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Research paper

Seasonal dynamics in photosynthesis of woody plants at the northern limit of Asian tropics: potential role of fog in maintaining tropical rainforests and agriculture in Southwest China

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The lowland tropical rainforests in Xishuangbanna, Southwest (SW) China, mark the northern limit of Asian tropics. Fog has been hypothesized to play a role in maintaining rainforests and tropical crop production in this region, but the physiological mechanism has not been studied. The goals of this study were to characterize the seasonal dynamics in photosynthesis and to assess the potential for fog to mitigate chilling-induced photodamage for tropical trees and crops in Xishuangbanna. We measured seasonal dynamics in light-saturated net photosynthetic rate (A_a), stomatal conductance (g_s), intercellular CO_2 concentration, quantum yield of Photosystem II (F_v/F_m) and maximum P700 changes (P_m ; indicates the amount of active PSI complex), as well as chilling resistance and fog (light/shading) effects on low temperature-induced decline in F_v/F_m and P_m for native tree and introduced lower latitude tree or woody shrub species grown in a tropical botanical garden. Despite significant decreases in A_a , g_s , P_m and F_v/F_m , most species maintained considerably high A_a during the cool season ($2.51\text{--}14.6\ \mu\text{mol m}^{-2}\text{ s}^{-1}$). Shaded leaves exposed to seasonal low temperatures had higher F_v/F_m than sun-exposed leaves in the cool season. All species could tolerate $1.4\ ^\circ\text{C}$ in the dark, whereas a combined treatment of low temperature and high light caused a distinctly faster decline in P_m and F_v/F_m compared with low temperature treatment alone. Because fog persistence avoids or shortens the duration of high light condition in the morning when the temperatures are still low, our results provide support for the hypothesis that fog reduces chilling damage to tropical plants in this region and thus plays a role in maintaining tropical rainforests and agriculture in SW China.

Keywords: Asian tropical rainforest, chilling, CO_2 assimilation, photoinhibition, Xishuangbanna.

Introduction

The lowland rainforests in Xishuangbanna autonomous prefecture in Yunnan province, Southwest (SW) China, account for the largest proportion of tropical rainforests in China and, at $21\text{--}22^\circ\text{N}$, mark the northern limit of tropical rainforests in Asia (Cao et al. 2006). Xishuangbanna is also known for its production of tropical crops (e.g., coffee, jackfruit) in China. Tropical rainforests are typically associated with little

climatic seasonality and year-round high temperatures and precipitation, therefore seasonal drought and cold typically set the geographic limits of tropical rainforests (Köppen 1901, Richards 1996, Givnish 2002, Peel et al. 2007). Although Xishuangbanna has a pronounced cool dry season with chilling temperatures and rainfall shortages (Cao et al. 2006), the tropical forests in this region are structurally, physiognomically and floristically similar to the rainforests from the lower latitude

tropics of Southeast Asia (Zheng et al. 2006, Zhu et al. 2006). Fog has been hypothesized to play a key role in buffering chilling and drought effects, thereby allowing tropical rainforests and tropical crop production to exist in this region (Cao et al. 2006), but the physiological mechanisms for this hypothesis have not been well studied. Dense radiation fog is frequent in the cool dry season, persisting from night until midday when the air temperature warms up.

Fog persistence influences photosynthesis of plants in two ways. On one hand, fog or cloud cover reduces photosynthetic photon flux density (PPFD) and consequently limits photosynthetic carbon gain (Graham et al. 2003, Zhang et al. 2011). On the other hand, fog has the potential to reduce chilling-induced photoinhibition. The photosynthetic processes of many tropical plants are chilling-sensitive, and chilling increases the likelihood of photoinhibition [both Photosystem I (PSI) and Photosystem II (PSII)] in tropical plants (Levitt 1980, Allen and Ort 2001, Kao et al. 2004, Huang et al. 2010a, Santini et al. 2013) because low temperatures affect light utilization but hardly light absorption of their leaves (Hetherington et al. 1989, Germino and Smith 2000, Santini et al. 2013). Fog persistence could reduce chilling-induced photoinhibition by avoiding or shortening the duration of high PPFDs in the early morning when the temperatures are still low. Although fog could also be a water source to plants to buffer the effects of rainfall shortages in the dry season (Cavelier and Goldstein 1989, Liu et al. 2004, Simonin et al. 2009), this study focused on understanding the effects of fog on protecting leaves from chilling-induced photodamage by studying well-watered plants in a tropical botanical garden.

The tropical rainforest in Xishuangbanna is an important component of the regional biodiversity, and understanding the ecophysiological mechanisms of its maintenance will help develop effective conservation, forest management and economic development strategies. Xishuangbanna harbors 16% of the plant diversity of China (Liu et al. 2002), and is included in the Indo-Burma diversity hotspot (Myers et al. 2000, Cao et al. 2006). However, the forests in this region have been under major threat of deforestation and rapidly expanding rubber plantations (Guo et al. 2002, Li et al. 2006, 2009, Qiu 2009, Ziegler et al. 2009). Notably, if fog plays an important role in maintaining the tropical rainforests in Xishuangbanna, the remaining rainforests may undergo degradation because deforestation and conversion of forest to pasture have a severe impact on cloud formation (Lawton et al. 2001) and the frequency of fog events is decreasing in Xishuangbanna according to the climatic record (Huang et al. 2001).

