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Review

On the interface of light-harvesting antenna complexes and reaction centers in oxygenic photosynthesis

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ABSTRACT

Photosynthetic pigment-protein complexes (PPCs) accomplish light-energy capture and photochemistry in natural photosynthesis. In this review, we examine three pigment protein complexes in oxygenic photosynthesis: light-harvesting antenna complexes and two reaction centers: Photosystem II (PSII), and Photosystem I (PSI). Recent technological developments promise unprecedented insights into how these multi–component protein complexes are assembled into higher order structures and thereby execute their function. Furthermore, the interfacial domain between light-harvesting antenna complexes and PSII, especially the potential roles of the structural loops from CP29 and the PB–loop of ApcE in higher plant and cyanobacteria, respectively, are discussed. It is emphasized that the structural nuances are required for the structural dynamics and consequently for functional regulation in response to an ever–changing and challenging environment.

1. Introduction

The thylakoid membrane in higher plants, algae, and cyanobacteria harbors all of the photosynthetic light reaction machineries: light-harvesting antenna complexes (LHCs, such as LHCI, LHCII in higher plants, phycobilisomes (PBSs) in red algae and cyanobacteria), Photosystem II (PSII), and Photosystem I (PSI). These Photosynthetic Pigment Protein Complexes (PPCs) usually contain a diverse collection of pigments that are arrayed in a proteinaceous matrix and are used for either light-energy harvesting or for photochemical reactions [1–7]. PPCs are not evenly distributed across all of the thylakoid membranes. In higher plants, the thylakoid membrane is structured into stacked and unstacked regions that are defined as granal and stromal thylakoids (see e.g., recent reviews [8–12] and therefor previous literature). Briefly, in higher plants, PSII is located mostly in the grana thylakoids [13], which is the basis for the biochemical preparation of PSII particles developed several decades ago using specific type of detergents [14], whereas PSI (and ATP synthase) are mostly located in the stromal thylakoids and the outer layers of grana. The cytochrome b_6f complex, a proton pump linking PSII and PSI by using mobile electron carriers [15], is distributed evenly throughout thylakoid membranes. In cyanobacteria, no consensus model for the thylakoid membrane organization has yet been reached [16]. However, emerging data indicate that lateral heterogeneity does exist in cyanobacteria [17–19]. This review focuses on the most recent progress on the supramolecular architecture of higher plant thylakoid PPCs and emerging information about PPCs organization in cyanobacteria, with a focus on the structural basis that dominates the inter–complex relationships and on the commonalities between these two groups of oxygenic phototrophs.

2. Atomic level interactions of PPCs in PSII

The Photosystem II core is a pigment-protein complex composed of around 20 subunits as well as other accessory, such as the PSII core antenna proteins CP43 and CP47, which contain 13 and 17 Chl *a* respectively [5]. The light-harvesting cross–section of the PSII core, however, is less than that of PSI, which contains 95 Chl *a* [4]. This results in unequal excitation of the two photosystems and thus can lead to unbalanced linear electron transfer. The light-harvesting cross–section of the PSII core is expanded by having either an integral membrane PPC associated with the PSII core in plants or an extrinsic membrane phycobilisome attached to the thylakoid membrane in cyanobacteria and red algae [20].

2.1. LHCII–PSII interactions in plants

In higher plants, LHCII is one of the PPCs comprised of intrinsic transmembrane helices holding chlorophyll *a* (Chl *a*) and chlorophyll *b*

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(Chl *b*) that are used for harvesting light energy and energy transmission to PSII and PSI as well. There are six Lhcb (b for LHCII) proteins [21], i.e., Lhcb1, Lhcb2, and Lhcb3, which form either homo– or hetero–trimers, and minor LHCs, Lhcb4 (CP29), Lhcb5 (CP26), Lhc6 (CP24). The sub-atomic structure of LHCII bound to PSII wasn't discovered until 2016 when *Liu* and co-workers solved the cryo–EM structure of the spinach PSII-LHCII supercomplex at 3.2 Å resolution [22]. They discovered that the PSII-LHCII supercomplex belongs to the C_2S_2–type (C: PSII core complex; S: strongly associated LHCII timer) particle previously defined by Boekema et al. [23]. The intrinsic membrane protein components in higher plant PSII share amazingly high similarities with those of cyanobacteria PSII core [5,22]. However PsbW, a 6.1 kDa low-molecular-weight protein and found exclusively in photosynthetic eukaryotes, was found to be mediating the association of the LHCII trimer with the PSII core complex. This work confirmed that PsbW plays an important role in stabilizing the supramolecular organization of LHCII-PSII in higher plants [24,25]. Two minor light-harvesting complexes CP26 and CP29 were univocally found associated with CP43 and CP47 proteins respectively, which corroborated previous reports [23,26–28], e.g., research by Nield and co-workers [29,30], when cryo–EM was under rapid development. Nield et al, essentially modeled LHCII, CP26, and CP29 onto the PSII structure using a 17 Å resolution 3D electron density map of the spinach supercomplex determined by cryo–EM and single particle analysis.

