PHOTOSYNTHETICA 43 (4): 567-574, 2005

Photosynthesis and photoinhibition after night chilling in seedlings of two tropical tree species grown under three irradiances

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Abstract

We investigated the physiological effect of night chilling (CN) on potted seedlings of two tropical tree species, *Calophyllum polyanthum* and *Linociera insignis*, in Xishuangbanna, southwest China. Seedlings grown under 8, 25, and 50 % daylight for five months were moved to a 4–6 °C cold storage house for three consecutive nights, and returned to the original shaded sites during the day. CN resulted in strong suppression of photosynthesis and stomatal conductance for *L. insignis*, and reduced photorespiration rates, carboxylation efficiency, and maximum photochemical efficiency of photosystem 2 (PS2) at dawn and midday for both species. CN increased dawn and midday rates of non-photochemical quenching, and the contents of malondialdehyde and H_2O_2 for both species. CN also induced inactivation or destruction of PS2 reaction centres. The impacts of CN on tropical seedlings increased with the number of CN. Shading could significantly mitigate the adverse effects of CN for both species. After 3-d-recovery, gas exchange and fluorescence parameters for both species returned to pre-treatment levels in most cases. Thus CN induced mainly stomatal limitation of photosynthesis for *L. insignis*, and non-stomatal limitation for *C. polyanthum*. *C. polyanthum* was more susceptible to CN than *L. insignis*. Fog, which often occurs in Xishuangbanna, could be beneficial to chilling sensitive tropical seedlings in this area through alleviating photoinhibition or photodamage by reducing sunlight.

Additional key words: *Calophyllum polyanthum*; carboxylation efficiency; chlorophyll fluorescence; fog; H_2O_2; *Linociera insignis*; malondialdehyde; reactive oxygen species; stomatal conductance.

Introduction

Tropical forests mainly occur in regions around the equator, but extend northward near the Tropic of Cancer in southwestern China (Cao and Zhang 1997, Zhu 1997). There, the Tibetan Plateau, the Yun-Gui Plateau, and the Hengduan mountain ranges protect tropical forests by blocking the movement of cold air from northern China. However, occasionally strong cold winds pass over the Yun-Gui Plateau and affect the area (Xu and Yu 1982). For example, in December 1999 a cold front affected the region for about 10 d. During this chilly period, the lowest temperature recorded at a tropical rain forest site was 2 ºC, while about 8 ºC appears in the same season of normal years. Large areas of tropical crops such as rubber trees, coffee, and mango were severely injured or died of chilling (Hong and Li 2001). Although there were no visible injuries to native tropical forest plants, the low temperature could have adversely affected their physiology and hence productivity. Physiological intolerance to lower temperatures could result in a competitive disadvantage with other adjacent plants in the community (Long *et al*. 1994).

In the wet tropics, most plants grow all the year round in a warm climate, and are particularly vulnerable to low temperatures (Greer 1990, Ortiz-Lopez *et al*. 1990). Temperatures between 6 and 10 °C could cause injury and even mortality to typical tropical plants (Crawford 1989). During the life cycle of a tropical tree, the seedling stage is most vulnerable to chilling. In northern tropical regions, such as Xishuangbanna of southwest China where this study was carried out, chilling temperature occurs only at night, but it is still warm during the day stimulating photosynthesis. The lowest night temperature

Received 2 December 2004, *accepted* 11 April 2005.
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Ackowledgements: We are grateful to Feng Zhi-Li, Cai Zhi-Quan, and Zhang Jiao-Ling for assistance, and Giles Thelen of the University of Montana and two anonymous reviewers for helpful suggestions on our earlier manuscript. This study was funded by the Project of Distinguished Scientists in the West from Chinese Academy of Sciences granted to YLF, and the Chinese Academy of Sciences through a research project (No. KSCX2–SW–116) granted to KFC.

recorded in normal years is 6 °C, but it is over 20 °C in the afternoon during the coolest season in Xishuangbanna. This kind of chilling temperature is different from that in temperate zone, where temperature is low day and night. The effect of night chilling (CN) should be different from that of simultaneous occurrence of low temperature together with moderate or high irradiance that is the case in temperate regions.

