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Effects of high temperature and high light on photosystem II activity in leaves of two *Bauhinia* species

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Abstract

It is, so far, unclear whether lianas and trees differ in photosynthetic thermotolerance and response to high temperature and high light. Here, photosynthetic thermotolerance was compared in the leaves of *Bauhinia brachycarpa* (tree) and *Bauhinia comosa* (liana). Moreover, the combined treatments of four temperatures (25, 35, 40, and 45°C) and two light intensities [500 and 2,000 μmol(photon) m^{-2} s^{-1}] were used to investigate the effects of high temperature and high light on PSII activity. The results showed that *B. brachycarpa* leaves exhibited higher photosynthetic thermotolerance, leaf mass per area, and Ca^{2+} concentration than those of *B. comosa*. As the temperature and light intensity increased, maximum quantum yield of PSII decreased significantly, particularly with greater declines in *B. comosa* than that in *B. brachycarpa*. Our results suggested that PSII was more sensitive to high temperature and high light in liana species *B. comosa* than in the congener tree species *B. brachycarpa.*

Additional key words: global warming; heat stress; photoinhibition; photoprotection.

Introduction

Lianas, an important component of tropical forests, strongly compete with co-occurring trees, which in turn can alter plant community composition and affect forest regeneration (Schnitzer and Bongers 2002, Schnitzer 2018). Both the richness and biomass of lianas increased in many tropical and secondary forests (Wright *et al*. 2004a, Schnitzer and Bongers 2011). High liana abundance has been indicated to suppress tree regeneration, increase tree mortality (Schnitzer and Bongers 2002, Ingwell *et al.* 2010, De Deurwaerder *et al.* 2018), and even reduce carbon storage in tropical forests (Durán and Sánchez-Azofeifa 2015).

It has been proposed that lianas had stronger stomatal regulation, more efficient hydraulic conductivity (Zhang *et al.* 2016, Chen *et al.* 2017), better seasonal adjustment in leaf turgor loss point (Maréchaux *et al.* 2017), and greater external mechanical stability of canopy terminal branches (Zhang *et al.* 2019), compared to the co-occurring trees. More recently, lianas have been suggested to have a seasonal growth advantage over co-occurring trees (Schnitzer and van der Heijden 2019). Together, these results provided potential physiological explanations for the faster growth strategy of lianas over trees.

With changes in the global climate, plant species may be significantly affected by global warming (Corlett and Westcott 2013). High temperature (HT) stress brings plant species closer to their physiological limits, especially in tropical forests (Doughty and Goulden 2008). The leaf surfaces exposed to direct sunlight occasionally reach the temperature of 7.6°C higher than that of the ambient air (Noffsinger 1961). However, it remains unclear how the photosynthetic performance of both lianas and trees is

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Abbreviations: F_0 – minimum dark-adapted fluorescence; F_m – maximum dark-adapted fluorescence; F_v/F_m – maximum quantum yield of PSII; HL – high light; HT – high temperature; LMA – leaf mass per area; LSP – light-saturation point; NPQ – nonphotochemical quenching; P_N – net photosynthetic rate; P_{Nmax} – light-saturated net photosynthetic rate; PT – photosynthetic thermotolerance; T_c – critical high temperature threshold for the change from inactivation to irreversible destruction of PSII; T_{cond} – threshold temperature of the leakage of ions from cells.

