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The Function of PsbS Protein in Plant Photosynthesis Regulation

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Abstract: Photosynthesis transforms sun light energy into chemical energy of organic compounds, which sustain almost all life on the planet. In high light conditions, the energy absorbed that excess their photosynthesis capacity can be formed ROS (Reactive Oxygen Species) that are very dangerous for plant. To prevent ROS and plant photoprotection, the plant develop a mechanism which harmlessly dissipate excess light energy absorbed as heat called NPQ (Non Photochemical Quenching). In this paper, we review the researches of PsbS protein of photosystem II which is known have a key role in the NPQ activation. The NPQ capacity is correlate to PsbS level in plant leaf. The protein PsbS is as sensor of lumenal pH for NPQ activation. It is also proposed reorganisation control of grana membrane in high light condition. This protein maybe is not bound pigments, but it is related to zeaxanthin for complete NPQ activation. So PsbS has the important role for resistance of plant to high light. The investigation of PsbS protein could open the photosynthesis light harvesting regulation perspective for improve plant productivity.
Keywords: Light, NPQ, photosynthesis, PsbS protein, ROS.

1. Introduction

Photosynthesis transforms light energy absorbed by light-harvesting pigment-protein complexes into chemical energy of organic compounds, which sustain almost all life on the planet. In high light conditions, excess energy absorbed can be transferred to molecular oxygen from triplet excited state chlorophylls (^{3}Chls*) with consequent production of ROS (Reactive Oxygen Species) that are dangerous for organisms. Triplet excited Chls are produced at high level from singlet excited Chls (^{1}Chl*) when photosynthesis is saturated and energy is not used for photochemistry. Triplet Chls can react with O_2 (which is triplet in the ground state) to form singlet excited O_2, which is a very reactive and oxidizing molecule.

In plants, photoprotective mechanisms have evolved at different levels to respond to light

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intensity changes, as the avoidance of excessive light by movement of leaves, cells or chloroplasts, or the regulation of light harvesting and excitation energy transfer to balance light absorption and utilization [1-3]. One fundamental photosynthesis regulation is the Non Photochemical Quenching process (NPQ), which is activated in order to quench singlet-excited Chls and harmlessly dissipate excess excitation energy as heat at the level of PSII and finally limit photooxydative damages in plants. NPQ is considered a feedback response because, similarly to enzymatic feedback controls, is activated by the low lumenal pH, a product of the photosynthetic light phase [4]. This is an important response to protect photosynthesis of plant and algae in high light environments [5-7]. However, the precise mechanism of NPQ is still not completely known.

In plants, one fundamental protein for NPQ activation is PsbS [6-11]. PsbS is the product of the nuclear gene psbS, it belongs to the Lhc superfamily and interacts in some way with PSII [12]. This protein has a key role in the activation of qE, the principal and fastest component of NPQ [9]. qE activation requires a low lumenal pH and PsbS is the sensor of low pH thanks to two lumenal protonable glutamates [11]. Full qE activation requires the synthesis of zeaxanthin through the xanthophyll cycle, but the relationship between zeaxanthin and PsbS is not clearly understood. Because of its essential contribution in NPQ for maintaining efficient photosynthesis and avoiding photooxydative damages and ultimately for survival of photosynthetic organisms, PsbS and qE are topics of considerable interest in plant physiology and biochemistry researches since long time [6,7,8,10,11,13-24]. Though PsbS activity is known to be triggered by low lumenal pH, the molecular mechanism by which this subunit regulates light excitation energy utilization within PSII is still debated. Moreover, its exact location in thylakoid membranes and its interaction with PSII are still unknown. In this review, we will summarize previous reports on PsbS and provide present understanding on its mechanism of action in qE.

2. NPQ components

Most of the light used for photosynthesis is absorbed by the light-harvesting pigment-protein complexes (LHCs) that are associated with the reaction centers. Light energy excites chlorophyll molecules from the ground state to a singlet excited state ($^1Chl^*$). The relaxation of an excited Chl to the ground state from the singlet state is realized in different ways: excitation energy transfer from Chl to Chl until the reaction centre to drive photochemical reaction; re-emission of a photon (fluorescence); dissipation as heat by internal conversion; dissipation as heat in a controlled pathway (NPQ); decay via the triplet state ($^3Chl^*$) (Figure 1). A $^3Chl^*$ can return to the ground state by energy transfer to the O_2 in the ground-state to generate singlet excited oxygen ($^1O_2^*$), which is an extremely damaging reactive oxygen species. At room temperature, Chl fluorescence originates essentially from PSII, and the yield of fluorescence is generally low (0.6%–3%) [25]. Non-photochemical processes that dissipate excitation energy (collectively called NPQ) also quench Chl fluorescence, since dissipative pathways are in competition each other [6]. Chl fluorescence is indeed used to measure indirectly, but precisely, NPQ and photochemistry.

Balance between energy used for photochemical reactions and dissipative pathways are important for plant resistance and productivity in the natural environment where light intensity changes continuously. Indeed, under conditions of excess light, plants use only a small part of the absorbed light energy for photochemical reactions, while up to 80% of the absorbed energy is dissipated as heat [26]. This mechanism known as non-photochemical chlorophyll quenching is triggered to dissipate excess absorbed light energy within the PSII antenna system as heat, preventing photodamage of the reaction center. Energy dissipation is based on at least four different mechanisms called qE, qT, qI as described by Muller et al (2001) [6] and qZ as proposed by Nilkens et al (2010) and Willelm et al (2011) [28,29]. They are recently discussed by Ruban et al (2012) [30]:

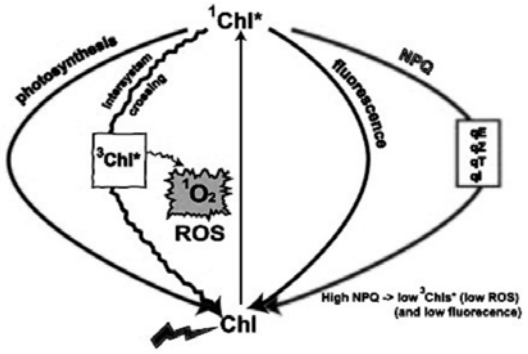

Figure 1. The use of the excitation energy of the chlorophylls. All pathways are in competition. Plants can control photosynthesis and NPQ. An increased NPQ is necessary to reduce 3Chl* formation (thus ROS formation) and can be detected as a concomitant decrease of fluorescence emission.

* The qT is a quenching associated to state transitions: in State II part of the major antenna LHCII of PSII migrates to PSI, thereby reducing the amount of excitation energy and fluorescence of PSII. This process contributes for a small component of NPQ (Figure 2) and relaxes within tens of minutes [6].

* The qI is a consequence of damaged reaction centers of PSII acting as weak energy traps in the absence of ΔpH and is described as photoinhibitory quenching. It shows very slow recovery in the range of hours in the dark after a period of illumination and it is not photoprotective [30].

* The recently proposed qZ component is a PsbS-independent but zeaxanthin-dependent quenching [28] that is related to zeaxanthin-dependent conformational changes in PSII antenna proteins [27]. Its formation and relaxation times are in the order of 10-15 min and correspond to the synthesis and epoxidation of zeaxanthin [28].

* The qE is the thylakoid energization-dependent quenching that is rapidly inducible and rapidly reversible and it needs the presence of a transmembrane thylakoid proton gradient (ΔpH). Activation and relaxation is within seconds to minutes [6,29,30]. The qE has been shown as a very effective short-term regulatory mechanism capable of protecting PSII in excess light conditions and is the main component of NPQ. For this reason, many investigations on qE have been performed in the last decades. However, so far the mechanism of energy quenching is still not completely elucidated and the mechanistic aspects are still debated and controversial [31-34].

