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Seedling Growth Strategies in *Bauhinia* Species: Comparing Lianas and Trees

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• *Background and Aims* Lianas are expected to differ from trees in their growth strategies. As a result these two groups of woody species will have different spatial distributions: lianas are more common in high light environments. This study determines the differences in growth patterns, biomass allocation and leaf traits in five closely related liana and tree species of the genus *Bauhinia*.
• *Methods* Seedlings of two light-demanding lianas (*Bauhinia tenuiflora* and *B. claviflora*), one shade-tolerant liana (*B. aurea*), and two light-demanding trees (*B. purpurea* and *B. monandra*) were grown in a shadehouse at 25 % of full sunlight. A range of physiological, morphological and biomass parameters at the leaf and whole plant level were compared among these five species.
• *Key Results* The two light-demanding liana species had higher relative growth rate (RGR), allocated more biomass to leaf production [higher leaf mass fraction (LMF) and higher leaf area ratio (LAR)] and stem mass fraction (SMF), and less biomass to the roots [root mass fraction (RMF)] than the two tree species. The shade-tolerant liana had the lowest RGR of all five species, and had a higher RMF, lower SMF and similar LMF than the two light-demanding liana species. The two light-demanding lianas had lower photosynthetic rates per unit area (A_{area}) and similar photosynthetic rates per unit mass (A_{mass}) than the trees. Across species, RGR was positively related to SLA, but not to LAR and A_{area}.
• *Conclusions* It is concluded that the faster growth of light-demanding lianas compared with light-demanding trees is based on morphological parameters (SLA, LMF and LAR), and cannot be attributed to higher photosynthetic rates at the leaf level. The shade-tolerant liana exhibited a slow-growth strategy, compared with the light-demanding species.

Key words: Relative growth rate, biomass allocation, shade tolerance, liana, tree, photosynthesis, *Bauhinia*.

INTRODUCTION

In tropical rain forests, resource availability (light, water and nutrients) varies over spatial and temporal scales. Plant species may adapt to different parts of these resource gradients, and are likely to differ in their ability to capture, use and conserve limiting resources. Spatial and temporal differences in resources availability within plant communities have led to the evolution of a variety of plant strategies (Grime, 1979; Schulze and Chapin, 1987). Plant performance is enhanced through morphological and physiological adaptations to the abiotic environment. In tropical rain forest understorey, light is the most limiting resource for plant growth and survival, although, in some forests, nutrient and water limitation can play a significant role as well (Whitmore, 1996). Light-demanding species that regenerate in gaps enhance growth through a high biomass investment in thin, productive leaves with high nitrogen concentrations and a high photosynthetic capacity (Kitajima, 1994; Poorter, 2005; Poorter and Bongers, 2006). At the same time they are well protected against excess radiation and suffer little from photoinhibition (Powles, 1984). Shade-tolerant species that regenerate in the shaded understorey enhance their survival through the

formation of thick well-protected long-lived leaves, and a large root system for below-ground carbohydrate storage (Kitajima, 1996; Canham *et al.*, 1999; Paz, 2003), thus reducing potential above-ground biomass loss due to herbivory, fire or falling debris.

Trees and woody climbers (lianas) are the two dominant life-forms in tropical forests. Compared with trees, liana abundance and diversity is higher in disturbed areas such as treefall gaps (Putz, 1984; Hegarty and Caballé, 1991; Schnitzer and Carson, 2001). A major factor in this difference may be the higher light levels in gaps, suggesting that lianas may require high light levels for establishment and survival, comparable to those of light-demanding tree species. However, a variety of shade tolerance strategies is found within canopy liana species (Gerwing, 2004) and there are also shade-tolerant liana species that can germinate and survive in the shade (Putz, 1984; Nabe-Nielsen, 2002; Sanches and Válio, 2002). Recently, lianas and trees were not found to be different in their regeneration requirements across seedling and sapling life stages (Gilbert *et al.*, 2006).

