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Evidence for the regulation of leaf movement by photosystem II activity

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ABSTRACT

Some light-demanding plants fold leaves under high light and open leaves under low light. Since paraheliotropism leaf movement under high light could be induced by environmental stresses that aggravate photoinhibition of photosystem II (PSII), we hypothesize that the leaf movement is regulated by PSII activity. To test this hypothesis, we examined photosynthetic gas exchange and chlorophyll fluorescence, diurnal changes in leaf angle, and maximum quantum yield of PSII (F_v/F_m) in a leaf-foldable canopy liana, *Bauhinia tenuiflora*, grown in an open field. The rate of CO_2 assimilation, electron transport rate, and non-photochemical quenching was saturated under light of 1000 μmol photons $m^{-2}\,s^{-1}$. After exposure to high light of 1000 μmol photons $m^{-2}\,s^{-1}$ and 2000 μmol photons $m^{-2}\,s^{-1}$ for 8 h, F_v/F_m decreased to 54% and 19%, respectively. The repair of photodamaged PSII was strongly suppressed when illuminated at high light. After high light treatment, the recovery of PSII activity under low light functions efficiently. During the daytime, the minimum values of F_v/F_m and leaf angle were 0.75° and 9°, respectively. In the early morning, high F_v/F_m was accompanied by large leaf angle. At noon, when F_v/F_m was lower than 0.8, *B. tenuiflora* strongly folded its leaves. In the afternoon, when F_v/F_m was higher than 0.8, leaf angle gradually increased. After treatment with 3-(3,4-dichlorophenyl)-1,1-dimethylurea (DCMU, an inhibitor of PSII), F_v/F_m and leaf angle decreased significantly. Based on these results, the leaf movement in *B. tenuiflora* can be regulated by PSII photoinhibition, suggesting that PSII photoinhibition plays a potential role in the regulation of leaf movement under environmental stresses.

1. Introduction

Light is the driving force for photosynthesis. However, excess light could induce photodamage to photosystem II (PSII) in leaves (Barber and Andersson, 1992; Prasil et al., 1992; Aro et al., 1993; Barth et al., 2001; Adir et al., 2003; Takahashi et al., 2009). Although sun leaves of light-demanding plants have several physiological mechanisms, such as cyclic electron flow (CEF) (Munekage et al., 2004; Takahashi et al., 2009; Huang et al., 2012a), non-photochemical quenching (NPQ) (Demmig-Adams, 1990; Niyogi et al., 1997, 1998, 2001; Müller et al., 2001; Li et al., 2002), and photorespiration (Takahashi et al., 2007), to protect PSII from photoinhibition under condition of excess light energy, PSII photoinhibition is inevitable in plants after exposure to high light for several hours (for review Takahashi and Badger, 2011).

An interesting natural phenomenon is that some light-demanding plants fold their leaves under high light intensity to diminish photodamage of PSII (Kao and Forseth, 1991, 1992; Pastenes et al., 2005; Huang et al., 2012b). Previous studies have suggested that leaf paraheliotropism under high light intensity could be induced by water and nutrient availability, and air temperature (Shackel and Hall, 1979; Oosterhuis et al., 1985; Fu and Ehleringer, 1989, 1991; Kao and Forseth 1991, 1992; Kao and Tsai, 1998; Bielenberg et al., 2003; Pastenes et al., 2005). These environmental stresses decrease photosynthetic CO_2 assimilation and then reduce the ability of plants to utilize light energy, which increases the production of reactive oxygen species (ROS) that aggravate PSII photoinhibition (Nishiyama et al., 2001, 2004, 2005, 2006, 2011; Murata et al., 2007) and accelerating PSII photodamage (Oguchi et al., 2009, 2011). It has been widely considered that the leaf paraheliotropism alleviates PSII photoinhibition under environmental stresses. However, it is unclear whether the leaf paraheliotropism under environmental stresses is regulated by the extent of PSII photoinhibition.

Abbreviations: An, Rate of CO_2 asimilation; ETR, Electron transport rate through photosystem II; PPFD, Photosynthetic photons flux density; F_v/F_m, Maximum quantum yield of photosystem II; NPQ, Non-photochemical quenching; PSII, photosystem II.

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In tropical rain forests, some light-demanding liana species form a typical mono-layered canopy. The high light intensity and low relative humidity in the canopy lead to high vapor potential deficit. These environmental characteristics in the canopy induce stomatal closure at noon, which depresses CO_2 assimilation (Zhang et al., 2009) and then increases the risk of PSII photoinhibition (Takahashi and Murata, 2005, 2006; Murata et al., 2007). A canopy liana species, *Bauhinia tenuiflora* (Leguminosae), significantly showed leaf paraheliotropism under high light intensity. In addition, *B. tenuiflora* showed relatively low capacities of CEF and NPQ than some non-foldable species (Huang et al., 2012b). Thus, leaves of *B. tenuiflora* displayed severe PSII photoinhibition after exposure to high light for several hours (Huang et al., 2012b). Under natural conditions, *B. tenuiflora* folds its leaves at noon and opens its leaves in the late afternoon. PSII activity of sun leaves is inhibited at noon and repaired in late afternoon (Allen et al., 2000; Hendrickson et al., 2004). Therefore, we hypothesize that the stronger PSII photoinhibition at noon regulates leaf folding and lower PSII photoinhibition in late afternoon regulates leaf opening in *B. tenuiflora*.

We examine photosynthetic gas exchange and chlorophyll fluorescence, diurnal changes in leaf angle and maximum quantum yield of PSII in *B. tenuiflora* grown in an open field. Our aim is to address whether PSII activity is an important signal for the regulation of leaf movement in *B. tenuiflora*.

