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Review

Molecular mechanism of photosystem I assembly in oxygenic organisms☆

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ABSTRACT

Photosystem I, an integral membrane and multi-subunit complex, catalyzes the oxidation of plastocyanin and the reduction of ferredoxin by absorbed light energy. Photosystem I participates in photosynthetic acclimation processes by being involved in cyclic electron transfer and state transitions for sustaining efficient photosynthesis. The photosystem I complex is highly conserved from cyanobacteria to higher plants and contains the light-harvesting complex and the reaction center complex. The assembly of the photosystem I complex is highly complicated and involves the concerted assembly of multiple subunits and hundreds of cofactors. A suite of regulatory factors for the assembly of photosystem I subunits and cofactors have been identified that constitute an integrative network regulating PSI accumulation. This review aims to discuss recent findings in the field relating to how the photosystem I complex is assembled in oxygenic organisms. This article is part of a Special Issue entitled: Chloroplast Biogenesis.

1. Introduction

Oxygenic photosynthesis is the principal reaction that converts sunlight energy into chemical energy for almost all life on Earth performed in cyanobacteria, green algae, and plants. The light reaction of photosynthesis is driven by photosystem I (PSI) and photosystem II (PSII) complexes, which use the trapped sunlight to excite the primary donors, leading to the linear electron transfer reactions. PSI catalyzes the sunlight-driven transmembrane electron transport: the oxidation of plastocyanin in the inner side of the thylakoid membrane and the reduction of ferredoxin in the stroma. PSI is the most efficient photoelectric apparatus in nature with the quantum efficiency of nearly 100%, in that every captured photon by PSI is used for electron translocation [1–4].

PSI plays important roles in photosynthetic acclimation to the changing environment mainly by participating in PSI cyclic electron transfer (CET), state transitions and adjustment of photosystem stoichiometry. In CET reactions, electrons from ferredoxin are recycled to PSI via plastoquinone, generating ATP without any accumulation of NADPH, which is thought to balance the ATP/NADPH ratio [5–7]. Two independent pathways have been identified in angiosperms. One is an antimycin A-sensitive pathway involving proton gradient regulation 5 (PGR5) and PGR5-like 1 (PGRL1) complexes. Another pathway involves NADH dehydrogenase-like (NDH) complex [7–11]. While the PGR5–PGRL1 pathway is required for efficient photosynthesis and photoprotection, the NDH pathway is thought to prevent overreduction of the chloroplast stroma, especially under stress conditions [5–7,9]. In bundle-sheath cells of C4 plants, the NDH complex was shown to be important for producing more ATP to concentrate CO_2 [12]. In *Chlamydomonas reinhardtii*, a major finding is that a supercomplex consisting of PSI, Cyt b_6f, Fd-$NADP^+$ reductase, light harvesting complex I/II (LHCI/LHCII), and PGRL1 mediates the CET. It was suggested that the formation and dissociation of this supercomplex not only balance the excitation energy of PSII and PSI, but also control the mode of photosynthetic electron flow [5,13]. In cyanobacteria, genetic analyses have elucidated two main routes for cyclic electron transport around PSI [14,15]. One route involves electron transfer from ferredoxin to plastoquinone mediated by the NDH-1L complex [14]. Another parallel route of CET depends on the gene product of *ssr2016*, which shows sequence similarity to PGR5 in *Arabidopsis* [16].

In addition, oxygenic organisms can redistribute excitation energy between PSI and PSII by state transitions [17,18]. During short-term adaptations of photosynthesis to changes of light quality, phycobilisome in cyanobacteria and LHCII in the green lineage can relocate between PSI and PSII to balance the distribution of the absorbed light energy [15,19–21]. State transitions are controlled by redox state of plastoquinone in cyanobacteria: reduction of plastoquinone triggers adaptation to "state II" in which more energy is transferred to PSI, while oxidation of plastoquinone triggers energy transfer to PSII [15,22]. However, no mutants related to state transitions have been identified in cyanobacteria so far. In *Chlamydomonas* and plants, the regulation of redox state of plastoquinone pool on state transitions is clearly more established as

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compared to cyanobacteria [20,23,24]. Under conditions when PSII is preferentially excited, the plastoquinone pool becomes reduced, which favors the binding of plastoquinone to the Q_0 site of the Cyt b_6f complex and leads to the activation of LHCII phosphorylation by Stt7/STN7 kinase. The phosphorylated LHCII migrates to PSI, thus increasing the cross-section of the PSI antenna [17,25,26]. This migration of LHCII is reversible as overexcitation of PSI will lead to the oxidation of plastoquinone pool. The oxidation of plastoquinone pool inactivates Stt7/STN7 but activates LHCII dephosphorylation performed by PPH1/TAP38 phosphates, and the dephosphorylated LHCII then migrates back to PSII [18,23,27,28]. In *Chlamydomonas*, it has been suggested that the state transitions are important for maintenance of the ATP homeostasis while the physiological role of state transitions in *Arabidopsis* is under discussion [20,29,30].