Lianas have been assumed to differ strikingly in growth strategies and biomass allocation patterns compared with tree species (Putz and Mooney, 1991). Lianas rely on surrounding plants for their structural support, and therefore they can make long and slender stems to forage for light

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in the high-light conditions of the forest canopy (Darwin, 1867; Putz and Mooney, 1991). As a result, they have height growth rates than can be seven times faster than that of trees (Schnitzer, 2005). Because they are not self-supporting, lianas may invest less biomass in stems and allocate more biomass to leaves (Darwin, 1867; Putz, 1983; Castellanos *et al.*, 1989; Niklas, 1994). The larger proportional investment in leaf mass and/or leaf area may then result in high growth rates in terms of biomass increment. To date only a few whole-plant growth studies have been carried out to test these hypotheses, and none of them has given a conclusive answer. Although lianas were assumed to be adapted for rapid growth (Putz, 1983; Hegarty and Caballé, 1991), Den Dubbelden and Verburg (1996) found that herbaceous climbing plants had lower relative growth rates than self-supporting species under controlled conditions. However, these results cannot be applied directly to woody plants because they have much higher support costs. A climbing habit would therefore especially be advantageous for woody plants, as this would allow them to cut back on support costs. Cornelissen *et al.* (1996) found indeed that temperate 'climbers' had faster whole-plant biomass growth rates than non-climbing species. However, they present data on only two woody climbers, whereas the rest of the 'lianas' were woody scramblers, with a totally different strategy. Neither did they present data on biomass fractions in leaves, stem and roots, and therefore did not test the biomass allocation hypothesis, and the plants were only 3 weeks old at final harvest, and were not likely to have developed the climbing habit. Teramura *et al.* (1991) present a literature review on growth data of temperate woody vines as shoot elongation, and their biomass allocation results are mostly for one species (kudzu, *Pueraria lobata*). Between 20 % and 60 % of above-ground biomass was in leaves, and 52–65 % of the plant biomass was invested in roots, both much higher than generally reported for temperate trees.

Lianas are also considered to be among the most deep-rooted species in tropical forests, perhaps because they have to invest so little in stem mass. There is evidence that their roots can grow below ground to a depth of several metres (Holbrook and Putz, 1996; Tyree and Ewers, 1996; Restom and Nepstad, 2004), and that they can tap deep sources of soil water to sustain high rates of water use (Jackson *et al.*, 1995). This would imply that lianas invest a large biomass fraction in a deep and extensive root system, resulting in higher water availability and, as a result, water use at the leaf level would be expected to be less efficient (Lambers *et al.*, 1998). Also these hypotheses have not been tested using a whole-plant perspective.

Here is presented a comparative growth analysis on biomass allocation, morphology and leaf physiology of five *Bauhinia* species. Within the genus *Bauhinia*, adaptive radiation has occurred into different life forms (trees and lianas) and different shade tolerance strategies (light-demanding versus shade-tolerant lianas). Generalizing results based on five species is difficult; however, by comparing only species from the same genus potential confounding phylogenetic differences are corrected for, and the contrast between lianas and trees is much clearer (Westoby, 1999). Within-genus variation in growth strategies is analysed and this variability related to the following hypotheses: (*a*) lianas have higher biomass growth rates than trees because less biomass has to be allocated to stem support and more biomass can be allocated to productive leaves; (*b*) shade-tolerant lianas are intermediate between light-demanding lianas and light-demanding trees in terms of growth rates and biomass allocation, based on the prediction that compared with light-demanding lianas they have less productive leaves, and compared with trees they have lower allocation to stem support.

MATERIALS AND METHODS

Study site and species

The study was conducted in Xishuangbanna (21°09′–22°33′N, 99°58′–101°50′E), SW China. Average annual temperature in Xishuangbanna is 21·4 °C. Average annual rainfall is 1539 mm, 85 % of which occurs in the rainy season (May–October). This still is a 'true' rain forest because heavy fog compensates partially for the reduced rainfall during the dry season (November to April). Five species of *Bauhinia* (three climbing lianas and two trees) were selected (Table 1). *Bauhinia claviflora* and *B. tenuiflora* are light-demanding liana species that are abundant in large canopy gaps. *Bauhinia aurea* is an extremely shade-tolerant liana that is found in the shaded understorey. *Bauhinia purpurea* and *B. monandra* are light-demanding tree species that are more abundant in canopy gaps (B. Wen and H. Zhu, pers. comm).

