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The biogenesis and maintenance of PSII: Recent advances and current challenges

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Abstract

The growth of plants, algae, and cyanobacteria relies on the catalytic activity of the oxygen-evolving PSII complex, which uses solar energy to extract electrons from water to feed into the photosynthetic electron transport chain. PSII is proving to be an excellent system to study how large multi-subunit membrane-protein complexes are assembled in the thylakoid membrane and subsequently repaired in response to photooxidative damage. Here we summarize recent developments in understanding the biogenesis of PSII, with an emphasis on recent insights obtained from biochemical and structural analysis of cyanobacterial PSII assembly/repair intermediates. We also discuss how chlorophyll synthesis is synchronized with protein synthesis and suggest a possible role for PSI in PSII assembly. Special attention is paid to unresolved and controversial issues that could be addressed in future research.

PSII: a sophisticated solar-driven nano-machine

PSII is one of 2 types of photosynthetic reaction center located in the thylakoid membranes of cyanobacteria, algae, and plants, the other being PSI (Shen 2015). From a functional point of view, PSII is a water:plastoquinone photo-oxidoreductase (EC number 1.10.3.9) catalyzing the light-driven reduction of plastoquinone to plastoquinol and the oxidation of water to molecular oxygen and protons. PSII also contributes to the proton-motive force used to drive ATP synthesis (Qi et al. 2023). Recent advances in structural biology especially cryogenic-electron microscopy (cryo-EM) have provided detailed, high-resolution structures of PSII complexes isolated from a variety of photosynthetic organisms (Cao et al. 2020). These data clearly document the conserved character of the central part of PSII, called the PSII core complex (RCCII).

Efficient assembly of PSII and its prompt repair in response to light-induced irreversible damage, or chronic photoinhibition, is vital for maintenance of PSII activity and growth. Both processes have been intensively studied, especially in cyanobacteria, which have provided the most detailed structural information. Figure 1 presents an overview of the cryo-EM structure of the dimeric oxygen-evolving PSII complex isolated from the cyanobacterium *Synechocystis* PCC 6803 (hereafter *Synechocystis*; Gisriel et al. 2022), which is widely used to study cyanobacterial PSII biogenesis. Each monomer is composed of 4 large and 17 small intrinsic and 4 extrinsic subunits and contains 35 chlorophylls (Chls), 10 β-carotenes, and several other cofactors. The chlorin cofactors involved in the initial steps of light-induced charge separation leading to reduction of plastoquinone and oxidation of water are bound to a central heterodimeric reaction center complex of the D1 and D2 subunits (RCII). The inner antennae, CP47 and CP43, bound symmetrically to D2 and D1, respectively, absorb light energy and deliver it to RCII to drive charge separation. CP43 is also involved with D1 in the ligation of the Mn_4CaO_5 metal cluster that oxidizes water (Ferreira et al. 2004; Umena et al. 2011; Shen 2015). These

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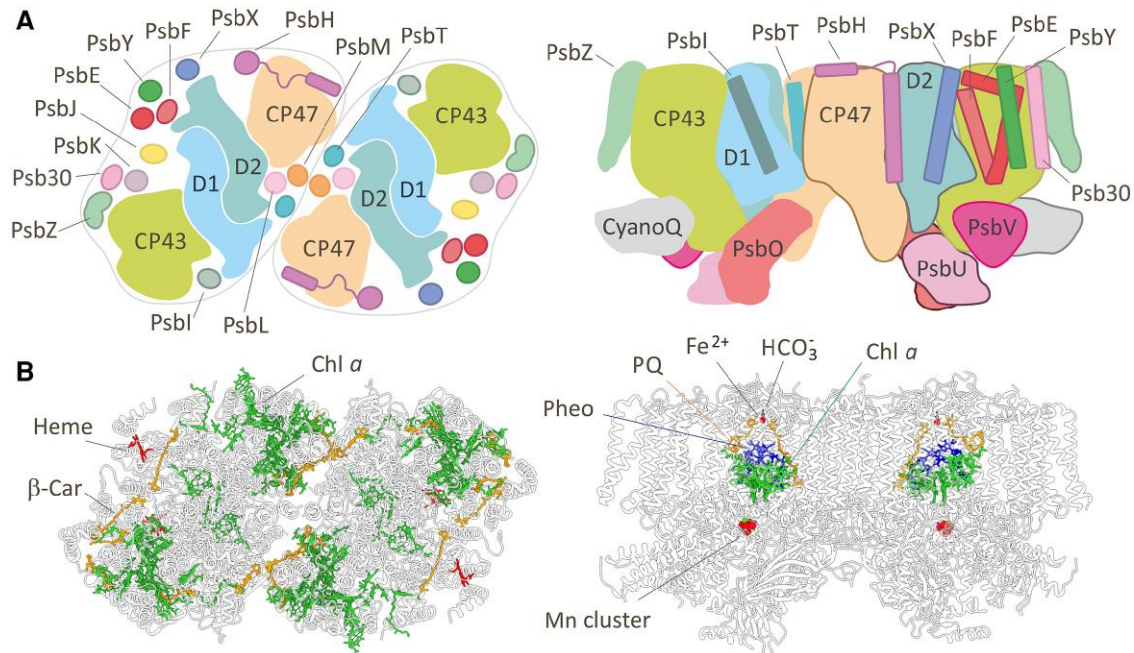
Figure 1. Proteins and cofactors of dimeric oxygen-evolving cyanobacterial PSII. **A)** Cartoon shows all subunits in the available structure of *Synechocystis* PSII (PDB: 7N8O) as a top view from the cytoplasmic side (left) and side-view along the membrane plane (right). **B)** The structure of the same complex highlighting the cofactors. The left side shows the location of chlorophyll *a* (Chl *a*), β-carotene (β-Car), and heme *b*; the right panel shows the plastoquinone (PQ), pheophytin *a* (Pheo), Chl *a*, non-heme iron, bicarbonate, and water-splitting Mn_4CaO_5 cluster associated with D1 and D2. Please note that the orientation of the structures in (**B**) corresponds to the cartoons in (**A**).

large subunits are surrounded by several smaller transmembrane subunits of less well-defined function.

In contrast to the very conserved core of PSII, different sets of proteins bind to the lumenal side of PSII to optimize the function of the Mn_4CaO_5 cluster (Ifuku and Noguchi 2016). *Synechocystis* PSII contains the PsbO, PsbU, PsbV, and PsbQ (also termed CyanoQ) subunits (Fagerlund and Eaton-Rye 2011), whereas in other cyanobacteria CyanoQ is detached during purification and is absent (Michoux et al. 2014). In the case of plant chloroplasts there are 4 extrinsic subunits: PsbO, PsbQ, PsbP, and PsbTn (Wei et al. 2016). The peripheral light-harvesting complexes that associate with PSII to form large PSII supercomplexes are even more diverse (Cao et al. 2020; You et al. 2023). In the case of cyanobacteria, the soluble phycobilisome docks onto the cytoplasmic surface of PSII (You et al. 2023), whereas transmembrane light-harvesting complexes are found in land plants (Lokstein et al. 2021).

The beginning of the journey: translation of core subunits and formation of modules

PSII assembly proceeds in a step-wise process via discrete assembly intermediates (Nixon et al. 2010; Komenda et al. 2012a; Nickelsen and Rengstl 2013) (Fig. 2). The abundance of these intermediates is generally low in wild type (WT) but can be enhanced in mutants blocked at specific stages of assembly (de

Vitry et al. 1989; Komenda et al. 2004) (Fig. 2). Assembly occurs in distinct membrane compartments (biogenesis centers or zones) in cyanobacteria, algae, and plants and is discussed in detail by Nickelsen et al. (this issue).

Although the organization of the PSII biogenesis center remains enigmatic, such a membrane domain should be abundant in the translation and translocation machineries engaged in the production of PSII core subunits. D1, D2, CP43, and CP47 are polytopic membrane proteins that are likely inserted into the membrane via the signal recognition particle (SRP) pathway (Hristou et al. 2019; for review, see Cymer et al. 2015). The cyanobacterial SRP consists of the Ffh protein and a small RNA molecule, which together scan the ribosome exit, recognize hydrophobic sequences, and target them to the SecYEG translocon, a transmembrane channel that allows translocation of nascent protein chains across the membrane. The translocon can associate with the YidC foldase/insertase, which assists the lateral exit of transmembrane helices (TMHs) from the translocon and the translocation of the periplasmic domains across the membrane (for review of YidC, see Hennon et al. 2015). YidC and its plastid homologue ALB3 are involved in the synthesis of all large cyanobacterial Chl-binding proteins of PSII and PSI (Pasch et al. 2005).

Integration of multi-spanning membrane proteins may proceed by either the stepwise integration of single transmembrane segments or by the cooperative insertion of 2 or more TMHs (Ota et al. 1998). However, the precise
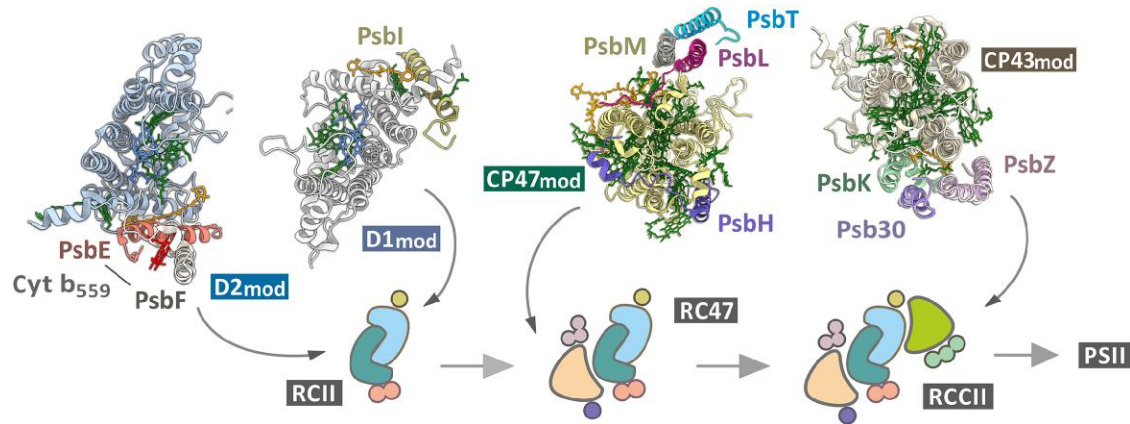
Figure 2. Modular de novo assembly of PSII. According to our model (Komenda et al. 2012a), PSII is built from 4 preassembled modules (D1$_{mod}$, D2$_{mod}$, CP47$_{mod}$ and CP43$_{mod}$) in a step-wise manner. Each module contains 1 core chlorophyll-binding subunit of PSII already associated with a set of small subunits (as indicated) and with pigment cofactors. D1$_{mod}$ and D2$_{mod}$ combine first to produce the RCII reaction center assembly complex, which associates with CP47$_{mod}$ to form the RC47 assembly complex that is then converted to the RCCII non–oxygen-evolving PSII intermediate by binding CP43$_{mod}$. The final steps of assembly to produce oxygen-evolving PSII involve light-driven assembly of the Mn$_4$CaO$_5$ cluster and attachment of the lumenal subunits and dimerization. The picture was prepared using the cryo-EM structure of *Synechocystis* PSII (PDB: 7N8O) (Gisriel et al. 2022).

mechanism for PSII subunits remains to be determined, especially the role of the SecA cytosolic motor (van Wijk et al. 1995; Wang et al. 2017b).

PSII core subunits bind a number of Chl cofactors and, at least in the case of CP43 and CP47, Chl molecules need to be inserted co-translationally as a prerequisite for correct folding (Shen et al. 1993; Manna and Vermaas 1997). The accumulation of D1 and D2 appears less Chl-dependent as unassembled D1 can be detected in *Synechocystis* mutants depleted in Chl (Kiss et al. 2019; Skotnicová et al. 2024) and D2 can be detected in Chl-free etioplasts (Müller and Eichacker 1999). As discussed later, PSII biogenesis needs to be tightly coordinated with Chl biosynthesis and turnover to deal safely with this highly phototoxic pigment. The presence of β-carotene is also critical for the biogenesis of PSII with the stability of the CP47 and CP43 Chl-binding antennae dramatically impaired in a *Synechocystis* mutant lacking this pigment (Sozer et al. 2010). However, in contrast to Chl, carotenoids can safely accumulate as free molecules in the membrane. It is thus expected that β-carotene is transferred spontaneously to apoproteins from a membrane pool during Chl incorporation to provide efficient photoprotection (Domonkos et al. 2013).

The assembly and stability of PSII is also dependent on lipids, which are integral components of PSII (Guskov et al. 2009), with phosphatidyl-glycerol and sulfoquinovosyl-diacylglycerol needed for stabilization of PSII dimers and stable binding of CP43 within PSII (Laczkó-Dobos et al. 2008; Nakajima et al. 2018).

During insertion into the membrane, or soon after, D1, D2, CP47, and CP43 bind pigments and other cofactors and associate with neighboring small membrane PSII subunits to form "assembly modules." These small, pigmented complexes exist in the membrane autonomously before associating with the other modules to form larger assembly complexes and the final oxygen-evolving PSII complex (Fig. 2). Except for the D1 assembly module (D1$_{mod}$), which probably needs to be produced de novo, the other 3 assembly modules (D2$_{mod}$, CP47$_{mod}$, and CP43$_{mod}$) can be recycled from photodamaged PSII (Komenda and Masojídek 1995; Yao et al. 2012).

Additionally, accessory factors not present in the final functional PSII complex associate transiently with assembly modules and larger assembly intermediates to promote or regulate assembly and protect vulnerable assembly intermediates from damage (Johnson and Pakrasi 2022).

D1 and D2 assembly modules

Apart from a few exceptions, such as *Euglena*, the D1 subunit is synthesized as a precursor protein (pD1) with a C-terminal extension in the range of 8 to 16 amino-acid residues. This extension is cleaved by the CtpA protease (Anbudurai et al. 1994) to reveal the free carboxyl group of the conserved C-terminal alanine residue of mature D1 (Nixon et al. 1992), which acts as a bidentate ligand to the Mn$_4$CaO$_5$ cluster (Umena et al. 2011). In cyanobacteria the 16 amino-acid extension is cleaved in 2 steps (Komenda et al. 2007a) via an intermediate form of D1 (iD1) (Inagaki et al. 2001). Whereas pD1 is only detected in an unassembled state, iD1 is present in the D1$_{mod}$ and larger subcomplexes (Komenda et al. 2004).

