



Special issue on Recent advances in photomodulation in higher plants, algae, and bryophytes

REVIEW

Effects of abiotic stress on photosystem II proteins

M. LANDI⁺ and L. GUIDI

Department of Agriculture, Food and Environment, University of Pisa, Via del Borghetto 80, 56124 Pisa, Italy

Abstract

Photosystem II (PSII) represents the most vulnerable component of the photosynthetic machinery and its response in plants subjected to abiotic stress has been widely studied over many years. PSII is a thylakoid membrane-located multiprotein pigment complex that catalyses the light-induced electron transfer from water to plastoquinone with the concomitant production of oxygen. PSII is rich in intrinsic (PsbA and PsbD, namely D1 and D2, CP47 or PsbB and CP43 or PsbC) but also extrinsic proteins. The first ones are more largely conserved from cyanobacteria to higher plants while the extrinsic proteins are different among species. It has been found that extrinsic proteins involved in oxygen evolution change dramatically the PSII efficiency and PSII repair systems. However, little information is available on the effects of abiotic stress on their function and structure.

Keywords: abiotic stress; extrinsic protein; intrinsic protein; photosynthesis; photosystem II.

Introduction

Photosynthesis is the process that converts sunlight into chemical energy utilized to synthesize organic compounds. It represents the most important process on the Earth carried out by higher plants, algae, and cyanobacteria. The process exploits solar radiation to induce a charge separation from chlorophyll (electron donor) to pheophytin (electron acceptor) which represents the key phenomenon of the whole process. This chemical event occurs in two complexes located inside the thylakoid membranes, photosystem II (PSII) and I (PSI). Briefly, a photosystem is a supramolecular protein that absorbs the sunlight through a light-harvesting complex (LHC), chlorophyll

(Chl)–protein complex that absorbs light and funnels the energy to the reaction centre Chl *a* molecule(s), using Foster resonance energy transfer. The reaction centre is the place where light energy is collected and used to power photosynthetic redox reactions, leading to the synthesis of ATP and NADPH. In higher plants, two photosystems show some differences such as (Caffarri *et al.* 2014):

- location in the thylakoid membranes: PSI is located in the non-appressed grana region and stroma lamellae while PSII is in the appressed grana region;
- different reaction centre: PSI is an iron–sulphur type reaction centre (type I) while PSII has a quinone type reaction centre (type II or Q-type). In addition, the core complex of PSI is made up of about 15 protein subunits

Highlights

- Intrinsic and extrinsic proteins of PSII help counteract light stress
- Abiotic stressors strongly influence PSII proteins dynamics
- Role of extrinsic proteins in PSII repairing cycle

Received 14 April 2022

Accepted 1 September 2022

Published online 3 October 2022

⁺Corresponding author

phone: +39 50 2216620

e-mail: marco.landi@unipi.it

Abbreviations: Chl – chlorophyll; ETC – electron transport chain; LHC – light-harvesting complex; NPQ – nonphotochemical quenching; OEC – oxygen-evolving complex; q_E – energy gradient quenching; q_I – photoinhibition quenching; q_T – state II–I transition quenching; q_Z – zeaxanthin-dependent quenching; ROS – reactive oxygen species.

Acknowledgements: The authors are extremely thankful to Prof. Claudia Büchel for the critical revision of the manuscript and her insightful comments and suggestions. The authors are also thankful to Dr. Ermes Lo Piccolo for the graphical support in figure realization.

Conflict of interest: The authors declare that they have no conflict of interest.

while that of PSII is a multi-subunit complex with about 25–30 subunits;

- the peak in light absorption: PSI has maximum absorption close to 682 nm, while PSII at 677 nm. In addition, due to the higher LHC complement of PSI as compared to PSII, the PSII supercomplex has a lower Chl *a/b* ratio and shows a higher Chl *b* peak near 650 nm. Finally, the presence of low-energy Chls which absorb at wavelengths above those of P700 is unique in PSI (Croce *et al.* 1996);

- involvement in water splitting: this process is only associated with PSII, as it generates a strong oxidant (P680⁺) necessary to carry out the thermodynamically not favoured process of water oxidation.

PSII is a large membrane-protein complex located in the thylakoids of the chloroplast of many organisms, from cyanobacteria to higher plants. It is a very organized complex that contains 20 subunits (17 transmembrane subunits and three membrane-peripheral extrinsic subunits) (Müh and Zouni 2020). Among the transmembrane subunits, proteins D1 and D2 constitute the reaction centre core of PSII directly associated with all cofactors involved in electron-transfer and water-splitting reactions (Ferreira *et al.* 2004, Umena *et al.* 2011, Büchel 2015, Müh and Zouni 2020). Other subunits surround the D1 (also known as photosystem A or PsbA) and D2 subunits and in particular, CP47 and CP43 in which the acronyms CP stands for Chl-protein complex having an important role in binding Chl molecules with the function of an inner light-harvesting complex. All these intrinsic proteins are encoded by chloroplast DNA. The proteins D1 and D2 bind Chls, pheophytin, plastoquinones, β -carotenes, and Fe whereas CP43 and CP47 bind only Chls and β -carotenes (Pospíšil and Yamamoto 2017, Müh and Zouni 2020). The other 13 transmembrane subunits with low molecular mass are PsbE, PsbF, PsbH, PsbI, PsbJ, PsbK, PsbL, PsbM, PsbT, PsbX, PsbY, PsbZ, and Psb30 (Shen *et al.* 2008, Umena *et al.* 2011, Müh and Zouni 2020). Finally, in plants and algae the three membrane-peripheral extrinsic proteins (PsbO, PsbP, and PsbQ), associated with the luminal side of PSII, are necessary to

maintain the water-splitting reactions (Roose *et al.* 2007, Enami *et al.* 2008, Ifuku 2014, Shen 2015). The basic structure of PSII is reported in Fig. 1.

Associated with the core complex, there is a peripheral-antenna system represented by a trimeric light-harvesting complex, the major antenna of PSII, and three monomers, the minor light-harvesting complex, named CP29, CP26, and CP24. These LHC complexes coordinate Chl *a* and *b* and several xanthophylls (Xu *et al.* 2017) and are associated with dimeric PSII cores to form PSII supra-complexes. Finally, a nucleus-encoded PsbS protein is a Δ pH-dependent kinetic modulator of the energy dissipation process in the LHCII, namely q_E suggested to be the major component of NPQ under high-light conditions (Li *et al.* 2000) The supercomplexes PSII-LHCII form semi-crystalline arrays in the thylakoid membrane (Dekker and Boekema 2005, Rantala *et al.* 2020) and are abundant in the stacked grana, but absent in the unstacked thylakoid membranes.