2. Materials and methods

2.1. Plant material and growth condition

A light-demanding plant that folds its leaves under high light intensity, *Bauhinia tenuiflora*, was chosen for this study. *Bauhinia tenuiflora* is a liana plant which forms a typical mono-layered canopy and is native to south China. The plants of *B. tenuiflora* were cultivated in an open field and with good water and nutrition conditions. It grows well in Xishuangbanna Tropical Botanical Garden (21°54′N, 101°46′E). During the study period (late August to early September in 2012), the maximum photosynthetic photon flux density (PPFD) at midday was up to 1850 μmol $m^{-2}\,s^{-1}$, the outdoor air temperatures at night and noon are about 24 °C and 34 °C, respectively.

2.2. Gas exchange and chlorophyll fluorescence measurements

Rates of CO_2 assimilation (An) were measured between 9:00 and 10:30 am with an open gas exchange system incorporating infrared CO_2 and water vapor analyzers (Li-6400, Li-Cor Inc. Lincoln, NE, USA). During the measurements, the water vapor pressure deficit was about 1.2 kPa, and atmospheric CO_2 concentration (C_a) was 400 μmol mol^{-1}. Leaves were illuminated by either a quartz halogen light source or red light-emitting diodes (656–680 nm; 6400–02, Li-Cor Inc.). Measurements of CO_2 assimilation rate in response to incident photosynthetic photon flux density (PPFD) were made between 2000 and 0 μmol photons $m^{-2}\,s^{-1}$ and at 30 °C with relative humidity of about 75%.

Chlorophyll fluorescence was measured simultaneously with the gas exchange measurements for leaves using fluorometer leaf chamber (6400–40, Li-Cor Inc. Lincoln, NE, USA). The fluorescence parameters F_m, F_s, and $F_m{}'$ were determined as previously described (Baker and Rosenqvist, 2004). F_s is the steady fluorescence under light-adapted state. F_m and $F_m{}'$ are the dark-adapted and light-adapted maximum fluorescence upon illumination of a pulse (800 ms) of saturating light (8000 μmol photons $m^{-2}\,s^{-1}$). The fluorescence parameters Φ_{PSII}, NPQ and ETR were calculated as follows (Genty et al., 1989):

$$\Phi_{PSII} = \frac{F'_m - F_s}{F'_m},$$

$$NPQ = \frac{F_m - F'_m}{F'_m},$$

$$ETR = 0.5 \times L_{abs} \times \Phi_{PSII} \times PPFD,$$

where 0.5 is the proportion of absorbed light reaching PSI or PSII, L_{abs} is the leaf absorptance and was assumed to be 0.85 in our present study. Φ_{PSII} Is the effective quantum yield of PSII. NPQ represents the ability of plants to dissipate excess light energy as heat through non-photochemical quenching. ETR represents the electron transport rate through PSII.

2.3. Photoinhibitory treatments and subsequent recovery

Detached leaves incubated in the presence or absence of chloramphenicol (CM, 3 mM, to inhibit the repair of photodamaged PSII) overnight in darkness were exposed to high light of 1000 or 2000 μmol photons $m^{-2}\,s^{-1}$ at 30 °C for 8 h. During these treatments, the leaves were dark acclimated in between, and F_v/F_m was measured. The maximum quantum yield of PSII was calculated as: $F_v/F_m = (F_m - F_0)/F_m$, where F_0 and F_m are the minimum and maximum fluorescence in the dark-adapted state, respectively. F_m was measured upon illumination of a pulse (300 ms) of saturating light (10,000 μmol photons $m^{-2}\,s^{-1}$). The value of F_v/F_m was measured by Dual-PAM-100 after 20 min dark adaptation (Kornyeyev and Holaday, 2008).

In order to evaluate the recovery of PSII activity after photoinhibition, six independent detached leaves of *B. tenuiflora* were placed flatly on water and exposed to strong light of 2000 μmol photons $m^{-2}\,s^{-1}$ at 30 °C for 2 h, and then allowed to recover at 30 °C and a light of 100 μmol photons $m^{-2}\,s^{-1}$ for 3 h. During these treatments, the leaves were dark acclimated in between, and F_v/F_m was measured.

To determine the effect of decreasing F_v/F_m on leaf angle, we examined the influence of 3-(3,4-dichlorophenyl)-1,1-dimethylurea (DCMU) (an inhibitor of PSII) on PSII activity and leaf angle. At 8:00 (solar time), we spray DCMU solution (70 μM) or water on leaves of *B. tenuiflora*, and subsequently measured F_v/F_m and leaf angle at 10:00 and 12:00. Because in rainy season, it usually rains in the afternoon in the study site, we used the data collected at 10:00 and 12:00 in the present study.

2.4. Diurnal leaf angle and F_v/F_m measurements

During a clear day, the diurnal changes in leaf angle (Fig. 1) and F_v/F_m were measured. Diurnal change in F_v/F_m was measured by a portable fluorometer (FMS-2, Hansatech, UK) after dark incubation for 20 min. The mean value of two halves was used to represent the F_v/F_m of a certain leaf.

