

Differences in the photosynthetic efficiency and photorespiration of co-occurring Euphorbiaceae liana and tree in a Chinese savanna

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Abstract

Lianas perform better than co-occurring trees in secondary forests or disturbed areas. Lianas and trees differ strikingly in water use strategy, which may result in a significant difference in photosynthetic light use between both growth forms. However, the difference in the photosynthetic efficiency and light energy dissipation between these two growth forms is poorly understood. Moreover, photorespiration is an important mechanism of photoprotection under conditions of high light. In this study, we used *Bridelia stipularis* (Linn.) Bl. (liana) and *Strophoblachia fimbriatylx* Boerl. (tree) in order to measure the response curves of the gas exchange and photosynthetic electron flow to the incident light gradients and intercellular CO₂ concentration, as well as the hydraulic conductivity. We tested whether the photochemical efficiency and photorespiration differed between both growth forms. Our results clearly demonstrated that *B. stipularis* possessed a significantly higher stem and leaf specific hydraulic conductivity, total electron flow, and maximum rate of ribulose-1,5-bisphosphate regeneration compared to the sympatric tree *S. fimbriatylx*. Correspondingly, *B. stipularis* exhibited a significantly higher photochemical quenching coefficient and electron flow to photorespiration relative to *S. fimbriatylx* under saturating light levels. We suggested that photorespiration might play an important role in photoprotection for both species under high light, but particularly for *B. stipularis*. These findings could enrich our knowledge of the superior photosynthetic and growth performance of lianas over the co-occurring trees.

Additional key words: hydraulic conductivity; photochemical quenching; photosynthetic electron flow.

Introduction

Lianas are an important growth form commonly found in tropical forests (Schnitzer and Bongers 2002). Their richness and growth performance have been highlighted over co-occurring trees (Schnitzer 2005, Schnitzer and Bongers 2011), particularly in secondary forests or disturbed areas (Putz 1984, Schnitzer and Carson 2010). More recently, the high abundance of lianas in seasonally dry forests has been explained by a stronger capacity of

dry-season uptake of deep soil water and stomatal adjustment of the water status, as well as higher wet-season photosynthesis over trees (Chen *et al.* 2015). However, the competition for light also affects the interactions between lianas and trees (Schnitzer *et al.* 2005, Chen *et al.* 2008). High light, particularly, in open or disturbed areas, may induce photo-oxidative damage of the photosynthetic apparatus (Nishiyama *et al.* 2001), which suppresses

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Abbreviations: A_s – sapwood area; A_L – total leaf area; Chl – chlorophyll; C_i – intercellular CO₂ concentration; g_s – stomatal conductance; HV – the Huber value; J_c – electron flow for RuBP carboxylation; J_{max} – maximum rate of RuBP regeneration; J_o – electron flow for RuBP oxygenation; J_T – total electron transport rate; K_h – water flow rate through the segment; K_L – leaf specific hydraulic conductivity; K_s – sapwood specific hydraulic conductivity; LSP – light saturation point, P_N – net CO₂ assimilation rate; q_P – photochemical quenching coefficient; R_D – dark respiration; ROS – reactive oxygen species; RuBP – ribulose-1,5-bisphosphate; V_{cmax} – maximum rate of RuBP carboxylation; Φ_{PSII} – actual photochemical efficiency of PSII.

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largely the photosynthetic performance of plants. Thus, high irradiance in open tropical forests and savanna may be a driving factor for determining an interspecific competition and the niche differentiation between lianas and trees (Schnitzer *et al.* 2005). There is, so far, little information about comparisons of the physiologically adaptive strategies to high light between lianas and trees. Therefore, the differences in the photochemical efficiency and the excessive light energy dissipation between these two growth forms are poorly understood.