Alteration of PSII components under stress

Light represents the pivotal factor in driving photosynthesis but, the irony of fate, an excess of light can also cause damage to the photosynthetic apparatus (Barber and Andersson 1992). Excess light induces a decline in photosynthetic performance, thus resulting in an excess of excitation energy at the chloroplast level (Bassi and Dall'Osto 2021). Therefore, plants must continuously balance the energy absorbed and utilized, basically adjusting the leaf light interception and dissipation by the photosynthetic pigment. The energy excess leads to a reduction in PSII activity and the electron transport chain becomes over-reduced (Nishiyama *et al.* 2001, Roach and Kreiger-Liszkay 2014, Alric and Johnson 2017, Barbato *et al.* 2020).

However, plants have evolved several photoprotective mechanisms against situations of light excess. One of these mechanisms is the nonphotochemical energy dissipation associated with the nonphotochemical quenching (NPQ)

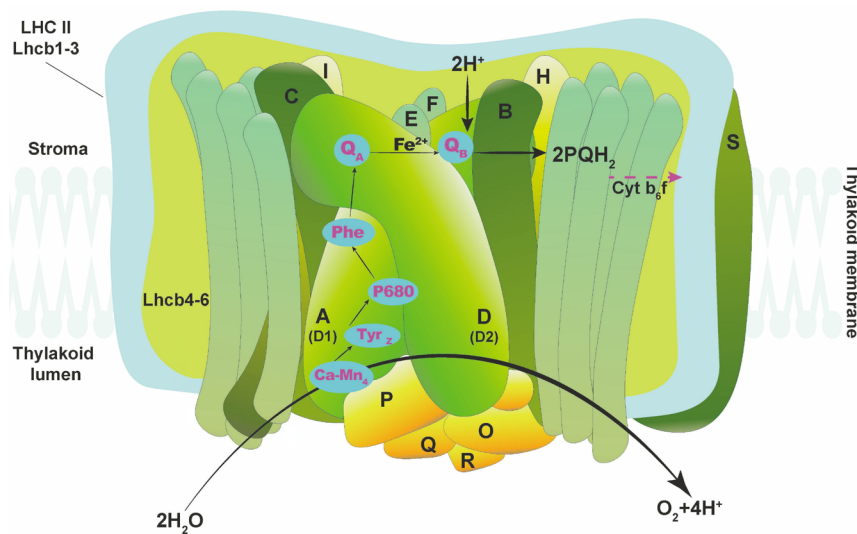


Fig. 1. Simplified structure of photosystem II (PSII) intrinsic and extrinsic proteins. Ca-Mn₄ – calcium-manganese cluster of oxygen evolving complex; Cyt *b₆f* – cytochrome *b₆f*; D1 – D1 protein; D2 – D2 protein; LHC II – light-harvesting complex of photosystem II; protein Tyr_z – tyrosine-161 of D1 protein; Phe – pheophytin; PQH₂ – mobile plastoquinone molecule; Q_A, Q_B – primary and secondary plastoquinone electron acceptors; P680 – core of photosystem II reaction center; A, B, C, D – intrinsic proteins of photosystem II; E, F, H, O, P, Q, R – extrinsic proteins of photosystem II.

of Chl fluorescence, which absolves the key role of reducing the amount of excited PSII Chl molecules under stressful conditions (Cazzaniga *et al.* 2013, Gururani *et al.* 2013, Murchie and Ruban 2020). NPQ consists of three components, described by the relaxation kinetics in dark conditions following an illumination period (Horton *et al.* 1996, Kress and Jahns 2017). The major and fast-released (within seconds to minutes) component is q_E , which is related to the increase in the ΔpH across the thylakoid membrane in the presence of PsbS and zeaxanthin (Horton *et al.* 1996, Ruban and Wilson 2021). The second component that relaxes slower than q_E , q_T , is attributable to the reversible phosphorylation of the LHCII that determines the state transition II–I (Quick and Stitt 1989, Kress and Jahns 2017). Finally, the third component, q_I , relaxes very slowly in time due to photoinhibition (Matsubara and Chow 2004, Nawrocki *et al.* 2021). There is another component, the long-lasting zeaxanthin-dependent quenching that occurs under certain environmental conditions (Demmig-Adams *et al.* 1998). This component, named q_Z , has been directly attributed to zeaxanthin accumulation and in particular to its binding to LHC protein specifically LHCb5 (Dall'Osto *et al.* 2005, Bassi and Dall'Osto 2021) and this component does not require a low lumen pH nor PsbS and thus does not represent a zeaxanthin-dependent q_E component (Nilkens *et al.* 2010, Kress and Jahns 2017).

As above reported, the nuclear-encoded PsbS protein plays a crucial role in the dissipation of excess light energy absorbed by PSII–LHCII into heat and, in this way, in the formation of nonphotochemical quenching q_E (Li *et al.* 2000, Bassi and Dall'Osto 2021). Kereïche *et al.* (2010) reported that this role is induced by the ability to control the macro-organization of the grana membranes in the chloroplast of higher plants. It has been also reported that PsbS, with the location of this protein in thylakoid membranes, is a mobile protein in the membranes (Teardo *et al.* 2007) and that its location is due to a reversible dimerization (Bergantino *et al.* 2003). However, Nicol *et al.* (2019) using an *Arabidopsis* mutant lacking LHCII trimers (*NoLHCII*), observed a decrease in NPQ of around 60% but the authors did not observe significant changes to the levels of PsbS, zeaxanthin or grana stacking and attributed the decrease in NPQ to the observed lack of upregulation of the minor antenna complexes and the absence of LHC trimers in the *NoLHCII* plants. From their results, the authors concluded that the majority of NPQ occurs in LHCII, but there is an additional site of PsbS-dependent quenching in the PSII core, most likely in the core antenna complexes CP43 and/or CP47.

During abiotic stress conditions, when the absorbed light exceeds that utilized by the biosynthetic pathways, another negative process is the generation of reactive oxygen species (ROS) in the chloroplasts because the electron transport chain (ETC) fails to generate NADPH, whilst directing electrons towards dioxygen in the photorespiration and the Mehler peroxidase reaction (Baker 2008, Bhattacharjee 2019). ROS induces lipid peroxidation and damages PSII proteins at the reaction

centre, antenna, and in the membrane near lipid molecules (Sasi *et al.* 2018). One of the most important adverse effects of ROS generation (and in particular of singlet oxygen) is the damage to the D1 protein; in particular, ROS may not directly damage PSII, but inactivate the repairing mechanisms of PSII (Allakhverdiev and Murata 2004, Nishiyama *et al.* 2004, Pinnola and Bassi 2018, Zavafer 2021). Indeed, in addition to the NPQ photoprotective mechanism, plants have developed an efficient PSII repairing mechanism aimed to preserve PSII from irreversible damage in conditions of excessive excitation energy (Nath *et al.* 2013a, Weisz *et al.* 2019). The PSII repairing cycle is a process in which the D1 protein is phosphorylated, dephosphorylated, and degraded by the action of a specific kinase (STN8; Nath *et al.* 2013b), phosphatase (PBCP; Samol *et al.* 2012), and protease (FtsHs and DEGs; Sun *et al.* 2007, Edelman and Mattoo 2008), respectively, and finally D1 is newly resynthesized and reassembled in the PSII (Tikkanen and Aro 2014, Weisz *et al.* 2019).

