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饱和白光引起的光系统 II 捕光复合体 (LHCII) 从反应中心复合体脱离不同于弱红光引起的状态 1 向状态 2 的转换

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摘要: 我们观测了不同光照预处理对拟南芥、小麦和大豆叶片光合作用和低温 (77K) 叶绿素荧光参数 *F*685、*F*735 和 *F*685 *F*735 的影响。野生型拟南芥叶片光合作用对饱和光到有限光转变的响应曲线是 V 型, 而缺乏叶绿体蛋白激酶的突变体 STN7 的这一曲线为 L 型。饱和白光可以引起拟南芥叶片 *F*685 *F*735 的明显降低, 但是 *F*735 没有明显增高, 而弱红光可以导致拟南芥叶片 *F*685 *F*735 的明显降低和 *F*735 的明显增高, 表明弱红光可以引起状态 1 向状态 2 的转变, 同时伴随从光系统 II 脱离的 LHC II 与光系统 I 的结合, 而饱和白光只能引起 LHC II 从光系统 II 反应中心复合体脱离。并且, 低温叶绿素荧光分析结果证明, 饱和白光可以引起大豆叶片 LHC Ⅱ 脱离, 但是不能引起小麦叶片 LHC II 脱离, 而弱红光可以引起小麦叶片的这种状态转换, 却不能引起大豆叶片的这种状态转换。因此, 饱和白光引起的野生型拟南芥和大豆叶片的 LHC Ⅱ 脱离不是一个典型的状态转换现象。

关键词: 拟南芥; 光系统 II 捕光复合体 (LHC II); 低温 (77K) 叶绿素荧光; 净光合速率; 可逆脱离; 状态转换

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Dissociation of Photosystem II Light-harvesting Complex (LHC II) from the Reaction Center Complex Induced by Saturating White Irradiation Differs from the Transition from State 1 to State 2 Induced by Weak Red Irradiation

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Abstract: The effects of different irradiance pre-treatments on leaf photosynthesis and low temperature (77K) chlorophyll fluorescence (LTCF) parameters *F*685, *F*735, and *F*685 *F*735 were observed in *Arabidopsis*, wheat, and soybean leaves. The curve of photosynthetic responsing to irradiance transition from saturating to limiting one in *Arabidopsis* wild-type leaves was the V pattern, while the curve in *Arabidopsis* mutant lacking chloroplast protein kinase STN7 was the L pattern. Saturating white irradiation (SWI) could induce the significantly decreased *F*685 *F*735 without a significantly increased *F*735, while weak red irradiation (WRI) could lead to the significantly declined *F*685 *F*735 with a significantly increased *F*735. The results showed that the attachment of dissociated LHC II to PS I in *Arabidopsis* wild-type leaves, indicating that WRI can cause the transition from state 1 to sate 2, while SWI can only induce LHC II dissociation from PSII reaction cen-

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ter complex . Moreover the results of LTCF analysis demonstrated that SWI could induce the LHC II dissociation in soybean but not wheat leaves, while WRI could cause the state transition in wheat but not soybean leaves . Hence the LHC II dissociation caused by SWI in *Arabidopsis* wild-type and soybean leaves was not a typical phenomenon of the state transition .

Key words: *Arabidopsis*; Light-harvesting complex of photosystem II (LHC II); Low temperature (77K) chlorophyll fluorescence; Net photosynthetic rate; Reversible dissociation; State transition

The largest efficiency of photosynthesis depends on the cooperation of the photosystem II (PS II) and photosystem I (PS I), while the cooperation relies on the balanced distribution of excitation energy between the two photosystems . However, due to the difference in radiation absorption property between the two photosystems and the change in quality of sunlight reaching the photosynthetic apparatus at different time during day, the received excitation energy is often unbalanced between the two photosystems . State transitions provide a mechanism whereby more balanced excitation of the two photosystems can be achieved (Fork and Satoh, 1986; Niyogi, 1999; Haldrup *et al.*, 2001) .

The state transition initially discovered by Murata (1969) and Bonaventura and Myers (1969) is involved in a reversible association of some light-harvesting complex II (LHC II) with either PSII or PSI . During the transition from state 1 to 2, some LHC IIs are phosphorylated, migrate to unstacked thylakoids, and attach to PS I (Bassi *et al.*, 1988; Vallon *et al.*, 1991; Allen, 1992; Samson and Bruce, 1995; Horton *et al.*, 1996; Gal *et al.*, 1997; Tan *et al.*, 1998; Lunde *et al.*, 2000; Snyders and Kohorn, 2001) . In reverse, these phosphorylated LHC IIs are dephosphorylated, return to stacked thylakoids, and re-attach to PS II when translating from state 2 to 1 . In these events, the protein kinase Stt7 or STN7 is required for LHC II phosphorylation and state transition (Depège *et al.*, 2003; Bellafiore *et al.*, 2005) .

