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The changing role of the small PSII subunits Psb27 and Psb28 during evolution

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Photosystem II (PSII) catalyzes the unique reaction of light-dependent water oxidation and subsequent reduction of plastoquinone at the beginning of the photosynthetic electron transport chain. The mature complex consists of at least 20 protein-subunits and over 80 cofactors. Further proteins are required for biogenesis and repair of PSII. Most of these proteins interact specifically with assembly intermediates during defined steps in PSII assembly. This review shall emphasize the function of the two factors Psb27 and Psb28 during the biogenesis and repair of PSII in cyanobacteria and give an impression of their potential biochemical, structural and physiological properties in plants considering the fact that they both have homologues in all oxygenic photosynthetic organisms.

We hypothesize that Psb28 may have retained its function in higher plants while the two Psb27 forms bind differently to PSII intermediates depending on PSII core phosphorylation state.

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Introduction

Photosystem II (PSII), the protein pigment complex embedded in the thylakoid membrane of plastids and cyanobacteria, catalyses the oxidation of water and the reduction of plastoquinone. The reaction centre (RC) where the electron transfer is initiated consists of the heterodimers D1 (PsbA) and D2 (PsbD) as well as the proteins PsbI and Cytb_{559} (Hankamer et al. 1997; Barber et al. 1987). Alongside with the two core antenna proteins CP43 and CP47 (Bassi and Dainese 1992; Boekema et al. 1995) a variety of different other factors like the manganese cluster of the oxygen evolving complex (OEC) (Ghanotakis and Yocum 1985) and the primary and secondary quinone electron acceptors (Q_A and Q_B) are attached to the RC complex (Broser et al. 2010; Ferreira et al. 2004).

While the structure and function of the fully assembled PSII is adequately known in cyanobacteria the assembly process remains to be further investigated and enlightened. Many acquainted and unknown co-factors are involved in this highly ordered process (Rokka et al. 2005). The first detectable intermediate of the PSII biogenesis is the previously mentioned RC complex consisting of the proteins D1, D2, PsbI and cytb_{559}. At first a subcomplex comprising D2 and cytb_{559} is formed (Komenda et al. 2004) which assembles with a D1 precursor (pD1) and PsbI. During the formation of the RC complex pD1 is processed into D1 by the protease CtpA (Nickelsen and Rengstl 2013). In the next step the inner antenna CP47 binds to the RC and thus the so called RC47 complex is built. Like D1 and D2 CP47 is previously integrated into the membrane separately and forms a subcomplex with other subunits of PSII like PsbH, PsbL PsbT and Psb28 (Boehm et al. 2012). Another subcomplex, containing CP43, binds to the formerly developed RC47 complex (Boehm et al. 2011) and the monomeric PSII emerges. Data from spinach revealed that during a light regulated process the Mn_4CaO_5 cluster alongside with the proteins PsbO, PsbP and PsbQ associates with the luminal side of the monomeric PSII (for review see: Dasgupta et al. 2008; Bricker et al. 2012). The functional PSII monomers then dimerize (Kouril et al. 2012), the minor antenna and the LHCII bind and form the PSII super-complex.

During periods of high light radiations reactive oxygen species (ROS) can occur which can damage the photosystem. The D1 proteins is the locus where most of this impairment takes place (Aro et al. 1993). The degradation of D1 is a scheduled breaking point to preserve the photosystem from further damage. To overcome the inflicted photoinhibition the damaged D1 protein has to be removed (Ohad et al. 1984) and exchanged with a new functional one (Mattoo et al. 1984). The damaged PSII (PSII*) is disassembled towards the RC47* complex and the non-functional D1 protein is exchanged with a new synthesized version (Komenda et al. 2012; Nixon et al. 2005). The synthesis of the functional PSII then follows the steps of the PSII biogenesis (Nixon et al. 2010). Also during PSII repair, auxiliary factors like Psb27 and Psb28 seem to play an important role.