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affected by global warming. HT usually combines with high light (HL) in the natural environment. PSII is a stress-sensitive component of the photosynthetic apparatus and is photoinhibited as a result of HT and HL (Hu *et al.* 2009). The heat-induced inactivation of PSII includes reversible and irreversible inactivation. The inactivation of PSII as a result of moderate HT can be reversed by transfer of cells to 25°C. However, the inactivation by heat stress higher than 45°C was irreversible in soybean (*Glycine max*) (Nishiyama *et al*. 2006a). Previous studies have suggested that moderate heat stress may inhibit the repair of photodamaged PSII (Takahashi *et al.* 2004), and strong heat stress has been shown to deactivate the oxygen-evolving complex (OEC) in PSII (Nash *et al.* 1985, Murata *et al.* 2007). Photosynthetic thermotolerance (PT) is defined as the change in excitation capacity of PSII under HT, and may be used to evaluate PSII performance in leaves under heat stress (Knight and Ackerly 2003, Zhang *et al*. 2012). There is a great variation in PT across species even grown in a common environment (Knight and Ackerly 2003), and it has been shown that the inter-species variation in PT was related to leaf lifespan, leaf mass per area (LMA), and leaf Ca^{2+} concentration (Zhang *et al*. 2012). A high LMA may limit the water transport efficiency, but promote heat resistance (Zhang *et al*. 2012, Sastry *et al*. 2018). PT has also exhibited high plasticity to seasonal changes and temperature treatments in the same species (Weng and Lai 2005). High light not only damages PSII activity directly, but also inhibits the repair of PSII *via* production of reactive oxygen species (ROS) inhibiting expression of the D1 protein at the translation step (Allakhverdiev *et al*. 2005, Nishiyama *et al*. 2005, 2006b, 2011; Takahashi and Murata 2008).

Lianas and trees differ strikingly in life growth forms and water use strategies (Chen *et al*. 2015, Zhang *et al*. 2016). Our previous study also suggested that lianas have higher stem and leaf-specific hydraulic conductivity, and photorespiration, than that of co-occurring trees under environmental stress-free conditions (Zhang *et al*. 2016). However, little is known about the different responses of PSII to HT and HL for lianas. Maximum quantum yield of PSII (F_v/F_m) is a reliable diagnostic indicator of photosynthetic function in response to environmental stresses, such as light, temperature, drought, and salt (Murata *et al.* 2007, Takahashi and Murata 2008). In the present study, we compared photosynthetic thermotolerance and the response of F_v/F_m to HT and HL in the leaves of *Bauhinia brachycarpa* (tree) and *Bauhinia comosa* (liana). We sought answers to the following three questions: (*1*) Does PT differ between two *Bauhinia* species with contrasting growth forms? (*2*) Does PSII activity in response to HT and HL differ between the two species? (*3*) Are the differences in PT and response of PSII activity to HT and HL associated with specific leaf traits (LMA and leaf element content)?

Materials and methods

The study site was located in Yuanjiang Savanna Ecosystem Research Station (23°27'N, 102°10'E, 481 m a.s.l.), in Yuanjiang County, Yunnan Province, China. Based on the meteorological record of 2012–2017, mean annual air temperature was 23.7°C, and mean annual precipitation was 732.8 mm. The midday air temperature can reach over 40°C in summer, with an extreme air temperature of 43.7°C at midday. The soil type was ferralic cambisol. The typical vegetation in this site was valley-type savanna with a mixture of co-occurring trees and lianas (Jin and Ou 2000, Zhang *et al*. 2016).

Plants: Five individuals of *B. brachycarpa* and *B. comosa* were selected from a long-term monitoring plot (100 × 100 m) for savanna ecosystem (23°28'25''N, 102°10'38''E, 565 m a.s.l.). When plants were growing under optimal conditions in August 2018, fully expanded and sun-exposed leaves from five individuals per species were used to assess photosynthesis and chlorophyll (Chl) fluorescence parameters.

Gas exchange: Photosynthetic light responses were measured between 9:00–11:00 h on sunny days using a *LI-6400*XT portable photosynthesis system (*Li-Cor*, Lincoln, NE, USA). Leaf temperature was set at 30°C and CO_2 concentration in the incoming air was 400 μmol(CO_2) mol^{-1} controlled by a *6400-01* CO_2 injector system (*Li-Cor*, Lincoln, NE, USA). Photosynthetic light responses were generated from measurements obtained at 2,000; 1,500; 1,000; 500, 200, 100, 50, 20, and 0 μmol(photon) m^{-2} s^{-1}. Steady-state photosynthesis was maintained for at least 3 min under each PPFD. The light-saturated net photosynthetic rate (P_{Nmax}) and light-saturation point (LSP) were fitted according to a nonrectangular hyperbola.