Similar to state transitions, the reversible dissociation of some LHC IIs induced by saturating irradiance (SI) (Hong and Xu, 1999; Chen and Xu, 2006) is also involved in LHC II phosphorylation and dissociation from PSII core complex (Allen *et al.*, 1981; Bennett, 1991; Harrison and Allen, 1991; Allen, 1992; McCormac *et al.*, 1994; Wollman, 2001) . Then, the questions rise: whether or not the reversible LHC II dissociation caused by SI is the same as state transition ? If not so, what is the difference between them ? In order to answer these questions, the effects of different radiation (saturating white irradiation, SWI, and weak red irradiation, WRI) pre-treatment on leaf photosynthesis and low temperature (77K) chlorophyll fluorescence parameters were observed in *Arabidopsis*, soybean and wheat .

Materials and Methods

Plant growth

The potted plants of soybean (*Glycine max*, cv . Baimangjie), wheat (*Triticum aestivum*, cv . Gaoyuan 602), and *Arabidopsis* (*Arabidopsis thaliana*, cv . Columbia) including the mutant *stn*7 offered by Dr . Vera Bonardi (Botanisches Institut, Development Biologie I, Ludwig-Maximilians- Universit t, Germany) and its wild type were grown in the phytotrons with 25 20℃ (day night) and a photosynthetic photon flux density (PPFD) of about 300 μmol m^{-2} s^{-1} (12 h 12 h light-dark cycle) for soybean and wheat or with 22℃ (day and night) and a PPFD of about 100 μmol m^{-2} s^{-1} (9 h 15 h light-dark cycle) for *Arabidopsis* . The plants were irrigated everyday to avoid water stress . Experiments were performed using fully expanded and healthy leaves .

Leaf irradiation and photosynthesis measurement

The plant leaves were first illuminated by limiting irradiance (LI: 300 μmol m^{-2} s^{-1}) until net photosynthetic rate (*Anet*) reached a steady state . Then, the limiting irradiance was replaced by saturating irradiance (SI: 750 μmol m^{-2} s^{-1}, LI-SI) for photosynthesis . After *Anet* rose gradually to a new steady state the irradiance was reduced back to limiting one (LI-SI-LI) until *Anet* reached again a steady state . In general, *Anet* reaches its steady state value after about 15 and 30 minutes of illumination at limiting and saturating irradiance, respectively . *Anet* was measured *in situ* at 350 μmol CO_2 mol^{-1} by a portable photosynthetic gas analysis system LI-COR 6400 with a LED light source (LI-COR Inc . Lincoln, Nebraska, USA) .

According to the procedure of irradiance changes mentioned above, the other leaves were illuminated by a metal halogen lamp (1 000 W) . A flowing layer of water was placed between the lamp and the leaves to remove heat . After illumination (LI and LI-SI) the leaves were immediately dropped into liquid nitrogen

for low-temperature (77K) chlorophyll fluorescence analysis.

Fully dark-adapted leaves were illuminated by WRI (650 nm, 20 μmol photons m^{-2} s^{-1}) for 20 min. The weak red radiation was obtained using an interference filter with a half wavelength width of 10 nm. After illumination these leaves were dark-adapted for 30 s and then put into liquid nitrogen for the 77K chlorophyll fluorescence analysis.

Low temperature chlorophyll fluorescence analysis

Low-temperature chlorophyll fluorescence was analyzed at 77K with a 44 W-fluorescence spectrofluorimeter built in our laboratory. *F*685, *F*735 and *F*685 *F*735 were measured and calculated as previously described (Hong and Xu, 1999).

Statistical analysis

Statistical analysis of all data including mean, standard error, and t-tests was made with Sigma Plot 8.0 (SPSS, Inc. USA).

Results

Photosynthetic response of *Arabidopsis* leaves to the change in irradiance

When irradiance was changed from saturating (750 μmol m^{-2} s^{-1}) to limiting one (300 μmol m^{-2} s^{-1}), *Anet* in *Arabidopsis* wild-type leaves declined immediately to a value lower than that at limiting irradiance before saturating irradiation. Then, *Anet* rose slowly to a stable value near to that at limiting irradiance before saturating irradiation (Fig.1: a). However, the responses of *Anet* in *Arabidopsis* mutant *stn*7 lacking chloroplast protein kinase STN7 to the irradiance transition were significantly different from those in *Arabidopsis* wild-type leaves. After irradiance was changed from saturating to limiting one, *Anet* in the mutant *stn*7 leaves decreased immediately to a stable value similar to that before saturating irradiation, namely, no slow rise followed the sharp drop in *Anet* (Fig.1: b). These results indicate that the photosynthetic response curves to irradiance transition from saturating to limiting one in *Arabidopsis* wild-type and mutant *stn*7 leaves are the V and L patterns, respectively.

