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REGULAR PAPER

The different effects of chilling stress under moderate light intensity on photosystem II compared with photosystem I and subsequent recovery in tropical tree species

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Abstract Tropical plants are sensitive to chilling temperatures above zero but it is still unclear whether photosystem I (PSI) or photosystem II (PSII) of tropical plants is mainly affected by chilling temperatures. In this study, the effect of 4°C associated with various light densities on PSII and PSI was studied in the potted seedlings of four tropical evergreen tree species grown in an open field, *Khaya ivorensis*, *Pometia tomentosa*, *Dalbergia odorifera*, and *Erythrophleum guineense*. After 8 h chilling exposure at the different photosynthetic flux densities of 20, 50, 100, 150 μmol m^{-2} s^{-1}, the maximum quantum yield of PSII (F_v/F_m) in all of the four species decreased little, while the quantity of efficient PSI complex (P_m) remained stable in all species except *E. guineense*. However, after chilling exposure under 250 μmol m^{-2} s^{-1} for 24 h, F_v/F_m was severely photoinhibited in all species whereas P_m was relative stable in all plants except *E. guineense*. At the chilling temperature of 4°C, electron transport from PSII to PSI was blocked because of excessive reduction of primary electron acceptor of PSII. F_v/F_m in these species except *E. guineense* recovered to ~90% after 8 h recovery in low light, suggesting the dependence of the recovery of PSII on moderate PSI and/or PSII activity. These results suggest that PSII is more sensitive to chilling temperature under the moderate light than PSI in tropical trees, and the photoinhibition of PSII and closure of PSII reaction centers can serve to protect PSI.

Keywords Tropical trees · Photosystem I · Photosystem II · Photoinhibition · Recovery

Abbreviations

CEF	Cyclic electron flow
F_o	Minimum chlorophyll fluorescence
F_m	Maximum chlorophyll fluorescence
F_v/F_m	Maximum quantum yield of PSII
NPQ	Non-photochemical quenching
PSI	Photosystem I
PSII	Photosystem II
P_m	Maximal change of P700 signal upon quantitative transformation of P700 from the fully reduced to the fully oxidized state
qP	Photochemical quenching
Q_A	Primary quinone electron acceptor of PSII

Introduction

The chilling temperature above zero is the major limitation to the distribution of tropical plants to higher latitudes and altitudes. Due to the exacerbation of fragmentation of tropical forests and increasing demand on tropical hardwood timber, afforestation using tropical high-quality timber species in marginal tropical areas is presently under practice. Occasionally, cold winds invade these areas for several days and cause severe damage to the introduced tropical crops and plants (Zhang and Xu 2000; Zhou et al. 2008). The selection of relatively chilling-resistant

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high-quality timber species is urgently needed. However, the study on chilling sensitivity of typical tropical trees is basically lacking.

Tropical plants are especially sensitive to chilling temperatures above zero because of the photoinhibition induced by the chilling-and-light stress (Aro et al. 1993a; Zhang and Scheller 2004; Zhang and Xu 2000; Zhou et al. 2008). Photoinhibition is regarded as a decline of photosynthetic efficiency under the conditions in which the input of photons exceeds the requirement for photosynthesis (Powles 1984). Under high irradiances, photosystem II (PSII) is very sensitive while photosystem I (PSI) is relatively stable (Aro et al. 1993a; Barber and Andersson 1992; Prasil et al. 1992). However, both PSII and PSI activities were significantly inhibited in cucumber treated at 4°C with the illumination of 200 μmol m^{-2} s^{-1} for 5 h (Sonoike 1999). Generally, at a chilling temperature combined with low illumination PSI is selectively damaged whereas photoinhibition of PSII is negligible in cold-sensitive species as cucumber (Terashima et al. 1994) and potato (Havaux and Davaud 1994). In cold-tolerant species such as barley (Teicher et al. 2000; Tjus et al. 1998, 1999) and winter rye (Ivanov et al. 1998), photoinhibition of PSI induced by chilling-and-light stress has also been reported. However, the photoinhibition of both PSI and PSII could not be induced by chilling in the dark as photoinhibition is induced by excess light energy which can induce photooxidation to the photosynthetic apparatus (Sonoike 1999; Zhang and Scheller 2004). Although light is an essential factor for photoinhibition of PSI, a chilling temperature plays a crucial role in causing its photoinhibition (Sonoike 1999). It is still unclear whether PSII or PSI in tropical plants is mainly affected by chilling temperatures associated with light.