3. Results

To explore the photosynthetic characterizes of *B. tenuiflora*, light response curves of An, ETR, and NPQ were measured at an atmospheric CO_2 concentration of 400 μmol mol^{-1} and 30 °C. The light response curve indicated that the maximum An at an atmospheric CO_2 concentration of 400 μmol mol^{-1} was about 8 μmol CO_2 $m^{-2}\,s^{-1}$ (Fig. 2A). The maximum value of ETR of *B. tenuiflora* was 107 μmol electrons $m^{-2}\,s^{-1}$ (Fig. 2B). The maximum value of NPQ was 1.8 in leaves of *B. tenuiflora* (Fig. 2C). The light saturating points of An, ETR and NPQ were approximately 1000 μmol photons $m^{-2}\,s^{-1}$ (Fig. 2). These results suggested that

Fig. 1. Photographs of opening and folding leaves of *Bauhinia tenuiflora*. The symbol θ indicates leaf angle.

leaves of *B. tenuiflora* cannot safely deal with excess light energy when exposed to light intensity above 1000 μmol photons $m^{-2} s^{-1}$.

After exposure to high light of 1000 or 2000 μmol photons $m^{-2} s^{-1}$ at 30 °C for 8 h, the value of F_v/F_m in leaves of *B. tenuiflora* decreased to 54% and 19%, respectively (Fig. 3). Since PSII photoinhibition is a result of imbalance of photodamage and repair, the decrease in F_v/F_m suggests that, under strong light intensity, the rate of PSII photodamage largely exceeds the rate of repair. Furthermore, chloramphenicol (CM, inhibits the repair of PSII activity) significantly accelerated PSII photoinhibition under high light (Fig. 3). To examine the repair process under low light, we monitored the recovery of F_v/F_m after photoinhibition by strong light. After exposure to light at 2000 μmol photons $m^{-2} s^{-1}$ for 2 h in air, the level of F_v/F_m decreased to 65% in leaves of *B. tenuiflora* (Fig. 4). When the detached leaves were subsequently exposed to low light at 100 μmol photons $m^{-2} s^{-1}$ in air to allow repair, the value of F_v/F_m recovered to 88% of the initial level in 2 h (Fig. 4), indicating that PSII activity increased by 23% (88% – 65% = 23%) in 2 h when illuminated under low light of 100 μmol photons $m^{-2} s^{-1}$. The value of F_v/F_m decreased to 57% in the CM-treated leaves of *B. tenuiflora* after exposure to 2000 μmol photons $m^{-2} s^{-1}$ for 2 h (Fig. 3B). If the repair process under 2000 μmol photons $m^{-2} s^{-1}$ functioned efficiently as well as under 100 μmol photons $m^{-2} s^{-1}$, the value of F_v/F_m just decreased to 80% (23% + 57% = 80%) after 2 h exposure to 2000 μmol photons $m^{-2} s^{-1}$. Actually, F_v/F_m decreased to 65% after 2 h exposure to 2000 μmol photons $m^{-2} s^{-1}$ (Fig. 4). Thus, these results indicated that the repair of photodamaged PSII was strongly suppressed under 2000 μmol photons $m^{-2} s^{-1}$. Similarly, under 1000 μmol photons $m^{-2} s^{-1}$, the repair process was also suppressed.

To understand the relationship between PSII photoinhibition and leaf folding in leaves of *B. tenuiflora*, diurnal changes in F_v/F_m and leaf angle were measured in a clear day. In early morning, the sunlight intensity was relatively low, and the F_v/F_m value was high,

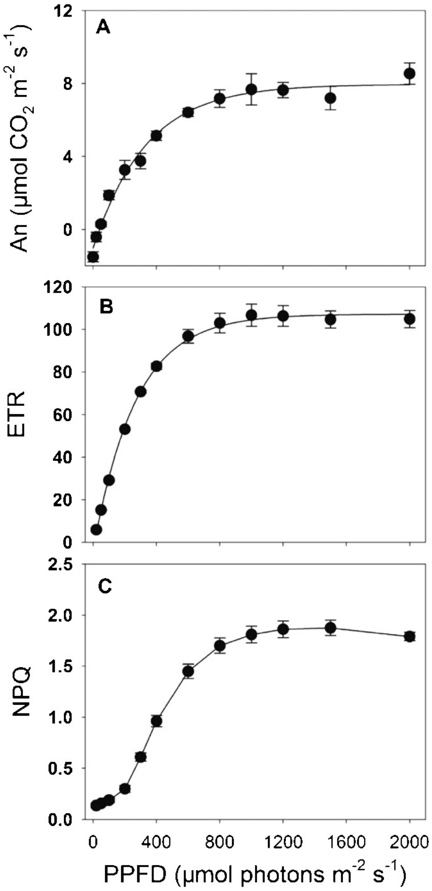

Fig. 2. Response of CO_2 assimilation (An), electron transport rate (ETR) and non-photochemical quenching (NPQ) to incident photosynthetic photon flux density (PPFD) for leaves of *Bauhinia tenuiflora* measured at 30 °C and 400 μmol mol^{-1} CO_2 concentration. The mean ± SE was calculated from four independent experiments.