In the day following a chilling night, photosynthetic enzyme activity was suppressed, stomatal limitation was increased, and photosynthesis was reduced (Flexas *et al*. 1999, Allen *et al*. 2000). Reduced photosynthesis can lead to the accumulation of excessive photon energy and photoinhibition. The excessive photon energy can be dissipated non-radiatively by several processes such as xanthophyll cycle, or be used up by photorespiration. If there is still excess energy, plants will produce reactive oxygen species such as $O_2^{\bullet-}$, •OH, and H_2O_2 through various processes, which cause the peroxidation of membrane lipids and destruction of the photosynthetic apparatus (Foyer *et al*. 1994). Malondialdehyde (MDA) is the product of membrane lipid peroxidation, and is also toxic to the photosynthetic apparatus.

Low temperature (Greer 1990, Ortiz-Lopez *et al*. 1990) and high irradiance (Feng *et al*. 2004) induce photoinhibition (Krause 1992) and photooxidation (Wise 1995) in tropical plants. The combined effects of low temperature and high irradiance are more significant than the individual effect of each stress (Long *et al*. 1994). Shading significantly mitigates the effects of chilling and promotes forest seedling establishment in areas where chilling is a problem (Ouander and Öquist 1991, Ball 1994, Egerton *et al*. 2000). During the winter season in Xishuangbanna, each day there is heavy fog cover from midnight to the following midday. The fog blocks direct sun and reduces irradiance by 60–90 %. Fog might probably mitigate CN effect on native tropical rainforest plants and introduced tropical crops in this region. In this report we investigated the effect of CN on photosynthesis and the effect of daylight on the physiological effect of CN in seedlings of two tropical montane rainforest tree species grown under three different daylights. The main objective of this study was to determine whether reducing daylight could alleviate the adverse effect of CN on tropical tree seedlings.

Materials and methods

This study was conducted in the Xishuangbanna Tropical Botanical Garden (21°56'N, 101°15'E, 600 m elevation), Chinese Academy of Sciences, which is situated in the southern part of Yunnan Province, southwest China. Climatic conditions are described in Feng *et al*. (2002) and Cao and Zhang (1997). The two native tropical tree species *Calophyllum polyanthum* Wall. *ex* Choisy (Clusiaceae) and *Linociera insignis* C.B. Clarke (Oleaceae) were chosen for the study. Both species occur in the tropical mountain rain forests, and are canopy species. Seedlings germinated from seeds were planted in 0.015 m^3 pots (1 seedling per pot) in shading house with 25 % daylight. The pots contained an 0.1 m layer of forest soil. One month later, two thirds of these seedlings were moved into shading houses with 8 and 50 % daylight, respectively. There were at least 15 healthy individuals per species per shading house. The plants were watered every day and fertilized with compound chemical fertilizers monthly. Seedlings were regularly sprayed with pesticides to control insects and diseases.

Four months after transferring the seedlings into different shading houses (late December 2000), 3–5 potted seedlings were moved into a dark cold storage house (4–6 °C) for 10 h per day for three consecutive nights. During the day the CN-treated seedlings were put back into the original shading houses. Net photosynthetic rate (P_N) and stomatal conductance for water (g_s) were measured on mature leaves of the CN and control (C) seedlings, using a portable photosynthesis system (*Li-Cor 6200*, *LI-COR*, Lincoln, NE, USA) and a LED radiation source with a photon flux density (PFD) of 600 μmol m^{-2} s^{-1}. Portions of intact leaves were enclosed in a 250-cm^3 cuvette. The relative humidity was about 60 % and CO_2 concentration in the cuvette was 360 μmol mol^{-1}. Measurements were taken in the morning (07:30–10:30) and again in the early afternoon (12:30–15:30). Photosynthesis CO_2 responses were determined with CO_2 concentrations ranging within 0–360 μmol mol^{-1}, using the CO_2 control system of the machine to regulate CO_2 concentration in the leaf chamber. P_N was measured when leaves were stabilized at each CO_2 concentration for about 3 min. The slope of the linear regression of intercellular CO_2 concentration (C_i) and P_N at the low C_i is the carboxylation efficiency (CE) and its intercept at y-axis (C_i = 0) is photorespiration rate (P_r; Cai and Xu 2000). Gas exchange measurements were taken every day during the CN treatment, and on the following three days. During this period, incident irradiance was low in the morning due to heavy fog (until about 10:30), with ambient atmospheric temperatures of 19–22 ºC. It was always clear in the afternoon, with ambient atmospheric temperatures of 27–29 ºC.