Further, data on photosynthetic performance of the tropical plants in the cool dry season are crucial in understanding the carbon balance and productivity of tropical forests and agricultural systems in this region. Ecosystem level gas exchange monitoring indicates a carbon sink function of the rainforests

in Xishuangbanna in the cool dry season (Zhang et al. 2006), suggesting positive carbon balance of the plants. However, to what extent leaves of different species can maintain positive net CO₂ assimilation in the cool dry season is not known. The objectives of this study were (i) to characterize the seasonal dynamics in photosynthetic performance of both native rainforest trees and introduced lower latitude woody plants including some crops at the northern limit of Asian tropics, (ii) to clarify the factors contributing to potential cool season declines in photosynthesis of plants in this region and (iii) to assess the potential for fog to reduce chilling-induced photoinhibition of tropical trees and crops during the cool season in Xishuangbanna, SW China.

Materials and methods

We performed this research at Xishuangbanna Tropical Botanical Garden (XTBG; 21°41'N, 101°25'E, elevation 570 m) in Mengla County, Yunnan Province, SW China. Mean annual temperature and mean annual precipitation at XTBG are 21.7 °C and 1560 mm (40 years average; data from Xishuangbanna Station for Tropical Rain Forest Ecosystem Studies). There is strong seasonality in air temperature and precipitation (Figure 1a). November to early March is referred to as the cool season, with average daily minimum temperature ranging from 12.0 to 16.6 °C (Figure 1a) and extreme low temperatures to 2 °C (Figure 1b). During the cool season, monthly rainfall totals are <50 mm (Figure 1a), but radiation fog is frequent (>20 days a month; Figure 1b). During foggy days of the cool season, fog usually lasts from night to midday (11:00–12:00 h; Figure 1c). Foggy days showed shorter time periods of combined chilling temperatures [<15 °C; according to Levitt (1980)] and high PPFD [>640 μmol m⁻² s⁻¹; according to Huang et al. (2010b)] than sunny days (Figure 1c and d). Chilling temperatures are defined as temperatures that are cool enough to induce injury but not enough to freeze the plant (Levitt 1980). For most warm climate plants, chilling temperatures range from 15 to 0 °C (Levitt 1980).

Eleven woody plant species were selected for this study, including three native tree species, and eight tree and shrub species introduced from lower latitudes (Table 1). *Shorea chinensis* is the emergent tree species and an important symbol of the Chinese tropical rainforest, while *Alstonia scholaris* and *Pometia tomentosa* are dominant overstory tree species in the forest. We selected these tree species as the representatives of the tropical rainforest trees in SW China because of their dominance and ecological importance (Cao et al. 2008). Among the introduced species, *Artocarpus heterophyllus* and *Coffea arabica* have been widely cultivated by local farmers as important tropical crops in this region. The *Garcinia mangostana* trees included in the study were 2 to 3 m tall, while the other tree species were 8 to 12 m tall. The shrub species