Under optimal conditions, a higher hydraulic efficiency can maintain a higher stomatal conductance (g_s) (Meinzer 2003, Santiago *et al.* 2004). Nonetheless, under conditions of environmental stress, such as a water deficit, high light, and high temperature, the decreasing g_s may limit CO_2 diffusion from the outer atmosphere to chloroplast carboxylation sites (Ackerly 2004, Santiago *et al.* 2004), leading to a lower intercellular CO_2 concentration (C_i). A lower influx of CO_2 results in the generation of reactive oxygen species (ROS), which suppresses D_1 protein synthesis (Nishiyama *et al.* 2001, 2011) and causes, consequentially, the photoinactivation of PSII under conditions of excessive light (Oguchi *et al.* 2009, 2011). To overcome the adverse effects of excessive photosynthetic excitation energy, the plants must balance the proportion of absorbed light devoted to carbon assimilation and that of a safe dissipation of excessive light energy by a variety of photoprotective mechanisms. It is well documented that the enhancement of photorespiration plays an important role in the safe dissipation of excessive light energy, especially in C_3 plants (Osmond and Grace 1995, Takahashi *et al.* 2007, Zhang *et al.* 2009, Hochberg *et al.* 2013). A previous report has suggested that ribulose-1,5-bisphosphate (RuBP) is oxygenated by Rubisco to produce glycerate-3-phosphate, which, in turn, continues the Calvin cycle (Leegood *et al.* 1995). Furthermore, the oxygenation of RuBP consumes twice more photo-

synthetic transport electrons than that of the carboxylation of RuBP (Laisk and Edwards 1998). Therefore, the photorespiratory pathway can protect photosystems from photoinactivation by consuming excessive photosynthetic transport electrons (Flexas *et al.* 1999, Takahashi *et al.* 2007). To date, no direct test has been performed to verify whether the activation of photorespiration differs between lianas and trees when they are exposed to high light.

As a result of the rain-shadow effects of the mountains, the valley type of savanna is widely distributed, with a total area of 80,000 km^2 , in dry and hot valleys of Southwest China. Its climate is characterized by a dry season that lasts over half a year, accompanied by high irradiance (Jin and Ou 2000). A valley type of savanna, with a mixture of trees and lianas with contrasting growth forms, dominates these valleys. In the open savanna, the lianas exhibited a higher growth performance than the co-occurring trees. In this study, we measured the gas exchange and the chlorophyll (Chl) fluorescence of *Bridelia stipularis* (Linn.) Bl. and *Strophoblachia fimbriatylx* Boerl., as well as the xylem hydraulic properties that were functionally coordinated with the leaf gas exchange (Patiño *et al.* 1995, Brodribb *et al.* 2002, Campanello *et al.* 2008, Hao *et al.* 2011). These two Euphorbiaceae species grow under similar environmental conditions in a valley type of savanna but differ strikingly in their growth forms (liana vs. tree). The following question and hypothesis were addressed: How do the photosynthetic performance and the partitioning of the photosynthetic electron flow, such as the net CO_2 assimilation rate (P_N), photochemistry, and photorespiration, differ between trees and lianas when they are exposed to excessive high light? We expected that liana *B. stipularis* receives a higher proportion of absorbed light energy used by PSII photochemistry and photorespiration, as well as it has a higher hydraulic efficiency and P_N compared with the co-occurring tree *S. fimbriatylx*.

Materials and methods

Study site: This study was carried out at the Yuanjiang Research Station for Savanna Ecosystems (YRSSE, 23°27'N, 102°10'E, 481 m a.s.l.) of Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Yuanjiang County, Yunnan Province, Southwest China. The climate is characterized by two distinct seasons: a rainy season (May to October) and a dry season (November to next April). Based on the YRSSE meteorological record from 2012 to 2014, the mean annual temperature is 24.9°C, with a mean monthly temperature ranging from 17.1°C (January) to 30.0°C (May). The number of days over the maximal and minimal temperatures of over 30°C and below 15°C was 244 and 63, respectively. The total mean annual precipitation was 662 mm, with 84.8% of the precipitation falling during the rainy season (Fig. 1). The soil is ferralitic cambisol, with a pH ranging from 5.2 to 6.3.

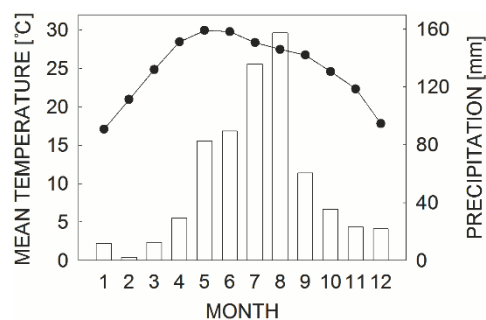


Fig. 1. Monthly mean air temperature (black circles) and monthly precipitation (vertical bars) in the study site. The values are the means of 2012 to 2014.

