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Phenotypic plasticity of lianas in response to altered light environment

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Abstract The growth, morphology and biomass allocation of 11 liana species (six light-demanding and five shade-tolerant) were investigated by growing plants in three contrasting light environments (i.e., field, forest edge and forest interior). Our objectives were to determine: (1) changes in plant traits at the species level; and (2) differences in light-demanding and shade-tolerant species in response to altered light environment. We found that all seedlings of liana species increased in total biomass, total leaf area, relative growth rate (RGR), net assimilation rate (NAR), height, basal diameter, root length, leaf number, root mass/total plant mass (RMR) and root-to-shoot dry biomass (R/S ratio), and decreased in leaf area ratio (LAR), specific leaf area (SLA), leaf size, stem mass-to-total plant mass ratio (SMR) and leaf mass-to-total plant mass ratio (LMR) with increasing light availability. Under the three light environments, the two types of species differed significantly in total biomass, total leaf area, RGR, NAR, LAR, SLA and leaf number, and not in leaf area. Only light-demanding species differed significantly in height, root length, basal diameter, RMR, SMR, LMR and R/S ratio. The mean plasticity index of growth and biomass allocation were relatively higher than the morphological variables, with significant differences between the two groups. Our results showed that liana species respond differently to changing light environments and that light-demanding species exhibit higher plasticity. Such differences may affect the relative success of liana species in forest dynamics.

Keywords Liana seedling · Functional traits · Phenotypic plasticity · Biomass allocation · Changes in light environment

Introduction

Light is one of the most important environmental factors, providing plants with a source of energy and controlled growth and development (Lambers et al. 2008). Rain forest species are often classified into two functional groups, based on seed germination and seedling establishment (Swaine and Whitmore 1988). Shade-tolerant species germinate, grow and survive in low light (e.g., forest interior), whereas light-demanding species need high levels of light (e.g., treefall gap, forest edge, and other disturbed forests) for their establishment. Light-demanding species grow under exposed conditions of the canopy. As the amount of light is not limited they maximize their photosynthetic capacity and usually exhibit high growth rate (Kitajima 1994; Poorter and Bongers 2006). Shade-tolerant species tend to have thicker leaves that are tougher and live longer and therefore have a lifetime light acquisition and carbon gain comparable to the shorter lived but more productive leaves of light-demanding species (Selaya and Anten 2010). The two groups of species also differ in response to altered light environment. Light-demanding species manifest higher plasticity in growth, morphology and physiology than shade-tolerant species, because they grow in a more variable environment (Bazzaz 1979; Huante and Rincon 1998; Valladares et al. 2000). However, no general consensus exists as greater, similar, and even lower plasticity has been found in pioneers compared with shade-tolerant species (Rozendaal et al. 2006).

Phenotypic plasticity is the ability of a genotype to produce distinct phenotypes under changing environmental conditions. It often involves ecologically relevant

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behavioral, physiological, morphological and life-history traits (Miner et al. 2005). Such plasticity may be of paramount importance for species to adjust to temporal and spatial variation in resource availability. Shade-grown plants typically invest in high aboveground biomass and also have thin leaves to optimize light capture and utilization. In contrast, plants grown under high light allocate relatively less biomass to leaves and more to roots to capture water and nutrients to sustain the high transpiration and growth rates (Brouwer 1962). The diversity of species may be partly explained by their potential for plastic response to the environment. Strong evidence suggests that plant species may differ remarkably in the extent of their plastic responses to comparable environmental challenges (Valladares et al. 2007).

Lianas (woody vines) are diverse and abundant in many tropical forests, especially in disturbed sites, such as treefall gaps (Putz 1984; Schnitzer and Carson 2001), forest margins (Laurance et al. 2001; Zhu et al. 2004; Londre and Schnitzer 2006), and other disturbed forests (Hegarty and Caballe 1991; DeWalt et al. 2000; Yuan et al. 2009). As the forest ecosystem is increasingly disrupted worldwide the relative importance of lianas is increased. The lianas play a role in many aspects of forest dynamics (Schnitzer and Bongers 2002): driving floristic changes, suppressing tree regeneration, exacerbating tree mortality, and decreasing whole-forest biomass and carbon sequestration (Schnitzer and Bongers 2011; Schnitzer et al. 2011). Understanding the response of lianas to environmental changes (such as light) is therefore important in predicting their impact on forests.