Experimental design

Seedlings that were 0·5–1 year old were collected from Xishuangbanna Botanical Garden and a nearby nursery during May 2004, at the start of the rainy season. Seedlings were transplanted into 20 × 30 cm pots containing topsoil from the nearby forest and then moved into a shadehouse. Four to six seedlings per species were harvested 4–6 weeks after bud expansion for measurements of biomass and biomass partitioning (leaves including petioles, stems and roots). The mean biomass of seedlings of the five species ranged from 4·6 to 11·6 g d. wt (*Bauhinia aurea* 11·6 g, *B. claviflora* 7·1 g, *B. monandra* 4·6 g, *B. purpurea* 5·7 g, *B. tenuiflora* 5·2 g). The remaining five to seven seedlings per species were grown in pots in the shadehouse at 25 % of full sunlight. This irradiance level is typical for a large gap in the forest, and was created using

TABLE 1. *Characteristics of the five* Bauhinia *species used in this study*

Species	Life form	Growth strategy	Species code
B. tenuiflora	Liana	Fast growth, light-demanding	BT
B. claviflora	Liana	Fast growth, light-demanding	BC
B. aurea	Liana	Slow growth, shade-tolerant	BA
B. purpurea	Tree	Fast growth, light-demanding	BP
B. monandra	Tree	Fast growth, light-demanding	BM

layers of neutral-density screen on a steel frame. Light availability [photosynthetic photon flux (PPF)] was measured using LI-190SA quantum sensors connected to a LI-1400 data logger (Li-Cor, Lincoln, NE, USA). All plants were watered on days without rain to maintain the soil near field capacity. Lianas were supported with dry bamboo shoots. At the end of the experiment (after approx. 6 months), physiological measurements were made for three or four plants per species, one leaf per plant. Morphological and biomass measurements were made for four to six plants per species. All lianas started to climb halfway the experiment and at the end all had a clear climbing habit.

Photosynthesis, N concentration and carbon isotope measurements

At the end of the experiment, the light-saturated CO_2 assimilation rate was measured under ambient CO_2 concentrations (approx. 400 ppm) and temperature ($25-27\,^{\circ}$C) using a portable Li-6400 photosynthesis system (Li-6400; Li-Cor). PPF density was set at 1600 μmol m^{-2}s^{-1} with the built-in red/blue LED light source (LI6400-02B). Light-response curves showed that this was sufficient to saturate photosynthesis for all species (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, UK) as an indicator of photoinhibition. Minimal (F_0) and maximal (F_m) fluorescence yields were measured on leaves after maintaining them in the dark for approx. 15 min. The 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 (0700 h) and at the middle of the day (1400 h). Diurnal photoinhibition was estimated as follows:

% diurnal photoinhibition $= 100 - 100 \times (F_v/F_{m\ 1400\ h})/(F_v/F_{m\ 0700\ h})$

After the photosynthesis measurements, leaves were collected and analysed for nitrogen concentration, $\delta^{13}C$ isotope ratio and biomass. $\delta^{13}C$ provides a time-integrated estimate of the ratio of photosynthesis to conductance and is therefore a good estimator of the intrinsic water-use efficiency (Farquhar and Richards, 1984). Leaves were ground to a fine powder for elemental analyses of $\delta^{13}C$ isotope ratio and N content. The $\delta^{13}C$ ratio was measured for all species but *Bauhinia aurea*. The $\delta^{13}C$ ratio was determined for 2 mg sub-samples using a Thermo Finnigan MAT stable isotope mass spectrometer (Bremen, German) at the Stable Isotope Laboratory in the Institute of Botany of the Chinese Academy of Sciences. Foliar N concentration (N_{mass},%) was measured by semi-micro Kjeldahl analysis using a wet digestion procedure. Photosynthetic nitrogen-use efficiency (PNUE, μmol CO_2 g^{-1} N s^{-1}) was determined as A_{mass} divided by N_{mass}.

Biomass allocation, morphology and plant growth

After harvest, plants were separated into leaves (including petioles), stems, and roots. Leaf areas were determined with a leaf area meter (LI-3100A; Li-Cor). Roots were washed in tap water. All tissues were dried to a constant weight at $70\,^{\circ}$C for 48 h. Specific leaf area (SLA, cm^2 leaf/g leaf), leaf area ratio (LAR, cm^2 leaf/g plant), leaf mass fraction (LMF, g leaf/g plant), stem mass fraction (SMF, g stem/g plant) and root mass fraction (RMF, g root/g plant) were calculated. Relative biomass growth rate (RGR, mg g^{-1} d^{-1}) was calculated as: RGR = [ln(final plant mass) – ln(initial plant mass)]/time. To this end the plants at initial and final harvest were randomly paired (cf. Causton and Venus, 1981).

