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Effect of diurnal irradiance on night-chilling tolerance of six rubber cultivars

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Abstract

The rubber tree (*Hevea brasiliensis*) is an important tropical crop with a high economic value that has been successfully cultivated in Xishuangbanna, China. Xishuangbanna has a long dry season (November–February) with cold nights and frequent fog events. Thus, it is important to select chilling-tolerant cultivars in order to understand better the role of fog in protecting rubber tree from chilling-induced photodamage. In this study, we examined the photosynthetic responses of six rubber tree cultivars (Lan 873, Yunyan 77-2, Yunyan 77-4, GT1, Reken 523, and Reyan 733-97) to night-chilling stress (0, 5, and 10°C) and two different irradiances (100 and 50% of full sunlight). Our results showed that all six cultivars could withstand nights at 10°C for three days, while night chilling at 0 and 5°C impaired photosynthesis, which was indicated by photoinhibition, decrease of soluble protein content, and accumulation of malondialdehyde. Reken 523 and Reyan 733-97 were more sensitive to night chilling than other cultivars. Low irradiance (50% of full sunlight) after the chilling treatment apparently mitigated the effect of night-chilling stress. It indicates that frequent fog events after cold nights might greatly contribute to the success of rubber tree cultivation in Xishuangbanna.

Additional key words: chlorophyll fluorescence; gas exchange; reactive oxygen species; soluble sugar content; stomatal conductance.

Introduction

The rubber tree (*Hevea brasiliensis*) is an important tropical crop with a high economic value, because its latex serves as the basic material for various rubber products. Its production zone is traditionally concentrated between 15°N and 10°S (Lemmens *et al.* 1995); however, it has been successfully cultivated as far north as 21–22°N in Xishuangbanna, autonomous prefecture, Yunnan Province, Southwest China. In this area, the first rubber plantations were established in 1956 in order to meet needs of national defense and economic development (Wu *et al.* 2001, Li *et al.* 2008), and the total cultivated area of rubber tree plantations reached 270,000 ha by 2010.

Chilling stress is one of the major abiotic factors that limit survival, growth, reproduction, and distribution of plant species (Boyer 1982, Allen and Ort 2001, Annicchiarico *et al.* 2001). Plants, which grow in tropical areas, are adapted to year-round warm temperatures and are relatively more vulnerable to chilling stress than those grown in temperate areas (Crawford 1989, Greer 1990, Zheng *et al.* 2009). It has been indicated that temperatures between 6 and 10°C can cause injury or even death to typical tropical plants (Crawford 1989).

The photosynthetic apparatus in chilling-sensitive plants displays physiological and biochemical dysfunctions under stress conditions, because photosynthetic enzymes are inactivated or degraded (Allen *et al.* 2000). The reduced photosynthesis may lead to accumulation of excess energy, especially at high irradiance (Hovenden and Warren 1998, Feng and Cao 2005). When excessive irradiance energy is not harmlessly dissipated as heat by nonphotochemical

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Abbreviations: C_i – intercellular CO_2 concentration; F_0 – minimal fluorescence yield of the dark-adapted state; FI – full irradiance treatment; F_m – maximum fluorescence yield of the dark-adapted state; F_v – variable fluorescence; F_v/F_m – maximal quantum yield of PSII photochemistry; g_s – stomatal conductance; I50 – treatment at 50% of full irradiance; MDA – malondialdehyde; P_{max} – light-saturated photosynthetic rate; ROS – reactive oxygen species.

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quenching, many reactive oxygen species (ROS), such as $O_2^{\bullet-}$, OH^-, and H_2O_2, are generated (Foyer *et al.* 1994). ROS may accelerate photoinhibition, which leads to peroxidation of membrane lipids and destruction of the photosynthetic apparatus (Asada 2006, Lei *et al.* 2014). Malondialdehyde (MDA), the product of membrane lipid peroxidation, is also toxic to the photosynthetic apparatus. ROS also inhibit the synthesis of some proteins, necessary for photodamage repair (Danon 2012).