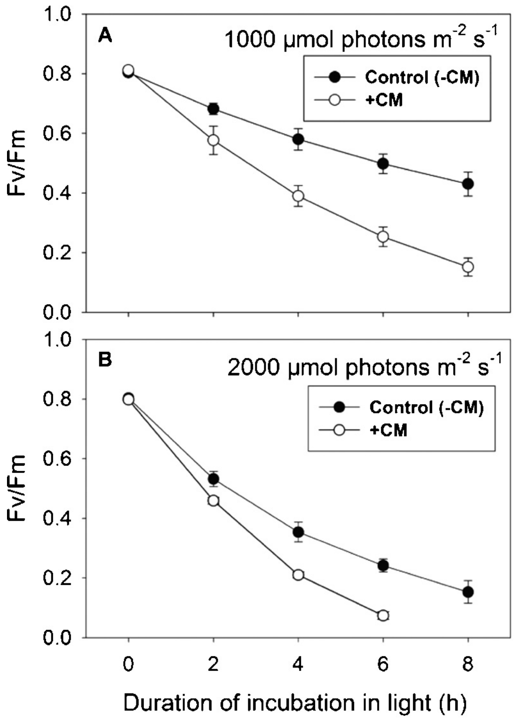

Fig. 3. Change in the maximum quantum yield of PSII (F_v/F_m) during exposure to high light in air in leaves of *Bauhinia tenuiflora*. Detached leaves incubated in the presence or absence of chloramphenicol (CM, 3 mM) overnight in darkness were exposed to light at 1000 μmol photons $m^{-2} s^{-1}$ or 2000 μmol photons $m^{-2} s^{-1}$. The F_v/F_m was measured after dark incubation for 20 min. Values are means ± SE ($n = 6$).

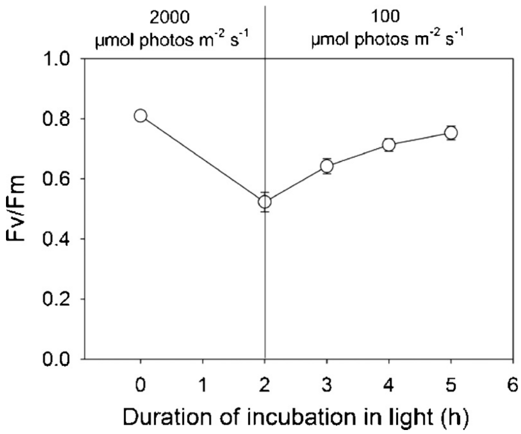

Fig. 4. Recovery of the maximum quantum yield of PSII (F_v/F_m) in air after photoinhibition in leaves of *Bauhinia tenuiflora*. Detached leaves floating on water were exposed to a high light of 2000 μmol photons m^{-2} s^{-1} for 2 h. Subsequently, the detached leaves were exposed to low light of 100 μmol photons m^{-2} s^{-1} for recovery. Values are means ± SE (n = 6).

accompanying by high degrees of leaf angle (Fig. 5). At noon, the sunlight intensity increases to a relatively high level, inducing PSII photoinhibition and leaf folding (Fig. 5). In the afternoon, the sunlight intensity gradually decreases (Fig. 5A), and the value of F_v/F_m and the leaf angle increased (Fig. 5B and C). The value of F_v/F_m was 0.83 at 8:00 and decreased to about 0.78 at noon. In the afternoon, F_v/F_m recovered and reached 0.81 at 18:00 (Fig. 5B). The leaf angle was maintained at high levels above 160° in early morning and late afternoon but decreased to a low level about 25° at noon (Fig. 5C).

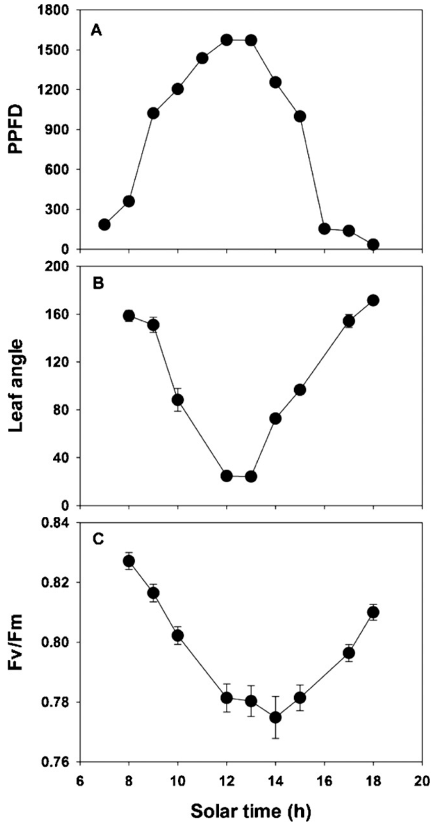

Fig. 5. Diurnal variation of photosynthetic photon flux density (PPFD), the maximum quantum yield of PSII (F_v/F_m) and leaf angle for leaves of *Bauhinia tenuiflora*. The mean ± SE was calculated from at least 10 independent experiments.

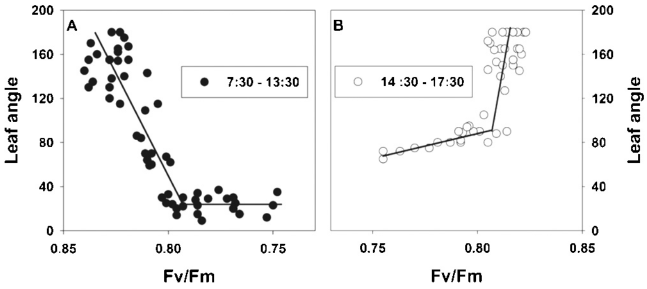

Fig. 6. Diurnal change in leaf angle as a function of the maximum quantum yield of PSII (F_v/F_m) for leaves of *Bauhinia tenuiflora*.

Pooling diurnal leaf angle and F_v/F_m indicated that leaf angle was significantly correlated with PSII activity. In the morning, when the value of F_v/F_m was higher than 0.80, the decrease in leaf angle was accompanied by a decrease in F_v/F_m (Fig. 6A). When F_v/F_m was lower than 0.80, the leaf angle was maintained at levels below 40° irrespective of F_v/F_m (Fig. 6A). In the late afternoon, when F_v/F_m recovered to the level above 0.8, the leaf angle increased quickly (Fig. 6B).