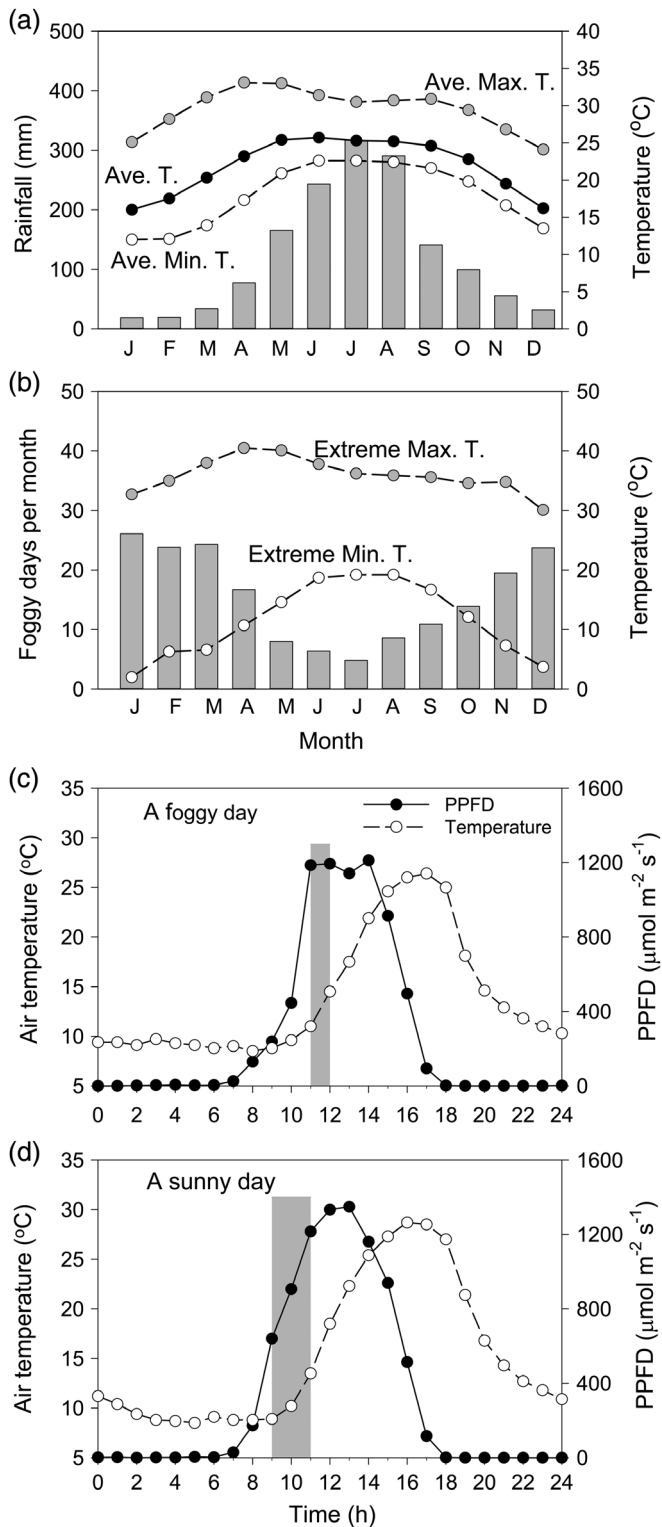


Figure 1. (a) Average monthly rainfall (bars), average maximum, minimum and average temperatures; (b) foggy days per month and extreme maximum, minimum temperatures (40 years average); (c and d) daily changes in PPFD and air temperature on a foggy day and a sunny day in the coldest period of the 2011–12 cool season (January 2012) in Xishuangbanna Tropical Botanical Garden (data from Xishuangbanna Tropical Rainforest Ecosystem Station). Shaded areas are periods with combined chilling temperatures ($<15^{\circ}\text{C}$) and high PPFD ($>640 \mu\text{mol m}^{-2} \text{s}^{-1}$).

Table 1. Plant species selected for this study, and their families, growth forms, and species codes used.

Species	Family	Growth form	Species code
Native species			
<i>Alstonia scholaris</i> (L.) R. Br.	Apocynaceae	Tree	AS
<i>Pometia tomentosa</i> (Bl.)	Sapindaceae	Tree	PT
Teysm. et Binn.			
<i>Shorea chinensis</i> (Wang Hsie)	Dipterocarpaceae	Tree	SC
H. Zhu			
Introduced species			
<i>Artocarpus champeden</i> Spreng.	Moraceae	Tree	AC
<i>Artocarpus heterophyllus</i> Lam.	Moraceae	Tree	AH
<i>Coffea arabica</i> L.	Rubiaceae	Shrub	CA
<i>Dombeya calantha</i> K. Schum.	Sterculiaceae	Shrub	DC
<i>Garcinia mangostana</i> L.	Clusiaceae	Tree	GM
<i>Morinda citrifolia</i> L.	Rubiaceae	Tree	MC
<i>Paullinia cupana</i> Kunth	Sapindaceae	Shrub	PC
<i>Theobroma cacao</i> L.	Sterculiaceae	Tree	TC

(*C. arabica*, *Dombeya calantha* and *Paullinia cupana*) were 1.5 to 2 m tall growing in open fields at the garden. The soil of the XTBG is sandy alluvium, and the plants were fertilized twice a year with compound fertilizer (Stanley, Inc., Shandong, China). Plants were kept well supplied with water by frequent irrigation, which allowed us to test the chilling effects on plants without the potential interference of soil water deficits.

Gas exchange measurements

In the warm and cool seasons, we measured light-saturated net photosynthetic rate per leaf area (A_n), stomatal conductance (g_s) and intercellular CO_2 concentration (C_i) in situ using a portable photosynthetic system (LI-6400, LI-COR, Lincoln, NE, USA). For each species, 6–14 sun-exposed newly fully developed mature leaves from different individuals (one leaf per individual) were selected for gas exchange measurements with the exception of *G. mangostana* and *Artocarpus champeden*, for which six leaves from two and three individuals, respectively, were used. Measurements were carried out on sunny days between 09:30 and 11:30 h; during the cool season measurements were made only after any fog had dispersed on days with relatively short fog persistence. All measurements were done at a PPFD of $1500 \mu\text{mol m}^{-2} \text{s}^{-1}$, and ambient temperature, humidity and CO_2 concentration. Average air temperature during the measurement period was 33.0°C in the warm season and 28.8°C during the cool season. Average relative humidity during the hours when photosynthesis was measured was 66.0% in the warm season and was 51.9% during the cool season. Air temperatures remained high in the mornings of the cool season after fog disappeared, while the average night temperatures were substantially lower in the cool season ($\sim 12^{\circ}\text{C}$) compared with that of the warm season ($\sim 24^{\circ}\text{C}$) (Figure 1b). Notably, leaf age may have had a confounding effect in assessing the influence of air temperatures on g_s and

A_a (Field 1983, 1987, Kitajima et al. 1997) because studied leaves in different seasons may vary in leaf ages. However, because trees in this region continuously flush leaves throughout the year and we selected newly fully developed leaves for physiological measurements, the leaf age effect on g_s and A_a should be minor.

Chlorophyll fluorescence and P700

Seasonal changes in leaf chlorophyll fluorescence and P700 redox state were determined with a Dual PAM-100 (Walz, Effeltrich, Germany). For each species, six 70- to 100-cm-long sun-exposed branches from different individuals (two and three individuals for *G. mangostana* and *A. champeden*; six individuals for other species) were collected in the late afternoon, immediately recut under water, maintaining the cut ends under water, and covered with black plastic bags. The maximum quantum yield of PSII (F_v/F_m) and maximum P700 changes during quantitative transformation from the fully reduced to the fully oxidized state (P_m ; indicating the amount of active PSI complex) were determined at predawn of the next morning in the laboratory. Leaf F_v/F_m was determined by illuminating the leaf with a white saturating light pulse (photon flux density $10,000 \mu\text{mol m}^{-2} \text{s}^{-1}$) for 600 ms. For P_m determination, leaves were preilluminated with a far-red light for 10 s, and then P_m was determined through applying a saturation pulse. P_m is the maximal change in P700 signal upon quantitative transformation of P700 from the fully reduced to the fully oxidized state and the amplitude of P_m depends on the maximum amount of photo-oxidizable P700. Therefore, P_m is a good indicator of the amount of active PSI complex. In order to infer the shading effects of fog on cool season declines in F_v/F_m , cool season F_v/F_m of sun-exposed and shaded leaves were compared for three species (*A. heterophyllus*, *Theobroma cacao*, *C. arabica*), which have enough shaded mature leaves with the same age as the studied sun-exposed leaves. Because same age sun-exposed and shaded leaves were in similar positions relative to the crown, they probably were exposed to similar temperature regimes.

