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Stimulation of Cyclic Electron Flow During Recovery After Chilling-Induced Photoinhibition of PSII

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Although cyclic electron flow (CEF) is essential for repair of PSII, it is unclear whether the CEF is stimulated and what the role of stability of PSI is during the recovery. In order to explore these two questions, mature leaves of *Dalbergia odorifera* were treated with the chilling temperature of 4°C under a photosynthetic flux density (PFD) of 650 μmol m^{-2} s^{-1} for 2 h and then were transferred to 25°C under a PFD of 100 μmol m^{-2} s^{-1} for recovery. The maximum quantum yield of PSII (F_v/F_m), the maximum photo-oxidizable P700 (P_m), the energy distribution in PSII and the redox state of P700 at 25°C under a PFD of 100 μmol m^{-2} s^{-1} were determined before and after chilling treatment and during subsequent recovery. We found that the CEF was significantly stimulated during the recovery after photodamage. There is a significant positive correlation between stimulation of CEF and photodamage of PSII during recovery. Our results indicated that CEF was significantly stimulated in order to enhance the synthesis of ATP for the fast repair of PSII. The stability of PSI activity favored the fast repair of PSII activity through stimulation of CEF.

Keywords: Chilling temperature • Cyclic electron flow • Photoinhibition • PSII • Recovery.

Abbreviations: CEF, cyclic electron flow; F_v/F_m, maximum quantum yield of PSII; LEF, linear electron flow; PFD, photosynthetic flux density; Y(CEF), quantum yield of cyclic electron flow; Y(I), efficient quantum yield of PSI; Y(II), efficient quantum yield of PSII; Y(NA), PSI acceptor side limitation; Y(ND), PSI donor side limitation; Y(NO), quantum yield of non-regulated energy dissipation; Y(NPQ), quantum yield of regulated energy dissipation.

Introduction

Exposure of leaves to moderate light and chilling temperature led to selective photodamage of PSII of tropical trees grown under high light (Huang et al. 2010). After short-term chilling treatment under high light, the photodamage of PSII activity could be quickly repaired under low light in several hours (He and Chow 2003, Zhang and Scheller 2004, Huang et al. 2010). This is caused by the fast turnover rate of D1 protein, and the damaged PSII subunits could be repaired and reused for assembly of the PSII complex (Aro et al. 1993). The fast synthesis of D1 protein and repair of damaged PSII subunits needs a large amount of ATP in a short time (Allakhverdiev et al. 2005); however, the damage to PSII could decrease the linear electron flow (LEF) and then reduce the synthesis of ATP. Therefore, ATP should be synthesized through other pathways. A possible pathway is the stimulation of cyclic electron flow (CEF) around PSI during the recovery of PSII.

Our previous study indicated that PSII activity could not be recovered if PSI is severely photodamaged (Huang et al. 2010), but the role of the stability of PSI in the fast repair of PSII is unclear. PSI involves two modes of electron flow, LEF and CEF. CEF around PSI helps the build-up of a trans-thylakoid membrane proton gradient, and favors the synthesis of ATP (Heber and Walker 1992, Bendall and Manasse 1995) and the recovery of PSII (Allakhverdiev et al. 2005). We speculated that CEF was stimulated during the recovery in order to increase the synthesis of ATP. Since CEF involves the activity of PSI, perhaps the severe damage to PSI would inhibit the stimulation of CEF and then decrease the synthesis of ATP and therefore block the recovery of PSII.

In the present study, mature leaves of the tropical tree *Dalbergia odorifera* were treated with the chilling temperature of 4°C associated with a photosynthetic flux density (PFD) of 650 μmol m^{-2} s^{-1} for 2 h and then were transferred to 25°C and a PFD of 100 μmol m^{-2} s^{-1} for an 8 h recovery. The following question was addressed: is CEF stimulated during the recovery for the fast repair of PSII activity?

