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REVIEW

Light-harvesting regulation from leaf to molecule with the emphasis on rapid changes in antenna size

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Abstract In the sunlight-fluctuating environment, plants often encounter both light-deficiency and light-excess cases. Therefore, regulation of light harvesting is absolutely essential for photosynthesis in order to maximize light utilization at low light and avoid photodamage of the photosynthetic apparatus at high light. Plants have developed a series of strategies of light-harvesting regulation during evolution. These strategies include rapid responses such as leaf movement and chloroplast movement, state transitions, and reversible dissociation of some light-harvesting complex of the photosystem II (LHCIIs) from PSII core complexes, and slow acclimation strategies such as changes in the protein abundance of light-harvesting antenna and modifications of leaf morphology, structure, and compositions. This review discusses successively these strategies and focuses on the rapid change in antenna size, namely reversible dissociation of some peripheral light-harvesting antennas (LHCIIs) from PSII core complex. It is involved in protective role and species dependence of the dissociation, differences between the dissociation and state transitions, relationship between the dissociation and thylakoid protein phosphorylation, and possible mechanism for thermal dissipation by the dissociated LHCIIs.

Keywords Chloroplast movement · Leaf movement · LHCII · Photosystem II · qE · Reversible dissociation

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Abbreviations

ATP	Adenosine triphosphate
A_{net} (or P_n)	Net photosynthetic rate
Chl	Chlorophyll
CP24	Lhcb6 (24 kDa) protein–pigment complex, a minor LHCII
CP26	Lhcb5 (26 kDa) protein–pigment complex, a minor LHCII
CP29	Lhcb4 (29 kDa) protein–pigment complex, a minor LHCII
CP43	A core antenna complex of PSII
$C_2S_2M_2N_2$	PSII supercomplex, a dimeric core complex with six different type (S, M, N, for strong or tight bound, middle-intensity bound, and loose bound, respectively) LHCII trimers
Cyt b_6f	Cytochrome b_6f complex
D1	D1 protein of the photosystem II core complex
D2	D2 protein of the photosystem II core complex
ΔpH	Trans-thylakoid membrane proton gradient
ELIP	Early light-induced protein
ETC	Electron transport chain
F_{685}	Chlorophyll fluorescence emissions peaked at 685 nm
F_{735}	Chlorophyll fluorescence emissions peaked at 735 nm
FSBA	5′-*p*-Fluorosulfonylbenzoyl adenosine
F_v/F_m	Maximal or potential photochemical efficiency of photosystem II in dark-adapted leaves
HLIP	High light-induced protein
LHC	Light-harvesting complex
LHCII	Light-harvesting complex of the photosystem II

LHCII-L	Loose bound LHCII
LHCII-M	Middle-intensity bound LHCII
LHCII-S	Strong bound LHCII
LHCSR	Light-harvesting complex of green algae
Lut	Lutein
NPQ	Non-photochemical quenching of chlorophyll fluorescence or excitation energy
P680	Chlorophyll *a* molecule of the PSII reaction center
PHOT	Phototropin
PGR5	Proton gradient regulator 5
PGRL1	Ferredoxin–plastoquinone reductase 1
PQ	Plastoquinone
PSI	Photosystem I
PSII	Photosystem II
PsbS	PsbS protein, a subunit of PSII
Phy	Phytochrome
qE	Chlorophyll fluorescence quenching or thermal dissipation dependent on trans-thylakoid membrane proton gradient or feedback de-excitation
qI	Photoinhibitory quenching
qT	State transition-dependent quenching
qZ	Zeaxanthin-dependent quenching
RC	Reaction center
STN7	Protein kinase for LHCII protein phosphorylation in higher plants
STN8	Protein kinase for PSII core protein phosphorylation
Stt7	Protein kinase from green algae
TM	Thylakoid membrane
Zea	Zeaxanthin

Introduction

Under natural conditions, sunlight is energy resource of plant photosynthesis. Deficiency of light inevitably limits photosynthesis. Excessive light, however, may induce photoinhibition of photosynthesis and even photodamage of the photosynthetic apparatus. Unfortunately, plants always live in the sunlight-fluctuating environment in nature. The sunlight intensity incident on the upper layer leaves of a canopy changes in a range of the photosynthetic photon flux densities from 0 in the night to about 2000 μmol m^{-2} s^{-1} at midday. So plants often encounter either light deficiency (in the early morning and toward evening, or on cloudy days, especially in those middle and bottom layer leaves of canopies) or light excess cases (around midday on clear days) since the saturating light intensity for photosynthesis in general is about 800–1600 μmol m^{-2} s^{-1} in most sun plants or sun leaves. Therefore, regulation of light harvesting is absolutely essential for photosynthesis in order to maximize light utilization at low light (LL) and avoid photodamage at high light (HL). During evolution, indeed, plants have developed a series of strategies to regulate light harvesting for photosynthesis.

The strategies of light-harvesting regulation include rapid and slow ones. The rapid regulation strategies, including leaf movement, chloroplast movement, state transitions, and reversible dissociation of the peripheral light-harvesting antenna from the photosystem II (PSII) core complex, can occur within several minutes. The slow regulation strategies, e.g., the changes in the protein abundance or size of light-harvesting antenna and the modifications of leaf morphology, structure, and components, are generally accomplished within several hours or days. These regulations operate, respectively, at the organ level via leaf movement, at the cell level via chloroplast movement, at the thylakoid membrane (TM) level via state transitions, or at the molecular level via changes in the contents of leaf compositions. Changes in the size of light-harvesting antenna include short-term response by reversible dissociation of light-harvesting complex of the PSII (LHCII) from the PSII core complex and long-term acclimation by light-intensity-dependent modification of development or gene expression.

On light-harvesting regulation, there have been many reports and review papers (e.g., Björkman and Demmig-Adams 1994; Horton et al. 1996, 2000; Horton 2012; Ruban 2013; Rochaix 2014; Ruban 2015). In this review, the strategies of light-harvesting regulation including leaf's morphological, physiological, and biochemical changes are discussed with the emphasis on rapid changes in antenna size.

Leaf movement

Hundreds of years ago, in fact, some scientists noted the circadian rhythm of leaf movement in plants, and Darwin (1880), the originator of the evolution theory, established the science of plant movement. In a recent review focusing on short-term mechanisms of plant response to light, Ruban (2015) definitively introduced Darwin's observations on the plant dia- and paraheliotropisms.

Under full intensity of sunlight, the leaves of many plants carry out the paraheliotropic leaf movement to lessen light absorption. Light-avoiding leaf movement of

some plants particularly in legumes (Koller 1990) is an important regulatory pattern of light harvesting. Under LL, and lower temperatures, light-accumulating leaf movement may enhance light absorption and raise leaf temperature, leading to an increase in photosynthesis, while light-avoiding or paraheliotropic leaf movement may decrease both light absorption and leaf temperature, eliminating damage of the photosynthetic apparatus under HL and high temperature. For instance, the paraheliotropic leaf movement protected water-stressed *Macroptilium atropurpureum* DC. Cv. Siratro leaves from damage due to excess light and high leaf temperature. When the leaves were restrained to a horizontal position, photodamage occurred, and the degree of this damage increased along with the prolonging of the exposure to HL (Ludlow and Björkman 1984). Some experimental results in *Bauhinia tenuiflora* suggested that leaf fold themselves under HL may remedy the deficiency of physiological photoprotection capacity (Huang et al. 2012). Similar to *B. tenuiflora*, leaf pose of *Calathea lutea* changed also under different light intensities: leaf blades opened and flattened, so that their green upper surfaces faced sunlight under LL in the early morning to maximize light absorption, while leaf blades closed and their white lower surfaces faced sunlight under HL around midday to minimize light absorption, as shown in Fig. 1 (Xu 2013).

Leguminous species perform leaf movement by means of the turgor pressure changes in the motor cells at the pulvinus in the base of each lamina.Under the light conditions, potassium ions enter the motor cells through their plasmalemma, accompanied by entering of mass water, whereby the turgor pressures of these cells increase, so that leaves become flat. On the contrary, in the dark conditions, the leaves fold because an opposite process occurs. Light is the primary driving force of leaf movement, and the movement is also regulated by leaf water status and temperature. The paraheliotropism or light-avoiding leaf movement may result in 40–70 % of incident light on leaf surface and leaf temperature 5–10 °C lower, compared with restrained leaves (Ludlow and Björkman 1984; Gamon and Pearcy 1989; Pastenes et al. 2005). Thus, light stress and photodamage are effectively alleviated.

For a long period, the molecular mechanism of leaf movement has been unclear. Until the year 2000, the discovery of sugar–phenol compounds controlling leaf movement revealed the mechanism (Ueda and Nakamura 2010). These phenolic compounds interact with some specific target proteins on the plasmalemma of the motor cells. Moreover, there are different switch compounds of leaf movement and their specific target proteins in different genus plants.

Fig. 1 Light-avoiding leaf movement. Leaf poses of *Calathea lutea* (Aubl.) Schult change with light intensity: leaf blades open and become flat, so that their *green upper surfaces* face sunlight under low light in the early morning (*above photo*), maximizing light absorption, while leaf blades close and their *white lower surfaces* face sunlight under high light around midday (*bottom photo*), thereby minimizing light absorption. These photos were taken at the Xishuangbanna Tropic Botanical Garden of Chinese Academy of Sciences in Southwest China

Chloroplast movement

In response to the changes in light intensity, chloroplast movement is also a rapid regulatory pattern of light harvesting. This regulatory pattern exists universally in plant kingdom. In the cell, chloroplasts are linked with the actin microfilaments of the cytoskeleton, and the latter controls the former to locate in a definite position within the cell. Under LL, chloroplasts arrange along the upper and lower cell walls vertical to the rays to maximize light capture, whereas they move to the side walls parallel to rays and shade themselves by mutually shielding each other to minimize incident light. Light is the driving force of chloroplast movement. In most species of plants, the effective wavelengths inducing chloroplast movement are in the blue light region, but red light is also effective in some lower plants such as fern and moss (Kadota et al. 2000). There have been some special reviews about chloroplast

movement (Haupt and Scheuerlein 1990; Wada et al. 2003; Sato and Kadota 2006).