Statistical analyses

For morphological and physiological variables, a one-way analysis of variance (ANOVA) was used to test for statistical differences among species, and the Fisher LSD test was used for *post-hoc* analysis. Data were checked for normality and homogeneity of variances, and a log$_{10}$ or square-root transformation was applied when necessary to satisfy the assumptions of ANOVA. To evaluate the underlying causes of interspecific variation in photosynthetic performance, the net photosynthetic rate (A_{mass}) was correlated with the nitrogen concentration (N_{mass}), which is an important component of RUBISCO. PNUE was correlated with the carbon isotope ratio to evaluate whether there is a trade-off between the photosynthetic nitrogen-use efficiency and photosynthetic water-use efficiency. To evaluate how RGR was affected by its underlying components, it was correlated with LAR (LMF × SLA, the morphological component) and A_{area} (as a proxy of NAR, the physiological component). Statistical analyses were done using SPSS 11·0 (SPSS, Chicago, IL, USA).

RESULTS

Growth, morphology and biomass allocation

The two light-demanding liana species had a higher RGR than the two light-demanding tree species, whereas the shade-tolerant liana *B. aurea* had the lowest RGR (ANOVA, $F = 98.5$, $P < 0.001$, Fig. 1A). LAR was significantly higher in the two light-demanding lianas compared with the other three species, whilst shade-tolerant *B. aurea* had similar LAR values as the two tree species ($F = 48.9$, $P < 0.001$, Fig. 1B). The SLA differed significantly among the five species (ANOVA, $F = 75.9$, $P < 0.001$). The SLA of the two light-demanding lianas was very high (>390 cm^2 g^{-1}) compared with the other three species ($190-230$ cm^2 g^{-1}). The shade-tolerant liana species, *B. aurea*, had a similar SLA to the tree species (Fig. 1C).

Distinct differences in biomass partitioning were found among the five species studied (Fig. 1D–F). The three liana species allocated more biomass to leaves than the two tree species ($F = 6.7$, $P = 0.004$). The light-demanding liana species allocated more to stems ($F = 39.8$, $P < 0.001$) and less to roots ($F = 71.0$, $P = 0.001$) than the tree species. The shade-tolerant liana, *B. aurea*, allocated
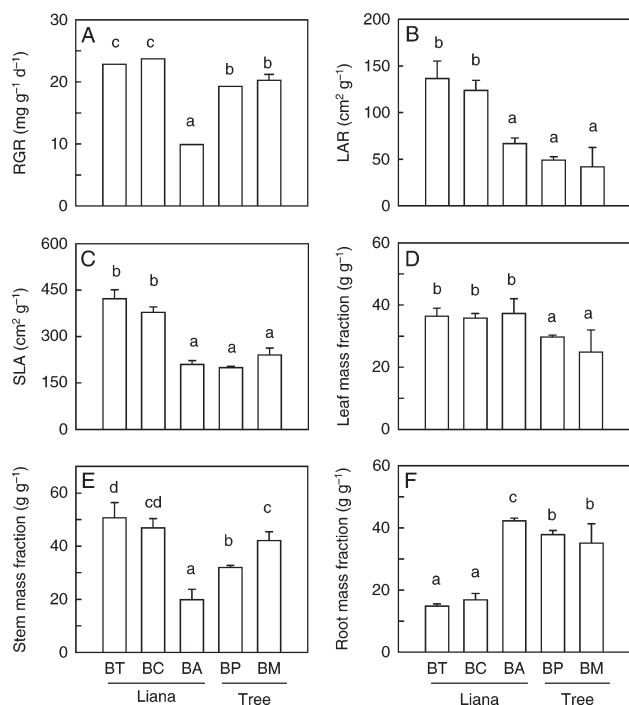
FIG. 1. Growth, morphology, and biomass distribution (means ± s.d.) in seedlings of five *Bauhinia* species. Significant differences (at $P < 0.05$) between species are indicated by different letters. Species codes are as defined in Table 1. RGR, Relative growth rate; SLA, specific leaf area; LAR, leaf area ratio.
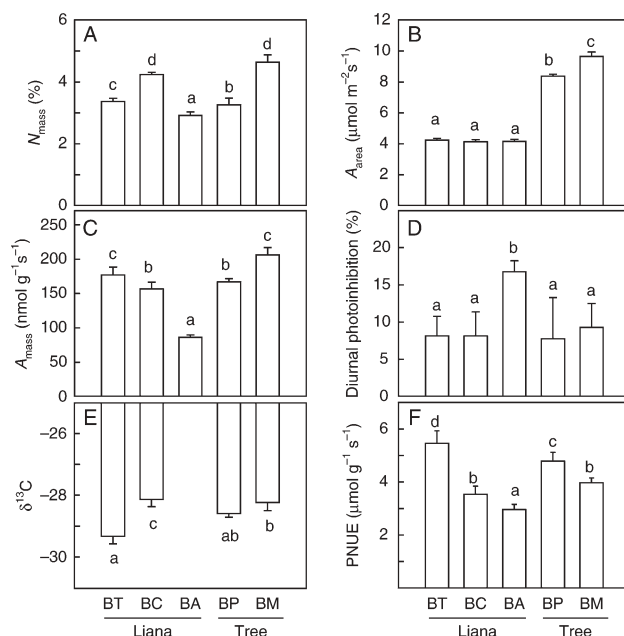