Light effects on the sensitivity of leaf F_v/F_m and P_m to low temperatures were determined for *C. arabica*, an important tropical crop in Xishuangbanna, in February 2010, when the plants were fully acclimated to cool season temperatures. Sun-exposed newly fully developed leaves were collected in the late afternoon. After dark acclimation in black plastic bags with wet paper towels for 12 h, F_v/F_m and P_m were determined for a sub-sample of leaves ($n = 6$) with the Dual PAM-100 to provide control values. Then the other groups of leaves (six leaves per group) were treated with different temperatures (10, 6, 4, 2, 0, -2, -4, -6, -8, -10, -12, -15 °C) using a cooling bath (Heto CBN 18-30, Hansatech Instruments, King's Lynn, Norfolk, UK) maintained by a HMT 200 Heto Thermostat temperature controlling system. Leaves were placed in clear plastic zip lock

bags and submerged into the cooling bath for 30 min. One set of leaves remained in the dark while the other set was illuminated ($650 \mu\text{mol m}^{-2} \text{s}^{-1}$) during the low temperature treatment. The light source was hanging over the cooling bath, and the incoming light was perpendicular to the adaxial leaf surface. After different low temperature treatments, leaves in clear plastic zip lock bags containing wet paper towels were placed in the dark at room temperature (~ 25 °C) for 12 h, following which leaf F_v/F_m and P_m were measured with the Dual PAM-100. Relative F_v/F_m and P_m were calculated as the percentage of control values. The relationship between relative F_v/F_m or P_m and treatment temperature was fitted with a sigmoid function.

Leaf chilling resistance and leaf lethal temperatures

The electrolyte leakage method was used to assess the chilling sensitivities of the 11 species used in the present study (Wilner 1960, Lipp et al. 1994). Six sun-exposed newly fully developed mature leaves from different individuals (two and three individuals for *G. mangostana* and *A. champeden*; six individuals for other species) were collected before sunrise, placed in plastic bags with wet paper towels to reduce water loss and transported to the laboratory for measurements. Leaves were punched into round discs of 1-cm diameter and were sealed into zip lock bags and incubated in the cooling bath at different temperatures (8, 6, 4, 2, 0, -2, -4, -6, -8 and -10 °C). After maintaining the samples at a particular target temperature for 30 min, a group of leaf samples were removed from the cooling bath, placed in 20 ml tubes and then 10 ml of deionized water was added to each tube. The solutions with leaf samples were held at room temperature for 24 h with occasional mixing and shaking. Electrical conductivity (EC) of the solution was then measured with an electrical conductance/resistance meter (Hanna HI 98311, Hanna instruments, Woonsocket, RI, USA). After EC measurements, the tubes were put into a boiling water bath to obtain the EC with complete ion leakage. Electrical conductivity of the solution with leaf samples was measured again after 24 h with occasional mixing and shaking. The relative EC, an indicator of membrane ion leakage, was calculated for each sample as a percentage:

$$\text{Relative EC} = \frac{\text{EC after the temperature treatment}}{\text{EC after boiling}} \times 100 \quad (1)$$

The temperature at 50% relative EC was defined as the leaf lethal temperature (LT_{50}), which is widely used as an indicator of freezing resistance (Lipp et al. 1994, Melcher et al. 2000).

Data analysis

Seasonal differences in A_a , g_s , C_i , F_v/F_m and P_m for each species were tested using one-way analysis of variance (ANOVA). The relationships between percent decrease in A_a and percent decrease in g_s , and between percent decrease in A_a and

percent decrease in F_v/F_m were explored using linear regressions. The relationship between relative F_v/F_m or P_m and treatment temperature was fitted with a sigmoid function: $y = a + b/[1 + e^{-(x-c)/d}]$. Curves were fit using Sigmaplot V12.5 (Systat Software, Inc., San Jose, CA, USA), and one-way ANOVA was carried out in SPSS V21 (IBM Corp., Armonk, NY, USA).

Results

The light-saturated net photosynthetic rates (A_a) of all the studied species except *D. calantha* and *A. champeden* were significantly lower in the cool season compared with the warm season. *Dombeya calantha* showed a significant increase in A_a , while that of *A. champeden* had no significant change (Figure 2a). The A_a of the studied species ranged from 5.81 to 15.4 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in the warm season and from 2.51 to 14.6 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in the cool season (Figure 2a). Stomatal conductance (g_s) of 10 of the 11 species studied was significantly lower in the cool season, while g_s of *D. calantha* showed no change in the cool season compared with the warm season (Figure 2b). Five of the 11 species exhibited significant declines in intercellular CO_2 concentration (C_i), three showed significant increases, while the rest showed no change in the cool season (Figure 2c). Seven out of the 11 species had significantly lower maximum quantum yield of PSII (F_v/F_m) and maximum P700 changes (P_m) in the cool season than in the warm season (Figure 3). One native (*A. scholaris*) and one introduced species (*D. calantha*) had no seasonal decline in both F_v/F_m and P_m . *Artocarpus heterophyllus* had a significant decline in P_m but not in F_v/F_m , while *S. chinensis* had a significant decline in F_v/F_m but not in P_m (Figure 3). The F_v/F_m values of two species (*G. mangostana* and *T. cacao*) were <0.70 in the cool season, suggesting irreversible photoinhibition. Percent cool season decline in A_a was positively correlated with percent decrease in g_s and percent decrease in F_v/F_m (Figure 4).