In addition to excess light, other environmental stresses can lead to photoinhibition, even though not directly, but rather by facilitating the inhibition of the PSII repairing mechanisms (Murata *et al.* 2007, Nishiyama and Murata 2014, Li *et al.* 2018). It has been widely reported as both photoinhibition and ROS, such as superoxide anion and singlet oxygen, induced by different abiotic stresses, *e.g.*, high or low temperature (Allakhverdiev and Murata 2004, Takahashi *et al.* 2009, Mattila *et al.* 2020), salinity (Allakhverdiev and Murata 2004, He *et al.* 2021, Pan *et al.* 2021), and constrained CO₂ fixation (Wang *et al.* 2014, Foyer 2018), can inhibit the translation of *psbA* mRNA and inactivate in this way the PSII repairing process. Finally, ROS can irreversibly alter the protein structure through the carbonylation process (Johansson *et al.* 2004, Akagawa 2021). Although photoprotective mechanisms can scavenge ROS, when the stress overcomes the protection mechanisms, protein oxidation can induce PSII protein cleavage and aggregation (Kale *et al.* 2017, Pospíšil and Yamamoto 2017).

In photoinhibition conditions, slight phosphorylation of PSII results in efficient photochemistry of LHCII and slower damage to PSII (Tikkanen *et al.* 2010, Tikkanen and Aro 2014, Wu *et al.* 2021a). In fact, in these conditions, no net damage to PSII occurs and a moderate amount of energy is transferred to PSI because phosphorylated LHCII move to the grana margins. However, when light is in excess and PSII proteins are phosphorylated at a very high rate, the PSII–LHCII supercomplex loses its structural integrity and the energy transfer toward PSI is unregulated (Tikkanen *et al.* 2010, Tikkanen and Aro 2014, Grinzato *et al.* 2020).

In addition, the PSII photoinhibition represents also a mechanism by which PSII can protect PSI from irreversible damage; Tikkanen *et al.* (2014) proposed that the regulation of PSII photoinhibition is the ultimate regulator of the photosynthetic electron transfer chain and provides a photoprotection mechanism against the formation of ROS and photodamage in PSI. In a general way, it is

possible that slowing down PSII photochemistry but also the redox chemistry can function as a protection system for the photosynthetic machinery against photodamage (Tikkanen *et al.* 2012).

An important aspect is a balance between the damage and repair of PSII, which represents the most dynamically regulated part of the light reactions in the thylakoid membrane (Tikkanen *et al.* 2008, Rantala *et al.* 2020). In addition to the phosphorylation process of LHCII, the PSII core proteins D1, D2, CP43, PsbH, and TSP9 can also be subjected to dynamic phosphorylation (Rochaix 2007, Johnson and Wientjes 2020), strictly related to the regulation of PSII turnover upon photodamage (Aro *et al.* 1993, Longoni and Goldschmidt-Clermont 2021). Even in moderate light conditions, the high oxidant power of P680⁺ can induce photodamage to the D1 protein; so, the dynamic degradation of the damaged D1 protein and its *de novo* synthesis and insertion in the PSII core is one of the prerequisites for aerobic organisms (Aro *et al.* 2005, Chen *et al.* 2020). In the past, it was postulated that the phosphorylation of the damaged D1 protein represents in plants a signal for migration of the damaged PSII from the grana to stroma lamellae where D1 is degraded, resynthesized, and inserted in the PSII (Aro *et al.* 1993). More recently it has been reported that the processes of phosphorylation and dephosphorylation in plants are not a key element for the D1 turnover (Bonardi *et al.* 2005) even though the PSII core phosphorylation facilitates the disassembly of the PSII–LHCII supercomplexes (Tikkanen *et al.* 2008, Fristedt *et al.* 2009) to increase the mobility of the PSII from grana to stroma lamellae under photoinhibition conditions (Rantala *et al.* 2020).

Using the *Arabidopsis* mutants with impaired capacity (*stin8*) or complete lack (*stin7 stin8*) in phosphorylation of PSII core proteins, Tikkanen *et al.* (2008) concluded that after the migration towards stroma thylakoids of the phosphorylated PSII core, a phosphatase, activated by the release of the CYP38 protein, dephosphorylates the damaged D1. In turn, D1 resulted as more susceptible to the degradation operated by a D1-specific protease. The protease FtsH (Adam and Sakamoto 2014) and DEG (Sun *et al.* 2007, Kato *et al.* 2012) are the two possible candidates for degradation of the D1 protein. Opposing this view, Fristedt *et al.* (2009) argued that the PSII core phosphorylation instead induces macroscopic rearrangements to the thylakoid membrane and allows the PSII repair cycle by decreasing the membrane cohesion. The different hypotheses on the roles of PSII core protein phosphorylation are not necessarily mutually exclusive.

PSII repair cycle: the role of extrinsic proteins PsbO, PsbP, PsbQ, and PsbR

The extrinsic proteins PsbO, PsbP, PsbQ, and PsbR (33, 23, 18, and 10 kDa, respectively) play a key role in maintaining the cluster of oxygen-evolving complex (OEC) represented by four Mn atoms, one Ca atom and five oxygen atoms (CaMn₄O₅). This structure is evolutionary conserved and identical from cyanobacteria to various algae and higher

plants and dates back to 2.4 billion years ago (Vinyard *et al.* 2013). An important role of the extrinsic protein PsbO, PsbP, and PsbQ, located at the luminal side, is the protection of the OEC under stress (Roose *et al.* 2007). For example, salinity harms the Mn cluster of OEC which induces a reduction of PSII activity (Allakhverdiev and Murata 2004). PsbO is very important in stabilizing the OEC (Popelkova and Yocum 2011) while the PsbP protein plays a role in optimizing Ca²⁺ and Cl⁻ availability for maintaining the Mn–Ca²⁺–Cl⁻ cluster of OEC (Bricker *et al.* 2013). In addition, the correct functioning of PsbQ requires the presence of Cl⁻ ions at low concentrations (< 3 mM) (Tomita *et al.* 2009). In addition to PsbO, PsbP, PsbQ, another protein, the 10-kDa PsbR protein, has been found in green algae structures and plant PSII and is involved in the protection of OEC in high-light conditions maintaining the standard rate of oxygen evolution (Suorsa *et al.* 2006). Its absence induces a strong decrease in oxygen evolution particularly in plants grown in low-light conditions (Suorsa *et al.* 2006).

In both high and low-temperature conditions, the PSII complex is the most susceptible part of the photosynthetic apparatus and in these stressed conditions, the extrinsic proteins PsbP, PsbQ, and PsbR disassociate from the OEC complex of PSII (Gupta *et al.* 2021).