Effects of saturating white irradiation pretreatment on 77K chlorophyll fluorescence parameters in *Arabidopsis* leaves

The 77K chlorophyll fluorescence parameters *F*685 and *F*685 *F*735 declined significantly, but *F*735 had no significant change in *Arabidopsis* wild-type leaves pre-illuminated by saturating white irradiation, compared with those in leaves pre-illuminated by limiting white irradiation (Fig.2: a). Nevertheless, in *Arabidopsis* mutant *stn*7 leave no significant change was observed in *F*685 and *F*685 *F*735 (Fig.2: b).

Effects of weak red irradiation pretreatment on 77K chlorophyll fluorescence parameters in *Arabidopsis* leaves

The 77K chlorophyll fluorescence parameters *F*685 and *F*685 *F*735 decreased significantly and *F*735 increased markedly in *Arabidopsis* wild-type leaves pre-il-

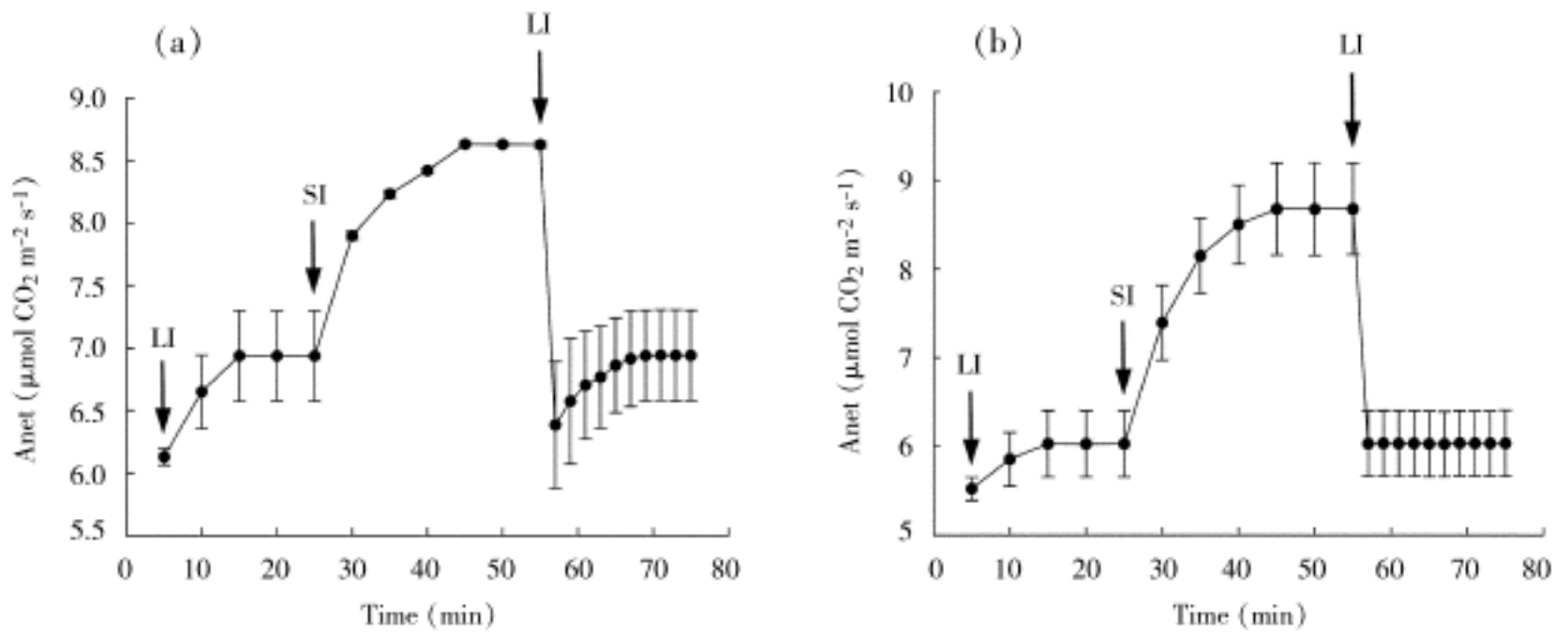

Fig. 1 Response of net photosynthetic rate (*Anet*) in *Arabidopsis* leaves to change in irradiance

(a) Wild type; (b) Mutant *stn*7. LI: limiting irradiance (300 μmol m^{-2} s^{-1}); SI: saturating irradiance (750 μmol m^{-2} s^{-1}).