The leaf lethal temperature, defined as the temperature at which 50% membrane leakage occurred, ranged from 1.44 to -8.52°C . *Coffea arabica* was the most chilling-sensitive species with a leaf lethal temperature of 1.44°C , and was also the only species with an above zero leaf lethal temperature. *Shorea chinensis* was the most chilling-resistant species (Figure 5).

No significant differences were found in F_v/F_m between sun-exposed and shaded leaves of *A. heterophyllus* in the cool season (Figure 3). This species showed no seasonal decline in F_v/F_m in sun-exposed leaves (Figures 3 and 6). The cool season F_v/F_m values of the shaded leaves of *T. cacao* and *C. arabica* were significantly higher than those of the sun-exposed leaves, and close to the warm season values of sun-exposed leaves (Figure 6).

A combination of low temperature and photoinhibitory light ($650 \mu\text{mol m}^{-2} \text{s}^{-1}$) resulted in a faster decline of F_v/F_m and

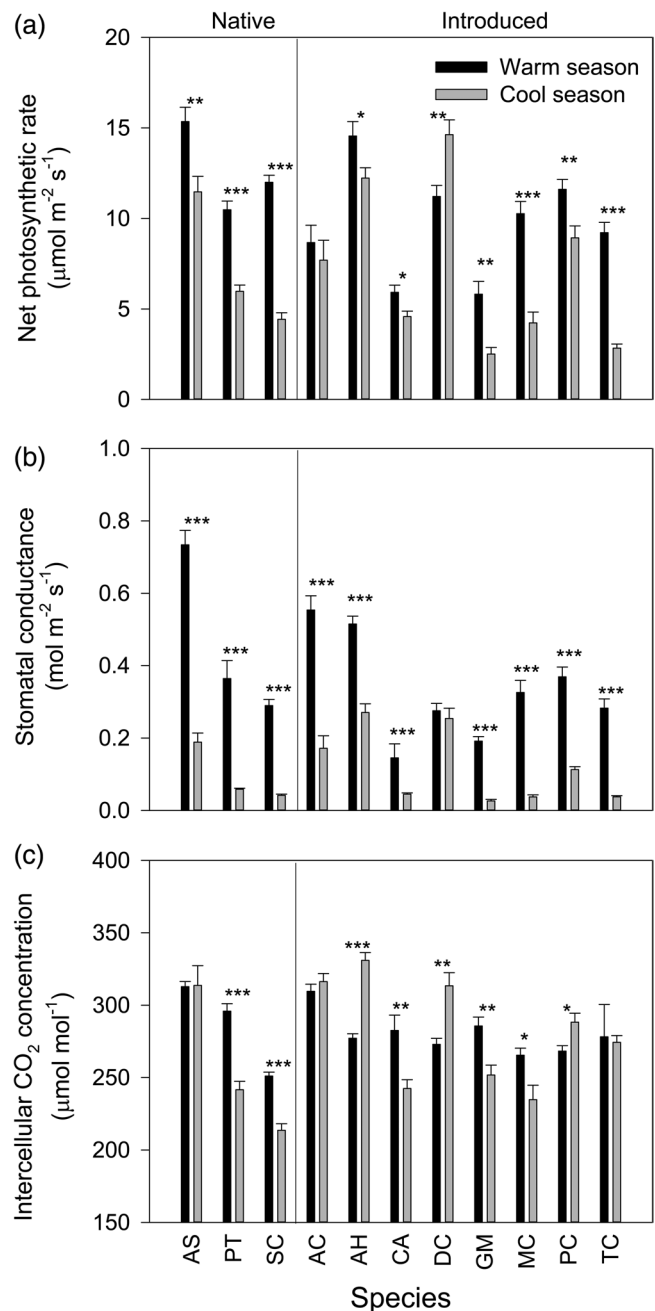


Figure 2. Net photosynthetic rates (a), stomatal conductance (b) and intercellular CO_2 concentrations (c) of different species in warm and cool seasons. Bars are means \pm SEs. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. Species codes are provided in Table 1.

P_m in *C. arabica* as the treatment temperature decreased compared with low temperature treatment alone (Figure 7). As the treatment temperature decreased, leaf P_m started to decrease at 4°C when the leaves were in the dark, and started to decrease at 6°C when the leaves were illuminated. Leaf F_v/F_m started to decrease distinctly at 0°C without light treatment, and started to decrease distinctly at 4°C when exposed to light (Figure 7b). The temperatures at which 50% loss of F_v/F_m and P_m occurred were 4 and 5°C higher when