Chlorophyll fluorescence emission was measured for the chilling-treated and control plants at dawn and around midday, using a portable pulse-modulated fluorometer (*FMS 2*, *Hansatech*, U.K.). The leaf was dark-adapted for at least 15 min, and the minimum fluorescence yield (F_0) was measured under a weak modulating beam. Maximum fluorescence yield (F_m) was determined by irradiating the dark-adapted leaf sample with a saturating pulse (5 000 μmol m^{-2} s^{-1}, 0.7 s). After the fluorescence yield dropped from F_m to close to F_0, "actinic light" source

(400 μmol m^{-2} s^{-1}) was switched on, and the fluorescence yield started to increase. When it became stable after about 150 s we recorded it as steady-state fluorescence yield (F_s). Afterwards, the leaf was again irradiated with a pulse of the saturating beam and the maximum light-adapted fluorescence yield (F_m') was determined. Finally, the minimum light-adapted fluorescence yield (F_0') was detected by turning off the "actinic light"and 3 s later switching on the far-red radiation source for 5 s. The maximum photochemical efficiency of photosystem 2 (PS2) was calculated as $F_v/F_m = (F_m - F_0)/F_m$. The non-photochemical quenching coefficient was calculated as $NPQ = (F_m/F_m' - 1)$ (Bilger and Björkman 1990), where F_m was the value measured at dawn. A decrease of the F_v/F_m value indicates the occurrence of photoinhibition of photosynthesis, while an increase of the F_0 value indicates either reversible inactivation or destruction of the reaction centres of PS2 (Chow 1994).

Leaves were sampled from seedlings around 09:30, and immediately frozen at –20 ºC. On the same day, H_2O_2 (following the method of Lin *et al*. 1988) and MDA contents (following Wang *et al*. 1986) of the leaves were determined. We extracted leaf H_2O_2 with cold acetone, then made the extract to react quantitatively with titanium tetrachloride and ammonia to produce peroxide-Ti complex. We collected the complex through centrifuging, washed it with cold acetone for five times, finally dissolved it in 1 M sulphuric acid. We measured absorbance of the solution at 410 nm, then calculated H_2O_2 content according to standard curve. We extracted leaf MDA with 10 % trichloroacetic acid, then made the extract to react quantitatively with 2-thiobarbituric acid at boiling water incubation for 20 min. We collected the suspension through centrifuging, then determined the absorbances at 532 and 600 nm. MDA content was computed with 155 as the extinction coefficient of MDA at 532 nm. As mentioned above, several reactive oxygen species can be produced in chilled leaves. Only H_2O_2 was measured in this study due to its direct effect on photosynthesis, and it was easier to detect than other reactive oxygen species. All physiological and biochemical measurements were also taken during the 3 d of the CN treatment and the following 3 d afterwards.