Results

Effects of chilling stress on PSI and PSII activities

PSII was very sensitive to the chilling temperature of 4°C associated with a PFD of 650 μmol m^{-2} s^{-1} whereas PSI activity

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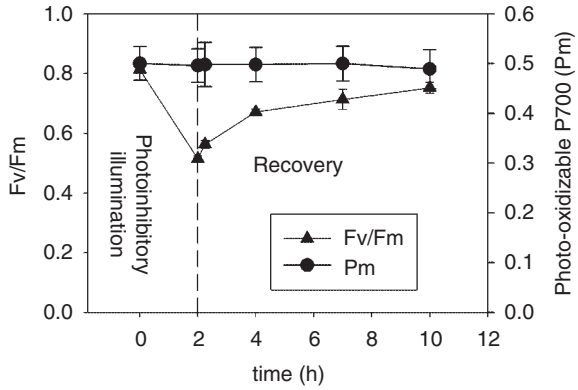

Fig. 1 Changes in F_v/F_m and maximum photo-oxidizable P700 (P_m) after a 2 h chilling treatment at 4°C and a photosynthetic flux density (PFD) of 650 μmol m^{-2} s^{-1}, and subsequent recovery at 25°C and a PFD of 100 μmol m^{-2} s^{-1}. The mean ± SE was calculated from three independent experiments.

was stable. After 2 h chilling treatment, the maximum quantum yield of PSII (F_v/F_m) decreased from 0.81 to 0.51, but the maximum photo-oxidizable P700 (P_m) did not decrease (**Fig. 1**). The quantum yield of thermal dissipation by non-functional PSII [Y(NF)] significantly increased to 0.25 after 2 h of chilling treatment (**Fig. 2A**). The yield of non-regulated energy dissipation [Y(NO)] at 25°C under a PFD of 100 μmol m^{-2} s^{-1} increased from 0.21 to about 0.45 after 2 h of chilling treatment (**Fig. 2B**). The value of the efficient quantum yield of PSII [Y(II)] at 25°C under a PFD of 100 μmol m^{-2} s^{-1} decreased from 0.73 to about 0.5 after 2 h of chilling treatment (**Fig. 2D**). The decrease in Y(II) induced by chilling treatment was mainly caused by a decrease in the maximum quantum yield, but not the coefficient of photochemical quenching (qP) (data not shown).

Recovery of PSII activity and stability of PSI activity

The F_v/F_m recovered rapidly, especially during the initial 2 h recovery. The F_v/F_m increased from 0.51 to 0.67 after a 2 h recovery and recovered to 0.75 after an 8 h recovery (**Fig. 1**). During the recovery, the quantity of maximum photo-oxidizable P700 remained very stable (**Fig. 1**). After 8 h of recovery, the quantum yield of dissipation by Y(NF) at 25°C decreased from 0.25 to 0.05 (**Fig. 2A**), the Y(NO) at 25°C under a PFD of 100 μmol m^{-2} s^{-1} decreased from 0.45 to 0.26 (**Fig. 2B**) and the yield of regulated energy dissipation [Y(NPQ)] increased from 0.04 to 0.14 (**Fig. 2C**). The Y(II) at 25°C under a PFD of 100 μmol m^{-2} s^{-1} increased from about 0.5 to 0.58 after a 2 h recovery and recovered to 0.6 after an 8 h recovery (**Fig. 2D**).

