PHYSIOLOGICAL ECOLOGY - ORIGINAL PAPER

Contrasting cost–benefit strategy between lianas and trees in a tropical seasonal rain forest in southwestern China

Shi-Dan Zhu · Kun-Fang Cao

Abstract Lianas are an important component of tropical forests and often abundant in open habitats, such as tree-fall gaps, forest edges, and disturbed forests. The abundance of lianas in tropical forests has been increasing as a result of global environmental change and increasing forest fragmentation. In order to understand this phenomenon in terms of leaf functional traits and to evaluate their competitive potential, we conducted a cost–benefit analysis of leaves from 18 liana species and 19 tree species in a tropical seasonal rain forest. The results revealed that lianas were scattered in a group distinct from trees along the first axis of a principal component analysis using 15 leaf ecophysiological traits, being located at the quick-return end of the leaf economics spectrum, with higher specific leaf area and photosynthetic rates (A), higher photosynthetic nitrogen (N) and phosphorus (P) use efficiencies, a lower leaf construction cost per unit leaf area (CC) and cost–benefit ratio (CC/A), and a shorter leaf life span (LLS). Trees showed the opposite trends. The results indicate that lianas can grow faster and capture resources more efficiently than trees in disturbed, open habitats. The positive relationship between LLS and CC/A revealed a trade-off between leaf construction cost and benefit over time. The 37 species analyzed had a mean foliar N/P ratio of 20, indicating that the forest was characterized by a P deficit. With an increasing atmospheric CO_2 concentration, the higher nutrient use efficiency could benefit lianas more than trees in terms of productivity, possibly also contributing to the increasing abundance of lianas in nutrient-limited tropical forests.

Keywords Leaf construction cost · Leaf life span · Nutrient use efficiency · Photosynthesis

Introduction

Lianas are an important component of tropical rain forests and are often abundant in open habitats such as tree-fall gaps, forest edges, secondary forests, and clearings (Laurance et al. 2001; Schnitzer 2005; Schnitzer and Bongers 2002; Schnitzer et al. 2000). With increasing forest fragmentation and global environmental change, such as an increasing atmospheric CO_2 concentration, the abundance of lianas in tropical forests has been increasing (Phillips et al. 2002; Wright et al. 2004a). For example, the abundance of liana species is 10% greater in fragmented rain forests than in the primary rain forests of southwestern China (Zhu et al. 2004). Lianas can reduce tree growth and increase tree mortality, thus influencing forest regeneration (Schnitzer and Bongers 2002). Consequently, comprehensive knowledge of the functional basis for their high abundance in open habitats is critical for an understanding of tropical forest composition and dynamics.

Wright et al. (2004b) have developed the "leaf economics spectrum", which is associated with the key traits of leaf functions ranging from quick to slow returns on investments of nutrients and dry mass in leaves. At the

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quick-return end are those species with high leaf nutrient concentrations, high rates of photosynthesis (A) and respiration, a high specific leaf area (SLA), and a short leaf life span (LLS). The slow-return end is associated with those species with the opposite traits. Previous studies have reported that lianas have a greater SLA and A (Cai et al. 2009), faster leaf expansion (Avalos and Mulkey 1999), and faster turnover rates (Avalos et al. 2007; Phillips et al. 2005) than co-occurring trees. Given the increase in the abundance of lianas in open habitats and their specific characteristics, we expect that lianas should be closer to the quick-return end of the leaf economics spectrum than trees.

Leaf construction (CC) and maintenance (MC) cost are two very important functional traits of plants because they are closely related to many aspects of plant ecological and physiological performance. The CC is a measure of the energy invested by plants to produce carbon skeletons and nitrogenous compounds (Eamus et al. 1999). It is indirectly related to nutrient use efficiency and relative growth rate (Griffin 1994; Lambers and Poorter 1992; Sobrado 1991; Williams et al. 1987) and can be used to assess the resistance of plant species to environmental stresses (Suárez 2003, 2005) and to analyze plant survival, growth, and distribution (Baruch and Goldstein 1999; Feng et al. 2008; Liao et al. 2007; Nagel and Griffin 2001; Song et al. 2007). The MC is related to those processes requiring energy, such as the maintenance of ion gradients across lipid membranes and the turnover of organic compounds, but which do not directly result in a net increase in dry matter (Eamus and Prichard 1998). Low MC is generally associated with long-lived and sclerophyllous leaves and high structural components (Eamus et al. 1999; Merino et al. 1982; Sobrado 1991). However, relatively little is known about how lianas and trees differ in terms of CC and MC.