Both low temperature (Greer 1990, Zheng *et al.* 2009, Huang *et al.* 2010a,b) and high irradiance (Feng *et al.* 2004) can cause damage to PSII of tropical plants (Krause 1992, Wise 1995). The combined effects of these factors are more significant than the individual effect of each factor alone (Long *et al.* 1994, Feng and Cao 2005).

Xishuangbanna is the northern limit of tropical rainforests in Asia and has a long cool dry season that lasts from November to February (Cao *et al.* 2006). In December and January, which are the coolest months, the lowest temperature is usually near 5°C in the morning, but in the afternoon temperatures reach over 20°C (Feng and Cao 2005, Zhang *et al.* 2014). In the cool season, dense fog events are very frequent, about 25 days per month (Zhang *et al.* 2014), and during those days irradiance is reduced by 60–90% (Feng and Cao 2005), especially during the morning hours, when temperatures are still low.

Rubber tree cultivation is successful in Xishuangbanna, but it may be affected in the future by global climatic changes and urbanization of tropical forests. Global climate change has led to more frequent periods of unusual chilling (Cohen *et al.* 2012, Liu *et al.* 2012), and extreme low temperatures (≤5°C), which occurred three times (December 28, 1993; December 27, 1999; and December 19, 2013) in the last 20 years in Xishuangbanna (Xishuangbanna Station for Tropical Rain Forest Ecosystem Studies). Urbanization and deforestation are considered to be contributing factors to the decreasing frequency of fog events in Xishuangbanna, which may seriously affect rubber tree cultivation in the future, since fog plays an important role in mitigating the effect of chilling (Huang *et al.* 2001). Thus, it is important to select chilling-tolerant cultivars and better understand the role of fog in protecting rubber trees from chilling-induced photodamage.

In this study, we examined the diurnal irradiance effect on night-chilling tolerance of six rubber tree cultivars. The main objectives were: (*1*) to identify chilling-tolerant genotypes and (*2*) to determine whether reduced irradiance could mitigate the effect of night-chilling stress in rubber trees.

Materials and methods

Experimental site, plants, and treatments: This study was conducted at the Yunnan Institute of Tropical Crops (22°0'N, 100°45'E), located in Jinghong, Xishuangbanna autonomous prefecture, Yunnan Province, China. The mean annual temperature in the study area is 21.5°C, and the mean annual precipitation is 1,162 mm.

Six popular rubber tree cultivars (Lan 873, Yunyan 77-2, Yunyan 77-4, GT1, Reken 523, and Reyan 733-97) were used in this study. In November 2010, seeds of GT1 were sown into an experimental field, and in March 2011, when the seedlings were about 60 cm tall, shoots from each cultivar were grafted onto them. The distance from the lowest point of the graft union to the ground surface was 30 cm. After the graft union healed, the upper portion of the rootstocks was removed. In May 2012, when the grafted saplings were about 60 cm tall, they were singly transplanted into 20 dm^3 pottery pots containing homogenized forest top soil. The saplings were grown outdoors under full irradiance and watered as necessary. On September 15, 30 similar sized seedlings from each cultivar were selected. Fifteen of them were transferred into a greenhouse at 50% full irradiance (I50), while the remaining 15 seedlings were left outdoors at full irradiance (FI).

In Xishuangbanna, low temperatures occur only at night (Feng and Cao 2005); therefore, chilling treatments were only applied at night in this study. On October 1, 15 seedlings at FI and 15 at I50 were randomly divided into three groups of five individuals each in order to be subjected to the night-chilling treatments. The three groups were transferred to a cold climate greenhouse where they were maintained at 0, 5, and 10°C for 12 h (18:00 to 06:00 h) in the dark for three consecutive nights. During the day (average maximum temperature was 30.7°C), each group was returned to the original site. After three nights of chilling treatments, the seedlings were maintained for another three days at the original sites in order to recover. Before and after the night- chilling treatments and after recovery, measurements of photosynthesis and chlorophyll (Chl) fluorescence were carried out *in vivo* using the youngest fully expanded leaves of each individual. Then, the same leaves were collected for determining the content of MDA, soluble proteins, and soluble sugars.