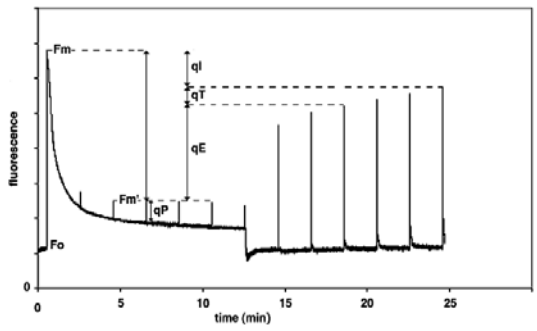

Figure 2. The components of NPQ, from [6], measured via Chl fluorescence measurement on Arabidopsis leaves. NPQ (qE + qT + qI) is related to the difference between Fm (maximal fluorescence of dark-adapted plants, which do not have NPQ activated) and Fm' (the maximal fluorescence during a light period). The rest of the Fm quenching during a light phase is related to photochemical quenching (qP). The recently proposed qZ component is not shown, but it would contribute to part of qE and qI shown in the figure. After switching off the actinic light, recovery of Fm' within a few minutes reflects relaxation of the qE component of NPQ. F_0 represents the minimal fluorescence of the system, related to inevitable energy losses.

Full qE activation is known to require four main components: i) a low lumenal pH; ii) the protein PsbS as sensor of lumenal pH; iii) the xanthophyll cycle (in particular zeaxanthin synthesis in high light); iv) the presence of some Lhcb proteins (PSII antenna complexes). These components interact each other in some way and if one is lacking, qE is decreased.

In the following session, we will discus the functional role of PsbS and zeaxanthin in energy quenching.

3. The conformation and location of PsbS

Properties of the PsbS protein have been analyzed in many plant species as Arabidopsis [9], maize [35], spinach [36], rice [18,23,37], tomato [38], *Marchantia polymorpha* [39], tobacco [40] and it has been concluded that this protein is accumulated in all land plants [41]. Nevertheless, it does not seem accumulated in the unicellular green alga *Chlamydomonas reinhardtii* under many growth conditions and in other unicellular green algae [41]. In these organisms, it seems that the LHCSR proteins, which also belong to the Lhc superfamily, replace PsbS for photoprotection by NPQ [42,43]. In the moss *Physcomitrella patens* both PsbS and LHCSR are found and participate in NPQ [44].

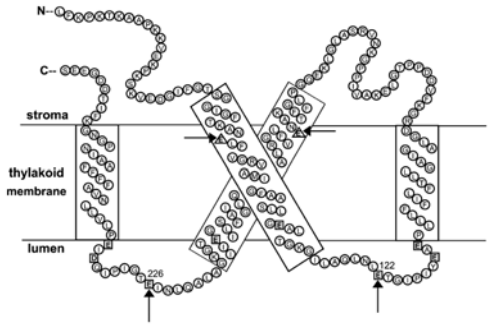

Figure 3. Topology of PsbS from [11] with indicated the two protonable lumenal glutamates (E122/E226).

In plants, PsbS was firstly isolated in spinach as a 22 kDa protein by Kim and co-workers [36]. It was found having a precursor sequence of 274-residue originated from a single-copy gene [45] and was called CP22 (Chlorophyll binding Protein of 22 KDa). Although PsbS is a member of the Lhc superfamily, which is composed by three helices membrane proteins, PsbS is predicted with four transmembrane helices [13,46]. Some glutamate and aspartate residues are present in the two lumenal loops in symmetrical position [47].

The biochemical, biophysical, and physiological properties of the PsbS protein were studied *in vitro* and in vivo in plants carrying a modified PsbS obtained by mutating these lumen-exposed glutamate/aspartate residues. Li and coworkers have used a site-directed mutagenesis approach to change one single glutamate in glutamine (EQ) or aspartate in asparagine (DN) or both the symmetrical residues at the same time [11]. Results showed that qE is reduced 50% in the single mutants E122Q and E226Q as compared with the control and to the level of the PsbS-KO mutant (*npq4.1*) in the double mutant E122Q-E226Q (Figure 4) [11]. PsbS is a DCCD (*N*,*N*′-dicyclohexylcarbodiimide) binding protein [11,47]. DCCD binds proton-active residues in hydrophobic environments and is an inhibitor of qE [48]. DCCD binding in plant carrying mutated PsbS was about 50% of the control in single mutants (E122Q or E226Q) and undetectable in the double mutant carrying glutamines at the place of glutamates (E122Q-E226Q) [11]. Thus these two glutamates (Figure 3) are strongly indicated as the residues responsible for pH sensitivity of PsbS [11,47]. PsbS is a 2-fold symmetrical protein and these two glutamates E122 and E226 seems to act independently and addictively in qE (Figure 4) [11,47,49]. Since DCCD binding to both glutamates is efficient only at low pH [11], it is very likely that a conformational change of PsbS after protonation brings these residues in a hydrophobic environment, necessary to activate PsbS and qE.

In intact chloroplasts and whole plants, PsbS seems to exist in dimeric or monomeric form depending on lumenal pH: the monomer is present at acidic pH and the dimer at alkaline pH. The dimer-to-monomer conversion is reversibly induced by light, which causes lumenal acidification by the electron transport chain [50]. PsbS conformational switch has been suggested to contribute in the reorganization of PSII supercomplex [16,22,51,52] necessary for the NPQ activation induced by variations in light intensity.

Even if it is clear that PsbS is mainly located in the grana membranes, the precise location of PsbS is still enigmatic. Different studies have been performed to find PsbS location, but results obtained are controversial. In spinach, Kim and coworker suggested that this protein is associated with the oxygen-evolving complex, although it is not needed for oxygen evolution function [13,36]. In accordance with this suggestion [53] reported that PsbS is found in PSII preparations depleted of LHC. It has been suggests that PsbS could localise near minor antennas in the PSII-LHCII supercomplex [54].

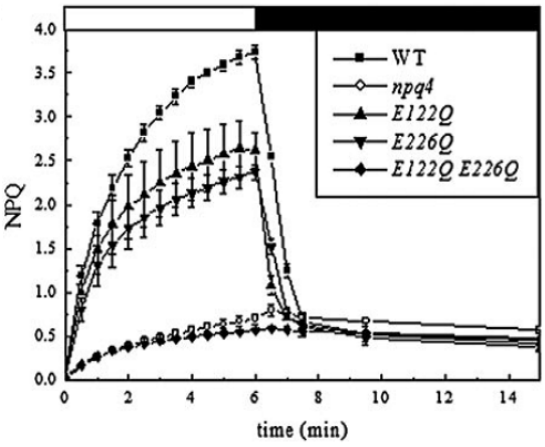

Figure 4. Effect of the mutations of the two glutamates E122 and E226 on NPQ, from [20].

On the contrary, using cryoelectron microscopy and single particle analysis in spinach, Nield and colleagues observed that PsbS protein is not located within the PSII-LHCII supercomplex, but it can be located in

the LHCII-rich regions that interconnect the supercomplex [55]. This is supported by other researches on purified PSII particles [56]. It had been also reported that PsbS can associate with PSII core in dimeric form in the dark and with LHCII antenna in monomeric form upon illumination [35] and the monomeric form would be the active form for qE. It was found to be present in numerous sucrose gradient fractions containing PSII supercomplex, but not bound to PSII [56]. Using immunoprecipitation studies, Teardo and co-authors reported that PsbS is associated with numerous thylakoid complexes including trimeric LHCII, CP29, PSI and ATP synthase [57]. However, the "sticky" behavior of PsbS [47,56] and the fact that PsbS was found to interact with several thylakoid complexes [57] on which it has no function (as PSI and ATP synthase), suggest that artificial aggregation during immunoprecipitation are possible. Thus, a conclusive answer for PsbS localization is still not available.