FIG. 2. Leaf physiological traits (means ± s.d.) in seedlings of five *Bauhinia* species. Significant differences (at $P < 0.05$) between species are indicated by different letters. Species codes are as defined in Table 1. N_{mass}, leaf nitrogen concentration; A_{area}, light-saturated photosynthetic rate based on leaf area; A_{mass}, light-saturated photosynthetic rate based on leaf mass; $\delta^{13}C$, carbon isotope discrimination (‰); PNUE, photosynthetic N-use efficiency. For *Bauhinia aurea* (BA) no $\delta^{13}C$ data were available.

more biomass to roots and less to stem than the four light-demanding species.

Leaf physiological traits

The species differed significantly in their leaf nitrogen concentration (N_{mass}) (Fig. 2A; ANOVA, $F = 306.9$, $P < 0.001$), with the shade-tolerant liana having the lowest value. A_{area} in the two tree species was significantly higher than that of the two light-demanding liana species ($F = 329.2$, $P < 0.001$), whereas A_{mass} was similar between these two groups (Fig. 2B and C). The shade-tolerant liana species had the lowest photosynthetic rate per unit mass (A_{mass}) and, alongside with the other lianas, the lowest photosynthetic rate per unit area (A_{area}). Pre-dawn F_v/F_m values were similar for all five species (approx. 0.82; data not shown). Diurnal photoinhibition was most severe in the shade-tolerant *B. aurea*, but was of similar magnitude in the four light-demanding species (Fig. 2D). Carbon isotope ratios ($\delta^{13}C$) were significantly different but with no consistent difference between liana and tree species (Fig. 2E, $F = 18.3$, $P = 0.001$). PNUE differed amongst species ($F = 28.3$, $P < 0.001$) and was lowest for the shade-tolerant liana (Fig. 2F).

Correlations between leaf attributes and growth characteristics

There was no significant correlation between leaf A_{mass} and N_{mass} concentration in the species studied and a significantly negative relationship between PNUE and $\delta^{13}C$ (Fig. 3).

To further analyse interspecific variation in growth rate, RGR was related to some of its underlying components. RGR was significantly correlated with SLA but not with LMF, LAR or A_{area} (Fig. 4). The shade-tolerant liana *B. aurea* in most cases seems to be deviating from the other species.

DISCUSSION

Do lianas grow faster than trees?