Many other stresses can alter the structure and functionality of PSII proteins. For example, Wu *et al.* (2021b) recorded the inhibition of the photosynthetic process in plants of *Phragmites australis* grown at high Cu concentrations related to a reduction in both Chl *a* and *b* contents but also a downregulation in the expression of PsbD, PsbO, and PsbA. Other trace elements such as Cd and Cr at toxic concentration induced negative effects on the structure of thylakoid complexes in *Chlorella variabilis* attributable to the generated oxidative stress (Zsiros *et al.* 2020). However, the mechanisms involved for the two elements are different: Cd induced the inhibition of PSII activity *via* degradation of PsbO (and also PsbA) proteins while the negative effects of Cr were due to the inhibition on the PSII side.

In addition, in the repair cycle of PSII, *i.e.*, in the D1 turnover, a key role is played by the extrinsic PSII proteins PsbO, PsbP, and PsbQ (Bricker *et al.* 2012). The mutation and absence of the PsbO subunit render PSII more vulnerable to photoinhibition (Henmi *et al.* 2004, Sasi *et al.* 2018), and Yamamoto *et al.* (2008) reported that PsbO is of utmost importance in protecting the structure of D1 from ROS production.

Some plant species only possess one PsbO isoform (*Oryza sativa* and *Pisum sativum*) whereas other species such as potato and *Arabidopsis* have two isoforms of PsbO (Sasi *et al.* 2018). The role of PsbO protein against photodamage during different abiotic stress has been reported. In particular, PsbO preserved and stabilized the PSII during drought stress (Pawłowicz *et al.* 2012) but this protein was partially degraded during cold treatment (Kosmala *et al.* 2009). Many researchers used PsbO mutants under abiotic stress conditions and sometimes they obtained contrasting results (Murakami *et al.*

2005, Dwyer *et al.* 2012, Gururani *et al.* 2012, 2013); in addition, there were also contrasting results between *PsbO* expression and plant growth under stress conditions (Pawłowicz *et al.* 2012, Gururani *et al.* 2013) likely attributable to the presence of different isoforms of *PsbO* in different plant species (Sasi *et al.* 2018). *PsbO* has also a function as a putative enzymatic GTPase regulating the phosphorylation state of the D1 process, the event associated with an efficient turnover of the D1 protein during the repairing mechanism (Bricker and Frankel 2011). In addition to *PsbO*, the other extrinsic proteins, *PsbP* and *PsbQ* play an important role in stabilizing the architecture of LHCII supercomplexes in higher plants; in particular, *PsbO* and *PsbP* under normal growth conditions (Ifuku *et al.* 2005, Che *et al.* 2020) and *PsbQ* during growth at low light intensity (Yi *et al.* 2006). The protein *PsbP* is important to maintain the Mn–Ca²⁺–Cl⁻ cluster within PSII (Seidler 1996, Ifuku and Nagao 2021) and some homologs of this protein are present in the thylakoid lumen (*e.g.*, the *PsbP*-like proteins PPL1 and 2) (Ishihara *et al.* 2007, Matsui *et al.* 2013). These PPL1 and 2 of PSII are involved in the response of photosynthesis under stress conditions. For example, Ishihara *et al.* (2007) reported that a *ppl1* mutant of *Arabidopsis* was more sensitive to high-intensity light than the wild type, and the recovery of PSII activity after photoinhibition was delayed in *ppl1* plants. On the other hand, Ishihara *et al.* (2007) also demonstrated that PPL2 is a novel thylakoid luminal factor required for the accumulation of the chloroplast NADH dehydrogenase complex.

PsbP with *PsbQ* proteins are strictly involved in the association of peripheral antennae to PSII, a process extremely dynamic that adjusts the photosynthetic light reactions to environmental changes (Cao *et al.* 2018). In particular, *PsbP* protein represents an assembly and/or stability factor for PSII in cyanobacteria (Knoppová *et al.* 2016) but also in higher plants (Bricker *et al.* 2012, 2013).

Extrinsic protein *PsbQ*, together with *PsbP*, are responsible for the interactions with both PSII intrinsic and light-harvesting complex (Ido *et al.* 2014, Cao *et al.* 2018) and other studies revealed that *PsbQ* can replace the N-terminal *PsbP* functional defect and in this way is involved in the *PsbP* stabilization in PSII (Ifuku *et al.* 2005). On the other hand, the *PsbQ* is required at low Cl⁻ concentrations (< 3 mM) for oxygen evolution (Miyao and Murata 1985, Gupta 2020).

In conclusion, the extrinsic proteins in PSII play a major role to protect the oxygen-evolving complex and, until now, few reports have indicated the possible role of abiotic stresses on these proteins. It is, however, underlined as changes in the expression of these extrinsic proteins dramatically decrease the PSII efficiency or change the repair PSII mechanisms (Sasi *et al.* 2018).

In addition, it has been proposed that *PsbP* is involved in binding manganese which is essential for photoactivation (Bondarava *et al.* 2007, Schmidt and Husted 2019) and, together with *PsbQ* protein, participates in grana stack formation (Anderson *et al.* 2008). Finally, the removal of *PsbP* protein induces defects at the reducing side of

the PSII because significantly slows the rate of electron transport from Q_A to Q_B (Roose *et al.* 2010).

Other low-molecular-mass proteins associated with PSII

In addition to the above reported in the PSII, there is a large number of proteins for which not much information about their role has been reported. Close to D2 protein, the *PsbE* and *PsbF*, α - and β -subunits of Cyt *b*₅₅₉, function as a safety valve to remove the excessive oxidative hole from the PSII donor side (Shevela *et al.* 2021). Cyt *b*₅₅₉ plays a protective role for the donor and acceptor side of PSII reaction centres against photoinhibition as evidenced by Chu and Chiu (2016) in site-direct mutagenesis studies that provide evidence for a possible physiological role of Cyt *b*₅₅₉ in the assembly and stability of PSII, protecting PSII against photoinhibition and modulating photosynthetic light harvesting.

Another plastome-encoded protein *PsbH* is reported in higher plants; it contributes to Chl-binding protein 43 kDa (CP43) in the formation of the inner LHC (Barber *et al.* 1997). This protein is a determinant of PSII activity but plays also a role in regulating PSII assembly/stability and repair of photodamaged PSII (Shi and Schröder 2004) and in protecting the PSII core and the thylakoid membrane from oxidative damage (Huang *et al.* 2016).

The *PsbI* protein, again a plastome-encoded protein, is located at the periphery of the reaction centre and strictly related to the core antenna protein CP43, is close to ChlZ(D1) and binds to D1 (Niield and Barber 2006, Pagliano *et al.* 2013). Studies with tobacco plants, in which the *PsbI* gene was deleted, demonstrated the importance of the *PsbI* protein for PSII functioning and the stabilization of PSII dimers and supercomplexes (Schwenkert *et al.* 2006). This seems to indicate that this subunit can play a role in the connection between the inner antenna CP43 and the outer antenna CP29 (Dekker and Boekema 2005).