PsbS was shown capable to enhance the dynamic of thylakoid membrane and its sensitivity to detergents [22]. It has been reported that PsbS can catalyze the dissociation of the PSII-LHCII supercomplex leading to a reorganization of the PSII supercomplexes, which seem a fundamental step for triggering energy quenching in high light [16,22,51,52,58,59,60]. Thereby, after protonation and conformational change, PsbS would dissociate LHCII complexes from PSII core and induce aggregation of LHCII, which would cause energy quenching in the antenna (see below).

4. Is PsbS a pigment binding protein?

PsbS capability to bind pigments is another question that has been discussed for longtime. To be the quencher site, PsbS needs to bind pigment. On the contrary, if no pigment is bound to this protein, this implies that PsbS can only be the sensor of low lumenal pH and would transfer the signal to the PSII-LHCII complex in some way.

PsbS has some sequence similarity to the Lhc chlorophyll-binding proteins of PSII [36]. Funk and colleagues reported that the PsbS is able to bind chlorophylls [46,61]. However, they also reported that PsbS, differently from other chlorophyll-binding proteins, is stable in the absence of pigments [8], in accordance to a previous report [45]. PsbS pigment binding ability was also analyzed by experiences of purification from thylakoids and by reconstitution experiments of the overexpressed protein in *E. coli* in presence of pigments (Chls and Cars): in no case PsbS was purified or refolded with some pigments bound, accordingly to the lack of most of the pigment binding sites present in the other Lhc proteins [20,47]. Results from Aspinall-O'Dea and co-authors, indicating zeaxanthin binding to PsbS *in vitro* [62], were found an experimental artifact [20]. In normal light conditions, the pigment and photosynthetic protein content do not change in the *npq4.1* mutant of Arabidopsis (lacking PsbS) as compared to the wild type [63].

In conclusion present knowledge strongly suggest that native PsbS protein does not bind chlorophylls or carotenoids, differently from others Lhc proteins, which maintain full pigment binding in the same conditions [47]. Alternatively, the binding of xanthophylls (especially zeaxanthin and lutein) to PsbS could be weak or only transient under qE condition [64].

5. Relation between PsbS and zeaxanthin in NPQ formation

The xanthophylls cycle consists in the reversible deepoxidation of violaxanthin into zeaxanthin via antheraxanthin by the action of the violaxanthin deepoxidase enzyme (VDE) and zeaxanthin epoxidase (ZE) [65]. Under conditions of excess light, zeaxanthin accumulates thanks to the action of the VDE, which is activated by the low lumenal pH generated by photochemical reactions [65]. In this condition, zeaxanthin binds one or more proteins of the PSII-LHCII macromolecular complex [66,67] and the PsbS protein is protonated, thus activating qE [11]. In the absence of PsbS (*npq4* mutant), NPQ is largely reduced. In the presence of PsbS, but in the absence of zeaxanthin (in the *npq1* mutant plant blocked in the xanthophyll cycle in high light), NPQ is reduced by ~50-70% with respect to wild type, but less than in the *npq4* mutant [9,20]. This indicates that the function of PsbS in qE activation is dominant compared to that one of zeaxanthin in the presence of ΔpH. Indeed, the absence of both PsbS and zeaxanthin show the same qE reduction as in the case of the single PsbS-KO mutant (Figure 5) [9]. It is suggested that zeaxanthin cannot perform its qE function if PsbS is absent, while PsbS can still induce qE without zeaxanthin. However, reports of [27,28] indicated that PsbS-independent/zeaxanthin-dependent NPQ components would exist.

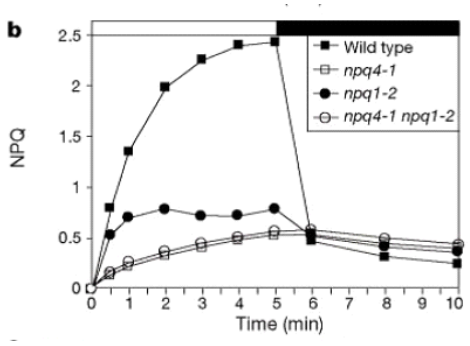

Figure 5. Non photochemical quenching phenotypes of *npq4-1* (no PsbS), *npq1-2* (no zeaxanthin), the double mutant and wild type plants. White bars above graphs indicate periods of illumination with high light (1250 μmol photons m^{-2} s^{-1}); black bars indicate darkness, from [9].

Transgenic plants over accumulating PsbS (L17 mutant of Arabidopsis) can enhance NPQ in the presence or absence of zeaxanthin [10,11,68,69]. A ΔF682 fluorescence signal in the difference spectrum between the quenched and unquenched states showed that a negative fluorescence peak at 682 nm is formed independently from zeaxanthin and is due to PsbS-specific conformational changes in the quenching site for qE [70]. Moreover, Johnson and colleagues observed that NPQ in *npq4* Arabidopsis leaves blocked in zeaxanthin formation by infiltration of DTT (dithiothreitol, inhibitor of violaxanthin de-epoxidase) was reduced compared with untreated leaves, but it was found to be not significantly different from DTT-infiltrated wild type leaves [17]. This suggests that PsbS can act independently from zeaxanthin in energy quenching activation, and zeaxanthin can activate qE independently from PsbS and enhance PsbS-dependent NPQ. It is evident that their interaction can strongly enhance photoprotection capacity in plants [11,20,24,28,30,69,71,72]. These suggest that it exist a synergistic effect between PsbS and zeaxanthin in NPQ formation.

6. Where is the quenching site?

It has been proposed that PsbS is the site of energy quenching [73]. However, to day, this proposition is unlike, because PsbS would not be able to bind pigments, as discussed before. Furthermore, qE seems activated also in the absence of PsbS, but on a longer time scale [19,24]. Hence it is very probable that PsbS does not quench directly singlet excited chlorophyll state [47], despite its key role in qE [9].

Previous research showed that minor antenna proteins, as CP26 and CP29, can bind DCCD [74,75], thus they can be protonated by low lumen pH as the PsbS protein. Using genetic approaches such as antisense or knock-out techniques to manipulate Lhcb content, it was found that the absence of CP26 has little effect on qE [76,77], elimination of CP29 decreases qE more than CP26 absence [60,76] and deletion of CP24 leads to the strongest decrease of qE [60,77,78]. However, in plants lacking both CP29 and CP24, qE shows a smaller reduction as compared to the single koCP24 mutant [71,79], and similar results were found for the koCP24/CP26 double mutant [60,77]. A deep investigation indicated that qE decrease in the koCP24 is not due to the presence of the quencher site in this subunit, but it is due the particular organisation of the complexes in the membranes and the reduced capacity of electron transport and thus ΔpH creation [77]. It is therefore unlikely that the quenching site is localized only in minor antenna complexes [30].

Indeed major antenna LHCII is also an important candidate to be the quencher. In *lhcb1-2* antisense plants, the capacity for non-photochemical quenching was reduced, but not completely deleted [71,80]. However, in Arabidopsis T-DNA koLhcb3 plants, the absence of Lhcb3, which is compensated by increased amounts of Lhcb1 and Lhcb2, did not result in any significant alteration of qE [81]. In conclusion, there are strong indications that the quenching site is not associated to one single subunit [30].

Using ultrafast fluorescence techniques on intact leaves, Holzwarth and coworker proposed that there are two independent NPQ quenching sites *in vivo*, which depend differently on the actions of PsbS and zeaxanthin. One site is formed in the functionally dissociated major light-harvesting complex LHCII and depends strictly on the PsbS protein, while the second site localize in the minor antennae of PSII and depends on the presence of zeaxanthin [34]. Both qE components would arise from a quenching mechanism based on a conformational change within the PSII antenna, optimized by Lhcb subunit-subunit interactions and tuned by the synergistic effects of PsbS and xanthophylls [71]. The second site is in agreement with the allosteric model of zeaxanthin in qE proposed by [82,83]. A model for PsbS action in qE is presented in the following section.