Photoreceptors

The phototropins (PHOTs), blue light receptor controlling chloroplast movement, have been identified by the genetic analysis of *Arabidopsis* (Kagawa et al. 2001; Jarillo et al. 2001; Sakai et al. 2001). Kagawa et al. (2001) isolated *Arabidopsis* mutant failing to show the typical light-avoiding chloroplast movement under HL, and identified the mutant gene and the blue light receptor protein controlling the movement, revealing the molecular mechanism of the light-avoiding chloroplast movement. Among the PHOTs, PHOT2 mediates both light-accumulating and light-avoiding chloroplast movements, while PHOT1 involves only in light-accumulating chloroplast movement (Sakai et al. 2001). These PHOTs regulate not only chloroplast movement, but also stomatal opening (Huala et al. 1997; Kinoshita et al. 2001) and stem phototropic curvature (Sakai et al. 2001). Through the adjustment of leaf phototropism, chloroplast relocation, and stomatal aperture, net photosynthetic rate is maximized, so the PHOTs are in fact the sensors of light direction and intensity for photosynthesis.

The PHOTs consist of the blue light absorption region and protein kinase region. The former absorbs blue light by the bound flavin mononucleotide (FMN) and promotes the kinase activity, and the latter is related to signal transduction (Kagawa 2003). The velocity of chloroplast avoidance movement is light intensity or fluence rate dependent, and the amount of light-activated PHOT2 likely plays a role in the movement (Kagawa and Wada 2004). In the dark conditions, the PHOTs are located at the cytoplasmic membranes (Gallagher et al. 1988; Palmer et al. 1993; Sharma et al. 1997; Sakamoto and Briggs 2002). However, after blue light illumination, some PHOTs leave the cell membranes and enter into the cytoplasm (Knieb et al. 2004).

In addition, the red light- and far-red light-absorbed phytochrome (Phy) is also involved in chloroplast movement of algae, moss, and fern. A study suggested that phytochromes A and B (phyA and phyB) may contribute to blue light-induced chloroplast movements by modulating the transition between the HL and LL responses mediated by PHOT1 and PHOT2. However, it is still unclear whether phyA and phyB are acting directly to enhance the LL response signal or they have different effects (DeBlasio et al. 2003).

Mechanism

The whole process of chloroplast movement includes at least three phases: photoperception, signal transduction, relocation and anchoring of chloroplasts. Moreover, the actin filaments may play important roles in the relocation and anchoring (Takagi 2003).

Although the two proteins bound directly to PHOT1 (Motchoulski and Liscum 1999; Inada et al. 2004) and 14-3-3 proteins (Ferl 1996) have been found to be binding partners of PHOTs, and PHOT-regulated activation of Ca^{2+}-permeable channels on the plasma membrane (Harada et al. 2003; Stoelzle et al. 2003) has also been observed, the precise downstream signal transduction events following light perception by PHOT are still unknown. It was thought that the motility systems for chloroplast movement are dependent on the actin filaments and myosin motors, and chloroplasts move along both tracks of the actin filaments and microtubules. Furthermore, some data suggested that red-light signals are transmitted to the microtubule system, whereas blue-light signals activate both the actin filaments and microtubule system, and that the actin filaments also change their organization after chloroplast photo-relocation (Sato and Kadota 2006).

Ecological significance

The adaptive advantage of chloroplast movement is to perform efficient photosynthesis in a fluctuating light environment. The light-accumulating movement under LL has long been considered as a means of maximizing light capture for photosynthesis. Therefore, the fern mutant with much lower sensitivity to LL (Kawai et al. 2003) cannot enhance light capture by light-accumulating movement under LL. On the other hand, the light-avoiding movement may protect the photosynthetic apparatus from photodamage under HL (Park et al. 1996). The experiments using *Arabidopsis* mutants defective in chloroplast avoidance movement showed that these mutants are more susceptible to photodamage and their leaf bleaching occurs faster than wild-type plants under HL (Kasahara et al. 2002). However, the chloroplast movement is essential or effective only for the plants grown in an environment fluctuating substantially in light intensity, whereas it is not very important for those plants grown in a constant light environment (Augustynowicz and Gabrys 1999).

In addition, the chloroplast "clumping phenomenon" in some succulent plants (Kondo et al. 2004) and aquatic plants (Sharon and Beer 2008; Sharon et al. 2011) may be also a protective mechanism against HL- or ultraviolet rays-induced damage to chloroplasts themselves and/or cell nucleotides by shading.

State transitions of the thylakoid membrane

State transitions of the TMs were found independently by Murata (1969) and Bonaventura and Myers (1969). These transitions are the regulatory mechanisms to maintain the

balances of light energy distribution and light excitations of reaction center (RC) chlorophyll (Chl) molecules between the two PSs (PSI and PSII). Due to the differences in light absorption characteristics between the two PSs and natural changes in sunlight quality or wavelength incident on leaf surface during a day, the light absorption and light excitation between the two PSs are often unbalanced, so the adjustment by state transitions are required (Fork and Satoh 1986).

PSI absorbs preferentially far-red light (wavelength more than 700 nm), whereas PSII absorbs preferentially red light (wavelength less than 700 nm). Thus, when the TMs are illuminated by red light the light energy absorbed by PSII is more than that absorbed by PSI, the membranes change into state 2, leading to an increase in the light energy absorbed by PSI and a new balance of the reached light energy between the two PSs. In contrast, when the TMs are illuminated by far-red light, the light energy absorbed by PSI is more than that absorbed by PSII, and the membranes change into state 1, thereby also resulting in a new balance of the light energy absorbed by RCs between the two PSs. Obviously, the state transitions are mainly some responses to changes in light quality, different from other strategies or patterns of light-harvesting regulations such as leaf movement and chloroplast movement which are always induced by changes in light intensity.

Mechanism

During state transitions, the key reactions are the protein phosphorylation and dephosphorylation of PSII light-harvesting complexes (LHCIIs). Plastoquinone (PQ) and cytochrome b_6f complex (Cyt b_6f) are probably the redox sensors of the protein phosphorylation regulation (Bennett 1991; Gal et al. 1997). When the TMs transform from state 1 to state 2, some phosphorylated LHCIIs dissociate from PSII core complexes, and migrate to and associate with PSI (Bassi et al. 1988; Vallon et al. 1991; Samson and Bruce 1995; Snyders and Kohorn 2001). The H subunit of PSI is essential for this association (Lunde et al. 2000). When the TMs transform from state 2 to state 1, the phosphorylated LHCIIs are dephosphorylated, and leave PSI and migrate to PSII, and then re-associate with PSII. A protein phosphatase PPH1 is specifically required for the dephosphorylation of LHCII (Shapiguzov et al. 2010). A recent study showed that one PSII supercomplex has four LHCII trimers ($C_2S_2M_2$), and the two loosely associated LHCII trimers leave the supercomplex and migrate to PSI during transition from state 1 to state 2 in *Arabidopsis thaliana* (Wientjes et al. 2013a).

Interestingly, protein phosphorylations during state transitions occur not only in the major light-harvesting complex LHCII, but also in some PSII core subunits and the minor LHCII such as CP29. For instance, in green alga 15 TM proteins including CP29 were phosphorylated during state transitions, and the phosphorylation sites of CP29 were different at state 1, state 2, and under HL (Turkina et al. 2006). It was postulated that CP26 and CP29 shuttle between PSII and PSI during state transitions, acting as docking sites for the trimeric LHCIIs on PSII and PSI (Takahashi et al. 2006).

Most people thought that during state transitions, the regulation of excitation energy distribution is achieved by the movement of some light-harvesting antenna from one PS to another, i.e., by changes in light absorption cross section of the two PSs, but not by a change in spillover of excitation energies between PSII and PSI (Malkin et al. 1986; Veeranjameyulu et al. 1991; Delosme et al. 1996). However, some studies suggested that the changes in excitation distribution are not only related to modification of light absorption cross section but also involved in spillover variation (Dau and Hansen 1988; Canaani 1990), and the spillover change is a faster response to the unbalance of light absorption between the two PSs (Tan et al. 1998).

Protein kinases

The protein kinases bound in the TMs catalyze the phosphorylation of LHCII during state transitions. The protein kinases Stt7 from green algae *Chlamydomonas* (Depege et al. 2003) and protein kinase for LHCII protein phosphorylation in higher plants (STN7) from terrestrial plants (Bonardi et al. 2005) have been identified. The redox status of the photosynthetic electron transport chain (ETC) directly controls state transitions. When the electron carriers of the ETC, for example, PQ, are reduced, the protein kinases for LHCII phosphorylation are activated, whereas these kinases become deactivated when the electron carriers are subsequently re-oxidized. In the kinase activation/deactivation process, the Cyt b_6f complex transmits the redox signal of electron carrier to the kinase (Zito et al. 1999). The effect of redox status of the PQ pool on the kinase has been demonstrated (Ruban and Johnson 2009).

After illumination by PSI-preferentially absorbed light for several days, the PSII antenna in terrestrial plants became larger, while the PSII antenna became smaller after illumination by PSII-preferentially absorbed light. No such change occurred in the STN7-deficient mutant after suffering same treatments, indicating that STN7 functions both in short-term response and long-term acclimation to light. Also, the slower growth of the *stn7* plants might be due to disturbance of transcriptional regulation rather than defects in state transitions (Bellafiore et al. 2005). It has been clarified that STN7 kinase is the only enzyme known so far that is common to both state transitions and long-term alterations in thylakoid composition (Pesaresi et al.