The two light-demanding lianas in the present study indeed had higher growth rates than the two light-demanding tree species (Fig. 1). Lianas are usually assumed to be adapted for rapid growth (Putz, 1983; Hegarty and Caballé, 1991) and a high RGR fits into that scheme. A higher RGR in plants is an important determinant of their distribution in productive habitats (those with a high availability of nutrients and light) because it can provide greater competitive ability (Poorter and Remkes, 1990; Cornelissen *et al.*, 1996; Poorter, 2005). In a comparative study of temperate woody species, the climbers and scramblers did indeed realize a higher RGR than the tree species (Cornelissen *et al.*, 1996). In contrast, the relative growth rate of herbaceous climbers was low compared with those of self-supporting species for seedlings grown in controlled environment chambers (Den Dubbelden and Verburg, 1996). Interestingly, equal growth rates for the liana and
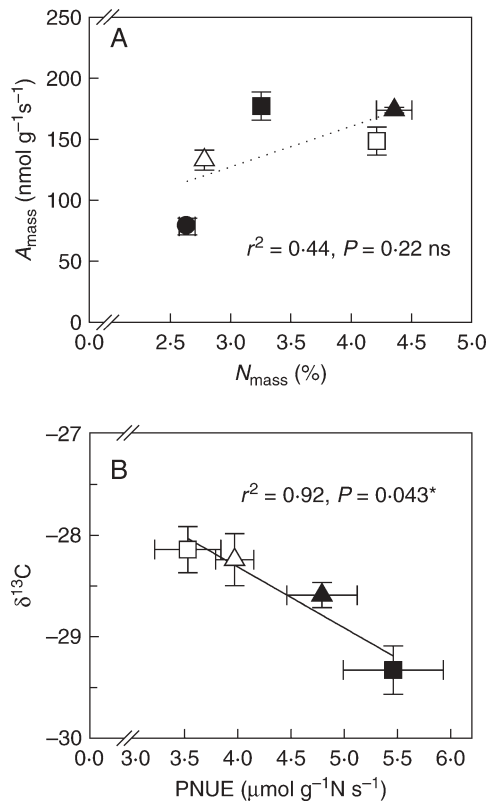
FIG. 3. Relationship between (A) net photosynthetic rate per unit dry mass (A_{mass}) and leaf N concentration (N_{mass}) and (B) photosynthetic nitrogen-use efficiency (PNUE) and $\delta^{13}C$ values (‰) for the species studied. Light-demanding lianas: BT, closed squares; BC, open squares; shade-tolerant liana: BA, closed circles, and light-demanding trees: BP, closed triangles; BM, open squares. See Table 1 for species' codes.
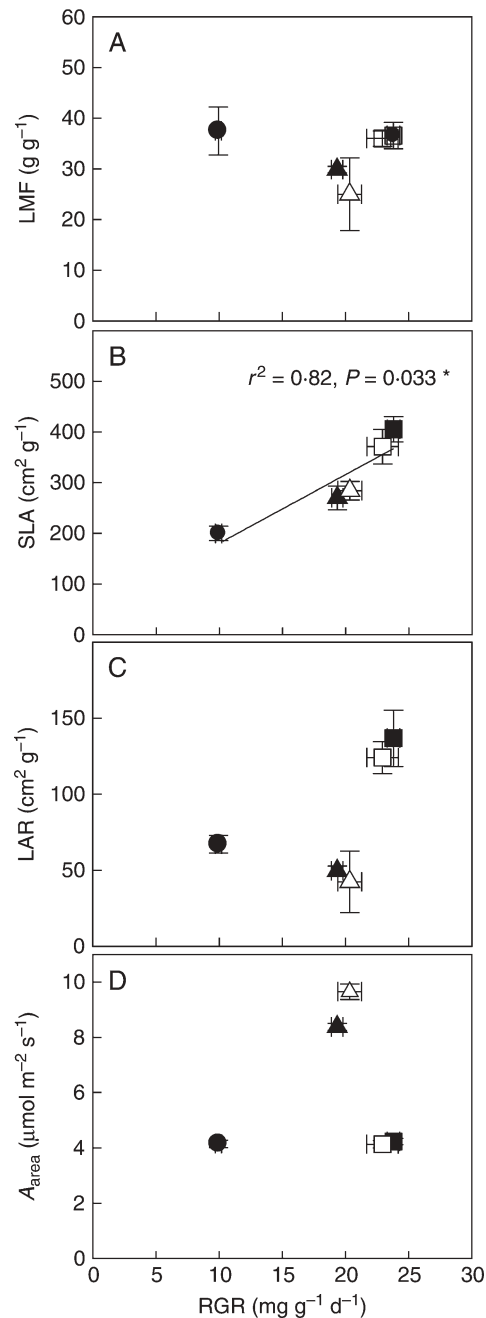

FIG. 4. Relationships between relative growth rates (RGR) and (A) leaf mass fraction (LMF), (B) specific leaf area (SLA), (C) leaf area ratio (LAR) and (D) net photosynthetic rates per unit area (A_{area}) for five *Bauhinia* species. Light-demanding lianas: BT, closed squares; BC, open squares; shade-tolerant liana: BA, closed circles, and light-demanding trees: BP, closed triangles; BM, open squares. See Table 1 for species' codes.

shrub growth form of *Toxicodendron diversilobum* were found when plants were grown in an experimental garden without competition, but the liana had higher growth rates in patchy natural habitats (Gartner, 1991).