Changes in Y(CEF), Y(CEF)/Y(II) and the redox state of P700 during recovery

The CEF was significantly stimulated during the recovery. After a 2 h chilling treatment, the value of Y(CEF)/Y(II) at 25°C under a PFD of 100 μmol m^{-2} s^{-1} increased from 0.15 to 0.53 and the value of Y(CEF) increased from 0.11 to 0.27 (**Fig. 3**). The values of Y(CEF)/Y(II) and Y(CEF) decreased gradually

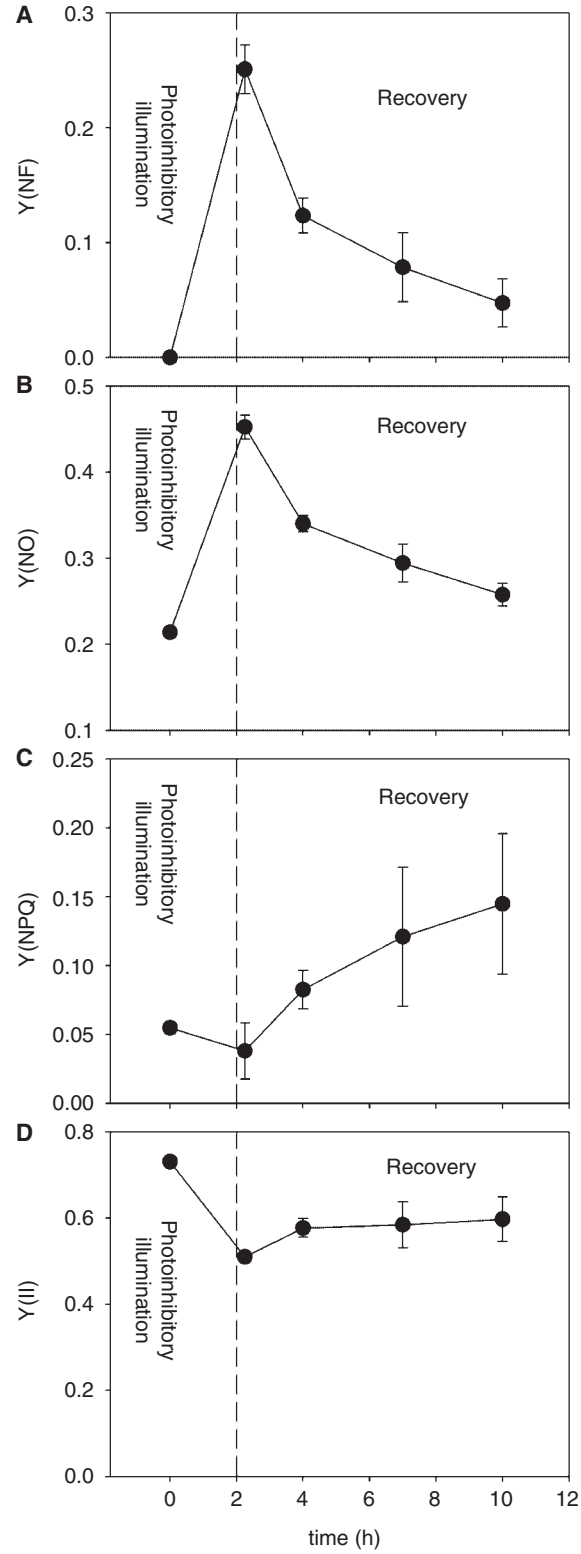

Fig. 2 Changes in Y(NF), Y(NO), Y(NPQ) and Y(II) at 25°C under a PFD of 100 μmol m^{-2} s^{-1} after a 2 h chilling treatment at 4°C and a PFD of 650 μmol m^{-2} s^{-1}, and subsequent recovery at 25°C and a PFD of 100 μmol m^{-2} s^{-1}. The mean ± SE was calculated from three independent experiments.