Adjacent to the *PsbE* and *PsbF* proteins of Cyt *b*₅₅₉ is located also the *PsbJ* protein; altogether these proteins form a channel for the diffusion of PQ/PQH2 involved in the PQ pool (Guskov *et al.* 2009).

Concluding remarks

Photosynthetic light absorption generates the P680⁺, a strong oxidant able to oxidize water in the OEC, a complex that is protected and stabilized by extrinsic proteins. These proteins play a key role in stabilizing the PSII that represents the most vulnerable components in the photosynthetic machinery. Nevertheless, little information is on the role of these proteins in the plant abiotic stress responses. In this review, the state of the art about the information on the effects of abiotic stresses on PSII protein is reported in an attempt to summarize existing information on the topic and stimulate further research on the matter.

References

- Adam Z., Sakamoto W.: Plastid proteases. – In: Theg S., Wollman F.A. (ed.): *Plastid Biology. Advances in Plant Biology*. Pp. 359-389. Springer, New York 2014.
- Akagawa M.: Protein carbonylation: molecular mechanisms, biological implications, and analytical approaches. – *Free Radic. Res.* **55**: 307-320, 2021.
- Allakhverdiev S.I., Murata N.: Environmental stress inhibits the synthesis *de novo* proteins involved in the photodamage-repair cycle of photosystem II in *Synechocystis* sp. PCC 6803. – *BBA-Bioenergetics* **1657**: 23-32, 2004.
- Alric J., Johnson X.: Alternative electron transport pathways in photosynthesis: a confluence of regulation. – *Curr. Opin. Plant Biol.* **37**: 78-86, 2017.
- Anderson J.M., Chow W.S., De Las Rivas J.: Dynamic flexibility in the structure and function of Photosystem II in higher plant thylakoid membranes: the grana enigma. – *Photosynth. Res.* **98**: 575-587, 2008.
- Aro E.-M., Suorsa M., Rokka A. *et al.*: Dynamics of photosystem II: a proteomic approach to thylakoid protein complexes. – *J. Exp. Bot.* **56**: 347-356, 2005.
- Aro E.-M., Virgin I., Andersson B.: Photoinhibition of Photosystem II. Inactivation, protein damage and turn over. – *BBA-Bioenergetics* **1143**: 113-134, 1993.
- Baker N.R.: Chlorophyll fluorescence. A probe of photosynthesis *in vivo*. – *Annu. Rev. Plant Biol.* **59**: 89-113, 2008.
- Barbato R., Tadini L., Cannata R. *et al.*: Higher order photoprotection mutants reveal the importance of ΔpH-dependent photosynthesis-control in preventing light induced damage to both photosystem II and photosystem I. – *Sci. Rep.-UK* **10**: 6770, 2020.
- Barber J., Andersson B.: Too much of a good thing: light can be bad for photosynthesis. – *Trends Biochem. Sci.* **17**: 61-66, 1992.
- Barber J., Nield J., Morris E.P. *et al.*: The structure, function and dynamics of photosystem two. – *Physiol. Plantarum* **100**: 817-827, 1997.
- Bassi R., Dall'Osto L.: Dissipation of light energy absorbed in excess: the molecular mechanisms. – *Annu. Rev. Plant Biol.* **72**: 47-76, 2021.
- Bergantino E., Segalla A., Brunetta A. *et al.*: Light- and pH-dependent structural changes in the PsbS subunit of photosystem II. – *P. Natl. Acad. Sci. USA* **100**: 15265-15270, 2003.
- Bhattacharjee S.: ROS and oxidative stress: origin and implication. – In: Bhattacharjee S. (ed.): *Reactive Oxygen Species in Plant Biology*. Pp. 1-31. Springer, New Delhi 2019.
- Bonardi V., Pesaresi P., Becker T. *et al.*: Photosystem II core phosphorylation and photosynthetic acclimation require two different protein kinases. – *Nature* **437**: 1179-1182, 2005.
- Bondarava N., Un S., Krieger-Liszkay A.: Manganese binding to the 23 kDa extrinsic protein of Photosystem II. – *BBA-Bioenergetics* **1767**: 583-588, 2007.
- Bricker T.M., Frankel L.K.: Auxiliary functions of the PsbO, PsbP and PsbQ proteins of higher plant Photosystem II: A critical analysis. – *J. Photoch. Photobio. B* **104**: 165-178, 2011.
- Bricker T.M., Roose J.L., Fagerlund R.D. *et al.*: The extrinsic proteins of Photosystem II. – *BBA-Bioenergetics* **1817**: 121-142, 2012.
- Bricker T.M., Roose J.L., Zhang P., Frankel L.K.: The PsbP family of proteins. – *Photosynth. Res.* **116**: 235-250, 2013.
- Büchel C.: Evolution and function of light harvesting proteins. – *J. Plant Physiol.* **172**: 62-75, 2015.
- Caffarri S., Tibiletti T., Jennings R.C., Santabarbara S.: A comparison between plant photosystem I and photosystem II architecture and functioning. – *Curr. Protein Pept. Sci.* **15**: 296-331, 2014.
- Cao P., Su X., Pan X. *et al.*: Structure, assembly and energy transfer of plant photosystem II supercomplex. – *BBA-Bioenergetics* **1859**: 633-644, 2018.
- Cazzaniga S., Dall'Osto L., Kong S.G. *et al.*: Interaction between avoidance of photon absorption, excess energy dissipation and zeaxanthin synthesis against photooxidative stress in *Arabidopsis*. – *Plant J.* **76**: 568-579, 2013.
- Che Y., Kusama S., Matsui S. *et al.*: *Arabidopsis* PsbP-like protein 1 facilitates the assembly of the Photosystem II supercomplexes and optimizes plant fitness under fluctuating light. – *Plant Cell Physiol.* **61**: 1168-1180, 2020.
- Chen J.-H., Chen S.-T., He N.-Y. *et al.*: Nuclear-encoded synthesis of the D1 subunit of photosystem II increases photosynthetic efficiency and crop yield. – *Nat. Plants* **6**: 570-580, 2020.
- Chu H.-A., Chiu Y.-F.: The roles of cytochrome *b₅₅₉* in assembly and photoprotection of Photosystem II revealed by site-directed mutagenesis studies. – *Front. Plant Sci.* **6**: 1261, 2016.
- Croce R., Zucchelli G., Garlaschi F.M. *et al.*: Excited state equilibration in the photosystem I-light-harvesting I complex: P700 is almost isoenergetic with its antenna. – *Biochemistry-US* **35**: 8572-8579, 1996.
- Dall'Osto L., Caffarri S., Bassi R.: A mechanism of nonphotochemical energy dissipation, independent from PsbS, revealed by a conformational change in the antenna protein CP26. – *Plant Cell* **17**: 1217-1232, 2005.
- Dekker J.P., Boekema E.J.: Supramolecular organization of thylakoid membrane proteins in green plants. – *BBA-Bioenergetics* **1706**: 12-39, 2005.
- Demmig-Adams B., Moeller D.L., Logan B.A., Adams III W.W.: Positive correlation between levels of retained zeaxanthin+ antheraxanthin and degree of photoinhibition in shade leaves of *Schefflera arboricola* (Hayata) Merrill. – *Planta* **205**: 367-374, 1998.
- Dwyer S., Chow W., Yamori W. *et al.*: Antisense reductions in the PsbO protein of photosystem II leads to decreased quantum yield but similar maximal photosynthetic rates. – *J. Exp. Bot.* **63**: 4781-4795, 2012.
- Edelman M., Mattoo A.K.: D1-protein dynamics in photosystem II: the lingering enigma. – *Photosynth. Res.* **98**: 609-620, 2008.
- Enami I., Okumura A., Nagao R. *et al.*: Structures and functions of the extrinsic proteins of photosystem II from different species. – *Photosynth. Res.* **98**: 349-363, 2008.
- Ferreira K.N., Iverson T.M., Maghlaoui K. *et al.*: Architecture of the photosynthetic oxygen-evolving center. – *Science* **303**: 1831-1838, 2004.
- Foyer C.H.: Reactive oxygen species, oxidative signaling and the regulation of photosynthesis. – *Environ. Exp. Bot.* **154**: 134-142, 2018.
- Fristedt R., Willig A., Granath P. *et al.*: Phosphorylation of photosystem II controls functional macroscopic folding of photosynthetic membranes in *Arabidopsis*. – *Plant Cell* **21**: 3950-3964, 2009.
- Grinzato A., Albanese P., Marotta R. *et al.*: High-light versus low-light: effects on paired Photosystem II supercomplex structural rearrangement in pea plants. – *Int. J. Mol. Sci.* **21**: 8643, 2020.
- Gupta R.: The oxygen-evolving complex: a super catalyst for life on earth, in response to abiotic stresses. – *Plant Signal. Behav.* **15**: 1824721, 2020.
- Gupta R., Sharma R.D., Rao Y.R. *et al.*: Acclimation potential of Noni (*Morinda citrifolia* L.) plant to temperature stress is