In the study reported here, we compared leaf construction and maintenance costs and benefits in terms of carbon gain between 19 tree species and 18 liana species in a tropical seasonal rain forest. We tested the prediction that the two groups exhibit different cost–benefit strategies. Specifically, the lianas should have leaves with a higher SLA and gas exchange rate, but lower CC and shorter LLS. These differences between lianas and trees may provide an explanation for the high abundance of lianas in high-light habitats.

Materials and methods

Study site and plant materials

This study was carried out in the Xishuangbanna Tropical Botanical Garden (XTBG; 21°54′N, 101°46′E, 580 m

a.s.l.), southern Yunnan, China. This region has a typical monsoon climate and thus has a distinct dry season from November to April. Mean annual total precipitation is about 1,500 mm, of which about 80% occurs in the wet season from May to October. Mean annual temperature is 21.4°C, with monthly temperatures ranging from 15.1 to 21.7°C. Although this region is at the margin of the tropics, the mountains and plateaus in the north and the west shelter it from cold winds in the winter. In addition, heavy fog occurs from midnight to noon every day in the first 4 months of the dry season, maintaining the soil moisture over a large proportion of the dry season. As a result, seasonal tropical rain forests flourish in this region, with a relatively high abundance of lianas (Zhu 1997; Zhu et al. 2006).

The study site is a fragmented forest with an areas of 100 ha that is located inside the XTBG. It was logged during the 1960s and 1970s but has been strictly protected since this time. The canopy height of this forest is about 15 m, which is about one-third to half of that of the primary seasonal rain forests of the area (Zhu et al. 2004). Nevertheless, many canopy species in this forest have reached the mature stage, while the abundance and diversity of lianas in this forest has increased over time (Tang et al. 1997; Zhu et al. 2004). We selected 18 liana species and 19 tree species in this forest (Table 1) based on the following criteria: (1) the species are common components of the forest according to an earlier community study (Tang et al. 1997, 1999); (2) the plants reach the forest canopy; (3) the trees do not carry any lianas.

Some species in this study are deciduous (Table 1), so we measured all of the leaf traits and gas exchange rates during the rainy season to avoid any seasonal effect on physiology and leaf traits. Twigs carrying newly and fully expanded, healthy sun-exposed leaves were harvested from the canopy crowns using a tree pruner attached to a long stick for the measurement of leaf traits. Three to five twigs from three to five different mature individuals per species were sampled. Leaf area was measured with a leaf area meter (Li-3000A; Li-Cor, Lincoln, NE), and then the leaves were oven-dried for 48 h at 70°C to determine the dry weight. The SLA was calculated as leaf area per dry mass. The dry leaves were then ground and homogenized for subsequent analyses.

Leaf life span

Leaf flushing and mortality were monitored twice a month between March 2007 and June 2008 for 60−100 leaves from three to five individuals for each species. Average LLS was determined in months following Reich et al. (1999).

Table 1 Species name, family, number of individuals sampled, leaf habit, and primary occurrence in different types of forest environments of 19 tree species and 18 liana species based on Li et al. (1996)