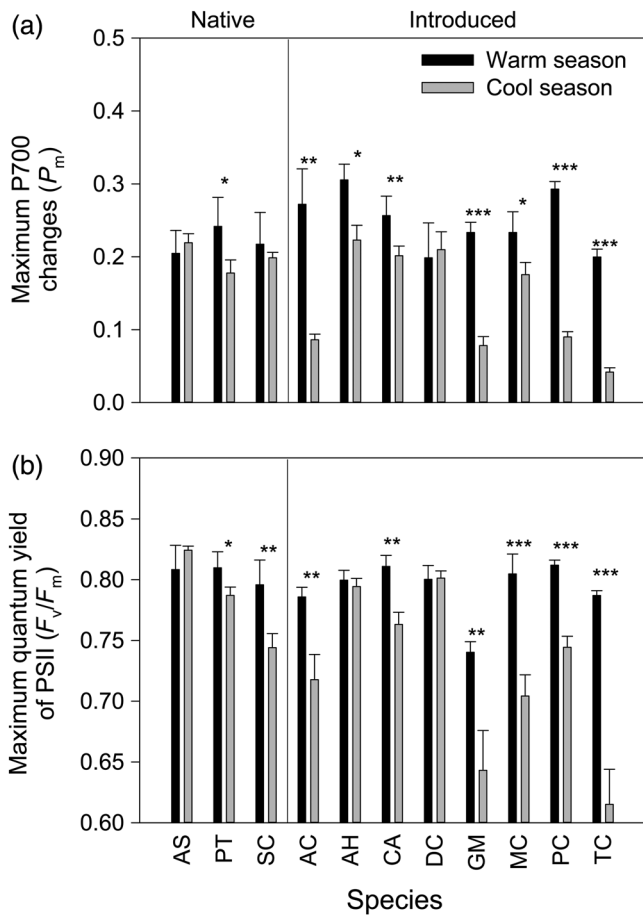


Figure 3. Maximum P700 changes (a) and maximum quantum yield of PSII (b) in warm and cool seasons. Bars are means + SEs. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. Species codes are provided in Table 1.

the leaves were illuminated than when the leaves were in the dark, respectively.

Discussion

Seasonal declines in net photosynthesis

Most of the studied tropical plants in Xishuangbanna, the northern limit of Asian tropics, significantly decreased their light-saturated net photosynthetic rate (A_a) in the cool dry season. However, most species maintained considerably high A_a in the unfavorable season ($2.51\text{--}14.6 \mu\text{mol m}^{-2} \text{s}^{-1}$), consistent with the finding of positive net carbon gain of the tropical rainforests in the cool season (Zhang et al. 2006) and high tropical crop production in Xishuangbanna. Additionally, because tissue respiration of tropical plants changes exponentially with changes in ambient temperatures (Slot et al. 2013), lower nocturnal respiratory carbon release from leaves, stems and roots in the cool season could contribute to the positive carbon balance of trees and thus help explain the high carbon sequestration rate of the forest in the cool season (Zhang et al. 2006).

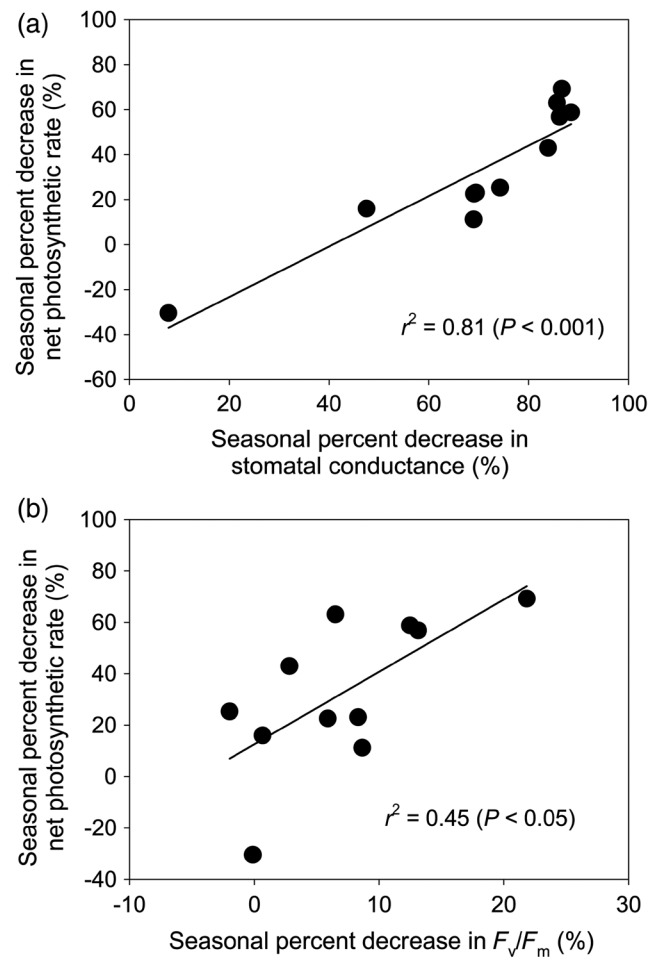


Figure 4. Percent decrease of net photosynthetic rate in the cool season in relation to percent decrease in stomatal conductance (a) and percent decrease in quantum yield of PSII (b). Lines are linear regressions fitted to the data.