Plant materials: The YRSSE established one long-term monitoring plot (100 m×100 m) in 2011. *Bridelia*

stipularis (Linn.) Bl. and *Strophoblachia fimbriatylx* Boerl. belong to the Euphorbiaceae family and are representatives of the liana and tree growth forms, respectively. They are the two dominant woody species in the Chinese savanna. Near the plot, five mature individuals were chosen for *B. stipularis* and *S. fimbriatylx* grown in a similar light environment in the open savanna. All of the individuals were exposed to full light over the crown surface. We selected sun-exposed and fully expanded leaves without herbivory damage. All of the measurements were carried out in August of 2013 in the middle of the rainy season with a mean air temperature of 31.0°C/25.5°C (day/night). The maximum PPFD reached above 1,800 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in the midday and was 600–1,000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in the morning. The soil water potential was –0.3MPa, and all of the sample individuals grew well without water stress. Thus, the differences in the eco-physiology were attributed to the growth forms rather than to the environmental conditions.

Gas exchange and Chl fluorescence measurements: The gas exchange and Chl fluorescence was measured simultaneously on sunny days using a portable *LI-6400* gas analysis system with a *6400-40* fluorescence chamber (*LI-6400*, *Li-Cor*, Lincoln, NE, USA). Each replicate was measured from the youngest fully matured and intact leaf from one sample individual of each species in the field. Therefore, there were, in total, five replicates for the parameters of leaf gas exchange and Chl fluorescence.

During predawn, the leaves were used to determine the maximum fluorescence yield (F_m), with a 0.8-s saturating pulse at 7,000 $\mu\text{mol}(\text{photon}) \text{m}^{-2} \text{s}^{-1}$, and the ground fluorescence yield (F_o). The light-response curves were measured after at least 20 min of light adaptation with a PPFD of 1,000 $\mu\text{mol}(\text{photon}) \text{m}^{-2} \text{s}^{-1}$. The light-response curves of the gas exchange and the Chl fluorescence were measured at 2,000; 1,500; 1,000; 500; 200; 100; 50; 20, and 0 $\mu\text{mol}(\text{photon}) \text{m}^{-2} \text{s}^{-1}$ and 30 °C; the relative humidity was approximately 80% under the CO_2 concentration of 400 $\mu\text{mol mol}^{-1}$. According to previous methods (Genty *et al.* 1989, Kramer *et al.* 2004), we determined the minimum (F_o') and maximum Chl fluorescence (F_m') of the light-adapted leaves, as well as the steady-state fluorescence under actinic light (F_s). The photochemical quenching coefficient (q_p) and the actual proportion of absorbed light energy used by PSII photochemistry (Φ_{PSII}) was calculated according to the following formula (Eq. 1, 2; Genty *et al.* 1989). Meanwhile, the total electron transport rate (J_T) was estimated according to the following formula (Eq. 3; Krall and Edwards 1992):

$$q_p = \frac{F_m' - F_s}{F_m' - F_o'} \quad (1)$$

$$\Phi_{\text{PSII}} = 1 - \frac{F_s}{F_m'} \quad (2)$$

$$J_T = 0.5 \times \alpha \times \text{PPFD} \times \Phi_{\text{PSII}} \quad (3)$$

where α is the ratio of radiation absorbed by the leaf compared to the incident radiation. In this study, α was

measured with a *USB-4000* spectrometer (*Ocean Optics*, Florida, USA) at wavelengths from 400 to 700 nm. The values of α were 0.919 and 0.843 for *B. stipularis* and *S. fimbriatylx*, respectively. The absorbed photons were assumed to distribute equally in PSI and PSII, thus, a factor of 0.5 was used in the calculation of the electron flow. The maximum leaf area-based CO_2 assimilation rate ($P_{N\text{max}}$) and the light-saturation point (LSP) were calculated according to the methods described by Prioul and Chatterier (1977). In addition, the electron flows for RuBP carboxylation (J_c) and oxygenation (J_o) were estimated according to the following formula (Valentini *et al.* 1995):

$$J_c = \frac{1}{3} \times [J_T + 8 \times (P_N + R_D)] \quad (4)$$

$$J_o = \frac{2}{3} \times [J_T - 4 \times (P_N + R_D)] \quad (5)$$

where P_N is leaf area-based net CO_2 assimilation rate under each PPFD and R_D is the dark respiration. In this study, R_D was calculated from light-response curves in the low light of 20–100 $\mu\text{mol}(\text{photon}) \text{m}^{-2} \text{s}^{-1}$.