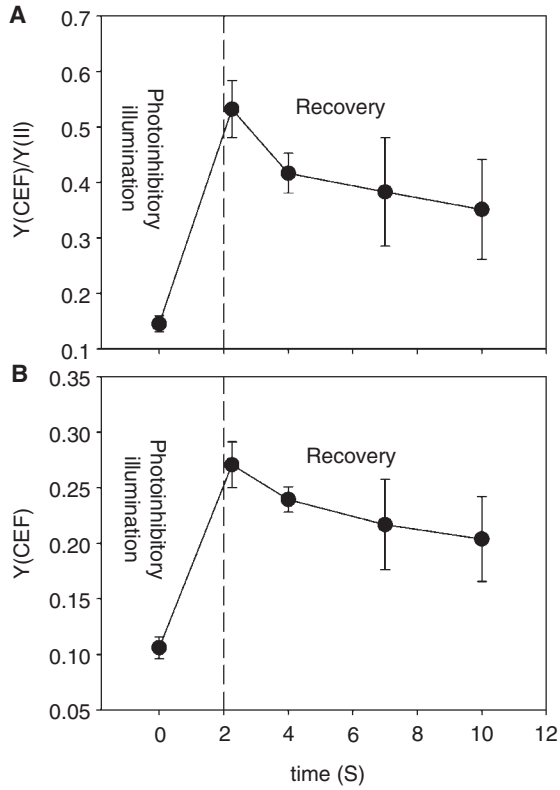

Fig. 3 Changes in Y(CEF) and Y(CEF)/Y(II) at 25°C under a PFD of 100 μmol m^{-2} s^{-1} after a 2 h chilling treatment at 4°C and a PFD of 650 μmol m^{-2} s^{-1}, and subsequent recovery at 25°C and a PFD of 100 μmol m^{-2} s^{-1}. The mean ± SE was calculated from three independent experiments.

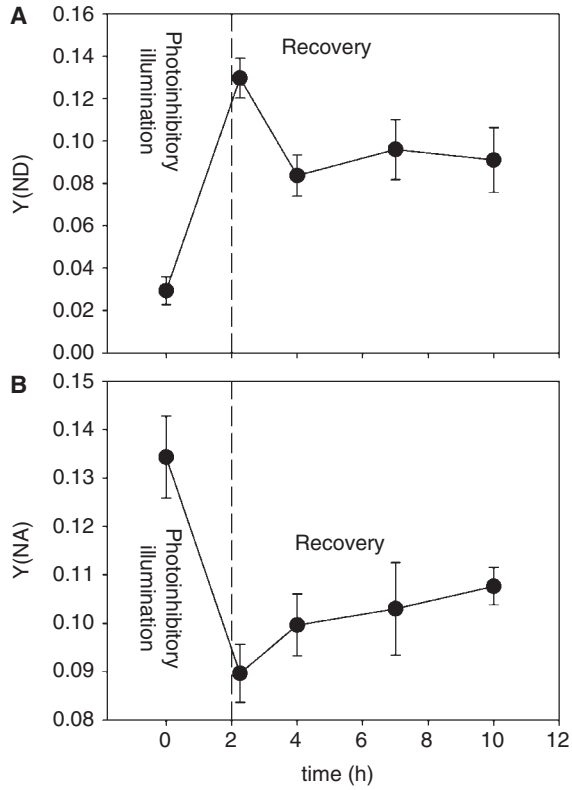

Fig. 4 Changes in Y(ND) and Y(NA) at 25°C under a PFD of 100 μmol m^{-2} s^{-1} after a 2 h chilling treatment at 4°C and a PFD of 650 μmol m^{-2} s^{-1}, and subsequent recovery at 25°C and a PFD of 100 μmol m^{-2} s^{-1}. The mean ± SE was calculated from three independent experiments.

with the recovery of PSII. PSI donor side limitation [Y(ND)] was higher during recovery compared with that before treatment. The value of Y(ND) at 25°C under a PFD of 100 μmol m^{-2} s^{-1} increased from 0.03 to 0.13 after a 2 h chilling treatment and decreased to 0.09 after an 8 h recovery (**Fig. 4A**). The value of Y(NA) at 25°C under a PFD of 100 μmol m^{-2} s^{-1} decreased from 0.134 to 0.09 after a 2 h chilling treatment and increased to 0.108 after an 8 h recovery (**Fig. 4B**).