2009). In the absence of the STN7 kinase, the high-efficiency LHCII [low non-photochemical quenching of chlorophyll fluorescence or excitation energy (NPQ)] overexcites PSII relative to PSI, leading to strong reduction of the ETC. Hence, strongly fluctuating light can induce drastic fluctuation in the redox state of the ETC and stunted growth of the *stn7* mutant (Tikkanen et al. 2010). Interestingly, the STN7 can phosphorylate not only the LHCII proteins but also the core antenna protein CP43, and the phosphorylation of CP43 is minimized under limiting light illumination and maximized at excess light (Tikkanen et al. 2010). This may imply that the STN7 kinase and CP43 play a role in photoprotection under conditions of excess light.

Other roles

Although state transitions may balance light absorption and coordinate electron transport between the two PSs, they are not essential for plant survival. There was no change in phenotype of *Arabidopsis* mutant failing to carry out state transitions because of lacking PSI-H subunit and STN7 (Lunde et al. 2003).

There is such a close interaction between the redox status of photosynthetic electron transporters and state transitions that state transitions may serve metabolic control and signal transduction (Eberhard et al. 2008). The mobile LHCII antenna accounts for 80 % of the total PSII antenna in *Chlamydomonas* but only 15–20 % in *Arabidopsis* (Delosme et al. 1996). Therefore, in green algae, the role of state transitions is not only balancing light absorptions of the two PSs, but also enhancing the function of PSI, being a switch from preferential noncyclic electron transport to preferential cyclic electron transport (Finazzi et al. 1999, 2002; Wollman 2001; Finazzi and Forti 2004). In *Chlamydomonas*, a supercomplex, including PSI, Cyt b_6f, ferredoxin–NADPH reductase, and the ferredoxin–PQ reductase (PGRL1; Hertle et al. 2013), is involved in the cyclic electron flow (Iwai et al. 2010). However, there is a study showing that the cyclic electron flow is redox controlled and is independent of state transitions in green algae (Takahashi et al. 2013). In *Arabidopsis*, PGRL1 and proton gradient regulator (PGR5) are involved in the switch between the linear and cyclic electron flows (DalCorso et al. 2008).

State transitions seem to be involved in coordinating the signal nets of gene expressions between nucleus and chloroplast (Bellafiore et al. 2005). One important dual role of state transitions in algae and higher plants is maintaining the redox poise of PQ pool and responding to metabolic needs (Rochaix 2014).

State transitions are often related to LL, whereas its physiological significance under HL seems to be an open problem. The Chl fluorescence analysis results of wheat suggested that the contribution of state transitions to photoprotection is much less than those of thermal dissipation mechanisms dependent, respectively, on the trans-TM proton gradient (ΔpH) and the xanthophyll cycle (Hong et al. 1999). However, the green algae seem to be different from higher plants in the role of state transitions under HL. In *Chlamydomonas reinhardtii*, HL may induce both *qE* and state transition from state 1 to state 2. Hence, besides *qE*, state transitions also play a photoprotective role during HL acclimation, most likely by decreasing hydrogen peroxide production (Allorent et al. 2013).

Challenge

It is generally considered that the balance of energy distribution and excitation between the two PSs is maintained by state transitions in the short term and by PS stoichiometry adjustment in the long term (Dietzel et al. 2008; Eberhard et al. 2008). Nevertheless, these concepts are recently challenged by some experimental results in *A. thaliana*: under all growth conditions [LL, moderate light (ML), HL, sunlight), a large part of the PSI population was complemented with one LHCII trimer, that is presented as PSI-LHCII (65, 54, and 40 % for LL, ML, and HL, respectively), exhibiting a typical character of state 2 (Wientjes et al. 2013b). These results imply that some LHCII trimers are still phosphorylated and linked with PSIs together, even though the protein kinase STN7 responsible for the transition to state 2 is inhibited under HL or that the inhibition of STN7 by HL is not absolute.

Recently, Tikkanen et al. (2011) presented a model describing the relationship between the LHCII protein phosphorylation via the STN7 kinase and NPQ: the NPQ and LHCII protein phosphorylations are activated under opposite light conditions and control cooperatively chloroplast redox balance under fluctuating light illumination. It seems that a long-held view about the possible role of state transitions is overturned.

Reversible dissociation of some LHCIIs: rapid changes in the size of light-harvesting antenna

Based on a reversible dissociation of LHCII from PSII at temperatures above 35 °C, it was proposed that LHCII dissociation could be a short-term regulatory mechanism for avoiding overexcitation and destruction of PSII in periods of very HL intensities during the course of a day (Sundby and Andersson 1985). Through similar experiments, Ruban and Trach (1991) added evidence from excitation fluorescence spectra for heat-induced LHCII dissociation but not for HL-induced LHCII dissociation and its protective role supposed by Sundby and Andersson (1985).

Experimental evidence for LHCII dissociation caused by high light

First, the sucrose gradient centrifugation experiments provided biochemical evidence for LHCII dissociation. After the centrifugation of the TMs, the amount of LHCII from saturating light-illuminated soybean leaves decreased in lower green layers but increased in upper green layers, compared to those from dark-adapted leaves, indicating that dissociations of some LHCIIs occur from PSII core complexes. Also the LHCII dissociation caused by illumination with saturating light was reversible, and the dissociation and the subsequent re-association in the dark conditions depended on phosphorylation and dephosphorylation of the thylakoid proteins, respectively (Hong and Xu 1999a).

Second, the measurements of PSII electron transport rate also provided strong biochemical evidence for LHCII dissociation. The light-saturated PSII electron transport rate changed little, while the light-limited PSII electron transport rate declined significantly in the thylakoids from soybean leaves pre-illuminated with saturating light (Cai and Xu 2002; Zhang and Xu 2003a, b; Chen and Xu 2006). This may be explained by the fact that the pre-illumination with saturating light induces dissociation of some LHCIIs from PSII core complexes, leading to the smaller antennae of these PSII core complexes. Under limiting light illumination, the smaller antennae must lead to a decreased PSII electron transport rate, but the rate measured under saturating light illumination did not decline since saturating light illumination can eliminate the unfavorable effect of the smaller antennae on the rate.

Third, the analyses of low-temperature (77 K) Chl fluorescence provided biophysical evidence for LHCII dissociation. At 77 K, the Chl fluorescence emissions peaked at 685 nm (F_{685}) and 735 nm (F_{735}) stem from PSII and PSI antennae, respectively. Although F_{685} comes from the PSII core antenna (Bassi et al. 1990; Krause and Weis 1991), the peripheral antennae of LHCIIs also contribute to F_{685} because photons absorbed by the LHCIIs can be transferred to the core antennae when they are linked to each other. A change in F_{685}, therefore, can show the changes in the association statuses of LHCII and PSII core complexes, provided there is no change in the amount of LHCII. The significant decreases in F_{685} and F_{685}/F_{735} of saturating light-illuminated soybean leaves indicated the occurrence of dissociation rather than damage or degradation of some LHCIIs. The possibility of LHCII damage or degradation was ruled out by subsequent rapid recovery of these parameters under the dark conditions (Hong and Xu 1999a; Cai and Xu 2002) or limiting light illumination, and by the unchanged amount of LHCII after illumination with saturating light (Chen and Xu 2006).

Fourth, the measurements of leaf gas exchange supplied the important physiological evidence for LHCII dissociation. As is well known, during photosynthesis, the light energy used by the RCs of PSII is largely from major LHCs or antennae LHCIIs. Also, the magnitude of net photosynthetic rate (P_n or A_{net}) depends on both light intensity and antenna size under limiting light illumination. Therefore, it is reasonably supposed that a decrease in the size of light-harvesting antenna due to saturating light illumination-induced dissociation of some LHCIIs must lead to a significant decline in leaf A_{net} measured under limiting light illumination. Leaf gas exchange experiments have demonstrated this supposition. After light-intensity transition from saturating to limiting one, A_{net} in soybean leaves declined first to a level much lower than that under limiting light illumination before illumination by saturating light; afterward it rose slowly within about 10 min to a steady level identical to that under limiting light illumination before illumination by saturating light. This phenomenon may be explained by the fact that under saturating light illumination, some LHCIIs dissociate from PSII core complexes, and the dissociated LHCIIs subsequently re-associate to these core complexes under limiting light illumination. In contrast with soybean, wheat had a different photosynthetic response to light-intensity transition. After light-intensity transition from saturating to limiting one, A_{net} in wheat leaves immediately dropped to a steady level identical to that under limiting light illumination before illumination by saturating light. In other words, in wheat leaves, there was no such a process where A_{net} declined first and then rose slowly in response to light-intensity transition. According to these different shapes of response curves, they were defined as V and L types or patterns for soybean and wheat, respectively (Chen and Xu 2006). Figure 2 is a scheme describing the two different responses to light-intensity transition from saturating to limiting one. It is worth noticing that the response patterns must be examined under saturating light and nonstress conditions; otherwise, the obtained result may be an artifact leading to a mistaken judgment about the response pattern.