The degree of photoinhibition is not only dependent on the extent of the gross damage to the photosynthetic apparatus but also the capacity for recovery. The chilling-induced photoinhibition of PSII in *Arabidopsis* can be completely repaired after 8 h recovery under a low light at 20°C (Zhang and Scheller 2004). The quick recovery of PSII photoinhibition is largely attributable to the fast turnover of D1 which is a marker protein of PSII activity (Aro et al. 1993a, b). The D1 synthesis has been proposed to occur during the PSII repair cycle (Adir et al. 1990; Aro et al. 1993a; Guenther and Melis 1990), and the other subunits of the PSII complex can be reused during the repair process (Barbato et al. 1992; van Wijk et al. 1995). However, the PSII repair cycle and the degradation and *de novo* synthesis of D1 protein were blocked at 4°C (Salonen et al. 1998). Studies on barley and *Arabidopsis* have indicated that PSI recovery from photoinhibition is a slow process (Teicher et al. 2000; Zhang and Scheller 2004) and needs several days. The slow recovery of PSI mainly due to all PSI core subunits is degraded more or less simultaneously, and almost no parts of the damaged complexes can be reused (Zhang and Scheller 2004).

Several protection mechanisms are contributive to prevent photoinhibition, such as cyclic electron flow around PSI (CEF) and non-photochemical quenching (NPQ) to dissipate excess absorbed light energy (Kim et al. 2001; Niyogi 1999). The development of CEF and NPQ in tobacco is affected by growth light. High-light plants showed a larger activity of CEF and a stronger NPQ than low-light plants (Miyake et al. 2005). Because of the important roles of CEF and NPQ in protecting plants from photoinhibition, the experiments involved in the photoinhibition induced by chilling-and-light stress should consider the growth light intensity. However, in the previous studies on the chilling effect on PSI almost all plant materials were grown at weak or moderate light of about 100–300 μmol m^{-2} s^{-1}. Little is known about the effect of chilling-and-light on PSI and PSII in plants grown at high light.

In this study, we investigated the effect of chilling associated with various ambient light intensities on PSI and PSII and subsequent recovery in seedlings of four tropical hardwood timber species grown in an open field in a marginal tropical area, of which three species are introduced from low tropics and one species is native. The following questions were addressed: (1) Is the chilling temperature of 4°C under moderate light harmful to the photosynthetic apparatus of the four tropical timber species? This temperature is close the extreme low temperature found in the study area. (2) Is PSI more sensitive to chilling-and-light stress than PSII in these tropical trees? (3) Is there any difference in relative sensitivity of PSI and PSII to this chilling temperature associated with different ambient light intensities?

Materials and methods

Plant materials

The following four evergreen tropical tree species were chosen for this study. *Khaya ivorensis* A. Chev (Meliaceae) is a large canopy species found in various habitat types in west and central tropical Africa but is most abundant in wet undisturbed evergreen forests. *Pometia tomentosa* (Blume) Teijsm. & Binn (Sapindaceae) is a dominant canopy species of tropical rain forests native to Sri Lanka, Indonesia, and southern Yunnan, China. *Dalbergia odorifera* T. Chen (Fabaceae) is native to the Hainan island of China and a light-demanding tree species that inhabits secondary forests. *Erythrophleum guineense* G. Don (Fabaceae) is a large canopy species native to tropical Africa. All of these species produce high-quality timber and their seedlings exhibit good growth performance in the Xishuangbanna

tropical botanical garden (21°54′N, 101°46′E) that is located in the northern boundary of the tropical zone. The potted and 2-year-old seedlings of the four species were raised in an open field. The photosynthetic flux density (PFD) over these seedlings during normal growth and the day–night cycle length are indicated in Fig. 1. The highest PFD on midday is up to 1,850 μmol m^{-2} s^{-1} in summer and 1,350 μmol m^{-2} s^{-1} in winter.