Photosynthetic thermotolerance was determined using *PlanTherm PT100* (*Photon Systems Instruments*, Czech Republic). Leaf segments taken from the middle of the sampled leaves were submerged in water bath with distilled water. The water temperature was gradually heated from 25°C up to 70°C (increase of 1–3°C min^{-1}). The conductivity and Chl fluorescence transients were continuously monitored with changes in the water temperature. The fluorescence (F_t) and temperature curves were used to determine the critical high temperature threshold (T_c), in which the change from inactivation to irreversible destruction of PSII occurred. Further, conductivity and temperature curves were used to determine the threshold temperature of the leakage of ions from cells (T_{cond}).

Leaf traits: More than 30 mature leaves from five individuals per species were sampled and the leaf area was determined with *Li-3000*A leaf area meter *(Li-Cor*, Nebraska, USA). The leaf dry mass was measured after oven-drying at 70°C for 48 h. The leaf mass per area (LMA) was calculated as the leaf dry mass divided by the total leaf area. The leaf samples were grinded to measure the leaf Ca^{2+} concentration [mg g^{-1}(DM)]. After the leaf samples were digested by HNO_3-$HClO_4$, leaf Ca^{2+} concentration was determined using an inductively coupled plasma atomic-emission spectrometer (*iCAP6300*, *Thermo Fisher Scientific*, USA).

HT and HL treatments: Detached leaves were exposed to the combined treatments of four temperatures (25, 35, 40, and 45°C) supplied by a water bath (*Jintan Science Analysis Instrument Co., Ltd.*, China), and two light intensities [500 and 2,000 μmol(photon) m^{-2} s^{-1}] continuously provided by an LED-light source for 2 h. Five replicates of each combined treatment were carried out. After each treatment, detached leaves were acclimated to darkness for 30 min. The Chl fluorescence parameters were evaluated using a *PAM-2100* fluorometer (*Heinz Walz*, Effeltrich, Germany). Minimal dark-adapted fluorescence (F_0) was determined for the dark-acclimated leaves. The intensity for the measurements of F_0 was 0.1 μmol(photon) m^{-2} s^{-1}. This low intensity of the exciting light allows the detection of F_0 (Ilík *et al*. 2018). Then, maximum dark-adapted fluorescence (F_m) was determined after a 0.8-s saturating pulse at 5,000 μmol(photon) m^{-2} s^{-1}. F_v/F_m was calculated as $(F_m - F_0)/F_m$.

Statistical analysis: The values of leaf photosynthetic and functional traits were presented as the means ± SE. Statistically significant differences in photosynthetic and leaf trait parameters between two species were performed by independent-sample *t*-test. Two-way analysis of variance (*ANOVA*) was performed to assess the effects of temperature and light on F_v/F_m. Significance level was set at $P<0.05$. Statistical analysis was performed using *SPSS 17.0* software (*SPSS Inc.*, Chicago, IL, USA). The figures were plotted with *Sigmaplot version 12.0* software.

Results

Comparison of light-response curves: There was no significant difference in P_N between the two species under low PPFDs of 20–200 μmol(photon) m^{-2} s^{-1}. However, *B. brachycarpa* exhibited higher values of P_N than that of *B. comosa* under the PPFDs, which were greater than 500 μmol(photon) m^{-2} s^{-1} (Fig. 1). The P_{Nmax} was significantly higher in *B. brachycarpa* [20.2 μmol(CO_2) m^{-2} s^{-1}] than that in *B. comosa* [16.2 μmol(CO_2) m^{-2} s^{-1}] (Fig. 2*A*). Light-saturation point (LSP) values were 1,137.6 and 893.6 μmol(photon) m^{-2} s^{-1} for *B. brachycarpa* and *B. comosa*, respectively. Both *Bauhinia* species are light-demanding plants, however, the tree species *B. brachycarpa* had a significantly higher LSP than the congener liana species *B. comosa* (Fig. 2*B*).

Comparison of PT: T_c was used to indicate the inactivation to irreversible destruction of PSII reaction centers (Bilger *et al.* 1984, Zhang *et al.* 2012). According to the parameters of PT, T_c was significantly higher in *B. brachycarpa* (47.2 ± 0.3°C) than that in *B. comosa* (45.8 ± 0.3°C) (Fig. 2*C*). T_{cond} was used to indicate the cell membrane thermostability under heat treatment (Ilík *et al*. 2018). The T_{cond} were 59.6 ± 0.5°C and 59.0 ± 0.3°C for *B. brachycarpa* and *B. comosa*, respectively, and no significant difference was found for the T_{cond} values between the two *Bauhinia* species (Fig. 2*D*).