The response curves of the leaf gas exchange to the intercellular CO_2 concentration (P_N/C_i) were made from 400, 200, 100, 50, 20, 400, 800; 1,200; 1,600; 2,000 $\mu\text{mol}(\text{CO}_2) \text{mol}^{-1}$ under a PPFD of 1,000 $\mu\text{mol m}^{-2} \text{s}^{-1}$. According to the method previously described by Long and Bernacchi (2003), the maximum rate of RuBP regeneration (J_{max}) and the maximum rate of RuBP carboxylation (V_{cmax}) were calculated based on the response curves of P_N/C_i . Meanwhile, the Rubisco content per leaf area was calculated according to the method described by Hymus *et al.* (2002).

$$\text{Rubisco } [\mu\text{mol m}^{-2}] = V_{\text{cmax}}/8 K_{\text{cat}} (K_{\text{cat}} = 3.3) \quad (6)$$

Hydraulic properties: Five terminal branches (diameter ~1 cm) with fully sun-exposed leaves from the upper canopy were harvested from five sample individuals of each species in the predawn. The branches were recut immediately under water and quickly transported to a nearby laboratory of the YRSSE. More than 50 cm long stem segments without twigs were used to determine the xylem hydraulic conductivity. Both ends of the stem segment were shaved with a sharp razor blade. The stem segment was connected to the hydraulic conductivity apparatus previously described by Hao *et al.* (2011). The pressure in this apparatus was induced by gravity. One end of the segment was connected to 0.1 mol L⁻¹ KCL solution with 7kPa pressure. The direction of injection solution flow always moves from base to top of the stems. The other end was connected to a pipette to measure the water flow rate through the segment (K_h , kg m s⁻¹ MPa⁻¹):

$$K_h = F/(dp/dx) \quad (7)$$

where F is the water flux through an excised stem segment (kg s⁻¹) and dp/dx is the pressure gradient causing the flow (MPa m⁻¹).

Afterwards, the sapwood of the segment was flushed

with a methyl blue solution, and the sapwood area (A_s , cm^2) was calculated by the mean value of the traverse section of the two ends of the stem segment. The sapwood specific hydraulic conductivity (K_s , $\text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$) is equal to K_h divided by A_s . The total leaf area (A_L) for every terminal branch was determined with a *Li-3000A* leaf area meter (*Li-Cor*, Nebraska, USA). The specific leaf hydraulic conductivity (K_L , $\text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$) was calculated as the ratio of K_h to A_L . Meanwhile, the Huber value (HV) was calculated as the ratio of A_s to A_L .

Results

Hydraulic properties: The liana species, *B. stipularis*, had a significantly higher K_s (3.70 vs. 1.56 $\text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$) than the co-occurring tree species, *S. fimbricalyx*. In parallel with the K_s , *B. stipularis* had a significantly higher K_L (6.26 vs. 2.81 $\text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$) than *S. fimbricalyx*. However, the HV values were 1.69×10^{-4} and 1.80×10^{-4} for *B. stipularis* and *S. fimbricalyx*, respectively, and no significant difference was found for the HV values between these two species.

Photochemistry and photosynthetic performance: The light-response curves at 30°C and the concentration of 400 $\mu\text{mol}(\text{CO}_2) \text{mol}^{-1}$ showed that *B. stipularis* had significantly higher q_p values compared to those of *S. fimbricalyx* under all of the PPFD levels (Fig. 2A). Correspondingly, the Φ_{PSII} values were significantly higher in *B. stipularis* than those in *S. fimbricalyx* regardless of the PPFD (Fig. 2B). At the concentration of 400 $\mu\text{mol}(\text{CO}_2) \text{mol}^{-1}$, the light-response curves showed that *B. stipularis* had higher C_i values than those of *S. fimbricalyx*, with the exception of that under the dark conditions [at

Data analysis: The statistical analyses were performed with *SPSS* version 16.0 software (*SPSS*, Chicago, IL, USA). The differences in the hydraulic properties and the photosynthetic and Chl fluorescence parameters between the two species were assessed by one-way analysis of variance (*ANOVA*) at a significant level $P < 0.05$. The figures were plotted with *SigmaPlot 10.0* software. The ecophysiological values were presented as the means $\pm$ SE for five replicates. However, the meteorological background values were the means recorded from 2012 to 2014.