The V pattern of photosynthetic response to light-intensity transition in soybean leaves cannot be explained by changes in stomatal conductance or photorespiratory rate. The substantial decline in A_{net} of soybean leaves after transition from saturating to limiting light one is mainly due to a lowered photosynthetic activity of mesophyll cells rather than due to a lowered stomatal conductance, because the lowest A_{net} was always accompanied by a maximal but not a minimal intercellular CO_2 concentration. Although, after light-intensity transition from saturating to limiting one, the lowered photorespiratory CO_2 evolution may lead to increased A_{net}, the adjustment of photorespiratory rate is much faster than change in the photosynthetic response

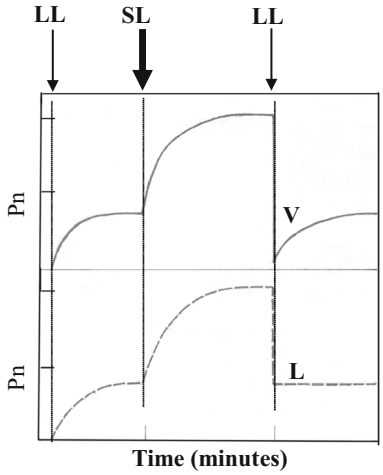

Fig. 2 Scheme describing the two patterns of leaf photosynthetic response to light-intensity transition from saturating to limiting one. The letter *L* and *V* represent, respectively, the two patterns (or types). The letters *LL* and *SL* indicate illuminations with limiting light and saturating light, respectively. P_n represents the net photosynthetic rate. After light intensity changes from saturating to limiting one, P_n first declines to a level lower than that steady level under limiting light illumination, then increases gradually to the steady level identical to that under limiting light illumination; the shape of P_n curve is similar to letter *V* for some plant species such as soybean and rice, while P_n drops immediately to the steady level without a gradual increase after light intensity changes from saturating to limiting one; i.e., the shape of P_n curve is similar to letter *L* for some plant species such as wheat and maize

curve. Moreover, wheat with higher photorespiratory rate has no slow rise of A_{net} after light-intensity transition (Chen and Xu 2006).

Interestingly, the two different patterns, L and V, of leaf photosynthetic response to light-intensity transition were also observed, respectively, in a rice mutant with decreased LHCII content and its wild type (Zhenhui 249) (Chen and Xu 2006), demonstrating the link between the V pattern of photosynthetic response and reversible LHCII dissociation. Perhaps the mutant having substantially decreased LHCII content seldom encounters the danger of photodamage to the photosynthetic apparatus by excess light, so the dissociation of some LHCIIs is not necessary for it under HL. For the V pattern of leaf photosynthetic response to light-intensity transition, of course, apart from the reversible dissociation of some LHCIIs, one perhaps has alternative explanation such as chloroplast movement. Nevertheless, the results of electron transport rate measurement from isolated thylakoids mentioned above may exclude the possibility.

In addition, the experiments of trypsin treatment inducing change in the PsbS protein amount provided new evidence for LHCII dissociation. The PsbS protein located between LHCII and PSII core complex plays an important role in thermal dissipation of excessive light energy, as shown by an excellent study (Li et al. 2000). PsbS is a highly hydrophobic polypeptide having four membrane-spanning helices, and its N-terminal domain and the domain between the second and third helices are susceptible to trypsin attack. When LHCII is removed from the PSII core complex and these domains are exposed to the stroma of chloroplast, the PsbS protein is easily degraded by trypsin (Kim et al. 1994). The experiments showed that trypsin treatment resulted in a remarkable decrease in the PsbS protein amount of the thylakoids from saturating light-illuminated but not in those from dark-adapted and dark-recovered soybean leaves. However, the trypsin treatment did not cause such a decrease in the PsbS protein amount of the thylakoids from saturating light-illuminated wheat leaves (Liao and Xu 2007). These results support the conclusion that saturating light illumination induces reversible dissociation of some LHCIIs from the PSII core complexes in soybean leaf but not in wheat leaf.

Besides these results listed above, there are even more reports about the light-induced dissociation of some LHCIIs from PSII core complex provided by other research groups (e.g., Miloslavina et al. 2008; Betterle et al. 2009; Holzwarth et al. 2009).

Protective role of the LHCII dissociation

Since light energy used by the PSII RCs during photosynthesis comes mainly from LHCIIs, saturating light illumination-caused dissociation of some LHCIIs must result in decrease of light energy transferred to the PSII RCs. Furthermore, the LHCII dissociation is linked with the protein kinase-dependent phosphorylation of thylakoid proteins. Then, it is reasonable to predict that the damage to the photosynthetic apparatus must occur under HL if the LHCII dissociation is inhibited by an inhibitor of the protein kinases. The prediction has been demonstrated by the experiments using an inhibitor of the protein kinases. Illumination with saturating light led to dissociation of some LHCIIs, but PSII activity and D1 protein amount largely unchanged in soybean leaves. In contrast with these results, 5′-*p*-fluorosulfonylbenzoyl adenosine (FSBA, an inhibitor of the protein kinases) treatment with saturating light illumination inhibited LHCII dissociation and significantly decreased PSII activity and the amount of the D1 protein, indicating that some damages of the photosynthetic apparatus occur. The damage induced by FSBA treatment may also result that other protein kinases (e.g., those involved in the photosynthetic carbon reduction cycle) rather than the thylakoid protein kinase are inhibited since FSBA is not a specific inhibitor. However, this possibility has been ruled out by similar results obtained in the experiments using isolated thylakoids instead of leaves, because there is no other protein kinase in isolated thylakoids (Zhang and Xu 2003a).

The protective role of reversible LHCII dissociation is relatively limited, since only 15–20 % of total LHCIIs are mobile between PSII and PSI in higher plants (Allen 1992). In other words, at very strong light intensity, the damage to the photosynthetic apparatus is yet unavoidable in spite of dissociation of some LHCIIs. For instance, after illumination with ML (700 μmol photons m^{-2} s^{-1}, saturated for photosynthesis) for 3 h, there were no significant changes in the light-saturated PSII electron transport rate, D1 protein level, and proportion of PSII dimer/monomer in soybean leaves grown at 250–300 μmol photons m^{-2} s^{-1} in a phytotron. Although PSII photochemical efficiency expressed as the ratio of variable fluorescence intensity to maximal fluorescence intensity (F_v/F_m) declined significantly, it could recover completely after 4 h under the dark conditions. After illumination with very strong light (2000 μmol photons m^{-2} s^{-1}) for 3 h, however, significant decreases in all parameters mentioned above were observed (Cai and Xu 2002). These results clearly indicate that the illumination with ML results in reversible downregulation of some PSIIs through reversible dissociation of some LHCIIs, while the illumination with very strong light leads to damage of some PSII RCs.

On PSII photodamage a new viewpoint is that light absorption by the manganese cluster in the oxygen-evolving complex of PSII causes primary photodamage, whereas excess light absorbed by LHCs induces the inhibition of PSII repair process mainly through the generation of reactive oxygen species (Takahashi and Badger 2011). In other words, photodamage is caused by the direct effect of light on oxygen-evolving complex, whereas the HL-induced accumulation of reactive oxygen species inhibits the de novo synthesis of the PSII RC proteins, in order to repair the photodamaged PSII (Kreslavski et al. 2013). The leaf movement and chloroplast movement together with reversible dissociations of some LHCIIs from the PSII core complexes mentioned above may alleviate or avoid the damage by efficiently decreasing light absorption. The reversible downregulations or inactivations of some PSII RCs (Hong and Xu 1999b) induced by reversible dissociations of some LHCIIs are in fact apparent inactivations (Cai and Xu 2002) due to light-harvesting antenna becoming smaller rather than damaging RC itself. Yes, indeed photo-inactivation of PSII is often a photoprotective strategy but not a damaging process for plants in the field under excessive light (Anderson et al. 1997).

Species dependence of the LHCII dissociation

It is worthy of paying attention to the fact that the reversible dissociation of some LHCIIs induced by saturating light is species-dependent (Chen and Xu 2006, 2007). This species dependence may not be related to classification in taxology or systematics because the photosynthetic response to light-intensity transition may display the two different patterns (V and L) in plants of the same family, for example, rice and wheat (*Gramineae*), soybean and peanut (*Leguminosae*). Nevertheless, it seems to be related to the pathway of photosynthetic carbon assimilation. All of the examined C_4 plants (maize, green bristlegrass and thorny amaranth) display the L pattern in the photosynthetic response to light-intensity transition. This is understandable or logical. The reversible dissociation of some LHCIIs is not required for C_4 plants because they need two extra adenosine triphosphate (ATP) molecules for assimilating one CO_2 into sugar compared with C_3 plants, so their photosynthesis is not light-saturated even at full sunlight without environmental stress.

Among more than 50 plant species examined, the V pattern of photosynthetic response to light-intensity transition is often observed in some plants grown well in shade habitats, for example, sweet viburnum and soybean, while the L pattern is frequently observed in those plants grown well in sun habitats, for example, ginko and cotton (Chen and Xu 2007). Then, it is hypothesized that the two plant types exhibiting V and L patterns of photosynthetic response originated, respectively, from shade habitat and sun habitat. This hypothesis has yet to be proved.

Differences between the LHCII dissociation and state transitions

Because of some similarities in LHCII dissociation and protein phosphorylation, the LHCII dissociation caused by saturating light illumination mentioned above is probably considered as a phenomenon of state transitions. Nevertheless, a basic or key character for the state transition from state 1 to state 2 is the close link of some LHCIIs dissociated from PSII core complexes with PSIs (Lunde et al. 2000; Kouril et al. 2005), whereas under saturating light illumination, the dissociated LHCIIs from PSII core complexes did not link with PSIs together, as shown by the analyses of low-temperature Chl fluorescence (Hong and Xu 1999a; Chen and Xu 2006, 2009). And state transitions occur always under LL because HL can lead to dephosphorylation of LHCII unfavorable for state transitions (Tikkanen et al. 2010), while the LHCII dissociation with photoprotective role occurs under HL (Chen and Xu 2009). Hence, the LHCII dissociation caused by HL is not a phenomenon of state transitions, at least not a typical one. Figure 3 shows some basic differences between the LHCII dissociation and state transitions.