Chl fluorescence: The measurements of leaf Chl fluorescence (PSII) were performed using a *Dual PAM-100* fluorometer (*Heinz Walz*, Effeltrich, Germany). At 05:00 h (11 h dark-adapted), when the studied plants could achieve the daily highest maximal quantum yield of PSII photochemistry (F_v/F_m), the minimum fluorescence yield of the dark-adapted state (F_0) was measured on each leaf (adaxial side) under a weak modulated red beam, then the maximum fluorescence yield of the dark-adapted state (F_m) was determined by irradiating (300 ms) the sampled leaf with a saturating white light pulse [10,000 μmol(photon) m^{-2} s^{-1}]. The F_v/F_m was calculated as $F_v/F_m = (F_m - F_0)/F_m$. $F_v = (F_m - F_0)$ is the variable fluorescence, reflecting the maximum quantum yield of PSII (Kramer *et al.* 2004, Zheng *et al.* 2009).

Gas exchange: In the morning when the plants achieved the highest photosynthetic rate, the light-saturated rate (P_{max}), stomatal conductance (g_s), and intercellular CO_2 concentration (C_i) were measured using a *Li-6400* portable photosynthesis system (*Li-Cor*, Lincoln, NE, USA) at a saturated irradiance of 1,200 μmol(photon) m^{-2} s^{-1}. Relative humidity and CO_2 concentration of the air in the reference chamber and leaf temperature were controlled automatically by the equipment at 80%, 380 μmol mol^{-1}, and 20°C, respectively.

MDA, soluble protein, and soluble sugar contents: MDA was extracted using 10% trichloroacetic acid and detected using 2-thiobarbituric acid (Hodges *et al*. 1999). Soluble proteins were extracted using phosphate buffer and detected using Coomassie Brilliant Blue G-250 (Wang *et al*. 1986). Soluble sugars were extracted as described by Ciha and Brun (1978) and quantified using phenol sulfuric acid assay with some modifications (Centrifuge was used to facilitate filtration process) (Zhang 1993).

Statistical analysis: Differences between treatments at the same irradiance were compared using one-way analysis of variance (*ANOVA*). The values of each variable before night-chilling treatment might be different between cultivars and the differences between groups in an absolute value (measured directly) of each variable after night chilling and recovery treatments might not reflect the differences in chilling tolerance between cultivars (Zheng *et al*. 2009). In order to evaluate the differences in chilling tolerance between cultivars, the relative values of each variable after night chilling and recovery treatments were calculated as the percentage of the absolute value to the value measured before night-chilling treatment. The effects of night-chilling treatment and irradiance on each cultivar were tested using two-way *ANOVA*. At the same irradiance and night-chilling treatment, the differences in chilling tolerance between cultivars were compared by one-way *ANOVA*. The correlations of P_{max} and C_i, P_{max} and F_v/F_m, P_{max} and MDA, F_v/F_m and MDA, P_{max} and soluble protein content, F_v/F_m and soluble protein content, P_{max} and soluble sugar content, and F_v/F_m and soluble sugar content were tested by *Pearson*'s correlation analysis. All analyses were performed using *SPSS 17.0* (*SPSS Inc*., Chicago, IL, USA).