In this review, we aim to compare the known function of Psb27 and Psb28 in cyanobacteria and discuss possible scenarios how these two small thylakoid associated proteins could work in higher plants.

Psb28

The first occurrence of this protein was in a PSII preparation from a PS I lacking mutant of Synechocystis sp. PCC 6803 (Ikeuchi et al. 1995). This cyanobacterium possesses two orthologues of this thylakoid membrane associated protein (Kashino et al. 2002; Srivastava et al. 2005). The first and more abundant orthologue (*Psb28-1*) is encoded by the gene *sll 1398* and the second one (*Psb28-2*) by the gene *slr 1739* (Srivastava et al. 2005). Bialek and colleagues (2013) suggested that Psb28-1 forms homomers (probably dimers) whereas Psb28-2 does not. The functional role of Psb28 dimerization is still under debate.

However, a 2D-Blue Native/SDS-PAGE revealed that the 13 kDa protein Psb28, which is loosely associated with the cytoplasmic side of the thylakoid membrane, is not linked to the functional PSII but to the assembly intermediate RC47 lacking the inner antenna CP43 (Dobakova et al. 2009). This suggests that Psb28-1 interacts with CP47. Like Psb28-1, the Psb28-2 protein also seems to interact with the CP43-less RC47 complex taking into account that this assembly intermediate could be isolated using a FLAG-tagged version of Psb28-2 (Boehm et al. 2012). The abundance of PS I in a Synechocystis sp. PCC 6803 strain lacking Psb28 was decreased as shown by a 77 K Chl fluorescence emission spectra. In addition, the *Δpsb28* line shows an accumulation of the Chl precursor protoporphyrin-IX which may display a hint for the correlation of Chl biosynthesis and PSII assembly (Dobakova et al. 2009). Interestingly another study where a different Synechocystis sp. PCC 6803 strain with a mutation in the *sll 1398* gene, resulting in an inactivation, showed no alteration in photosystem stoichiometry and Chl biosynthesis compared to the wild type (Sakata et al. 2013). Although former studies showed that Psb28 is associated with the CP43-less PSII assembly intermediate and not the functional monomer, an investigation of a *psbJ* deletion mutant of *Thermosynechococcus elongatus* showed an accumulation of a monomeric PSII complex, containing the proteins Psb28 and Psb27 (Nowaczyk et al. 2012). Interestingly, this monomer also contains the inner antenna CP43 which was proposed to be stabilized by Psb27 during assembly. Hence, this complex appears as novel and presumably short-lived intermediate in PSII biogenesis.

Genes formerly located in the plastid tend to be transferred to the nucleus of their host and the translated protein is post-translationally transferred to the plastid. The *psb28* gene of plants for example is located at the nucleus while in most algae it is located in the plastid. The diatom *Thalassiosira pseudonana* possesses two nearly identical copies of the *psb28* gene. One of which is encoded in the nucleus and the other on the plastome (Jiroutová et al. 2010). This could be an example for the translocation of genes from the plastid to the nucleus. Compared with cyanobacterial Psb28, little is known about the orthologues of this protein in photosynthetic eukaryotes. A comparison of Psb28 orthologues from different species, performing oxygenic photosynthesis, shows that the protein has highly conserved domains and features (Figure 1).