Pooling the data obtained just after chilling treatment and during the recovery, Y(CEF), Y(CEF)/Y(II) and Y(NO) were strongly and negatively correlated with F_v/F_m (**Fig. 5A–C**). Y(CEF) was strongly and negatively correlated with Y(II) (**Fig. 6**).

Discussion

Stability of the PSI complex favors the fast recovery of PSII activity

After 2 h chilling treatment at 4°C under a PFD of 650 μmol m^{-2} s^{-1}, PSII was significantly inhibited whereas PSI remained very stable. During the recovery, PSII activity recovered quickly and no significant change occurred in PSI activity. Our previous study indicated that the stability of PSI activity contributes to the fast recovery of PSII activity (Huang et al. 2010), but the underlying mechanism is unclear. In our present study, we found that the stability of the PSI complex favors the stimulation of CEF which helps the generation of ATP that was used for the fast recovery of PSII. If the majority of PSI complexes were damaged and degraded, CEF could not be stimulated and the generation of ATP would be blocked, which would delay the complete recovery of PSII, even leading to death of leaves (Kudoh and Sonoike 2002, Huang et al. 2010). Our result showing the fast recovery of PSII is different from the slow recovery of PSII in cucumber leaves after chilling treatment reported by Kudoh and Sonoike (2002). In their study, cucumber was grown under low light of 190 μmol m^{-2} s^{-1} and PSI was severely damaged after 12 h chilling treatment. Since CEF could not be well developed under a low growth light intensity (Miyake et al. 2005) and fast recovery of PSII from photodamage is dependent on moderate PSI activity, we speculated that the slow recovery of PSII as indicated by Kudoh and Sonoike (2002) resulted from the severe damage to PSI which stunted CEF. We concluded that the stability of the PSI complex is essential for the fast recovery of PSII activity because of strong stimulation of CEF. Taking into account the

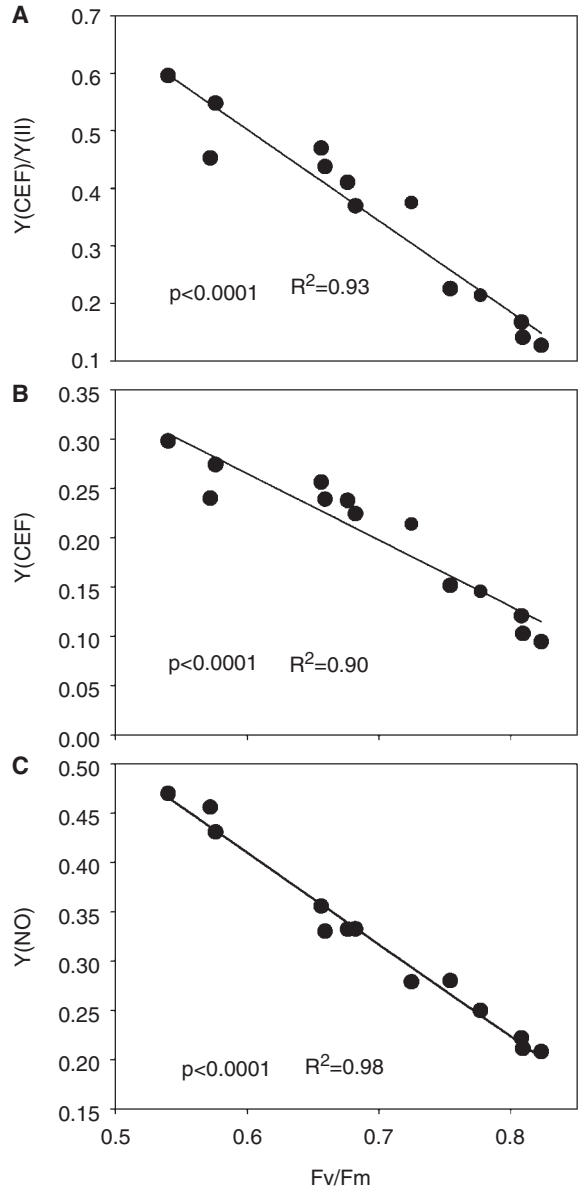

Fig. 5 Changes in Y(CEF), Y(CEF)/Y(II) and Y(NO) at 25°C under a PFD of 100 μmol m^{-2} s^{-1} as a function of F_v/F_m for leaves treated at 4°C and a PFD of 650 μmol m^{-2} s^{-1} and subsequently recovered at 25°C and a PFD of 100 μmol m^{-2} s^{-1}.