Results

Night-chilling treatments significantly decreased P_{max}, g_s, and soluble protein content across all groups in all cultivars and did not recover to pretreatment levels, except for g_s of Lan 873 grown at I50 and treated at 10°C (Figs. 1–3; Figs. 1S, 3S, 6S, *supplements available online*). The soluble sugar content significantly increased after the night-chilling treatment across all groups in all cultivars, while it returned to pretreatment levels after recovery in all groups at 5 and 10°C (Fig. 7S, *supplement available online*; Fig. 3*C*). C_i values after the night-chilling treatments at the three different temperatures were not significantly different compared to those found before night chilling in any cultivar, except for GT1 and Reken 523 that were significantly lower across groups (Fig. 4S, *supplement available online*). In all cultivars left outdoor under FI, F_v/F_m values were not significantly different after night chilling at 10°C from those measured before the night chilling, while F_v/F_m values after night chilling at 0 or 5°C significantly decreased and did not recover to pretreatment levels (Fig. 2S, *supplement available online*; Fig. 1*B*).

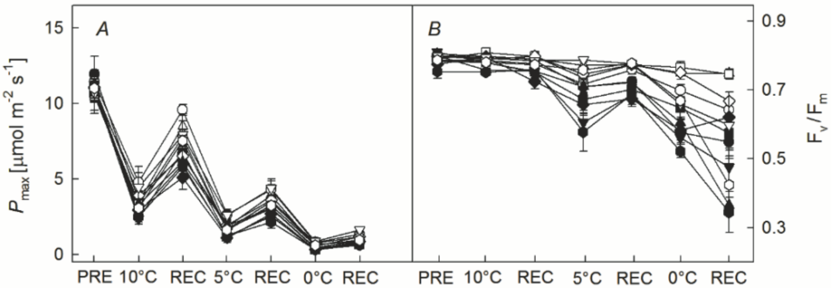

Fig. 1. Light-saturated photosynthetic rate (P_{max}) (*A*) and maximal quantum yield of PSII photochemistry (F_v/F_m) (*B*) of six rubber tree cultivars (●,○ Lan 873; ▼,Δ Yunyan 77-2; ■,□ Yunyan 77-4; ◆,◇ GT1; ▲,▽ Reken 523; and ⬢,⬡ Reyan 733-97) before and after night-chilling treatment at 0, 5, or 10°C and subsequent recovery in full irradiance (*full symbols*) and 50% of full irradiance (*open symbols*). PRE – pretreatment; REC – recovery.

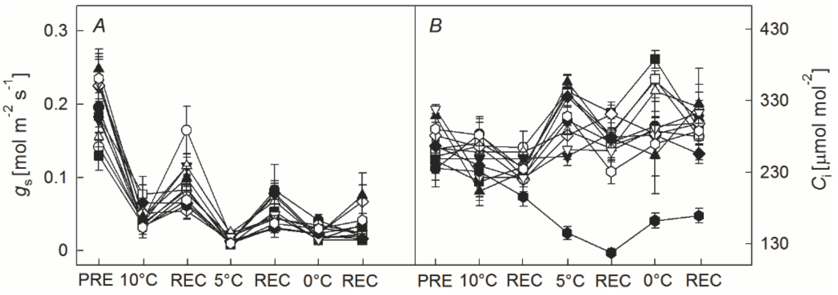

Fig. 2. Stomatal conductance (g_s) (*A*) and intercellular CO_2 concentration (C_i) (*B*) of six rubber tree cultivars (●,○ Lan 873; ▼,Δ Yunyan 77-2; ■,□ Yunyan 77-4; ◆,◇ GT1; ▲,▽ Reken 523; and ⬢,⬡ Reyan 733-97) before and after night-chilling treatment at 0, 5, or 10°C and subsequent recovery in full irradiance (*full symbols*) and 50% of full irradiance (*open symbols*). PRE – pretreatment; REC – recovery.