Photoinhibitory treatment and recovery condition

The chilling experiment and physiological measurements were conducted during January and February (the coldest months of a year) in 2009 and 2010. During this period, the outdoor air temperatures at night and noon are ~10 and ~25°C, respectively. Three to six seedlings of each species were placed in a cool room at 4°C with the marked leaves illuminated under a photosynthetic flux density (PFD) of 250 μmol m^{-2} s^{-1} for 24 h, and then transferred to an outdoor shadow site for recovery. During the initial 8 h recovery, the PFD was 100–200 μmol m^{-2} s^{-1} and the air temperature was ~23°C. From 8 to 24 h recovery, these seedlings were exposed to weak light or in the darkness with the temperature varied from ~13 in the night to ~23°C during the day. For each species, four to eight detached leaves placed on wet tissue papers were chilled at 4°C under the PFDs of 20, 50, 100, 150 μmol m^{-2} s^{-1} for 8 h, respectively, for determination of effect of low light under chilling on PSII and PSI.

Chlorophyll fluorescence measurements

At various time intervals during the chilling treatment and the recovery, the in vivo chlorophyll fluorescence of PSII was measured by Dual PAM-100 (Heinz Walz, Effeltrich, Germany) connected to a computer with control software. The following parameters were calculated: maximum quantum yield of PSII $= F_v/F_m = (F_m - F_o)/F_m$ and $(1 - qP) = (F'_s - F'_o)/(F'_m - F'_o)$, where F_o and F'_o is the minimum fluorescence in the dark-adapted state and light-adapted state respectively, and F_m and F'_m is the dark-adapted and light-adapted maximum fluorescence upon illumination of pulse (600 ms) of saturating light (10,00 μmol m^{-2} s^{-1}). F'_s is the steady-state fluorescence after light adaptation. F_o and F_m were determined after 15 min dark-adaptation.

Photochemical quenching, qP, is usually used as an indicator of the redox level of the primary quinone electron acceptor of PSII (Q_A). Photoinhibition is strongly correlated with the redox state of Q_A (Huner et al. 1996; Oquist et al. 1993). The parameter 1 − qP can be used to indicate the excitation pressure in PSII or the proportion of closed PSII reaction centers. Therefore, the difference in 1 − qP light response curves between 25 and 4°C is very useful for the understanding of the photoinhibition of PSI and PSII. Six to eight untreated detached leaves were light-adapted (450 μmol m^{-2} s^{-1}) for 10 min before measurement of 1 − qP light response curve, and qP was recorded after 2 min exposure to each of the PFDs (27, 58, 100, 131, 221, 344, 536, 830 μmol m^{-2} s^{-1}). The chlorophyll fluorescence measured at 4°C was corrected to that at 25°C according to the equation,

$$\text{F\_standard}\ (T) = -0.003106 \times \text{temperature (in K)} + 1.932.$$

P700 measurement

At various time intervals during the chilling treatment and the recovery, the maximal P700 changes (P_m) were determined with saturation pulses using Dual PAM-100. The leaves were dark-adapted for 15 min before the measurement. After far-red preillumination for 10 s, P_m was determined through the application of a saturation pulse. It represents the maximal change in P700 signal upon quantitative transformation of P700 from the fully reduced to the fully oxidized state. At a defined optical property, the amplitude of P_m depends on the maximum amount of photo-oxidizable P700, which is a good parameter for representing the quantity of efficient PSI complex.

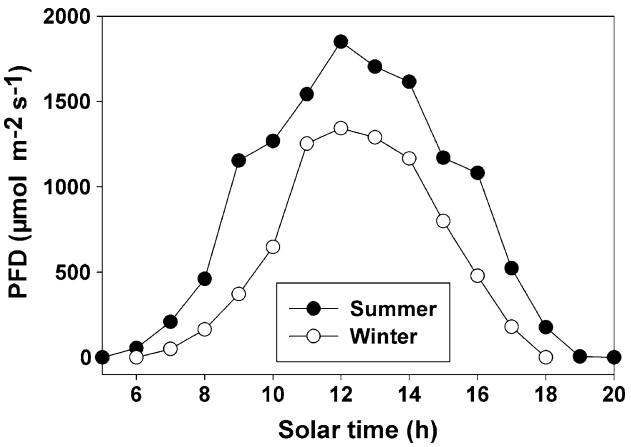

Fig. 1 Diurnal change in photosynthetic flux density (PFD) during a representative clear day in the summer and winter, respectively, recorded by Xishuangbanna Station for Tropical Rain Forest Ecosystem Studies (XSTRE) (100 m away from the nursery garden)

Results

Photoinhibition and subsequent recovery of PSII activity

During the treatment with chilling temperature under moderate illumination (4°C and 250 μmol m^{-2} s^{-1}) for