Relationship between the LHCII dissociation and protein phosphorylation

Based on the inhibition of dark recovery of low-temperature Chl fluorescence parameters by NaF, an inhibitor

of the protein phosphatases, it was deduced that the reversible dissociation of some LHCIIs from PSII core complexes is related to LHCII protein phosphorylation (Hong and Xu 1999a). However, the deduction encountered a severe challenge. Some experimental results showed that under LL less than growth light intensity, the LHCII phosphorylation level was higher, and the phosphorylation levels of PSII core proteins, e.g., CP43, D1, and D2, were lower; by contrast, HL stimulated the phosphorylation of PSII core proteins, but inhibited LHCII protein kinase, leading to dephosphorylation of LHCII proteins (Rintamaki et al. 2000; Hou et al. 2003; Tikkanen et al. 2010). Moreover, PSII core protein and LHCII protein phosphorylations require two different protein kinases for PSII core protein phosphorylation (STN8) and STN7, respectively (Bonardi et al. 2005). Consistent with expectation, the curve of photosynthetic response to transition of light intensity from saturating to limiting one was the V pattern in *Arabidopsis* wild type, while the curve was the L pattern in *its* mutant lacking STN7 (Chen and Xu 2009). The fact seems to imply that the reversible dissociation of some LHCIIs is indeed linked with LHCII protein phosphorylation. Obviously, more experimental studies are required to establish whether the reversible dissociation of some LHCIIs under saturating light illumination is dependent on LHCII protein phosphorylation.

Interestingly, a model describing the different roles in excitation energy distribution of PSII core protein phosphorylation and LHCII protein phosphorylation (Tikkanen et al. 2010) suggested that under LL LHCII protein phosphorylation leads to a balanced distribution of excitation energy between the two PSs, whereas under HL, phosphorylation occurs in PSII core proteins rather than LHCII proteins, so that excitation energy absorbed by LHCIIs neither transfers to PSII nor to PSI, and is dissipated by NPQ. This is to some extent consistent with the hypothesis that the saturating light-induced reversible dissociation of some LHCIIs may protect PSII from photodamage. On the

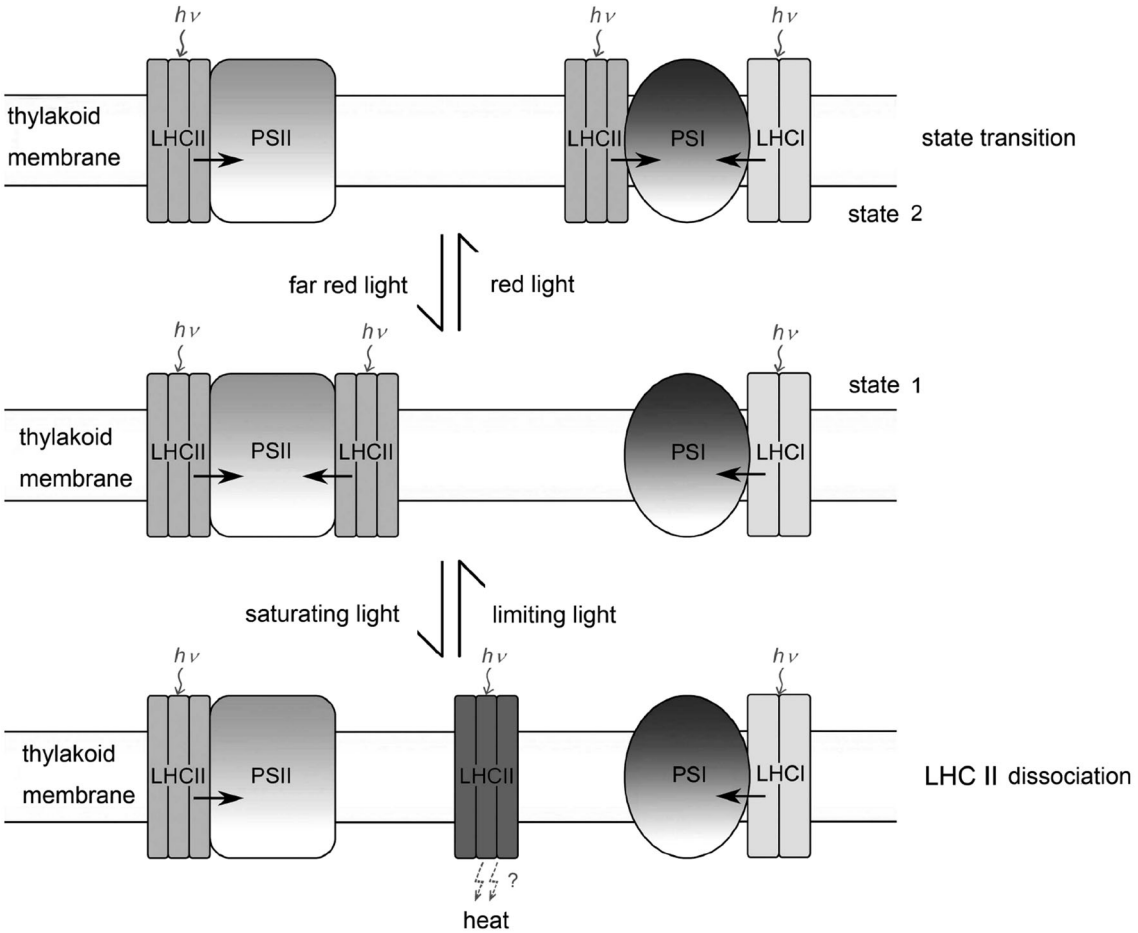

Fig. 3 Scheme depicting the differences between saturating light-caused LHCII reversible dissociation and state transitions induced by light quality change. *hv* photons, *LHCI* light-harvesting complex of photosystem I, *LHCII* light-harvesting complex of photosystem II, *PSI* photosystem I reaction center complex, *PSII* photosystem II reaction center complex. The *arrows* between two complexes indicate the direction of light energy transport

basis of this model and those facts that, under HL and low temperature, the subunit CP29 located between PSII core complex dimer and LHCII trimer was phosphorylated (Yakushevska et al. 2003) and that CP29 was a determinant of photoprotection (de Bianchi et al. 2011), it is assumed that the saturating light-induced reversible dissociation of some LHCIIs and subsequent thermal dissipation by the dissociated LHCIIs may be the results of CP43, D1, and D2 as well as CP29 phosphorylations rather than due to LHCII protein phosphorylation and repelling one another because of their negative charges (HPO_4^{2-}). This requires that some LHCIIs along with CP29 dissociate from PSII core complex and the dissociated LHCIIs do not associate with PSI. This hypothesis still needs further investigation.

Since the discovery of the TM protein phosphorylation (Bennett 1977), scientists have found 16 phosphorylation sites of 13 TM proteins and two membrane periphery proteins (Aro et al. 2004). The important factor regulating the ratio of phosphorylated/non-phosphorylated D1 proteins is the redox status of electron transport components between the two PSs, but not the light intensity itself. All factors affecting photosynthetic energy supply and consumption, including biological and abiotic stresses, can induce a high-level and light-intensity-independent D1 protein phosphorylation (Salonen et al. 1998). Although the D1 protein phosphorylation/dephosphorylation alone has no effect on the electron transport activity of PSII (Zhang et al. 2002), its successive phosphorylation and dephosphorylation are essential to the repair cycle of the D1 protein. The PSII core phosphatase is specifically responsible for dephosphorylation of the PSII core proteins (Samol et al. 2012). Besides the protective role of D1 protein phosphorylation from D1 degradation and the balancing role of LHCII protein phosphorylation in light-energy distribution between the two PSs by state transitions, the phosphorylations of the PSII core and LHCII proteins may optimize the photosynthetic electron transport of higher plant chloroplasts under fluctuating light. On the contrary, due to failure of these protein phosphorylations, the *stn7* and *stn7stn8* kinase mutants of *Arabidopsis* displayed severely stunted phenotypes under strongly fluctuating light conditions (Tikkanen et al. 2010).

Possible mechanisms for energy dissipation by the dissociated LHCIIs

Although the fitness advantage of rapid regulation of light harvesting has been elegantly demonstrated by a significant difference in seed yield between *Arabidopsis* mutants and their wild type (Kühlheim et al. 2002), the mechanism for the rapid regulation of light harvesting is not yet clear. Perhaps, the reversible LHCII dissociation from PSII core complex under saturating light illumination mentioned above is such a rapid regulation of light harvesting in plant photosynthesis. It can balance the absorption and utilization of light energy to maximize light utilization of PSII RCs under LL and to avoid photodamage to the centers under HL. Then, what is the molecular mechanism of energy dissipation by the dissociated LHCII under saturating light illumination? It is likely that the thermal dissipation is dependent on ΔpH or feedback de-excitation (*qE*). *qE* is induced by ΔpH, occurs in PSII antenna, and is involved in xanthophylls (Niyogi 1999). Recently, Ruban et al. (2012) reviewed the current state of the research on photoprotective molecular mechanism of *qE*. This mechanism may include four key elements: trigger (ΔpH), site (antenna), mechanics (antenna dynamics), and quenchers.

Link between *qE* and the LHCII dissociation

There has been evidence suggesting that upon formation of *qE,* a part of the major LHCIIs undergoes separation from the PSII core complexes (Miloslavina et al. 2008; Holzwarth et al. 2009). And the dissociation is dependent on ΔpH, PsbS, and zeaxanthin (Zea). The *Arabidopsis* mutants, *npq4* (lack of the PsbS protein) and *npq1* (lack of Zea), did not show the light-dependent LHCII dissociation and activation of NPQ, and the dissociation of a five-subunit complex, composed of the monomeric CP29 and CP24 and the trimeric LHCII-M, was indispensable for the onset of NPQ under HL (Betterle et al. 2009). Moreover, a recent study has provided direct structural evidence that formation of the photoprotective state requires a reorganization of PSII–LHCII supercomplexes involving dissociation of LHCII from PSII and its aggregation, and the reorganization can occur on a timescale consistent with formation and relaxation of *qE* (Johnson et al. 2011). Interestingly, the long-term treatment with lincomycin (a chloroplast protein synthesis inhibitor) led to a decreased PSII RC concentration; an increased LHCII component (a large part of which was separated from PSII RC complexes); a reduction in the photochemistry yield; and an increased NPQ in *Arabidopsis* plants, indicating that NPQ originates in LHCII antenna (Belgio et al. 2012).