During long-term changes in the metabolic demand, adjustment of photosystem complex stoichiometry is needed to allow for optimal photosynthesis under conditions which favor either of the two photosystems [31–33]. The contents of PSII and Cyt b_6f increased with light intensity while the PSI content only increased under very low light conditions [34,35]. The Stt7/STN7 kinase, together with Stl1/STN8 kinase required for the phosphorylation of the PSII core proteins, is involved in this photosynthetic acclimation process [26,36].

The biochemical and physiological functions of PSI mentioned above depend on the complex structure of PSI in which many protein subunits and cofactors are precisely assembled. PSI represents one of the largest and most complex macromolecular assemblies in nature and the basic structure of PSI has been conserved from cyanobacteria to higher plants during the course of evolution [2,37]. The X-ray crystal structures of PSI from cyanobacteria and higher plants have been determined at 2.5 Å and 3.3 Å resolutions, respectively [3,38,39]. While most of the cyanobacterial PSI complex functions as a trimer, in which each monomer contains 12 subunits and 127 cofactors [38,40], the PSI complex from higher plants functions as a large monomer containing at least 19 subunits and nearly 200 cofactors [3,39]. Of the PSI subunits, two large subunits PsaA and PsaB form a heterodimer that constitutes the core of the reaction center and harbors the electron transport chain. PsaC contains [4Fe–4S] clusters F_A and F_B and also participates in the electron transfer reactions. While the small PsaC, PsaD and PsaE subunits in the stromal side are essential for the binding of ferredoxin, the PsaF and PsaN subunits are involved in the interaction with plastocyanin in the lumen [41–43]. The other small integral subunits are either important for the stability of the complex in cyanobacteria or involved in the interaction with LHCI and LHCII in higher plants [43,44].

Although our current knowledge of PSI structure and function has advanced, how these subunits and cofactors are assembled into a functional complex in the thylakoid membrane is largely unknown (see a review [45]). Understanding the PSI complex assembly process will help us understand its high efficiency of energy transformation and its potential application in biomimetic solar-to-fuel system. Compared to the PSII assembly process, PSI assembly is much more rapid, which makes it very difficult to isolate the assembly intermediate complex [45]. Combination of data from structural biology, genetics and in-vitro reconstitution studies from various oxygenic organisms has yielded a preliminary understanding of PSI assembly procedure [45]. The PsaB subunit is first synthesized and integrated into the thylakoid membrane as an anchor for PsaA in *C. reinhardtii* [46]. These two large subunits form a heterodimer that accounts for half of the molecular mass of the mature PSI complex and then PsaC, together with PsaD and PsaE, is integrated into the stromal side. PsaK and PsaG bind to the PSI core complex after the integration of LHCI in the late step of PSI assembly [47]. The assembly sequence of the other small peripheral and integral subunits remains unknown.

The highly ordered and rapid PSI assembly process may likely be assisted by many auxiliary protein factors to ensure the proper incorporation of the subunits and cofactors. Recently, many auxiliary proteins involved in the biosynthesis of the PSI complex have been identified by genetic and biochemical methods in various photosynthetic organisms. These protein factors can be classified into four categories according to their functions: (1) subunit assembly factors that act as chaperones assisting the proper folding and incorporation of the subunits into the thylakoid membrane; (2) cofactor assembly factors that bring the cofactors into the nascent proteins, such as Hcf101 and CnfU/Nfu2 [48,49]; (3) regulators that are involved in maintaining the stability of the PSI complex, such as BtpA [50,51]; and (4) trans-acting factors involved in PSI gene expressions at different post-transcription steps including RNA processing, stability, editing, splicing, and translation (for a review, see [52]). Not surprisingly, many of the auxiliary protein factors are highly conserved from cyanobacteria to higher plants considering the conserved PSI structure and assembly process.