Each value in this figure is the mean of three leaves with standard error expressed as a vertical bar

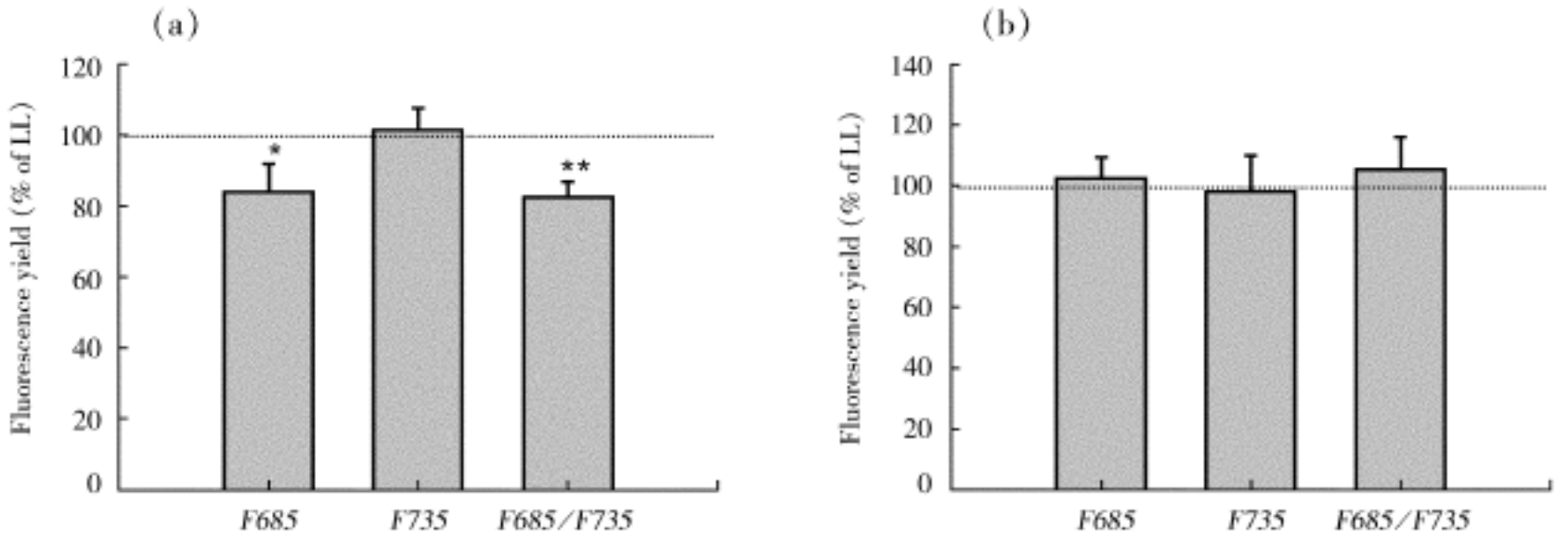

Fig . 2 Changes in 77K chlorophyll fluorescence parameters *F*685, *F*735, and *F*685 *F*735 of *Arabidopsis* leaves caused by pre-illumination with saturating irradiance

(a) Wild type; (b) Mutant *stn*7 . In this figure the parameter values are expressed as the percentages of limiting irradiance (LI, 300 μmolm^{-2}s^{-1}) -pre-illuminated leaves, and each value is the mean of 3-4 repeats with standard error expressed as a vertical bar . LI: limiting irradiance (300 μmolm^{-2}s^{-1}); SI: saturating irradiance (750 μmolm^{-2}s^{-1}) . Asterisks * and ** indicate respectively significant ($p < 0.05$) and very significant ($p < 0.01$) differences between SI-pre-illuminated and LI-pre-illuminated leaves

luminated by weak red irradiation, compared with those of dark control leaves (Fig.3: a) . However, no significant change in these parameters was observed in the mutant *stn*7 leaves pre-illuminated by weak red irradiation (Fig.3: b) .

Changes in 77K chlorophyll fluorescence parameters in soybean leaves induced by weak red irradiation or saturating white irradiation pretreatment

Compared with dark control or pre-illumination with limiting white irradiation, pre-illumination with weak red irradiation or saturating white irradiation led to significant decreases in *F*685 and *F*685 *F*735 without significantly increased *F*735 in soybean leaves (Fig.4: a, b), indicating that neither saturating white irradiation nor weak red irradiation can cause the transition from state 1 to state 2 .

Changes in 77K chlorophyll fluorescence parameters in wheat leaves induced by pre-illumination with weak red irradiation or saturating white irradiation

In wheat leaves the pre-illumination with weak red irradiation led to significantly decreased *F*685 and