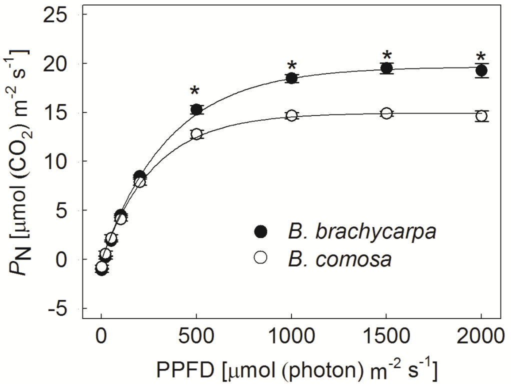

Fig. 1. Comparisons of light-response curves in the leaves of *Bauhinia brachycarpa* and *B. comosa*. *Asterisks* indicate significant differences of P_N between *B. brachycarpa* and *B. comosa* ($P<0.05$). The results were displayed as means ± SE ($n = 5$).

LMA and leaf Ca^{2+} concentration: *B. brachycarpa* had significantly greater LMA and leaf Ca^{2+} concentration than that of *B. comosa* (Fig. 2*E,F*). This result suggested that *B. comosa* leaves may be more vulnerable to irreversible thermal damage than those of *B. brachycarpa*.

The effects of HT and HL on F_v/F_m: The F_v/F_m was significantly affected by light intensity and temperature in both *Bauhinia* species (Table 1, two-way *ANOVA*). Under both 500 and 2,000 μmol(photon) m^{-2} s^{-1}, F_v/F_m decreased as the treatment temperature increased (Fig. 3). At moderate light and high temperatures (40 and 45°C), the F_v/F_m values were significantly higher in *B. brachycarpa* than that in *B. comosa* (Fig. 3*A*). At the high light, the F_v/F_m of *B. brachycarpa* was significantly higher at all temperatures (Fig. 3*B*).

Discussion

Environmental stresses, such as salt, heat, and drought stress, enhance photoinhibition of PSII (Murata *et al.* 2007, Nishiyama *et al.* 2005, 2006a,b; Takahashi and Murata 2008). The extent of photoinhibition is determined by the balance between photodamage to PSII and subsequent repair (Murata *et al.* 2007, Takahashi and Murata 2008). In this study, F_v/F_m values varied inversely with elevated temperature and light intensity for both *Bauhinia* species, with a greater decrease in F_v/F_m values in *B. comosa* (Fig. 3). This result indicated that PSII activity was more sensitive to HT and HL in *B. comosa* than in *B. brachycarpa*. *B. brachycarpa* had higher LMA, leaf Ca^{2+} concentration, and T_c than that of *B. comosa* (Fig. 2). Considering the close association between photosynthetic thermotolerance and leaf traits (Knight and Ackerly 2003, Zhang *et al.* 2012, Sastry *et al.* 2018), the higher T_c of *B. brachycarpa* may be related to the higher values of LMA and leaf Ca^{2+} concentration.

Previous studies have indicated that a higher LMA is linked to a longer leaf lifespan and a higher carbon-cost of deploying a new leaf (Wright *et al.* 2004b, Onoda *et al.* 2011). The longer-living leaves may experience a higher