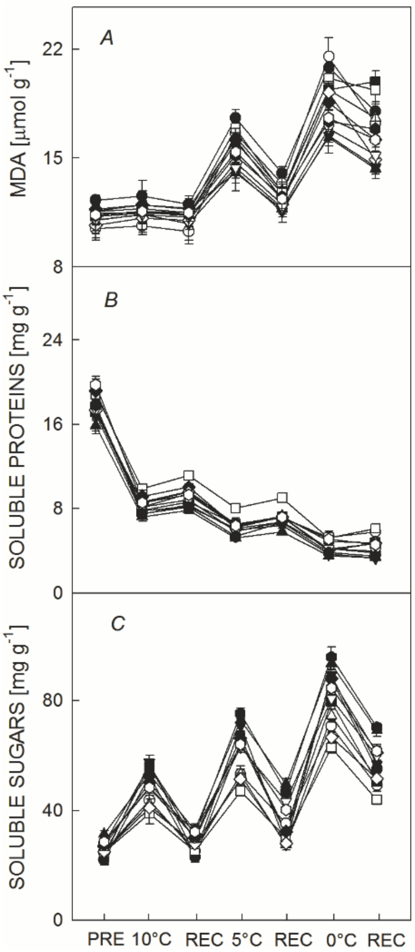

Fig. 3. Malondialdehyde (MDA) (*A*), soluble protein (*B*), and soluble sugar (*C*) contents of six rubber tree cultivars (●,○ Lan 873; ▼,△ Yunyan 77-2; ■,□ Yunyan 77-4; ◆,◇ GT1; ▲,▽ Reken 523; and ⬢,⬡ Reyan 733-97) before and after night chilling treatment at 0, 5, or 10°C and subsequent recovery in full irradiance (*full symbols*) and 50% of full irradiance (*open symbols*). PRE – pretreatment; REC – recovery.

All cultivars grown at I50 showed similar F_v/F_m patterns as those under FI, while it returned to pretreatment levels after recovery in all groups treated at 5°C, except for Yunyan 77-2 (Fig. 2S). At both irradiances, night chilling at 10°C had no significant effect on the MDA content in any cultivar, while after night chilling at 5°C, the MDA content significantly increased and returned to pretreatment levels after recovery in all cultivars (Fig. 5S, *supplement available online*; Fig. 3*A*). MDA significantly increased after night chilling at 0°C in all cultivars and did not return to the pretreatment levels, except for Yunyan 77-4 (Figs. 5S, 3*A*).

In all cultivars, irradiance had a significant effect on the relative value of P_{max}, F_v/F_m, and MDA, soluble sugar and soluble protein contents, except for the relative value of the soluble protein content in GT1, Reken 523, and Reyan 733-97 and the relative value of the soluble sugar content in Reken 523 (Table 1S, *supplement available online*). It had no significant effect on the relative value of g_s and C_i (data not shown). The relative values of P_{max} and the MDA content showed no significant differences before and after the night-chilling treatment or recovery across all groups in all cultivars (Table 1S). The relative value of F_v/F_m after recovery was significantly different between the groups treated at 0°C and recovered under I50 and FI (Table 1S). The relative value of soluble proteins was not significantly different between cultivars, except for groups treated at 0°C and recovered under FI and those treated at 0 or 10°C and recovered under I50 (Table 1S). The relative value of soluble sugar contents was not significantly different between cultivars, except for groups treated at 5°C and 10°C and recovered under FI (Table 1S). Across all cultivars, P_{max} significantly increased with increasing F_v/F_m, but it decreased with increasing C_i (Fig. 4). Both F_v/F_m and P_{max} were significantly positively correlated with the soluble protein content (Fig. 5*B*,*E*) and negatively correlated with the MDA and soluble sugar content (Fig. 5*A*,*C*,*D*,*F*).

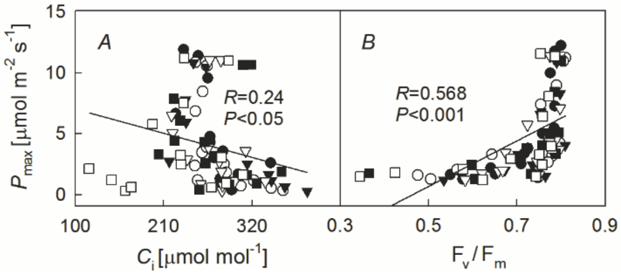

Fig. 4. Mean value of light-saturated photosynthetic rate (P_{max}) as a function of mean values of intercellular CO_2 concentration (C_i) (*A*) and maximal quantum yield of PSII photochemistry (F_v/F_m) (*B*) of six rubber tree cultivars (● Lan 873, ○ Yunyan 77-2, ▼ Yunyan 77-4, ▽ GT1, ■ Reken 523, and □ Reyan 733-97) before and after night-chilling treatment at 0, 5, or 10°C and subsequent recovery under full irradiance and 50% of full irradiance.