important role of PSI activity in the fast recovery of PSII, the photoprotection of PSI and the development of CEF should be considered when tropical trees are planted in subtropical and marginal tropical areas. Since high growth light could activate the development of CEF and make PSI insensitive to chilling and light stress in tropical trees (data not shown), the resistance of light-demanding plants to chilling and light stress can be enhanced under high growth light. After short-term chilling and light stress, although PSII reactive centers were damaged, their recovery was very fast because of the stability of PSI activity and significant stimulation of CEF.

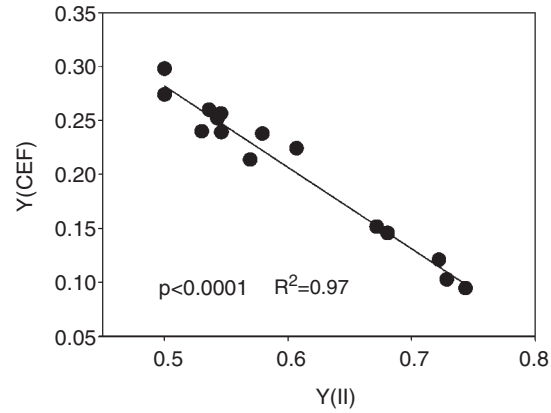

Fig. 6 Changes in Y(CEF) at 25°C under a PFD of 100 μmol m^{-2} s^{-1} as a function of Y(II) for leaves treated at 4°C and a PFD of 650 μmol m^{-2} s^{-1} and subsequently recovered at 25°C and a PFD of 100 μmol m^{-2} s^{-1}.

Changes in energy distribution in PSII and the redox state of P700 during recovery

Y(NO) and Y(NF) gradually decreased and Y(II) gradually increased during recovery. Y(NO) is a parameter indicative of photodamage. Our results indicated that Y(NO) was negatively correlated with F_v/F_m (**Fig. 5C**). We conclude that in addition to F_v/F_m, Y(NO) is another good indicator of PSII photodamage. The fast decrease in Y(NO) was caused by an increase in Y(NPQ) rather than by an increase in Y(II). The increase in Y(NPQ) indicated that more excess energy excitation was dissipated harmlessly as heat, which led to the decrease in oxidative stress, i.e. the generation of reactive oxygen species (ROS). Since ROS not only directly cause photodamage to PSII but also inhibit the recovery of PSII through inhibiting protein synthesis (Asada 1996, Asada 1999, Niyogi 2000, Nishiyama et al. 2001, Nishiyama et al. 2004), the increase in Y(NPQ) indicated that the risk of photoinhibition of PSII decreased and the recovery could go on wheels.

The value of Y(NA) during recovery was significantly lower than before treatment. Since Y(NA) represents the over-reduction of the PSI acceptor side which contributes to photoinhibition of PSI, the lower Y(NA) during recovery indicated that PSI was well protected against photoinhibition (Shuvalov et al. 1986, Golbeck 1987, Golbeck and Bryant 1991). It has been reported that inhibition of LEF from PSII to PSI and stimulation of CEF around PSI are two main mechanisms for the photoprotection of PSI (Satoh 1970, Sonoike 1995, Kim et al. 2001, Kudoh and Sonoike 2002, Munekage et al. 2002, Shikanai 2007). In our present study, LEF was significantly inhibited and CEF was significantly stimulated after chilling treatment; therefore, we conclude that the strong stimulation of CEF and inhibition of LEF protected PSI from photoinhibition.