Species	Family	Number	Leaf habit	Distribution
Tree				
Kopsia officinalis Tsiang et P. T. Li	Apocynaceae	5	E	Disturbed forest
Vatica xishuangbannaensis G. D. Tao et J. H. Zhang	Dipterocarpaceae	5	E	Primary forest
Shorea chinensis (Wang Hsie) H. Zhu	Dipterocarpaceae	5	E	Primary forest
Bischofia javanica BL.	Euphorbiaceae	3	D	Secondary forest
Baccaurea ramiflora Lour.	Euphorbiaceae	5	E	Primary forest
Bauhinia variegata L. var. candida (Roxb.) Voigt.	Fabaceae	5	D	Secondary forest
Millettia leptobotrya Dunn	Fabaceae	5	E	Primary forest
Castanopsis indica (Roxb.) A. DC.	Fagaceae	4	E	Disturbed forest
Phoebe lanceolata (Wall. ex Nees) Nees	Lauraceae	5	E	Primary forest
Barringtonia macrostachya (Jack) Kurz	Lecythidaceae	3	E	Primary forest
Lagerstroemia tomentosa Presl	Lythraceae	5	D	Disturbed forest
Albizia lucidior (Steud.) I. Nielsen	Mimosaceae	3	D	Disturbed forest
Streblus indicus (Bureau) Corner	Moraceae	3	E	Primary forest
Syzygium latilimbum Merr. et Perry	Myrtaceae	3	E	Primary forest
Syzygium szemaoense Merr. et Perry	Myrtaceae	4	E	Secondary forest
Heliciopsis terminalis (kurz) Sleum.	Proteaceae	4	E	Secondary forest
Homalium laoticum Gagnep. var. glabretum C. Y. Wu	Samydaceae	3	E	Primary forest
Litchi chinensis Sonn. var. euspontanea Huse	Sapindaceae	3	E	Primary forest
Microcos chungii (Merr.) Chun	Tiliaceae	3	D	Secondary forest
Liana				
Artabotrys hongkongensis Hance	Annonaceae	3	E	Primary forest
Uvaria macrophylla Roxb.	Annonaceae	3	D	Secondary forest
Beaumontia grandiflora Wall.	Apocynaceae	4	E	Primary forest
Ecdysanthera rosea Hook. et Arn.	Apocynaceae	3	E	Forest borders
Dregea volubilis (L. F.) Benth. ex Hook. f.	Asclepiadaceae	3	D	Disturbed forest
Stixis suaveolens (Roxb.) Pierre	Capparaceae	4	E	Secondary forest
Combretum latifolium BL.	Combretaceae	4	D	Secondary forest
Quisqualis indica Linn.	Combretaceae	5	D	Secondary forest
Argyreia wallichii Choisy	Convolvulaceae	3	E	Primary forest
Bridelia insulana Hance	Euphorbiaceae	5	D	Secondary forest
Phyllanthus flexuosus (Sieb. et Zucc.) Muell.-Arg.	Euphorbiaceae	3	D	Forest borders
Bauhinia tenuiflora Watt ex C. B. Clarke	Fabaceae	5	E	Secondary forest
Millettia pachycarpa Benth.	Fabaceae	5	E	Secondary forest
Mucuna macrocarpa Wall.	Fabaceae	3	E	Primary forest
Gnetum parvifolum (Warb.) C. Y. Cheng ex Chun	Gnetaceae	3	E	Primary forest
Ziziphus attopensis Pierre	Rhamnaceae	5	E	Primary forest
Poikilospermum suaveolens (Blume) Merr.	Urticaceae	3	E	Primary forest
Tetrastigma campylocarpum (Kurz) Planch.	Vitaceae	3	E	Primary forest

E Evergreen, *D* deciduous

Leaf nutrients, leaf construction, and maintenance costs

All chemical analyses were processed in the Biogeochemical Laboratory of XTBG. Total organic nitrogen concentration (N) was determined by Kjeldhal analysis. Protein concentration was estimated by multiplying the N concentration by 6.25 (Merino et al. 1984), and phosphorus concentration (P) was determined using atomic absorption spectrum-photometry. Lipid concentration was analyzed gravimetrically from soluble diethylether extracts, and leaf ash concentration was determined gravimetrically after combustion of the samples for 4 h at 500°C.

The heat of combustion was determined with a bomb calorimeter (SDCM-IIIa; Sundy Instrument, Hunan, China),

and ash-free heat of combustion was calculated by converting the heat of combustion on a total dry mass basis to the corresponding ash-free mass. The construction cost (g glu g^{-1}) was defined as the amount of glucose required to produce 1 g biomass out of glucose and minerals (Eamus et al. 1999; Poorter et al. 2006) and was calculated from the equation given in Williams et al. (1987):

$$CC = [(0.06968 \, Hc - 0.065)(1 - Ash) + 7.5(KN/14.0067)]/0.89$$

where Hc is the ash-free heat of combustion (kJ g^{-1}), ash is the ash concentration (g g^{-1}), N is the nitrogen concentration (g g^{-1}), and K is the oxidation state of the N source (+5 for nitrate or -3 for ammonium). We used K = -3 and considered ammonium to be the main source of N at the study site (Sha et al. 2000).

The MC (g glu kg^{-1} day^{-1}) was calculated following Merino et al. (1984) using biochemical pathway analysis and the following maintenance coefficients: lipid, 0.0425; protein, 0.0405; ash, 0.008.