Results

Under the same daylight, *Calophyllum* usually had much lower P_N, g_s, CE, and P_r than *Linociera* (Fig. 1*A–L*). CN induced reductions in these characteristics for both species, and its adverse effects on the four parameters increased with the increase of CN. The reductions in CE were greater for *Calophyllum* than for *Linociera* (Fig. 1 *G–I*), while the reduction in P_N and g_s showed the reverse pattern, especially in the early afternoon (Fig. 1 *A–F*). Under CN and high daylight treatments, early afternoon P_N and g_s in *Linociera* were lower even than in *Calophyllum* (Fig. 1*A, B, D*). After termination of the CN treatment, both species showed recovery in the four parameters (Fig. 1*A–L*). After 3-d-recovery, the four parameters increased to nearly pre-treatment values, except for P_N of *Linociera* under 50 % daylight. P_N and g_s were significantly less in the early afternoon than in the morning for both species on the days of the chilling treatment and recovery (Fig. 1*A–F*), but the differences were much greater in *Linociera* than in *Calophyllum*. The reductions induced by CN in P_N, g_s, CE, and P_r increased with increasing daylight (Fig. 1*A–L*), which suggested that shading could mitigate CN adverse effects on tropical seedling in Xishuangbanna.

The diurnal change patterns of F_v/F_m (Fig. 2*A–C*) were opposite to those of incident PFD (data not shown) for both species without the chilling treatment on a clear day. F_v/F_m decreased with the increase of PFD in the morning, and increased with the decrease of PFD in the afternoon, but the lowest values of F_v/F_m occurred about 2 h later than the highest PFD. The F_v/F_m reductions in each species increased with increasing irradiance, and were larger for *Calophyllum* than for *Linociera* at each irradiance (Fig. 2*A–C*). Diurnal fluctuations of F_v/F_m were very small for both species grown under 8 % daylight. Diurnal reduction of F_v/F_m indicated occurrence of dynamic (reversible) photoinhibition. CN increased the diurnal fluctuations of F_v/F_m (data not shown), and its adverse effect on F_v/F_m was small at 8 % daylight.

CN resulted in reduced dawn and midday F_v/F_m values for both species under all irradiances (Fig. 3*A–D*). The lower dawn and diurnal F_v/F_m values indicated occurrence of chronic and dynamic photoinhibition (Long *et al*. 1994). Photoinhibition was exacerbated with the increase of the CN and the daylight regimes. Decreasing daylight alleviated CN effects on F_v/F_m. Under 25 and 50 % daylights, *Calophyllum* displayed more severe chilling induced photoinhibition than *Linociera*. After termination of CN, both species showed recovery from the chilling induced photoinhibition, indicated by the increase of dawn and midday F_v/F_m values. Three days later, the dawn and midday F_v/F_m of both species had nearly recovered to the values of the control plants.

Under all three irradiances, dawn and midday F_0 values for both species increased with the amount of CN (Fig. 3*E–H*), indicating occurrence of reversible inactivation or irreversible destruction of PS2 reaction centres. After the chilling treatment, F_0 gradually decreased and reached the pre-treatment levels on the third day of recovery. With increasing daylights, dawn and midday F_0 values of both species increased. The increase in F_0 in relation to irradiance was more pronounced during the chilling treatment. In *Linociera* seedlings grown under 25 and 50 % daylight, the midday values of F_0 were higher than the dawn values. However, *Calophyllum* showed

a reverse pattern; the CN induced a greater increase in dawn F_0 compared to the midday values. Furthermore, dawn F_0 of *Calophyllum* seedlings in 50 % daylight were substantially higher than the midday values on the third day of chilling treatment.

Diurnal changes in NPQ (Fig. 3*I–L*) coincided with the changes of incident PFD (data not shown). CN treatment resulted in an increase in NPQ for both species under all growth irradiances. As the numbers of chilling nights increased, the NPQ became greater. For *Calophyllum*, after termination of the CN treatment, midday NPQ decreased each day, and reached pre-treatment levels after 3 d of recovery, but dawn NPQ values were still higher than pre-treatment levels. In contrast, during the 3 d recovery *Linociera* had only a slow decrease in midday NPQ for seedlings grown under 8 and 25 % sunlight,