The architecture of the supramolecular organizations of LHCII–PSII stayed in focus, and the applications of cryo–EM further facilitated the elucidation of the detailed structure of LHCII–PSII at higher organization levels (Fig. 1). Two groups reported $C_2S_2M_2$ (M for moderately bound LHCIIs) from *Pisum sativum* at 2.7– and 3.2–Å [31] and *Arabidopsis thaliana* at an overall resolution of 5.3 Å respectively [32]. CP24, another minor LHC, was found closely associated with CP29 and seems to play a pivotal role in mediating excitation energy transfer from M–LHCII to the CP29 that is bound to CP47 in PSII (Fig. 1). All these remarkable achievements lead not only to higher resolution elucidation of an even larger LHC-PSII complex, but also on the combinatorial methodology of using physiologically relevant biochemical preparations and state-of-the-art cryo–EM techniques. $C_2S_2M_2$ supercomplexes from stacked and unstacked thylakoids were prepared using different pH and Ca^{2+} solutions [31]. All these studies, together with previous publications, contributed to the existing knowledge of the structural location of how higher PPCs are organized relative to each other. It is now clear that one strong S–LHCII feeds energy directly through a close interaction with CP43 and PsbW proteins of the PSII core, and that CP29 mediates energy transfer from one moderately bound M–LHCII to the PSII core assisted by CP24.

The LHCII–PSII structure also expands the concept that grana is the only region where PSII is located, rather, PSII is also located in stromal, unstacked thylakoids [33]. Over the years, PSII was considered largely enriched in granal thylakoids and the ease of biochemical preparation developed several decades ago also reinforced such concept. It seems that the PSII–LHCII supercomplexes are highly unstable and heterogeneous. Subjection of plant thylakoid membranes to a detergent treatment will often produce a population of PSII cores with different amounts of LHCII and minor light-harvesting proteins attached [34,35]. This could be due to protein crowding heterogeneity in the thylakoids and subsequently the altered sensitivity to detergent treatment. The structural roles of lipid molecules in the assembly of the plant PSII–LHCII supercomplex should also be taken into account in the context of chloroplast development and any real life biotic or abiotic stress conditions [36]. At the present time almost all of the LHC–PSII components are identified except PsbS and PsbR [22,31,32,37]. The structural location of PsbS is considered as an important piece of information to interpret Non-Photochemical Quenching (NPQ) in plant photoprotection. However, if all PPCs are packed in a crowded manner and energetically coupled, one could argue that the structural location of PsbS may not matter, since light–induced acidification of the

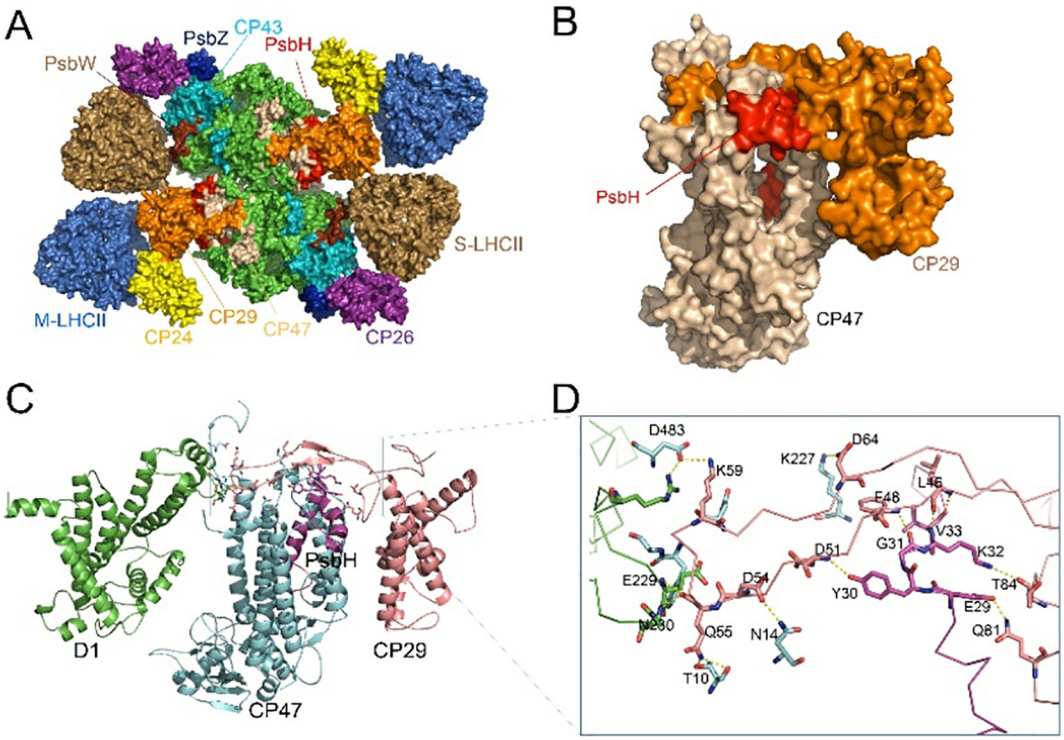

Fig. 1. Structure of PSII supercomplex and interaction of CP29 with its binding partners. A, Overall structure of the $C_2S_2M_2$–type PSII–LHCII supercomplex from *Pisum sativum*. B, surface representation of CP29 (orange) binding to CP47 (wheat) and PsbH (red), L–shape loop region winding on the stromal surface of PSII, passing PsbH, and ending at the interface of CP47 and D1 protein (not shown). C, molecular interaction of CP29 (brown) with CP47 (cyan), PsbH (purple), and D1 (green). D, atomic interactions CP29 loop with CP47, PsbH, and D1 proteins on the stromal side, highlighting H–bond and salt–bridging network on the stromal side of PSII. (PDBID: 5xnl).

thylakoid lumen will activate the PsbS–dependent (pH sensitive) mechanism and subsequently lead to all the coupled energy dissipation as heat. No structural location of PsbR has been found, although biochemical data support its structural proximity to PsbJ and PsbP [38,39].