The effect of DCMU on PSII activity and leaf angle was examined in intact leaves. The DCMU-treated leaves showed significantly lower F_v/F_m and leaf angle than the H_2O-treated leaves. Values for PPFD at 10:00 and 12:00 (solar time) were 643 and 1181 μmol photons m^{-2} s^{-1}, respectively. At 10:00, F_v/F_m was 0.76 and 0.67 in the H_2O and DCMU-treated leaves, respectively, and the respective leaf angle was 107° and 70° (Fig. 7). At 12:00, F_v/F_m was 0.74 and 0.64 in the H_2O and DCMU-treated leaves, respectively, and the respective leaf angle was 84° and 44° (Fig. 7). These results indicated that when the PSII activity was depressed, the leaf angle decreased subsequently.

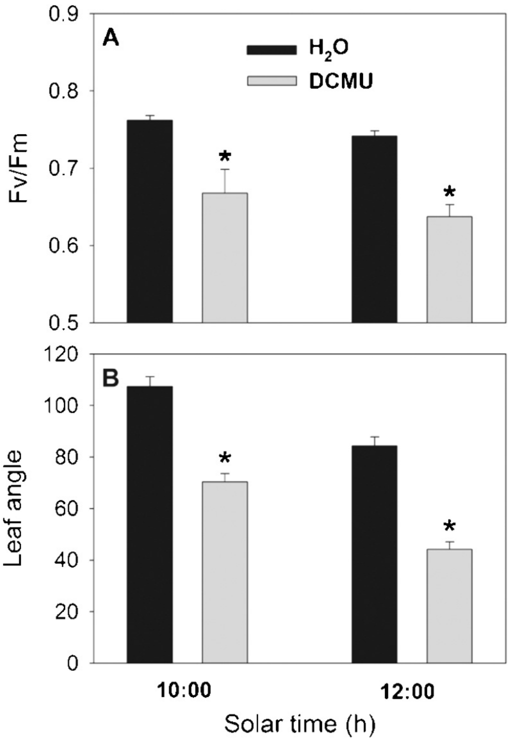

Fig. 7. Effect of 3-(3,4-dichlorophenyl)-1,1-dimethylurea (DCMU) (an inhibitor of PSII) on PSII activity and leaf angle. The mean ± SE was calculated from six independent experiments. Asterisks indicate a significant difference in the DCMU-treated leaves compared with the H_2O-treated leaves.

4. Discussion

PSII photoinhibition has often been considered as an unavoidable reaction. It is conceivable that leaf paraheliotropism alleviates PSII photoinhibition under environmental stresses. However, the coordination of PSII activity and leaf movement is unclear. Here we provide evidence that the leaf movement is closely correlated with PSII activity. PSII photoinhibition can regulate leaf movement in *B. tenuiflora*, which prevents irreversible damage of PSII and optimize CO_2 assimilation.

The leaf-foldable species *B. tenuiflora* displayed relatively low capacities of CO_2 assimilation and ETR (Fig. 2A and B). At light of 1000 μmol photons m^{-2} s^{-1}, CO_2 assimilation and ETR reached the maximum values. These results indicated that when exposed to light intensity above 1000 μmol photons m^{-2} s^{-1}, the absorbed light energy exceeds the utilization for photosynthesis in leaves of *B. tenuiflora*. The excess absorbed light energy leads to production of ROS that cause photodamage to PSII and inhibit the repair of photodamaged PSII complex (Nishiyama et al., 2001, 2004, 2005, 2006, 2011; Oguchi et al., 2009, 2011). Plants use NPQ to harmlessly dissipate excess light energy as heat and then diminish the production of ROS. In leaves of *B. tenuiflora*, although NPQ was activated under high light, the capacity of NPQ was relatively low (Fig. 2C, Huang et al., 2012b). Furthermore, *B. tenuiflora* displayed a lower CEF capacity compared with the non-foldable species *Microcos paniculata* (Huang et al., 2012b). Because CEF and NPQ are two important mechanisms involved in photoprotection for PSII, the relatively low capacities of CEF and NPQ led to severe PSII photoinhibition in leaves of *B. tenuiflora* after exposure to strong light (Fig. 3).

PSII photoinhibition is a net result of the imbalance of photodamage and repair. When the rate of photodamage exceeds the rate of repair, PSII photoinhibition should occur. The rate of photodamage to PSII is directly controlled by the intensity of light (Allakhverdiev and Murata, 2004; Nishiyama et al., 2004) but not by the rate of electron transport through PSII (Allakhverdiev et al., 2005). In addition, the rate of repair of photodamaged PSII is closely related with light intensity and the rate of electron transport through PSII (Allakhverdiev and Murata, 2004; Allakhverdiev et al., 2005). High light induces the production of ROS, which inhibit the repair of photodamaged PSII. In the leaves of *B. tenuiflora*, the repair process was strongly inhibited when illuminated under high light of 1000 and 2000 μmol photons m^{-2} s^{-1} (Figs. 3 and 4). Under low light, absorbed light energy can be utilized by photosynthesis and there is little excess energy. As a result, the repair of photodamaged PSII functions efficiently under low light (Fig. 4).