The *Synechocystis* D1$_{mod}$ has recently been isolated and found to contain close to stoichiometric amounts of the small PsbI subunit and the Ycf48 assembly factor (Knoppová et al. 2022). The lumenal Ycf48 protein (and its plant homologue HCF136) is important for PSII accumulation,
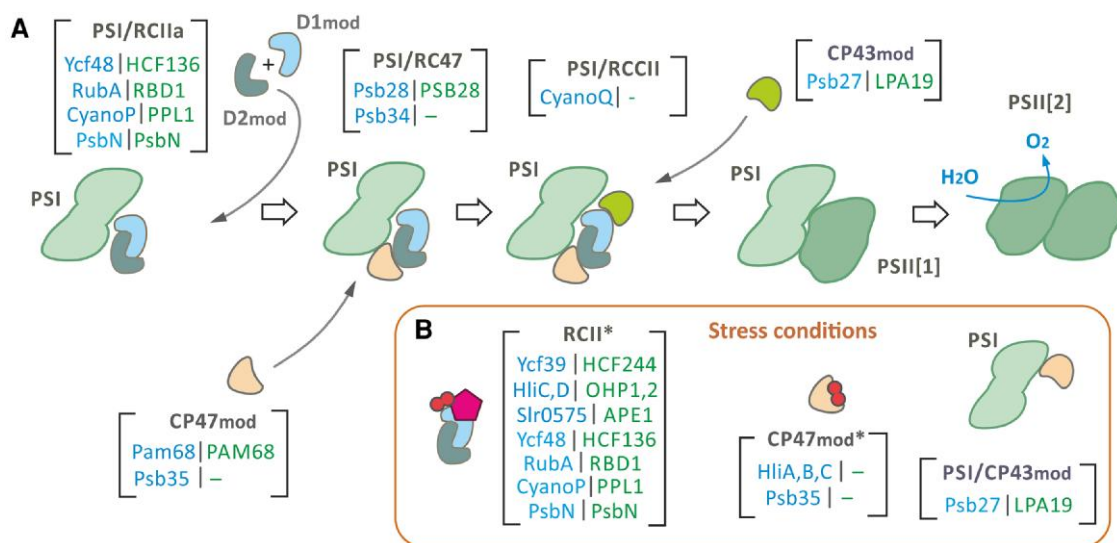
Figure 3. Scheme for involvement of PSI in PSII biogenesis in *Synechocystis*. **A)** Under low-stress conditions, the assembly of PSII begins with the formation of RCIIa reaction center complexes with the assistance of early assembly factors indicated in square brackets. According to our working model (see the text), the PSI monomeric core is either in close vicinity or in physical contact with RCIIa and serves as a scaffold for the later assembly steps. In this scheme, factors involved in each assembly step are listed below the name of the corresponding module or assembly intermediate (blue and green signify cyanobacterial and eukaryotic homologues). It should be noted that some factors are present in multiple assembly complexes (e.g. the RubA rubredoxin-domain protein has been identified in RCIIa, RC47, and RCCII complexes). **B)** Under stress conditions, such as high light, PSI complexes are not produced, and the synthesis of CP47$_{mod}$ and CP43$_{mod}$ is also weakened due to the lack of available Chl. PSII biogenesis is achieved through an alternative pathway that involves the RCII* intermediate, which is photo-protected by the associated Ycf39-HliC/D subcomplex (Ycf39/Hlips). Unlike RCIIa, RCII* exists as an individual entity. The CP47$_{mod}$ and CP43$_{mod}$ antenna mainly originate from disassembled (damaged) PSII. CP47m is photoprotected by HliA/C and HliB/C heterodimers, while free CP43$_{mod}$ can associate with PSI, which serves as a sink for absorbed excitation energy.

more so in chloroplasts (Meurer et al. 1998; Plücken et al. 2002) than cyanobacteria (Komenda et al. 2008). Ycf48/HCF136 is a 7-bladed beta-propeller protein that acts early in assembly by binding to D1$_{mod}$ and facilitating formation of the RCII complex (Yu et al. 2018) (Fig. 3). Ycf48 also co-purifies with YidC suggesting engagement of Ycf48 with lumenally exposed regions of D1 early in translation, possibly to aid folding and the binding of Chl (Yu et al. 2018).

The isolated *Synechocystis* D2$_{mod}$ contains D2 and cytochrome b$_{559}$ (Cyt b$_{559}$) as anticipated from earlier studies in barley (Müller and Eichacker 1999) and *Synechocystis* (Komenda et al. 2008; Fig. 2). Cyt b$_{559}$ consists of a heme *b* molecule ligated by 2 small proteins [PsbE (alpha) and PsbF (beta)]. Deletion of PsbE or PsbF abolishes PSII assembly (Pakrasi et al. 1988; Morais et al. 1998; Swiatek et al. 2003) by preventing accumulation of D2 (Shukla et al 1992; Komenda et al. 2004). Mutation of the His ligands to the heme profoundly impairs the assembly, photoprotection, and repair of PSII (Morais et al. 2001; Hung et al. 2010; Hamilton et al. 2014), but the precise role of Cyt b$_{559}$ remains enigmatic (Pospíšil 2011).

Also found at substoichiometric levels in D2$_{mod}$ is CyanoP, a protein distantly related to the PsbP extrinsic subunit of chloroplast PSII and the PPL1 subunit (Thornton et al. 2004; Michoux et al. 2010) implicated in PSII assembly in plants (Che et al. 2020). CyanoP appears to protect D2$_{mod}$

from proteolysis, with its absence leading to overaccumulation of newly synthesized D1$_{mod}$ (Knoppová et al. 2016).

Other proteins that co-purify at low levels with D2$_{mod}$ include 2 proteins, Slr0575 and Slr1470, with homologues in chloroplasts (Knoppová et al. 2022). While the function of Slr1470 remains to be determined, Slr0575 has a stabilizing effect on D2 in *Synechocystis* (Knoppová et al. 2022). The plant homologue of Slr0575 called APE1 appears to be important for the acclimation of Arabidopsis to high irradiance (Walters et al. 2003), but its effect on RCII formation in chloroplasts remains unknown. A preliminary report suggests that growth of the *Chlamydomonas ape1* null mutant (Chazaux et al. 2019) is more photosensitive, which agrees with a possible role in RCII formation/stability.

Both the isolated D1$_{mod}$ and D2$_{mod}$ contain Chl and β-carotene but lack Pheo (Knoppová et al. 2022). Given the potential loss of pigment during purification, it remains unclear how many pigments bind to each module in vivo.

Structure of the photochemically active RCII complex

The RCII complex, formed from the association of D1$_{mod}$ and D2$_{mod}$, has been isolated from a *Synechocystis* strain lacking CP47 (Knoppová et al. 2014; Knoppová et al. 2022) and its cryo-EM structure recently determined (Zhao et al. 2023).

Isolated RCII is photochemically active and performs primary charge separation between the P680 electron donor and Pheo electron acceptor (Knoppová et al. 2022). All the expected pigment cofactors of D1/D2 are present in very similar positions to that found in high resolution structures of PSII core complexes (Umena et al. 2011; Wei et al. 2016; Gisriel et al. 2022), except for the loss of 1 β-carotene on the D2 side of the complex, which most probably occurred during purification (Knoppová et al. 2022). Also absent are the plastoquinone electron acceptors, Q_A and Q_B, and the Mn cluster, while the non-heme iron is clearly recognized in the structure. Because it is ligated by 4 histidine residues, 2 provided by D1 and 2 by D2, its insertion most probably occurs during the formation of the heterodimer. The origin of the 2 Pheo molecules in D1/D2 is enigmatic because there is no evidence for the existence of a general, PSII-specific magnesium dechelatase activity essential for generating Pheo a from Chl a.

The RCII structure also reveals how the Ycf48 assembly factor docks onto the lumenal surface of the complex. In most cyanobacteria the protein is processed at the N terminus, and the resulting N-terminal Cys residue (Cys29 in *Synechocystis*) is lipidated, whereas in chloroplasts lipidation is absent (Knoppová et al. 2021) and the protein contains an additional 19 amino-acid insertion located between blades 3 and 4 (Yu et al. 2018). A conserved arginine-rich patch of Ycf48 interacts with acidic residues on the luminal surface of the D1 protein, while the C-terminal tail of D1 binds into a groove on Ycf48. These regions of D1 ligate the metal ions of the Mn_4CaO_5 cluster, and therefore binding of Ycf48 to D1 blocks ligation of Mn ions and formation of the oxygen-evolving cluster. This mechanism avoids photooxidative damage potentially induced by the premature binding of Mn ions to D1 and ensures that assembly of the cluster occurs at the appropriate stage of assembly. Steric clashes between Ycf48 and the lumenal loops of CP47 and CP43 might contribute to detachment of Ycf48 upon formation of larger assembly complexes, although other proteins might participate (Zhao et al. 2023).

Another assembly factor co-purifying with RCII is rubredoxin A (RubA) named after its cytoplasmic rubredoxin domain (Wastl et al. 2000), which is attached to the membrane via a single TMH at its C terminus. In most cyanobacteria the *rubA* gene is located immediately upstream of the *ycf48* gene, suggesting a functional relationship. Indeed, a RubA-Ycf48 fusion protein substitutes for both the RubA and Ycf48 functions, suggesting their proximity in PSII (Kiss et al. 2019). RubA is conserved across oxygenic phototrophs, and a function in PSII was initially suggested by its co-localization with *Guillardia* PSII particles (Wastl et al. 2000). By contrast, RubA in the cyanobacterium *Synechococcus* 7002 was originally proposed to play a role in the biogenesis of Fe-S clusters in PSI (Shen et al. 2002). Later analyses of knockout mutants have confirmed a primary role in PSII function (Calderon et al. 2013; García-Cerdán et al. 2019; Kiss et al. 2019), with the PSI deficiency seen in cyanobacterial mutants

an indirect effect (Kiss et al. 2019). Accumulation of a D1 degradation product in a *Chlamydomonas rubA* null mutant (Calderon et al. 2023) implies a role in the correct folding and/or stabilization of $D1_{mod}$. One possibility is that the rubredoxin domain binds ferrous ions and that RubA delivers the non-heme iron to the acceptor side of PSII, thereby stabilizing the D1 structure; however, convincing evidence is still lacking, and a redox role cannot yet be excluded (Kiss et al. 2019; Calderon et al. 2023).

CyanoP, detected in $D2_{mod}$ (Knoppová et al. 2016), remains bound to RCII, although in sub-stoichiometric amounts (Knoppová et al. 2022). CyanoP is apparently much less important for PSII biogenesis than Ycf48 because the CyanoP null mutant behaves like WT. In the absence of D2, CyanoP co-purifies with Ycf48 (Knoppová et al. 2016), indicating an interaction between Ycf48 and CyanoP that may increase the efficiency of RCII formation from $D1_{mod}$ and $D2_{mod}$. Unfortunately, both CyanoP and RubA are absent from the recent RCII cryo-EM structure, and their exact locations within RCII remain unknown (Zhao et al. 2023). Whether PLP1, the closest plant homologue to CyanoP, fulfils a similar role to CyanoP in chloroplasts remains unclear.

Also detected in RCII complexes of *Synechocystis* is PsbN (Knoppová et al. 2022), of unknown function, which had previously been assigned a role in the early steps of PSII assembly in tobacco (Torabi et al. 2014).

Role of the Ycf39/Hlips complex in photoprotection

The RCII complex (named RCIIa in Knoppová et al. 2022) containing Ycf48, CyanoP, and RubA is detectable in *Synechocystis* grown under standard growth conditions (Fig. 3) and probably represents a cyanobacterial "default" assembly path. Increased irradiance induces the accumulation of a larger form of RCII (designated RCII* in *Synechocystis*), which is associated with binding of an additional pigment/protein complex consisting of the Ycf39 assembly factor (Ermakova-Gerdes and Vermaas 1999; Knoppová et al. 2014) and 2 members of the High-light-inducible protein (Hlip) family termed HliC and HliD (Dolganov et al. 1995; Fig. 3). These Hlip subunits are also designated ScpB and ScpE, respectively, as they are small cab-like proteins (Scps) related to the light-harvesting Chl-a/b−binding proteins found in chloroplasts (Funk and Vermaas 1999; see below).

The HliC/D pair and 2 other *Synechocystis* Hlips (HliA and HliB) have been shown to bind 4 to 6 Chls and 2 carotenoids in an energy dissipative configuration that leads to the conversion of the absorbed light energy into heat (Staleva et al. 2015; Shukla et al. 2018; Pazderník et al. 2019; Konert et al. 2022). Ycf39 is a member of the atypical short-chain alcohol dehydrogenase/reductase (SDR) family and is of unknown function. Although the Ycf39/Hlips complex is not essential for assembly of PSII, and synthesis of D1 is not markedly affected under low stress conditions, the incorporation of

newly synthesized D1 into PSII is affected in the mutant under high light (Knoppová et al. 2014). The HliC/D pair bound to RCII via Ycf39 is therefore likely to play a photoprotective role in dissipating energy absorbed by RCII (Knoppová et al. 2014). Hlips also have the capacity to scavenge free Chls, which would otherwise elicit the generation of singlet oxygen (Sinha et al. 2012) and might participate in Chl recycling (Knoppová et al. 2014), but this role needs further confirmation.

Although progress in understanding the early steps of PSII assembly in plants has been slower in comparison with cyanobacteria, recent evidence suggests that the initial steps are highly conserved. The equivalent complex to Ycf39/Hlips in chloroplasts consists of HCF244 and a pair of Hlip homologues named one-helix protein 1 (OHP1) and one-helix protein 2 (OHP2), which co-purify with RCII and, by analogy, probably play a photoprotective role (Myouga et al. 2018; Li et al. 2019; Maeda et al. 2022). In Arabidopsis all 3 components of the HCF244/OHPs complex are needed for normal D1 synthesis and accumulation of PSII (Link et al. 2012; Chotewutmontri and Barkan 2020; Hey and Grimm 2020), whereas in *Chlamydomonas*, the requirement of OHP2 and HCF244 homologues for D1 synthesis is less strict (Wang et al. 2023).

CP43-less PSII intermediate (RC47)

The next step in PSII assembly involves the attachment of CP47$_{mod}$ to RCII to form the non-oxygen-evolving RC47 complex (Fig. 2). The binding of CP47$_{mod}$ is rapid, and RCII is hardly detectable in vivo under optimal growth conditions (de Vitry et al. 1989; Komenda et al. 2004).