2.2. PBS–PSII in red algae and cyanobacteria

PBSs capture sections of the solar spectrum that chlorophyll molecules fail to absorb and transmit to two reaction centers where photochemistry takes place [1,2,40]. A PBS is an ensemble of chromophore-associated water-soluble acidic polypeptides called phycobiliproteins (PBPs) and often colorless basic subunits called linker proteins. PBSs can be classified into two types, depending on the presence of allophycocyanin (APC): CpcG-PBS and CpcL-PBS [41–43]. The former can also be further classified into: hemidiscoidal [44], hemiellipsoidal [45], block–type [46] and bundle–type [47]. These conventional PBSs consist of a core from which several rod-like subcomplexes protrude [44,48,49]. Phycocyanin (PC) is the major PBP in the rod, and allophycocyanin is the major PBP in the core with fluorescence emission peaking close to that of chlorophylls in PSII and PSI [2]. Light is harvested by hundreds of chromophores and the excitation energy is then transferred to the energy–transducing RCs via only two sites, terminal energy emitter, i.e., allophycocyanin B (AP-B) and the core–membrane linker (L_{cm}) with the former preferentially serving for PSI [50] and the later for PSII [51,52].

Although spatial orientations of the chromophores in the PBS and chlorophylls in the reaction centers dictate an efficient energy transfer, the exact PBS–RCs interaction remains unclear [48,52,53]. ApcE, also called the core-membrane linker or L_{cm}, is a multi-domain protein with a molecular mass of 70–130 kDa [54] containing two to four (depending on the species) repetitive domains that are homologs of the Pfam00427 domain [55,56]. ApcE appears to be essential for the assembly of the APC discs to cylinders, and subsequently the bi–, or tri–, or penta– cylindrical PBS core [49]. The N-terminal portion of ApcE, or the PB domain shares high similarity to the ApcA [57]. During PBS assembly, the PB domain replaces one ApcA in the trimeric $(\alpha\beta)_3$ disc [48]. The PB domain, however, is interrupted by a so called “PB–loop” insertion that presumably protrudes to and is involved in the attachment of the PBS to the photosynthetic membrane [57,58], so ApcE is also called an anchor protein. The function of the “PB–loop”, however, remains a mystery.

In early research, the PB–domain (containing 54 amino acid (AA) residues) was genetically deleted from ApcE, and the shortened ApcE was found to be functionally equivalent to the wild type of ApcE [59]. That the assembly of PBSs was not disturbed in this truncated ApcE mutant enabled the authors to conclude that the PB–loop is dispensable for the PBS biogenesis and function. A similar truncation mutant was recently generated: Zlenko et al., deleted a peptide fragment corresponding to the PB–loop containing 59 AA [60]. The authors discovered that deletion of PB–loop reduced the energetic coupling of PBS–PSII and it seems that the PB–loop participates in PBS anchoring to the PSII complexes. Fluorescence induction analysis further indicated that deletion of the PB–loop also disturbed the “state transitions” and the orange carotenoid protein–dependent PBS fluorescence quenching as well. It should be noted that the two labs haven't used identical deletion mutants (54 AA vs 59 AA in the loop region) to address the function of the PB–loop.

Already very early in the history of PBS–PSII research, the focus was laid on investigating the detailed excitation energy transfer from PBS to the reaction center [61,62] as well as on the structure of this complex network. Extensive efforts have been made to determine the intact PBS–PSII/PSI structure, but limited progress has been made [63]. The first observations of the PBS–PSII complex was from Zhao's group, who isolated an intact PBS–PSII complex from *Anabeana* and probed by using single–particle electron microscopy in combination with biochemical and molecular analysis [51]. They provided direct evidence that ApcE and ApcF are critical for the formation of a protrusion at the bottom of the PBS, which plays an important role in mediating PBS interactions with PSII. This tight association between the PBS and PSII agrees with a previous report that demonstrated the formation of a PBS–PSII–PSI megacomplex in vivo via protein cross–linking and mass spectrometry analysis [52]. Another interesting observation came from an ApcF deletion mutant [51]. Cryo–EM data showed that peripheral rods attached to the bottom of the cores of PBS, indicative of the importance of a C–terminal extension of ApcF (compared with ApcB) for building up the PBS core directionality or polarity, in case of a promiscuous attaching of the peripheral rods. These data could also be used to interpret earlier research showing that ApcF is critical for energy transfer from the PBS to PSII [64,65], since deletion of ApcF consequently abolishes the structural integrity of the PBS interface that associates with PSII.