0 $\mu\text{mol}(\text{photon}) \text{m}^{-2} \text{s}^{-1}$] (Fig. 2C). Under low PPFD [20–100 $\mu\text{mol}(\text{photon}) \text{m}^{-2} \text{s}^{-1}$], there was no significant difference in P_N between the two species, but *B. stipularis* had higher P_N values than those of *S. fimbricalyx* when the PPFD reached above 200 $\mu\text{mol}(\text{photon}) \text{m}^{-2} \text{s}^{-1}$ (Fig. 2D).

Under conditions of 30°C and 400 $\mu\text{mol}(\text{CO}_2) \text{mol}^{-1}$, *B. stipularis* had a significantly higher $P_{N\text{max}}$ calculated from the light-response curves compared with that of *S. fimbricalyx* (Fig. 3A). In addition, *B. stipularis* had a significantly higher LSP than *S. fimbricalyx* (Fig. 3B).

Photosynthetic electron flow: The light-response curves showed that J_T , J_e , and J_o did not differ significantly between the two species under PPFD that were lower than 200 $\mu\text{mol}(\text{photon}) \text{m}^{-2} \text{s}^{-1}$ (Fig. 4). However, when the PPFD reached more than 500 $\mu\text{mol}(\text{photon}) \text{m}^{-2} \text{s}^{-1}$, *B. stipularis* had significantly higher J_T , J_e , and J_o values compared with those of *S. fimbricalyx*. Specifically, under saturating light, the maximum J_e values were 100 and 52 $\mu\text{mol}(\text{photon}) \text{m}^{-2} \text{s}^{-1}$ for *B. stipularis* and *S. fimbricalyx*, respectively (Fig. 4B). In addition, the maximum J_o values

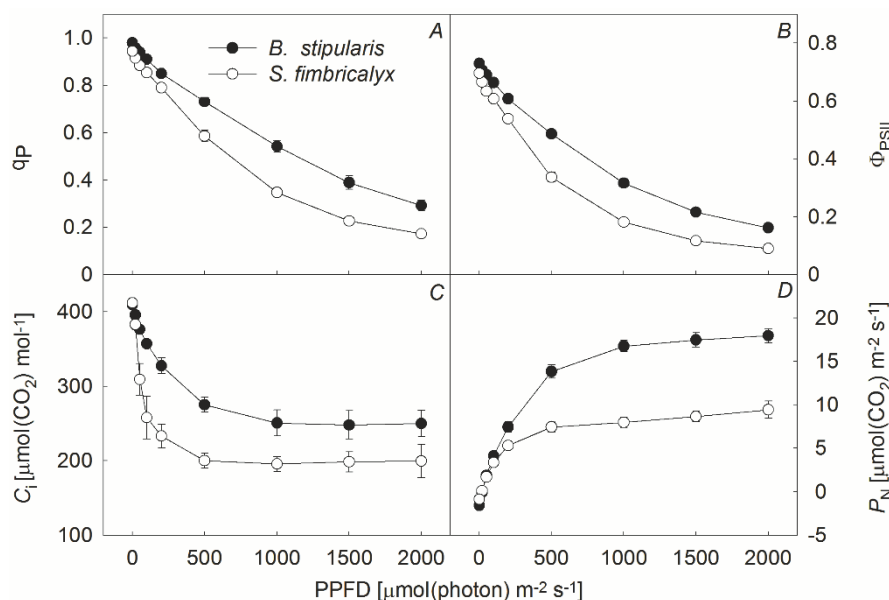


Fig. 2. Light-response curves of the coefficient of (A) photochemical quenching (q_p), (B) the effective quantum use of PSII (Φ_{PSII}), (C) the intercellular concentration of CO_2 (C_i), and (D) the net CO_2 assimilation rate (P_N) in *Bridelia stipularis* and *Strophoblachia fimbricalyx*. The values are the means $\pm$ SE for five replicates.