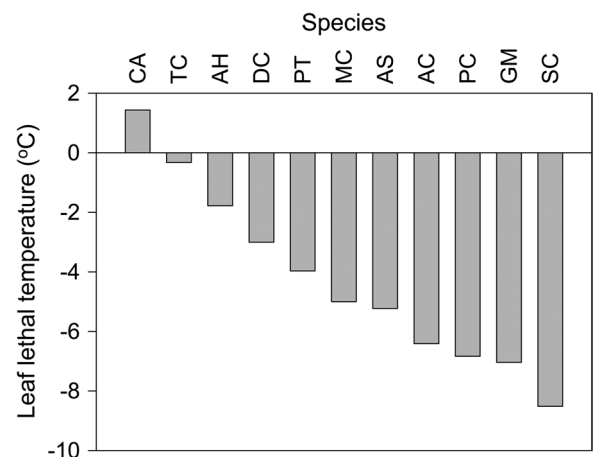


Figure 5. Leaf lethal temperatures, the temperatures causing 50% of membrane leakage, of different species. Species codes are provided in Table 1.

The strong correlation between percent decrease in A_a and percent decrease in g_s and F_v/F_m across species suggests that stomatal closure and photoinhibition are two factors associated

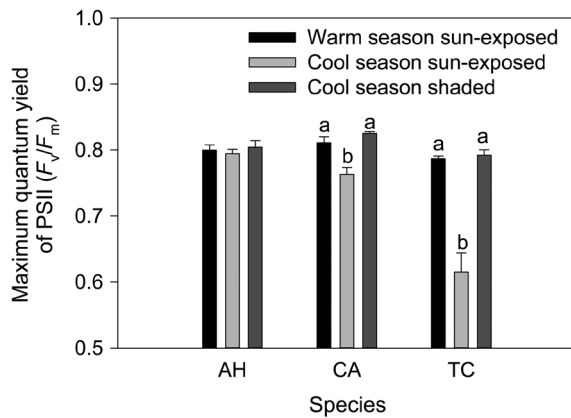


Figure 6. Quantum efficiency of PSII of sun-exposed and shaded leaves. Bars topped by the same letter do not differ significantly ($P > 0.05$) within species.

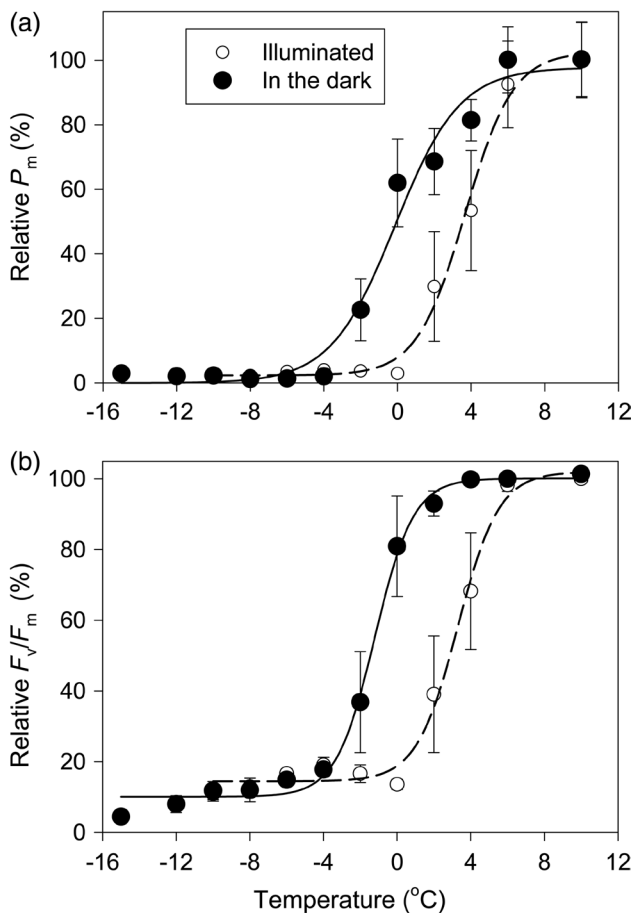


Figure 7. Maximum P700 changes (a) and maximum quantum yield of PSII (b) of *C. arabica* as a function of the treatment temperature. Points are means \pm SEs, and the lines are sigmoid functions fitted to the data. Closed points and solid lines indicate samples only treated with different temperatures, while open points and dashed lines indicate samples treated with a combination of different temperatures and light illumination ($650 \mu\text{mol m}^{-2} \text{s}^{-1}$).

with seasonal decline in A_a . Because of frequent watering and water input from fog interception in this region (Liu et al. 2004), the seasonal decline in A_a and g_s is probably the result

of chilling effects rather than soil water deficits. Chilling can reduce stomatal conductance (g_s) either through directly interfering with guard cell function or through indirectly stimulating stomatal closure by reducing Rubisco activity and increasing intercellular CO_2 concentration (C_i) (Allen and Ort 2001). Notably, among the nine species exhibiting significant seasonal decline in A_a and g_s , four showed no decline or even increases in C_i in the cool season. Therefore, g_s may not be the limiting factor in A_a in the cool season for these four species, and their A_a are probably more limited by decreased enzyme activity and/or photosynthetic electron transport efficiency in the cool season (Levitt 1980, KingstonSmith et al. 1997, Allen et al. 2000, Allen and Ort 2001, Bertamini et al. 2005, Huang et al. 2010a, Santini et al. 2013). In addition, lower night-time respiratory carbon release in cool seasons could lead to a higher concentration of carbohydrates retained in leaves, which may consequently inhibit A_a (Azcon-Bieto 1983).