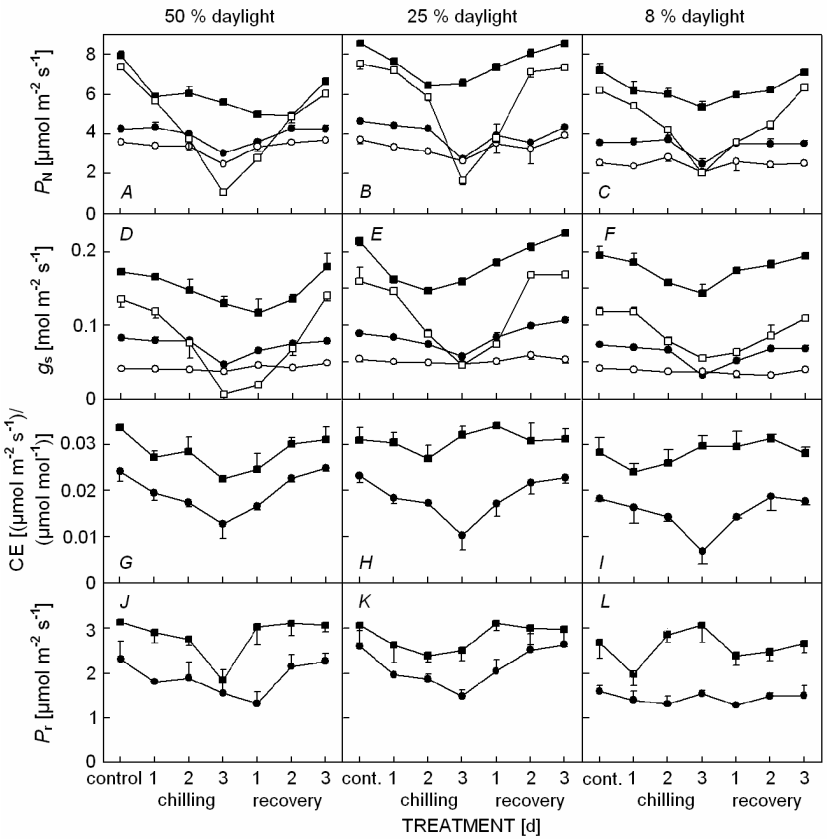

Fig. 1. Morning (*filled symbols*) and early afternoon (*open symbols*) values of photosynthetic rate, P_N (*A, B, C*), stomatal conductance, g_s (*D, E, F*), carboxylation efficiency, CE (*G, H, I*), and photorespiration, P_r (*J, K, L*) in *Linociera insignis* (*squares*) and *Calophyllum polyanthum* (*circles*) grown under 8, 25, and 50 % daylight. Measurements were taken before the night chilling treatment (control), on three days with night chilling treatment (chilling 1–3), and during three days of recovery (recovery 1–3). Mean ± SE (n = 3–5).

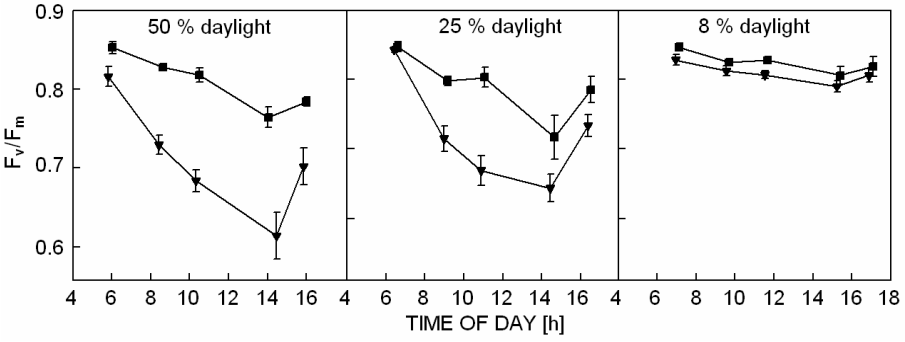

Fig. 2. Diurnal fluctuations of maximum photochemical efficiency of photosystem 2, F_v/F_m for *Linociera insignis* (*squares*) and *Calophyllum polyanthum* (*circles*) grown under 50 (*A*), 25 (*B*), and 8 (*C*) % daylight, detected on a clear day before night-chilling treatment. Mean ± SE (n = 3–5).

and had continued increase in NPQ under 50 % sunlight. *Linociera* had higher NPQ than *Calophyllum* at each irradiance.