Lianas are usually considered light-demanding because of their rapid growth under high-light conditions (Richards 1996). Nevertheless, contrasting evidence supporting the regeneration of lianas also exists (Gerwing 2004). Shade-tolerant species of liana that germinate and survive in deeply shaded forests also exist (Putz 1984; Carter and Teramura 1988; Nabe-Nielsen 2002; Sanches and Válio 2002a; Gilbert et al. 2006; Yuan et al. 2015). Furthermore, lianas rely on the surrounding plants for their structural support, and therefore, may invest less biomass in stems and more in leaves (Putz 1983; Castellanos et al. 1989; Niklas 1994). However, studies fail to support this hypothesis, e.g., Kaneko and Homma (2006) showed that liana species (*Hydrangea petiolaris*) did not invest more in leaves and reproductive organs than the three *Hydrangea* shrub species. Cai et al. (2007) investigated the differences in growth patterns, biomass allocation and leaf traits in five closely related liana and tree species of the genus *Bauhinia* species. They found that the faster growth of light-demanding lianas compared with light-demanding trees is based on functional traits (i.e., specific leaf area, leaf mass ratio, and leaf area ratio), and cannot be attributed to higher photosynthetic rates at the leaf level. Cai et al. (2008) further analyzed the responsiveness to light and nutrient availability of the five *Bauhinia* species, and suggested that lianas were no more responsive to variation in light and nitrogen availability than trees. However, all the above studies compared only a few liana species with non-climbing species (i.e., trees or shrubs), and it might be difficult to generalize the results to all lianas. Sanches and Válio (2002b) studied the initial growth of a few seedlings of liana and herbaceous vine species in the forest margins and under forest canopy. They found that the climbers showed high rates of growth in sunlight when compared with those under canopy, but with a diverse response of morphological and physiological traits (e.g., leaf area, specific leaf area (SLA), leaf mass ratio (LMR), chlorophyll a and b, as well as chlorophyll a/b ratio).

In this study, the growth, morphology and biomass allocation of 11 liana species were investigated by growing plants in three contrasting light environments, i.e., open field (high light), forest edge (intermediate light) and forest interior (low light). Six of the species' seedlings are principally found in gaps or forest edge environments, whereas the other five species are principally found in shaded understory. Our objectives were to determine: (1) how plant traits change under altered light environment at the species level; (2) differences in light-demanding species from shade-tolerant species in response to altered light environment. We found that plants use their plasticity to invest in organs that capture the most limiting resources (e.g., light and water). High plasticity occurred in light-demanding plants rather than shade-tolerant species.

Materials and methods

Study site

The experiment was carried out in the Ailao Mountains Subtropical Forest Ecosystem Research Station (24º32′N, 101°01′E), the Chinese Academy of Sciences. The study area exhibits a typical mountainous monsoon climate. Annual mean precipitation in 1991–1995 averaged 1931.1 mm, of which 85.0 % occurred during the rainy season from May to October. The average annual temperature is 11.3 °C with an average of 5.4 °C in January to 16.4 °C in July (Qiu and Xie 1998). The predominant vegetation is mid-montane moist evergreen broad-leaved primary forest, which accounts for nearly 80 % of the total area, along with secondary patches within the forest. The forest flora consists of a combination of tropical and temperate species, including those endemic to the region (Wu and Fan 1990). Canopy tree species are mainly composed of *Castanopsis wattii*, *Lithocarpus xylocarpus*, *Schima noronhae* and *Lithocarpus jingdongensis*, and evenly distributed within the forest (Liu et al. 2001). The forest reaches 20–25 m in height, with a closed canopy (>90 %).

Species

Eleven liana species (Table 1), which are native to the studied region (Yuan et al. 2009, 2015) were selected.

Table 1 Summary of the species studied: climbing type (*H* hook climbers, *S* stem twiners, *R* root climbers, *T* tendril climbers), life form (*E* evergreen species, *D* deciduous species), regeneration habitats (*G* gap, *E* edge, *U* understory), source of plant material (*S* seed, *T* transplanted seedling from forest)

Species	Family	Species code	Climbing type	Life form	Regeneration habitat	Guild	Adult stature	Source
Rosa longicuspis	Rosaceae	RL	H	E	G; E	L	Canopy	S
Actinidia callosa	Actinidiaceae	AC	S	D	G; E	L	Canopy	S
Celastrus angulatus	Celastraceae	CA	S	D	G; E	L	Canopy	S
Holboellia latifolia	Lardizabalaceae	HL	S	E	G; E	L	Canopy	T
Kadsura coccinea	Schisandraceae	KC	S	E	G; E	L	Canopy	T
Parthenocissus himalayana	Vitaceae	PH	R	D	G; E	L	Canopy	T
Euonymus vagans	Celastraceae	EV	R	E	U	S	Canopy	T
Jasminum urophyllum	Oleaceae	JU	S	E	U	S	Canopy	T
Hydrangea anomala	Saxifragaceae	HA	R	D	U	S	Canopy	T
Heterosmilax japonica	Smilacaceae	HJ	T	E	U	S	Canopy	T
Embelia procumbens	Myrsinaceae	EP	S	E	U	S	Understory	T