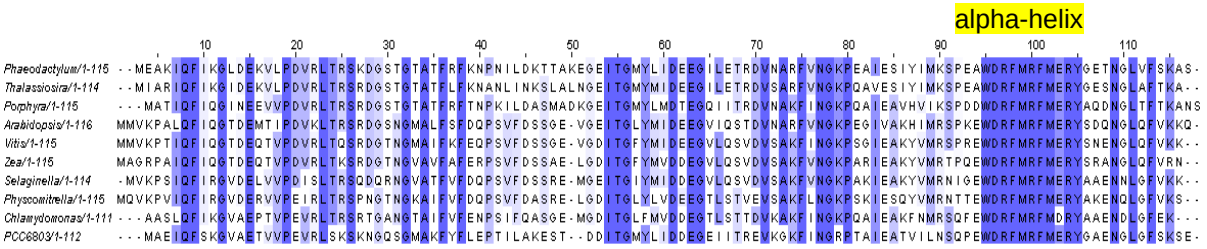

Figure 1: Alignment of Psb28 from different photosynthetic organisms. The figure shows the alignment of amino acid sequences from the organisms (top to bottom) *Phaeodactylum tricornutum*, *Thalassiosira pseudonana*, *Porphyra purpurea*, *Arabidopsis thaliana*, *Vitis vinifera*, *Zea mays*, *Selaginella moellendorffii*, *Physcomitrella patens*, *Chlamydomonas reinhardtii* und Synechocystis sp. PCC 6803. Matching amino acids are marked with a blue background.

Psb28 from Synechocystis sp. PCC 6803 is composed of 7 β-strands, one long α-helix and two short 3_{10} helices (Yang et al. 2011). Due to the high degree of conservation we modelled the structure of the Arabidopsis protein (At4g38660) against the Synechocystis structure (PDB: 2KVO; Yang et al. 2011) using the SWISS Model Server (Arnold et al. 2006). The secondary structure is highly conserved - this is especially true for the distribution of polar residues (Figure 2). Especially the exterior long C-terminal helix is nearly completely conserved might form an ionic interaction docking site for PSII reaction center proteins.

The distribution of polar and hydrophobic residues in the two molecules shows high similarities. Although little is known about Psb28 in other photosynthetic organisms, the fact that the amino acid sequence is highly conserved and that the protein shows a similar distribution pattern of polar and hydrophobic amino acids in the 3D structure leads to the conclusion that it may have a comparable function in plants as in cyanobacteria. The Arabidopsis protein carries a predicted chloroplast transit peptide with high confidence (TargetP score=0.93; Emanuelsson et al. 2000). Psb28 was found in thylakoids and the stroma by high-throughput mass spectrometric analyses (Peltier et al. 2004, 2006) but its

exact localization is to date unknown, and the function is not verified in any higher plant. Gene expression data point towards the notion that Psb28 is needed for photosynthetic activity since expression levels are highest in young leaves (http://bar.utoronto.ca/efp), and the *Psb28* transcript is co-regulated with other photosynthesis associated genes (http://bar.utoronto.ca/expressionAngler). Future experiments will clarify the role of Psb28 in PSII biogenesis, regulation or repair of higher plants.