As regards the link between NPQ and LHCII dissociations, it seems that there are some contradictory views and results. For instance, it was suggested that NPQ is a widespread event within the antenna, involving most, if not all, LHCII complexes, unlikely involving any selective detachment of LHCII from PSII (Johnson and Ruban 2009). Furthermore, a recent study showed that the functional antenna size of PSII during NPQ does not decrease, bringing the existence of a pool of detached LHCII complexes into question (Belgio et al. 2014). This result seems to disprove the hypothesis of energetic uncoupling of LHCII from PSII core complex during NPQ.

qE site

qE is located in LHCII instead of the RC (Horton et al. 1996). In plants, LHCII is not only an important regulator of light harvesting for photosynthesis but also a primary site of the thermal dissipation (Elrad et al. 2002). Under light excess conditions, LHCII can reversibly transform from effective light-harvesting state to thermal dissipation state, providing photoprotective mechanism for the photosynthetic apparatus (Pascal et al. 2005). A study showed that in vivo, there are at least two different NPQ sites in higher plants: a PsbS-dependent site (Q1) in the major LHCII detached from PSII and aggregated [middle-intensity-bound LHCII (LHCII-M), and loosely bound LHCII (LHCII-L)]; and a Zea-dependent site (Q2) in the minor antennae remaining associated with PSIIs such as CP29 and CP24. Also differently from Q1, the activation of Q2 is independent of PsbS, but strongly dependent on Zea (Holzwarth et al. 2009; Jahns and Holzwarth 2012). In addition to the major LHCII, the minor antenna complexes may also contribute to *qE* (Ballottari et al. 2010). It was postulated that the dissociated LHCII–CP24–CP29 complex is in a quenched state (Betterle et al. 2009). Recently, it was found that individual LHCII trimers possess an intrinsic capacity to switch reversibly between quenched and unquenched states using single molecule fluorescence spectroscopy (Krüger et al. 2010). The light-induced acidification of the thylakoid lumen leads to the activation of violaxanthin de-epoxidase (VDE) and then conversion of the xanthophylls bound to the LHC proteins to Zea, inducing conformational changes and switch from an efficient light-harvesting state to a thermally dissipated state in these proteins. Moreover, some conditions promoting both LHCII aggregation and NPQ may prolong the dwell time in the dissipated state (Krüger et al. 2012). Many results have suggested that *qE* occurs in the light-harvesting antenna. For example, mutant plants lacking most LHCII antenna possessed much decreased *qE* level; crosslinker that binds to protein could block *qE* due to restricting the transition of isolated LHCII from efficient light harvesting to protective states; *qE* and isolated trimeric LHCII responded in the same way to pH, antimycin A, magnesium, etc.; and *qE* was almost entirely dependent on the presence of LHCII-bound lutein (Lut) and Zea (Ruban 2013). And *qE* may occur at multiple sites rather than one site within the LHCII antennae, including CP24, CP29, and major LHCII (Rochaix 2014).

According to the Horton model, the LHCII antenna has four different structural/functional states: 1–4. The state 1 is dark-adapted, and violaxanthin-containing unquenched one. Illumination induces violaxanthin de-epoxidation and protonation of the LHCII antenna, leading to a deeply quenched state 4 by promoting LHCII aggregation. When Zea is not formed, LHCII is partially aggregated and quenched state 3. During *qE* relaxation, the LHCII antenna still contains Zea, and remains partially aggregated and quenched state 2, because it will take much longer time for the epoxidation of Zea back into violaxanthin than that for the relaxation of ΔpH (Ruban et al. 2012). Under conditions of light excess, the ΔpH triggers a reversible transformation from effective light-harvesting state to thermal dissipation state by feedback control, as shown in Fig. 4.

PsbS protein: regulator of *qE*

The nuclear-encoded PsbS protein consisting of about 205 amino acids has a molecular mass of 22 kDa (Bonente et al. 2008a, b). It may be a regulator of *qE* (Niyogi 2005). In *Arabidopsis*, mutants lacking PsbS *qE* was almost totally absent (Li et al. 2000). Also, overexpression of PsbS enhanced *qE* proportionally (Li et al. 2002). PsbS acts as a sensor of the thylakoid lumen pH and activates *qE* rapidly, likely through protonation of its acidic domains exposed to the lumen and promotion of antenna hetero-oligomer dissociation from PSII core complex (Betterle et al. 2009). Moreover, the PsbS protein controls the interactions and associations between the TM protein complexes (Horton et al. 2008; Betterle et al. 2009; Kereiche et al. 2010). PsbS and Zea may have different role in *qE*: the former seems to have an acceleration effect while the latter has a deceleration effect on *qE* recovery kinetics (Ruban et al. 2012). The PsbS protein may act as a catalyst of the LHCII conformational change (Horton et al. 2000, 2005; Bonente et al. 2008a, b), but in the absence of the PsbS protein a larger ΔpH is required to trigger the reorganization of the PSII–LHCII macro-structure linked with *qE*. Interestingly,

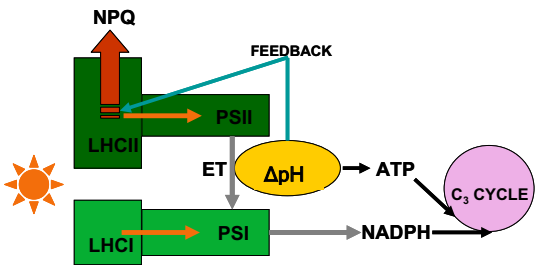

Fig. 4 The model illustrating the feedback regulation of light harvesting for photosynthesis by ΔpH, which is referred to Ruban (2013). ΔpH switches reversibly from light-harvesting state to energy dissipation state of the major antenna LHCII when ΔpH increases to a threshold due to excess light and/or ATP production going beyond its use. *ET* electron transport, *NPQ* non-photochemical quenching or thermal dissipation of excitation energy (*red heavy arrow*), *PSI* the core complex of photosystem I, *PSII* the core complex of photosystem II, *ΔpH* trans-thylakoid membrane proton gradient. *Orange-colored*, *gray*, and *black arrows* represent light energy, electric energy, and chemical energy transport, respectively, while *blue arrow* shows the feedback control by ΔpH

it was reported that the PsbS protein exists in dimeric state associated with PSII core complex in the dark conditions, while it undergoes monomerization and associates with LHCII upon illumination (Bergantino et al. 2003).

In ecological opinion, there are two kinds of thermal dissipation by the light-harvesting system: one is flexible, Zea-facilitated, PsbS-associated and controlled by ΔpH, and another is inflexible or sustained, associated with both Zea retention and PSII core rearrangement and/or degradation. The former can change into the latter at low temperatures. The molecular mechanisms for the two kinds of thermal dissipation, however, are not yet clear (Demmig-Adams and Adams 2006). It has been suggested that the presence of the PsbS protein leads to an increase in the fluidity of the membrane, accelerating the NPQ induction-necessary re-organization of the PSII macrostructure (Goral et al. 2012). Moreover, *qE* may be involved in a PsbS-catalyzed re-organization of PSII supercomplexes in the grana membrane, mediating the transition between the unquenched and quenched states (Kouril et al. 2012). However, further researches are needed to test the hypothesis.

Differently from higher plants, *C. reinhardtii* exhibits a restricted ability of NPQ upon illumination. Also most of the limited NPQ is due to state transition instead of *qE*. *qE* can be observed only when the photosynthetic capacity of cells is impaired either by lowering to ~0 °C or in mutants lacking ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) activity (Finazzi et al. 2006). The limited NPQ ability in the green alga probably is related to lack of the PsbS protein. Despite the presence of *PsbS* genes, the PsbS protein has not been detected in this green alga (Allmer et al. 2006). However, this alga has light-harvesting complex of green algae (*LHCSR*) genes absent from vascular plants and the LHCSR protein accumulation induced by HL is correlated with *qE* capacity, indicating that vascular plants and algae use different proteins in dissipation of excess light energy (Peers et al. 2009). The PSII–LHCII–LHCSR3 supercomplex formed in the HL-grown *C. reinhardtii* cells performs energy dissipation probably through following molecular steps: LHCSR3 synthesis, link of LHCSR3 with the PSII–LHCII supercomplex, protonation of LHCSR3, and change in the antenna conformation whereby to form a quenching center within the supercomplex (Tokutsu and Minagawa 2013). It should be pointed out that LHCSR is both a sensor of ΔpH and a quenching site of excess light energy in algae, whereas PsbS is only a sensor of ΔpH or regulator of *qE* but not quenching sites of excess light energy in land plants (Rochaix 2014).

Roles of zeaxanthin and lutein in *qE*

There are two different xanthophyll cycles in land plants. One is the violaxanthin cycle present in all land plants: violaxanthin is reversibly converted to Zea via antheraxanthin. Another is the Lut epoxide cycle existent only in some species: Lut epoxide is reversibly converted to Lut. Both cycles are involved in the switching of PSII from a light-harvesting state (with epoxidized xanthophylls under LL) to an energy dissipating state (with de-epoxidized xanthophylls under HL; Jahns and Holzwarth 2012). High level of Zea accelerates the formation of *qE* and retards its relaxation (Johnson et al. 2008; Nilkens et al. 2010). In *qE*, Zea may play two different roles: the direct role in energy transfer from Chl to Zea (Frank et al. 2000) or in electron transfer to a neighboring Chl, forming a Zea^{+}/Chl^{-} state (Holt et al. 2005; Ahn et al. 2008; Avenson et al. 2008, 2009), and the indirect role as an allosteric regulator controlling the efficiency and kinetics of *qE* (Johnson et al. 2008). Lut has three important functions: structural stabilization of antenna proteins, light harvesting and transfer of excitation energy to Chl, and quenching of ^{3}Chl and ^{1}Chl states in NPQ (Jahns and Holzwarth 2012).