During the diurnal course, the minimum leaf angle was 9°, and the minimum value of F_v/F_m was 0.75 (Fig. 6). These results indicated that leaf folding in *B. tenuiflora* protected PSII against irreversible photodamage when exposed to strong light at noon. On a clear day, the relative humidity decreases, and the vapor pressure deficit increases at noon compared with the morning, as a result, leaves close their stomata to reserve water potential. The decrease in stomatal conductance induces a decline of photosynthetic CO_2 fixation (Wingler et al., 2000; Flexas et al., 2002; Flexas and Medrano, 2002; Zhang et al., 2009), which could increase the generation of ROS that induce photo-oxidative damage to PSII (Oguchi et al., 2009, 2011) and inhibit PSII repair (Takahashi and Murata, 2005, 2006; Murata et al., 2007). To avoid severe PSII photoinhibition under high light, *B. tenuiflora* folds its leaves to diminish the absorption of light energy, which not only decreases the rate of photodamage of PSII but also favor the repair of photodamaged PSII.

In the morning, the increase in sunlight intensity induced a decrease in the F_v/F_m value of *B. tenuiflora* (Fig. 5). Meanwhile, the leaf angle gradually decreased (Fig. 5). At noon, when the F_v/F_m was below 0.8, the leaf angle was smaller than 40° (Fig. 6A). When PSII activity was depressed by DCMU, the leaf angle decreased subsequently (Fig. 7). These results indicated that leaf folding in *B. tenuiflora* was closely related with the decrease in PSII activity. Since PSII activity is very sensitive to high light in leaves of *B. tenuiflora* (Figs. 3 and 4), regulation of leaf folding by PSII photoinhibition is an efficient strategy that quickly responses to high sunlight. Through leaf folding, *B. tenuiflora* can decline the absorbed light energy, which alleviates further photodamage to PSII activity.

In the afternoon, the sunlight intensity gradually decreases, which is accompanied by increases in PSII activity (Fig. 5). When the value of F_v/F_m was higher than 0.8, leaf angle increased in *B. tenuiflora* (Fig. 6B). Since low light decreases the rates of PSII photodamage and ROS production, the relatively low light in the afternoon favors the repair of photodamaged PSII (Figs. 4and 5). If *B. tenuiflora* fold its leaves in the late afternoon, the absorbed light intensity should be very low. Since photosynthetic rate is mainly limited by light intensity in *B. tenuiflora* when exposed to light intensity below 400 μmol photons m^{-2} s^{-1} (Fig. 2A), leaf folding in the late afternoon should decrease the rate of CO_2 assimilation and then impede the gain of carbohydrate. The increase in leaf angle in the afternoon enhances the absorption of light energy, which increases the rate of photosynthetic CO_2 fixation. Therefore, our results suggest that the regulation of leaf movement by PSII photoinhibition optimizes photosynthetic CO_2 fixation in the afternoon. The similar phenomenon has been found in another species *Robinia pseudoacacia* (Arena et al., 2008).

Previous studies on leaf movement mainly focus on the effect of environmental stresses (water and nutrition deficit, light intensity and air temperature) on leaf movement (Shackel and Hall, 1979; Oosterhuis et al., 1985; Fu and Ehleringer, 1989, 1991; Kao and Forseth, 1991, 1992; Kao and Tsai, 1998; Pastenes et al., 2005). Little is known about the effect of PSII activity on leaf movement. High temperature and water deficit induces a decrease in stomatal conductance, which leads to a decrease in the intercellular CO_2 concentration and then reduces the rate of photosynthetic CO_2 assimilation (Golding and Johnson, 2003; Zhang et al., 2009). Nutrition deficit decreases the rubisco concentration, reducing the capacity of photosynthetic CO_2 assimilation (Evans and Terashima, 1988; Yamori et al., 2011). The decrease in CO_2 assimilation led to the generation of ROS. High light aggravates PSII photoinhibition not only due to high rate of photodamage of PSII bur also production of ROS. The regulation of leaf movement by PSII photoinhibition in *B. tenuiflora* suggested that leaf paraheliotropism under environmental stresses is probably induced by the decrease in PSII activity.

Bauhinia tenuiflora is a liana plant that forms a typical monolayered canopy in tropical rain forests. Its leaves are always exposed to strong sunlight in natural conditions. The long-term transport of water from root to canopy increases the potential of leaf water deficit (Ewers et al., 1989). Furthermore, the high light and low relative humidity in the canopy lead to stomatal closure in *B. tenuiflora*, which can depresses CO_2 assimilation (Zhang et al., 2009) and then aggravates PSII photoinhibition (Murata et al., 2007). Because regulation of leaf movement by PSII photoinhibition can diminish PSII photoinhibition and optimize photosynthetic CO_2 fixation, we assume that the regulation of leaf movement by PSII photoinhibition is probably an important strategy in *B. tenuiflora* for acclimating to the environmental condition in the canopy.

5. Conclusion

In summary, leaf folding is an important mechanism for alleviating PSII photoinhibition in *Bauhinia tenuiflora*. The regulation of leaf movement by PSII activity in *Bauhinia tenuiflora* mainly has two functions: one is alleviating PSII photoinhibition, and the other one is optimizing photosynthetic CO$_2$ fixation. Furthermore, our results suggest that leaf paraheliotropism under environmental stresses is probably regulated by the decrease in PSII activity.

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References

Adir, N., Zer, H., Sochat, S., Ohad, I., 2003. Photoinhibition – a historical perspective. Photosynth. Res. 76, 343–370.

Allakhverdiev, S.I., Murata, N., 2004. Environmental stress inhibits the synthesis de novo of proteins involved in the photodamage-repair cycle of photosystem II in *Synechocystis* sp. PCC 6803. Biochim. Biophys. Acta 1657, 23–32.