7. Action mechanism of PsbS in photoprotection

The role of PsbS on PSII-LHCII supercomplex reorganization for qE activation

The largest purifiable PSII supercomplex consists of two PSII cores (C2), two copies of CP29, CP26 and CP24, two strongly bound LHCII trimers (S2) and two trimers bound with moderate strength (M2), and it is called C2S2M2 [84]. It has been suggested for a long time that the structural changes within the grana membrane, where PSII supercomplexes

localize, could provide a physiological mechanism for regulating the partitioning of energy between utilization in photosynthesis and dissipation by NPQ [26,85].

Recently, it has been proposed that in the quenched state, the PSII-LHCII supercomplex is reorganized by dissociation of PSII core complex and antenna and/or clustering of PSII core units and LHCII antenna aggregates [52,85], in a process controlled by PsbS [22,30,34,51,52,86].

Using electron microscopy and fluorescence spectroscopy analysis on thylakoids prepared from wild type, PsbS-deficient and PsbS overexpressing Arabidopsis plants, Kiss and colleagues observed that reorganization of PSII-LHCII during thylakoid re-stacking could be regulated by the level of PsbS. The Mg^{2+} requirement in this process was negatively correlated with the level of PsbS [22]. Moreover, the increase of the amplitude of the psi-type CD signal originating from features associable to the PSII-LHCII organization is also correlated to the PsbS level [22].

It was also found that the content of PsbS would regulate the PSII organisation in the grana membrane [16]. Indeed, it was observed that PSII units assembled into semicrystalline arrays in grana membranes are higher in the absence of PsbS, lower in wild type and not found in membrane enriched in PsbS (L17 mutant) [16]. Therefore in the presence of PsbS, thylakoid membranes would become more dynamic and in its absence the association of the supercomplexes would be stronger [16,22]. PsbS would therefore regulate the interaction between LHCII and PSII and/or between PSII complexes in the grana membranes organisation [16,22].

Consistently with these findings, it was also reported a PsbS-dependent change in the distance between PSII core complexes observed by electron microscopy, implying a reorganization of the PSII-LHCII macrostructure occurring during illumination [51]. This was supported by biochemical analysis showing that a part of the C2S2M2 supercomplex, consisting of the LHCII M-trimer, CP24, and CP29 (B4C subcomplex), is dissociated by light treatment and dependent on the presence of PsbS [51].

In addition, using freeze-fracture electron microscopy, combined with laser confocal microscopy employing the fluorescence recovery after photobleaching technique in intact spinach chloroplasts, Johnson and coworker proposed that the formation of the photoprotective state requires a structural reorganization of the photosynthetic membrane involving dissociation of LHCII from PSII and its aggregation [52]. The structural changes, which occur rapidly and reversibly, are manifested by a reduced mobility of Lhc antenna chlorophyll proteins [52]. The LHCII aggregates may cause specific changes in the LHCII pigment population able to regulate energy flow. This hypothesis is supported by spectroscopic analyses on purified LHCII in the quenched and unquenched states indicating a conformational change between these two states [32,58]. This supercomplex reorganization could be related to the two quenchings Q1 and Q2 proposed by [34].

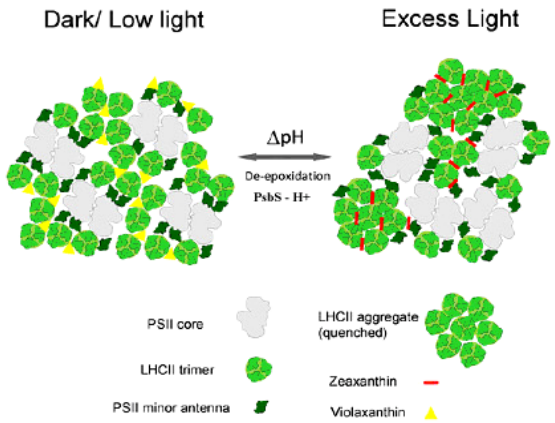

Figure 6. Model describing the reorganization of the PSII-LHCII supercomplexes under the combined action of PsbS, zeaxanthin and lumen pH, from [30]. Aggregates of LHCII would be formed in high light conditions and would dissipate excitation energy as heat.

Johnson and colleagues [52] suggested that the structural rearrangement lead to the formation of internal dissipative pigment interactions, and energy quenching occurs in accordance with the xanthophyll-chlorophyll models proposed by [33,87,88,89] or chlorophyll-chlorophyll quenching model [90].

Therefore today, the results on the molecular basis for quenching mechanisms support the hypothesis that reversible and flexible reorganisation of PSII-LHCII supercomplexes triggers energy quenching formation (Figure 6) promoted by PsbS under the control of low lumen pH [16,22,29,30,52,58,59,86].

Low lumen pH as a signal for photoprotection

During the photosynthetic process, a ΔpH in the thylakoid lumen is generated from the water photooxydation reaction in the oxygen evolving complex and during electron transfer at the level of Cyt b_6f complex. Besides activating ATP synthase for ATP synthesis, ΔpH is indispensable for the qE component of NPQ. The ΔpH regulation of energy quenching is a flexible and rapid regulation of PSII activity. Low lumenal pH activates NPQ via PsbS protonation [9,11,20], which causes its conformational change [11,35], and through the activation of the xanthophylls cycle [91,92].

In addition, it was found that both PsbS-dependent and PsbS-independent NPQ depend on lumen pH. In wild type leaves infiltrated with nigericin, a protonophore that dissipates the ΔpH, NPQ decreases strongly even in the presence of PsbS [52,93]. On the contrary, in the absence of PsbS, NPQ shows a strong increase when ΔpH is enhanced by a diaminodurene treatment [19]. Transient qE, particularly visible on dark adapted plants in the first minutes after switching on a low light, is also dependent on the PsbS protein and is determined by a transient low lumenal pH due to a delay in the activation of the Calvin cycle that causes proton accumulation [94].

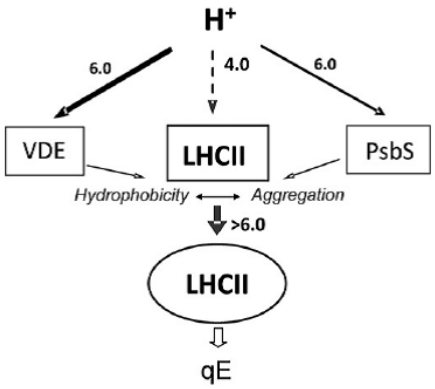

Figure 7. Model explaining the action of PsbS and the xanthophylls cycle in pH-dependent energy quenching. The proposed pKa of LHCII is ~4.0 [95,96], too low for qE activation by physiological lumen pH values of ~5.8 [97]. However when PsbS and VDE, which would have a pK for their activation of ~6.0 [98], bind protons, together they would trigger the aggregation of LHCII increasing the hydrophobicity of the environment of the qE-active residues and shifting the pKa of LHCII to ~6.0, thus activating qE at physiological lumen pH values, from [30].

In short, the initiation of qE involves two lumen pH-dependent processes, the activation of the xanthophylls cycle and the protonation of PsbS. It is proposed that PsbS could interact with xanthophylls cycle for regulation of PSII antenna reorganization by regulating the pK for qE activation [19]. In the absence of zeaxanthin and PsbS, the pH necessary for PSII-LHCII reorganisation would be very low and thus qE activated to a minor extent at a given pH. In presence of PsbS/zeaxanthin, the pK of qE would increase, allowing a faster and more efficient thermal dissipation during the light induced decrease of lumenal pH [30]. It is also proposed that the LHCII complex, which presents several acidic residues exposed to the lumen, may be protonated in qE condition. Protonation would be necessary for their "aggregation" and energy quenching. PsbS and zeaxanthin could have a role by increasing the pKa of some important residues of LHCII. In their absence, pKa would be very low and LHCII would remain unprotonated even at high light (low lumenal pH), with little activation of the energy quenching (Figure 7) [30,52].