- mediated through photosynthetic electron transport rate. – *Plant Signal. Behav.* **16**: 1865687, 2021.
- Gururani M.A., Upadhyaya C.P., Strasser R.J. *et al.*: Physiological and biochemical responses of transgenic potato plants with altered expression of PSII manganese stabilizing protein. – *Plant Physiol. Bioch.* **58**: 182-194, 2012.
- Gururani M.A., Upadhyaya C.P., Strasser R.J. *et al.*: Evaluation of abiotic stress tolerance in transgenic potato plants with reduced expression of PSII manganese stabilizing protein. – *Plant Sci.* **198**: 7-16, 2013.
- Guskov A., Kern J., Gabdulkhakov A. *et al.*: Cyanobacterial photosystem II at 2.9 Å-resolution and the role of quinones, lipids, channels and chloride. – *Nat. Struct. Mol. Biol.* **16**: 334-342, 2009.
- He W., Yan K., Zhang Y. *et al.*: Contrasting photosynthesis, photoinhibition and oxidative damage in honeysuckle (*Lonicera japonica* Thunb.) under iso-osmotic salt and drought stresses. – *Environ. Exp. Bot.* **182**: 104313, 2021.
- Henmi T., Miyao M., Yamamoto Y.: Release and reactive-oxygen-mediated damage of the oxygen-evolving complex subunits of PSII during photoinhibition. – *Plant Cell Physiol.* **45**: 243-250, 2004.
- Horton P., Ruban A.V., Walters R.G.: Regulation of light harvesting in green plants. – *Annu. Rev. Plant Phys.* **47**: 655-684, 1996.
- Huang W., Yang Y.J., Hu H. *et al.*: Evidence for the role of cyclic electron flow in photoprotection for oxygen-evolving complex. – *J. Plant Physiol.* **194**: 54-60, 2016.
- Ido K., Nield J., Fukao Y. *et al.*: Cross-linking evidence for multiple interactions of the PsbP and PsbQ proteins in a higher plant photosystem II supercomplex. – *J. Biol. Chem.* **289**: 20150-20157, 2014.
- Ifuku K.: The PsbP and PsbQ family proteins in the photosynthetic machinery of chloroplasts. – *Plant Physiol. Bioch.* **81**: 108-114, 2014.
- Ifuku K., Nagao R.: Evolution and function of the extrinsic subunits of Photosystem II. – In: Shen J.R., Satoh K., Allakhverdiev S.I. (ed.): *Photosynthesis: Molecular Approaches to Solar Energy Conversion. Advances in Photosynthesis and Respiration*. Pp. 429-446. Springer, Cham 2021.
- Ifuku K., Yamamoto J., Ono T. *et al.*: PsbP protein, but not PsbQ protein, is essential for the regulation and stabilization of Photosystem II in higher plants. – *Plant Physiol.* **139**: 1175-1184, 2005.
- Ishihara S., Takabayashi A., Ido K. *et al.*: Distinct function for the two PsbP-like proteins PPL1 and PPL2 in the chloroplast thylakoid lumen. – *Plant Physiol.* **145**: 668-679, 2007.
- Johansson E., Olsson O., Nyström T.: Progression and specificity of protein oxidation in the life cycle of *Arabidopsis thaliana*. – *J. Biol. Chem.* **279**: 22204-22208, 2004.
- Johnson M.P., Wientjes E.: The relevance of dynamic thylakoid organisation to photosynthetic regulation. – *BBA-Bioenergetics* **1861**: 148039, 2020.
- Kale R., Hebert A.E., Frankel L.K. *et al.*: Amino acid oxidation of the D1 and D2 proteins by oxygen radicals during photoinhibition of Photosystem II. – *P. Natl. Acad. Sci. USA* **114**: 2988-2993, 2017.
- Kato Y., Sun X., Zhang L., Sakamoto W.: Cooperative D1 degradation in the Photosystem II repair mediated by chloroplastic proteases in *Arabidopsis*. – *Plant Physiol.* **159**: 1428-1439, 2012.
- Kereiche S., Kiss A.Z., Kouřil R. *et al.*: The PsbS protein controls the macro-organisation of photosystem II complexes in the grana membranes of higher plant chloroplasts. – *FEBS Lett.* **584**: 759-764, 2010.
- Knoppová J., Yu J., Konik P. *et al.*: CyanoP is involved in the early steps of Photosystem II assembly in the cyanobacterium *Synechocystis* sp. PCC 6803. – *Plant Cell Physiol.* **57**: 1921-1931, 2016.
- Kosmala A., Bocian A., Rapacz M. *et al.*: Identification of leaf proteins differentially accumulated during cold acclimation between *Festuca pratensis* plants with distinct levels of frost tolerance. – *J. Exp. Bot.* **60**: 3595-3609, 2009.
- Kress E., Jahns P.: The dynamics of energy dissipation and xanthophyll conversion in *Arabidopsis* indicate an indirect photoprotective role of zeaxanthin in slowly inducible and relaxing components of non-photochemical quenching of excitation energy. – *Front. Plant Sci.* **8**: 2094, 2017.
- Li L., Aro E.-M., Millar A.H.: Mechanisms of photodamage and protein turnover in photoinhibition. – *Trends Plant Sci.* **23**: 667-676, 2018.
- Li X.P., Björkman O., Shih C. *et al.*: A pigment-binding protein essential for regulation of photosynthetic light harvesting. – *Nature* **403**: 391-395, 2000.
- Longoni F.P., Goldschmidt-Clermont M.: Thylakoid protein phosphorylation in chloroplasts. – *Plant Cell Physiol.* **62**: 1094-1107, 2021.
- Matsui S., Ishihara S., Ido K. *et al.*: Functional analysis of PsbP-like protein 1 (PPL1) in *Arabidopsis*. – In: Kuang T., Lu C., Zhang L. (ed.): *Photosynthesis Research for Food, Fuel and the Future. Advanced Topics in Science and Technology in China*. Pp. 415-417. Springer, Berlin-Heidelberg 2013.
- Matsubara S., Chow W.S.: Populations of photoinactivated photosystem II characterized by Chl fluorescence lifetime *in vivo*. – *P. Natl. Acad. Sci. USA* **101**: 18234-18239, 2004.
- Mattila H., Mishra K.B., Kuusisto I. *et al.*: Effects of low temperature on photoinhibition and singlet oxygen production in four natural accessions of *Arabidopsis*. – *Planta* **252**: 19, 2020.
- Miyao M., Murata N.: The Cl⁻ effect on photosynthetic oxygen evolution: interaction of Cl⁻ with 18-kDa, 24-kDa and 33-kDa proteins. – *FEBS Lett.* **180**: 303-308, 1985.
- Müh F., Zouni A.: Structural basis of light-harvesting in the photosystem II core complex. – *Protein Sci.* **29**: 1090-1119, 2020.
- Murakami R., Ifuku K., Takabayashi A. *et al.*: Functional dissection of two *Arabidopsis* PsbO proteins: PsbO1 and PsbO2. – *FEBS J.* **272**: 2165-2175, 2005.
- Murata N., Takahashi S., Nishiyama Y., Allakhverdiev S.I.: Photoinhibition of photosystem II under environmental stress. – *Biochim. Biophys. Acta* **1767**: 414-421, 2007.
- Murchie E.H., Ruban A.V.: Dynamic non-photochemical quenching in plants: from molecular mechanism to productivity. – *Plant J.* **101**: 885-896, 2020.
- Nath K., Jajoo A., Poudyal R.S. *et al.*: Towards a critical understanding of the photosystem II repair mechanism and its regulation during stress conditions. – *FEBS Lett.* **587**: 3372-3381, 2013a.
- Nath K., Poudyal R.S., Eom J.S. *et al.*: Loss-of-function of OsSTN8 suppresses the photosystem II core protein phosphorylation and interferes with the photosystem II repair mechanism in rice (*Oryza sativa*). – *Plant J.* **76**: 675-686, 2013b.
- Nawrocki W.J., Liu X., Raber B. *et al.*: Molecular origins of induction and loss of photoinhibition-related energy dissipation q_i. – *Sci. Adv.* **7**: eabj0055, 2021.
- Nicol L., Nawrocki W.J., Croce R.: Disentangling the sites of non-photochemical quenching in vascular plants. – *Nat. Plants* **5**: 1177-1183, 2019.
- Nield J., Barber J.: Refinement of the structural model for the Photosystem II supercomplex of higher plants. –