3. Structural basis of the LHC to the PSII core

3.1. Loop anchoring of CP29 to plant PSII core through CP47

All minor light harvesting proteins, CP29, CP26, and CP24, are involved in mediating LHCII–PSII assembly (Fig. 1), although future studies of the biogenesis process are needed to support this hypothesis. In the cryo–EM structure of both spinach and pea, the long N–terminal region of CP29 was resolved for the first time [22,31]. This 87 amino acid residue domain was not observed in the previous crystal structure owing to its structural flexibility or probably proteolysis [66] and is completely absent in CP26 and CP24. The cryo–EM structure shows this region forms two motifs (Motif I, P12–K41, and motif II, P42–F87) [22]. CP29 associated with PSII through not only transmembrane hydrophobic interactions with CP47 but also through this L–shaped loop region, which, like an arm, winds its way nearly parallel to the stromal surface of CP47 and PsbH, holding PSII through the PSII stromal side extrinsic region (Fig. 1B). The CP29 loop completely passes over the stromal side of CP47 and structurally associates with D–E loop of D1 protein [67] (Fig. 1C). It seems that a hydrogen bonding (H–bond) and salt bridging network plays a central role on the stromal side of this quartet, i.e., CP29, CP47, D1, and PsbH (Fig. 1D): two pair of salt bridges CP29:K^{59}–CP47:D^{483} and CP29:D^{64}– CP47:K^{227} and multiple pairs of H–bond. Interestingly, CP47:D^{483} interacts with CP29 through K^{59} and is also within the salt bridging contact with D1:R^{225} (2.7–3.1 Å). So, electrostatic interaction does contribute to the interaction between CP29 and PSII through three components of PSII: PsbH, CP47, and the D1 protein. Protein–protein interactions dictate the efficient excitation energy transfer from LHCII to the PSII core.

The originally assigned strongly bound LHCII (S-LHCII) trimer relies on a close association with PsbW and PsbI protein, two single transmembrane small peptides, in PSII core. The N–terminal loop of CP29 is distinct compared with the other two minor light harvesting antenna proteins, i.e., CP24 and CP26. Why evolution has produced such a structure and what could be the function of it require further investigation. Is it possible though that M–LHCII which is associated with CP24 and CP29 has different excitation energy transfer regulatory mechanism than S–LHCII which is associated with PSII core only through PsbW and PsbI and another minor LHC, CP26? Structural dynamics and reorganization of PPCs on the thylakoids are important regulatory processes that adapt photosynthetic organisms to changing environments. At the molecular level, it is evolutionarily advantageous to sense the real time status of light-driven electron transfer and subsequently to respond to altered physio-chemical condition in favor of photoprotection and fine-tuning of the photosynthetic machinery functionality. Recent data indicated that only S–LHCII is sensitive to pH conditions [68]. Although this research was performed in vitro, however, pH (or proton gradient across the thylakoid membrane) is known to be directly related to photosynthetic electron transfer [68]. This

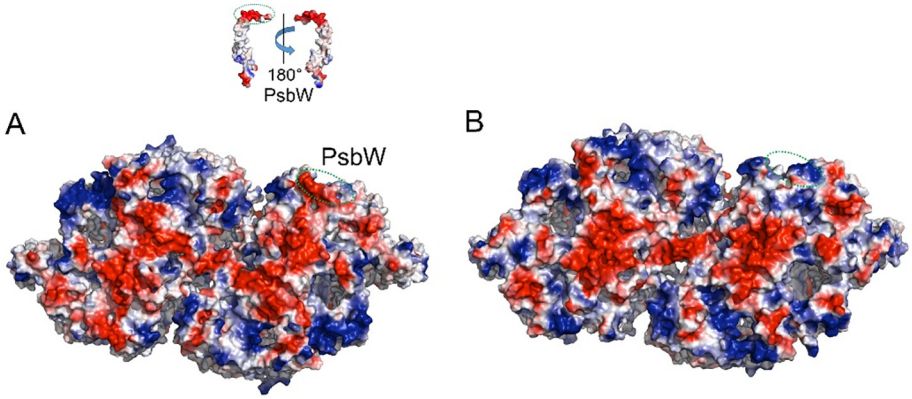

Fig. 2. Surface charge distribution of higher plant PSII core (A, PDBID: 5xnl) and cyanobacteria PSII (B, PDBID: 3wu2). Inset, surface charge of PsbW, highlighting negatively charged domain (red) and positively charge domain (blue).

result indeed challenges the original assignment of S–, M–, and L–trimmers of LHCII [23,34,35,69]. Biochemical preparations of PPCs rely on using different detergents. The insensitivity of one type of PPC higher order structure organizations to a specific type of detergent is not necessarily relevant to their physiological features that has to be considered in the context of physiological pH, ion strength, metabolite concentration, cellular viscosity, etc. In short, classification of LHCII into S–, M–, and L–type may not reflect their physical binding strength under physiological conditions. The effects of electrostatic interactions between LHCII and PSII core complex awaits further experiments.