Analysis of a His-tagged derivative of CP47$_{mod}$ from *Synechocystis* indicates that CP47$_{mod}$ binds a virtually complete set of Chl and β-carotene molecules (Boehm et al. 2011). The conserved Pam68 factor containing 2 TMHs (Armbruster et al. 2010) is thought to act early in the synthesis of CP47 by binding to the apopolypeptide to promote Chl-binding. It was speculated that the coordination of Pam68, YidC, and Ycf48 fixes the nascent CP47 subunit in a position that is amenable to Chl binding (Bučinská et al. 2018). In chloroplasts PAM68 acts in concert with the DEAP2 factor, with the lack of both proteins resulting in loss of functional PSII (Keller et al. 2023).

CP47$_{mod}$ contains several neighboring small transmembrane subunits: PsbH, PsbL, PsbM, and PsbT (Boehm et al. 2011). PsbM and PsbT form part of the interface between the PSII monomers within the dimer (Umena et al. 2011) and contribute to the formation of the PSII dimer (Bentley et al. 2008). Loss of either PsbL or PsbT has multiple effects, including modification of the properties of Q$_A$ and Q$_B$ and enhanced sensitivity to photodamage (Luo et al 2014; Fagerlund et al. 2020). The single TMH of PsbH interacts with helices II and III of CP47, and its N-terminal tail is folded over the cytoplasmic (stromal) surface of CP47. PsbH helps

bind Chl and β-carotene and its binding to CP47 might help detach Pam68 (Bučinská et al. 2018).

RC47 is relatively abundant in oxygenic phototrophs and represents a heterogeneous mixture of complexes formed during both assembly and repair of PSII (Adir et al. 1990; Barbato et al. 1992; Komenda and Masojídek 1995; Boehm et al. 2012b). Since CP43 provides a Glu ligand to the Mn$_4$CaO$_5$ cluster (Ferreira et al. 2004), RC47 assembly complexes lack the Mn$_4$CaO$_5$ cluster but are still capable of light-driven electron transfer from tyrosine Y$_z$ to Q$_A$ (Rögner et al. 1991; Boehm et al. 2012b). A subpopulation of RC47 containing the early assembly factors Ycf48, RubA, and CyanoP has also been detected and may represent PSII in the process of repair (Knoppová et al. 2016; Yu et al. 2018; Kiss et al. 2019).

The Psb28 subunit is present in both RC47 and in larger core complexes containing CP43 (RCCII) (Kashino et al. 2002; Dobáková et al. 2009; Sakata et al. 2013; Bečková et al. 2017a) (Fig. 3). Early crosslinking experiments proposed that the extrinsic Psb28 subunit was in contact with the cytoplasmic N-terminal tails of both Cyt b$_{559}$ subunits (Weisz et al. 2017). However, the latest cryo-EM structures have revealed that D1, D2, and CP47 are the main interacting partners (Xiao et al. 2021; Zabret et al. 2021). Binding of Psb28 induces substantial structural changes to the cytoplasmic regions of D1 and D2 so that the Q$_B$ pocket is distorted, the non-heme iron is ligated by residue Glu241 in the D2 subunit, rather than by bicarbonate in oxygen-evolving PSII, and binding of CP43$_{mod}$ is destabilized.

These substantial conformational changes may stabilize reduced Q$_A$ and protect PSII from photodamage by reducing the production of singlet oxygen from Chl triplet states produced via charge recombination (Brinkert et al. 2016; Zabret et al. 2021). Furthermore, attachment of Psb28 to the cytoplasmic surface of RC47 aids photoprotection by preventing docking of the phycobilisome. Nevertheless, the physiological function of Psb28 is still not yet clear. Levels of RC47 are almost undetectable in a *psb28* null mutant of *Synechocystis* and assembly as well as repair seem to proceed faster than in WT (Dobáková et al. 2009, Bečková et al. 2017a). Binding of Psb28 therefore seems to block assembly of a fraction of newly assembled PSII at the stage of RC47 (or RCCII with weakly bound CP43), perhaps to confer a special function to a subpopulation of RC47, such as in Chl biosynthesis (see below).

In *Synechocystis* 2 Hlip heterodimers (HliA/C and HliB/C) associate with CP47$_{mod}$ during stress (Fig. 3) and are detected in RC47 as well as in the PSII core complex (RCCII) (Promnares et al. 2006; Yao et al. 2007; Konert et al. 2022). These Hlips are likely to photoprotect PSII assembly intermediates containing CP47, but definitive evidence is lacking. Cyanobacteria also contain a protein, designated Psb34, with a long N-terminal tail similar in primary structure to the N-termini of HliA/HliB but lacking the Chl-binding domain. Cryo-EM structures have revealed that N-terminal part of Psb34 binds to the cytoplasmic side of RC47 and RCCII in the vicinity of Psb28 (Xiao et al. 2021; Zabret et al. 2021). It

has been suggested that Psb34 binds to the same binding site as Hlip heterodimers and so promotes detachment of Hlip heterodimers during the later stages of PSII formation (Rahimzadeh-Karvansara et al. 2022). In contrast the recently discovered Psb35 subunit binds to $CP47_{mod}$ and other PSII assembly intermediates containing $CP47_{mod}$, helping to stabilize the binding of Hlips and increase the stability of these complexes in the dark (Pascual-Aznar et al. 2021).

Building the PSII core (RCCII)

Attachment of $CP43_{mod}$ to RC47 forms the RCCII complex. Free $CP43_{mod}$, which consists of CP43 and small PSII subunits PsbZ, PsbK, and Psb30 (Boehm et al. 2011; Komenda et al. 2012a; Fig. 2), is relatively abundant in membranes (Vermaas et al. 1988; Komenda et al. 2004) and, like $CP47_{mod}$, probably contains its full complement of Chl and carotenoid cofactors (Boehm et al. 2011). The PsbK subunit is needed for stable attachment of $CP43_{mod}$ to RC47 (Komenda et al. 2012b), but the role of PsbZ is unclear (Bishop et al. 2007); however, the tobacco PsbZ null mutant shows a lower level of PSII-LHCII supercomplex (Swiatek et al. 2001). The small PsbJ subunit (Fig. 1) has not been detected in the isolated $CP43_{mod}$ or RC47 complexes and might bind to RCCII late in assembly (Choo et al. 2022).

The $CP43_{mod}$ also associates with the Psb27 assembly factor (Nowaczyk et al. 2006), which binds to the large lumenal loop of CP43 (loop E) interconnecting TMHs 5 and 6 (Liu et al. 2011; Komenda et al. 2012b) and assists its attachment to RC47 (Komenda et al. 2012b). Psb27 folds into a robust 4-helix bundle (Cormann et al. 2009; Mabbitt et al. 2009; Michoux et al. 2012; Xingxing et al. 2018), which may protect PSII from lumenal proteases (Komenda et al. 2012b).

Psb27 is associated with isolated PSII complexes that lack a functional Mn cluster (Nowaczyk et al. 2006; Roose and Pakrasi 2008). Recent cryo-EM structures suggest that binding of Psb27 to CP43 may impede binding of PsbO to maintain diffusional access of Ca^{2+} and Mn^{2+} ions into PSII to enable assembly of the Mn cluster (Huang et al. 2021, Zabret et al. 2021). However, there is little difference in the structures of inactive PSII with and without bound Psb27 (Huang et al. 2021; Zhao 2023), so the role of Psb27 may be to inhibit assembly of the Mn cluster by constraining the conformational flexibility of the large lumenal loop of CP43 (Avramov et al. 2020; Tokano et al. 2020). Psb27 thus could stabilize a pool of "back-up" PSII complexes in the membrane that can be rapidly photoactivated following detachment of Psb27 (Komenda et al. 2012b), possibly driven by binding of CyanoQ, whose binding site overlaps that of Psb27 (Gisriel and Brudvig 2022). Recent ideas also suggest that Psb27-containing complexes are subject to nonphotochemical quenching of excitation energy to help prevent photodamage (Johnson et al. 2022).

Psb27 (Nowaczyk et al. 2006), like CyanoP (Ishikawa et al. 2005), Ycf48 (Knoppová et al. 2021), and CyanoQ/PsbQ (Fagerlund and Eaton-Rye 2011), is a lipoprotein, which might help anchor PSII complexes in biogenesis regions via its lipid moiety, whereas the chloroplast homologues are not lipidated which may be related to differences in how and where PSII is assembled.

Although the binding sites and precise roles of Psb27 in chloroplasts remain to be determined, a tobacco Psb27 homologue was recently detected in a novel monomeric PSII assembly intermediate containing the PSBS subunit (Fantuzzi et al. 2023), and Arabidopsis homologues have been implicated in PSII repair (Psb27-1, Chen et al. 2006) and the maturation of D1 (Psb27-2, Wei et al. 2010).

Assembly of the Mn cluster

Formation of oxygen-evolving PSII involves light-driven assembly of the Mn_4CaO_5 cluster (in a process termed photoactivation) and subsequent attachment of the lumenal extrinsic subunits, which shield the active cluster. Early studies in *Synechocystis* suggested that the tetratricopeptide PratA protein present in the periplasm was involved in pre-loading D1 with Mn early in assembly before the RCCII is formed (Stengel et al. 2012). However, this now seems unlikely given the recent structure of the Ycf48-binding site in PSII, which prevents binding of Mn to mature and precursor forms of D1 (Zhao et al. 2023). It is therefore more likely that Mn binds to PSII later in the assembly process after release of Ycf48 and after formation of RCCII, when the full complement of amino-acid ligands to the cluster are available.

The photoactivation process is known to consist of light-dependent and light-independent events (Bao and Burnap 2016), but the molecular details remain unclear. The first step is the light-driven oxidation of a single Mn^{2+} ion bound at a high-affinity binding site within D1 (Diner and Nixon 1992; Nixon and Diner 1992) close to Y_z, the immediate oxidant of the cluster. Recent cryo-EM structures of PSII complexes lacking the intact cluster have provided hints on the location of this Mn^{2+} ion in both cyanobacterial (Zabret et al. 2021) and plant complexes (Graça et al. 2021). The C-terminal tails of D1 and D2 are difficult to model in PSII structures lacking the Mn cluster, suggesting a high degree of flexibility (Gisriel et al 2020; Huang et al. 2021; Zabret et al. 2021; Zhao et al. 2023). It is likely that assembly of the Mn cluster is coupled to local conformational changes in D1 so that residues in the D1 tail and CP43 correctly ligate the cluster. These structural changes then trigger reorientation of the D2 C-terminal tail and the lumenal loop of CP43 to permit binding of PsbO and the other extrinsic proteins to the lumenal surface of PSII to bind and seal off the Mn cluster (Zhao 2023).

Cyanobacterial oxygen-evolving PSII exists in the form of both a dimer and monomer, although the isolated dimer is more active than the monomer (Nowaczyk et al. 2006). It has been assumed that the oxygen-evolving PSII dimer is assembled from active PSII monomers. However, recent cryo-EM analyses have revealed that isolated dimeric PSII complexes are heterogeneous (Huang et al. 2021; Lambertz
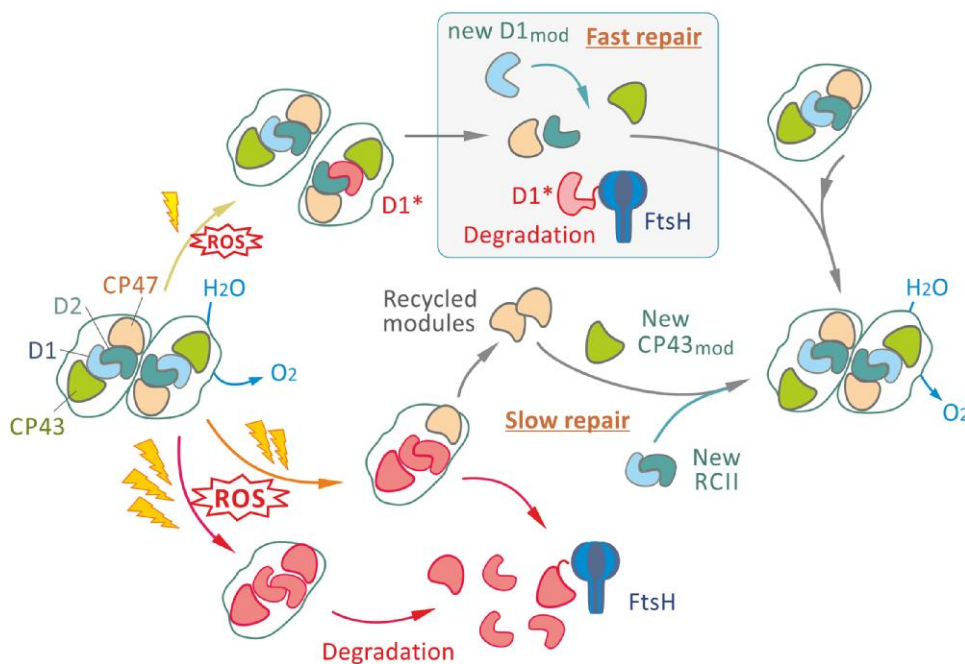
Figure 4. Scheme for PSII repair. The dimeric PSII inactivated by light is partially disassembled and can be promptly repaired by detachment of CP43mod, fast FtsH-mediated D1 degradation, D1 synthesis, and reassembly of the active dimeric PSII (Fast repair, upper box). Under harsh oxidative stress when fast repair cannot cope with the high rate of oxidative inactivation, other PSII subunits are also oxidized by ROS and their replacement and reassembly into the active dimeric PSII is also needed (Slow repair, lower part of the scheme).

et al. 2023; Zhao 2023). Besides fully assembled active dimers, PSII complexes can be found as inactive dimers and semi-active dimers with just 1 of the 2 complexes containing an assembled cluster (Zhao 2023), and dimers with Psb27 bound to 1 or both complexes (Lambertz et al. 2023). Thus, assembly of the Mn cluster appears to occur by parallel pathways involving both monomeric and dimeric complexes.

PSII is a mosaic of new and recycled components formed during cycles of disassembly and assembly

PSII is a weak link in photosynthesis due to its vulnerability to light-induced irreversible damage caused by the production of reactive oxygen species (ROS) in PSII and by the reactivity of highly oxidizing species needed to drive the oxidation of water (Diner and Rappaport 2002; Pospíšil 2009). Photodamage is an inevitable intrinsic feature of the complex and several "donor" and "acceptor" side mechanisms have been proposed depending on the site of primary impairment (for review, see Vass 2012). Although there is no general agreement on which mechanism prevails in nature, all involve formation of highly oxidizing species that irreversibly damage protein and co-factors within PSII.

