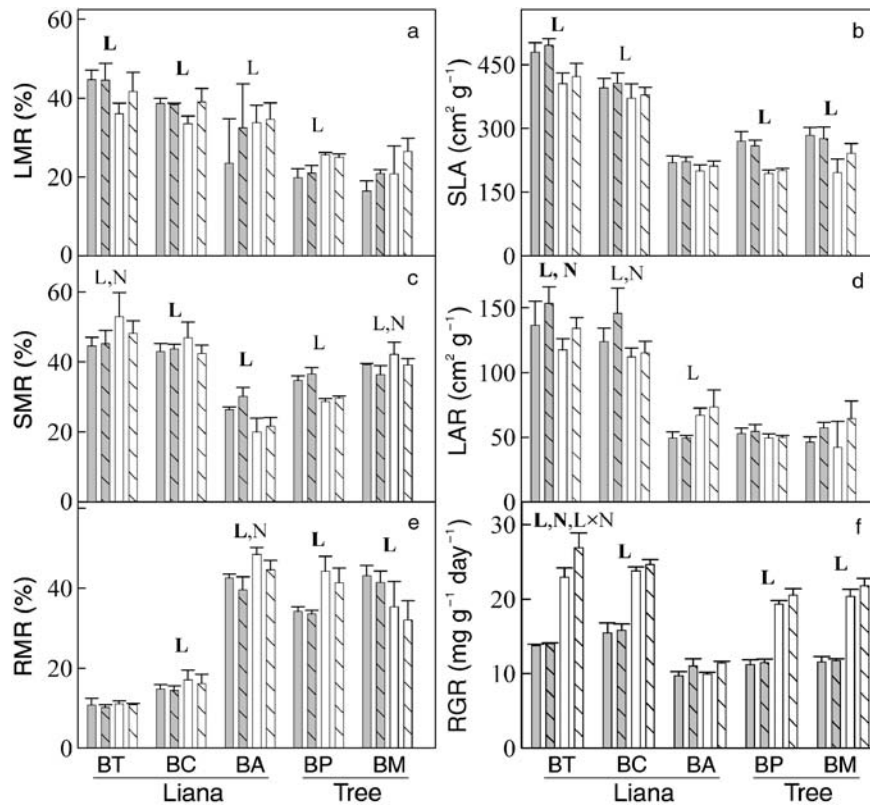


Figure 2. Mean values (\pm SD) of whole-plant traits for each species and treatment. Open and closed bars represent 25 and 5% of full sunlight, respectively. Hatched bars represent N fertilization. Significant treatment effects are indicated by L (light) and N (nitrogen) for each species ($P < 0.05$). Bold letters indicate $P < 0.01$. Species abbreviations: BT, *Bauhinia tenuiflora*; BC, *B. claviflora*; BA, *B. aurea*; BP, *B. purpurea*; and BM, *B. monandra*.

action for A_a and A_m , indicating that the two light-demanding tree species realize especially high photosynthetic rates when both light and nutrients are abundant, whereas the lianas generally did not (Figures 1a and 1b).

Phenotypic plasticity

The plasticity index (PI_v) calculated across all light and nutrient conditions ranged from 0.031 to 0.598. The plasticity index differed significantly among variables (one-way ANOVA, $F_{11,47} = 4.0$, $P < 0.001$), and was lowest for $\delta^{13}C$ (0.07) and highest for RGR (0.40) and $\%F_v/F_m$ (0.45) (post-hoc test, $P < 0.05$) (Table 2). The species did not differ significantly in

the plasticity of their physiological traits (ANOVA, $F_{4,24} = 0.83$, $P = 0.52$), morphological traits ($F_{4,25} = 0.34$, $P = 0.85$) and all traits combined ($F_{4,54} = 1.21$, $P = 0.32$). The mean PI_v of the *Bauhinia* species was higher in response to increased irradiance than in response to nutrient addition, and this pattern was found for physiological traits, morphological traits and all traits combined (Figure 3). For the studied species, the maximum RGR along the light and nutrient gradients (RGR_{max}) was significantly correlated with the plasticity of RGR (Figure 4) but not with the plasticity of its morphological (SLA, LMR, LAR) and physiological (A_a) components ($r = -0.47$ to 0.57 , $P > 0.05$ in all cases).

Table 2. Phenotypic plasticity indices ($PI_v = (\max - \min)/\max$) for 12 variables of five *Bauhinia* species in response to solar irradiance and N addition. Means of morphological, physiological and total variables were not significantly different between species ($P > 0.05$, ANOVA). Abbreviations: A_a and A_m , light-saturated photosynthetic rate based on leaf area and leaf mass, respectively; N_m , leaf nitrogen concentration; PNUE, photosynthetic nitrogen-use efficiency; $\delta^{13}C$, carbon isotope ratio; $\%F_v/F_m$, diurnal photoinhibition; LMR, leaf mass to plant mass ratio; SMR, stem mass to plant mass ratio; RMR, root mass to plant mass ratio; SLA, specific leaf area; LAR, leaf area to plant mass ratio; and RGR, relative growth rate.