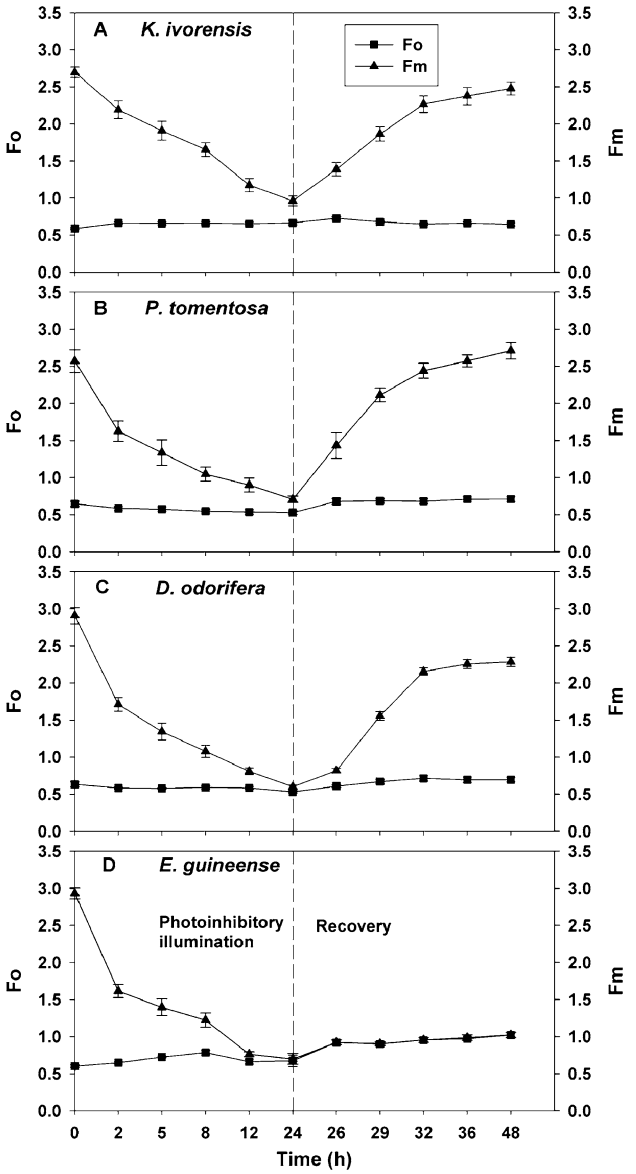

Fig. 2 Changes in F_o and F_m in the four species during the chilling treatment at 4°C under the photosynthetic flux density of 250 μmol m^{-2} s^{-1} and subsequent recovery under natural shade condition. The mean ± SE were calculated from three to six plants

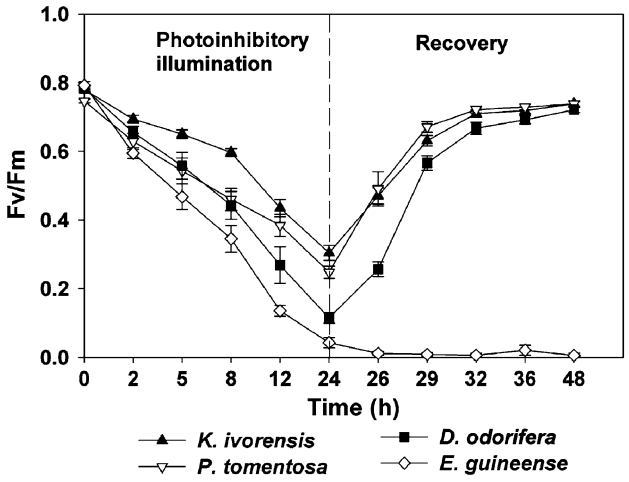

Fig. 3 Changes in F_v/F_m in the four species during the chilling treatment at 4°C under the photosynthetic flux density of 250 μmol m^{-2} s^{-1} and subsequent recovery under natural shade conditions. The mean ± SE were calculated from three to six plants