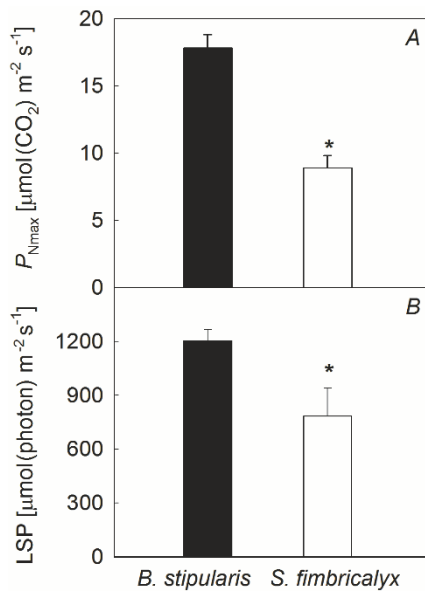


Fig. 3. Comparison of (A) the maximum net CO_2 assimilation rate (P_{Nmax}) and the light-saturating point (B) in *Brideliya stipularis* and *Strophoblachia fimbricalyx*. * – significant differences between the two species at a significance level of $P < 0.05$. The values are the means $\pm$ SE for five replicates.

were 49 and 28 $\mu\text{mol}(\text{photon}) \text{ m}^{-2} \text{ s}^{-1}$ for *B. stipularis* and *S. fimbricalyx*, respectively, indicating a higher electron flow for photorespiration in *B. stipularis* than that in *S. fimbricalyx* under excessive light. The light-saturating point (LSP) of J_o was approximately 1,000 $\mu\text{mol}(\text{photon}) \text{ m}^{-2} \text{ s}^{-1}$ for the leaves in *B. stipularis*, which was much higher than that of the leaves in *S. fimbricalyx* [approximately 500 $\mu\text{mol}(\text{photon}) \text{ m}^{-2} \text{ s}^{-1}$] (Fig. 4C).

Rubisco content and the light-saturated photosynthetic capacity: *B. stipularis* had a significantly higher leaf Rubisco content, which was expressed as per unit of leaf area (2.1 vs. 0.9 $\mu\text{mol m}^{-2}$), than that of *S. fimbricalyx*. Consequently, *B. stipularis* had significantly a higher

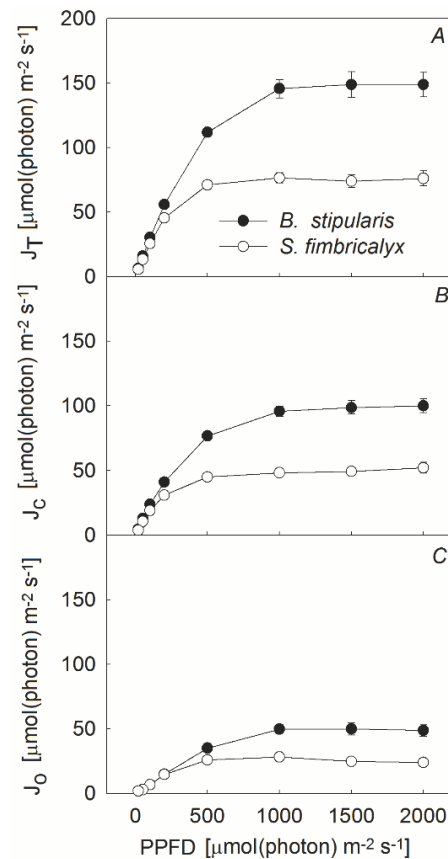


Fig. 4. Light-response curves of (A) the total electron flow through PSII (J_T), (B) the electron flow devoted to the carboxylation of RuBP (J_C), and (C) the electron flow devoted to the oxygenation of RuBP (J_o) to incident PPFD for the leaves in *Brideliya stipularis* and *Strophoblachia fimbricalyx*. The values are the means $\pm$ SE for five replicates.

V_{cmax} (56 vs. 23 $\mu\text{mol m}^{-2} \text{ s}^{-1}$) than that of *S. fimbricalyx*, which was calculated using the response curves of P_N/C_i under conditions of 30°C and PPFD of 1,000 $\mu\text{mol}(\text{photon}) \text{ m}^{-2} \text{ s}^{-1}$. Additionally, *B. stipularis* had a significantly higher J_{max} (58 vs. 27 $\mu\text{mol m}^{-2} \text{ s}^{-1}$) than *S. fimbricalyx*.

Discussion

The aim of the present study was to test how co-occurring and sympatric lianas and trees differ in their photosynthetic efficiency and photorespiration when they were exposed to conditions of excessive high light. In line with our hypothesis, our results suggested that the liana *B. stipularis* had a significantly higher hydraulic efficiency and a higher photosynthetic efficiency and electron flow for photorespiration than the tree *S. fimbricalyx*. These findings added a new insight for explaining the better photosynthetic performance of the lianas over the co-occurring trees.