Classification of the species in light-demanding and shade-tolerant species was based on differences in regeneration requirements (*L* light-demanding, *S* shade-tolerant)

Species selection was based on differences in shade tolerance or regeneration, including six light-demanding species and five shade-tolerant species (Yuan et al. 2008, 2015; species guilds see Table 1). The adults of all species climb to the forest canopy, except *Embelia procumbens*, which is a typical understory liana. Due to lack of seedlings for the three light-demanding species (i.e., *Rosa longicuspis*, *Actinidia callosa* and *Celastrus angulatus*) in the forest, we collected fresh seeds for germination in a greenhouse in March, 2013. The seedlings of the other eight species were transplanted from the forest.

Experimental design

We designed three light environments, i.e., field, forest edge and forest interior (50 m from edge into forest interior). During June 2013, we transplanted the germinated seedlings and wild types into 20 × 30 cm plastic pots (one plant per pot and 40 plots in total, for each species) containing topsoil from the nearby forest and then moved into a shade house for material preparation (10 % of full sun light). All plants were watered on days without rain to maintain the soil near field capacity.

At the end of April 2014, 24 pots per species with similar plant size (i.e., height or length) were selected for the experiment. Of these, six plants (pots) per species for each treatment (i.e., field, forest edge and forest interior) were moved for growth experiment (each plant was tagged and supported with a dry bamboo shoot), which lasted 6 months (at the end of October, totaled 184 days). The remaining six plants were used for initial measurement. During this experimental period, the fallen leaves of deciduous species were collected for each plant species and treatment and retained in paper bags for the final measurements (i.e., leaf number, area, and biomass).

During the preparation period of the seedlings, there was no death. During the experimental period, all the plants survived, except three plants of *Rosa longicuspis*, in the forest interior, and one *Embelia procumbens*, which died in the field.

Plant functional traits

At the initial and final harvest, basal diameter, height, root length, leaf number (and leaflets counted in compound leaves), leaf area and leaf (including petiole), stem and root mass were determined. Liana's height was defined as either actual height of upright individuals or the length of climbing individuals, measured from the plant stem base to the apex.

After harvest, plants were separated into leaves (including petioles), stems and roots. All leaves in each species were photocopied by EPSON V700 scanner and analyzed with an image analysis system (ImageTool Version 2.0) to calculate leaf area. Roots were washed in tap water. All the tissues were dried to a constant weight at 70 °C for 48 h.

From the primary data the following variables were derived: root mass ratio (RMR; root mass/total plant mass, in g g^{-1}), stem mass ratio (SMR; stem mass/total plant mass, in g g^{-1}), leaf mass ratio (LMR; leaf + petiole mass/total plant mass, in g g^{-1}), R/S ratio (root-to-shoot dry biomass), specific leaf area (SLA; leaf area/leaf mass, in cm^2 g^{-1}), leaf area ratio (LAR; leaf area/total plant mass, in cm^2 g^{-1}), and mean leaf size (total leaf area/total leaf number, in cm^2) (Poorter 1999; Cornelissen et al. 2003; Pérez-Harguindeguy et al. 2013). The relative growth rate (RGR, dry biomass increment per unit total plant biomass per unit time) for each treatment was calculated as: $RGR = (\ln W_2 - \ln W_1)/t$, the net assimilation rate (NAR, the rate of dry matter production per unit leaf area) as: $NAR = [(W_2 - W_1)/t] \times [(\ln A_2 - \ln A_1)/(A_2 - A_1)]$, where W is the total plant dry biomass in grams, A is the total leaf area in cm^2 and t is time in days (Hunt 1978).

Statistical analysis

The differences in growth, morphology and biomass allocation variables of each species in the three light environments (field, forest edge and forest interior) were tested using a one-way ANOVA ($P = 0.05$). The Fisher LSD test was used for post hoc analysis. Plant responses were analyzed using a two-way ANCOVA, with light and species as fixed factors. Plant biomass may differ between light environments and species at the end of the experiment, and biomass was therefore included as a covariable in the analysis. Data were checked for normality and homogeneity of variances, and an ln- or square-root transformation was used when necessary to satisfy the assumptions of ANCOVA.

To compare the plasticity in growth, morphology and biomass allocation, we calculated a plasticity index for each measured variable in each species, following Valladares et al. (2000). The index ranged from zero to one and represents the difference between the maximum and minimum mean value of a variable among treatments divided by the maximum value. Finally, a mean plasticity index was calculated for growth, morphology and biomass allocation variables, respectively. Independent-sample *t* test was used to compare the differences of mean plasticity index of growth, morphology and biomass allocation between the two functional group species. Statistical analyses were done using SPSS 19.0 (SPSS, Chicago, IL, USA).