Discussion

Night chilling decreased P_{max}: Night-chilling treatments significantly decreased P_{max} of rubber saplings in all cultivars under both irradiances (Figs. 1*A*, 1S). The effect of night chilling on F_v/F_m was less significant than that on P_{max} (Figs. 1*A*,*B*; 1S, 2S; Table 1S), which indicated that net photosynthesis was more affected than the maximum

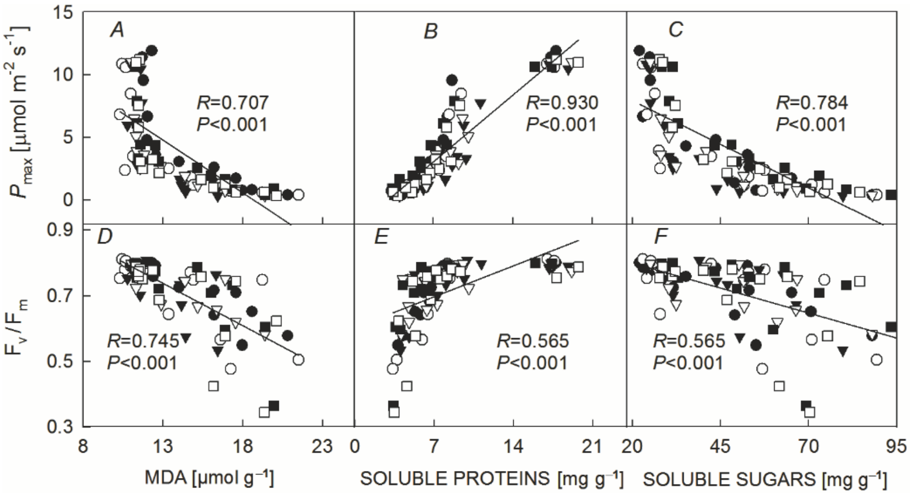

Fig. 5. Mean values of light-saturated photosynthetic rate (P_{max}) (*A*,*B*,*C*) and maximal quantum yield of PSII photochemistry (F_v/F_m) (*D*,*E*,*F*) as a function of mean values of malondialdehyde (MDA), soluble protein and soluble sugar contents of six rubber tree cultivars (● Lan 873, ○ Yunyan 77-2, ▼ Yunyan 77-4, ▽ GT1, ■ Reken 523, and □ Reyan 733-97) before and after night-chilling treatment at 0, 5, or 10°C and subsequent recovery under full irradiance and 50% of full irradiance.