In this study, the liana *B. stipularis* had a significantly higher sapwood and leaf specific hydraulic efficiency (as

indicated by higher K_s and K_L) and a correspondingly higher photochemical efficiency (higher q_P , Φ_{PSII} , and P_{Nmax}) compared with those of the tree *S. fimbricalyx* grown in a Chinese savanna (Figs. 2, 3A). Some previous studies have indicated that there is a functional coordination of hydraulic conductivity and photosynthesis across or within species (Brodribb and Feild 2000, Brodribb *et al.* 2002, Santiago *et al.* 2004, Campanello *et al.* 2008, Hao *et al.* 2011). In line with our hypothesis, our results were consistent with an above hydraulic-photosynthetic coordination. More importantly, this link indicated that the photochemistry and the CO_2 assimilation capacity were strongly affected by the hydraulic efficiency.

It has been noted that hydraulic conductivity is directly linked to leaf water demands as a result of transpiration (Brodribb and Feild 2000), which may affect CO₂ diffusion from the outer atmosphere to chloroplast carboxylation sites and thereby affect the intercellular concentration of CO₂ and carbon assimilation (Ackerly 2004, Santiago *et al.* 2004). Because K_L is an important index of the water supply status of the leaves attached to the braches (Brodribb and Feild 2000), it would be expected that a higher K_L value would indicate a better leaf water supply. Under optimal conditions, a higher K_L allows the leaves to maintain a higher g_s and C_i, and subsequently maintain a greater photochemistry and a CO₂ assimilation rate (Sperry 2000, Meinzer 2002, Ackerly 2004). In this study, *B. stipularis* had a higher K_s and K_L to support a higher stomatal water loss (higher g_s, data not shown), hence maintaining a higher P_N. Taking into consideration of hydraulic – photosynthetic coordination, the higher photosynthetic efficiency of *B. stipularis* relative to *S. fimbriicalyx* may be well explained by the distinct hydraulic transport efficiency between the two growth forms.

Under conditions of high light, photoinhibition may occur when the excess excitation energy largely exceeds the amount of energy used by photosynthesis (Takahashi and Murata 2008). When the linear electron flow (LEF) in the acceptor side was inhibited under high-light conditions, the ability to consume NADPH (a product of LEF) decreased greatly (Carpentier 1997). As a result, excessive NADPH and ATP were overaccumulated. If excess excitation energy could not be dissipated in safe forms, the generation of ROS suppresses the synthesis and repair of the D₁ protein (Murata *et al.* 2012), thereby the photochemical efficiency decreases and PSII may be photoinhibited (Oguchi *et al.* 2011). In this study, with the increasing PPFD, the J_o values increased for both *B. stipularis* and *S. fimbriicalyx* and the ratio of J_o/J_T was maintained above 0.3 under saturating high light, both for *B. stipularis* and *S. fimbriicalyx* (Fig. 4C), indicating that the photorespiratory pathway was strongly activated and that a considerable proportion of the photosynthetic transport electrons were consumed by the photorespiration process. Under conditions of high light, an increase in J_o has been indicated to be the main photosynthetic electron sink (Hochberg *et al.* 2013). Photorespiration can also promote the repair of the D₁ protein, subsequently, the repair of the photodamaged PSII complexes (Takahashi *et al.* 2007, Takahashi *et al.* 2009). Furthermore, the carbon released by the photorespiration process can increase C_i, which is essential for photosynthetic carbon fixation (Hochberg *et al.* 2013). In this study, P_N and the electron flow for photorespiration increased simultaneously with the increasing PPFD for both *B. stipularis* and *S. fimbriicalyx* (Figs. 2D, 4C). Therefore, the activation of photorespiration plays an important role in the safe dissipation of excessive excitation energy, as well as favouring carbon assimilation under excessive high light (Osmond 1981).