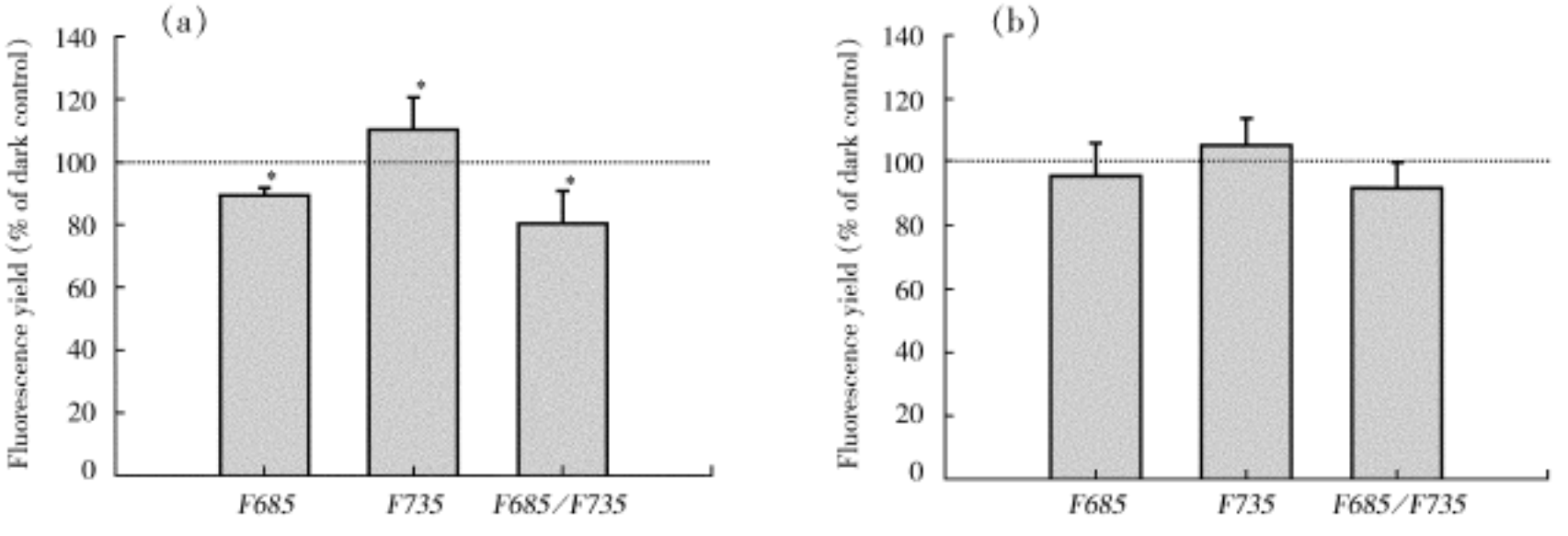

Fig . 3 Changes in 77K chlorophyll fluorescence parameters *F*685, *F*735, and *F*685 *F*735 of *Arabidopsis* leaves caused by pre-illumination with weak red irradiation

(a) Wild type; (b) Mutant *stn*7 . In this figure the parameter values are expressed as the percentages of dark control leaves, and each value is the mean of 3-4 repeats with standard error expressed as a vertical bar . Asterisk * indicates that differences between weak red irradiation-pre-illuminated and dark control leaves are significant ($p < 0.05$)