Carbon isotope ratio

The δ^{13}carbon (C) value of leaves is widely used to estimate the efficiency of long-term water use in natural vegetations (Farquhar et al. 1989; Holtum and Winter 2005). Because of the high expense of δ^{13}C analyses, we selected ten species for each of the two growth forms. The leaf stable C richness was analyzed at the Institute of Botany, Chinese Academy of Sciences using an elemental analyzer (Flash EA 1112; Thermo Electron, Waltham, MA) interfaced to an isotope ratio mass spectrometer (Thermo Finnigan MAT DELTAplusXP; Thermo Electron). δ^{13}C was calculated as:

$$\delta^{13}C \ (\text{‰}) = (R_{sample} - R_{standard})/R_{standard} \times 1{,}000\text{‰}$$

where R_{sample} and $R_{standard}$ were the ratios of ^{13}C/^{12}C in the sample and in the Pee Dee Belemnite standard, respectively.

Leaf gas exchange rate

On sunny days in August in the wet season, maximum net CO_2 assimilation rate (A) was measured in mature sun leaves on branches accessible from the ground. This measurement was performed in the field between 8:00 and 11:30 solar time with a Li 6400 portable photosynthesis system (LiCor). The photosynthetic photon flux density (PPFD) was set between 1,000 and 1,500 µmol m^{-2} s^{-1}, which corresponds to photosynthetic saturation for all species. Three to five individuals were selected for each photosynthetic measurement and five to six sun leaves were selected

from each individual. Photosynthetic nitrogen (PNUE) and P use efficiencies (PPUE) were calculated as A/N and A/P, respectively. The cost–benefit ratio was calculated as CC/A.

Statistical analyses

The multivariate associations of the 15 leaf traits (except for δ^{13}C) shown in Table 2 were analyzed with a principal component analysis (PCA) using $\log_{10}$-transformed values of the means of the leaf traits. A multivariate analysis of variance (MANOVA) was conducted to examine the difference between lianas and trees using the raw data of the 15 leaf traits and species scores for the first two PCA axes as dependent variables.

Reich et al. (1997) developed a model suggesting a trade-off between photosynthetic rates, CC, and LLS across a global data set regardless of growth form. The LLS increases with decreasing photosynthetic rates and increasing CC. To further examine the major differences in the C cost–benefit between liana and trees, the relationships between LLS and A_{mass}, CC_{area}, and CC/A were analyzed by linear regression for lianas and trees, respectively. If the slopes were not significantly different between the liana and tree regression lines, the difference in the regression intercepts was examined by ANCOVA. All statistical analyses were conducted using the SPSS software package (SPSS, Chicago, IL).

Results

The MANOVA results revealed that the two groups differed significantly for the 15 leaf traits (Table 2). The first two axes of the PCA explained 75% of the total variation of the 15 leaf traits (Table 3). Axis 1 correlated positively with SLA, A_{area}, A_{mass}, PNUE, and PPUE and negatively with CC_{area}, CC/A, and LLS; this difference represents a contrast between "quick-return leaves" and "slow-return leaves". Axis 2 correlated positively with N_{mass}, N_{area}, P_{area} MC_{mass}, and MC_{area} and was thus associated with leaf nutritional status and maintenance costs (Table 3).

The lianas and trees were separated along the first axis of the PCA (Table 3). The lianas were grouped on the right and were associated with higher SLA, A_{area}, A_{mass}, PNUE, and PPUE, lower CC_{area} and CC/A, and shorter LLS; the trees showed the opposite pattern (Fig. 1). Three families analyzed in this study comprise both lianas and trees: Apocynaceae, Euphorbiaceae, and Fabaceae. The comparison of leaf traits between the liana and tree species in first two families and genus *Bauhinia* followed the same pattern as the whole set of species (Table 4). The 37 species studied has a mean foliar N/P ratio of 20, suggesting that the forest under study had a P deficit.

Table 2 Leaf traits, trait abbreviations, units of traits and mean values of leaf traits for 19 tree species and 18 liana species (δ^{13}C from ten species for each growth form), and the results of the MANOVA