8. Role physiological of PsbS in plant photosynthesis regulation

Photosynthesis regulation is a complex network of mechanisms necessary to adapt photosynthesis to different environmental conditions and finally optimise plant fitness. Photosynthesis can be regulated at many levels, such as at a macroscopic level (leaf movement), microscopic level (chloroplast movement) or molecular level (long-term responses such as regulations of gene expression to optimise metabolism and photosynthesis and, of course, short-term responses modulating photochemistry) [2,3]. Since photochemical reactions are at the beginning of the whole metabolism in photosynthetic organism, numerous researches investigate all steps of photosynthesis to fully understand this fundamental process and its regulation and finally to provide strategies to improve natural or create artificial photosynthesis.

However so far, photosynthesis improvements have been obtained mainly at a plant level (leaf shape and orientation) rather than at a molecular level, and the possibilities to improve photosynthetic efficiency are recently discussed by different authors [29,99,100,101,102]. Since the very first photosynthetic events are the light harvesting and excitation energy transfer to reaction centres, and the main regulation at this level is NPQ, these topics have been at the centre of many researches to understand the mechanistic aspects (see [30] for a recent review), as well the physiological importance. The de-excitation of singlet excited Chls by heat dissipation (NPQ) is fast (in the order of few seconds). Thus, it was assumed that such a photoprotective mechanism is important to control PSII photoinhibition under high light to dissipate excess absorbed energy and under variable light to rapidly match available excitation energy and photosynthetic capability. The importance of PsbS on plant fitness was indeed demonstrated under variable light [103,104,105], while under constant high light conditions other photoprotective mechanisms can compensate, at least partially, for the lack of PsbS [14,103].

Plants acclimated to different light conditions showed that the amount of PsbS is adjusted to some extent to the intensity of the light and it is lowered when plants are grown under low light compared to high light [44,106,107]. Similarly, an investigation on the

presence of the PsbS protein in different green organisms suggested that deep-water algae accumulate less PsbS than sun-exposed algae [41]. This suggest that, if competition for excitation energy between NPQ and photochemical activity is not significant under saturating light, it could be important in low light for photosynthesis optimization and PsbS down-regulation would be important for optimal photochemistry. Indeed, it was observed that the L17 mutant overexpressing PsbS, which has a higher NPQ capacity, shows a decreased growth in low light [108]. This would be in some way similar to what found for the *npq2* mutant of Arabidopsis, which accumulates zeaxanthin even at low light. This mutant would waste useful energy in low light due to some unnecessary NPQ activation, leading to a reduced growth as compared to wild type plants [27]. PsbS accumulation is not abolished even at low light, probably because plants evolved in natural environment where conditions can rapidly change. PsbS presence could reduce plant performances in low light, but this would be a price to pay to stand with variable illuminated habitats. Thus, it might be possible to optimize photosynthesis in nature light condition by PsbS overexpression [2] and in not natural and controlled environments where light is strongly liming by elimination of its present in plant. Since plants have evolved in natural environments, the photosynthetic apparatus may not be well adapted for the optimised conditions encountered in certain agricultural systems. Regulations necessary to improve stress resistance and plant survival in nature might reduce photosynthesis potential. Thus, improvement of photosynthesis might be possible (see [29,99,101] for some reviews).

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References

[1] K.K. Niyogi, Photoprotection revisited: Genetic and molecular approaches, Annu.Rev.Plant Physiol.Plant Mol.Biol. 50 (1999) 333.

[2] Z. Li, S. Wakao, B.B. Fischer, K.K. Niyogi, Sensing and responding to excess light, Annu Rev Plant Biol 60 (2009) 239.

[3] P.A. Davis, R.P. Hangarter, Chloroplast movement provides photoprotection to plants by redistributing PSII damage within leaves, Photosynth Res (2012).

[4] C.A. Wraight, A.R. Crofts, Energy-dependent quenching of chlorophyll alpha fluorescence in isolated chloroplasts, Eur J Biochem 17 (1970) 319.

[5] G.H. Krause, C. Vernotte, J.M. Briantais, Photoinduced quenching of chlorophyll fluorescence in intact chloroplasts and algae, Biochim.Biophys.Acta 679 (1982) 116.

[6] P. Muller, X.P. Li, K.K. Niyogi, Non-photochemical quenching. A response to excess light energy, Plant Physiol 125 (2001) 1558.

[7] P. Horton, A.V. Ruban, Molecular design of the photosystem II light-harvesting antenna: photosynthesis and photoprotection, J.Exp.Bot. 56 (2005) 365.

[8] C. Funk, I. Adamska, B.R. Green, B. Andersson, G. Renger, The nuclear-encoded chlorophyll-binding photosystem II-S protein is stable in the absence of pigments, J.Biol.Chem. 270 (1995) 30141.

[9] X.P. Li, O. Bjorkman, C. Shih, A.R. Grossman, M. Rosenquist, S. Jansson, K.K. Niyogi, A pigment-binding protein essential for regulation of photosynthetic light harvesting, Nature 403 (2000) 391.

[10] X.P. Li, P. Muller-Moule, A.M. Gilmore, K.K. Niyogi, PsbS-dependent enhancement of feedback de-excitation protects photosystem II from photoinhibition, Proc Natl Acad Sci U S A 99 (2002) 15222.

[11] X.P. Li, A.M. Gilmore, S. Caffarri, R. Bassi, T. Golan, D. Kramer, K.K. Niyogi, Regulation of photosynthetic light harvesting involves