3.2. PsbW–PsbI–CP43–D1–PsbO axis

S–LHCII interacts with PSII core through CP43 and PsbW, the latter being exclusive to eukaryotes. The PsbW protein has several unique features that foreshadow an important function in linking “S–LHCII” to PSII and being sensitive to pH. It has a negatively charged C–terminal domain on the stromal side as well as an N–terminal domain that is exposed on the luminal side (Fig. 2, inset). Replacement of two of the three negatively charged N–terminal amino acids with neutral amino acids and three positively charged histidines completely abolished the dimeric PSII supercomplex assembly [70]. No mutagenesis experiments have yet been performed on the C–terminal domain. However, it is so negatively charged compared to the N–terminal domain that it consequently changes the plant PSII core local surface charges and pronouncedly differentiates the plant PSII from the cyanobacterial PSII core structure (Fig. 2). A close look at the recently resolved PSII structure indicated a complex hydrogen bonding and salt–bridging network on both terminal domain (Fig. 3). The interactions between LHCII and CP43/D1 are mediated by PsbW and PsbI trough intrinsic membrane hydrophobic interactions as well as a hydrogen bonding network on both stromal and luminal sides (Fig. 3B, C). The N–terminal region of PsbW extends to the luminal surface and interacts with PsbO through at least one pair of salt–bridging (PsbO: R^{81}–PsbW:E^{9}) and multiple hydrogen–bonding networks (Fig. 3C). Higher plant PsbO proteins tend to have a longer N–terminal region compared to other oxygenic phototrophs, such as *Chlamydomonas* and cyanobacteria. The structure and function of the N–terminal domain have been intensely researched by multiple groups [71–73]. It was suggested that PsbO undergoes proton–induced protein conformational changes that accommodate released protons during PSII light-driven electron transfer by rearranging a complex hydrogen bond network [74]. Protons are pumped across the thylakoid membrane into the lumen making it acidic down to the range between 5.8 and 6.5 [75]. It remains unknown how these hydrogen bonds (Fig. 3C, F) on the thylakoid lumen are affected after lumen acidification resulting from light-driven electron transfer. PsbO is a natively unfolded protein and provides a structural scaffold and is a sensor of a hydrogen-bonding network in photosynthetic water oxidation [76]. PsbO undergoes catalytically relevant structural dynamics that are even coupled over a long distance to hydrogen–bonding changes at the Mn_4CaO_5 cluster. Salt bridging between PsbO and PsbW and the close interaction of PsbO N–terminal extension and PsbW (Fig. 3C) could indicate a feedback regulatory mechanism to fine tune excitation energy transfer from LHCII to the PSII core. Whether the preferred decoupling of S–LHCII from the PSII core is mediated through altered PsbO–PsbW interaction remains for future research.

At the S–LHCII–CP43 interface, there are three phosphatidylglycerol (PG) molecules on the stromal side, two of which are hydrogen bonded to the side chain of the E^{46}-E^{48} region of PsbW and in van der Waals contact with the backbone of W^{34}-S^{42}. One monogalactosyldiacylglycerol (MGDG), hydrogen–bonded to CP43 and PsbW on the luminal side is also in van der Waals contact with CP26. It's speculative whether any conformational changes resulting from electron transfer in the PSII core could alter the interactions of the core with its antenna through connecting molecules as described (Fig. 3). It has been long interesting as to why PSII has involved numerous low molecular subunits by introducing one small peptide, i.e., PsbW to the crew of PSII core, higher plant PSII gains the capability of adjusting its core interactions with S–LHCII upon pH changes. PsbS also contains protonatable amino acids that senses the signal from ΔpH and triggers the process of NPQ [77], realizing effective photoprotection. On the luminal side of PsbW, there are an array of conserved amino acids with apparent pKa around 3.7–4.0. Low pH triggered S–LHCII disassociation from PSII core could synergistically contribute to S–LHCII aggregation (with other LHCII?), which is less efficient in light harvesting. PsbS plays an essential role to trigger LHCII aggregation and thus NPQ [78,79]. It seems that other PSII components could also participate in the strategy to cope with light-energy harvesting regulation, but not be an essential part of the fastest component of NPQ, i.e., qE [80,81].

3.3. PB–loop of ApcE to cyanobacterial PSII

The structure of the phycobilisome from the red alga *Griffithsia pacifica* provides a firm structural basis for understanding the complex assembly and the mechanisms of energy transfer within PBS in both red algae and cyanobacteria [48]. The PBS contains a triangular core with the top cylinder (two APC trimers) sitting on two basal cylinders consisting of only three APC trimers. Even this block type of PBS is considered different than the hemispherical PBS, the core structure is likely to be evolutionally derived from the core of the latter by elimination of the exterior trimers of all three cylinders. The C2–symmetry of the PBS core could mirror the C2–symmetry of photosystem II (PSII) as the most functional form of PSII is a dimer. How then does the PBS interact with PSII? We can consider the red algal PBS core as a chassis, and can then