Positive correlation between PSII photodamage and stimulation of CEF during recovery

Our results indicated that the stimulation of CEF is positively correlated with the extent of PSII photodamage

during recovery (**Figs. 5, 6**). After severe photodamage to PSII, the recovery of PSII activity is necessary to avoid accumulation of PSII photodamage. Since the recovery of PSII is dependent on fast turnover of D1 protein and fast repair of photodamaged PSII subunits, the fast recovery of PSII would consume a lot of ATP in a short time which could not be synthesized wholly through LEF because of the PSII photodamage (Allakhverdiev et al. 2005). Consequently, a large part of the ATP must be synthesized through other pathways. Fortunately, plants can increase the synthesis of ATP through stimulating the CEF around PSI if PSI is not severely photodamaged. Our results indicated that when F_v/F_m decreased from 0.82 to 0.54, Y(CEF) was stimulated from 0.1 to 0.3 and Y(CEF)/Y(II) increased from 0.13 to 0.6. The extent of stimulation of CEF is negatively correlated with the value of F_v/F_m and Y(II). The decreases in F_v/F_m and Y(II) indicated the photodamage of PSII. These results indicated that CEF was stimulated during the recovery of PSII. CEF contributes to the build-up of a trans-thylakoid membrane proton gradient which induces the synthesis of ATP (Heber and Walker 1992, Bendall and Manasse 1995). More ATP was synthesized by the stimulation of CEF and used for the synthesis of D1 protein and repair of photodamaged PSII subunits. With the repair of photodamaged PSII subunits, the demand for synthesis of ATP decreased during subsequent recovery. As a result, the extent of stimulation of CEF decreased in later recovery.

In conclusion, we found that there is a significant positive correlation between the extent of PSII photodamage and stimulation of CEF during recovery. The stimulation of CEF decreased gradually with the recovery of PSII activity. Severe photodamage of PSII induced strong stimulation of CEF which helps the synthesis of ATP, contributing to fast repair of PSII subunits. We concluded that the stability of PSI activity favors the fast repair of PSII activity through stimulation of CEF.

Materials and Methods

Plant materials

The chilling-sensitive tropical tree *D. odorifera* T. Chen (Fabaceae) is native to Hainan island of China, a light-demanding tree species inhabiting secondary forests. The trees produce high-quality timber and their seedlings exhibit good growth performance in the Xishuangbanna tropical botanical garden (21°54′N, 101°46′E) located in the northern boundary of the tropical zone. The 3-year-old seedlings were cultivated in an open field. The highest PFD at midday is up to 1,850 μmol m^{-2} s^{-1} in summer and 1,550 μmol m^{-2} s^{-1} in winter.

Photoinhibitory treatment and subsequent recovery

The chilling experiment and physiological measurements were conducted in April. During this period, the outdoor air temperatures at night and noon are ~17°C and ~30°C respectively.

Intact leaves on branches immersed in water were placed in a cool room at 4°C and were illuminated under a PFD of 630 μmol m^{-2} s^{-1} for 2 h, and then allowed to recover under a temperature of 25°C and a PFD of 100 μmol m^{-2} s^{-1}.

Photosynthetic measurements

The Chl fluorescence and P700 redox state measurement were determined in vivo with detached leaves using a Dual-PAM-100 (Heinz Walz). The F_v/F_m and P_m were determined after dark adaptation for 15 min. All the PSI and PSII photosynthetic measurements in the light were determined at 25°C and a PFD of 100 μmol m^{-2} s^{-1} after 15 min light adaptation.