The most striking differences between the light-demanding lianas and trees were in biomass partitioning. The larger investment in leaf mass (LMF) and/or leaf area (LAR) resulted in high biomass growth rates of the light-demanding lianas compared with the trees (Fig. 1). This higher LMF of lianas was consistent with results of other studies in both tropical and temperate forests; Putz (1983) found that lianas had a larger leaf biomass per unit basal area than trees. The two light-demanding lianas in the present experiment had higher SMF than the two trees (Fig. 1), contrasting sharply with the general postulation that climbers allocate less biomass to support tissue than self-supporting species (Darwin, 1867; Putz, 1984; Bell *et al.*, 1988). The larger investment in stem biomass of light-demanding lianas may maximize height growth (Richards, 1952; for herbaceous climbers, see Den Dubbelden and Verburg, 1996), enabling them to forage rapidly for a better light environment higher up in the forest canopy. If this trend continues over time then the growth-differences between lianas and trees may even be stronger in later ontogenetic stages (Selaya, 2007).

In looking for a functional explanation for growth differences, RGR is broken down into the product of net assimilation rate (NAR, dry mass gain per unit leaf area per day) and leaf area ratio (LAR). LAR is the product of specific leaf area (SLA) and leaf mass fraction (LMF) (Evans, 1972) and investment in leaf area generally improves light interception (Lambers and Poorter, 1992;

Poorter, 2001, 2005). Our light-demanding lianas indeed have a higher LAR than the two tree species (Fig. 1) and thus are likely to have a higher light-capturing ability and total photosynthetic carbon gain. However, lianas have a similar photosynthetic capacity per unit leaf biomass (A_{mass}) as trees, and the photosynthetic capacity per unit leaf area (A_{area}) is even lower (Fig. 2). The higher RGR of the light-demanding lianas may be attributable to their higher SLA and LMF (leading to higher LAR; Fig. 4), and not to the leaf physiological traits measured. This is in accordance with studies comparing fast-growing and slow-growing woody species (Kitajima, 1994; Cornelissen *et al.*, 1996; Poorter, 1999). Alternatively, a higher RGR could also be the result of lower respiration rates in faster-growing species (Lambers *et al.*, 1998)

The lack of photosynthetic differences (A_{mass}) is in contrast to the prediction that lianas differ from trees in those leaf traits related to efficient use of resources (Teramura *et al.*, 1991; Selaya *et al.*, 2007). When liana–tree species pairs were examined, the two light-demanding lianas indeed had higher SLA, but physiological differences in leaves were inconsistent (Figs 1 and 2). High SLA is a common trait contributing to faster growth because larger assimilatory surfaces are produced for a given amount of biomass (Veneklaas and Poorter, 1998; Poorter, 2005). A_{mass} represents the maximum rate of carbon capture per unit biomass invested and thus provides a better prediction of whole-plant growth than A_{area} (Givnish, 1988). The A_{mass} was similar among light-demanding lianas and trees, suggesting that these species are either similarly efficient at utilizing light energy, or have similar amounts of carboxylating enzymes. In contrast to the expectation that photosynthetic rates were positively related to leaf N concentrations (Evans, 1989), no correlation was found across species (Fig. 3A), suggesting that N availability is not the limiting factor for photosynthesis. This lack of correlation may be attributed to a different leaf N allocation between photosynthetic machinery and to photoprotection. Alternatively, stomatal conductance rather than N availability limits photosynthesis. With a decrease in stomatal conductance, water loss decreases and thus water-use efficiency increases. However, less of the total photosynthetic capacity is used due to lower CO_2 uptake, leading to reduced PNUE (Lambers *et al.*, 1998). This well-known trade-off between water-use efficiency and nitrogen-use efficiency (Field and Mooney, 1986) is confirmed by the present results (Fig. 3B). Lianas and trees may have different positions on this trade-off axis, but this is not confirmed by the present results. This may also be due to confounding factors such as cross-species differences in leaf thickness and leaf anatomy (Vitousek *et al.*, 1990).