Variable	Abbreviations	Unit	Tree (mean $\pm$ SE)	Liana (mean $\pm$ SE)
Specific leaf area	SLA	cm^2 g^{-1}	158.34 $\pm$ 9.64	203.66 $\pm$ 14.99
Leaf N per unit dry mass	N$_{mass}$	mg g^{-1}	22.22 $\pm$ 1.96	28.79 $\pm$ 1.25
Leaf N per unit leaf area	N$_{area}$	g m^{-2}	1.42 $\pm$ 0.10	1.50 $\pm$ 0.10
Leaf P per unit dry mass	P$_{mass}$	mg g^{-1}	1.12 $\pm$ 0.08	1.58 $\pm$ 0.13
Leaf P per unit leaf area	P$_{area}$	g m^{-2}	0.07 $\pm$ 0.01	0.08 $\pm$ 0.01
Net photosynthetic rate per unit leaf area	A$_{area}$	μmol m^{-2} s^{-1}	8.39 $\pm$ 0.52	11.80 $\pm$ 0.49
Net photosynthetic rate per unit dry mass	A$_{mass}$	nmol g^{-1} s^{-1}	137.93 $\pm$ 15.11	239.97 $\pm$ 20.47
Photosynthetic nitrogen use efficiency	PNUE	μmol CO$_2$ (mol N)$^{-1}$ s^{-1}	93.19 $\pm$ 9.36	120.37 $\pm$ 8.81
Photosynthetic phosphorus use efficiency	PPUE	mmol CO$_2$ (mol N)$^{-1}$ s^{-1}	4.13 $\pm$ 0.42	5.16 $\pm$ 0.51
Leaf construction cost per unit dry mass	CC$_{mass}$	g glu g^{-1}	1.38 $\pm$ 0.01	1.37 $\pm$ 0.01
Leaf construction cost per unit leaf area	CC$_{area}$	g glu m^{-2}	93.32 $\pm$ 5.86	72.35 $\pm$ 4.27
Leaf maintenance cost per unit dry mass	MC$_{mass}$	g glu kg^{-1} day^{-1}	9.48 $\pm$ 0.63	11.69 $\pm$ 0.51
Leaf maintenance cost per unit leaf area	MC$_{area}$	g glu m^{-2} day^{-1}	0.62 $\pm$ 0.04	0.61 $\pm$ 0.03
The cost–benefit ratio	CC/A	g s μmol^{-1}	12.42 $\pm$ 1.38	6.27 $\pm$ 0.41
Leaf life span	LLS	Month	10.16 $\pm$ 0.50	8.50 $\pm$ 0.43
Carbon isotope ratio	δ^{13}C	‰	-30.37 ± 0.46	-29.34 ± 0.48

MANOVA tests	Wilks' Lambda	df	F	P
Growth forms	0.388	15,21	2.213	0.046

MANOVA Multivariate analysis of variance; *SE* standard error

Leaf life span was significantly and negatively correlated with A$_{mass}$, and the intercept of the fitted linear regression was significantly higher ($P < 0.01$, ANCOVA) for the lianas than for the trees (Fig. 2a), indicating a higher A$_{mass}$ at a given LLS in the lianas than in the trees. LLS was also significantly and positively correlated with CC$_{area}$, where the intercept of the linear regression was significantly higher ($P < 0.01$) for the trees than for the lianas (Fig. 2b), indicating that the trees had higher CC$_{area}$ than the lianas at a given LLS. LLS was significantly and positively correlated with CC/A, and the slope of the linear regression was significantly steeper ($P < 0.01$) for the trees than for the lianas (Fig. 2c), indicating that the trees used more energy than the lianas in terms of structural cost relative to photosynthesis with increasing LLS.

Discussion

The results confirmed our hypothesis that lianas and trees are two plant groups that represent different cost–benefit strategies: lianas were found at the quick-return end, whereas trees were at the opposite end (Fig. 1). Lianas had higher SLA and A, lower CC and shorter LLS, which are typical characteristics of fast-growing species (Baruch and Goldstein 1999; Lambers and Poorter 1992; Poorter and Bongers 2006). In addition, lianas have a very high leaf to

stem biomass ratio while relying on the host trees for mechanical support, resulting in a higher proportion of assimilation biomass than trees (Putz 1984; Schnitzer and Bongers 2002). These traits give lianas a high advantage over trees in the competition for light in open habitats, such as tree-fall gaps and disturbed forests, and even in the forest canopy.

The relationship between LLS and CC/A found in this study (Fig. 2) revealed a trade-off between leaf construction cost and benefit over time (Eamus and Prichard 1998; Shipley et al. 2006). The significant differences in these relationships between lianas and trees indicated that the lianas tend to have shorter-lived and more effective leaves and to invest less energy in immobile defensives, such as lignin and cell-wall components, which in turn contributed to their lower construction costs (Griffin 1994). Cheaper and shorter-lived leaves may contribute to fast growth rates, but they are also more susceptible to herbivores. However, natural selection favors species with a faster growth rate and lower defense level in resource-rich habitats (Coley et al. 1985), such as tree-fall gaps, forest edges, and disturbed forests.