intrathylakoid lumen pH sensing by the PsbS protein, J Biol Chem 279 (2004) 22866.
[12] U. Ljungberg, H.E. Akerlund, B. Andersson, Isolation and characterization of the 10-kDa and 22-kDa polypeptides of higher plant photosystem 2, Eur J Biochem 158 (1986) 477.
[13] S. Kim, E. Pichersky, C.F. Yocum, Topological studies of spinach 22 kDa protein of Photosystem II, Biochim Biophys Acta 1188 (1994) 339.
[14] T. Golan, P. Muller-Moule, K.K. Niyogi, Photoprotection mutants of Arabidopsis thaliana acclimate to high light by increasing photosynthesis and specific antioxidants, Plant Cell Environ 29 (2006) 879.
[15] L. Kalituho, T. Grasses, M. Graf, J. Rech, P. Jahns, Characterization of a nonphotochemical quenching-deficient Arabidopsis mutant possessing an intact PsbS protein, xanthophyll cycle and lumen acidification, Planta 223 (2006) 532.
[16] S. Kereiche, A.Z. Kiss, R. Kouril, E.J. Boekema, P. Horton, The PsbS protein controls the macro-organisation of photosystem II complexes in the grana membranes of higher plant chloroplasts, FEBS Lett 584 (2010) 759.
[17] M.P. Johnson, A.V. Ruban, Arabidopsis plants lacking PsbS protein possess photoprotective energy dissipation, Plant J 61 (2010) 283.
[18] S. Hubbart, O.O. Ajigboye, P. Horton, E.H. Murchie, The photoprotective protein PsbS exerts control over CO(2) assimilation rate in fluctuating light in rice, Plant Journal 71 (2012) 402.
[19] M.P. Johnson, A.V. Ruban, Restoration of rapidly reversible photoprotective energy dissipation in the absence of PsbS protein by enhanced DeltapH, J Biol Chem 286 (2011) 19973.
[20] G. Bonente, B.D. Howes, S. Caffarri, G. Smulevich, R. Bassi, Interactions between the photosystem II subunit PsbS and xanthophylls studied in vivo and in vitro, J Biol Chem 283 (2008) 8434.
[21] G. Bonente, M. Ballottari, T.B. Truong, T. Morosinotto, T.K. Ahn, G.R. Fleming, K.K. Niyogi, R. Bassi, Analysis of LhcSR3, a protein essential for feedback de-excitation in the green alga Chlamydomonas reinhardtii, PLoS Biol 9 (2011) e1000577.
[22] A.Z. Kiss, A.V. Ruban, P. Horton, The PsbS protein controls the organization of the photosystem II antenna in higher plant thylakoid membranes, Journal of Biological Chemistry 283 (2008) 3972.
[23] I. Kasajima, K. Ebana, T. Yamamoto, K. Takahara, M. Yano, M. Kawai-Yamada, H. Uchimiya, Molecular distinction in genetic regulation of nonphotochemical quenching in rice, Proc Natl Acad Sci U S A 108 (2011) 13835.
[24] A.V. Ruban, E.H. Murchie, Assessing the photoprotective effectiveness of non-photochemical chlorophyll fluorescence quenching: A new approach, Biochim Biophys Acta 1817 (2012) 977.
[25] G.H. Krause, E. Weis, Chlorophyll fluorescence and photosynthesis: The basics, Ann.Rev.Plant Physiol. 42 (1991) 313.
[26] P. Horton, A.V. Ruban, R.G. Walters, Regulation of Light harvesting in Green Plants, Annu.Rev.Plant Physiol.Plant Mol.Biol. 47 (1996) 655.
[27] L. Dall'Osto, S. Caffarri, R. Bassi, A mechanism of nonphotochemical energy dissipation, independent from PsbS, revealed by a conformational change in the antenna protein CP26, Plant Cell 17 (2005) 1217.
[28] M. Nilkens, E. Kress, P. Lambrev, Y. Miloslavina, M. Muller, A.R. Holzwarth, P. Jahns, Identification of a slowly inducible zeaxanthin-dependent component of non-photochemical quenching of chlorophyll fluorescence generated under steady-state conditions in Arabidopsis, Biochim Biophys Acta 1797 (2010) 466.
[29] C. Wilhelm, D. Selmar, Energy dissipation is an essential mechanism to sustain the viability of plants: The physiological limits of improved photosynthesis, J Plant Physiol 168 (2011) 79.
[30] A.V. Ruban, M.P. Johnson, C.D. Duffy, The photoprotective molecular switch in the photosystem II antenna, Biochim Biophys Acta 1817 (2012) 167.
[31] N.E. Holt, D. Zigmantas, L. Valkunas, X.P. Li, K.K. Niyogi, G.R. Fleming, Carotenoid cation formation and the regulation of photosynthetic light harvesting, Science 307 (2005) 433.
[32] A.V. Ruban, R. Berera, C. Ilioaia, I.H.M. van Stokkum, J.T.M. Kennis, A.A. Pascal, H. van Amerongen, B. Robert, P. Horton, R. van Grondelle, Identification of a mechanism of photoprotective energy dissipation in higher plants, Nature 450 (2007) 575.
[33] S. Bode, C.C. Quentmeier, P.N. Liao, N. Hafi, T. Barros, L. Wilk, F. Bittner, P.J. Walla, On the regulation of photosynthesis by excitonic interactions between carotenoids and chlorophylls, Proc Natl Acad Sci U S A 106 (2009) 12311.

[34] A.R. Holzwarth, Y. Miloslavina, M. Nilkensb, P. Jahnsb, Identification of two quenching sites active in the regulation of photosynthetic light-harvesting studied by time-resolved fluorescence, Chemical Physics Letters 483 (2009) 262.

[35] E. Bergantino, A. Segalla, A. Brunetta, E. Teardo, F. Rigoni, G.M. Giacometti, I. Szabo, Light- and pH-dependent structural changes in the PsbS subunit of photosystem II, Proc Natl Acad Sci U S A 100 (2003) 15265.

[36] S. Kim, P. Sandusky, N.R. Bowlby, R. Aebersold, B.R. Green, S. Vlahakis, C.F. Yocum, E. Pichersky, Characterization of a spinach psbS cDNA encoding the 22 kDa protein of photosystem II, FEBS Lett 314 (1992) 67.

[37] T. Iwasaki, Y. Saito, E. Harada, M. Kasai, K. Shoji, M. Miyao, N. Yamamoto, Cloning of cDNA encoding the rice 22 kDa protein of Photosystem II (PSII-S) and analysis of light-induced expression of the gene, Gene 185 (1997) 223.

[38] M. Wallbraun, S. Kim, B.R. Creen, B. Piechulla, E. Pichersky, Nucleotide Sequence of a Tomato psbS Gene, Plant Physiol Biochem 106 (1994) 1703.

[39] R. Harrer, R. Bassi, M.G. Testi, C. Sch„fer, Nearest-neighbor analysis of a photosystem II complex from Marchantia polymorpha L.(liverwort), which contains reaction center and antenna proteins, Eur.J.Biochem. 255 (1998) 196.

[40] A.D. Heiber, O. Kawabata, H.Y. Yamamoto, Significance of the lipid phase in the dynamics and functions of the xanthophyll cycle as revealed by PsbS overexpression in tobacco, Plant Cell Physiol 45 (2005) 92.

[41] G. Bonente, F. Passarini, S. Cazzaniga, C. Mancone, M.C. Buia, M. Tripodi, R. Bassi, S. Caffarri, The occurrence of the psbS gene product in Chlamydomonas reinhardtii and in other photosynthetic organisms and its correlation with energy quenching, Photochem Photobiol 84 (2008) 1359.

[42] G. Peers, T.B. Truong, E. Ostendorf, A. Busch, D. Elrad, A.R. Grossman, M. Hippler, K.K. Niyogi, An ancient light-harvesting protein is critical for the regulation of algal photosynthesis, Nature 462 (2009) 518.

[43] G. Bonente, S. Pippa, S. Castellano, R. Bassi, M. Ballottari, Acclimation of Chlamydomonas reinhardtii to different growth irradiances, J Biol Chem 287 (2012) 5833.

[44] C. Gerotto, A. Alboresi, G.M. Giacometti, R. Bassi, T. Morosinotto, Role of PSBS and LHCSR in Physcomitrella patens acclimation to high light and low temperature, Plant Cell Environ 34 (2011) 922.

[45] N. Wedel, R. Klein, U. Ljungberg, B. Andersson, R.G. Herrmann, The single-copy gene psbS codes for a phylogenetically intriguing 22 kDa polypeptide of photosystem II, FEBS Lett 314 (1992) 61.

[46] C. Funk, W.P. Schr”der, B.R. Green, G. Renger, B. Andersson, The Intrinsic 22 kDa Protein Is a Chlorophyll-Binding Subunit of Photosystem II, FEBS Lett. 342 (1994) 261.

[47] P. Dominici, S. Caffarri, F. Armenante, S. Ceoldo, M. Crimi, R. Bassi, Biochemical properties of the PsbS subunit of photosystem II either purified from chloroplast or recombinant, Journal of Biological Chemistry 277 (2002) 22750.

[48] A.V. Ruban, R.G. Walters, P. Horton, The Molecular Mechanism of the Control of Excitation Energy Dissipation in Chloroplast Membranes - Inhibition of DeltapH- Dependent Quenching of Chlorophyll Fluorescence by Dicyclohexylcarbodiimide, FEBS Lett 309 (1992) 175.

[49] X. Li, A. Phippard, J. Pasari, K. Niyogi, Structural-functional analysis of Photosystem II subunit S (PsbS) in vivo, Functional Plant Biology 29 (2002) 1131

[50] E. Bergantino, A. Brunetta, E. Touloupakis, A. Segalla, I. Szabo, G.M. Giacometti, Role of the PSII-H subunit in photoprotection: novel aspects of D1 turnover in Synechocystis 6803, J Biol Chem 278 (2003) 41820.

[51] N. Betterle, M. Ballottari, S. Zorzan, S. de Bianchi, S. Cazzaniga, L. Dall'osto, T. Morosinotto, R. Bassi, Light-induced dissociation of an antenna hetero-oligomer is needed for non-photochemical quenching induction, J Biol Chem 284 (2009) 15255.

[52] M.P. Johnson, T.K. Goral, C.D. Duffy, A.P. Brain, C.W. Mullineaux, A.V. Ruban, Photoprotective energy dissipation involves the reorganization of photosystem II light-harvesting complexes in the grana membranes of spinach chloroplasts, Plant Cell 23 (2011) 1468.