Species	Physiological variables							Morphological variables							Total mean
	A_a	A_m	N_m	PNUE	$\delta^{13}C$	$\%F_v/F_m$	Mean	LMR	SMR	RMR	SLA	LAR	RGR	Mean	
<i>B. tenuiflora</i>	0.074	0.221	0.059	0.250	0.092	0.460	0.19	0.193	0.158	0.081	0.181	0.234	0.525	0.23	0.211
<i>B. claviflora</i>	0.107	0.049	0.050	0.230	0.105	0.400	0.16	0.140	0.102	0.160	0.088	0.324	0.372	0.20	0.177
<i>B. aurea</i>	0.241	0.196	0.096	0.130	–	0.598	0.25	0.323	0.340	0.182	0.100	0.327	0.155	0.24	0.244
<i>B. purpurea</i>	0.462	0.270	0.374	0.200	0.053	0.366	0.29	0.226	0.215	0.241	0.282	0.090	0.453	0.25	0.269
<i>B. monandra</i>	0.454	0.292	0.300	0.220	0.031	0.433	0.29	0.380	0.139	0.257	0.310	0.125	0.471	0.28	0.284

Discussion

Responses to light and nutrients

Increased light availability affected all measured variables, but the effects of N addition were less pronounced than the effects of increased irradiance (Table 1, Figures 1 and 2), indicating that light may be a more important limiting factor than N for the growth of tropical rain forest species (Graham et al. 2003, Cai et al. 2007a). Alternatively, this result may indicate that species show an asymptotic response to an increase in resource availability, and that the treatment regimes we used covered different parts of the resource gradients for light and nutrients. The irradiances that we used were quite low (5 and 25% of full sunlight), corresponding to the linear increasing part of the asymptotic response curve (Poorter 1999), whereas the nutrient regimes were relatively high (forest topsoil versus topsoil plus N addition), perhaps corresponding to the saturating part of the response curve. Other studies have shown that fertilization of forest soil results in modest growth responses (Raaimakers 1994), whereas dilution (Metcalfe et al. 2002) or trenching of the forest soil results in much stronger growth responses (Coomes and Grubb 2000, Tanner and Barberis 2007). In general, plant responses to light or nutrient availability tended to enhance the acquisition of resources that were in most limiting supply, which is in line with the resource equilibrium hypothesis of Brouwer (1963). In low light, plants had a high SLA, which enhanced light capture, and in high light, plants had a high RMR, which enhanced the uptake of water and nutrients, and high A_n , which enhanced growth (cf. Poorter and Nagel 2000, Poorter 2005). Similarly, when nutrient availability was low, plants had a high RMR to capture more nutrients, and at high nutrient availability they had a high LMR, SLA, and LAR resulting in greater light capture and enhanced growth (cf. Poorter and Nagel 2000). We found significantly interactive effects of light and nutrients only on leaf physiological traits and not on morphological traits or biomass allocation patterns (Table 1), in agreement with previous studies

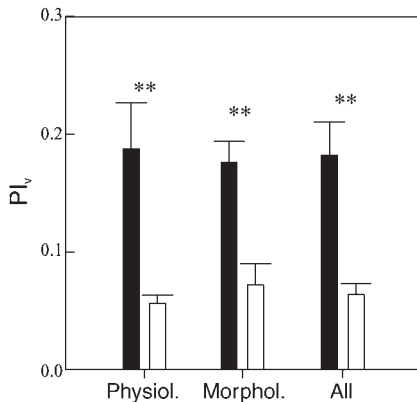


Figure 3. Phenotypic plasticity indices ($PI_v = (\max - \min)/\max$) of physiological, morphological and all traits combined of five *Bauhinia* species in response to light (closed bars) and nutrient addition (open bars). Asterisks indicate a significant difference: ** = $P < 0.01$.

(Latham 1992, Fownes and Harrington 2004, Portsmouth and Niinemets 2007). Perhaps our study plants needed more time to respond to the interactive effects of light and nutrients. Physiological responses occur on the time scale of seconds to weeks (Niinemets and Valladares 2004, Cai et al. 2005), whereas morphological responses at the whole-plant level may occur on the time scale of weeks to months (Popma and Bongers 1991).

Soil nutrient availability is often inversely related to irradiance (Bazzaz and Wayne 1994), suggesting that light \times nutrient interactions play an important role in plant growth responses along many natural gap-understory gradients. The significant light \times nutrient interactions on leaf physiological traits and RGR that we observed support this suggestion (Table 1). Plants exhibit an impressive ability to compensate for imbalances in the availability of environmental resources (Niinemets and Valladares 2006). Nevertheless, plant growth in natural environments is affected in complex ways by multiple interactions between water and nutrients (Mittler 2006), interactions between different nutrients (de Groot et al. 2003), and between nutrients and light (Grubb et al. 1996, Portsmouth and Niinemets 2007). As our study and previous work demonstrated, all of these interactions should be taken into consideration because interactive effects cannot be predicted from single factor combinations.