Lianas and trees compete intensively for soil water and nutrients (Schnitzer et al. 2005). The cheaper and shorter lived leaves of lianas are associated with higher PNUE (this study; Poorter and Bongers 2006; Sobrado 1991) because a larger fraction of organic N is allocated to
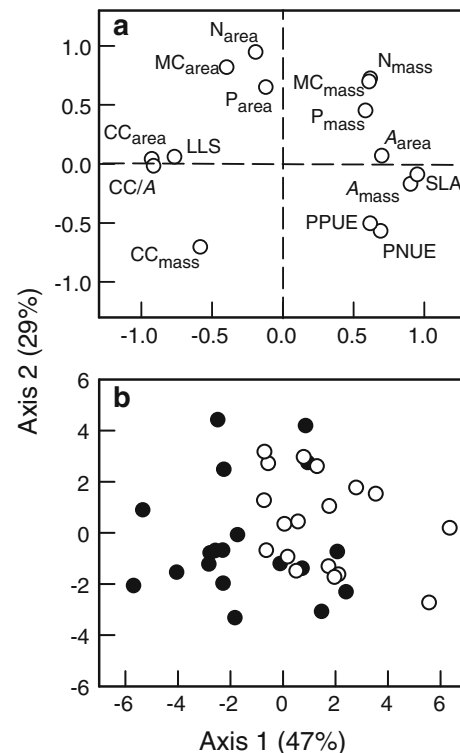
Table 3 Factor loading, eigenvalues, the percentage of variance explained, and MANOVA tests of the first two principal components

Variable	PC 1	PC 2
SLA	0.908	−0.177
N_{mass}	0.625	0.717
N_{area}	−0.187	0.940
P_{mass}	0.590	0.445
P_{area}	−0.114	0.643
A_{area}	0.706	0.062
A_{mass}	0.957	−0.097
PNUE	0.698	−0.576
PPUE	0.623	−0.511
CC_{mass}	−0.577	−0.712
CC_{area}	−0.921	0.034
MC_{mass}	0.616	0.691
MC_{area}	−0.392	0.813
CC/A	−0.907	−0.024
LLS	−0.760	0.052
Eigenvalues	7.016	4.296
% of variance	46.770	28.638
Cumulative %	46.770	75.408

MANOVA tests for two growth forms	F	P
Wilks' Lambda	9.130	0.001
Tests of between-subjects effects		
PC 1	16.139	0.000
PC 2	1.225	0.276

Abbreviations are as given in Table 2

Fig. 1 Principal component analysis for (**a**) the 15 leaf traits and (**b**) the 19 tree species (*filled circles*) and 18 liana species (*open circles*) for the first two axes. Abbreviations are as given in Table 2. All of the leaf traits were measured in the wet season

thylakoids and Rubisco (Poorter and Evans 1998), thus resulting in higher A. We found mean foliar N/P ratios of >16, which is in agreement with the results of Cai and Bongers (2007) from a tropical montane rain forest of the same area, and suggests that the forest used in our study was P-limited (Koerselman and Meuleman 1996). In addition, the lianas analyzed in our study showed a higher PPUE than the trees. Consequently, the higher nutrient use efficiency gives lianas a competitive advantage over trees in this nutrient-limited forest.

There was no significant difference in the $\delta^{13}C$ value measured in the wet season between the lianas and trees. Holtum and Winter (2005) also found that the $\delta^{13}C$ values of canopy leaves of lianas did not significantly differ from those of the adjacent upper-canopy trees. A water deficit in the dry season can affect physiological activity (Cao 2000) and growth rates (Engelbrecht et al. 2005). However, Cai et al. (2009) compared 16 tree species with 18 liana species and found that the lianas had a higher A_{mass} throughout a year and an increased $\delta^{13}C$ with no decreasing PNUE in the dry season. Lianas thus perform better than trees during a seasonal drought (Schnitzer 2005).