Allakhverdiev, S.I., Nishiyama, Y., Takahashi, S., Miyairi, S., Suzuki, I., Murata, N., 2005. Systematic analysis of the relation of electron transport and ATP synthesis to the photodamage and repair of photosystem II in *Synechocystis*. Plant Physiol. 137, 263–273.

Allen, D.J., Ratner, K., Giller, Y.E., Gussakovsky, E.E., Shahak, Y., Ort, D.R., 2000. An overnight chill induces a delayed inhibition of photosynthesis at midday in mango (*Mangifera indica* L.). J. Exp. Bot. 51, 1893–1902.

Arena, C., Vitale, L., De Santo, A.V., 2008. Paraheliotropism in *Robinia pseudoacacia* L.: an efficient strategy to optimise photosynthetic performance under natural environmental conditions. Plant Biol. 10, 194–201.

Aro, E.M., Virgin, I., Andersson, B., 1993. Photoinhibition of photosystem II. Inactivation, protein damage and turnover. Biochim. Biophys. Acta 1143, 113–134.

Baker, N.R., Rosenqvist, E., 2004. Applications of chlorophyll fluorescence can improve crop production strategies: an examination of future possibilities. J. Exp. Bot. 55, 1607–1621.

Barber, J., Andersson, B., 1992. Too much of a good thing: light can be bad for photosynthesis. Trends Biochem. Sci. 17, 61–66.

Barth, C., Krause, G.H., Winter, K., 2001. Responses of photosystem I compared with photosystem II to high-light stress in tropical shade and sun leaves. Plant Cell Environ. 24, 163–176.

Bielenberg, D.G., Miller, J.D., Berg, V.S., 2003. Paraheliotropism in two *Phaseolus* species: combined effects of photon flux density and pulvinus temperature, and consequences for leaf gas exchange. Environ. Exp. Bot. 49, 95–105.

Demmig-Adams, B., 1990. Carotenoids and photoprotection in plants: a role for the xanthophyll zeaxanthin. Biochim. Biophys. Acta 1020, 1–24.

Evans, J.R., Terashima, I., 1988. Photosynthetic characteristics of spinach leaves grown with different nitrogen treatments. Plant Cell Physiol. 29, 157–165.

Ewers, F.W., Fisher, J.B., Chiu, S.T., 1989. Water transport in the liana *Bauhinia fassoglensis* (Fabaceae). Plant Physiol. 91, 1625–1631.

Flexas, J., Bota, J., Escalona, J.M., Sampol, B., Medrano, H., 2002. Effects of drought on photosynthesis in grapevines under field conditions: an evaluation of stomatal and mesophyll limitations. Funct. Plant Biol. 29, 461–471.

Flexas, J., Medrano, H., 2002. Energy dissipation in C3 plants under drought. Funct. Plant Biol. 29, 1209–1215.

Fu, Q.A., Ehleringer, J.R., 1989. Helitropic leaf movements in common beans controlled by air temperature. Plant Physiol. 91, 1162–1167.

Fu, Q.A., Ehleringer, J.R., 1991. Modification of paraheliotropic leaf movement in *Phaseolus vulgaris* by photon flux density. Plant Cell Environ. 14, 339–343.

Genty, B., Briantais, J.M., Baker, N.R., 1989. The relationship between the quantum yield of photosynthetic electron transport and quenching of chlorophyll fluorescence. Biochim. Biophys. Acta 990, 87–92.

Golding, A.J., Johnson, G.N., 2003. Down-regulation of linear and activation of cyclic electron transport during drought. Planta 218, 107–114.

Hendrickson, L., Ball, M.C., Wood, J.T., Chow, W.S., Furbank, R.T., 2004. Low temperature effects on photosynthesis and growth of grapevine. Plant Cell Environ. 27, 795–809.

Huang, W., Yang, S.J., Zhang, S.B., Zhang, J.L., Cao, K.F., 2012a. Cyclic electron flow plays an important role in photoprotection for the resurrection plant *Paraboea rufescens* under drought stress. Planta 235, 819–828.

Huang, W., Zhang, S.B., Cao, K.F., 2012b. Evidence for leaf fold to remedy the deficiency of physiological photoprotection for photosystem II. Photosynth. Res. 110, 185–191.

Kao, W.Y., Forseth, I.N., 1991. The effects of nitrogen, light and water availability on tropic leaf movements in soybean (*Glycine max*). Plant Cell Environ. 14, 287–293.

Kao, W.Y., Forseth, I.N., 1992. Diurnal leaf movement, chlorophyll fluorescence and carbon assimilation in soybean grown under different nitrogen and water availabilities. Plant Cell Environ. 15, 703–710.

Kao, W.Y., Tsai, T.T., 1998. Tropic leaf movements, photosynthetic gas exchange, leaf δ13C and chlorophyll a fluorescence of three soybean species in response to water availability. Plant Cell Environ. 21, 1055–1062.

Kornyeyev, D., Holaday, A.S., 2008. Corrections to current approaches used to calculate energy partitioning in photosystem 2. Photosynthetica 46, 170–178.

Li, X.P., Müller-, Moule, P., Gilmore, A.M., Niyogi, K.K., 2002. PsbS-dependent enhancement of feedback de-excitation protects photosystem II from photoinhibition. Proc. Natl. Acad. Sci. U. S. A. 99, 15222–15227.

Müller, P., Li, X.P., Niyogi, K.K., 2001. Non-photochemical quenching: response to excess light energy. Plant Physiol. 125, 371–374.