Results

Growth, morphology and biomass allocation

Total biomass, total leaf area, RGR and NAR of all species were significantly higher in the field and at forest edge than in the forest interior ($P < 0.05$), and most of them showed the highest value in the field (Fig. 1a–d). All these growth variables differed significantly under the three light environments in both light-demanding and shade-tolerant species.

Among the morphology variables, seedlings of liana species increased in height, basal diameter, root length, leaf number, and decreased in LAR, SLA and leaf size with increasing light availability. In the forest interior, the height of all the species was the lowest under the three light environments, except *Embelia procumbens* (Fig. 1e). Light-demanding species showed significant differences under the different light environments, with *Rosa longicuspis* and *Parthenocissus himalayana* reaching the highest altitude in the field, and *Actinidia callosa*, *Celastrus angulatus*, *Holboellia latifolia* and *Kadsura coccinea* at the forest edge. On the contrary, there was no significant difference among the shade-tolerant species, except *Jasminum urophyllum*, which was significantly taller at the forest edge and in the field than in the forest interior. Basal diameter (Fig. 1f) and root length (Fig. 1g) were greater in the field than at the forest edge and in the forest interior. Except for a few cases, light-demanding species differed significantly among the three light environments, unlike shade-tolerant species.

Fig. 1 Liana functional traits in response to altered light environment: **a** total biomass; **b** total leaf area; **c** RGR; **d** NAR; **e** height; **f** basal diameter; **g** root length; **h** SLA; **i** LAR; **j** leaf size; **k** leaf number. *RGR* relative growth rate, *NAR* net assimilation rate, *SLA* specific leaf area, *LAR* leaf area ratio. Species codes are as defined in Table 1. Data are means ± SD ▶

The SLA (Fig. 1h) and LAR (Fig. 1i) of all species were significantly lower in the field than at forest edge and in the forest interior ($P < 0.05$). All of them reached the highest value in the forest interior, excluding the LAR of *Kadsura coccinea*, and LAR and SLA of *Embelia procumbens*. LAR and SLA differed significantly under the three light environments in both light-demanding and shade-tolerant species.

The leaf size in all species (Fig. 1j) was smaller in the field than at the forest edge and in the forest interior, without any significant differences under the three light environments among both light-demanding and shade-tolerant species, excluding *Holboellia latifolia* and *Jasminum urophyllum*. The leaf number in all the species (Fig. 1k) was higher in the field than at the forest edge and in the forest interior, except *Actinidia callosa* and *Celastrus angulatus*, which reached the highest value at forest edge. Contrary to leaf size, both light-demanding and shade-tolerant species showed significant differences under the three light environments, except *Heterosmilax japonica*.