Specific adaptations have been discovered that increase the intrinsic resistance of PSII from damage. These include synthesis of a specific form of cyanobacterial D1 in high light that contains a Glu residue rather than a Gln in the vicinity of the photoactive Pheo that reduces the production of singlet

oxygen via charge recombination (Vass 2011). In the case of the extremely light-resistant alga *Chlorella ohadii*, an additional protein binds close to the Q_B-binding site in oxygen-evolving PSII, possibly to reduce oxidative damage (Fadeeva et al. 2023). Whether expression of this protein will confer photoprotection in other organisms is unknown.

Once damaged, rather than resynthesize PSII de novo, complexes are "repaired" by selectively degrading the damaged subunit, replacing it by a newly synthesized subunit and recycling the undamaged components (Fig. 4). D1 is preferentially inactivated because it binds most of the co-factors that cause damage through oxidative side-reactions (Ferreira et al. 2004) and is the subunit that is replaced most often during so-called rapid D1 turnover. Under stress conditions, not only D1 but also D2, CP43, and finally CP47 are irreversibly damaged and replaced (Komenda and Masojídek 1995; Jansen et al. 1999; Yao et al. 2012). Thus, it is now clear that PSII repair is a much broader concept and can include the replacement of 1 (D1), 2 (D1, D2), 3 (D1, D2 and CP43), or more PSII subunits while the remaining "undamaged" subunits are recycled (see Fig. 4).

As D1 lies at the heart of the PSII complex, replacement requires partial detachment of the CP43mod to allow the fast degradation of the damaged D1 copy and insertion of a new version. Although replacement of D1 is widely assumed to take place in the RC47 complex, it cannot be totally excluded that damaged PSII disassembles into the individual modules (CP47mod, D2mod, CP43mod, and damaged D1mod) and then rapidly reassembled using a newly synthesized D1mod similar to that seen for de novo assembly. The recent

suggestion that PSII repair may involve a novel $CP47_{mod}$/$CP43_{mod}$ complex lacking the RCII complex (Weisz et al. 2019) remains highly controversial (Bečková et al. 2022).

Since the incorporation of newly synthesized D1 into RC47 is extremely fast, the co-translational incorporation of D1 into RC47 was originally proposed (Zhang et al. 1999). Given the known structure of the heterodimeric D1/D2 complex (Fig. 1) and assuming sequential insertion of D1 helices into the membrane, only the last 2 TMHs (IV and V) of D1 (Fig. 1) will potentially interact co-translationally with the corresponding helices of D2.

Currently it is far from clear what triggers disassembly of damaged PSII. Early studies using isolated chloroplast thylakoids (Adir et al. 1990; Barbato et al. 1992) or cyanobacterial cells with inhibited protein synthesis (Komenda and Masojídek 1995) suggested that monomerization of dimeric PSII preceded D1 degradation (Fig. 4). The interface between PSII monomers contains a belt of lipid molecules that is important for dimer stability (Guskov et al. 2009). Activation of a lipase, which would cleave these lipids, could potentially induce monomerization and indeed a PSII-associated lipase, LipA, has recently been implicated in D1 degradation in *Synechocystis* (Jimbo and Wada 2023). This lipase could also be involved in the detachment of CP43, since a lipid layer is also located between CP43 and D1 within PSII (Guskov et al. 2009). In addition, oxidative damage to PSII, such as to a bound cofactor, lipid or protein side-chain damage, may weaken the binding of $CP43_{mod}$ to RC47. Indeed, recent work has identified an important role for an oxidized Trp residue in the N-terminal tail of D1 in the detachment of CP43 (Kato et al. 2023).

On the other hand, additional auxiliary proteins may interact with RCCII to facilitate controlled disassembly and repair and so minimize the production of ROS from damaged complexes, which would otherwise inhibit protein synthesis (Nishiyama et al. 2001). This is especially important in eukaryotes, where damaged complexes migrate laterally in membranes to sites of protein synthesis/degradation (Puthiyaveetil et al. 2014). A possible *Chlamydomonas* PSII "repair" complex has recently been isolated and characterized by cryo-EM (Liu et al. 2023). The complex contains 3 additional, previously unidentified protein factors that participate in the detachment of PsbO and the CP29 antenna and blockage of the Q_B site. In chloroplasts, the phosphorylation of PSII core subunits (CP43, D2, D1, PsbH) is widely assumed to regulate PSII disassembly. However, these conclusions have relied heavily on the analysis of kinase and phosphatase knockout mutants that may have impacts outside PSII (Longoni and Goldschmidt-Clermont 2021).

Proteases involved in PSII repair

The main players involved in degrading damaged PSII subunits belong to the FtsH family of ATP-dependent membrane-embedded metalloproteases (Yi et al. 2022). *Synechocystis*, like most cyanobacteria, encodes 4 different FtsH subunits, with a heterohexameric complex of SynFtsH2 and SynFtsH3 (the FtsH2/3 complex) responsible for selective degradation of D1

(Silva et al. 2003; Boehm et al. 2012a) and for removal of mutated proteins and assembly intermediates (Komenda et al. 2006). For D1, the proposed mechanism involves recognition of the N-terminal tail of damaged D1 by the FtsH protease complex and subsequent processive degradation (Nixon et al. 2005; Komenda et al. 2007b).

From a phylogenetic viewpoint, FtsH2 (a type-B subunit) and FtsH3 (a type-A subunit) emerged early in the evolution of oxygenic photosynthesis (Shao et al. 2018). The corresponding homologues in algae and plants appear to fulfil the same role as SynFtsH2/3 (Sakamoto et al. 2003; Malnoë et al. 2014). The FtsH2/3 complex also co-purifies with preparations of $D2_{mod}$ and RCII from *Synechocystis* (Knoppová et al. 2022), which supports a role in the degradation of both D1 and D2 within RCII (Krynická et al. 2015). The FtsH2/3 complex also interacts with prohibitin, a member of the band 7 protein family, which might regulate FtsH activity (Boehm et al. 2009; Boehm et al. 2012a).

Accumulation of the FtsH2/3 protease complex in *Synechocystis* is dependent on the Psb29 subunit, which was originally identified as a PSII assembly factor (Kashino et al. 2002). Psb29 interacts directly with FtsH, but it remains unclear whether it is involved in assembly or stabilization of FtsH complexes (Bečková et al. 2017b). The plant homologue of Psb29, termed Thylakoid Formation 1, THF1 (Keren et al. 2005), is expected to play a similar role in chloroplasts (Bečková et al. 2017b). The *Chlamydomonas* CrFtsH1/2 complex exhibits increased turnover in the light (Wang et al. 2017a), with accumulation dependent on the peptidyl-prolyl cis-trans isomerization activity of immunophilin CYN28 (Fu et al. 2023); in *Arabidopsis*, FtsH turnover requires the EngA GTPase, which suggests a possible role for phosphorylation in FtsH action (Kato et al. 2018).

By contrast, the homo-oligomeric SynFtsH4 complex, which is also found in *Synechocystis* thylakoids, is not involved in the degradation of damaged PSII subunits; rather, it controls the level of Hlips and possibly other PSII assembly factors (Krynická et al. 2023). What determines the substrate specificity of FtsH complexes remains unknown.

Selective D1 degradation in cyanobacteria is synchronized with the synthesis of D1 so that when the D1 subunit is not available the degradation of damaged D1 is postponed and is closely followed by degradation of D2 (Komenda and Barber 1995; Mulo et al. 1997; Komenda et al. 2000; Masuda et al. 2023). The mechanism for this synchronization is unclear but might reflect the degradation of damaged D1 by FtsH attached to the Sec translocon (Yu et al. 2018).

The second group of proteases involved in the degradation of PSII components, especially D1, in chloroplasts are the Deg serine proteases, which are located in both the stroma and lumen and are considered as back-up proteases that cleave exposed loops of D1 and, possibly, other proteins to enhance FtsH-mediated degradation (Kato and Sakamoto 2009). Although important for conferring resistance to light stress, the *Synechocystis* Deg proteases do not play an important role in D1 degradation (Barker et al. 2006).

Chl biosynthesis and delivery to PSII during biogenesis

As already noted, unbound Chl is phototoxic and synthesis of Chl-binding proteins needs to be strictly synchronized with Chl biosynthesis and organized in a way to prevent leakage of Chl molecules into the membrane. The terminal enzyme of the Chl biosynthesis pathway, Chl synthase, is associated with the YidC insertase in cyanobacteria (Chidgey et al. 2014) and possibly in plants (Proctor et al. 2018), which has led to speculation that the Chl biosynthesis enzymes are organized close to the translocon (Sobotka 2014) and that newly formed Chl passes directly from the Chl synthase to the nascent polypeptide chain (Chidgey et al. 2014) in a co-translational mechanism, as suggested from early studies (Eichacker et al. 1990; Mullet et al. 1990). However, some Chls are now known to be bound at the interface of two subunits in photosynthetic complexes suggesting some post-translational binding of Chl. Also, analysis of purified $D1_{mod}$ and $D2_{mod}$ indicates that at least some Chl molecules are inserted after the folding and formation of modules (Knoppová et al. 2022). Nonetheless, it is likely that this post-translational Chl insertion still occurs in close vicinity of the translocon (and Chl synthase), where a limited pool of free Chl might be present. Its toxicity could be mitigated by Hlips and a high concentration of carotenoids. The stable assembly of D1 and D2 into the RCII complex requires Chl (Knoppová et al. 2022) with insertion facilitated by Ycf48 (Yu et al. 2018). The fact that this assembly factor can be co-isolated with YidC (Yu et al. 2018) supports the preloading of $D1_{mod}$ and $D2_{mod}$ with pigments on the periphery of the translocon.

Analysis of a wide range of PSII assembly mutants suggests that Chl biosynthesis is dependent on the ongoing assembly of PSII in cyanobacteria (Bečková et al. 2017a; Yu et al. 2018; Kiss et al. 2019) and chloroplasts (Plücken et al. 2002; García-Cerdán et al. 2019; Che et al. 2022). These mutants are PSI deficient, which appears to be a consequence of such regulation. Possibly, PSII assembly intermediates may interact with Chl biosynthesis enzymes, stabilize them and channel new Chl into newly synthesized Chl-binding proteins. This hypothesis is supported by detection of Mg-protoporphyrin IX monomethylester cyclase in RC47 and/or RCCII assembly intermediates containing Psb28 (Dobáková et al. 2009) but needs further support.

Importantly, the lifetime of Chl exceeds that of individual PSII Chl-binding proteins, and hence Chl is recycled (Yao et al. 2012). As yet, the Chl-binding proteins involved in this process remain unknown. D1, D2, and partly CP43 are synthesized in *Synechocystis* even when de novo Chl biosynthesis is inhibited, suggesting that they can utilize previously synthesized Chl molecules released from other Chl-binding proteins (Kopečná et al. 2013; Hollingshead et al. 2016). By contrast, synthesis of CP47 and formation of PSI trimers are dependent on the sufficient supply of new Chl occurring under optimal growth conditions when fast cell proliferation

occurs (Kopečná et al. 2012). This would indicate that PSI monomers need additional Chls to trimerize, and that this Chl could then be released upon monomerization.

A possible role for PSI in PSII biogenesis

The recent co-isolation of PSII assembly modules and assembly intermediates with PSI complexes has provided biochemical evidence for the possible involvement of PSI in PSII biogenesis (Fig. 3). Affinity purification of various PSII assembly intermediates and PSI complexes has led to the isolation of $CP43_{mod}$ (Fig. 3; Komenda et al. 2012b; Kopečná et al. 2015; Strašková et al. 2018) and RC47 (Kiss et al. 2019; Pascual-Aznar et al. 2021) complexes bound to monomeric PSI complexes as well as $CP47_{mod}$ and RCCII bound to trimeric PSI (Bečková et al. 2017a; Pascual-Aznar et al. 2021). Although more work is needed to confirm the structure and physiological relevance of these complexes (Zhao et al. 2023), these results suggest that the biogenesis pathways of PSI and PSII may be intertwined (Fig. 3). This is further supported by findings that some assembly factors like Psb27 (Komenda et al. 2012b), Ycf48 (Yu et al. 2018), and Psb35 (Pascual-Aznar et al. 2021) seem to be shared by both PSI and PSII. PSI may therefore play a role as a scaffold that transiently binds PSII assembly modules and intermediates to supply them with its own weakly bound Chl molecules and photoprotect them by dissipating excess light energy via excitation energy transfer (or "spill-over") to PSI (Bečková et al. 2017a; Strašková et al. 2018; Fig. 3).

Future outlook

Thanks to the dramatic progress in structural biology, especially cryo-EM, we are entering an era where structures of low-abundance complexes involved in PSII assembly and repair can be rapidly determined. A combination of affinity purification of tagged complexes from WT and mutants and cryo-EM will allow us to address the binding sites and possible functions of the many accessory factors so far implicated in PSII biogenesis (see Johnson and Pakrasi 2022 for recent list). Some of these are specific for cyanobacteria or chloroplasts and probably reflect specific adaptations.

Key questions to address in the future include how Chl is handled during the synthesis of Chl-binding proteins and during degradation of damaged PSII subunits and how the Mn_4CaO_5 cluster is assembled in PSII during the process of photoactivation. In terms of PSII repair, cryo-EM analysis combined with mass spectrometry of PSII complexes isolated from cells at various stages of photodamage will reveal insights into the modifications and accompanying structural changes that occur to trigger selective D1 degradation. So far work in this area has been restricted to identifying sites of damage in isolated PSII complexes (Kale et al. 2017). Ultimately, it might even be possible to obtain snapshots of PSII complexes undergoing assembly/repair in situ using advanced cryo-tomography

techniques as recently applied in the red alga *Porphyridium purpureum* (You et al. 2023) to study PSI/PSII megacomplexes. Ultimately, fundamental knowledge in this area might be exploited to improve the efficiency of PSII assembly and repair, especially under abiotic stress conditions, to increase biomass yields.

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J.K., R.S., and P.J.N. conceptualized the review outline; J.K. wrote the original draft and R.S. and P.J.N. reviewed and edited it; R.S. prepared the figures; J.K., R.S., and P.J.N. finalized the manuscript.