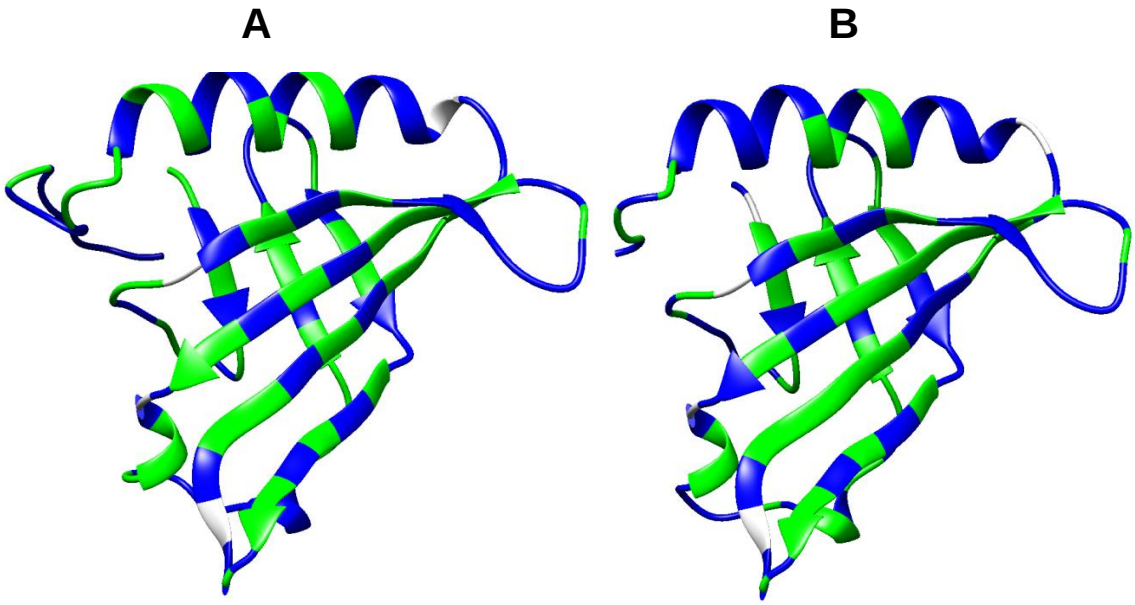

Figure 2: 3D structures of Psb28 from Synechocystis sp. and *Arabidopsis thaliana*. The 3D structure of the protein from *Arabidopsis thaliana* (B) was obtained with the SWISS-MODEL workspace (Arnold et al. 2006) using the known structure of the Synechocystis sp. PCC 6803 (PDB: 2KVO) (A). Polar residues are shown in blue and hydrophobic residues in green.

Psb27 in cyanobacteria

The ability of PSII to use light energy in order to split water into protons, electrons und oxygen is a unique "invention" throughout evolution. This somewhat delicate process is carried out by the oxygen evolving complex (OEC) carrying the manganese-calcium cluster which is located at the luminal site of PSII. Many peripheral subunits are required to stabilize this complex PsbO-family proteins are required for proper function in all oxygen evolving photosynthetic organisms. Small luminal subunits of cyanobacterial origin like PsbU and PsbV are replaced by PsbP, PsbR and PsbQ in green algae and higher plants. OEC attachment to the PSII core is thought to be one of the latest steps in PSII assembly since a premature activity of the OEC would cause photooxidative damage to the nascent photosystem. A lot of effort has been made to investigate how a premature binding of the OEC is prevented. The small lumenal lipoprotein Psb27 was suggested to occupy the PsbO binding site during assembly and especially repair of PSII monomers (Nowaczyk et al. 2006) in the cyanobacterium *Thermosynechococcus elongatus*. Psb27 is not essential for PSII biogenesis but facilitates the recruitment of OEC subunits during assembly and repair (Roose and Pakrasi 2008) in Synechocystis. Meanwhile several structures are solved (Michoux et al. 2012; Cormann et al. 2009; Mabbitt et al. 2009) revealing that Psb27 is an antiparallel 4-helix bundle protein with conserved aromatic residues stabilizing the hydrophobic core. Some conserved polar residues are found on the accessible surface of the helices have been considered to be important for protein-protein interaction.

Docking solutions and biochemical data suggest an interaction with the core antenna CP43 (Michoux et al. 2012; Liu et al. 2011; Komenda et al. 2012). The exact binding interface is still under debate. Acidic residues in the loop between helices 2 und 3 of Psb27 crosslinks basic residues in the luminal loop of CP43. These data is supported by protease protection assays which pinpoint the CP43-loop for Psb27 binding (Komenda et al. 2012). The mechanism of Psb27 binding and release could be due to a conformational change of the CP43 loop domain (Liu et al. 2013) induced by D1-processing. Hence, the interaction force of Psb27 to CP43 is loosened if D1 is inserted correctly into the growing PSII complex ejecting Psb27 and opening the way for assembly of OEC components like PsbO in order to form the fully active PSII complex.