[53] D.F. Ghanotakis, C.M. Waggoner, N.R. Bowlby, D.M. Demetriou, G.T. Babcock, C.F. Yocum, Comparative structural and catalytic properties of oxygen- evolving photosystem II preparations, Photosynth.Res. 14 (1987) 191.

[54] E. Thidholm, V. Lindstrom, C. Tissier, C. Robinson, W.P. Schroder, C. Funk, Novel approach reveals localisation and assembly pathway of the PsbS and PsbW proteins into the photosystem II dimer, Febs Letters 513 (2002) 217.

[55] J. Nield, C. Funk, J. Barber, Supermolecular structure of photosystem II and location of the PsbS protein, Philos.Trans.R.Soc.Lond B Biol.Sci. 355 (2000) 1337.

[56] S. Caffarri, R. Kouril, S. Kereiche, E.J. Boekema, R. Croce, Functional architecture of higher plant photosystem II supercomplexes, Embo J 28 (2009) 3052.

[57] E. Teardo, P.P. de Laureto, E. Bergantino, F. Dalla Vecchia, F. Rigoni, D. Szabo, G.M. Giacometti, Evidences for interaction of PsbS with photosynthetic complexes in maize thylakoids, Biochimica Et Biophysica Acta-Bioenergetics 1767 (2007) 703.

[58] A.A. Pascal, Z.F. Liu, K. Broess, B. van Oort, H. van Amerongen, C. Wang, P. Horton, B. Robert, W.R. Chang, A. Ruban, Molecular basis of photoprotection and control of photosynthetic light-harvesting, Nature 436 (2005) 134.

[59] P. Horton, M.P. Johnson, M.L. Perez-Bueno, A.Z. Kiss, A.V. Ruban, Photosynthetic acclimation: does the dynamic structure and macro-organisation of photosystem II in higher plant grana membranes regulate light harvesting states?, Febs J 275 (2008) 1069.

[60] Y. Miloslavina, S. de Bianchi, L. Dall'Osto, R. Bassi, A.R. Holzwarth, Quenching in Arabidopsis thaliana mutants lacking monomeric antenna proteins of photosystem II, J Biol Chem 286 (2011) 36830.

[61] C. Funk, G. Renger, I. Adamska, B. Andersson, P. Schr"der, The PS II-S polypeptide. An atypical CAB protein, From Light to Biophere Vol.I, Kluwer, Dordrecht, 1995, pp. 339-342.

[62] M. Aspinall-O'Dea, M. Wentworth, A. Pascal, B. Robert, A. Ruban, P. Horton, In vitro reconstitution of the activated zeaxanthin state associated with energy dissipation in plants, Proc Natl Acad Sci U S A 99 (2002) 16331.

[63] X.P. Li, A.M. Gilmore, K.K. Niyogi, Molecular and global time-resolved analysis of a psbS gene dosage effect on pH- and xanthophyll cycle-dependent nonphotochemical quenching in photosystem II, J Biol Chem 277 (2002) 33590.

[64] T. Barros, A. Royant, J. Standfuss, A. Dreuw, W. Kuhlbrandt, Crystal structure of plant light-harvesting complex shows the active, energy-transmitting state, Embo J 28 (2009) 298.

[65] B. Demmig-Adams, Carotenoids and photoprotection in plants: A role for the xanthophyll zeaxanthin, Biochim.Biophys.Acta 1020 (1990) 1.

[66] A.V. Ruban, P. Horton, The xanthophyll cycle modulates the kinetics of nonphotochemical energy dissipation in isolated light-harvesting complexes, intact chloroplasts, and leaves of spinach, Plant Physiol 119 (1999) 531.

[67] R. Bassi, S. Caffarri, Lhc proteins and the regulation of photosynthetic light harvesting function by xanthophylls, Photosynthesis Research 64 (2000) 243.

[68] S. Crouchman, A. Ruban, P. Horton, PsbS enhances nonphotochemical fluorescence quenching in the absence of zeaxanthin, FEBS Lett 580 (2006) 2053.

[69] A. Zia, M.P. Johnson, A.V. Ruban, Acclimation- and mutation-induced enhancement of PsbS levels affects the kinetics of non-photochemical quenching in Arabidopsis thaliana, Planta 233 (2011).

[70] I.S. Zulfugarov, A. Tovuu, B. Dogsom, C.Y. Lee, C.H. Lee, PsbS-specific zeaxanthin-independent changes in fluorescence emission spectrum as a signature of energy-dependent non-photochemical quenching in higher plants, Photochem Photobiol Sci 9 (2010) 697.

[71] M.P. Johnson, M.L. Perez-Bueno, A. Zia, P. Horton, A.V. Ruban, The zeaxanthin-independent and zeaxanthin-dependent qE components of nonphotochemical quenching involve common conformational changes within the photosystem II antenna in Arabidopsis, Plant Physiol 149 (2009) 1061.

[72] P. Jahns, A.R. Holzwarth, The role of the xanthophyll cycle and of lutein in photoprotection of photosystem II, Biochim Biophys Acta 1817 (2012) 182.

[73] K.K. Niyogi, X.P. Li, V. Rosenberg, H.S. Jung, Is PsbS the site of non-photochemical quenching in photosynthesis?, J Exp Bot 56 (2005) 375.

[74] R.G. Walters, A.V. Ruban, P. Horton, Higher plant light-harvesting complexes LHCIIa and LHCIIc are bound by dicyclohexylcarbodiimide during inhibition of energy dissipation, Eur.J.Biochem 226 (1994) 1063.

[75] R.G. Walters, A.V. Ruban, P. Horton, Identification of proton-active residues in a higher plant light- harvesting complex, Proc.Natl.Acad.Sci.USA 93 (1996) 14204.

[76] J. Andersson, R.G. Walters, P. Horton, S. Jansson, Antisense inhibition of the photosynthetic antenna proteins CP29 and CP26: Implications for the mechanism of protective energy dissipation Plant Cell 13 (2001) 1193.

[77] S. de Bianchi, L. Dall'Osto, G. Tognon, T. Morosinotto, R. Bassi, Minor antenna proteins CP24 and CP26 affect the interactions between photosystem II Subunits and the electron transport rate in grana membranes of Arabidopsis, Plant Cell 20 (2008) 1012.

[78] L. Kovacs, J. Damkjaer, S. Kereiche, C. Ilioaia, A.V. Ruban, E.J. Boekema, S. Jansson, P. Horton, Lack of the light-harvesting complex CP24 affects the structure and function of the grana membranes of higher plant chloroplasts, Plant Cell 18 (2006) 3106.

[79] P. Jahns, G.H. Krause, Xanthophyll cycle and energy-dependent fluorescence quenching in leaves from pea plants grown under intermittent light, Planta 192 (1994) 176.

[80] J. Andersson, M. Wentworth, R.G. Walters, C.A. Howard, A.V. Ruban, P. Horton, S. Jansson, Absence of the Lhcb1 and Lhcb2 proteins of the light-harvesting complex of photosystem II - effects on photosynthesis, grana stacking and fitness, Plant Journal 35 (2003) 350.

[81] J.T. Damkjaer, S. Kereiche, M.P. Johnson, L. Kovacs, A.Z. Kiss, E.J. Boekema, A.V. Ruban, P. Horton, S. Jansson, The photosystem II light-harvesting protein Lhcb3 affects the macrostructure of photosystem II and the rate of state transitions in Arabidopsis, Plant Cell 21 (2009) 3245.

[82] P. Horton, A.V. Ruban, M. Wentworth, Allosteric regulation of the light-harvesting system of photosystem II, Philos Trans R Soc Lond B Biol Sci 355 (2000) 1361.