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References

Adir N, Shochat S, Ohad I. Light-dependent D1 protein synthesis and translocation is regulated by reaction center II. Reaction center II serves as an acceptor for the D1 precursor. J Biol Chem. 1990:**265**(21): 12563–12568. https://doi.org/10.1016/S0021-9258(19)38381-4

Anbudurai PR, Mor TS, Ohad I, Shestakov SV, Pakrasi HB. The *ctpA* gene encodes the C-terminal processing protease for the D1 protein of the photosystem II reaction center complex. Proc Natl Acad Sci U S A. 1994:**91**(17):8082–8086. https://doi.org/10.1073/pnas.91.17.8082

Armbruster U, Zühlke J, Rengstl B, Kreller R, Makarenko E, Rühle T, Schünemann D, Jahns P, Weisshaar B, Nickelsen J, et al. The Arabidopsis thylakoid protein PAM68 is required for efficient D1 biogenesis and photosystem II assembly. Plant Cell. 2010:**22**(10): 3439–3460. https://doi.org/10.1105/tpc.110.077453

Avramov AP, Hwang HJ, Burnap RL. The role of Ca^{2+} and protein scaffolding in the formation of nature's water oxidizing complex. Proc Natl Acad Sci U S A. 2020:**117**(45):28036–28045. https://doi.org/10.1073/pnas.2011315117

Bao H, Burnap RL. Photoactivation: the light-driven assembly of the water oxidation complex of photosystem II. Front Plant Sci. 2016:**7**: 578. https://doi.org/10.3389/fpls.2016.00578

Barbato R, Friso G, Rigoni F, Dalla Vecchia F, Giacometti GM. Structural changes and lateral redistribution of photosystem II during donor side photoinhibition of thylakoids. J Cell Biol. 1992:**119**(2):325–335. https://doi.org/10.1083/jcb.119.2.325

Barker M, de Vries R, Nield J, Komenda J, Nixon PJ. The deg proteases protect *Synechocystis* sp. PCC 6803 during heat and light stresses but are not essential for removal of damaged D1 protein during the photosystem two repair cycle. J Biol Chem. 2006:**281**(41):30347–30355. https://doi.org/10.1074/jbc.M601064200

Bečková M, Gardian Z, Yu J, Konik P, Nixon PJ, Komenda J. Association of Psb28 and Psb27 proteins with PSII-PSI supercomplexes upon exposure of *Synechocystis* sp. PCC 6803 to high light. Mol Plant. 2017a:**10**(1):62–72. https://doi.org/10.1016/j.molp.2016.08.001

Bečková M, Sobotka R, Komenda J. Photosystem II antenna modules CP43 and CP47 do not form a stable 'no reaction centre complex' in the cyanobacterium *Synechocystis* sp. PCC 6803. Photosynth Res. 2022:**152**(3):363–371. https://doi.org/10.1007/s11120-022-00896-w

Bečková M, Yu J, Krynická V, Kozlo A, Shao S, Koník P, Komenda J, Murray JW, Nixon PJ. Structure of Psb29/Thf1 and its association with the FtsH protease complex involved in photosystem II repair in cyanobacteria. Philos Trans R Soc Lond B Biol Sci. 2017b:**372**(1730): 20160394. https://doi.org/10.1098/rstb.2016.0394

Bentley FK, Luo H, Dilbeck P, Burnap RL, Eaton-Rye JJ. Effects of inactivating psbM and psbT on photodamage and assembly of photosystem II in *Synechocystis* sp. PCC 6803. Biochemistry. 2008:**47**(44): 11637–11646. https://doi.org/10.1021/bi800804h

Bishop CL, Ulas S, Baena-Gonzalez E, Aro EM, Purton S, Nugent JH, Mäenpää P. The PsbZ subunit of photosystem II in *Synechocystis* sp. PCC 6803 modulates electron flow through the photosynthetic electron transfer chain. Photosynth Res. 2007:**93**(1–3):139–147. https://doi.org/10.1007/s11120-007-9182-0

Boehm M, Nield J, Zhang P, Aro EM, Komenda J, Nixon PJ. Structural and mutational analysis of band 7 proteins in the cyanobacterium *Synechocystis* sp. strain PCC 6803. J Bacteriol. 2009:**191**(20):6425–6435. https://doi.org/10.1128/JB.00644-09

Boehm M, Romero E, Reisinger V, Yu J, Komenda J, Eichacker LA, Dekker JP, Nixon PJ. Investigating the early stages of photosystem II assembly in *Synechocystis* sp. PCC 6803: isolation of CP47 and CP43 complexes. J Biol Chem. 2011:**286**(17):14812–14819. https://doi.org/10.1074/jbc.M110.207944

Boehm M, Yu J, Krynická V, Barker M, Tichý M, Komenda J, Nixon PJ, Nield J. Subunit organization of a *Synechocystis* hetero-oligomeric thylakoid FtsH complex involved in photosystem II repair. Plant Cell. 2012a:**24**(9):3669–3683. https://doi.org/10.1105/tpc.112.100891

Boehm M, Yu J, Reisinger V, Beckova M, Eichacker LA, Schlodder E, Komenda J, Nixon PJ. Subunit composition of CP43-less photosystem II complexes of *Synechocystis* sp. PCC 6803: implications for the assembly and repair of photosystem II. Philos Trans R Soc Lond B Biol Sci. 2012b:**367**(1608):3444–3454. https://doi.org/10.1098/rstb.2012.0066

Brinkert K, De Causmaecker S, Krieger-Liszkay A, Fantuzzi A, Rutherford AW. Bicarbonate-induced redox tuning in photosystem II for regulation and protection. Proc Natl Acad Sci U S A. 2016:**113**(43): 12144–12149. https://doi.org/10.1073/pnas.1608862113

Bučinská L, Kiss É, Koník P, Knoppová J, Komenda J, Sobotka R. The ribosome-bound protein Pam68 promotes insertion of chlorophyll into the CP47 subunit of photosystem II. Plant Physiol. 2018:**176**(4): 2931–2942. https://doi.org/10.1104/pp.18.00061

Calderon RH, de Vitry C, Wollman FA, Niyogi KK. Rubredoxin 1 promotes the proper folding of D1 and is not required for heme b_{559} assembly in Chlamydomonas photosystem II. J Biol Chem. 2023:**299**(3): 102968. https://doi.org/10.1016/j.jbc.2023.102968

Calderon RH, García-Cerdán JG, Malnoë A, Cook R, Russell JJ, Gaw C, Dent RM, de Vitry C, Niyogi KK. A conserved rubredoxin is necessary for photosystem II accumulation in diverse oxygenic photoautotrophs. J Biol Chem. 2013:**288**(37):26688–26696. https://doi.org/10.1074/jbc.M113.487629

Cao P, Pan X, Su X, Liu Z, Li M. Assembly of eukaryotic photosystem II with diverse light-harvesting antennas. Curr Opin Struct Biol. 2020:**63**:49–57. https://doi.org/10.1016/j.sbi.2020.03.007

Chazaux M, Caffarri S, Da Graça J, Cuiné S, Floriani M, Brzezowski P, Peltier G, Genty B, Alric J, Johnson X. ACCLIMATION OF PHOTOSYNTHESIS TO THE ENVIRONMENT 1 regulates Photosystem II Supercomplex dynamics in response to light in *Chlamydomonas reinhardtii*. bioRxiv 966580. February 29, 2020, preprint: not peer reviewed. https://doi.org/10.1101/2020.02.26.966580

Che Y, Kusama S, Matsui S, Suorsa M, Nakano T, Aro EM, Ifuku K. Arabidopsis PsbP-like protein 1 facilitates the assembly of the photosystem II supercomplexes and optimizes plant fitness under fluctuating light. Plant Cell Physiol. 2020:61(6):1168–1180. https://doi.org/10.1093/pcp/pcaa045

Che L, Meng H, Ruan J, Peng L, Zhang L. Rubredoxin 1 is required for formation of the functional photosystem II core complex in Arabidopsis thaliana. Front Plant Sci. 2022:13:824358. https://doi.org/10.3389/fpls.2022.824358

Chen H, Zhang D, Guo J, Wu H, Jin M, Lu Q, Lu C, Zhang L. A Psb27 homologue in Arabidopsis thaliana is required for efficient repair of photodamaged photosystem II. Plant Mol Biol. 2006:61(4–5):567–575. https://doi.org/10.1007/s11103-006-0031-x

Chidgey JW, Linhartová M, Komenda J, Jackson PJ, Dickman MJ, Canniffe DP, Koník P, Pilný J, Hunter CN, Sobotka R. A cyanobacterial chlorophyll synthase-HliD complex associates with the Ycf39 protein and the YidC/Alb3 insertase. Plant Cell. 2014:26(3):1267–1279. https://doi.org/10.1105/tpc.114.124495

Choo P, Forsman JA, Hui L, Khaing EP, Summerfield TC, Eaton-Rye JJ. The PsbJ protein is required for photosystem II activity in centers lacking the PsbO and PsbV lumenal subunits. Photosynth Res. 2022:151(1):103–111. https://doi.org/10.1007/s11120-021-00862-y

Chotewutmontri P, Barkan A. Light-induced *psbA* translation in plants is triggered by photosystem II damage via an assembly-linked autoregulatory circuit. Proc Natl Acad Sci U S A. 2020:117(35):21775–21784. https://doi.org/10.1073/pnas.2007833117

Cormann KU, Bangert JA, Ikeuchi M, Rögner M, Stoll R, Nowaczyk MM. Structure of Psb27 in solution: implications for transient binding to photosystem II during biogenesis and repair. Biochemistry. 2009:48(37):8768–8770. https://doi.org/10.1021/bi9012726

Cymer F, von Heijne G, White SH. Mechanisms of integral membrane protein insertion and folding. J Mol Biol. 2015:427(5):999–1022. https://doi.org/10.1016/j.jmb.2014.09.014

de Vitry C, Olive J, Drapier D, Recouvreur M, Wollman FA. Posttranslational events leading to the assembly of photosystem II protein complex: a study using photosynthesis mutants from *Chlamydomonas reinhardtii*. J Cell Biol. 1989:109(3):991–1006. https://doi.org/10.1083/jcb.109.3.991

Diner BA, Nixon PJ. The rate of reduction of oxidized redox-active tyrosine, Z$^+$, by exogenous Mn^{2+} is slowed in a site-directed mutant, at aspartate 170 of polypeptide D1 of photosystem II, inactive for photosynthetic oxygen evolution. Biochim Biophys Acta. 1992:1101(2):134–138. https://doi.org/10.1016/0005-2728(92)90196-9

Diner BA, Rappaport F. Structure, dynamics, and energetics of the primary photochemistry of photosystem II of oxygenic photosynthesis. Annu Rev Plant Biol. 2002:53(1):551–580. https://doi.org/10.1146/annurev.arplant.53.100301.135238

Dobáková M, Sobotka R, Tichý M, Komenda J. Psb28 protein is involved in the biogenesis of the photosystem II inner antenna CP47 (PsbB) in the cyanobacterium *Synechocystis* sp. PCC 6803. Plant Physiol. 2009:149(2):1076–1086. https://doi.org/10.1104/pp.108.130039

Dolganov NA, Bhaya D, Grossman AR. Cyanobacterial protein with similarity to the chlorophyll a/b binding proteins of higher plants: evolution and regulation. Proc Natl Acad Sci U S A. 1995:92(2):636–640. https://doi.org/10.1073/pnas.92.2.636

Domonkos I, Kis M, Gombos Z, Ughy B. Carotenoids, versatile components of oxygenic photosynthesis. Prog Lipid Res. 2013:52(4):539–561. https://doi.org/10.1016/j.plipres.2013.07.001

Eichacker LA, Soll J, Lauterbach P, Rüdiger W, Klein RR, Mullet JE. In vitro synthesis of chlorophyll a in the dark triggers accumulation of chlorophyll a apoproteins in barley etioplasts. J Biol Chem. 1990:265(23):13566–13571. https://doi.org/10.1016/S0021-9258(18)77385-7

Ermakova-Gerdes S, Vermaas W. Inactivation of the open reading frame slr0399 in *Synechocystis* sp. PCC 6803 functionally complements mutations near the Q(A) niche of photosystem II. A possible role of Slr0399 as a chaperone for quinone binding. J Biol Chem. 1999:274(43):30540–30549. https://doi.org/10.1074/jbc.274.43.30540

Fadeeva M, Klaiman D, Caspy I, Nelson N. Structure of Chlorella ohadii photosystem II reveals protective mechanisms against environmental stress. Cells. 2023:12(15):1971. https://doi.org/10.3390/cells12151971

Fagerlund RD, Eaton-Rye JJ. The lipoproteins of cyanobacterial photosystem II. J Photochem Photobiol B. 2011:104(1–2):191–203. https://doi.org/10.1016/j.jphotobiol.2011.01.022

Fagerlund RD, Forsman JA, Biswas S, Vass I, Davies FK, Summerfield TC, Eaton-Rye JJ. Stabilization of photosystem II by the PsbT protein impacts photodamage, repair and biogenesis. Biochim Biophys Acta Bioenerg. 2020:1861(10):148234. https://doi.org/10.1016/j.bbabio.2020.148234

Fantuzzi A, Haniewicz P, Farci D, Loi MC, Park K, Büchel C, Bochtler M, Rutherford AW, Piano D. Bicarbonate activation of the monomeric photosystem II-PsbS/Psb27 complex. Plant Physiol. 2023:192(4):2656–2671. https://doi.org/10.1093/plphys/kiad275

Ferreira KN, Iverson TM, Maghlaoui K, Barber J, Iwata S. Architecture of the photosynthetic oxygen-evolving center. Science. 2004:303(5665):1831–1838. https://doi.org/10.1126/science.1093087

Fu W, Cui Z, Guo J, Cui X, Han G, Zhu Y, Hu J, Gao X, Li Y, Xu M, et al. Immunophilin CYN28 is required for accumulation of photosystem II and thylakoid FtsH protease in Chlamydomonas. Plant Physiol. 2023:191(2):1002–1016. https://doi.org/10.1093/plphys/kiac524

Funk C, Vermaas W. A cyanobacterial gene family coding for single-helix proteins resembling part of the light-harvesting proteins from higher plants. Biochemistry. 1999:38(29):9397–9404. https://doi.org/10.1021/bi990545+

García-Cerdán JG, Furst AL, McDonald KL, Schünemann D, Francis MB, Niyogi KK. A thylakoid membrane-bound and redox-active rubredoxin (RBD1) functions in de novo assembly and repair of photosystem II. Proc Natl Acad Sci U S A. 2019:116(33):16631–16640. https://doi.org/10.1073/pnas.1903314116

Gisriel CJ, Brudvig GW. Comparison of PsbQ and Psb27 in photosystem II provides insight into their roles. Photosynth Res. 2022:152(2):177–191. https://doi.org/10.1007/s11120-021-00888-2