Psb27 in eukaryonts

While the structure of the PSII core between cyanobacteria and eukaryonts is highly conserved the latter ones differ in

their light-harvesting complexes. Some e.g. red algae retained phycobilisomes similar to that of cyanobacteria (Watanabe and Ikeuchi 2013). In some eukaryonts like brown algae and diatoms the major antenna system are the so called fucoxanthin-chlorophyll *a*,*c* binding proteins (FCP). In green algae and plants the chlorophyll *a*,*b* binding proteins are CAB = LHC (light harvesting system; Bassi and Dainese 1992). The antenna and the photosystems form the functional PS-LHC superkomplexes (Boekema et al. 1995; Dekker and Boekema 2005). This fact has consequences for the function of PSII assembly factors like Psb27 which work prior to PSII super-complex assembly. Psb27 is ubiquitous in every organism carrying out oxygenic photosynthesis, hence there is at least one copy in eukaryonts with a conservation grade of roughly 30%.

Chlorobionta contain a second gene ca. 30% related to its cyanobacterial ancestor. Comparison of the two Psb27 proteins (Psb27-H1 and Psb27-H2) reveals that the 4-helical structure might have retained but the distribution of charged amino acid in helix 3 is considerably changed (Figure 3). This suggest different interaction partners in the greens which could be novel OEC subunits like PsbR and PsbQ or differences in posttranslational modification of PSII proteins. Also, the novel occurrence of LHC-type integral antenna could require the second Psb27 protein for PSII assembly and repair, or the ability to perform phosphorylation on PSII core proteins requires a second Psb27 protein (see below and Figure 4).

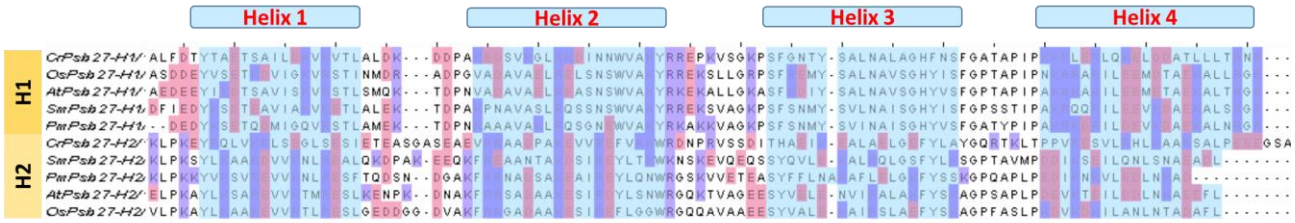

Figure 3: Alignment of Psb27-H1 and Psb27-H2 of green algal and plant species. The sequences are trimmed to the start of the native proteins in *Arabidopsis thaliana* (AtPsb27-H1). Predicted helices are indicated as blue boxes in the alignment. Acidic residues (D, E) are depicted in red; basic residues (R, K) are given in dark blue. The yellow boxes indicate whether the protein belongs to the Psb27-H1 or Psb27-H2 family.

Psb27-H1 in higher plants

Deducing from database information both *psb27* genes are expressed in green parts of Arabidopsis and respond to Norflurazon and Lincomycin implying that their expression depends on functional chloroplast (Genevestigator.com). *Psb27-H1* (At1g03600) is induced upon plastoquinone-oxidation when treated with PSI favoring light (Bräutigam et al. 2009; Geo Profiles GSE9235). *Psb27-H2* (At1g05385) was not redox-regulated. Maybe PSII-assembly and repair are differentially regulated which is reflected by the differences in gene expression between the two *psb27* genes.