[83] M.L. Perez-Bueno, M.P. Johnson, A. Zia, A.V. Ruban, P. Horton, The Lhcb protein and xanthophyll composition of the light harvesting antenna controls the DeltapH-dependency of non-photochemical quenching in Arabidopsis thaliana, FEBS Lett 582 (2008) 1477.

[84] J.P. Dekker, E.J. Boekema, Supramolecular organization of thylakoid membrane proteins in green plants, Biochim.Biophys.Acta 1706 (2005) 12.

[85] P. Horton, A.V. Ruban, D. Rees, A.A. Pascal, G. Noctor, A.J. Young, Control of the light-harvesting function of chloroplast membranes by aggregation of the LHCII chlorophyll-protein complex, FEBS Lett 292 (1991) 1.

[86] Y. Miloslavina, A. Wehner, P.H. Lambrev, E. Wientjes, M. Reus, G. Garab, R. Croce, A.R. Holzwarth, Far-red fluorescence: a direct spectroscopic marker for LHCII oligomer formation in non-photochemical quenching, FEBS Lett 582 (2008) 3625.

[87] P. Horton, M. Wentworth, A. Ruban, Control of the light harvesting function of chloroplast membranes: The LHCII-aggregation model for non-photochemical quenching, Febs Letters 579 (2005) 4201.

[88] T.K. Ahn, T.J. Avenson, M. Ballottari, Y.C. Cheng, K.K. Niyogi, R. Bassi, G.R. Fleming, Architecture of a charge-transfer state regulating light harvesting in a plant antenna protein, Science 320 (2008) 794.

[89] P.N. Liao, C.P. Holleboom, L. Wilk, W. Kuhlbrandt, P.J. Walla, Correlation of Car S(1) --> Chl with Chl --> Car S(1) energy transfer supports the excitonic model in quenched light harvesting complex II, J Phys Chem B 114 (2010) 15650.

[90] M.G. Muller, P. Lambrev, M. Reus, E. Wientjes, R. Croce, A.R. Holzwarth, Singlet energy dissipation in the photosystem II light-harvesting complex does not involve energy transfer to carotenoids, Chemphyschem 11 (2010) 1289.

[91] A.M. Gilmore, Mechanistic aspects of xanthophyll cycle-dependent photoprotection in higher plant chloroplasts and leaves, Physiological Plantarum 99 (1997) 197.

[92] K.K. Niyogi, A.R. Grossman, O. Bjorkman, Arabidopsis mutants define a central role for the xanthophyll cycle in the regulation of photosynthetic energy conversion, Plant Cell 10 (1998) 1121.

[93] P. Joliot, G.N. Johnson, Regulation of cyclic and linear electron flow in higher plants, Proc Natl Acad Sci U S A 108 (2011) 13317.

[94] L. Kalituho, K.C. Beran, P. Jahns, The transiently generated nonphotochemical quenching of excitation energy in Arabidopsis leaves is modulated by zeaxanthin, Plant Physiol 143 (2007) 1861.

[95] A.V. Ruban, A.J. Young, A.A. Pascal, P. Horton, The effects of illumination on the xanthophyll composition of the photosystem II light-harvesting complexes of spinach thylakoid membranes, Plant Physiol. 104 (1994) 227.

[96] H.E. Akerlund, B. Andersson, A. Persson, P.A. Albertsson, Isoelectric points of spinach thylakoid membrane surfaces as determined by cross partition, Biochim Biophys Acta 552 (1979) 238.

[97] D.M. Kramer, C.A. Sacksteder, J.A. Cruz, How acidic is the lumen, Photosynth. Res. 60 (1999) 151.
[98] P. Jahns, D. Latowski, K. Strzalka, Mechanism and regulation of the violaxanthin cycle: the role of antenna proteins and membrane lipids, Biochim Biophys Acta 1787 (2009) 3.
[99] X.G. Zhu, S.P. Long, D.R. Ort, Improving photosynthetic efficiency for greater yield, Annu Rev Plant Biol 61 (2010) 235.
[100] E.H. Murchie, M. Pinto, P. Horton, Agriculture and the new challenges for photosynthesis research, New Phytol 181 (2009) 532.
[101] E.H. Murchie, K.K. Niyogi, Manipulation of photoprotection to improve plant photosynthesis, Plant Physiol 155 (2011) 86.
[102] J. Beckmann, F. Lehr, G. Finazzi, B. Hankamer, C. Posten, L. Wobbe, O. Kruse, Improvement of light to biomass conversion by de-regulation of light-harvesting protein translation in Chlamydomonas reinhardtii, J Biotechnol 142 (2009) 70.
[103] C. Kulheim, J. Agren, S. Jansson, Rapid regulation of light harvesting and plant fitness in the field, Science 297 (2002) 91.
[104] N.M. Krah, B.A. Logan, Loss of psbS expression reduces vegetative growth, reproductive output, and light-limited, but not light-saturated, photosynthesis in Arabidopsis thaliana (Brassicaceae) grown in temperate light environments, Am J Bot 97 (2010) 644.
[105] S. Hubbart, O.O. Ajigboye, P. Horton, E.H. Murchie, The photoprotective protein PsbS exerts control over CO(2) assimilation rate in fluctuating light in rice, Plant J 71 (2012) 402.
[106] I.S. Zulfugarov, O.K. Ham, S.R. Mishra, J.Y. Kim, K. Nath, H.Y. Koo, H.S. Kim, Y.H. Moon, G. An, C.H. Lee, Dependence of reaction center-type energy-dependent quenching on photosystem II antenna size, Biochim Biophys Acta 1767 (2007) 773.
[107] M. Ballottari, L. Dall'Osto, T. Morosinotto, R. Bassi, Contrasting behavior of higher plant photosystem I and II antenna systems during acclimation, J Biol Chem 282 (2007) 8947.
[108] T. Roach, A. Krieger-Liszkay, The role of the PsbS protein in the protection of photosystems I and II against high light in Arabidopsis thaliana, Biochim Biophys Acta 1817 (2012) 2158.

Chức năng của protêin PsbS trong điều chỉnh quang hợp ở thực vật

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Tóm tắt: Quá trình quang hợp chuyển hóa năng lượng ánh sáng mặt trời thành năng lượng hóa học trong các hợp chất hữu cơ cung cấp cho hầu hết các dạng sống trên trái đất. Khi năng lượng ánh sáng hấp thụ vượt quá khả năng quang hợp của cây, nó có thể chuyển thành ROS (Reactive Oxygen Species) gây nguy hiểm cho cây. Trong điều kiện đó, cây phát triển một cơ chế tỏa ra năng lượng ánh sáng dư thừa ở dạng nhiệt được gọi là NPQ (Non Photochemical Quenching), để chống lại ROS bảo vệ cho cây. Trong bài tổng quan này, chúng tôi giới thiệu về một protêin của hệ quang hóa II, protêin PsbS được biết có vai trò chìa khóa trong sự hoạt hóa NPQ. Sự tăng hay giảm NPQ tỉ lệ với hàm lượng protêin PsbS trong lá cây. Các nghiên cứu trước đây chỉ ra rằng PsbS hoạt động như một cảm biến độ pH thấp của lumen trên màng thylakoid, một yếu tố quan trọng để hoạt hóa NPQ. Protêin PsbS còn được đề xuất kiểm soát sự tổ chức lại cấu trúc màng grana để hoạt hóa NPQ trong điều kiện ánh sáng cao. Protêin này có vẻ như không kết hợp với sắc tố quang hợp vậy nên nó không phải là điểm dập tắt năng lượng, nhưng nó có quan hệ với zeaxanthin để kích hoạt đầy đủ NPQ. Vì vậy, PsbS có vai trò rất quan trọng trong tính chống chịu ánh sáng cao của thực vật. Nghiên cứu protêin này mở ra một triển vọng điều chỉnh sự sử dụng năng lượng ánh sáng hấp thụ trong quang hợp để tăng năng xuất cây trồng.

Từ khóa: Ánh sáng, NPQ, protêin PsbS, quang hợp, ROS.