A high investment in roots can contribute in balancing the demands of nutrient and light energy capture (Huston and Smith, 1987). The light-demanding lianas in this study, however, had lower RMF than the two trees, which is in contrast with the hypothesis that lianas invest more in roots by having deep root systems and being drought tolerant in the dry season (Schnitzer, 2005). Teramura *et al.* (1991) showed in their review of temperate woody vines that lianas had over 50 % (*Pueraria lobata*) to even 70 %

(*Rubus corylifolius*) of biomass in their roots, far above values typically found for temperate trees in other studies. Nonetheless, the low RMF of our light-demanding lianas does not necessarily leads to a lower absorption ability for nutrients and water; root biomass *per se* is not directly indicative of the total absorptive area of the root system, and alterations to the root system architecture can occur without a change in total root biomass (Hodge, 2004). Specific root length (total root length/root biomass) or root length per unit mass have been suggested to be a more exact method for measuring the potential ability of a plant to absorb water and nutrition resources (Eissenstat and Caldwell, 1988; Hodge, 2004). Although such data were not collected, the two light-demanding lianas with fibrous root systems had a larger root surface area and longer roots than the other three species with tap roots (Z.-Q. Cai, personal observation). If lianas have better access to soil water resources than trees, then they are also expected to have inherently low photosynthetic water-use efficiency. Yet, the $\delta^{13}C$ did not differ in a consistent way between lianas and trees (Fig. 2), perhaps because plants were grown at a high water availability in this pot experiment and thus did not need to be efficient in their water use, or because of the already-mentioned cross-species differences in other factors.

And the shade tolerant liana?

It was expected that the shade-tolerant liana *B. aurea* would be intermediate between the light-demanding lianas and the trees, based on the prediction that compared with light-demanding lianas they have less productive leaves, and compared with trees they have lower allocation to stem support. *Bauhinia aurea* was not intermediate for any of the measured parameters. In fact, the shade-tolerant liana had the lowest RGR and SMF of all species. Differences between the shade-tolerant and light-demanding lianas paralleled, however, the differences that are commonly observed between shade-tolerant and light-demanding trees (Poorter, 2005; Poorter and Bongers, 2006); the RGR was lower than that of the light-demanding lianas because of a low LAR, SLA and low mass-based nitrogen and PNUE. RMF of the shade-tolerant liana was larger than the light-demanding lianas, in agreement with the large RMF widely reported for young seedlings of shade-tolerant species (Kitajima, 1994; Paz, 2003; Poorter, 2005). A greater allocation below ground can decrease the risk of herbivory loss (Blundell and Peart, 2001). SMF was the lowest, and consistent with a shade-tolerant sit-and-wait strategy (Clark and Clark, 1992), low RGR (Veneklaas and Poorter, 1998; Poorter, 1999) and no active foraging, in contrast to the light-demanding lianas. The relatively low LAR of *B. aurea* compared with the light-demanding lianas may be related to the conservation of carbon rather than to maximization of photosynthetic surface area (Grime, 1979; Kitajima, 1994). The large reduction in F_v/F_m after strong midday light suggests inefficiency at dissipating excess light, as is commonly found in shade-tolerant species (Powles, 1984; Houter and Pons, 2005).

CONCLUSIONS

The light-demanding liana species had higher LMF and SMF, and lower RMF than the light-demanding trees. Competition for light in light-demanding lianas appears to have favoured both rapid shoot extension (ensuring that leaves are displayed above those of competitors) and production of high leaf area, which can be achieved by a high biomass allocation to leaves and by producing 'cheap' leaves (high SLA). The faster growth of the light-demanding lianas could be explained by morphological traits, such as higher SLA, LAR and LMF, and was not attributed to physiological traits, such as higher photosynthetic rates and nitrogen concentrations at the leaf level. Compared with the four light-demanding *Bauhinia* species, the shade-tolerant *B. aurea* had a different growth strategy. The present study on five *Bauhinia* species shows that, even within a genus, species growth (and their underlying factors) is rather variable, and that this variation is related to life form (lianas versus trees) and to light demand.

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