- BBA-Bioenergetics **1757**: 353-361, 2006.
- Nilkens M., Kress E., Lambrev P. *et al.*: Identification of a slowly inducible zeaxanthin-dependent component of non-photochemical quenching of chlorophyll fluorescence generated under steady-state conditions in *Arabidopsis*. – BBA-Bioenergetics **1797**: 466-475, 2010.
- Nishiyama Y., Allakhverdiev S.I., Yamamoto H. *et al.*: Singlet oxygen inhibits the repair of photosystem II by suppressing the translation elongation of the D1 protein in *Synechocystis* sp. PCC 6803. – Biochemistry-US **43**: 11321-11330, 2004.
- Nishiyama Y., Murata N.: Revised scheme for the mechanism of photoinhibition and its application to enhance the abiotic stress tolerance of the photosynthetic machinery. – Appl. Microbiol. Biot. **98**: 8777-8796, 2014.
- Nishiyama Y., Yamamoto H., Allakhverdiev S.I. *et al.*: Oxidative stress inhibits the repair of photodamage to the photosynthetic machinery. – EMBO J. **20**: 5587-5594, 2001.
- Pagliano C., Saracco G., Barber J.: Structural, functional and auxiliary proteins of photosystem II. – Photosynth. Res. **116**: 167-188, 2013.
- Pan T., Liu M., Kreslavski V.D. *et al.*: Non-stomatal limitation of photosynthesis by soil salinity. – Crit. Rev. Environ. Sci. Technol. **51**: 791-825, 2021.
- Pawłowicz I., Kosmala A., Rapacz M.: Expression pattern of the psbO gene and its involvement in acclimation of the photosynthetic apparatus during abiotic stresses in *Festuca arundinacea* and *F. pratensis*. – Acta Physiol. Plant. **34**: 1915-1924, 2012.
- Pinnola A., Bassi R.: Molecular mechanisms involved in plant photoprotection. – Biochem. Soc. T. **46**: 467-482, 2018.
- Popelkova H., Yocum C.F.: PsbO, the manganese-stabilizing protein: Analysis of the structure–function relations that provide insights into its role in photosystem II. – J. Photoch. Photobio. B **104**: 179-190, 2011.
- Pospišil P., Yamamoto Y.: Damage to photosystem II by lipid peroxidation products. – BBA-Gen. Subjects **1861**: 457-466, 2017.
- Quick W.P., Stitt M.: An examination of the factors contributing to non-photochemical quenching of chlorophyll fluorescence in barley leaves. – BBA-Bioenergetics **977**: 287-296, 1989.
- Rantala M., Rantala S., Aro E.-M.: Composition, phosphorylation and dynamic organization of photosynthetic protein complexes in plant thylakoid membrane. – Photoch. Photobio. Sci. **19**: 604-619, 2020.
- Roach T., Kreiger-Liszky A.: Regulation of photosynthetic electron transport and photoinhibition. – Curr. Protein Pept. Sci. **15**: 351-362, 2014.
- Rochaix J.D.: Role of thylakoid protein kinases in photosynthetic acclimation. – FEBS Lett. **581**: 2768-2775, 2007.
- Roose J.L., Frankel L.K., Bricker T.M.: Documentation of significant electron transport defects on the reducing side of Photosystem II upon removal of the PsbP and PsbQ extrinsic proteins. – Biochemistry-US **49**: 36-41, 2010.
- Roose J.L., Wegener K.M., Pakrasi H.B.: The extrinsic proteins of Photosystem II. – Photosynth. Res. **92**: 369-387, 2007.
- Ruban A.V., Wilson S.: The mechanism of non-photochemical quenching in plants: localization and driving forces. – Plant Cell Physiol. **62**: 1063-1072, 2021.
- Samol I., Shapiguzov A., Ingelsson B. *et al.*: Identification of a photosystem II phosphatase involved in light acclimation in *Arabidopsis*. – Plant Cell **24**: 2596-2609, 2012.
- Sasi S., Venkatesh J., Daneshi R.F. *et al.*: Photosystem II extrinsic proteins and their putative role in abiotic stress tolerance in higher plants. – Plants-Basel **7**: 100, 2018.
- Schmidt S.B., Husted S.: The biochemical properties of manganese in plants. – Plants-Basel **8**: 381, 2019.
- Schwenkert S., Umate P., Dal Bosco C. *et al.*: PsbI affects the stability, function, and phosphorylation patterns of photosystem II assemblies in tobacco. – J. Biol. Chem. **281**: 34227-34238, 2006.
- Seidler A.: The extrinsic polypeptides of Photosystem II. – BBA-Bioenergetics **1277**: 35-60, 1996.
- Shen J.R.: The structure of Photosystem II and the mechanism of water oxidation in photosynthesis. – Annu. Rev. Plant Biol. **66**: 23-48, 2015.
- Shen J.R., Henmi T., Kamiya N.: Structure and function of photosystem II. – In: Fromme P. (ed.): Photosynthetic Protein Complexes: A Structural Approach. Pp. 83-106. Wiley-Blackwell, Weinheim 2008.
- Shevela D., Kern J.F., Govindjee *et al.*: Photosystem II. – eLS **2**: 1-20, 2021.
- Shi L.X., Schröder W.P.: The low molecular mass subunits of the photosynthetic supracomplex, photosystem II. – BBA-Bioenergetics **1608**: 75-96, 2004.
- Sun X.W., Peng L.W., Guo J.K. *et al.*: Formation of DEG5 and DEG8 complexes and their involvement in the degradation of photodamaged photosystem II reaction center D1 protein in *Arabidopsis*. – Plant Cell **19**: 1347-1361, 2007.
- Suorsa M., Sirpiö S., Allahverdiyeva Y. *et al.*: PsbR, a missing link in the assembly of the oxygen-evolving complex of plant photosystem II. – J. Biol. Chem. **281**: 145-150, 2006.
- Takahashi S., Whitney S.M., Badger M.R.: Different thermal sensitivity of the repair of photodamaged photosynthetic machinery in cultured *Symbiodinium* species. – P. Natl. Acad. Sci. USA **106**: 3237-3242, 2009.
- Teardo E., de Laureto P.P., Bergantino E. *et al.*: Evidences for interaction of PsbS with photosynthetic complexes in maize thylakoids. – BBA-Bioenergetics **1767**: 703-711, 2007.
- Tikkanen M., Aro E.-M.: Integrative regulatory network of plant thylakoid energy transduction. – Trends Plant Sci. **19**: 10-17, 2014.
- Tikkanen M., Grieco M., Kangasjärvi S., Aro E.-M.: Thylakoid protein phosphorylation in higher plant chloroplasts optimizes electron transfer under fluctuating light. – Plant Physiol. **152**: 723-735, 2010.
- Tikkanen M., Grieco M., Nurmi M. *et al.*: Regulation of the photosynthetic apparatus under fluctuating growth light. – Philos. T. Roy. Soc. B **367**: 3486-3493, 2012.
- Tikkanen M., Mekala N.R., Aro E.-M.: Photosystem II photoinhibition-repair cycle protects Photosystem I from irreversible damage. – BBA-Bioenergetics **1837**: 210-215, 2014.
- Tikkanen M., Nurmi M., Kangasjärvi S., Aro E.-M.: Core protein phosphorylation facilitates the repair of photodamaged photosystem II at high light. – BBA-Bioenergetics **1777**: 1432-1437, 2008.
- Tomita M., Ifuku K., Sato F., Noguchi T.: FTIR evidence that the PsbP extrinsic protein induces protein conformational changes around the oxygen-evolving Mn cluster in Photosystem II. – Biochemistry-US **48**: 6318-6325, 2009.
- Umeha Y., Kawakami K., Shen J.R., Kamiya N.: Crystal structure of oxygen-evolving photosystem II at a resolution of 1.9 Å. – Nature **473**: 55-60, 2011.
- Vinyard D.J., Ananyev G.M., Dismukes G.C.: Photosystem II: the reaction center of oxygenic photosynthesis. – Annu. Rev. Biochem. **82**: 577-606, 2013.
- Wang Y., Noguchi K., Ono N. *et al.*: Overexpression of plasma membrane H⁺-ATPase in guard cells promotes light-induced stomatal opening and enhances plant growth. – P. Natl. Acad. Sci. USA **111**: 533-538, 2014.
- Weisz D.A., Johnson V.M., Niedzwiedzki D.M. *et al.*: A novel chlorophyll protein complex in the repair cycle of photo-