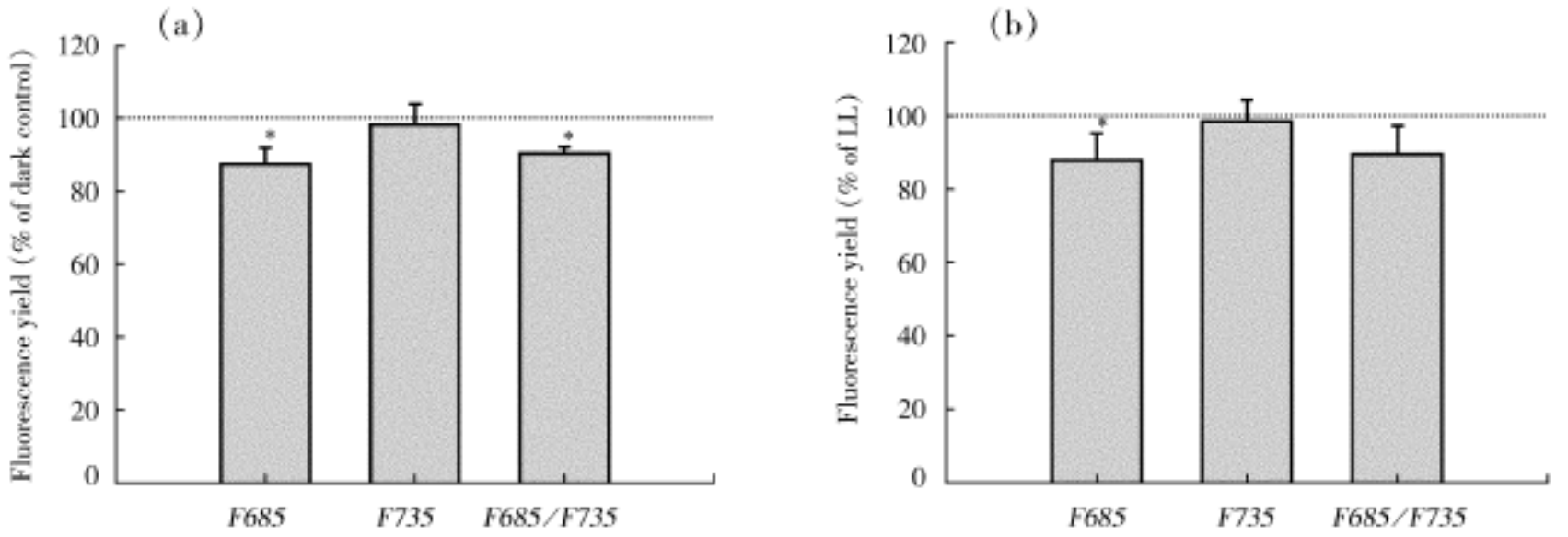

Fig. 4　Changes in 77K chlorophyll fluorescence parameters *F*685, *F*735, and *F*685 *F*735 of soybean leaves caused by pre-illumination with weak red irradiation (a, 20 μmolm^{-2}s^{-1}) or saturating white irradiation (b, SI, 750 μmolm^{-2}s^{-1}). In this figure the parameter values are expressed as the percentages of dark control leaves (a) or limiting irradiance (LI, 300 μmolm^{-2}s^{-1}) -pre-illuminated leaves (b), and each value is the mean of 3-4 repeats with standard error expressed as a vertical bar. Asterisk * indicates that the differences between weak red irradiation-pre-illuminated and dark control leaves or between SI-pre-illuminated and LI-pre-illuminated leaves are significant ($p < 0.05$)

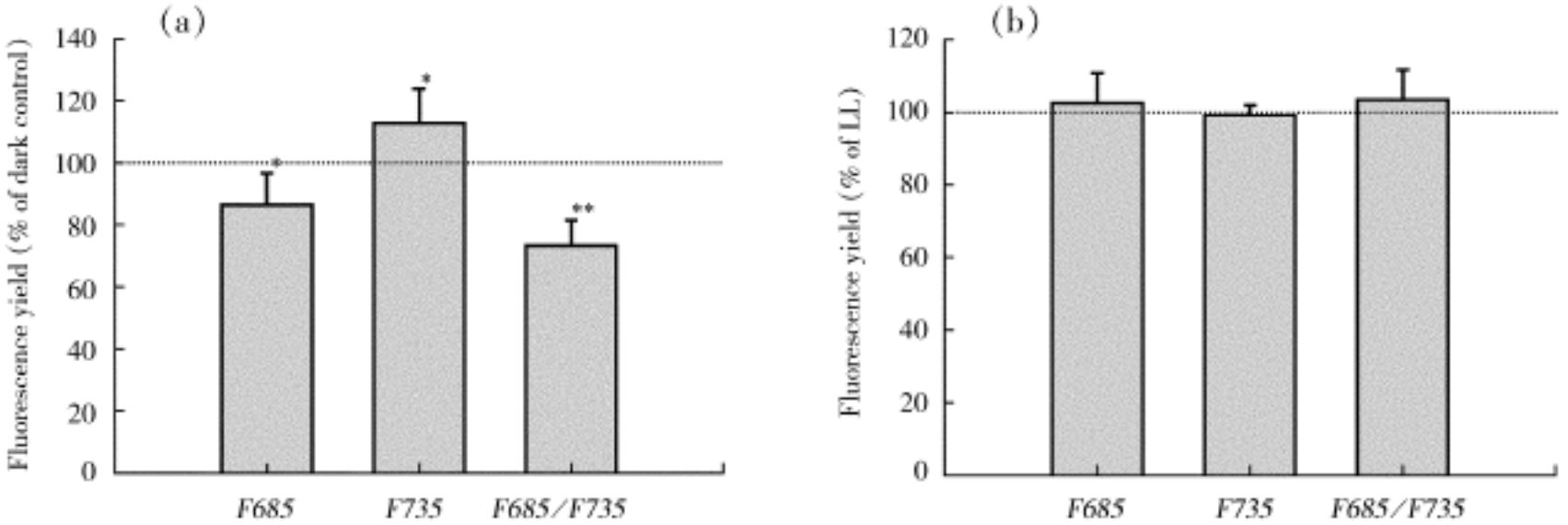

Fig. 5　Changes in 77K chlorophyll fluorescence parameters *F*685, *F*735, and *F*685 *F*735 of wheat leaves caused by pre-illumination with weak red irradiation (a, 20 μmolm^{-2}s^{-1}) or saturating white irradiation (b, SI, 750 μmolm^{-2}s^{-1}). In this figure the parameter values are expressed as the percentages of dark control (a) or limiting white irradiation (LI, 300 μmolm^{-2}s^{-1}) -pre-illuminated (b) leaves, and each value is the mean of 3-4 repeats with standard error expressed as a vertical bar. Asterisks * and ** indicate respectively significant ($p < 0.05$) and very significant ($p < 0.01$) differences between weak red irradiation-pre-illuminated and dark control leaves or between SI-pre-illuminated and LI-pre-illuminated leaves

*F*685 *F*735 accompanied by remarkably increased *F*735 (Fig.5: a). However, the pre-illumination with saturating white irradiation could not induce such changes in these parameters (Fig.5: b), indicating that weak red irradiation rather than saturating white irradiation can induce the transition from state 1 to state 2.