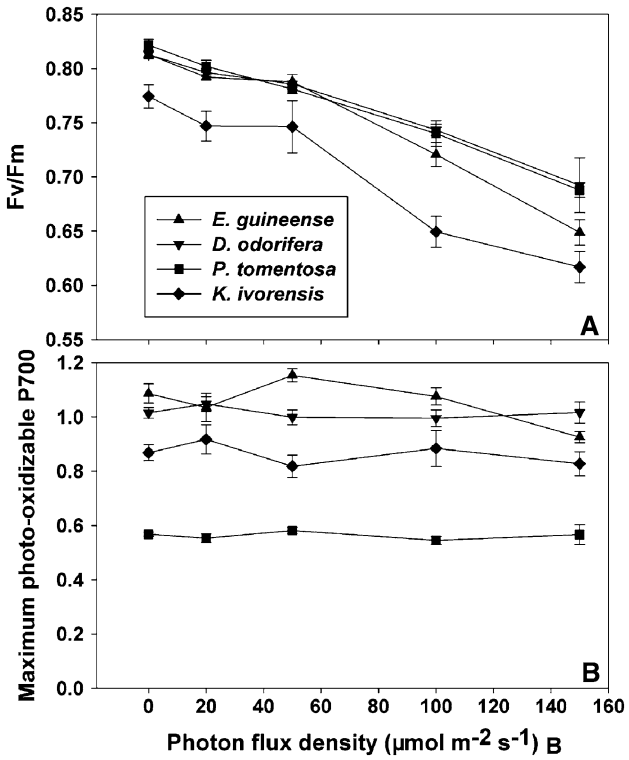

Fig. 4 The effects of chilling under different photosynthetic flux densities (PFDs) for 8 h on F_v/F_m and the maximum photo-oxidizable P700 of the four tropical tree species. Leaf samples placed on wetter paper were exposure to the chilling temperature of 4°C under the PFDs of 20, 50, 100, and 150 μmol m^{-2} s^{-1}. The mean ± SE were calculated from four to eight detached leaves from four to eight independent plants

24 h, F_o varied little in all species except *E. guineense* in which F_o slightly increased (Fig. 2). F_m progressively and strongly decreased during the chilling treatment, by 64% in *K. ivorensis*, 73% in *P. tomentosa*, 79% in *D. odorifera*, and 76% in *E. guineense* after 24 h exposure to the chilling-and-light stress (Fig. 2). Consequently, the maximum quantum yield of PSII (F_v/F_m) after 24 h the chilling stress was reduced by 62% in *K. ivorensis*, 67% in *P. tomentosa*, 85% in *D. odorifera*, and 95% in *E. guineense* (Fig. 3). In contrast, no inhibition of F_v/F_m was observed in these four species treated with 4°C in darkness for 24 h (data not show).

After 8 h exposure to the chilling temperature of 4°C under the different PFDs of 20, 50, 100, and 150 μmol m^{-2} s^{-1}, F_v/F_m showed much slighter decrease (Fig. 4a) than 8 h

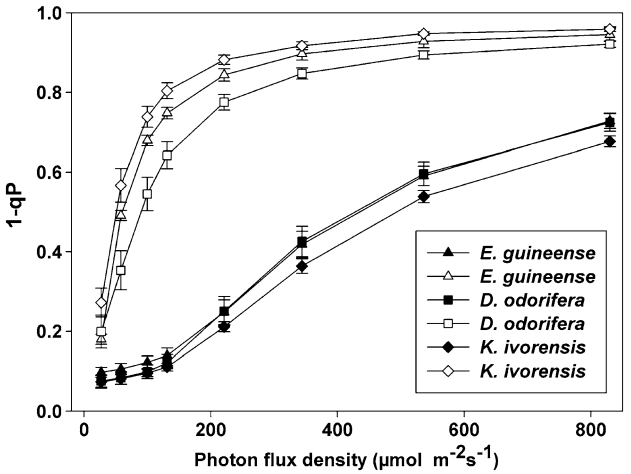

Fig. 5 Difference in the light response changes of 1 − qP at 4°C (*open symbols*) and 25°C (*closed symbols*) among three tree species. The mean ± SE were calculated from six to eight plants