Recently, a new component of NPQ, the Zea-dependent quenching, *qZ*, was defined (Nilkens et al. 2010). Differently from those three components (*qE*, energy- or pH-dependent quenching; *qT*, state transition quenching; and *qI*, photoinhibitory quenching) distinguished previously by Horton and Hague (1988), *qZ* is a slowly developing (10–30 min) and slowly relaxing (10–60 min) component, a kind of 'memory state' of HL stress (Horton et al. 2005). It seems that Zea is involved in all NPQ mechanisms except *qT*, operating in the major LHCIIs (*qE*), minor LHCIIs (*qZ*), and RCs (*qI*). Furthermore, in NPQ, the important role of Zea is mainly the de-excitation of excited singlet Chl (^{1}Chl*), while the unique function of Lut is the deactivation of excited triplet Chl (^{3}Chl*; Jahns and Holzwarth 2012). As for *qI*, it was proposed that *qI* is induced by the synthesis of Zea under HL and based on the conformational change in the CP26 upon binding of Zea to the allosteric site L2. Different from *qE*, *qI* is independent of both pH and PsbS. Nevertheless, *qI* and *qE* are connected through the availability of Zea for activation of PsbS. Thus, the stored Zea upon previous exposure to HL is able to trigger *qE* more rapidly (Dall'Osto et al. 2005).

Physical mechanisms

At excess light the LHCII antenna can be switched into a thermal dissipation state rapidly and reversibly (Ruban et al. 2007). It has been proposed that *qE* could be a consequence of pigment–pigment interactions within the LHCII antenna. And the Chl–Chl or Chl–carotenoid dimers may take part in this quenching (Horton et al. 1996, 2005; Pascal et al. 2005; Miloslavina et al. 2008; Holzwarth et al. 2009). Femtosecond transient absorption measurements on TMs showed selective formation of a carotenoid radical

cation upon excitation of Chl under conditions of maximal, steady-state feedback de-excitation. Using transgenic *Arabidopsis* plants, some studies confirmed that the carotenoid radical cation formation is linked the feedback de-excitation and needs Zea synthesized during HL exposure. During feedback de-excitation, the mechanism for excess energy dissipation consists of energy transfer from excited Chl molecules to a Chl–Zea heterodimer, its charge separation, and subsequent charge recombination (Holt et al. 2005). The charge transfer mechanism regulating light harvesting may operate in three minor antenna complexes: CP29, CP26, and CP24 located between PSII core complex and major LHCII complex, and the reversible conformational change of CP29 may regulate switching on or off in energy and charge transfer state of the Chl–Zea heterodimer during *qE* (Ahn et al. 2008), but not in major LHCII (Avenson et al. 2008). In addition, there have been some data supporting the viewpoint that quenching of excitation energy may be due to a Chl–Chl rather than Chl–carotenoids charge transfer (Muller et al. 2010).

Another mechanism different from the charge transfer one mentioned above operates in major LHCII trimer, and is involved in energy transfer from an excited Chl molecule to a carotenoid Lut 1. It is so called the energy transfer or excitonic interaction (Bode et al. 2009) or excitonic coupling mechanism. There has been the evidence that the quenching of excited Chl within LHCII complex is accompanied by formation of excited carotenoids Lut 1 (Ruban et al. 2007). The possible quenching sites are two Chl regions: Chl *b* 606–607 and Chl *a* 610–611–612–Lut 620 (Liu and Chang 2008). Furthermore, some studies have shown that excitonic interactions between Chls and xanthophylls may be involved in *qE* (Bode et al. 2009; Liao et al. 2010). In order to draw a refined picture of possible energy transfer or excitonic interactions in photosynthetic light-harvesting and dissipation channels, future studies need to answer which membrane organization, proteins, and pigments are predominantly involved in the changes leading to switch from light harvesting to energy dissipation (Holleboom and Walla 2014). Interestingly, it has been proposed that Lut can act as a participant of the charge transfer mechanism in the CP26 (Avenson et al. 2009). Figure 5 is an assumed scheme describing possible physical mechanisms for energy dissipation in major and minor LHCIIs.

Alteration in the LHCII protein abundance: slow changes in the size of light-harvesting antenna

The reversible dissociation of some LHCIIs from PSII core complexes is a fast response to short-term (several minutes) HL, while the decrease in the abundance of LHCII proteins is a slow acclimation to long-term (several hours or days) HL (Teramoto et al. 2002).

The core complex of PSII consists of D1, D2, Cyt b_{559}, CP43, and CP47. Each dimer of PSII core complex may bind eight main periphery antennae of LHCII trimers. The main components of LHCII trimer are Lhcb1–3 (28, 27, and 25 kDa). The main role of the Lhcb1–3 is light harvesting for photosynthesis. In addition, the Lhcb1 and Lhcb2 also have a role in the acclimation of the photosynthetic apparatus to different light conditions, and the Lhcb3 may act as an intermediary in light energy transfer from the Lhcb1/Lhcb2 antennae to the PSII core (Standfuss and Kühlbrandt 2004). The LHCII monomer isolated from spinach leaves associates with eight Chl *a* and six Chl *b* molecules, and has four binding sites of carotenoid molecules (Liu et al. 2004). However, most monomers of PSII–LHCII super-molecular complex contain only two or three but not four LHCII trimers. This means that there are some dissociated or LHCII-L trimers (Dekker and Boekema 2005). Probably, PSII core complex associates with only one LHCII trimer by Lhcb4 (CP29) and Lhcb5 (CP26), forming a basic super-molecular complex. Also this is considered as the main existing pattern of PSII in plants grown under HL (Boekema et al. 1999; Frigerio et al. 2007). In plants grown under middle- and low-intensity light, PSII associates with even more one Lhcb6 (CP24) monomer and two LHCII trimers (LHCII-M and loose bound LHCII-L) in order to enhance the capacity of light harvesting (Melis 1991; Ballottari et al. 2007). Thus, PSII–LHCII supercomplexes include two layers of Lhcb protein: the inner layer composed by CP26, CP29, and the strong bound LHCII (LHCII-S) trimer, and the outer layer consisting of CP24 and at least two LHCII trimers (M and L; Betterle et al. 2009). In other words, light intensity of plant growth have a strong effect on the amount of free and bound LHCIIs, leading to a modified ratio between different types of PSII supercomplexes, namely a PSII dimeric core (C_2) with LHCII trimer in different amounts and types (S, M), for example, $C_2S_2M_2$, C_2S_2M, C_2S_2 (Kouril et al. 2012). For example, C_2S_2 and $C_2S_2M_2$ are in general the PSII supercomplexes of plants grown, respectively, under HL and under LL (Daum et al. 2010). However, the $C_2S_2M_2$ was also observed in the HL-grown *Arabidopsis* (Kouril et al. 2012). Furthermore, the $C_2S_2M_2$ was the dominant form of PSII and the major target of structural re-arrangement due to the downregulation of Lhcb3 and Lhcb6 antenna proteins (Kouril et al. 2013). In addition, it seems to have "extra" LHCII trimers which are not present in PSII supercomplex. The exact location of these extra trimers in the TM is unknown (Van Amerongen and Croce 2013). A study showed that some extra trimers attach to PSI in the light but detach again in the dark and also under light stress conditions (Wientjes et al. 2013a).