In this study, the maximum values of J_o were 49 and 28 μmol(photon)⁻¹ m⁻² s⁻¹ under saturating light for *B. stipularis* and *S. fimbriicalyx*, respectively, exhibiting a significantly higher magnitude of electron flow for photorespiration in *B. stipularis* than that in *S. fimbriicalyx* (Fig. 4C). We speculate that the difference in the magnitude of photorespiration was greatly attributed to the Rubisco activation state. The leaves of *B. stipularis* had the significantly higher leaf Rubisco content than those of *S. fimbriicalyx*. Although the link between the leaf Rubisco content and its activation state was indirect (Hymus *et al.* 2002), the higher leaf Rubisco content supported faster RuBP regeneration under optimal conditions. In this study, the curves of P_N/C_i showed that *B. stipularis* had a significantly higher J_{max} than *S. fimbriicalyx*. Indeed, *B. stipularis* had a significantly higher J_T and J_e than *S. fimbriicalyx* under high light (when PPFD>1,000, Fig. 4A,B) in the light-response curves under the conditions of 30°C and 400 μmol(CO₂) mol⁻¹. Concomitantly, more photosynthetic transport electrons needed to be dissipated in a harmless form in *B. stipularis* than in *S. fimbriicalyx* in order to overcome the photoinhibition of PSII and improve the energetic balance. In this study, *B. stipularis* showed a greater electron flow for photorespiration than that in *S. fimbriicalyx* under saturating high light (Fig. 4C). Therefore, more excessive photosynthetic transport electrons were consumed by photorespiration and more electrons were utilized in the photosynthetic apparatus in *B. stipularis* than that in *S. fimbriicalyx* under high light. Additionally, photorespiration helped maintain a higher flux of intercellular CO₂ and carbon assimilation in *B. stipularis* relative to *S. fimbriicalyx* (higher C_i and P_{Nmax}, Fig. 2C,D).

Conclusion: In summary, we found that there were significant differences in the photosynthetic efficiency and photorespiration of two Euphorbiaceae liana and tree species. Specifically, *B. stipularis*, with a higher hydraulic conductivity, had a significantly higher photochemical efficiency and magnitude of electron flow for photorespiration than that of *S. fimbriicalyx*, which had a lower hydraulic conductivity. These two Euphorbiaceae species grew in similar open savanna areas. However, the hydraulic and photosynthetic advantages in *B. stipularis* over *S. fimbriicalyx* highlighted the fast growth strategy of the liana. Patiño *et al.* (1995) highlighted the differences in the hydraulic architectures and the growth strategies between the freestanding and hemiepiphytic *Ficus* species. To the best of our knowledge, this is the first report on the differences of the photosynthetic efficiency and photorespiration between the co-occurring liana and tree. These findings can provide direct evidence that lianas have advantageous photosynthesis and growth performance over the co-occurring trees under humid and warm conditions.

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ERRATUM

Erratum to: Leaf area estimation in muskmelon by allometry

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Erratum to: Photosynthetica

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Corrected Fig. 1 (the x-axis of panel A has a wrong caption in the original article):

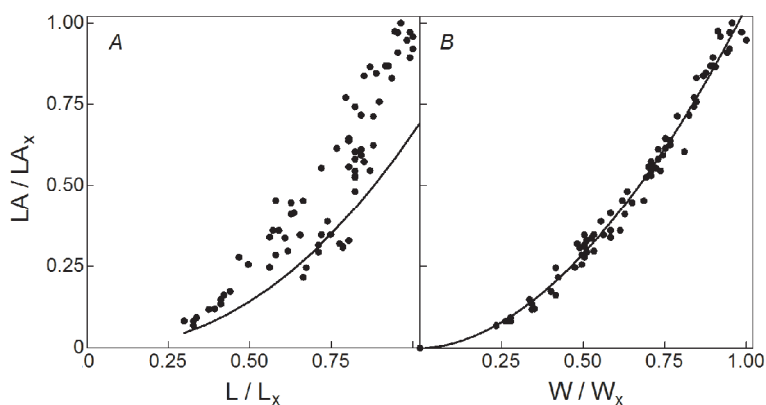


Fig. 1. Allometric curves for (A) relative leaf length (L/L_x) and (B) relative leaf width (W/W_x) of muskmelon related to relative leaf area (LA/LA_x), for 75 samples obtained 22 d from transplanting. L_x – maximum leaf length; W_x – maximum leaf width; LA_x – maximum leaf area. The fit indicators R^2 , absolute sum of squares, and $Sy.x$, standard deviation of residuals, were: (A) 0.9981, 34.89, and 0.6913; (B) 0.9854, 0.00876, and 0.03465, respectively.

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The publisher and authors apologize for these errors and for inconveniences they may have caused.