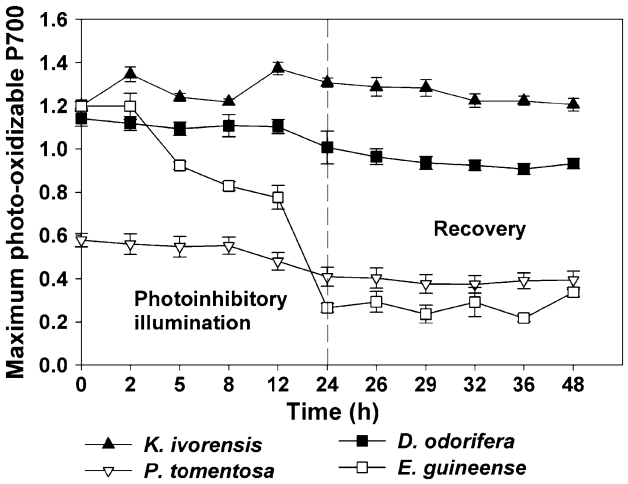

Fig. 6 Changes in maximum photo-oxidizable P700 in the four species during the chilling treatment at 4°C under the photosynthetic flux density of 250 μmol m^{-2} s^{-1} and subsequent recovery under natural shade conditions. The mean ± SE were calculated from three to six plants

chilling exposure under 250 μmol m^{-2} s^{-1}, but with an increased inhibition with the irradiance intensity. The inhibition of F_v/F_m is no more than 20% even under 150 μmol m^{-2} s^{-1} in *E. guineense* (Fig. 4a).

During the recovery, F_o attained higher values than during the chilling treatment in the four species, especially in *E. guineense* (Fig. 2); F_m showed a progressive and rapid significant increase in these species except *E. guineense*, in which F_m remained at a very low level (Fig. 2). After experiencing the severe photoinhibition of PSII in *K. ivorensis*, *P. tomentosa*, and *D. odorifera*, the F_v/F_m values were recovered to 91, 97, and 85% of their original values, respectively, under a low light (100–200 μmol m^{-2} s^{-1}) condition for 8 h (Fig. 3). However, the same as the case of F_m, no recovery of F_v/F_m in *E. guineense* was observed (Fig. 3). The treated leaves of this species died several days later.

We used 1 − qP to indicate the excitation pressure in PSII or the proportion of closed PSII reaction centers. The light response curves showed that the excitation pressure of PSII at 4°C was much higher than at 25°C in three species especially under PFDs (Fig. 5). At 4°C, the excitation pressure rapidly increased with PFD at low light and reached the values between 0.65 and 0.8 among the three species at the PFD of 131 μmol m^{-2} s^{-1}. In contrast, at 25°C this increased much slowerly than at 4°C but progressively with PFD and reached about 0.7 or so at the PFD of 830 μmol m^{-2} s^{-1}.

Photoinhibition and subsequent recovery of PSI activity

After 24 h chilling exposure under the PFD of 250 μmol m^{-2} s^{-1}, the quantity of efficient PSI complex (P_m) decreased by 78% in *E. guineense*, but by 29% in *P. tomentosa*, and only 12% in *D. odorifera* (Fig. 6). In *K. ivorensis* an unexpected result was observed, P_m increased slightly during the chilling-and-light treatment (Fig. 6). However, P_m in the four species showed no decrease after 2 h the chilling-and-light treatment and even maintained stable after 8 h the chilling treatment in all species except *E. guineense*. There were no changes in P_m with 24 h treatment at 4°C in the dark for all of the four species (Fig. 7).

After 8 h chilling treatment under the different constant low PFDs of 20, 50, 100, and 150 μmol m^{-2} s^{-1}, P_m remained stable in the four species except *E. guineense* (Fig. 4b). In this latter species, P_m decreased by 14% after

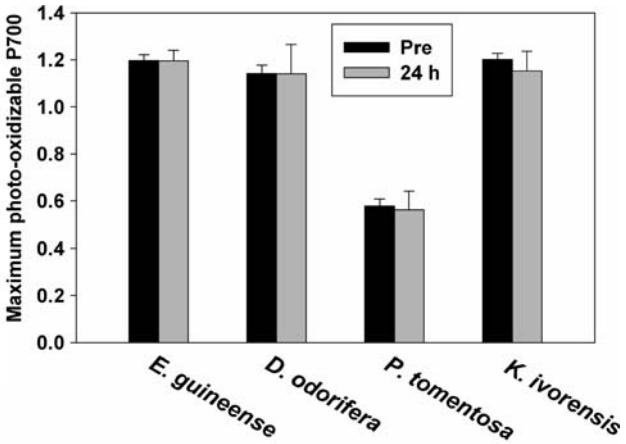

Fig. 7 Changes in maximum photo-oxidizable P700 in the four species after the 24 h the dark-and-chilling treatment. *Black bars* denote the values for pretreatment, and *gray bars* denote the values upon 24 h chilling treatment. The mean ± SE were calculated from three to six plants

8 h chilling treatment associated with the PFD of 150 μmol m^{-2} s^{-1} (Fig. 4b).