The 12 kD protein Psb27-H1 was found in mass spectrometric analysis of Arabidopsis chloroplasts (Friso et al. 2004) and biochemically in the thylakoid lumen (Hou et al. 2015). Interestingly, Psb27 co-purified in tobacco monomeric PSII preparations (Haniewicz et al. 2013) suggesting a role in PSII biogenesis or repair. The knockout of *psb27-H1* (At1g03600) in Arabidopsis has a fully functional PSII under low light conditions (Dietzel et al. 2011) but is very sensitive to high light resulting in accumulation of photoinhibited PSII (Chen et al. 2006; Hou et al. 2015). They concluded that Psb27 is required for D1 repair but a direct binding of Psb27 to PSII during photoinhibition could not be shown. Another problem was that the mutant line used in the studies above carries an additional mutation in the *lhcb5* gene causing the lack of the minor antenna CP26 (Hou et al. 2015) making it hard to distinguish between the phenotype caused by *psb27* from that caused by *cp26* mutation. Clearly, the lowered quantum yield of PSII can be assigned to *psb27* deletion since the *cp26*-ko does not show a severe PSII-phenotype (Bianchi et al. 2008). But how about assembly of PSII-supercomplexes? CP26 connects the LHCII-S-Trimer to the CP43-site of PSII - a disruption would cause an instability of PSII supercomplexes (Hou et al. 2015; Dietzel et al. unpublished).

But is there a contribution of Psb27 to stability of PSII-supercomplexes? There is evidence supporting this assumption. Additional *psb27*-knockdown lines with intact CP26 show lowered accumulation of PSII-SCs and faster state transition (Dietzel et al. 2011; Dietzel unpublished). PSII-super-complexes have to be disassembled before PSII repair. Such a process was described in Arabidopsis after high light treatment (Rokka et al. 2005). Since *psb27* mutants are very sensitive to high light the PSII-SCs will disintegrate faster after photoinhibition – this might explain the relatively small amount of PSII-SCs in *psb27* mutants and the faster PSII-remodeling. In cyanobacteria Psb27 stabilizes the inactive PSII binding to CP43 in order to prevent premature OEC-assembly, hence assuming a conserved function in higher plants one would expect that monomeric PSII accumulates in *psb27* mutants and a disturbed PSII-SC organization in OEC-mutants which is indeed the case in mutants lacking PsbQ and PsbR (Allahverdiyeva et al. 2013).

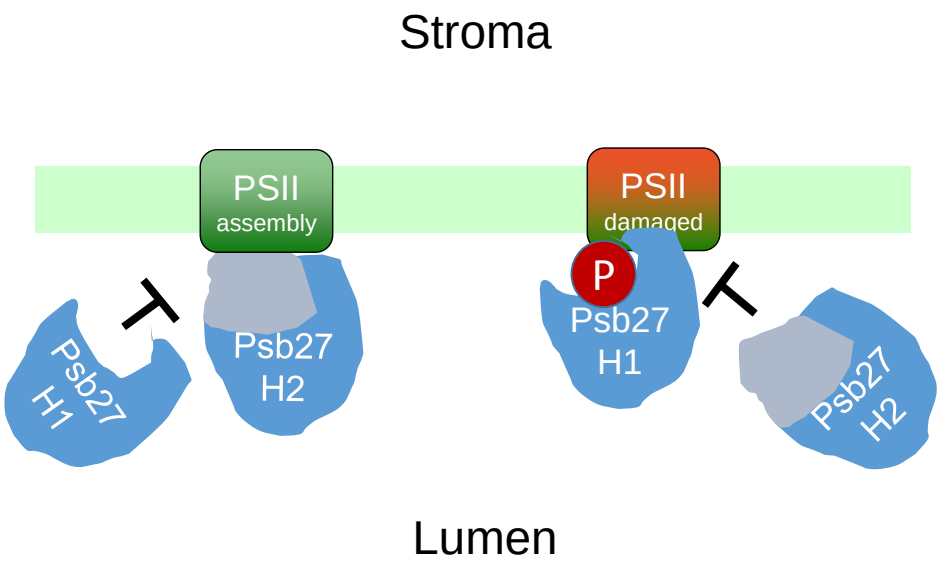

Figure 4: Working model on specificity of Psb27-H1 and Psb27-H2 in higher plants. During assembly the PSII core (green) is not phosphorylated. By this means Psb27-H2 (blue-grey) can bind and Psb27-H1 binding is blocked (black arrow). After photodamage the PSII core gets phosphorylated (red-green) which enables Psb27-H1 (blue) to bind. Phosphorylation prevents binding of Psb27-H2.