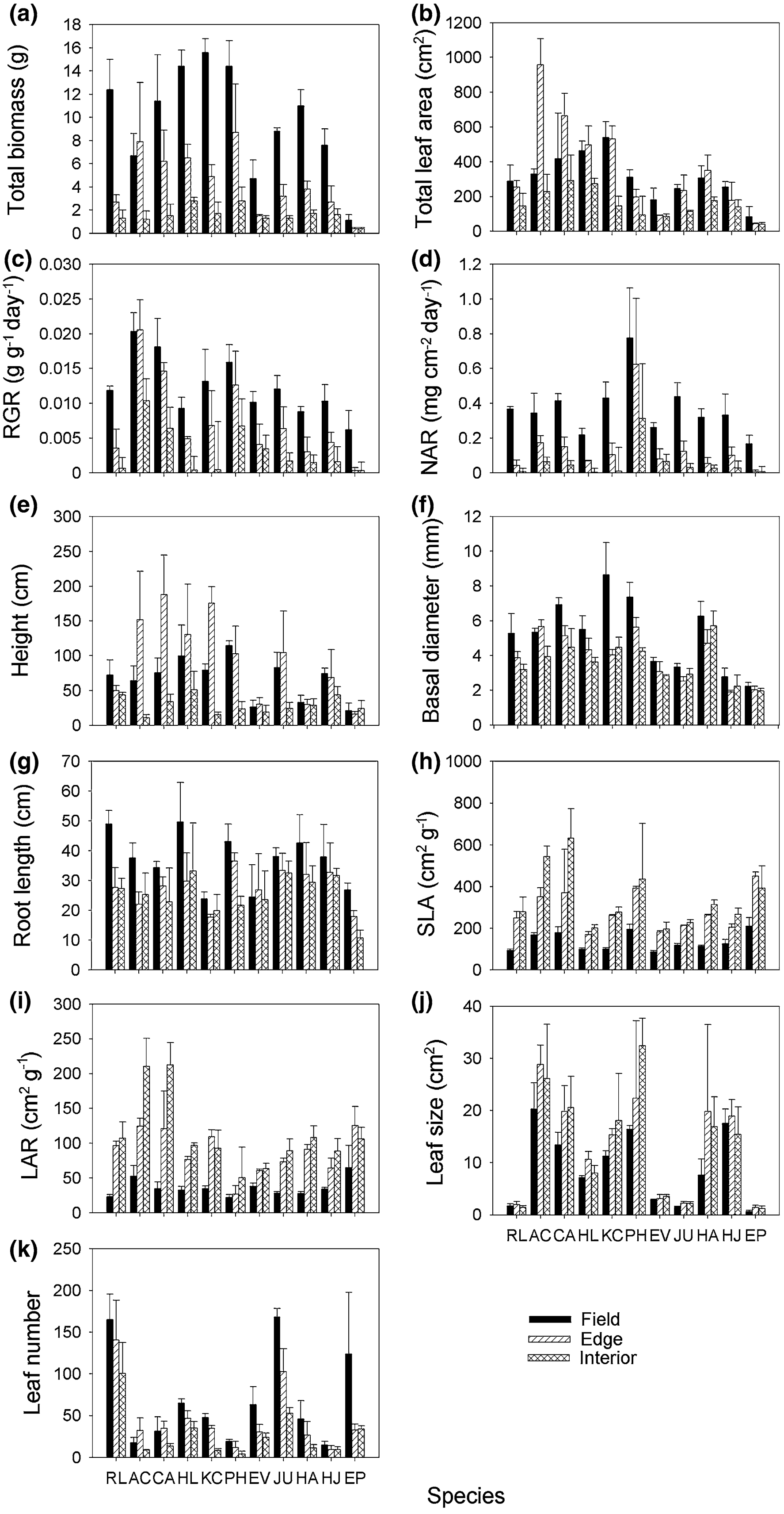
In general, RMR and R/S ratios were higher in the field than at the forest edge and in the forest interior (Fig. 2a, d), whereas LMR followed the opposite pattern (Fig. 2c) while SMR was higher at forest edge than in the field and in the forest interior (Fig. 2b). RMR, SMR, LMR and R/S ratio differed significantly under the three light environments for light-demanding species, unlike shade-tolerant species, except for *Jasminum urophyllum* (Fig. 2).

Interaction between light and species: relative significance

The two-way ANCOVA explained much of the variation in variable values, with a mean R^2 of 0.84 (range 0.65–0.91, Table 2). Biomass at the final harvest had no effect on biomass allocation, but showed a strong effect on seedling growth and morphological variables, except root length and leaf size. Both light and species had significant effect on the 15 variables of growth, morphology and biomass allocation. There were significant light vs. species interactions among all the variables, except RGR, NAR, root length and leaf size.

Phenotypic plasticity

The plasticity index was calculated for each species across the three light environments (Table 3). RGR and NAR showed the highest mean plasticity index, while basal diameter was the lowest. The mean plasticity index


(a)
Total biomass (g)
0
2
4
6
8
10
12
14
16
18
(b)
Total leaf area (cm^2)
0
200
400
600
800
1000
1200
(c)
RGR (g g^{-1} day^{-1})
0
0.005
0.010
0.015
0.020
0.025
0.030
(d)
NAR (mg cm^{-2} day^{-1})
0
0.2
0.4
0.6
0.8
1.0
1.2
(e)
Height (cm)
0
50
100
150
200
250
300
(f)
Basal diameter (mm)
0
2
4
6
8
10
12
(g)
Root length (cm)
0
10
20
30
40
50
60
70
(h)
SLA (cm^2 g^{-1})
0
200
400
600
800
1000
(i)
LAR (cm^2 g^{-1})
0
50
100
150
200
250
300
(j)
Leaf size (cm^2)
0
10
20
30
40
RL AC CA HL KC PH EV JU HA HJ EP
(k)
Leaf number
0
50
100
150
200
250
RL AC CA HL KC PH EV JU HA HJ EP
Species
Field
Edge
Interior