The contents of H_2O_2 and MDA increased with increasing numbers of chilling nights for both species (Fig. 4*A–F*). Over the 3-d recovery, H_2O_2 and MDA contents decreased, but for *Calophyllum* they were still higher than pre-treatment values on the 3rd d of recovery. H_2O_2 and MDA contents for *Linociera* were not measured on the 3rd d of recovery. H_2O_2 and MDA contents increased with daylight for both species. Under each irradiance, *Calophyllum* had markedly higher contents of H_2O_2 and MDA than *Linociera*.

Discussion

CN induced depression of P_N during the subsequent day for both studied species (Fig. 1*A–C*), which is consistent with previous studies (Martin *et al*. 1981, Flexas *et al*. 1999, Allen *et al*. 2000). Chilling-induced reductions of P_N and g_s were greater in *Linociera* than in *Calophyllum* (Fig. 1*A–F*). In contrast, chilling-induced reduction of CE was greater in *Calophyllum* than in *Linociera* (Fig. 1*G–I*). These results indicated that CN induced mainly stomatal limitation of photosynthesis in *Linociera*, and non-stomatal limitation in *Calophyllum*. Stomatal control in response to chilling has been found in many chilling-sensitive plants such as tomato (Martin *et a*l. 1981), grape (Flexas *et al*. 1999), and mango (Allen *et al*. 2000). Reduced g_s or closure of stomata on the day following CN was beneficial to plants because transpiration was reduced and plant water balance was maintained, as water absorption from the soil by roots and the hydraulic conductivity of plants were adversely affected by CN. Some plants vulnerable to chilling were unable to close stomata in response to an abrupt decrease to chilling temperatures, resulting in excessive water loss and possibly leaf wilting (Pardossi *et al*. 1992, Wilkinson *et al*. 2001).

The high H_2O_2 and MDA contents (Fig. 4*A-F*) in *Calophyllum* could be the partial causes of its strong reduction in P_N and CE during CN treatment. Both reactive oxygen species and MDA could suppress the activity of photosynthetic enzymes. CN decreased ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBPCO) activity in *Calophyllum* and *Amomum villosum* (Liang *et al*. 2004) judged by decreased CE. CN disrupted circadian rhythms of the activity of sucrose phosphate synthase and nitrate reductase in tomato (Jones *et al*. 1998), and of the gene expression of chlorophyll binding protein and RuBPCO activase (Martino-Cart and Ort 1992). Low temperature could also inhibit leaf starch mobilization at night (for review see Leegood and Edwards 1996), which could lead to feedback inhibition of photosynthate to photosynthesis by reducing return of inoirganic phosphate