The severe photoinhibition of PSI in *E. guineense* induced by the chilling treatment under 250 μmol m^{-2} s^{-1} for 24 h was not followed by any recovery after 24 h under the favorable condition (Fig. 6). During the recovery for 24 h the changes in P_m in other species were very small while P_m in *E. guineense* was maintained at the very low level (Fig. 6).

Discussion

Photoinhibition of PSII and PSI

The maximum PSII quantum yield (F_v/F_m) in all of the four tropical tree species was photoinhibited strongly by the chilling treatment under the PFD of 250 μmol m^{-2} s^{-1} (Fig. 3). This is in contrast with the previous studies that indicated that PSII was slightly photoinhibited by chilling-and-light stress in several chilling-sensitive species such as cucumber, potato, and *Arabidopsis* (Havaux and Davaud 1994; Terashima et al. 1994; Zhang and Scheller 2004). Our results indicated that the decrease in F_v/F_m in the four plant species during the chilling-light treatment was mainly due to the quenching of F_m (Fig. 2), which is the characteristic of photoinhibition (Briantais et al. 1988). The strong decrease in F_m indicates that the PSII cooperativity was inhibited and a large proportion of PSII reaction centers were destroyed (Krause and Weis 1991). Although the persistency of NPQ for hours in the dark could result in decrease of F_v/F_m as reported in *Aegialitis annulata* which has limited carbon-fixation capacity (Gilmore and Bjorkman 1995), the four species in this study have high carbon-fixation capacity. Furthermore, the fact of little inhibition of F_v/F_m after 8 h chilling treatment under the different low PFDs of 20, 50, and 100 μmol m^{-2} s^{-1} in the four species indicated that the decrease in F_v/F_m in the present four species could be resulted from photodamage but not from persistency of NPQ. The photodamage of PSII is related to degradation of D1 protein, which was not measured in this study. However, the previous study showed that the decrease of F_v/F_m was closely accompanied by decrease in D1 protein content (Tyystjarvi and Aro 1996).

Our results indicated that after cold acclimation by natural low temperature in the marginal tropical area, PSII of the four tropical tree species was not susceptible to chilling treatment under low light intensity (0–150 μmol m^{-2} s^{-1}). This contradicts the previous findings on that PSII of chilling-sensitive plant species were very sensitive to chilling stress even associated with low temperature (Terashima et al. 1994; Sonoike 1999). We speculated that the high growth light intensity and the cold acclimation by natural low temperature enhanced the resistance of the present four tropical species to chilling stress under low light.

The efficiency of PSI in all four species except *E. guineense* was little affected by the chilling treatment under the low PFDs (0–150 μmol m^{-2} s^{-1}, Fig. 4b). This contradicts the previous findings on that PSI in chilling-sensitive species were very sensitive to chilling temperature associated with low irradiance (Sonoike 1999; Sonoike and Terashima 1994; Terashima et al. 1994; Zhang and Scheller 2004). Apparently, the sensitivity of PSI to chilling-and-light stress varies among the present species. Not all species showed preferential sensitivity of PSI to chilling-and-light stress, such as tobacco (Barth and Krause 1999) and the three species in present study. The mechanism of photoinhibition of PSI itself may be different among plant species (Sonoike 2006). Since the electron flow from PSII is a necessary cause for the photoinhibition of PSI (Havaux and Davaud 1994; Sonoike 1995), the photoinhibition of PSII could be regarded as a mechanism to protect PSI from photodamage (Tjus et al. 1998). The insusceptibility of PSI to chilling stress under the low light in this study is largely attributable to the closure of PSII reaction centers (Fig. 5). Under the low light at 4°C, the primary acceptor of PSII, Q_A, was in excessively reduced state (Fig. 5) which led to blockage of linear electron flow from PSII to PSI, and thereby protecting PSI from photoinhibition. The plants of this study were grown in high light so that they probably well developed the protective mechanism of PSI such as cyclic electron transfer system, which is an important mechanism to alleviate the photoinhibition of PSI under the chilling stress (Miyake et al. 2005). Although the excessive closure of PSII reaction centers could protect PSI from photoinhibition, on the other hand, it resulted in severe photo-oxidative stress on PSII reaction centers.