Although our study indicates that lianas have several physiological advantages over trees, this does not mean that lianas can replace trees and totally occupy the open sites. Lianas depend on trees for the mechanical support needed to grow upwards. Schnitzer et al. (2000) found that liana abundance was positively correlated with pioneer tree abundance and negatively correlated with shade-tolerant tree abundance, suggesting that the competitive advantage of lianas over trees diminishes during the forest succession. Gilbert et al. (2006) investigated the growth and survival of lianas and trees using seedlings of 22 liana and 31 tree species and saplings of 30 tree species. They found that the two groups exhibited similar trade-offs between growth and survival, thus enabling the coexistence and mainte-nance of species diversity of both lianas and trees.

According to Li et al. (1996), 56% of the liana species used in this study favor disturbed and secondary forests. However, other studies have demonstrated a wide range of shade tolerance in lianas (Gilbert et al. 2006; Putz 1984; Santiago and Wright 2007). Some of the liana species included in our study (e.g., *Bauhinia tenuiflora*, *Combretum latifolium*) that favor secondary forests are also able to persist in the deep shade of primary forests, while other liana species studied here, such as *Mucuna macrocarpa*, *Ziziphus attopensis*, and *Poikilospermum suaveolens*, occur

Table 4 Comparison of leaf ecophysiological traits between the tree and liana species within the same taxonomic families

Family	Growth form	SLA	A_{mass}	A_{area}	CC_{area}	CC/A	PNUE	PPUE
Apocynaceae								
Kopsia officinalis	Tree	158.50 ± 2.04	113.60 ± 6.20	7.65 ± 0.14	92.90 ± 0.92	12.14 ± 0.41	71.96 ± 2.98	4.15 ± 0.11
Beaumontia grandiflora	Liana	160.89 ± 3.35	189.69 ± 14.98	11.79 ± 0.44	85.67 ± 1.00	7.27 ± 0.82	102.45 ± 8.94	5.77 ± 0.61
Ecdysanthera rosea	Liana	182.86 ± 1.39	189.99 ± 6.75	10.39 ± 0.28	74.82 ± 0.61	7.20 ± 0.14	96.41 ± 1.55	6.26 ± 0.47
Euphorbiaceae								
Bischofia javanica	Tree	116.71 ± 3.89	99.78 ± 3.42	8.55 ± 0.07	119.26 ± 4.09	13.95 ± 0.45	87.63 ± 3.34	3.74 ± 0.15
Baccaurea ramiflora	Tree	136.67 ± 8.33	67.79 ± 5.35	4.96 ± 0.11	101.98 ± 9.99	20.56 ± 2.85	64.86 ± 7.54	2.03 ± 0.25
Bridelia insulana	Liana	166.91 ± 3.01	206.13 ± 7.40	12.35 ± 0.39	82.93 ± 1.69	6.71 ± 0.38	141.46 ± 6.61	5.74 ± 0.23
Phyllanthus flexuosus	Liana	234.42 ± 3.17	254.82 ± 5.78	10.87 ± 0.16	58.76 ± 0.95	5.41 ± 0.16	151.45 ± 5.60	5.12 ± 0.27
Fabaceae								
Bauhinia variegata	Tree	218.52 ± 8.45	224.64 ± 16.14	10.28 ± 0.18	63.27 ± 4.17	6.15 ± 0.56	153.70 ± 9.57	8.20 ± 0.54
Millettia leptobotrya	Tree	202.01 ± 1.42	177.76 ± 7.15	11.18 ± 0.32	66.68 ± 0.81	7.58 ± 0.27	62.92 ± 2.78	4.53 ± 0.18
Bauhinia tenuiflora	Liana	368.24 ± 2.95	399.54 ± 13.30	10.85 ± 0.2	36.94 ± 0.26	3.40 ± 0.21	173.17 ± 3.99	13.02 ± 0.31
Millettia pachycarpa	Liana	168.91 ± 1.16	203.53 ± 7.48	12.05 ± 0.22	80.03 ± 0.23	6.64 ± 0.33	78.66 ± 4.27	4.54 ± 0.27
Mucuna macrocarpa	Liana	196.62 ± 7.12	272.12 ± 3.97	13.84 ± 0.40	70.04 ± 1.21	5.06 ± 0.09	164.39 ± 2.81	5.39 ± 0.12