Gisriel CJ, Wang J, Liu J, Flesher DA, Reiss KM, Huang HL, Yang KR, Armstrong WH, Gunner MR, Batista VS, et al. High-resolution cryo-electron microscopy structure of photosystem II from the mesophilic cyanobacterium, *Synechocystis* sp. PCC 6803. Proc Natl Acad Sci U S A. 2022:119(1):e2116765118. https://doi.org/10.1073/pnas.2116765118

Gisriel CJ, Zhou K, Huang H-L, Debus RJ, Xiong Y, Brudvig GW. Cryo-EM structure of monomeric photosystem II from *Synechocyst* 2020:4(10):2131–2148. https://doi.org/10.1016/j.joule.2020.07.016

Graça AT, Hall M, Persson K, Schröder WP. High–resolution model of Arabidopsis photosystem II reveals the structural consequences of digitonin–extraction. Sci Rep. 2021:11(1):15534. https://doi.org/10.1038/s41598-021-94914-x

Guskov A, Kern J, Gabdulkhakov A, Broser M, Zouni A, Saenger W. Cyanobacterial photosystem II at 2.9-A resolution and the role of quinones, lipids, channels and chloride. Nat Struct Mol Biol. 2009:16(3):334–342. https://doi.org/10.1038/nsmb.1559

Hamilton ML, Franco E, Deák Z, Schlodder E, Vass I, Nixon PJ. Investigating the photoprotective role of cytochrome b-559 in photosystem II in a mutant with altered ligation of the haem. Plant Cell Physiol. 2014:55(7):1276–1285. https://doi.org/10.1093/pcp/pcu070

Hennon SW, Soman R, Zhu L, Dalbey RE. Yidc/Alb3/Oxa1 family of insertases. J Biol Chem. 2015:**290**(24):14866–14874. https://doi.org/10.1074/jbc.R115.638171

Hey D, Grimm B. ONE-HELIX PROTEIN1 and 2 form heterodimers to bind chlorophyll in photosystem II biogenesis. Plant Physiol. 2020:**183**(1):179–193. https://doi.org/10.1104/pp.19.01304

Hollingshead S, Kopečná J, Armstrong DR, Bučinská L, Jackson PJ, Chen GE, Dickman MJ, Williamson MP, Sobotka R, Hunter CN. Synthesis of chlorophyll-binding proteins in a fully segregated Δycf54 strain of the cyanobacterium Synechocystis PCC 6803. Front Plant Sci. 2016:**7**:292. https://doi.org/10.3389/fpls.2016.00292

Hristou A, Gerlach I, Stolle DS, Neumann J, Bischoff A, Dünschede B, Nowaczyk MM, Zoschke R, Schünemann D. Ribosome-associated chloroplast SRP54 enables efficient cotranslational membrane insertion of key photosynthetic proteins. Plant Cell. 2019:**31**(11): 2734–2750. https://doi.org/10.1105/tpc.19.00169

Huang G, Xiao Y, Pi X, Zhao L, Zhu Q, Wang W, Kuang T, Han G, Sui SF, Shen JR. Structural insights into a dimeric Psb27-photosystem II complex from a cyanobacterium Thermosynechococcus vulcanus. Proc Natl Acad Sci U S A. 2021:**118**(5):e2018053118. https://doi.org/10.1073/pnas.2018053118

Hung CH, Hwang HJ, Chen YH, Chiu YF, Ke SC, Burnap RL, Chu HA. Spectroscopic and functional characterizations of cyanobacterium Synechocystis PCC 6803 mutants on and near the heme axial ligand of cytochrome b559 in photosystem II. J Biol Chem. 2010:**285**(8): 5653–5663. https://doi.org/10.1074/jbc.M109.044719

Ifuku K, Noguchi T. Structural coupling of extrinsic proteins with the oxygen-evolving center in photosystem II. Front Plant Sci. 2016:**7**:84. https://doi.org/10.3389/fpls.2016.00084

Inagaki N, Yamamoto Y, Satoh K. A sequential two-step proteolytic process in the carboxyl-terminal truncation of precursor D1 protein in Synechocystis sp. PCC6803. FEBS Lett. 2001:**509**(2):197–201. https://doi.org/10.1016/s0014-5793(01)03180-5

Ishikawa Y, Schröder WP, Funk C. Functional analysis of the PsbP-like protein (sll1418) in Synechocystis sp. PCC 6803. Photosynth Res. 2005:**84**(1–3):257–262. https://doi.org/10.1007/s11120-005-0477-8

Jansen MA, Mattoo AK, Edelman M. D1-D2 protein degradation in the chloroplast. Complex light saturation kinetics. Eur J Biochem. 1999:**260**(2):527–532. https://doi.org/10.1046/j.1432-1327.1999.00196.x

Jimbo H, Wada H. Deacylation of galactolipids decomposes photosystem II dimers to enhance degradation of damaged D1 protein. Plant Physiol. 2023:**191**(1):87–95. https://doi.org/10.1093/plphys/kiac460

Johnson VM, Biswas S, Roose JL, Pakrasi HB, Liu H. Psb27, a photosystem II assembly protein, enables quenching of excess light energy during its participation in the PSII lifecycle. Photosynth Res. 2022:**152**(3): 297–304. https://doi.org/10.1007/s11120-021-00895-3

Johnson VM, Pakrasi HB. Advances in the understanding of the life-cycle of photosystem II. Microorganisms. 2022:**10**(5):836. https://doi.org/10.3390/microorganisms10050836

Kale R, Hebert AE, Frankel LK, Sallans L, Bricker TM, Pospíšil P. Amino acid oxidation of the D1 and D2 proteins by oxygen radicals during photoinhibition of photosystem II. Proc Natl Acad Sci U S A. 2017:**114**(11):2988–2993. https://doi.org/10.1073/pnas.1618922114

Kashino Y, Koike H, Yoshio M, Egashira H, Ikeuchi M, Pakrasi HB, Satoh K. Low-molecular-mass polypeptide components of a photosystem II preparation from the thermophilic cyanobacterium Thermosynechococcus vulcanus. Plant Cell Physiol. 2002:**43**(11): 1366–1373. https://doi.org/10.1093/pcp/pcf168

Kato Y, Hyodo K, Sakamoto W. The photosystem II repair cycle requires FtsH turnover through the EngA GTPase. Plant Physiol. 2018:**178**(2):596–611. https://doi.org/10.1104/pp.18.00652

Kato Y, Kuroda H, Ozawa SI, Saito K, Dogra V, Scholz M, Zhang G, de Vitry C, Ishikita H, Kim C, et al. Characterization of tryptophan oxidation affecting D1 degradation by FtsH in the photosystem II quality control of chloroplasts. Elife. 2023:**12**:RP88822. https://doi.org/10.7554/eLife.88822

Kato Y, Sakamoto W. Protein quality control in chloroplasts: a current model of D1 protein degradation in the photosystem II repair cycle. J Biochem. 2009:**146**(4):463–469. https://doi.org/10.1093/jb/mvp073

Keller JM, Frieboes MJ, Jödecke L, Kappel S, Wulff N, Rindfleisch T, Sandoval-Ibanez O, Gerlach I, Thiele W, Bock R, et al. Eukaryote-specific assembly factor DEAP2 mediates an early step of photosystem II assembly in Arabidopsis. Plant Physiol. 2023:**193**(3): 1970–1986. https://doi.org/10.1093/plphys/kiad446

Keren N, Ohkawa H, Welsh EA, Liberton M, Pakrasi HB. Psb29, a conserved 22-kD protein, functions in the biogenesis of photosystem II complexes in Synechocystis and Arabidopsis. Plant Cell. 2005:**17**(10): 2768–2781. https://doi.org/10.1105/tpc.105.035048

Kiss É, Knoppová J, Aznar GP, Pilný J, Yu J, Halada P, Nixon PJ, Sobotka R, Komenda J. A photosynthesis-specific rubredoxin-like protein is required for efficient association of the D1 and D2 proteins during the initial steps of photosystem II assembly. Plant Cell. 2019:**31**(9):2241–2258. https://doi.org/10.1105/tpc.19.00155

Knoppová J, Sobotka R, Tichy M, Yu J, Konik P, Halada P, Nixon PJ, Komenda J. Discovery of a chlorophyll binding protein complex involved in the early steps of photosystem II assembly in Synechocystis. Plant Cell. 2014:**26**(3):1200–1212. https://doi.org/10.1105/tpc.114.123919

Knoppová J, Sobotka R, Yu J, Bečková M, Pilný J, Trinugroho JP, Csefalvay L, Bína D, Nixon PJ, Komenda J. Assembly of D1/D2 complexes of photosystem II: binding of pigments and a network of auxiliary proteins. Plant Physiol. 2022:**189**(2):790–804. https://doi.org/10.1093/plphys/kiac045

Knoppová J, Yu J, Janouškovec J, Halada P, Nixon PJ, Whitelegge JP, Komenda J. The photosystem II assembly factor Ycf48 from the cyanobacterium Synechocystis sp. PCC 6803 is lipidated using an atypical lipobox sequence. Int J Mol Sci. 2021:**22**(7):3733. https://doi.org/10.3390/ijms22073733

Knoppová J, Yu J, Konik P, Nixon PJ, Komenda J. CyanoP is involved in the early steps of photosystem II assembly in the cyanobacterium Synechocystis sp. PCC 6803. Plant Cell Physiol. 2016:**57**(9): 1921–1931. https://doi.org/10.1093/pcp/pcw115

Komenda J, Barber J. Comparison of psbO and psbH deletion mutants of Synechocystis PCC 6803 indicates that degradation of D1 protein is regulated by the QB site and dependent on protein synthesis. Biochemistry. 1995:**34**(29):9625–9631. https://doi.org/10.1021/bi00029a040

Komenda J, Barker M, Kuviková S, de Vries R, Mullineaux CW, Tichý M, Nixon PJ. The FtsH protease slr0228 is important for quality control of photosystem II in the thylakoid membrane of Synechocystis sp. PCC 6803. J Biol Chem. 2006:**281**(2):1145–1151. https://doi.org/10.1074/jbc.M503852200

Komenda J, Hassan HA, Diner BA, Debus RJ, Barber J, Nixon PJ. Degradation of the photosystem II D1 and D2 proteins in different strains of the cyanobacterium Synechocytis PCC 6803 varying with respect to the type and level of psbA transcript. Plant Mol Biol. 2000:**42**(4):635–645. https://doi.org/10.1023/a:1006305308196

Komenda J, Knoppová J, Kopečná J, Sobotka R, Halada P, Yu J, Nickelsen J, Boehm M, Nixon PJ. The Psb27 assembly factor binds to the CP43 complex of photosystem II in the cyanobacterium Synechocystis sp. PCC 6803. Plant Physiol. 2012b:**158**(1):476–486. https://doi.org/10.1104/pp.111.184184

Komenda J, Kuviková S, Granvogl B, Eichacker LA, Diner BA, Nixon PJ. Cleavage after residue Ala352 in the C-terminal extension is an early step in the maturation of the D1 subunit of photosystem II in Synechocystis PCC 6803. Biochim Biophys Acta. 2007a:**1767**(6): 829–837. https://doi.org/10.1016/j.bbabio.2007.01.005

Komenda J, Masojídek J. Functional and structural changes of the photosystem II complex induced by high irradiance in cyanobacterial cells. Eur J Biochem. 1995:**233**(2):677–682. https://doi.org/10.1111/j.1432-1033.1995.677_2.x

Komenda J, Nickelsen J, Tichý M, Prášil O, Eichacker LA, Nixon PJ. The cyanobacterial homologue of HCF136/YCF48 is a component

of an early photosystem II assembly complex and is important for both the efficient assembly and repair of photosystem II in *Synechocystis* sp. PCC 6803. J Biol Chem. 2008:**283**(33):22390–22399. https://doi.org/10.1074/jbc.M801917200

Komenda J, Reisinger V, Müller BC, Dobáková M, Granvogl B, Eichacker LA. Accumulation of the D2 protein is a key regulatory step for assembly of the photosystem II reaction center complex in *Synechocystis* PCC 6803. J Biol Chem. 2004:**279**(47):48620–48629. https://doi.org/10.1074/jbc.M405725200

Komenda J, Sobotka R, Nixon PJ. Assembling and maintaining the photosystem II complex in chloroplasts and cyanobacteria. Curr Opin Plant Biol. 2012a:**15**(3):245–251. https://doi.org/10.1016/j.pbi.2012.01.017

Komenda J, Tichý M, Prášil O, Knoppová J, Kuviková S, de Vries R, Nixon PJ. The exposed N-terminal tail of the D1 subunit is required for rapid D1 degradation during photosystem II repair in *Synechocystis* sp PCC 6803. Plant Cell. 2007b:**19**(9):2839–2854. https://doi.org/10.1105/tpc.107.053868

Konert MM, Wysocka A, Koník P, Sobotka R. High-light-inducible proteins HliA and HliB: pigment binding and protein-protein interactions. Photosynth Res. 2022:**152**(3):317–332. https://doi.org/10.1007/s11120-022-00904-z

Kopečná J, Komenda J, Bučinská L, Sobotka R. Long-term acclimation of the cyanobacterium *Synechocystis* sp. PCC 6803 to high light is accompanied by an enhanced production of chlorophyll that is preferentially channeled to trimeric photosystem I. Plant Physiol. 2012:**160**(4):2239–2250. https://doi.org/10.1104/pp.112.207274

Kopečná J, Pilný J, Krynická V, Tomčala A, Kis M, Gombos Z, Komenda J, Sobotka R. Lack of phosphatidylglycerol inhibits chlorophyll biosynthesis at multiple sites and limits chlorophyllide reutilization in *Synechocystis* sp. Strain PCC 6803. Plant Physiol. 2015:**169**(2):1307–1317. https://doi.org/10.1104/pp.15.01150

Kopečná J, Sobotka R, Komenda J. Inhibition of chlorophyll biosynthesis at the protochlorophyllide reduction step results in the parallel depletion of photosystem I and photosystem II in the cyanobacterium *Synechocystis* PCC 6803. Planta. 2013:**237**(2):497–508. https://doi.org/10.1007/s00425-012-1761-4

Krynická V, Shao S, Nixon PJ, Komenda J. Accessibility controls selective degradation of photosystem II subunits by FtsH protease. Nat Plants. 2015:**1**(12):15168. https://doi.org/10.1038/nplants.2015.168

Krynická V, Skotnicová P, Jackson PJ, Barnett S, Yu J, Wysocka A, Kaňa R, Dickman MJ, Nixon PJ, Hunter CN, et al. Ftsh4 protease controls biogenesis of the PSII complex by dual regulation of high light-inducible proteins. Plant Commun. 2023:**4**(1):100502. https://doi.org/10.1016/j.xplc.2022.100502