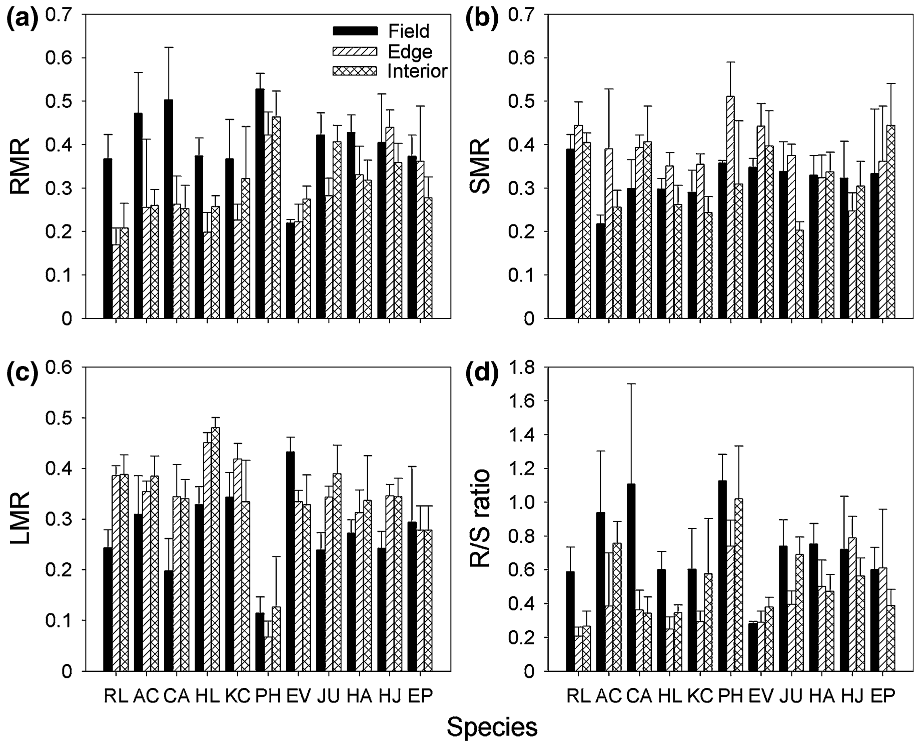


Fig. 2 Liana biomass allocation under the three light environments (field, forest edge and forest interior): **a** RMR; **b** SMR; **c** LMR; **d** R/S ratio; *RMR* root mass ratio, *SMR* stem mass ratio, *LMR* leaf mass ratio; and *R/S ratio* root-to-shoot dry biomass ratio. Species codes are as defined in Table 1. Data are means ± SD

of growth and biomass allocation were relatively higher than that of morphology. However, the leaf number and R/S ratio showed a relatively higher mean plasticity index, when compared with the other morphological and biomass allocation variables.

The mean plasticity index of growth, morphology and biomass allocation differed significantly between light-demanding and shade-tolerant species (growth: $t = 2.70$, $P = 0.024$; morphology: $t = 3.40$, $P = 0.008$; biomass allocation: $t = 2.64$, $P = 0.027$; Fig. 3). No significant differences were found in the mean plasticity index of total variables between the two functional group species ($t = 0.84$, $P = 0.422$).

Discussion

Response to altered light environment

This study demonstrated that both light-demanding and shade-tolerant liana species differed significantly in growth variables among the three light environments. The total biomass, total leaf area, RGR and NAR of the eleven liana species were significantly higher in the field and at forest edge than in the forest interior, and most of the species exhibited the highest value in the field (Fig. 1a–d). On the other hand, under low light conditions (i.e., shade house and forest interior), nearly all trial seedlings survived, with considerably smaller and shorter stature compared with seedling growth at the forest edge and in the field. This indicated that lianas prefer high-light environments to forest interior, and fully captured the high irradiance for their growth and development. The finding also explains the rapid growth under high-light conditions, such as treefall gaps, forest edge, and disturbed forest ecosystems.

Plant response includes increases or reductions in certain traits due to phenotype plasticity. Seedlings of liana species increased in height, basal diameter, root length, leaf number, and decreased in LAR, SLA and leaf size with increasing light availability. Plants that grow in a shady environment invest relatively more in photosysthesis and other resources in leaf area, with a high LAR and SLA (Lambers et al. 2008). A high SLA is advantageous in a low-light environment, where photoreception is of primary importance (Poorter 1999) as seen in the current study.

RMR and R/S ratio were higher in the field than at the forest edge and in the forest interior. The LMR and SMR followed the opposite pattern by investing biomass in roots in the field, and the shade lianas invest in leaves suggesting that plants use their plasticity to allocate resources to areas that capture the most limiting resource (e.g., light, water, and nutrients). The altered pattern of this study is consistent with other studies for trees (Gyimah and Nakao 2007). Poorter and Nagel (2000) carried out a meta-analysis of the studies, and found that the responses to light, nutrients and water were

Table 2 Results of a two-way ANCOVA with light ($N = 3$) and species ($N = 11$) as fixed factors and ln (1 + biomass) as covariable