The fluorescence parameters were calculated as follows: $F_v/F_m=(F_m-F_o)/F_m$, $Y(II)=(F_m'-F_s')/F_m'$, $Y(NO)=F_s'/F_m$, $Y(NPQ)=1-Y(II)-Y(NO)$ (Kramer et al. 2004), $Y(NF)=F_s'/(F_m)_{PI}-F_s'/F_m$ (Kornyeyev and Hendrickson 2007), where F_o represents the minimum fluorescence in the dark-adapted state and light-adapted state, respectively, and F_m and F_m' represent the maximum fluorescence upon illumination with a pulse (600 ms) of saturating light (10,000 μmol m^{-2} s^{-1}) in the dark-adapted state and light-adapted state, respectively. $(F_m)_{PI}$ represents the maximum level of Chl fluorescence in a sample that was dark acclimated after photoinhibitory treatment. F_s' is the light steady-state fluorescence. F_v/F_m represents the maximum quantum yield of PSII. Y(II) is the effective quantum yield of PSII. Y(NO) is the quantum yield of non-regulated energy dissipation of PSII. Y(NO) consists of the non-photochemical quenching due to photoinactivation and constitutive thermal dissipation that is very stable and was not affected by environmental stresses (Busch et al. 2009). A high Y(NO) value indicates that both photochemical energy conversion and protective regulatory mechanisms are inefficient. Therefore, it is indicative of the plant having serious problems in coping with the incident radiation. Y(NPQ) is the quantum yield of regulated energy dissipation of PSII. A high Y(NPQ) value indicates that the absorbed light energy is excessive and shows the efficiency of dissipation of excessive excitation energy into harmless heat. Y(NF) indicates the quantum yield of thermal dissipation by non-functional PSII.

The parameters related to PSI are calculated as follows: Y(ND) = 1 − P700 red, Y(I) = P700 red − Y(NA), $Y(NA)=(P_m-P_m')/P_m$. The maximal P700 changes (P_m) were determined with saturation pulses using a Dual-PAM-100. The leaves were dark adapted for 15 min before the measurement. After far-red pre-illumination 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 an efficient PSI complex. P_m' was determined similarly to P_m but without far-red pre-illumination. This method was taken from Klughammer and Schreiber (1994). Y(ND) represents the fraction of overall P700 that is oxidized in a given state due to a lack of donors,

which is enhanced by a trans-thylakoid proton gradient (photosynthetic control at the cytochrome *b/f* complex as well as down-regulation of PSII) and photodamage to PSII. The photochemical quantum yield of PSI, Y(I), is defined by the fraction of overall P700 that in a given state is reduced and not limited by the acceptor side. Y(NA) represents the fraction of overall P700 that cannot be oxidized by a saturation pulse in a given state due to a lack of acceptors; it is enhanced by dark adaptation (deactivation of key enzymes of the Calvin–Benson cycle) and damage at the site of CO_2 fixation. The saturating pulse used in P700 measurement is 10,000 $\mu mol\, m^{-2}\, s^{-1}$. The yield of CEF, Y(CEF), is calculated as Y(CEF) = Y(I) − Y(II). The ratio of the quantum yield of CEF to the LEF is calculated as Y(CEF)/Y(II) = [Y(I) − Y(II)]/Y(II).

Some experts recently pointed out that Y(II) and Y(I) may be determined in different parts of the leaf tissue by the Dual-PAM-100. The Chl fluorescence signal mainly originates from leaf mesophyll near the leaf surface, while the P700 signal comes from the whole tissue, and therefore LEF may be underestimated and consequently CEF would be overestimated. The method for measuring the P700 redox state was originally reported in Klughammer and Schreiber (1994) and has been widely referred to in previous studies on CEF (Golding and Johnson 2003, Chow and Hope 2004, Miyake et al. 2005, Fan et al. 2008, Jia et al. 2008). Although the measurement of CEF by the Dual-PAM-100 may not be perfect, the Dual-PAM-100 presently is a very good commercial instrument for P700 measurement because of the synchronicity of measuring Chl fluorescence and P700. Even though there might be some overestimation of CEF, we believe that the trend in change in the ratio of CEF to LEF in response to chilling treatment is reliable.

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