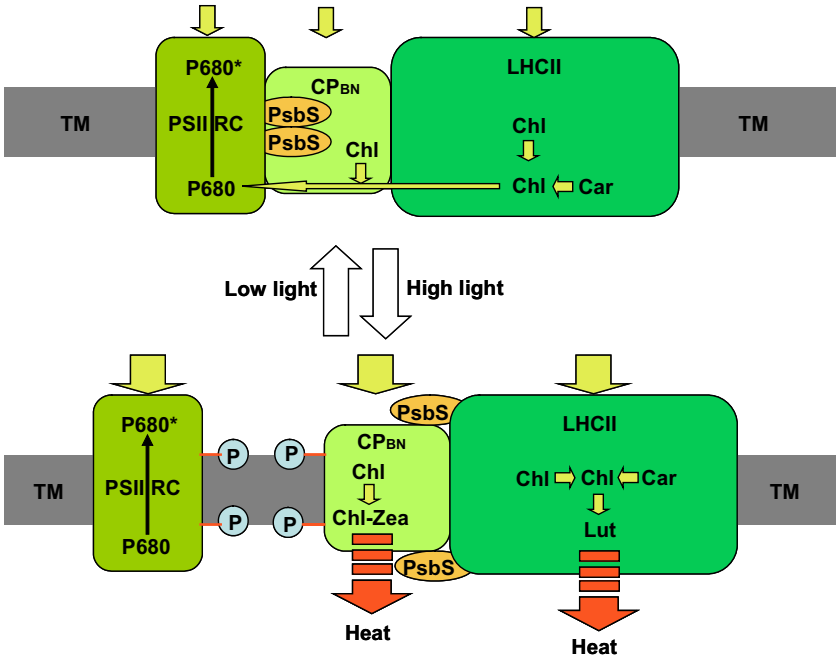

Fig. 5 An assumed model of reversible switch between light-harvesting and energy dissipation states of LHCII based on some references cited in the context. At high light conditions, some subunits of PSII core complex (PSII RC) such as D1 protein and CP43 and the minor antenna CP29 are phosphorylated, then the phosphorylated CP29 along with the major antenna LHCII dissociates from PSII RC due to electrostatic repelling one another of their $H_2PO_4^-$. At the same time, the dimer of the PsbS protein changes into monomers; then, these monomers attach to the LHCII and CP29, leading to the conformational changes of these antenna proteins and switch from ling state to thermal dissipation state. At this moment, the entire light energy absorbed by chlorophyll molecules is transferred to luteins within major LHCII and the heterodimers of chlorophyll–zeaxanthin within minor CP29, and then, this energy is dissipated as heat using energy transfer (excitonic coupling) and charge transfer (Chl* → Chl–Zea → $Chl^{-\bullet}$–$Zea^{+\bullet}$ → Chl–Zea, as shown in Holt et al. 2005) mechanisms, respectively. Here, *Chl* chlorophyll, *Chl–Zea* heterodimer of chlorophyll and zeaxanthin molecules, *LHCII* major antenna complex of PSII, CP_{BN} minor antenna complex of PSII, CP29, CP26, or CP24, *Lut* lutein, *P* $H_2PO_4^-$, *P680* chlorophyll *a* molecule of PSII reaction center, *P680** excitation state chlorophyll *a* molecule of PSII reaction center, *PsbS* PsbS protein, a subunit of PSII, *TM* thylakoid membrane. The *yellow arrows* within complexes show energy transfer direction. The *yellow arrows* outside the complexes show the incident light, and the *heavy arrows* indicate high light, while the *red arrows* represent thermal dissipation

It was recently found that the antenna size of PSII in *C. reinhardtii* is larger than that of higher plants. There are at least six LHCII trimers per dimeric core, namely the $C_2S_2M_2N_2$ supercomplex is present in *C. reinhardtii*. Also the CP24/CP29/LHCII-M is substituted by CP29/LHCII-M/LHCII-N, and LHCII-N trimer stabilizes the binding of LHCII-M trimer in the supercomplex (Drop et al. 2014).

After being transferred from LL to HL environments for several hours, the antennae of PSII of higher plants or green algae become smaller. These light-intensity-dependent changes in antenna sizes occur mainly in PSII-bound Lhcb1, Lhcb2, and Lhcb6 (CP24) proteins, bur rarely in Lhcb4 (CP29), Lhcb5 (CP26), and PSI-bound Lhca proteins (Ballottari et al. 2007). The changing into smaller of antenna size is related to both a decrease in protein synthesis and an increase in protein decomposition, and the decrease in the antenna proteins is mainly due to the declining of their syntheses (McKim and Durnford 2006). Along with the increase in light intensity, the decomposition of the antenna proteins enhanced in spinach, *Arabidopsis*, and barley leaves (Frigerio et al. 2007). Moreover, this regulation of protein synthesis occurred at posttranscriptional level but not at transcriptional level (Ballottari et al. 2007; Frigerio et al. 2007). Chloroplast redox signal, chloroplast gene expression signal, and the intermediates of Chl synthesis take part in the regulation of antenna protein (LHCB) gene expression (Strand et al. 2003; Koussevitzky et al. 2007). For example, the accumulation of Mg-protoporphyrin IX inhibited the expression of nucleus gene *LHC* (Strand et al. 2003). Light-harvesting antenna size and light-harvesting gene expression were controlled by the PQ redox state at the posttranscriptional level (Frigerio et al. 2007; Floris et al. 2013).

Modifications of leaf morphology, structure, and components

The acclimation of the photosynthetic apparatus to light environment is a complex progress, and it is performed by many ways. Apart from the slow changes in the sizes of light-harvesting antennae mentioned above, there are many

kinds of modification occurring in leaf morphology, structure, and components during acclimation.

First, the internal angles between leaf blade and stem become smaller to decrease light absorption of leaves in HL-acclimated plants (Mooney et al. 1977).

Second, leaf surface characters are changed in plants grown under intensive light. In general, 5–10 % of light incident on leaf surface is reflected. In some desert plants, the reflected light by the accumulated wax, salt, and grown pubescences on leaf surface may reach 20–25 % of the incident light (Mooney et al. 1977; Ehleringer and Björkman 1978; Ehleringer et al. 1981; Barker et al. 1997). These changes in leaf surface characters are the results of plant acclimation to unfavorable environmental conditions such as HL and drought.

Third, leaf thickness, layer numbers of the palisade cells, and chloroplast's ultrastructure are also altered after transferring plants from LL to HL conditions or the other way around for a longer term. For example, compared with sun and HL-acclimated plants, shade and LL-acclimated plants have more grana per chloroplast, with higher ratio of appressed to non-appressed TMs, larger antennae, and more PSII RCs relative to PSI RCs (Anderson 1986, 1999; Anderson et al. 1988). Obviously, these changes in chloroplast's ultrastructure are beneficial to light harvesting for photosynthesis under LL. Meanwhile, the TM is also a highly flexible system. HL can lead to a significant reduction in the diameter and partial unstacking of grana disks (Khatoon et al. 2009; Herbstova et al. 2012).

Fourth, the contents of some components in leaf are modified when changes occur in light, temperature, and/or water conditions. Among these changed leaf compositions, Chl and anthocyanin play important roles in regulation of light harvesting. In general, Chl content increases in the leaves grown under LL to enhance light harvesting (Murchie and Horton 1997), while contents of the phenol-like components such as anthocyanin (absorption peak at 450–550 nm) raises under HL, low-temperature, or ultraviolet radiation conditions to alleviate photodamage to the photosynthetic apparatus. For example, anthocyanin was accumulated to a higher concentration in the upper epidermal cells of *Mahonia repens* leaves when photosynthesis was limited by low temperature in winter (Grace et al. 1998). The phenol-like compounds may absorb intensive visible light and ultraviolet radiation (Merzlyak et al. 2008), decreasing the light intensity incident on chloroplasts, and act as antioxidants for protection from oxidative damage. Of plant-phenolic compounds, anthocyanin is increasingly noticed (Gould 2010), and the hypothesis about its role in protecting chloroplasts from unfavorable effects of excessive light is becoming more attractive. Compared with glabrous-green leaves, both containing anthocyanin and pubescent leaves of grapevine (*Vitis vinifera*) had greater dark-adapted PSII photochemical efficiencies and net photosynthetic rates as well as smaller midday de-epoxidation states of the xanthophylls cycle pigments, indicating that anthocyanin and pubescence can alleviate effectively light stress (Liakopoulos et al. 2006).

In addition, under HL conditions, the early light-induced protein (ELIP) accumulates in the major LHCII antenna system (Heddad et al. 2006). The ELIP accumulation is controlled by blue and UV-A radiation absorbed by the photoreceptor cryptochrome and dependent on light intensity (Kleine et al. 2007). This protein performs some protective roles by transient binding of free Chl molecules released from photodamaged Chl binding proteins and preventing the formation of singlet oxygen (generated by the reaction of free excited Chl in the triplet state with molecular oxygen), and/or by serving as sinks of excitation energy (Montane and Kloppstech 2000; Teramoto et al. 2004). Similar to ELIPs of higher plants, the HL-induced protein (HLIP) of cyanobacteria can also prevent the formation of reactive oxygen species by serving as transient carrier of Chl and/or participating in NPQ by the direct interaction of HLIPs with PSs or indirect modification of photosynthetic complex (Havaux et al. 2003). Moreover, HLIPs may stabilize the PSI complex by triggering PSI trimerization at high light (Wang et al. 2008).

In fact, LHC proteins are an extended LHC protein superfamily, including the best characterized LHC proteins such as the major and minor LHCIIs and the PsbS protein as well as the stress-induced ELIP and HLIP located in TMs of cyanobacteria and all photosynthetic eukaryotes. In a review about molecular design of the PSII light-harvesting antenna, Horton and Ruban (2004) illustrated the evolutionary and functional relationships between LHC-like proteins involved in light harvesting and photoprotection. It appears that plant LHCII trimer is the end-product of evolution process from a PsbS ancestor to ELIP, and then to LHC protein. It has been considered that all these proteins originate from a common ancestor having one trans-membrane helix (Jansson 2006; Engelken et al. 2010, 2012).

Concluding remarks

In light-harvesting regulation, in general, the rapid responses such as leaf movement and chloroplast movement occur in existing leaves/chloroplasts, whereas the slow acclimations such as the changes in LHCII protein abundance and modifications of leaf morphology, structure, and components occur in developing leaves/chloroplasts. All regulatory strategies, both fast and slow, are cooperative but not exclusive each other. The ingenious cooperation between rapid and slow strategies ensures for plants effective and safe utilization of light energy, namely

maximizing light absorption under LL and avoiding photodamage to the photosynthetic apparatus under HL in the fluctuating light environment. Although there have been many studies and hypotheses about ling regulation, many questions and some contradictory interpretations about *qE* remain; especially the molecular mechanisms for the reversible dissociation and thermal dissipation of some major LHCIIs from PSII core complexes under HL are unclear yet. For instance, whether the dissociated LHCIIs are linked with the PsbS protein, CP29, and CP24 or not, how the dissociated LHCIIs dissipate the light energy absorbed, which of the two physical mechanisms (charge transfer and energy transfer or excitonic coupling) is predominant one during *qE*, and what is the physiological role of HL-induced TM reorganization and LHCII aggregation. These questions should be probed further, and studying the *qE*-lacked mutants (*npq4* and *npq1*—the *npq4* lacks the PsbS protein, whereas the *npq1* lacks the VDE) may be useful in future investigation of LHCII dissociation. Answering these questions is undoubtedly beneficial not only for deep understanding of the natural photosynthesis but also for applying its principles and inspirations to artificial photosynthesis for finding solutions to the urgent problems such as food, energy resources, and environment in the world.

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