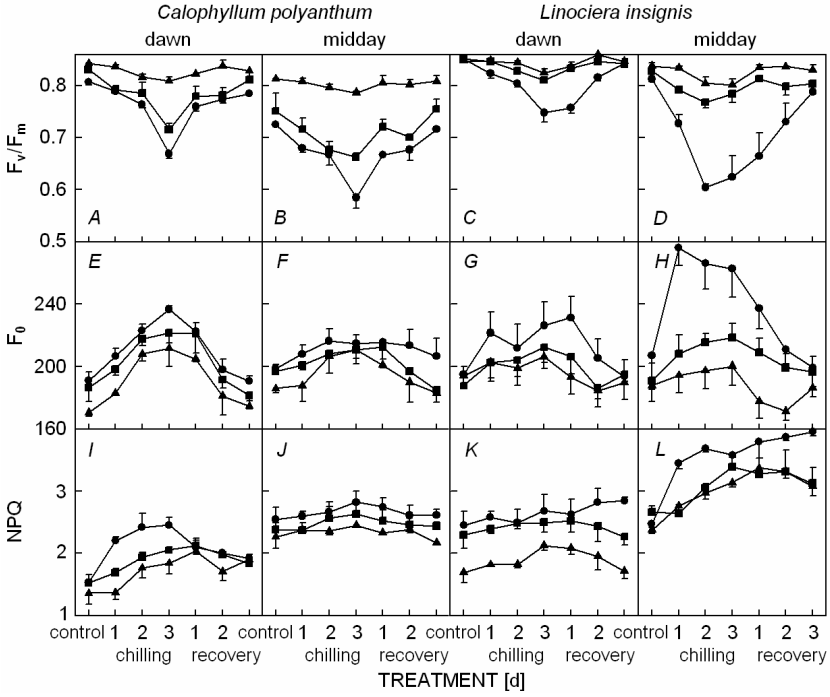

Fig. 3. Dawn and midday values of maximum photochemical efficiency of photosystem 2, F_v/F_m (*A-D*), non-photochemical quenching coefficient, NPQ (*E-H*), and minimum fluorescence yield, F_0 (*I-L*) in *Calophyllum polyanthum* and *Linociera insignis* grown under 8 (*triangles*), 25 (*squares*), and 50 (*circles*) % daylight. Measurements were taken before night chilling treatment (control), on three days with night chilling treatment (chilling 1–3), and during three days of recovery (recovery 1–3). Mean ± SE (n = 3–5).

to chloroplast (Stitt 1991). Non-stomatal limitation of photosynthesis could be associated with all these effects of CN.

Inhibition of photorespiration by CN in *Calophyllum* and *Linociera* (Fig. 1*J–I*) could further weaken their capacity for photoprotection. Along with the suppression of photosynthesis and CE, CN resulted in acceleration of dynamic and chronic photoinhibition (Fig. 3*A–D*; Nir *et al*.1997, Allen *et al*. 2000), and also increased dawn and midday values of NPQ and F_0 in both species (Fig. 3*E–L*). These patterns indicated that enhanced photoinhibition induced by CN was partly associated with increased thermal dissipation, and also with accelerated inactivation or destruction of PS2 reaction centres. Inactivation or destruction of PS2 reaction centres could produce an increase in F_0 (Chow 1994). Acceleration of predawn thermal dissipation after CN has been reported for various plant species (Adams and Baker 1998, Verhoeven *et al*. 1998). In the leaves of over-wintering plants under low night temperatures, transformation from zeaxanthin (Z) and antheranthin (A) to violaxanthin is impaired, and a high content of (Z+A)-dependent thermal dissipation is maintained overnight (Adams and Baker 1998, Verhoeven *et al*. 1998). This could be a cause of the low photochemical efficiency in many over-wintering evergreen plants (Adams *et al*. 1995, Egerton *et al*. 2000).