Data are given as the mean ± standard error (SE) for each species

Abbreviations and units are as given in Table 2
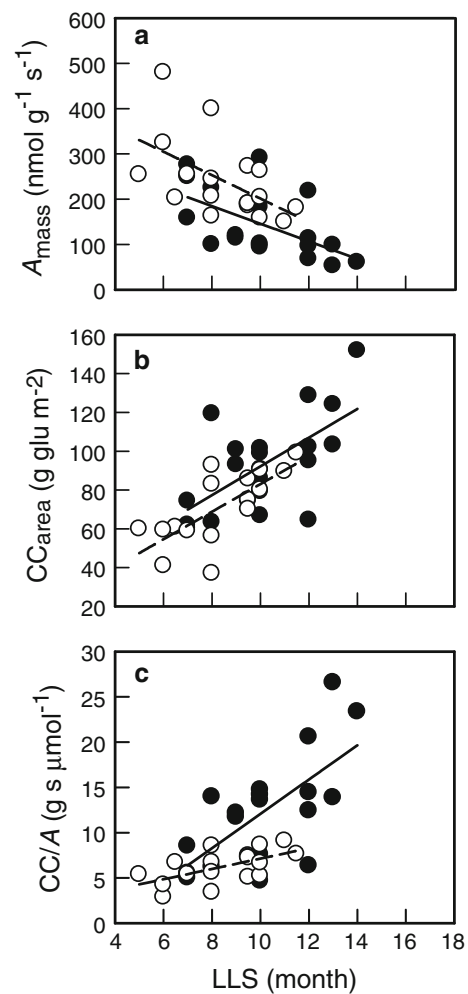
Fig. 2 Relationships between leaf life span (*LLS*) and **a** maximum net CO_2 assimilation rate per unit mass (A_{mass}), **b** leaf construction cost per unit area (CC_{area}), **c** cost–benefit ratio (CC/A) for the 19 tree species (*filled circles*, *solid lines*) and the 18 liana species (*open circles*, *dashed lines*). **a** For lianas, $A_{mass} = 460.11 - 25.90$ LLS, $r^2 = 0.30$, $P = 0.018$; for trees, $A_{mass} = 339.92 - 19.42$ LLS, $r^2 = 0.33$, $P = 0.011$. **b** For lianas, $CC_{area} = 11.89 + 7.11$ LLS, $r^2 = 0.53$, $P = 0.001$; for trees, $CC_{area} = 18.06 + 7.41$ LLS, $r^2 = 0.40$, $P = 0.004$. **c** For lianas, CC/A $= 1.41 + 0.57$ LLS, $r^2 = 0.36$, $P = 0.009$; for trees, CC/A $= -6.88 + 1.89$ LLS, $r^2 = 0.45$, $P = 0.002$

in dense forests, even though they possess the leaf characteristics of fast-growing species in disturbed habitats (data not shown). These growth characteristics indicate the high capacity of lianas to acclimatize to light and supports the hypothesis that lianas share attributes of both light-demanding and shade-tolerant species (Schnitzer and Bongers 2002). The high leaf acclimation potential of lianas has been reported in several studies (Avalos and Mulkey 1999; Cai et al. 2007; Salzer et al. 2006; Sanches and Válio 2008).

The quick-return strategy of lianas combined with their high nutrient use efficiency in tropical forests could

promote their growth as the concentration of atmospheric CO_2 concentration. Elevated atmospheric CO_2 concentration enhances the photosynthesis and productivity of C_3 plants. Results from earlier studies indicate that rising CO_2 levels stimulate the plant growth of tropical forest understorey species in general (Würth et al. 1998) and the competitive ability of lianas in deep shade in particular (Granados and Körner 2002). However, tropical forests are usually associated with poor soil nutrients, particularly P (Reich and Oleksyn 2004). This condition could act as a constraint on the stimulating effect of elevated atmospheric CO_2 levels on the productivity of tropical forest plants (LeBauer and Treseder 2008; Xia and Wan 2008), but the degree of the constraint would be less severe on lianas than on trees because of their differing nutrient use efficiency, possibly explaining the increasing abundance of lianas in tropical forests.

In summary, the quick-return strategy of lianas enables them to grow faster and capture resources more efficiently than forest trees, thus giving them a competitive advantage over these trees in open tropical forest habitats, such as tree-fall gaps, forest edges, and disturbed forests. The higher nutrient use efficiency could also benefit lianas more than trees in terms of an increased productivity from the increasing atmospheric CO_2 concentration. With increasing disturbances in tropical forests and increasing atmospheric CO_2 concentration, lianas are likely to increase both their abundance and their effect in the forest dynamics of tropical forests. Nevertheless, the dependence of lianas on trees for physical support and the similar trade-off of the life history traits between lianas and trees will allow their co-existence in tropical forests.

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