Different responses among *Bauhinia* species

The type of response to light and nutrient availability was related to growth form (liana or tree) and shade tolerance (light-demanding or shade-tolerant). The two light-demanding lianas exhibited a greater adjustment in LAR and leaf area than the two light-demanding trees in response to light and nutrients. Growth increases caused by N addition were not associated with enhanced rates of photosynthetic capacity in the light-demanding lianas. Instead, growth in these species was stimulated by the allocation of biomass to increased production of leaf area (e.g., high LAR) and stem tissue (Figure 2). Increased growth due to changes in resource allocation, through development of greater leaf area rather than through

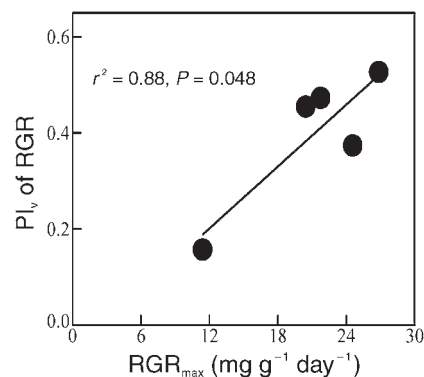


Figure 4. Relationship between potential maximum relative growth rate (RGR_{\max}) and the plasticity (PI_v) of relative growth rate (RGR) across light and nutrient gradients of five *Bauhinia* species.

an increase in productivity of individual leaves, has been observed in other woody species following fertilization (Baddeley et al. 1994, Lovelock et al. 2004). The greater phenotypic plasticity in LAR suggests that lianas perform better than trees in heterogeneous environments, especially when there is strong competition for light (Selaya et al. 2007). However, these results are not fully in agreement with hypotheses that a highly variable plant structure is advantageous because it allows plants to use environmental resources more efficiently and achieve higher growth rates (Givnish 1986): the light-demanding lianas and trees showed only limited variation in the plasticity of their growth responses to light and nutrient availabilities (Table 2). The two light-demanding tree species showed the largest plasticity in their physiological attributes (e.g., N_m , A_a) in response to light and nutrients, whereas the two light-demanding lianas did not respond. This may indicate that N availability has only a partially limiting effect on photosynthesis in tree species, whereas it is not a limiting factor for photosynthesis in lianas. A possible mechanism explaining the non-limitation of photosynthesis by N in lianas is that lianas have a more extensive root system that enables them to exploit a greater range of soil conditions (Schnitzer 2005).

Our data demonstrate that closely related species can respond differently, both morphologically and physiologically, to nutrient and light availabilities, but that their responses nevertheless have similar consequences for RGR. All species showed a similar modest increase in RGR in response to nutrients (i.e., there was no significant species \times nutrient interaction, Table 1), and only the shade-tolerant species failed to respond to increased light by an increase in RGR (Figure 2f). Therefore, the species show little or no cross-over in their rank performance in different light and nutrient environments, in contrast to the findings of other studies (Latham 1992, Grubb et al. 1996, Portsmouth and Niinemets 2007). Thus, inherent differences in species traits, rather than the capacity to respond plastically to resource heterogeneity determine the coexistence of these closely related *Bauhinia* species (Cai et al. 2007b); the light-demanding lianas grew better than the tree seedlings across a range of light and nutrient conditions (post-hoc test, $P < 0.05$, Figure 2f; cf. Schnitzer 2005) because of their greater LMR, SLA, and LAR (Figure 2; Cai et al. 2007b). The higher RGR of light-demanding lianas may be an important determinant of their distribution in productive habitats (i.e., with high availability of light and nutrients), which is mediated through their greater competitive ability (Grime and Hunt 1975, Poorter and Bongers 2006).

Phenotypic plasticity

Lianas experience temporally and spatially heterogeneous environments during ontogeny (Ray 1990, Teramura et al. 1991) and we predicted that they have a high phenotypic plasticity in response to environmental changes. Although all species showed significantly greater phenotypic plasticity in physiological traits, morphological traits and all traits combined in response to light than to nutrients (Figure 3), the mean plastic-

ity of measured variables was similar in lianas and trees across all light and nutrient conditions. The light-demanding species were no more plastic than the shade-tolerant species, contradicting the hypothesis of Bazzaz (1979). The differences in phenotypic plasticity depended on the variable measured (Table 2). It is often assumed that, in heterogeneous environments, species with high phenotypic plasticity have a growth advantage over, and thus outcompete, species with low phenotypic plasticity (Lortie and Aarssen 1996, Valladares et al. 2006), although plasticity is not always strongly related to fitness (Givnish 2002). We found a significant linear relationship between RGR_{max} and the plasticity of RGR in our study species (Figure 4), supporting the specialization hypothesis that faster-growing species are more plastic in RGR (Lortie and Aarssen 1996).

In conclusion, our study demonstrated that even closely related species can respond differently to changes in light and nutrient availability. Although the species showed a similar degree of plasticity to variation in resource availability overall, they differed in the pattern of response. Lianas exhibited greater phenotypic plasticity in LAR, whereas trees exhibited greater phenotypic plasticity in physiological traits. However, these different types of responses resulted in similar increases in RGR in response to increased light and nutrient availabilities. Species coexistence along light and nutrient gradients is therefore not determined by interspecific differences in plasticity, but by inherent differences in their overall growth characteristics.

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