Although a positive correlation between percent cool season decline in A_a and in F_v/F_m was found, the cool season decline in F_v/F_m could be the result rather than the cause of decreased A_a . Decreased A_a and therefore increased reactive oxygen species under stress can cause direct damage to PSII reaction centers (Oguchi et al. 2009, 2011) and inhibit the repair of photodamaged PSII (Murata et al. 2007). The percent seasonal decline in F_v/F_m was within 25% in the 11 studied species, while PSII complexes are suggested to be in excess of the number needed by 40% in *Capsicum annuum* and *Arabidopsis thaliana* (Lee et al. 1999, Kornyejev et al. 2006). In contrast, P_m showed a much greater decline ($\sim 70\%$) in the cool season than that of F_v/F_m ($\sim 20\%$) in four species (*A. champeden*, *G. mangostana*, *P. cupana*, *T. cacao*; Figure 3). This suggests that PSI of these species is more sensitive to seasonal low temperatures than PSII [see Havaux and Devaud (1994), Terashima et al. (1994), but see Huang et al. (2010a)], and thus could be the reason for decreased A_a in some of the species. Decreased PSI activity has been associated with decreased A_a in *A. thaliana*, and maintaining PSI activity has been suggested to be important in maintaining A_a (Kornyejev et al. 2006). However, in *A. champeden*, PSI declined by 68% in the cool season while its A_a showed no significant decline. This may be because *A. champeden* maintains excessive PSI during summer, or may be because seasonal changes in leaf structure influence P_m measurement, which needs further studies.

Potential role of fog in mitigating chilling-induced photoinhibition

Our results suggest that the shading effects of fog may mitigate chilling-induced photodamage during the cool season. Even the most chilling-sensitive species (*C. arabica*) can tolerate temperatures as low as 1.4°C in the dark according to the membrane leakage measurements (Figure 5). Also, leaf P_m and F_v/F_m in *C. arabica* did not decrease until 6°C (P_m) or 2°C (F_v/F_m) when

the leaves were in the dark. Therefore, chilling temperatures alone may have limited impact on leaf photosynthesis. In contrast, a combination of photoinhibitory light and low temperatures caused much faster decline in P_m and F_v/F_m in this species and the lethal temperatures (50% loss of P_m or F_v/F_m) of the leaf samples under photoinhibitory light were $\sim 4.0^\circ\text{C}$, which could occur in the cool season (Figure 1b). Therefore, the seasonal declines in A_a , P_m and F_v/F_m are more likely the result of a combination of chilling and high light stress than from the direct chilling temperature effects (Allen and Ort 2001, Huang et al. 2010a). This is consistent with the shaded leaves having much higher F_v/F_m than the sun-exposed leaves in the cool season, comparable to the values in the warm season. Because fog persistence in the morning prevents leaves from experiencing high light when the temperatures are still low or at least shortened the time period with combined high light and low temperatures, fog could avoid or reduce chilling-induced photodamage to leaves. Moreover, clear days typically have lower night and early morning temperatures because infrared emission from the earth surface rapidly escapes into the space (Supit and Van Kappel 1998, Sun et al. 2000, Bojanowski et al. 2013), which would worsen the photoinhibition and further suggest the importance of fog in mitigating chilling stress. Notably, although the light environment of shaded leaves was similar to that sun-exposed leaves experienced during the fog, shaded leaves may not be a perfect substitute for sun-exposed leaves in studying shading effects of fog due to structural and physiological differences between sun-exposed and shaded leaves (Boardman 1977). However, because shaded leaves are generally more sensitive to photoinhibition than sun-exposed leaves (Powles and Critchley 1980), high F_v/F_m in shaded leaves in the cool season indeed supports our statement that shading protects leaves from chilling-induced photoinhibition. Experiments illuminating leaves with photoinhibitory light in the foggy morning can be used to further confirm the physiological role of fog in mitigating chilling light stress.

The frequency of fog events in the studied region has been decreasing according to the climatic record (Huang et al. 2001), which may increase the exposure of tropical plants (forest trees and crops) to the combination of chilling temperatures and high light stress in the mornings of the cool season, and consequently reduce their productivity. The linkage between leaf chilling tolerance and plant mortality has not been studied for plants in Xishuangbanna. However, because leaf resistance to low temperatures is of importance for plant growth, survival and distribution (Sakai et al. 1981, Taschler and Neuner 2004), plants that are more chilling resistant may have higher fitness and higher vigor to compete with neighboring plants that are chilling sensitive. This is consistent with the result that the most dominant species in the rainforest in this marginal tropical region (*S. chinensis*) was the most chilling-resistant species among the 11 species studied. Therefore, we suggest that

a further decrease in fog persistence may result in changes in forest composition, degradation of the tropical rainforests and decreased yields of tropical crops in this region. Although the relationship between deforestation and the persistence of fog has not been established for Xishuangbanna, deforestation and conversion of forest to pasture lifts cloud base height and would decrease the area of cloud forests and limit their distributions in higher elevations in Costa Rica (Lawton et al. 2001). Thus, the potential impact of forest and land use management on fog persistence should be taken into account in the future.

Conclusions

Most of the tropical plants in Xishuangbanna studied here significantly decreased their net photosynthetic rates in the cool dry season, which was associated with both lower stomatal conductance and photoinhibition. However, their net CO_2 assimilations were still considerably high during the cool season. Shaded leaves had lower degree of cool season photoinhibition than sun-exposed leaves, and a combination treatment of low temperature and photoinhibitory light caused much faster decline in P_m and F_v/F_m compared with low temperature treatment alone. Because fog persistence avoids or shortens the duration of high light when the temperatures are low in the early morning, our results provide support for the hypothesis that fog mitigates chilling-induced photodamage of plants and plays a role in maintaining both tropical rainforests and tropical crop production in SW China.

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Conflict of interest

None declared.

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