The recovery of PSII and PSI

This study indicated that in three of the four tropical tree species, even with severe photoinhibition of PSII, its recovery could occur quickly (Fig. 3). This is in contrast with the slow recovery of PSII after chilling-induced photoinhibition in cucumber (Kudoh and Sonoike 2002), but similar to the case of *Arabidopsis* (Zhang and Scheller 2004). Kudoh and Sonoike (2002) reported that the recovery of PSII function after moderate chilling-induced photoinhibition took 4–5 days. The fast recovery of the maximum PSII quantum yield is likely to be due to the fast turnover of D1 protein which has half-times of 1–2 h (Sundby et al. 1993; Neidhardt et al. 1998) and the fact that most damaged PSII core subunits can be reused without de novo synthesis (van Wijk et al. 1995).

Erythrophleum guineense failed to recover from the severe photoinhibition of PSII induced by the chilling-and-

light stress (Fig. 3). Probably, one cause of this could be due to the severe photoinhibition of PSI, resulting in a loss of capacity for cyclic electron flow which might otherwise aid the repair of PSII, e.g. by providing ATP for biochemical reactions required to replace the damaged D1 protein by newly synthesized D1 (Taniguchi et al. 1993). The severe photoinhibition of PS II in *E. guineense* (Fig. 3) implied severely impaired linear electron flow. Linear electron flow sustained by residual functional PSII is important for recovery of photoinhibited PSII complexes for a number of reasons as summarized by Sun et al. (2006), e.g. provision of ATP, provision of reducing equivalents for the translational regulation of D1 protein, efficient translation of D1 protein, and integration of D1 protein into PSII reaction centers. Our results indicate that the low-light recovery from severe photoinhibition of PSII requires moderate activity of one or both photosystems.

The recovery of PSI was much slower than PSII, and the quantity of efficient PSI complex even slightly but progressively decreased during the initial 8 h of recovery (Fig. 6). This is consistent with findings from cucumber (Kudoh and Sonoike 2002) and *Arabidopsis* (Zhang and Scheller 2004). This progressive decrease during recovery could be explained by the fact that the inactivated PSI complex was not degraded at 4°C during treatment but degraded during recovery and the degradation of damaged chlorophyll after returning to normal growth temperature (Kudoh and Sonoike 2002; Zhang and Scheller 2004). It is suggested that all core subunits of inactivated PSI complex are degraded under normal temperature and no parts of the damaged complex can be reused (Zhang and Scheller 2004). Therefore, the complete recovery of the quantity of efficient PSI complex would need at least several days. The death of treated leaves of *E. guineense* indicated that the failure in the recovery of the quantity of efficient PSI complex would be fatal when severe photoinhibition of both PSI and PSII occurred simultaneously.

The above results revealed that *E. guineense* is not a suitable timber tree species for afforestation in subtropical and marginal tropical areas. Although the other three species showed much less chilling-induced photoinhibition of PSI than *E. guineense* and fast recovery of PSII after severe photoinhibition with the 24 h chilling treatment, an occasional chilling stress lasting 1 week or longer time may be fatal to these tree species because of the severe cumulative photoinhibition and continuous blockage of repair of damaged photosynthetic reaction centers. Severe chilling stress occasionally occurs in marginal tropical areas in southern China, and leads to the damage of some introduced tropical economic plants such as coffee (Zhang and Xu 2000) and mangosteen (Zhou et al. 2008). Therefore, afforestation using tropical tree species in marginal tropical areas must take into account their sensitivity to chilling stress. Our results suggest that the sensitivity of PSII to chilling-and-light stress is an important limitation to the distribution of tropical tree species to higher latitudes and altitudes.

In conclusion, the results of this study indicated that in these four tropical tree species PSII was more sensitive to chilling temperature under moderate light than PSI. Chilling temperature combined with darkness or low light (0–150 μmol m^{-2} s^{-1}) has no significant effect on PSI and PSII reaction centers in tropical tree species after fully cold acclimation. The severely photoinhibited PSII complexes can be quickly repaired in three of the four species and the recovery of the maximum quantum yield of PSII after severe photoinhibition was dependent on moderate activity of one or both photosystems. We conclude that the photoinhibition of PSII and closure of PSII reaction centers under chilling stress serve to protect PSI in tropical trees from chilling-and-light stress. The present results have important implications for the understanding of the chilling sensitivity of chilling-sensitive species under natural conditions.

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