Psb27-H2 in higher plants

The second Psb27 homologue (Psb27-H2, At1g05385) exclusively occurs in the green line. It is slightly larger than Psb27-H1 (15 kD) and possesses a considerably lower isolectric point (~5.5) than its paralogue Psb27-H1. Loss of function caused a reduction in PSII polypeptides and lowered PSII quantum yield and therefore, was named ***L**ow **P**SII **A**ccumulation 19* (LPA19). It binds to monomeric PSII probably via interaction with the mature D1-C-terminus, interestingly, it does not bind the RC47-assembly complex lacking CP43. The authors concluded from pulse-chase experiments that Psb27-H2 (LPA19) facilitates the D1 maturation during PSII assembly (Wei et al. 2010). Homology modeling suggests that it is a four-helix bundle protein as its ancestor cyanoPsb27 with a conserved hydrophobic core architecture. The pattern of charged amino acids in the third and fourth helix appears strikingly different from that of cyano-Psb27 and Psb27-H1 (Figure 3) (Mabbitt et al. 2014) implying different interaction partners. helix 1 and 2 are very similar in charge distribution in contrast to helix 3 which is heavily charged in Psb27-H2 while in Psb27-H1 there is virtually no charged residue. helix 4 contains more basic residues in Psb27-H1. An interesting point is that the N-terminus of the Psb27-H1 is acidic and basic for Psb27-H2 and *vice versa* the loop region between helices 2 and 3 (Figure 3).

Functional and structural differences of Psb27-H1 and Psb27-H2 – implications for binding and regulation

But, why do exclusively chlorobionta need LPA19 for this process? Assuming that both proteins have one structural "similar half" comprising helices 1 and 2 which might be functionally conserved and one part which is differently charged and may function in another step in assembly (or regulation) of PSII. One may hypothesize that the "conserved" half of Psb27-H1 and Psb27-H2 bind the same site – this would imply that they interfere with each other and cause a disaster making a functional assembly of PSII impossible. How could an interference between Psb27-H1 and Psb27-H2 be prevented?

A possible answer is PSII core phosphorylation. Phosphorylation of PSII proteins (especially D1 and D2) facilitate the repair of photodamaged PSII (Tikkanen et al. 2008). It is very likely that Psb27-H1 is involved in this process. For PSII-assembly D1 and D2 phosphorylation is negligible since mutants not phosphorylating the PSII-core proteins (*stn8* and *stn7/stn8,* Bellafiore et al. 2005; Bonardi et al. 2005) do not show any disturbance of PSII assembly. A working model for higher plants could be that Psb27-H1 recognizes phosphorylated PSII-core proteins (probably D1 or CP43) which can be deduced from docking solutions in cyanobacteria (Michoux et al. 2012) (Figure 4). Core phosphorylation prevents Psb27-H2 from binding to PSII. It may bind exclusively the non-phosphorylated PSII-core during de novo assembly where Psb27-H1 now is not able to attach.

Conclusion

Although Psb27 and Psb28 are conserved in photosynthetic eukaryonts it is not recommendable to transfer the wealth of knowledge obtained in cyanobacteria to higher plants or other photosynthetic organisms. Psb28 is found in every organism carrying out oxygenic photosynthesis. In eukaryonts Psb28 is mostly encoded by a single copy gene.

The protein seems to be structurally and functionally conserved and thus, retained its function throughout evolution. Psb27 instead has duplicated indicating that at least one of the two Psb27 proteins now fulfills a different function in higher plants. It will be a challenging task to explore the functions of both Psb27 proteins and Psb28 in the future.

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