Munekage, Y., Hashimoto, M., Miyake, C., Tomizawa, K.I., Endo, T., Tasaka, M., Shikanai, T., 2004. Cyclic electron flow around photosystem I is essential for photosynthesis. Nature 429, 579–582.

Murata, N., Takahashi, S., Nishiyama, Y., Allakhverdiev, S.I., 2007. Photoinhibition of photosystem II under environmental stress. Biochim. Biophys. Acta. 1767, 414–421.

Nishiyama, Y., Allakhverdiev, S.I., Murata, N., 2006. A new paradigm for the action of reactive oxygen species in the photoinhibition of photosystem II. Biochim. Biophys. Acta 1757, 742–749.

Nishiyama, Y., Allakhverdiev, S.I., Yamamoto, H., Hayashi, H., Murata, N., 2004. Singlet oxygen inhibits the repair of photosystem II by suppressing the translation elongation of the D1 protein in *Synechocystis* sp. PCC 6803. Biochemistry 43, 11321–11330.

Nishiyama, Y., Yamamoto, H., Allakhverdiev, S.I., Inaba, M., Yokota, A., Murata, N., 2001. Oxidative stress inhibits the repair of photodamage to the photosynthetic machinery. EMBO J. 20, 5587–5594.

Nishiyama, Y., Allakhverdiev, S.I., Murata, N., 2005. Inhibition of the repair of photosystem II by oxidative stress in cyanobacteria. Photosynth. Res. 84, 1–7.

Nishiyama, Y., Allakhverdiev, S.I., Murata, N., 2011. Protein synthesis is the primary target of reactive oxygen species in the photoinhibition of photosystem II. Physiol. Plant. 142, 35–46.

Niyogi, K.K., Bjorkman, O., Grossman, A.R., 1997. Chlamydomonas xanthophyll cycle mutants identified by video imaging of chlorophyll fluorescence quenching. Plant Cell 9, 1369–1380.

Niyogi, K.K., Grossman, A.R., Bjorkman, O., 1998. *Arabidopsis* mutants define a central role for the xanthophyll cycle in regulation of photosynthetic energy conversion. Plant Cell 10, 1121–1134.

Niyogi, K.K., Shih, C., Chow, W.S., Pogson, B.J., DellaPenna, D., Bjorkman, O., 2001. Photoprotection in a zeaxanthin and lutein deficient double mutant of *Arabidopsis*. Photosynth. Res. 67, 139–145.

Oguchi, R., Terashima, I., Chow, W.S., 2009. The involvement of dual mechanisms of photoinactivation of photosystem II in *Capsicum annuum* L. plants. Plant Cell Physiol. 50, 1815–1825.

Oguchi, R., Douwstra, P., Fujita, T., Chow, W.S., Terashima, I., 2011. Intra-leaf gradients of photoinhibition induced by different color lights: implications for the dual mechanisms of photoinhibition and for the application of conventional chlorophyll fluorometers. New Phytol. 191, 146–159.

Oosterhuis, D.M., Walker, S., Eastham, J., 1985. Soybean leaflet movements as an indicator of crop water stress. Crop Sci. 25, 1101–1106.

Pastenes, C., Pimentel, P., Lillo, J., 2005. Leaf movements and photoinhibition in relation to water stress in field-grown beans. J. Exp. Bot. 56, 425–433.

Prasil, O., Adir, N., Ohad, I., 1992. Dynamics of photosystem II: mechanism of photoinhibition and recovery processes. In: Barber, J. (Ed.), Topics in Photosynthesis. Elsevier, Amsterdam, The Netherlands, pp. 295–348.

Shackel, K.A., Hall, A.E., 1979. Reversible leaflet movements in relation to drought adaptation of cowpeas, *Vigna unguiculata* (L.) Walp. Aust. J. Plant. Physiol. 6, 265–276.

Takahashi, S., Badger, M.R., 2011. Photoprotection in plants: a new light on photosystem II damage. Trends Plant Sci. 16, 53–60.

Takahashi, S., Bauwe, H., Badger, M.R., 2007. Impairment of the photorespiratory pathway accelerates photoinhibition of photosystem II by suppression of repair but not acceleration of damage processes in *Arabidopsis*. Plant Physiol. 144, 487–494.

Takahashi, S., Milward, S.E., Fan, D.Y., Chow, W.S., Badger, M.R., 2009. How does cyclic electron flow alleviate photoinhibition in *Arabidopsis*? Plant Physiol. 149, 1560–1567.

Takahashi, S., Murata, N., 2005. Interruption of the Calvin cycle inhibits the repair of photosystem II from photodamage. Biochim. Biophys. Acta 1708, 352–361.

Takahashi, S., Murata, N., 2006. Glycerate-3-phosphate, produced by CO$_2$ fixation in the Calvin cycle, is critical for the synthesis of the D1 protein of photosystem II. Biochim. Biophys. Acta 1757, 198–205.

Wingler, A., Lea, P.J., Quick, W.P., Leegood, R.C., 2000. Photorespiration: metabolic pathways and their role in stress protection. Philos. Trans. R. Soc. London B. Biol. Sci. 355, 1517–1529.

Yamori, W., Nagai, T., Makino, A., 2011. The rate-limiting step for CO$_2$ assimilation at different temperatures is influenced by the leaf nitrogen content in several C$_3$ crop species. Plant Cell Environ. 34, 764–777.

Zhang, J.L., Meng, L.Z., Cao, K.F., 2009. Sustained diurnal photosynthetic depression in uppermost-canopy leaves of four dipterocarp species in the rainy and dry seasons: does photorespiration play a role in photoprotection? Tree Physiol. 29, 217–228.