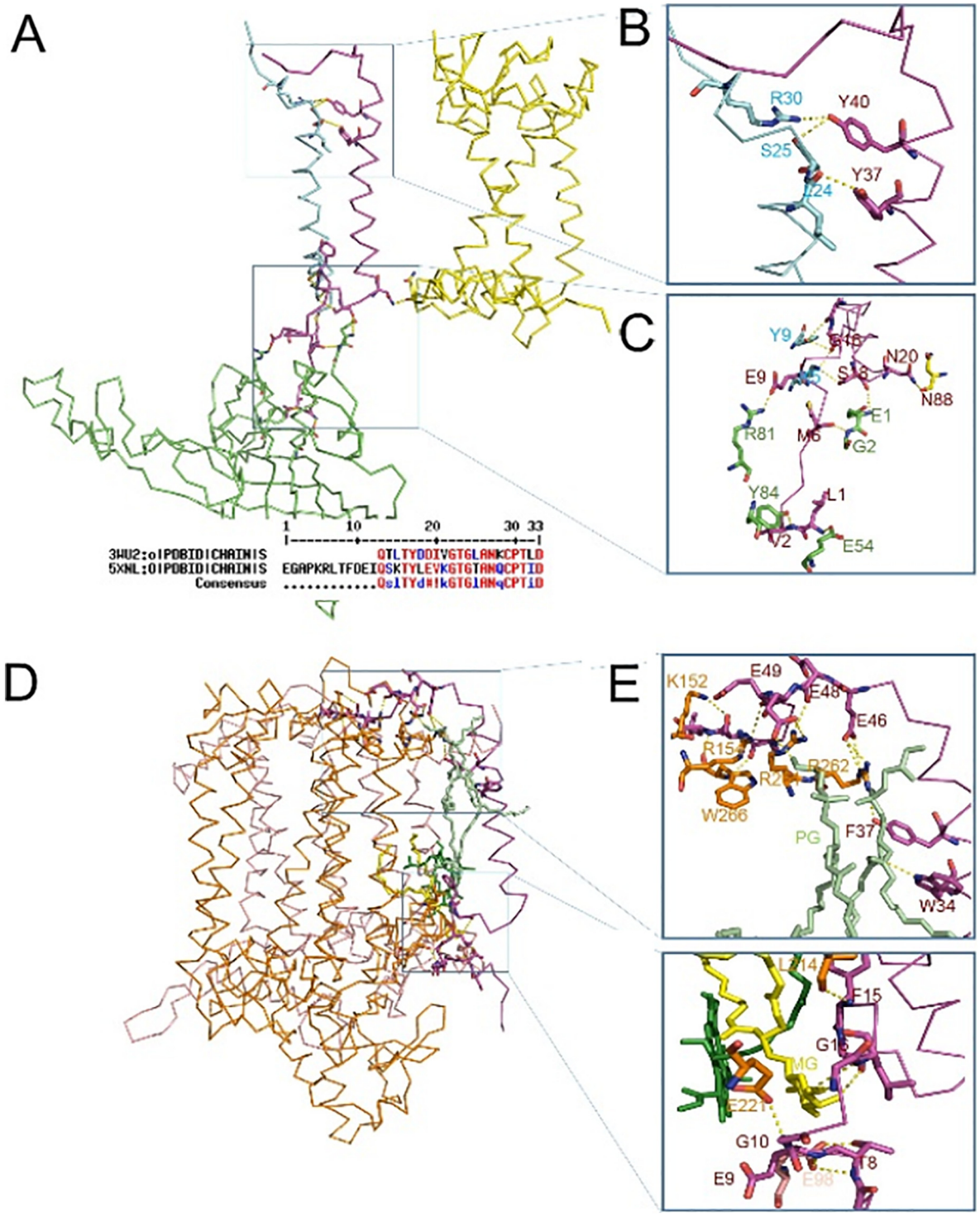

Fig. 3. Atomic interaction network of PsbW microenvironment. A, PsbW (purple, line), CP29 (yellow, line), PsbI (cyan, line), and PsbO (green, line). H–bonding between PsbW and PsbI. Inset, alignment of cyanobacteria and higher plant PsbO N–terminal sequences, highlighting eukaryotic exclusive N–terminal extension that participates in the association with PsbW (C). Overall structure (D) and atomic network of PsbW, CP43 (orange), D1 (green), phosphatidylglycerol (PG, lime), monogalactosyldiacylglycerol (MGDG, yellow), and a chlorophyll *a* molecule in D1 protein (Fig. E and F).

"build" a typical cyanobacterial PBS, e.g., *Synechocystis* sp. PCC 6803 PBS, by using structurally available APC data from the Protein Data Bank (PDB) in combination with structure prediction and modeling of those unavailable structures (Fig. 4). Detailed information about such model building will be published elsewhere.

The most active photosystem II reaction center (PSII) is considered as a dimer [5,82]. Shown in Fig. 4A is the most stretched top view from the stromal side, about 180 Å in length from one PsbZ in one monomer to another in the second monomer. The top view of PSII, however, shows a comparatively flat surface (the reducing side of PSII) compared to that of PSI [4,52]. In PSII, there are about 70 Chl *a* per PSII dimer. The major light-harvesting complex in red alga and cyanobacteria is the phycobilisome, which contains more than 400 pigments and is attached to the PSII reducing side, dramatically increasing the light-harvesting