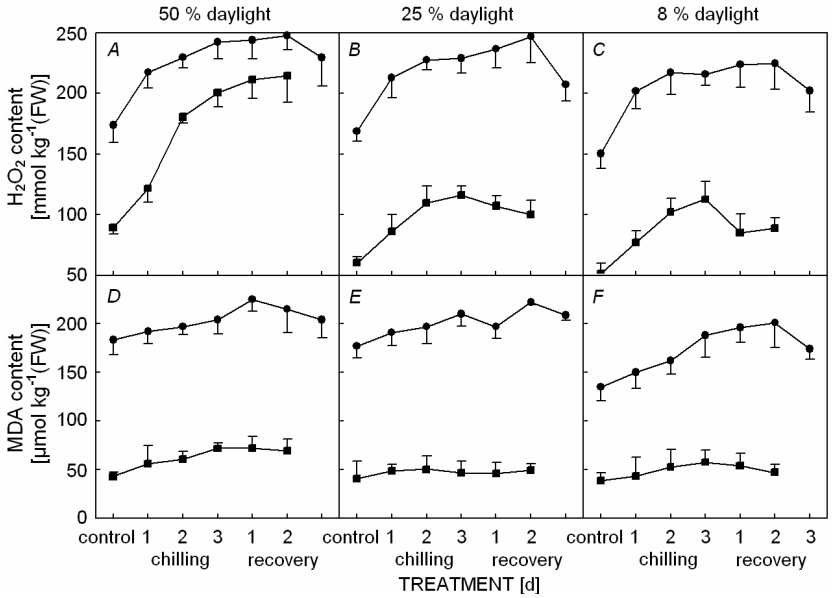

Fig. 4. Contents of H_2O_2 (*A, B, C*) and malondialdehyde, MDA (*D, E, F*) in *Linociera insignis* (*squares*) and *Calophyllum polyanthum* (*circles*) grown under 50, 25, and 8 % daylight, detected before night chilling treatment (control), on three days with night chilling treatment (chilling 1–3), and during three days of recovery (recovery 1–3). Mean ± SE (n = 3–5).

Calophyllum was more vulnerable to CN than *Linociera* as shown by its greater chilling-induced reduction in CE (Fig. 1*G-I*) and F_v/F_m (Fig. 3*A–D*), lower reduction in g_s (Fig. 1*D-F*), and higher MDA and H_2O_2 contents (Fig. 4*A-F*). Greater chilling-induced photoinhibition in *Calophyllum* could be related to lower photosynthetic (Fig. 1*A*) and thermal dissipation (Fig. 3*I–L*) rates compared to *Linociera*. Further, with or without chilling, *Calophyllum* always had much higher MDA and H_2O_2 contents than *Linociera* (Fig. 4*A–F*). It was likely that before the chilling treatment *Calophyllum* had already been subjected to decreased temperature in the winter season, illustrated by its low P_N and CE (Fig. 1*A–I*), low dawn F_v/F_m (Fig. 2*A*, 3*A*), and high MDA and H_2O_2 contents (Fig. 4*A–F*). The introduced fruit trees *Artocarpus altilis* (Parkinson) Fosberg and *Garcinia mangostana* L. grown in an open site in the Xishuangbanna Tropical Botanical Garden greatly reduced P_N and photochemical efficiency during a regular winter (unpublished data). The winter suppression did not occur in the native species *Artocarpus heterophyllus* Lam grown at the same site. Therefore, the physiology of some chilling sensitive tropical plants was affected by reduced temperatures in the cool season of this northern tropical area. With declining irradiance, chilling-induced photoinhibition became less severe (Fig. 3*A–D*), and the contents of MDA and H_2O_2 were lower (Fig. 4*A–F*). The shading treatments mitigated chilling-induced photoinhibition, as found in other studies (Allen *et al*. 2000, Egerton *et al*. 2000).

Every day during the winter season in Xishuangbanna, there is heavy fog cover from midnight until noontime of the following day. The fog blocks direct sun, thereby reducing the adverse effects of CN on tropical plants. However, due to deforestation in this region, the length of the foggy season and daily fog duration have been reduced (Liu and Li 1996). Moreover, global warming might make this region drier, shortening the lengths of daily foggy hours and the foggy season, which

might hurt species that are vulnerable to chilling temperatures and soil water deficit, leading to species composition changes in the tropical forests of the region. Once a severe cold front invades the region (often associated with clear days without fog), chilling susceptible species such as *Calophyllum* growing in gaps (high irradiance) would suffer from chilling induced photoinhibition and photooxidation. These stresses could result in reduced production, and a competitive disadvantage with adjacent plants that are little or not affected by chilling.

In summary, *Linociera* had much higher P_N than *Calophyllum*. CN resulted in a stronger depression of photosynthesis for *Linociera* than for *Calophyllum*. The depression of P_N was largely related to stomatal limitation for *Linociera*. On the other hand, night chilling induced stronger impairment of RuBPCO activity, more severe chronic photoinhibition of photosynthesis, and possibly more severe membrane injury for *Calophyllum* than for *Linociera*. Shading significantly mitigated adverse effect of CN for both species.

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