- system II. – P. Natl. Acad. Sci. USA **116**: 21907-21913, 2019.
- Wu G., Ma L., Yuan C. *et al.*: Formation of light-harvesting complex II aggregates from LHCII–PSI–LHCI complexes in rice plants under high light. – J. Exp. Bot. **72**: 4938-4948, 2021a.
- Wu J., Hu J., Wang L. *et al.*: Responses of *Phragmites australis* to copper stress: A combined analysis of plant morphology, physiology and proteomics. – Plant Biol. **23**: 351-362, 2021b.
- Xu P., Roy L.M., Croce R.: Functional organization of photosystem II antenna complexes: CP29 under the spotlight. – BBA-Bioenergetics **858**: 815-822, 2017.
- Yamamoto Y., Aminaka R., Yoshioka M. *et al.*: Quality control of photosystem II: impact of light and heat stresses. – Photosynth. Res. **98**: 589-608, 2008.
- Yi X., Hargett S.R., Frankel L.K., Brickel T.M.: The PsbQ protein is required in *Arabidopsis* for Photosystem II assembly/stability and photoautotrophy under low light conditions. – J. Biol. Chem. **281**: 26260-26267, 2006.
- Zavafer A.: A theoretical framework of the hybrid mechanism of photosystem II photodamage. – Photosynth. Res. **149**: 107-120, 2021.
- Zsiros O., Nagy G., Patai R. *et al.*: Similarities and differences in the effects of toxic concentrations of cadmium and chromium on the structure and functions of thylakoid membranes in *Chlorella variabilis*. – Front. Plant Sci. **11**: 1006, 2020.

© The authors. This is an open access article distributed under the terms of the Creative Commons BY-NC-ND Licence.