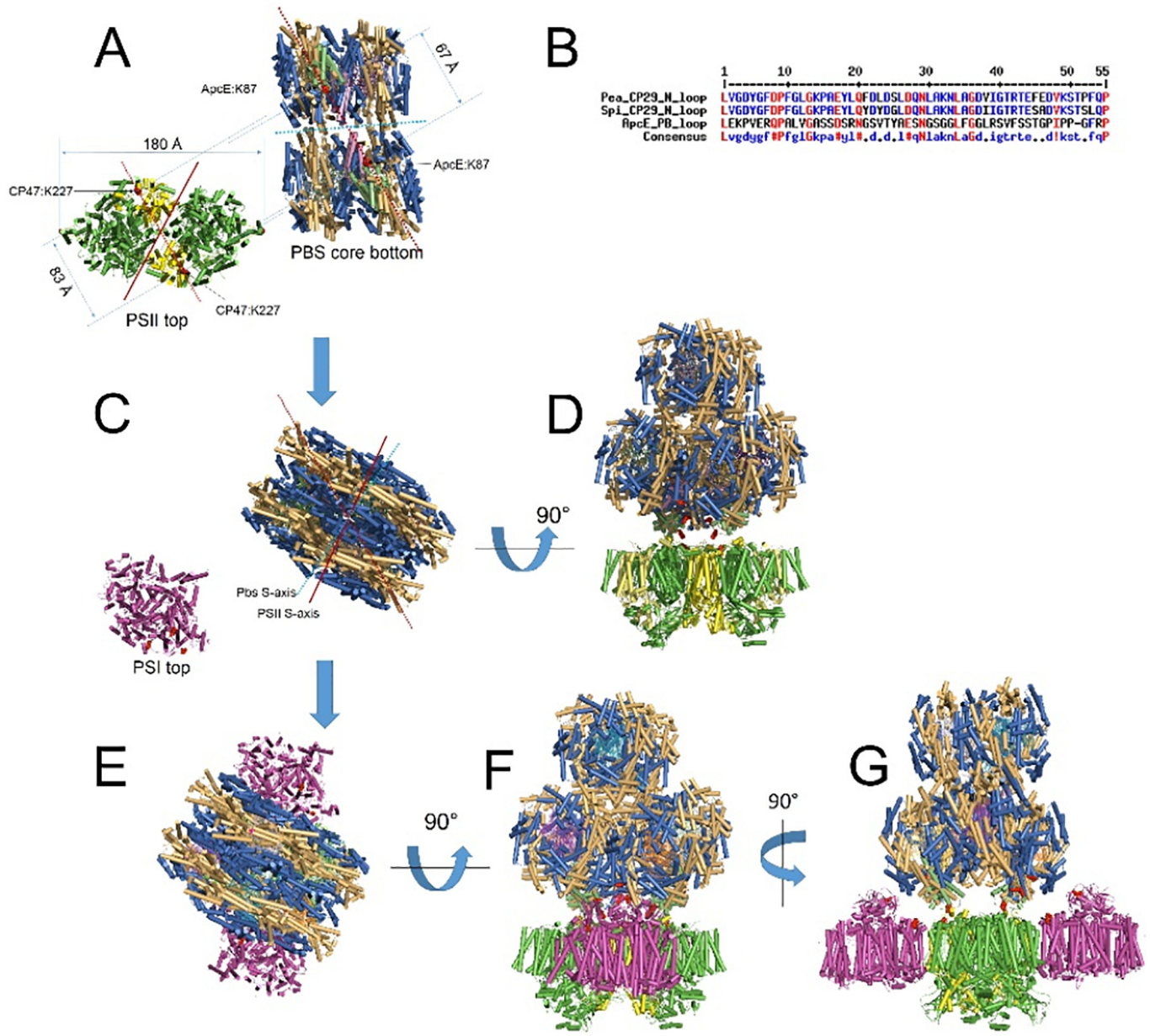

Fig. 4. Structural model of cyanobacteria megacomplex. A, cyanobacteria PSII (top view), symmetrical axis (red line). Two CP47:K^{227} in dimeric PSII (red sphere), alignment line (dashed red); PBS core bottom view, ApcA (wheat), ApcB (blue), ApcF (light purple), ApcE (green), ApcE:K^{87} (red sphere). The distance between two CP47:K^{227} and between two CP47:K^{227} are labeled. B, sequence alignment of loop region from CP29 and PB–loop of ApcE. C, Top view of PBS core covering a PSII dimer guided by overlapping axes. D, side view of PBS–core–PSII, PSII (fully stretched). E, PSI docking to PBS–core guided by cross–links of ApcB and PsaA [52], top view. F, side view of PBS–PSII–PSI, PSII fully stretched. G, side view of PBS–PSII–PSI, PSI on far sides. PDBID: PSII (3wu2), PSI (1jbo).

cross-section. Only the PBS core is shown here. ApcE and ApcD have long been considered as the terminal energy emitters in the PBS core [49], funneling energy directly to PSII and PSI as well [53]. A few years ago, a cross-linking experiment in combination with a mass spectrometry study indicated that there are two lysine residues of ApcE that are essentially bound to the reducing side of PSII in cyanobacteria [52]. When an in silico generated ApcE PB domain [52] was modeled in the PBS core [48], the distance of these two ApcE: K^{87} on PBS core was measured as 67 Å apart. These two Ks are indeed located on the PB-loop. On the PSII reducing side, the amino acid residues that were found to be cross-linked to ApcE, respectively, are K^{227} from the CP47 protein. As shown in this picture, they are measured as 83 Å, so 67 Å vs 83 Å, generally consistent with the crosslinking chemistry [83–85]. Guided by this information, here is a proposed model: a PBS core sits on the top of a PSII dimer with two ApcE PB-loops touching CP47 guided by overlapping of two lines that pass two pairs of lysines: ApcE:-K87–ApcE:K87 and CP47:K227–CP47:K227, respectively. The two PBS core basal cylinders don't form a perfectly flat surface as PSII does on its stromal side. Rather, only the PB-loop of ApcE tends to touch CP47, while the distal end rises up to an acute angle (tilted). Two basal cylinders tend to form an acute X shape, with one trimer containing ApcE and ApcF touching the surface of the flat PSII stromal side and the distal end of the basal cylinder rising up away from the flat PSII stromal side in contrast to the trimer that contains ApcD, which tends to get closer to the thylakoid membrane. Previous research also indicated that PSI is also found cross-linked to the PBS core, specifically through ApcB: K^{17} and PsaA: K^{30} [52]. Note that the N-terminal domain of PsaA has a long loop with increased flexibility. The first 10 amino acids residues actually were not resolved in the crystal structure [4]. In the model (Fig. 4F, G), ApcD is also in proximity within cross–linker reactivity arm span

range. The thylakoid membrane is very dynamic in terms of the distribution of reaction center proteins and other respiratory protein complexes [17,18,86–89]. It is interesting to see that the loop region that connects CP29 to CP47 (Fig. 1B, C, D) shares some identity with the PB–loop of ApcE (Fig. 4B). However, the surface charge of these two loops are significantly different: acidic in CP29 and very basic in PB–loop in ApcE, indicative of possible binding mechanisms. TM patches containing enriched either PSI, PSII or both may indicate the functional requirements of coping with dynamic eco-physiological conditions. This model (Fig. 4G), however, doesn't necessarily exclude other models. It seems that the structural basis exists to allow all three pigment protein complexes, i.e., PBS, PSI, PSII to come to proximity and form a huge entity, facilitating the energy transfer and regulation.