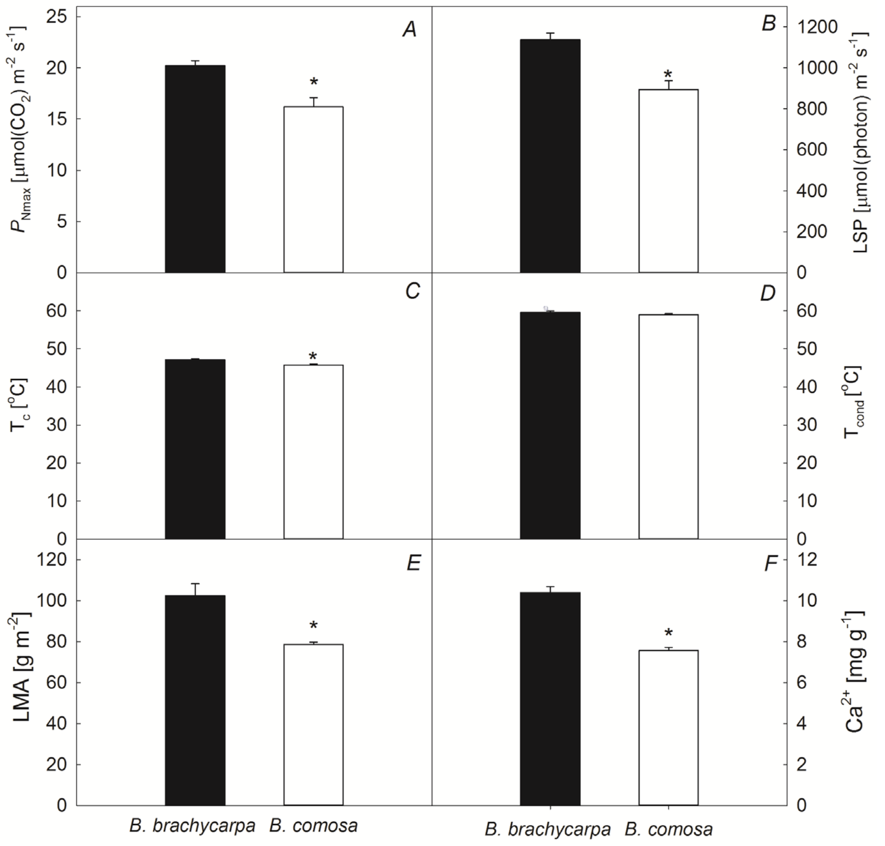

Fig. 2. Comparisons of photosynthetic and nutrient parameters in the leaves of *Bauhinia brachycarpa* and *B. comosa*. Light-saturated net photosynthetic rate (P_{Nmax}) (*A*), light-saturation point (LSP) (*B*), the critical high temperature threshold where the change from inactivation to irreversible destruction of PSII occurs (T_c) (*C*), the threshold temperature of the leakage of ions from cells (T_{cond}) (*D*), leaf mass per area (LMA) (*E*), and leaf Ca^{2+} concentration (Ca) (*F*). *Asterisks* indicate significant differences between *B. brachycarpa* and *B. comosa* ($P<0.05$). The results were displayed as means ± SE ($n = 5$).

Table 1. Two-way *ANOVA* results of the effects of high light and high temperature on maximum quantum yield of PSII (F_v/F_m) in *Bauhinia brachycarpa* and *B. comosa* leaves.

Species	Temperature		Light		Temperature × Light	
	F	Sig.	*F*	Sig.	*F*	Sig.
Bauhinia brachycarpa	30.76	<0.001	264.04	<0.001	7.89	<0.001
Bauhinia comosa	67.89	<0.001	295.28	<0.001	0.58	0.633

risk of heat stress. It has been shown that the PT of some species is positively correlated to the leaf lifespan (Zhang *et al*. 2012). The higher LMA in *B. brachycarpa* indicates slower turnover and higher need for heat resistance compared to *B. comosa*. In addition, Knight and Ackerly (2003) reported that species with higher LMA have high expression levels of the heat shock proteins (HSPs), which are involved in maintaining of protein structural stability, alleviate cell membrane damage, and reduce protein misfolding (Swindell *et al.* 2007, Qi *et al.* 2019). Moreover, Ca^{2+} has been suggested to play an important role in maintaining the structural rigidity of the cell wall and cell membrane permeability during heat stress (Hepler 2005). Heat shock-triggered Ca^{2+} mobilization may be a universal response under heat stress to improve the thermotolerance in plant leaves (Wu and Jinn 2010). The higher Ca^{2+} concentration may promote the thermostability of OEC, and, owing to lesser accumulation of ROS, partly maintain photochemical efficiency of PSII (Tan *et al.* 2011). Thus, the higher LMA and leaf Ca^{2+} concentration may be related to higher thermotolerance in *B. brachycarpa*.