Group	Variable	Light		Species		Light × species		Biomass		b	R^2
		F	*P*	*F*	*P*	*F*	*P*	*F*	*P*		
Growth	Total biomass	184.4	***	16.0	***	5.4	***				0.91
	Total leaf area	40.6	***	15.0	***	3.2	***	69.7	***	357.02	0.89
	RGR	5.3	**	34.9	***	0.3	ns	57.9	***	0.01	0.93
	NAR	4.8	**	13.6	***	0.7	ns	27.4	***	0.24	0.87
Morphology	Height	40.8	***	4.4	***	3.7	***	16.2	***	50.15	0.84
	Root length	5.0	**	4.5	***	1.3	ns	3.5	ns	6.58	0.69
	Basal diameter	6.5	**	22.7	***	4.9	***	10.5	**	0.93	0.92
	SLA	4.7	**	16.0	***	2.5	**	8.4	**	−93.75	0.86
	LAR	8.1	**	21.5	***	5.5	***	12.4	**	−31.21	0.91
	Leaf size	5.1	**	18.5	***	1.1	ns	0.6	ns	2.01	0.82
	Leaf number	5.1	**	45.2	***	4.0	***	16.3	***	35.48	0.91
Biomass allocation	RMR	18.8	***	10.6	***	2.9	**	0.5	ns	0.02	0.77
	SMR	10.0	***	5.3	***	1.8	*	1.3	ns	0.04	0.65
	LMR	4.8	**	22.3	***	2.7	**	0.3	ns	−0.01	0.83
	R/S ratio	13.4	***	8.5	***	2.4	**	0.4	ns	−0.06	0.73

F-values, levels of significance (*P*), regression coefficient (b) and coefficient of determination (R^2) are shown. *RGR* relative growth rate, *NAR* net assimilation rate, *SLA* specific leaf area, *LAR* leaf area ratio, *RMR* root mass ratio, *SMR* stem mass ratio, *LMR* leaf mass ratio, *R/S ratio* root-to-shoot dry biomass. Levels of significance: *ns* not significant; $*P < 0.05$; $**P < 0.01$; $***P < 0.001$

consistent with the prediction of the 'functional equilibrium' theory stating that plants respond to a decrease in aboveground resources with increased allocation of biomass to shoots (leaves), whereas they respond to a decrease in underground resources with increased allocation to roots. Furthermore, nearly all the R/S ratio values were lower than 1, suggesting that plants generally allocated higher mass to shoots than to roots, which is favorable for accumulation of photosynthetic products, and met the needs of plant growth and development. All liana species, excluding the understory liana, *Embelia procumbens*, reached the greatest height at the forest edge and in the field, and allocated more resources to canopy development, and stem elongation, which enabled rapid growth and a competitive advantage (Wright 2002).

Functional response to changes in light environment

The results presented in this study show that light-demanding species differed from shade-tolerant species in response to altered light environment. The results are in accordance with the response to edge effects of lianas in the forests studied (Yuan et al. 2016), where liana species responded differently to edge effects, including species present exclusively at or near the edges (within 20 m of the edge). The species density decreased with increasing distance from the edge, and insensitive to edge effects, which showed minor variation or random fluctuation throughout the gradient.

Among the three light environments, significant differences between light-demanding and shade-tolerant species were found in the plasticity of seven of the fifteen variables. The two functional group species differed significantly in total biomass, total leaf area, RGR, NAR, LAR, SLA and leaf number, and not in leaf area. Only light-demanding species differed significantly in height, root length, basal diameter, RMR, SMR, LMR and R/S ratio. The plasticity response of height and root length may reflect an important growth strategy for light-demanding lianas, in terms of enhanced light access and water use, respectively.

Phenotypic plasticity

Our data demonstrate that the mean plasticity index of growth, morphology and biomass allocation variables was significantly greater for light-demanding than for shade-tolerant species. The result was consistent with the hypothesis of Bazzaz (1979), and other studies (Huante and Rincon 1998; Valladares et al. 2000) demonstrating a greater phenotypic plasticity in pioneer species. Plasticity is generally thought to be the greatest for pioneer species, as they occur in variable, heterogeneous environments with high resource availability. Nevertheless, this hypothesis was rejected by Rozendaal et al. (2006), as short-lived pioneers showed the lowest plasticity to

Table 3 Phenotypic plasticity index, (maximum–minimum)/maximum, for 15 variables of eleven lianas in response to changes in light environment