Laczkó-Dobos H, Ughy B, Tóth SZ, Komenda J, Zsiros O, Domonkos I, Párducz A, Bogos B, Komura M, Itoh S, et al. Role of phosphatidylglycerol in the function and assembly of photosystem II reaction center, studied in a cdsA-inactivated PAL mutant strain of *Synechocystis* sp. PCC6803 that lacks phycobilisomes. Biochim Biophys Acta. 2008:**1777**(9):1184–1194. https://doi.org/10.1016/j.bbabio.2008.06.003

Lambertz J, Meier-Credo J, Kucher S, Bordignon E, Langer JD, Nowaczyk MM. Isolation of a novel heterodimeric PSII complex via strep-tagged PsbO. Biochim Biophys Acta Bioenerg. 2023:**1864**(2):148953. https://doi.org/10.1016/j.bbabio.2022.148953

Li Y, Liu B, Zhang J, Kong F, Zhang L, Meng H, Li W, Rochaix JD, Li D, Peng L. OHP1, OHP2, and HCF244 form a transient functional complex with the photosystem II reaction center. Plant Physiol. 2019:**179**(1):195–208. https://doi.org/10.1104/pp.18.01231

Link S, Engelmann K, Meierhoff K, Westhoff P. The atypical short-chain dehydrogenases HCF173 and HCF244 are jointly involved in translational initiation of the psbA mRNA of Arabidopsis. Plant Physiol. 2012:**160**(4):2202–2218. https://doi.org/10.1104/pp.112.205104

Liu H, Huang RY, Chen J, Gross ML, Pakrasi HB. Psb27, a transiently associated protein, binds to the chlorophyll binding protein CP43 in photosystem II assembly intermediates. Proc Natl Acad Sci U S A. 2011:**108**(45):18536–18541. https://doi.org/10.1073/pnas.1111597108

Liu Z, Li A, You T, Pang X, Wang Y, Tian L, Li X. Structural basis for an early stage of the photosystem II repair cycle in *Chlamydomonas reinhardtii*. Research Square. 2023. Online article. Preprint, not peer reviewed. Available at: https://www.researchsquare.com/article/rs-3272545/v1. https://doi.org/10.21203/rs.3.rs-3272545/v1

Lokstein H, Renger G, Götze JP. Photosynthetic light-harvesting (antenna) complexes-structures and functions. Molecules. 2021:**26**(11):3378. https://doi.org/10.3390/molecules26113378

Longoni FP, Goldschmidt-Clermont M. Thylakoid protein phosphorylation in chloroplasts. Plant Cell Physiol. 2021:**62**(7):1094–1107. https://doi.org/10.1093/pcp/pcab043

Luo H, Jackson SA, Fagerlund RD, Summerfield TC, Eaton-Rye JJ. The importance of the hydrophilic region of PsbL for the plastoquinone electron acceptor complex of photosystem II. Biochim Biophys Acta. 2014:**1837**(9):1435–1446. https://doi.org/10.1016/j.bbabio.2014.02.015

Mabbitt PD, Rautureau GJ, Day CL, Wilbanks SM, Eaton-Rye JJ, Hinds MG. Solution structure of Psb27 from cyanobacterial photosystem II. Biochemistry. 2009:**48**(37):8771–8773. https://doi.org/10.1021/bi901309c

Maeda H, Takahashi K, Ueno Y, Sakata K, Yokoyama A, Yarimizu K, Myouga F, Shinozaki K, Ozawa SI, Takahashi Y, et al. Characterization of photosystem II assembly complexes containing ONE-HELIX PROTEIN1 in Arabidopsis thaliana. J Plant Res. 2022:**135**(2):361–376. https://doi.org/10.1007/s10265-022-01376-x

Malnoë A, Wang F, Girard-Bascou J, Wollman F-A, de Vitry C. Thylakoid FtsH protease contributes to photosystem II and cytochrome b_6f remodeling in *Chlamydomonas reinhardtii* under stress conditions. Plant Cell. 2014:**26**(1):373–390. https://doi.org/10.1105/tpc.113.120113

Manna P, Vermaas W. Mutational studies on conserved histidine residues in the chlorophyll-binding protein CP43 of photosystem II. Eur J Biochem. 1997:**247**(2):666–672. https://doi.org/10.1111/j.1432-1033.1997.00666.x

Masuda T, Inomura K, Gao M, Armin G, Kotabová E, Bernát G, Lawrenz-Kendrick E, Lukeš M, Bečková M, Steinbach G, et al. The balance between photosynthesis and respiration explains the niche differentiation between *Crocosphaera* and *Cyanothece*. Comput Struct Biotechnol J. 2023:**21**:58–65. https://doi.org/10.1016/j.csbj.2022.11.029

Meurer J, Plücken H, Kowallik KV, Westhoff P. A nuclear-encoded protein of prokaryotic origin is essential for the stability of photosystem II in Arabidopsis thaliana. EMBO J. 1998:**17**(18):5286–5297. https://doi.org/10.1093/emboj/17.18.5286

Michoux F, Boehm M, Bialek W, Takasaka K, Maghlaoui K, Barber J, Murray JW, Nixon PJ. Crystal structure of CyanoQ from the thermophilic cyanobacterium Thermosynechococcus elongatus and detection in isolated photosystem II complexes. Photosynth Res. 2014:**122**(1):57–67. https://doi.org/10.1007/s11120-014-0010-z

Michoux F, Takasaka K, Boehm M, Komenda J, Nixon PJ, Murray JW. Crystal structure of the Psb27 assembly factor at 1.6 Å: implications for binding to photosystem II. Photosynth Res. 2012:**110**(3):169–175. https://doi.org/10.1007/s11120-011-9712-7

Michoux F, Takasaka K, Boehm M, Nixon PJ, Murray JW. Structure of CyanoP at 2.8 A: implications for the evolution and function of the PsbP subunit of photosystem II. Biochemistry. 2010:**49**(35):7411–7413. https://doi.org/10.1021/bi1011145

Morais F, Barber J, Nixon PJ. The chloroplast-encoded alpha subunit of cytochrome b-559 is required for assembly of the photosystem two complex in both the light and the dark in *Chlamydomonas reinhardtii*. J Biol Chem. 1998:**273**(45):29315–29320. https://doi.org/10.1074/jbc.273.45.29315

Morais F, Kühn K, Stewart DH, Barber J, Brudvig GW, Nixon PJ. Photosynthetic water oxidation in cytochrome *b*-559 mutants containing a disrupted heme-binding pocket. J Biol Chem. 2001:**276**(34):31986–31993. https://doi.org/10.1074/jbc.M103935200

Müller B, Eichacker LA. Assembly of the D1 precursor in monomeric photosystem II reaction center precomplexes precedes chlorophyll

a-triggered accumulation of reaction center II in barley etioplasts. Plant Cell. 1999:**11**(12):2365–2377. PMID: 10590164

Mullet JE, Klein PG, Klein RR. Chlorophyll regulates accumulation of the plastid-encoded chlorophyll apoproteins CP43 and D1 by increasing apoprotein stability. Proc Natl Acad Sci U S A. 1990:**87**(11): 4038–4042. https://doi.org/10.1073/pnas.87.11.4038

Mulo P, Tyystjärvi T, Tyystjärvi E, Govindjee, Mäenpää P, Aro EM. Mutagenesis of the D-E loop of photosystem II reaction centre protein D1. Function and assembly of photosystem II. Plant Mol Biol. 1997:**33**(6):1059–1071. https://doi.org/10.1023/a:1005765305956

Myouga F, Takahashi K, Tanaka R, Nagata N, Kiss AZ, Funk C, Nomura Y, Nakagami H, Jansson S, Shinozaki K. Stable accumulation of photosystem II requires ONE-HELIX PROTEIN1 (OHP1) of the light harvesting-like family. Plant Physiol. 2018:**176**(3):2277–2291. https://doi.org/10.1104/pp.17.01782

Nakajima Y, Umena Y, Nagao R, Endo K, Kobayashi K, Akita F, Suga M, Wada H, Noguchi T, Shen JR. Thylakoid membrane lipid sulfoquinovosyl-diacylglycerol (SQDG) is required for full functioning of photosystem II in *Thermosynechococcus elongatus*. J Biol Chem. 2018:**293**(38):14786–14797. https://doi.org/10.1074/jbc.RA118.004304

Nickelsen J, Rengstl B. Photosystem II assembly: from cyanobacteria to plants. Annu Rev Plant Biol. 2013:**64**(1):609–635. https://doi.org/10.1146/annurev-arplant-050312-120124

Nishiyama Y, Yamamoto H, Allakhverdiev SI, Inaba M, Yokota A, Murata N. Oxidative stress inhibits the repair of photodamage to the photosynthetic machinery. EMBO J. 2001:**20**(20):5587–5594. https://doi.org/10.1093/emboj/20.20.5587

Nixon PJ, Barker M, Boehm M, de Vries R, Komenda J. FtsH-mediated repair of the photosystem II complex in response to light stress. J Exp Bot. 2005:**56**(411):357–363. https://doi.org/10.1093/jxb/eri021

Nixon PJ, Diner BA. Aspartate 170 of the photosystem II reaction center polypeptide D1 is involved in the assembly of the oxygen-evolving manganese cluster. Biochemistry. 1992:**31**(3):942–948. https://doi.org/10.1021/bi00118a041

Nixon PJ, Michoux F, Yu J, Boehm M, Komenda J. Recent advances in understanding the assembly and repair of photosystem II. Ann Bot. 2010:**106**(1):1–16. https://doi.org/10.1093/aob/mcq059

Nixon PJ, Trost JT, Diner BA. Role of the carboxy terminus of polypeptide D1 in the assembly of a functional water-oxidizing manganese cluster in photosystem II of the cyanobacterium *Synechocystis* sp. PCC 6803: assembly requires a free carboxyl group at C-terminal position 344. Biochemistry. 1992:**31**(44):10859–10871. https://doi.org/10.1021/bi00159a029

Nowaczyk MM, Hebeler R, Schlodder E, Meyer HE, Warscheid B, Rögner M. Psb27, a cyanobacterial lipoprotein, is involved in the repair cycle of photosystem II. Plant Cell. 2006:**18**(11):3121–3131. https://doi.org/10.1105/tpc.106.042671

Ota K, Sakaguchi M, Hamasaki N, Mihara K. Assessment of topogenic functions of anticipated transmembrane segments of human band 3. J Biol Chem. 1998:**273**(43):28286–28291. https://doi.org/10.1074/jbc.273.43.28286

Pakrasi HB, Williams JG, Arntzen CJ. Targeted mutagenesis of the psbE and psbF genes blocks photosynthetic electron transport: evidence for a functional role of cytochrome b559 in photosystem II. EMBO J. 1988:**7**(2):325–332. https://doi.org/10.1002/j.1460-2075.1988.tb02816.x

Pasch JC, Nickelsen J, Schünemann D. The yeast split-ubiquitin system to study chloroplast membrane protein interactions. Appl Microbiol Biotechnol. 2005:**69**(4):440–447. https://doi.org/10.1007/s00253-005-0029-3

Pascual-Aznar G, Konert G, Bečková M, Kotabová E, Gardian Z, Knoppová J, Bučinská L, Kaňa R, Sobotka R, Komenda J. Psb35 protein stabilizes the CP47 assembly module and associated high-light inducible proteins during the biogenesis of photosystem II in the cyanobacterium *Synechocystis* sp. PCC 6803. Plant Cell Physiol. 2021:**62**(1):178–190. https://doi.org/10.1093/pcp/pcaa148

Pazderník M, Mareš J, Pilný J, Sobotka R. The antenna-like domain of the cyanobacterial ferrochelatase can bind chlorophyll and carotenoids in an energy-dissipative configuration. J Biol Chem. 2019:**294**(29): 11131–11143. https://doi.org/10.1074/jbc.RA119.008434

Plücken H, Müller B, Grohmann D, Westhoff P, Eichacker LA. The HCF136 protein is essential for assembly of the photosystem II reaction center in Arabidopsis thaliana. FEBS Lett. 2002:**532**(1–2):85–90. https://doi.org/10.1016/s0014-5793(02)03634-7

Pospíšil P. Production of reactive oxygen species by photosystem II. Biochim Biophys Acta. 2009:**1787**(10):1151–1160. https://doi.org/10.1016/j.bbabio.2009.05.005

Pospíšil P. Enzymatic function of cytochrome b559 in photosystem II. J Photochem Photobiol B. 2011:**104**(1–2):341–347. https://doi.org/10.1016/j.jphotobiol.2011.02.013

Proctor MS, Chidgey JW, Shukla MK, Jackson PJ, Sobotka R, Hunter CN, Hitchcock A. Plant and algal chlorophyll synthases function in *Synechocystis* and interact with the YidC/Alb3 membrane insertase. FEBS Lett. 2018:**592**(18):3062–3073. https://doi.org/10.1002%2F1873-3468.13222

Promnares K, Komenda J, Bumba L, Nebesarova J, Vacha F, Tichy M. Cyanobacterial small chlorophyll-binding protein ScpD (HliB) is located on the periphery of photosystem II in the vicinity of PsbH and CP47 subunits. J Biol Chem. 2006:**281**(43):32705–32713. https://doi.org/10.1074/jbc.M606360200

Puthiyaveetil S, Tsabari O, Lowry T, Lenhert S, Lewis RR, Reich Z, Kirchhoff H. Compartmentalization of the protein repair machinery in photosynthetic membranes. Proc Natl Acad Sci U S A. 2014:**111**(44):15839–15844. https://doi.org/10.1073/pnas.1413739111

Qi M, Zhao Z, Nixon PJ. The photosynthetic electron transport chain of oxygenic photosynthesis. Bioelectricity. 2023:**5**(1):31–38. https://doi.org/10.1089/bioe.2023.0003

Rahimzadeh-Karvansara P, Pascual-Aznar G, Bečková M, Komenda J. Psb34 protein modulates binding of high-light-inducible proteins to CP47-containing photosystem II assembly intermediates in the cyanobacterium *Synechocystis* sp. PCC 6803. Photosynth Res. 2022:**152**(3):333–346. https://doi.org/10.1007/s11120-022-00908-9

Rögner M, Chisholm DA, Diner BA. Site-directed mutagenesis of the psbC gene of photosystem II: isolation and functional characterization of CP43-less photosystem II core complexes. Biochemistry. 1991:**30**(22):5387–5395. https://doi.org/10.1021/bi00236a009