Discussion

Using a genetic approach it has demonstrated that the chloroplast thylakoid-associated serine-threonine protein kinase, Stt7, is required for the phosphorylation of LHC II and for state transition in *Chlamydomonas* (Depège *et al.*, 2003). Similarly, it has been shown that *Arabidopsis* mutant *stn*7 lacking chloroplast protein kinase STN7 cannot perform LHC II phosphorylation and state transition (Bellafiore *et al.*, 2005). Based on the V pattern of leaf photosynthetic response curve in *Arabidopsis* wild type (Chen and Xu, 2006),

it is supposed that the curve of its mutant *stn*7 should be the L pattern . The experimental results reported here (Fig.1) confirm this supposition, providing new evidence for SI-induced reversible dissociation of some LHC IIs from the PSII reaction center complex . The L pattern of the photosynthetic response curve in *Arabidopsis* mutant *stn*7 is obviously due to STN7 loss blocking the phosphorylation of LHC II and whereby dissociation of LHC II from the PS II core complex . The saturating irradiation-caused some LHC IIs dissociation from the PSII in *Arabidopsis* wild type suggests that STN7 is not inactivated at saturating irradiation . This is not consistent with that the protein kinase Stt7 required for LHC II phosphorylation is inactivated at high irradiation reported by Rintam ki *et al*. (2000) . Whether this contradiction originates from different tolerance to high irradiation of STN7 and Stt7 from different species (higher plant and green alga) is worth studying .

The reversible dissociation of LHC II induced by illumination with saturating irradiation, we observed, is not a phenomenon of state transitions . There are some important differences between the two things .

First, they had different mechanic characteristics for LHCIIs dissociation from PSII reaction center complex . The state transition from state 1 to state 2 is characterized not only by the dissociation of LHC II from PS II but also by the migration and attachment of dissociated LHC II to PS I (Bassi *et al.*, 1988; Vallon *et al.*, 1991; Allen, 1992; Samson and Bruce, 1995; Horton *et al.*, 1996; Gal *et al.*, 1997; Tan *et al.*, 1998; Lunde *et al.*, 2000; Snyders and Kohorn, 2001) . Lunde *et al*. (2000) have excellently demonstrated that not only does LHC II functionally connect to PSI in state 2, but also this connection is essential for state transition . At 77K the chlorophyll fluorescence emissions peaked at 685 nm (*F*685) and 735 nm (*F*735) stem from PS II and PS I antennae, respectively . Although *F*685 comes from the core antenna of PS II (Bassi *et al.*, 1990; Krause and Weis, 1991), the peripheral antenna LHC II also contributes to *F*685 because photons absorbed by LHC II can be transferred to the core antenna when they are linked to each other . A change in *F*685 or *F*735, therefore, can reflect the change in the status of association of LHC II and PS II core complex or LHCII and PSI core complex, respectively . In the study reported here the pre-illumination with saturating irradiation led to decreased *F*685 and *F*685 *F*735 without increased *F*735 in *Arabidopsis* wild type (Fig.2: a) . Therefore, the saturating irradiation-induced dissociation of LHC II, as shown by the decreased *F*685 and *F*685 *F*735, is not a phenomenon of state transition (from state1 to state 2) because the dissociated LHCII did not attach PSI, as shown by the unchanged *F*735 (Fig.2: a) .

Second, they are induced by different irradiation factors . The results reported here showed that the pre-illumination with weak red irradiation could cause the decreases in *F*685 and *F*685 *F*735 and increase in *F*735, indicating the occurrence of state transition from state 1 to state 2 in *Arabidopsis* wild type (Fig.3) and wheat (Fig.5: a) . However, that the pre-illumination with saturating white irradiation could not induce such changes in these chlorophyll fluorescence parameters, indicating no occurrence of the state transition in *Arabidopsis* wild type (Fig.2: a) and wheat (Fig.5: b) . Obviously, the induction of LHC II dissociation and the state transition depends on different irradiation, saturating white irradiation and weak red irradiation, respectively . Also, the state transition is induced only by low irradiation rather than high irradiation (Walter and Horton, 1991; Lunde *et al.*, 2002) .

Third, they perform different functions . The reversible LHC II dissociation caused by saturating illumination is a protective strategy from photodamage of the PS II reaction centers (Zhang and Xu, 2003), while state transitions serve to balance excitation energy distribution of the two photosystems (Fork and Satoh, 1986; Niyogi, 1999; Haldrup *et al.*, 2001; Kruse, 2001) . The contribution of state transition is quite limited in protecting the photosynthetic apparatus from photodamage, and the protective role is much smaller than the xanthophylls cycle- and $\triangle$pH across thylakoid membrane-dependent energy dissipation processes (Fork *et al.*, 1986; Demmig-Adams and Adams, 1992; Shen *et al.*, 1996; Hong and Xu, 1999; Hong *et al.*, 1999; Demming-Adams, 2003) .