Group	Variable	Species											
		RL	AC	CA	HL	KC	PH	EV	JU	HA	HJ	EP	Mean
Growth	Total biomass	0.89	0.85	0.87	0.81	0.89	0.81	0.72	0.85	0.85	0.79	0.64	0.82
	Total leaf area	0.49	0.76	0.56	0.45	0.73	0.70	0.53	0.54	0.50	0.46	0.53	0.57
	RGR	0.96	0.85	0.91	0.98	0.95	0.85	0.86	0.96	0.94	0.93	0.93	0.92
	NAR	0.98	0.81	0.89	0.98	0.98	0.96	0.75	0.93	0.92	0.92	0.95	0.92
	Mean	0.83	0.82	0.81	0.81	0.89	0.83	0.72	0.82	0.80	0.78	0.76	0.81
Morphology	Heights	0.39	0.93	0.82	0.61	0.91	0.79	0.38	0.77	0.12	0.61	0.35	0.61
	Root length	0.44	0.41	0.33	0.40	0.30	0.50	0.12	0.15	0.31	0.16	0.59	0.33
	Basal diameter	0.40	0.32	0.35	0.35	0.48	0.43	0.24	0.24	0.25	0.32	0.09	0.32
	SLA	0.67	0.69	0.72	0.51	0.64	0.55	0.57	0.48	0.64	0.53	0.53	0.59
	LAR	0.79	0.75	0.84	0.66	0.69	0.57	0.40	0.69	0.75	0.62	0.49	0.66
	Leaf size	0.30	0.30	0.35	0.32	0.38	0.49	0.22	0.35	0.62	0.19	0.57	0.37
	Leaf number	0.77	0.87	0.74	0.68	0.88	0.67	0.61	0.83	0.91	0.87	0.77	0.77
	Mean	0.54	0.61	0.59	0.50	0.61	0.57	0.36	0.50	0.51	0.47	0.48	0.52
Biomass allocation	RMR	0.67	0.81	0.70	0.59	0.64	0.42	0.39	0.50	0.39	0.43	0.50	0.55
	SMR	0.28	0.75	0.54	0.42	0.41	0.77	0.38	0.56	0.31	0.51	0.58	0.50
	LMR	0.51	0.47	0.69	0.42	0.38	0.83	0.40	0.57	0.46	0.43	0.53	0.52
	R/S ratio	0.79	0.90	0.86	0.71	0.77	0.65	0.48	0.66	0.54	0.61	0.67	0.86
	Mean	0.56	0.73	0.70	0.54	0.55	0.67	0.41	0.57	0.43	0.50	0.57	0.61
	Total mean	0.66	0.68	0.65	0.54	0.66	0.66	0.59	0.66	0.64	0.60	0.61	0.63

Species codes are as defined in Table 1

RGR relative growth rate, *NAR* net assimilation rate, *SLA* specific leaf area, *LAR* leaf area ratio, *RMR* root mass ratio, *SMR* stem mass ratio. *LMR* leaf mass ratio, *R/S ratio* root-to-shoot dry biomass

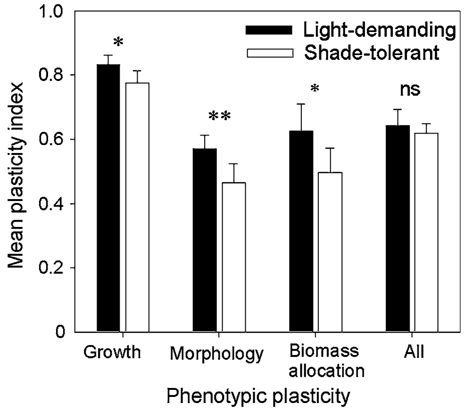


Fig. 3 Mean phenotypic plasticity index of the growth, morphology, biomass allocation and all variables combined, of light-demanding (*closed bars*) and shade-tolerant (*open bars*) species. *Asterisks* indicate a significant difference: $*P < 0.05$; $**P < 0.01$; *ns* not significant. Data are means ± SD

irradiance. They hypothesized that plasticity was the largest for tall species that experience large ontogenetic changes in irradiance during their life cycle.

In this study, growth and morphological variables changed with the plant size (Table 2). The regression slope shows altered plant variables with biomass. The SLA, LAR, LMR and R/S ratio declined with biomass, whilst the other traits increased with biomass.

Conclusions

In summary, the growth variables of all liana species were significantly higher in the field and at the forest edge than in the forest interior. However, seedlings of liana species increased in height, basal diameter, root length, leaf number, and decreased in LAR, SLA and leaf size with increased light availability. This result indicates that light is the most important factor explaining the success of lianas in high light environments. Plants use their plasticity to invest in areas that capture the most limiting resource (e.g., light, water, and nutrients). Furthermore, our results demonstrated that only light-demanding species differed significantly in height, root length, basal diameter, RMR, SMR, LMR and R/S ratio among the three light environments, and light-demanding species have a higher plasticity. Thus, lianas respond differently to altered environments with a diverse role in forest dynamics.

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