That PBS sits on the top of a PSII dimer makes the energy transfer from PBS to PSII very efficient, in contrast to the side-on orientation of the PBS on PSI. It is conceivable that this PBS–PSI–PSII megacomplex acts as a module to distribute energy flow between two photosystems. The N-terminal core antenna domain of PsaA and PsaB in PSI and the core antenna complexes PsbC and PsbB in PSII share a conserved structural motif of six transmembrane α-helices [90]. The cross-linking results support the idea that the PBS–RC energy transfer is via the core antenna domains (PSI) or core antenna subunit of PSII, specifically CP47, rather than directly to the electron transfer domains of the RC. How the lowest energy sink (or pigment) in the core antenna complex plays a role regulating the energy flow from the terminal energy emitter of PBS to where the charge separation site in RC remains for a future research effort [91–93].

Physical interactions between the PBS core and PSII have been suggested as essential for excitation energy migration from low-energy APC in the PBS to Chl *a* in PSII [94,95]. However, the enigmatic 'supercomplex' comprising PBS-PSII has never been consistently detected and isolated [53] owing to weak and easily disrupted interactions between these complexes. The weak coupling of PBS–PSII–PSI is best considered as an energy transfer complex that directs excitations to one or the other photosystem and not as a complex that includes the complete electron transport chain. Energy transfer requires an intimate physical association of the various complexes due to its strong distance dependence and short lifetime of the pigment excited states. The electron transport processes connecting the photosystems and the cytochrome b_6f complex involve mobile components that can interact via diffusion either within the membrane (quinones) or in the luminal space (plastocyanin) and, therefore, do not have a strict requirement for an intimate physical contact.

The concept of a PSI-PSII megacomplex is not new in higher plants. It is estimated that about 50% of the photosystem reaction centers form a PSI–PSII megacomplex in *Arabidopsis thaliana* that allows the deep trap in PSI to effectively dissipate excitation energy from PSII [96–101]. Whether the PBS–PSII–PSI complex in cyanobacteria plays a similar dissipating function remains for future research. There is another dilemma: PSII is constantly damaged and repaired upon light illumination at a rate far higher than found for PSI. Functionally closed and open PSII varies with light intensity and quality and other environmental conditions as well. For example, it was reported from the Vermaas lab that the half-life time of D1 protein (key PSII component) is less than 60 min [102], which means that dark adaption of cells for even 5 or 10 min will lead to significant transcriptomic and proteomic changes to photosynthetic components. Upon light activation, the ratio of open/closed PSII varies. How closed and open PSII structurally and energetically couple to light harvesting LHCII and phycobilisomes in higher plants and cyanobacteria respectively remains unclear. Energy redistribution has been suggested to be achieved by movement of light harvesting complexes between PSII and PSI [103–105] or "spillover" model [106–108] or a recent "uncoupled" model [101]. Therefore, although the importance of energy redistribution is understood in vivo, its mechanism remains controversial. The most difficult question at the top of different technological interrogations is: How heterogeneous are all the pigment protein complexes distributed across all the thylakoid membranes? Are these models exclusive? Are there any thylakoid regions or patches in which one model is dominant over the others? Caution must also be taken to apply physical instruments and mathematical modeling to probe energy transfer from LHC in general to PSII, PSI, or PSII–PSI pools unless the heterogeneity of PSII upon different light conditions is known in vivo.

It seems that in some thylakoid membrane regions, PSI is highly enriched [18] and PBS is less required, while in other regions, PSII is highly enriched and arranged in an array as previously reported with PBS [109]. This region may need more PBS for light harvesting. However, there are also some regions in the thylakoid membrane where both PSII PSI are present, which allows the merger of three intensely studied photosynthetic events of light harvesting (PBS) [16,17,110,111], water oxidation and plastocyanin:ferredoxin oxidoreduction in one module in oxygenic photosynthesis (Fig. 4G). Assembly, dissociation, or uncoupling of this region are significant for the direct balancing of the energy flow from LHC to the two photosystems. There are still many unresolved issues including the molecular mechanism that governs the assembly/disassembly of the higher order structure of PPCs. Future studies will focus on regulation of the higher order structure of PPCs in thylakoid membranes, so-called state transitions, and the mechanisms whereby cells precisely control the PPCs stoichiometry to adapt to changes in environmental conditions.

4. Conclusions and perspectives

It is important to realize that the higher order structures described here are by far more significant from a functional perspective. The principle of weak interactions holding all these complexes together is of great physiological and evolutionary importance. It is well understood and accepted that the pH difference across the thylakoid membrane can trigger a cascade of physiological responses not only by driving APT synthesis but also poising for feedback control of energy dissipation as heat through multiple mechanisms. All these processes seem to be happening at different time scales around the PSII reaction center core. It seems that both green lineage and the cyanobacterial systems have evolved strategies to optimize the physiology that matches the cellular requirements. It has been hypothesized that all these mechanisms have a significant impact upon plant productivity and potentially upon artificial photosynthesis and re–engineering of natural photosynthesis and the future improvement of crops.

Transparency document

The Transparency document associated with this article can be found, in online version.

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Declaration of competing interest

The Authors declare that there are no competing interests associated with the manuscript.

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