photochemical efficiency. Although g_s significantly decreased by night chilling (Figs. 2*A*, 1S), the reduction of P_{max} was not caused by low C_i concentration, since C_i was not significantly reduced by night chilling (Figs. 2*B*, 4S), and the correlation of P_{max} with C_i was also negative (Fig. 4*A*). Stomatal closure might be a protective response to chilling stress. The reduction of P_{max} was probably limited by the decreased enzyme activity and/or photosynthetic electron transport efficiency due to night chilling (Allen and Ort 2001, Bertamini *et al.* 2005, Huang *et al.* 2010a, Santini *et al.* 2013, Zhang *et al.* 2014). The significantly positive correlation of P_{max} and F_v/F_m with the soluble protein content (Fig. 5*B*,*E*) indicated that the decrease in the soluble protein content might be related to the reduction of P_{max}. More than half of the soluble proteins are important components of the photosynthetic apparatus and photodamage repair process (Pell *et al.* 1994, Asada 2006, Danon 2012), and soluble proteins also play an important role in osmotic adjustment (He *et al.* 2013). MDA, which is the product of membrane lipid peroxidation, was significantly increased after the night-chilling treatments at 5 and 0°C, indicating that night chilling might induce the accumulation of ROS and impair cell membranes of the photosynthetic system (Thomashow 1999, Mai *et al.* 2009, Lei *et al.* 2014). MDA and ROS can suppress the activities of photosynthetic enzymes, such as Rubisco. In this study, night chilling significantly increased the soluble sugar content in all cultivars (Figs. 3*C*, 7S). The rapid increase of soluble sugars to low temperatures was also identified in other plant species (Sasaki *et al.* 1996, Wanner and Junttila 1999, Klotke *et al.* 2004). Soluble sugars function as osmoprotectants, buffering low temperatures, while relatively high concentrations may trigger leaf senescence (Ma *et al.* 2009).

Cultivars differ in chilling tolerance: The night-chilling treatment at 10°C had no significant effect on F_v/F_m and MDA content, but increased the soluble sugar content, which returned to the pretreatment concentrations after a 3-d recovery (Figs. 2S, 5S, 7S). P_{max} was significantly decreased by the night-chilling treatment at 10°C and returned to 45–85% of pretreatment levels after a 3-d recovery (Table 1S). Our results were consistent with a previous study of Mai *et al.* (2009), in which rubber trees were shown to withstand 4 d of chilling at 10°C and 50% of its photosynthetic ability was recovered after 3 d at 28°C. We suggest that night chilling at 10°C for several days does not cause any irreversible damage in the photosynthetic apparatus of rubber trees; however, night chilling at 0–5°C in combination with subsequent full irradiance can cause evident photodamage in rubber trees.

No significant differences were identified between cultivars in the relative values of P_{max} and MDA at any night chilling treatment and subsequent recovery (Table 1S). For the relative values of F_v/F_m, the soluble protein content, and the soluble sugar content, significant differences among cultivars were only found after some night-chilling treatments and/or subsequent recoveries (Table 1S). Among cultivars, Reken 523 and Reyan 733-97 were less tolerant to the night-chilling treatments at 0 and 5°C.

Fog can mitigate the effect of night-chilling stress on photosystems: Irradiance had a significant effect on the relative values of P_{max}, MDA, and soluble sugar content in all cultivars, except for Reken 523, and on the relative value of soluble protein content in Lan 873, Yunyan 77-2, and Yunyan 77-4 (Table 1S). The effect of night chilling in combination with subsequent I50 was weaker than that with FI (Table 1S), suggesting that shade may mitigate the effect of night-chilling stress on photosystems. During the cool season (November to February), dense fog, which reduces irradiance by 60–90%, occurs frequently in Xishuangbanna from midnight until the following midday (Feng and Cao 2005). Low temperatures significantly affect irradiance utilization, but not as much as irradiance absorption by of leaves (Germino and Smith 2000, Santini *et al.* 2013). Fog shortens or eliminates periods of high irradiance during the morning hours in which temperatures are still low (Zhang *et al.* 2014), decreasing the risk of ROS production due to excessive energy absorption by leaves, and accelerating recovery from night chilling. Consequently, fog may play an important role in mitigating the effect of night-chilling stress in rubber trees.

In summary, our results showed that all six rubber tree cultivars could withstand night chilling at 10°C for three days, while night chilling at 0 and 5°C could impair photosynthesis by different physiological processes, such as photoinhibition, decrease of soluble protein content, and accumulation of MDA (Fig. 5). Reken 523 and Reyan 733-97 were more sensitive to night chilling than Lan 873, Yunyan 77-2, Yunyan 77-4, and GT1. Recovery at 50% of full irradiance mitigated the effect of night- chilling stress, which shows that frequent fog events in Xishuangbanan might greatly contribute to the success of the rubber tree cultivation.

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