Roose JL, Pakrasi HB. The Psb27 protein facilitates manganese cluster assembly in photosystem II. J Biol Chem. 2008:**283**(7):4044–4050. https://doi.org/10.1074/jbc.M708960200

Sakamoto W, Zaltsman A, Adam Z, Takahashi Y. Coordinated regulation and complex formation of yellow variegated1 and yellow variegated2, chloroplastic FtsH metalloproteases involved in the repair cycle of photosystem II in Arabidopsis thylakoid membranes. Plant Cell. 2003:**15**(12):2843–2855. https://doi.org/10.1105/tpc.017319

Sakata S, Mizusawa N, Kubota-Kawai H, Sakurai I, Wada H. Psb28 is involved in recovery of photosystem II at high temperature in *Synechocystis* sp. PCC 6803. Biochim Biophys Acta. 2013:**1827**(1): 50–59. https://doi.org/10.1016/j.bbabio.2012.10.004

Shao S, Cardona T, Nixon PJ. Early emergence of the FtsH proteases involved in photosystem II repair. Photosynthetica. 2018:**56**(SPECIAL ISSUE):163–177. https://doi.org/10.1007/s11099-018-0769-9

Shen JR. The structure of photosystem II and the mechanism of water oxidation in photosynthesis. Annu Rev Plant Biol. 2015:**66**(1):23–48. https://doi.org/10.1146/annurev-arplant-050312-120129

Shen G, Eaton-Rye JJ, Vermaas WF. Mutation of histidine residues in CP47 leads to destabilization of the photosystem II complex and to impairment of light energy transfer. Biochemistry. 1993:**32**(19): 5109–5115. https://doi.org/10.1021/bi00070a019

Shen G, Zhao J, Reimer SK, Antonkine ML, Cai Q, Weiland SM, Golbeck JH, Bryant DA. Assembly of photosystem I. I. Inactivation of the rubA gene encoding a membrane-associated rubredoxin in the cyanobacterium Synechococcus sp. PCC 7002 causes a loss of

photosystem I activity. J Biol Chem. 2002:**277**(23):20343–20354. https://doi.org/10.1074/jbc.M201103200

Shukla MK, Llansola-Portoles MJ, Tichý M, Pascal AA, Robert B, Sobotka R. Binding of pigments to the cyanobacterial high-light-inducible protein HliC. Photosynth Res. 2018:**137**(1):29–39. https://doi.org/10.1007/s11120-017-0475-7

Shukla VK, Stanbekova GE, Shestakov SV, Pakrasi HB. The D1 protein of the photosystem II reaction-centre complex accumulates in the absence of D2: analysis of a mutant of the cyanobacterium *Synechocystis* sp. PCC 6803 lacking cytochrome b559. Mol Microbiol. 1992:**6**(7):947–956. https://doi.org/10.1111/j.1365-2958.1992.tb01544.x

Silva P, Thompson E, Bailey S, Kruse O, Mullineaux CW, Robinson C, Mann NH, Nixon PJ. Ftsh is involved in the early stages of repair of photosystem II in *Synechocystis* sp PCC 6803. Plant Cell. 2003:**15**(9):2152–2164. https://doi.org/10.1105/tpc.012609

Sinha RK, Komenda J, Knoppová J, Sedlářová M, Pospíšil P. Small CAB-like proteins prevent formation of singlet oxygen in the damaged photosystem II complex of the cyanobacterium *Synechocystis* sp. PCC 6803. Plant Cell Environ. 2012:**35**(4):806–818. https://doi.org/10.1111/j.1365-3040.2011.02454.x

Skotnicová P, Srivastava A, Aggarwal D, Talbot J, Karlínová I, Moos M, Mareš J, Bučinská L, Koník P, Šimek P, et al. A thylakoid biogenesis BtpA protein is required for the initial step of tetrapyrrole biosynthesis in cyanobacteria. New Phytol. 2024:**41**(3):1236–1249. https://doi.org/10.1111/nph.19397

Sobotka R. Making proteins green; biosynthesis of chlorophyll-binding proteins in cyanobacteria. Photosynth Res. 2014:**119**(1–2):223–232. https://doi.org/10.1007/s11120-013-9797-2

Sozer O, Komenda J, Ughy B, Domonkos I, Laczkó-Dobos H, Malec P, Gombos Z, Kis M. Involvement of carotenoids in the synthesis and assembly of protein subunits of photosynthetic reaction centers of *Synechocystis* sp. PCC 6803. Plant Cell Physiol. 2010:**51**(5):823–835. https://doi.org/10.1093/pcp/pcq031

Staleva H, Komenda J, Shukla MK, Šlouf V, Kaňa R, Polívka T, Sobotka R. Mechanism of photoprotection in the cyanobacterial ancestor of plant antenna proteins. Nat Chem Biol. 2015:**11**(4):287–291. https://doi.org/10.1038/nchembio.1755

Stengel A, Gügel IL, Hilger D, Rengstl B, Jung H, Nickelsen J. Initial steps of photosystem II de novo assembly and preloading with manganese take place in biogenesis centers in *Synechocystis*. Plant Cell. 2012:**24**(2):660–675. https://doi.org/10.1105/tpc.111.093914

Strašková A, Knoppová J, Komenda J. Isolation of the cyanobacterial YFP-tagged photosystem I using *GFP-Trap*. Photosynthetica. 2018:**56**(SPECIAL ISSUE):300–305. https://doi.org/10.1007/s11099-018-0771-2

Swiatek M, Kuras R, Sokolenko A, Higgs D, Olive J, Cinque G, Müller B, Eichacker LA, Stern DB, Bassi R, et al. The chloroplast gene ycf9 encodes a photosystem II (PSII) core subunit, PsbZ, that participates in PSII supramolecular architecture. Plant Cell. 2001:**13**(6):1347–1367. https://doi.org/10.1105/tpc.13.6.1347

Swiatek M, Regel RE, Meurer J, Wanner G, Pakrasi HB, Ohad I, Herrmann RG. Effects of selective inactivation of individual genes for low-molecular-mass subunits on the assembly of photosystem II, as revealed by chloroplast transformation: the psbEFLJ operon in Nicotiana tabacum. Mol Genet Genomics. 2003:**268**(6):699–710. https://doi.org/10.1007/s00438-002-0791-1

Thornton LE, Ohkawa H, Roose JL, Kashino Y, Keren N, Pakrasi HB. Homologs of plant PsbP and PsbQ proteins are necessary for regulation of photosystem ii activity in the cyanobacterium *Synechocystis* 6803. Plant Cell. 2004:**16**(8):2164–2175. https://doi.org/10.1105/tpc.104.023515

Tokano T, Kato Y, Sugiyama S, Uchihashi T, Noguchi T. Structural dynamics of a protein domain relevant to the water-oxidizing complex in photosystem ii as visualized by high-speed atomic force microscopy. J Phys Chem B. 2020:**124**(28):5847–5857. https://doi.org/10.1021/acs.jpcb.0c03892

Torabi S, Umate P, Manavski N, Plöchinger M, Kleinknecht L, Bogireddi H, Herrmann RG, Wanner G, Schröder WP, Meurer J. Psbn is required for assembly of the photosystem II reaction center in Nicotiana tabacum. Plant Cell. 2014:**26**(3):1183–1199. https://doi.org/10.1105/tpc.113.120444

Umena Y, Kawakami K, Shen JR, Kamiya N. Crystal structure of oxygen-evolving photosystem II at a resolution of 1.9 Å. Nature. 2011:**473**(7345):55–60. https://doi.org/10.1038/nature09913

van Wijk KJ, Knott TG, Robinson C. Evidence for SecA- and delta pH-independent insertion of D1 into thylakoids. FEBS Lett. 1995:**368**(2):263–266. https://doi.org/10.1016/0014-5793(95)00668-y

Vass I. Role of charge recombination processes in photodamage and photoprotection of the photosystem II complex. Physiol Plant. 2011:**142**(1):6–16. https://doi.org/10.1111/j.1399-3054.2011.01454.x

Vass I. Molecular mechanisms of photodamage in the photosystem II complex. Biochim Biophys Acta. 2012:**1817**(1):209–217. https://doi.org/10.1016/j.bbabio.2011.04.014

Vermaas WF, Ikeuchi M, Inoue Y. Protein composition of the photosystem II core complex in genetically engineered mutants of the cyanobacterium *Synechocystis* sp. PCC 6803. Photosynth Res. 1988:**17**(1–2):97–113. https://doi.org/10.1007/BF00047683

Walters RG, Shephard F, Rogers JJ, Rolfe SA, Horton P. Identification of mutants of Arabidopsis defective in acclimation of photosynthesis to the light environment. Plant Physiol. 2003:**131**(2):472–481. https://doi.org/10.1104/pp.015479

Wang F, Dischinger K, Westrich LD, Meindl I, Egidi F, Trösch R, Sommer F, Johnson X, Schroda M, Nickelsen J, et al. One-helix protein 2 is not required for the synthesis of photosystem II subunit D1 in Chlamydomonas. Plant Physiol. 2023:**191**(3):1612–1633. https://doi.org/10.1093/plphys/kiad015

Wang F, Qi Y, Malnoë A, Choquet Y, Wollman FA, de Vitry C. The high light response and redox control of thylakoid FtsH protease in *Chlamydomonas reinhardtii*. Mol Plant. 2017a:**10**(1):99–114. https://doi.org/10.1016/j.molp.2016.09.012

Wang S, Yang CI, Shan SO. Seca mediates cotranslational targeting and translocation of an inner membrane protein. J Cell Biol. 2017b:**216**(11):3639–3653. https://doi.org/10.1083/jcb.201704036

Wastl J, Duin EC, Iuzzolino L, Dörner W, Link T, Hoffmann S, Sticht H, Dau H, Lingelbach K, Maier UG. Eukaryotically encoded and chloroplast-located rubredoxin is associated with photosystem II. J Biol Chem. 2000:**275**(39):30058–30063. https://doi.org/10.1074/jbc.M004629200

Wei L, Guo J, Ouyang M, Sun X, Ma J, Chi W, Lu C, Zhang L. LPA19, a Psb27 homolog in Arabidopsis thaliana, facilitates D1 protein precursor processing during PSII biogenesis. J Biol Chem. 2010:**285**(28):21391–21398. https://doi.org/10.1074/jbc.M110.105064

Wei X, Su X, Cao P, Liu X, Chang W, Li M, Zhang X, Liu Z. Structure of spinach photosystem II-LHCII supercomplex at 3.2 Å resolution. Nature. 2016:**534**(7605):69–74. https://doi.org/10.1038/nature18020

Weisz DA, Johnson VM, Niedzwiedzki DM, Shinn MK, Liu H, Klitzke CF, Gross ML, Blankenship RE, Lohman TM, Pakrasi HB. A novel chlorophyll protein complex in the repair cycle of photosystem II. Proc Natl Acad Sci U S A. 2019:**116**(43):21907–21913. https://doi.org/10.1073/pnas.1909644116

Weisz DA, Liu H, Zhang H, Thangapandian S, Tajkhorshid E, Gross ML, Pakrasi HB. Mass spectrometry-based cross-linking study shows that the Psb28 protein binds to cytochrome b_{559} in photosystem II. Proc Natl Acad Sci U S A. 2017:**114**(9):2224–2229. https://doi.org/10.1073/pnas.1620360114

Xiao Y, Huang G, You X, Zhu Q, Wang W, Kuang T, Han G, Sui SF, Shen JR. Structural insights into cyanobacterial photosystem II intermediates associated with Psb28 and Tsl0063. Nat Plants. 2021:**7**(8):1132–1142. https://doi.org/10.1038/s41477-021-00961-7

Xingxing C, Jiuyang L, Huan Z, Fudong L, Shuya Z, Min X, Ke R, Yuhua W, Aigen F. Crystal structure of Psb27 from Arabidopsis thaliana determined at a resolution of 1.85 Å. Photosynth Res. 2018:**136**(2):139–146. https://doi.org/10.1007/s11120-017-0450-3

Yao DC, Brune DC, Vermaas WF. Lifetimes of photosystem I and II proteins in the cyanobacterium *Synechocystis* sp. PCC 6803. FEBS Lett. 2012:**586**(2):169–173. https://doi.org/10.1016/j.febslet.2011.12.010

Yao D, Kieselbach T, Komenda J, Promnares K, Prieto MA, Tichy M, Vermaas W, Funk C. Localization of the small CAB-like proteins in photosystem II. J Biol Chem. 2007:**282**(1):267–276. https://doi.org/10.1074/jbc.M605463200

Yi L, Liu B, Nixon PJ, Yu J, Chen F. Recent advances in understanding the structural and functional evolution of FtsH proteases. Front Plant Sci. 2022:**13**:837528. https://doi.org/10.3389/fpls.2022.837528

You X, Zhang X, Cheng J, Xiao Y, Ma J, Sun S, Zhang X, Wang HW, Sui SF. In situ structure of the red algal phycobilisome-PSII-PSI-LHC megacomplex. Nature. 2023:**616**(7955):199–206. https://doi.org/10.1038/s41586-023-05831-0

Yu J, Knoppová J, Michoux F, Bialek W, Cota E, Shukla MK, Strašková A, Pascual Aznar G, Sobotka R, Komenda J, et al. Ycf48 involved in the biogenesis of the oxygen-evolving photosystem II complex is a seven-bladed beta-propeller protein. Proc Natl Acad Sci U S A. 2018:**115**(33):E7824–E7833. https://doi.org/10.1073/pnas.1800609115

Zabret J, Bohn S, Schuller SK, Arnolds O, Möller M, Meier-Credo J, Liauw P, Chan A, Tajkhorshid E, Langer JD, et al. Structural insights into photosystem II assembly. Nat Plants. 2021:**7**(4):524–538. https://doi.org/10.1038/s41477-021-00895-0

Zhang L, Paakkarinen V, van Wijk KJ, Aro EM. Co-translational assembly of the D1 protein into photosystem II. J Biol Chem. 1999:**274**(23):16062–16067. https://doi.org/10.1074/jbc.274.23.16062

Zhao Z. Structural investigations of photosystem II assembly [PhD thesis]. London, UK: Department of Life Sciences, Imperial College London; 2023.

Zhao Z, Vercellino I, Knoppová J, Sobotka R, Murray JW, Nixon PJ, Sazanov LA, Komenda J. The Ycf48 accessory factor occupies the site of the oxygen-evolving manganese cluster during photosystem II biogenesis. Nat Commun. 2023:**14**(1):4681. https://doi.org/10.1038/s41467-023-40388-6