In this study, both *Bauhinia* species showed a significant decline in PSII activity under the 40 and 45°C treatments in moderate light [500 μmol(photon) m^{-2} s^{-1}] (Fig. 3*A*). This is in agreement with the finding that the heat stress may lead to an imbalance in the electron flow from OEC toward the acceptor side of PSII in the direction of PSI reaction center (De Ronde *et al.* 2004). After exposure to a HL treatment of 2,000 μmol(photon) m^{-2} s^{-1}, the decline in F_v/F_m was further aggravated for both *Bauhinia* species than that in moderate light [500 μmol(photon) m^{-2} s^{-1}], even under an optimal growth temperature (25°C) (Fig. 3*B*). Due to the effect of a photoinhibitory light intensity, the increase of temperature above 25°C led to further decrease of F_v/F_m (Fig. 3*B*) as a result of the combined HL and HT stress (Zhang *et al.* 2012, Dongsansuk *et al.* 2013, Takahashi and Murata 2008, Nishiyama *et al.* 2004, 2006b, 2011).

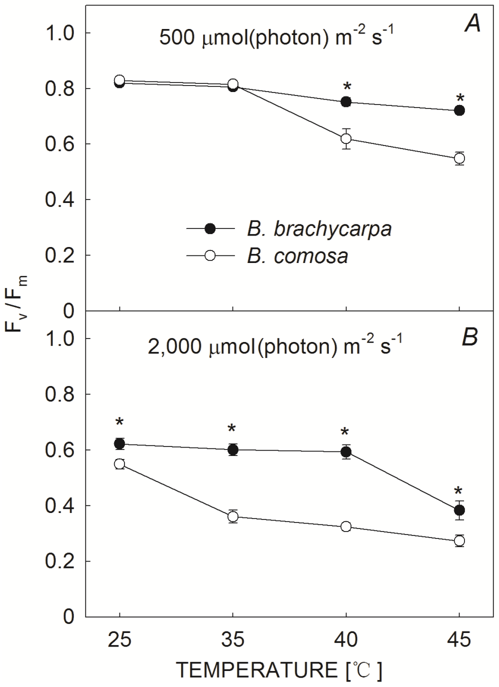

Fig. 3. Changes in the maximum quantum yield of PSII (F_v/F_m) during exposure to high light and high temperature in detached leaves of *Bauhinia brachycarpa* and *B. comosa*. *Asterisks* indicate significant differences of F_v/F_m between *B. brachycarpa* and *B. comosa* ($P<0.05$). The results were displayed as means ± SE ($n = 5$).

Lianas have been reported to have a higher hydraulic efficiency and a faster growth strategy than co-occurring trees (Zhang *et al.* 2016, Chen *et al.* 2017). Moreover, lianas allocated more excited light energy used for photorespiration to promote photoprotection compared to trees under current climate conditions (Zhang *et al*. 2016). In this study, *B. comosa* showed a greater decline in PSII activity under HT and HL than that of *B. brachycarpa* (Fig. 3). More sensitive PSII in liana species may decrease the photosynthetic carbon gain and growth performance. The findings of this study suggest that the growth advantage of lianas over trees might be weakened or even disappear due to global warming, which may alter species composition and forest regeneration.

Conclusion: The leaves of the tree species *B. brachycarpa* exhibited higher PT than those of the congener liana *B. comosa*. This may be related to the higher LMA and leaf Ca^{2+} concentration in *B. brachycarpa*. Further, PSII was more sensitive to the combined HT and HL stress in the liana than in the tree. Despite the lianas seem to have a seasonal growth advantage over co-occurring trees (Schnitzer and Bongers 2011, Schnitzer and van der Heijden 2019), the higher sensitivity of the photosynthetic apparatus may negatively affect photosynthetic carbon gain and subsequently the growth performance and fitness (McAlpine *et al*. 2008, Imbamba and Tieszen 2010, Slot and Winter 2017), under the expected global warming. In order to predict the long-term responses of co-occurring lianas and trees to the climate change, further studies are required to elucidate the integrated effect of the extreme temperatures, drought, and high light on the hydraulic and photosynthetic processes.

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