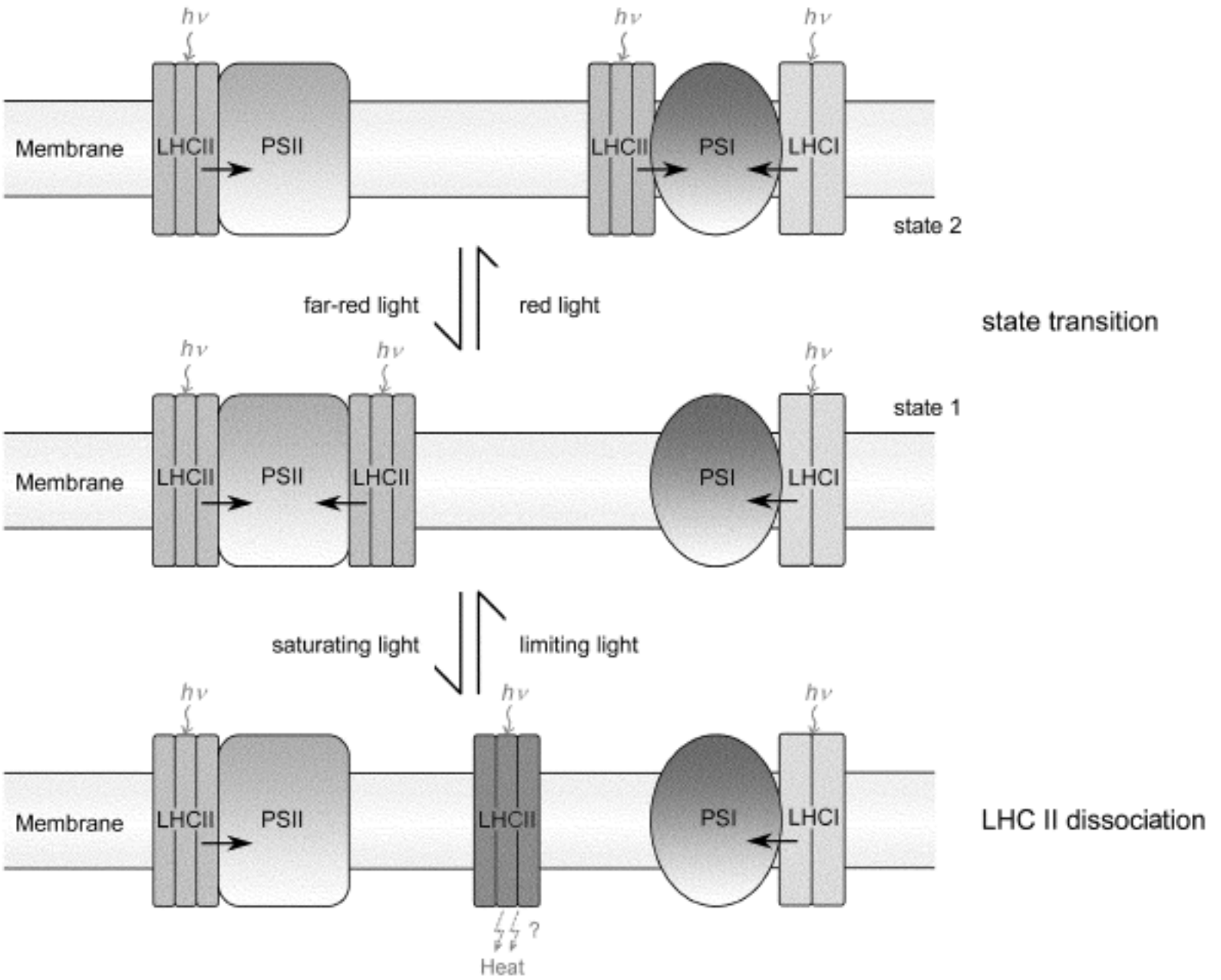

Fig . 6 Schematic model describing the differences between reversible LHC II dissociation induced by irradiance change and state transition induced by radiation quality change

PSII: photosystem II reaction center complex; PSI: photosystem I reaction center complex; LHC II: PS II light-harvesting complex; LHCI: PS I light-harvesting complex; hv: radiation energy . The arrows between two complexes indicate the direction of radiation energy transport

Main differences in induction irradiation, characteristics, and function between the reversible dissociation of LHC II and state transition are summarized in Fig. 6 .

Surprisingly, the weak red irradiation could induce significant decreases in $F685$ and $F685$ $F735$ but not cause a remarkable increase in $F735$ of soybean leaves (Fig. 4: a), indicating that the LHC II dissociation from PS II is not followed by the attachment of dissociated LHC II to PS I, namely, no typical state transition from state 1 to state 2 occurs in soybean leaves . Perhaps under the irradiation absorbed predominantly by PS II soybean leaves are able to balance excitation energy distribution between the two photosystems only by LHC II dissociation from PS II without attachment of dissociated LHC II to PS I and whereby decrease in radiation absorption of PS II . Whether the supposition is correct or not ? What controls the attachment of dissociated LHC II to PS I ? Further studies are required to answer these questions .

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