There are a series of excellent reviews focused on the structure and function of PSI [2,4,37,53–55] and the biogenesis of PSI [45,52,56]. In recent years, much progress has been made in understanding the structure, function, and biogenesis of PSI. In this review, we discuss recent findings in the field relating to how the PSI complex is assembled in oxygenic organisms. First, we focus on the evolution of PSI structure, mainly concerning the light harvesting complex, subunit composition and the oligomeric state of PSI from cyanobacteria to higher plants. Second, the function of the identified assembly factors for PSI subunits and cofactors is summarized. Finally, the networks of regulatory factors and the dynamic regulation of PSI biogenesis are discussed.

2. Evolution of subunit composition and oligomeric state of PSI

The PSI complex is composed of the reaction center complex which is responsible for light harvesting, charge separation and electron transport and the antenna complex which is involved in light harvesting and excitation energy transfer [57]. Although the principal structure of PSI is largely conserved from cyanobacteria to plants during the course of evolution, the light harvesting proteins, the subunit composition and especially the oligomeric state of PSI from various oxygenic organisms have changed to adapting to their natural habitats.

2.1. Evolution of structural components of PSI

2.1.1. The antenna complex

The antenna complex in PSI is much variable in different oxygenic organisms during evolution depending on their natural environments [21,58]. Cyanobacteria are descendents of primordial photosynthetic organisms that appeared in the oceans under aquatic protection. The light harvesting antenna in cyanobacteria is a phycobilisome complex, which is composed of chromophore-containing phycobiliproteins and linker-polypeptides (Table 1). The phycobilisome complex absorbs shorter wavelengths of light in the deep water and transfers the light energy to the intrinsic core antenna system composed of mainly chlorophyll *a* molecules, and the collected light energy is then used for charge separation and electron transfer reactions [59,60].

The eukaryotic photosynthetic organisms have evolved chlorophyll-carotenoid binding proteins assembled as LHCI, which increases the effective absorption cross-section of PSI [61]. However, the LHCI complex has undergone some differentiation in algae and higher plants during evolution, probably as a result of adaptation to specific environmental conditions (Table 1). The LHCI in *C. reinhardtii* is much larger than LHCI in higher plants and composed of nine Lhca antennas (Lhca1–9) [61,62]. The LHCI in higher plants contains four stably associated Lhca (Lhca1–4) proteins [63]. Lhca5 and Lhca6 are not present in the PSI crystal structures in pea plants [3]. These two low-expressed subunits are required for the formation of the PSI–LHCI–NDH supercomplex [10,64]. The composition and structure of PSI in the moss *Physcomitrella patens*, a transitional photosynthetic organism from aquatic to terrestrial life, have been studied by biochemical and mass spectrometry methods. The light harvesting complex in *P. patens* consists of four Lhca proteins (Lhca1–3, Lhca5) and forms a higher-plant-like PSI

Table 1
Subunit composition and oligomeric state of PSI in oxygenic organisms.

	Thermosynechococcus elongatus BP-1[a]	*Chroococcidiopsis* sp. TS-821[b]	*C. reinhardtii*[c]	*P. patens*[d]	*P. sativum*[e]
Core proteins	PsaA-F, PsaI-L, M, X	PsaA-F, PsaI-L, M, X	PsaA-F, PsaI-L, G, H, N, O	PsaA-F, PsaI-L, G, H, M, O	PsaA-F, PsaI-L, G, H, N, O
Light-harvesting proteins	Phycobili-protein, linker protein	Phycobili-protein, linker protein	Lhca1–9	Lhca1–3, Lhca5	Lhca1–4, Lhca5, 6
Oligomeric state	Trimer	Tetramer, dimer	Monomer	Monomer	Monomer

[a] [38].
[b] [74].
[c] [62].
[d] [65].
[e] [3,10].

superstructure since this superstructure resembles the structure of PSI–LHCI complexes isolated from *Arabidopsis* [65].

2.1.2. The reaction center complex

Compared to the antenna complex, the PSI reaction center complex is more conserved in the oxygenic organisms [37,55]. The PSI reaction center complex commonly contains PsaA–F and PsaI–L in the oxygenic organisms (Table 1). Among these common subunits, the PsaA–E is involved in the electron transfer reactions [3,56]. However, the function of other subunits, such as PsaF and PsaL, differs in cyanobacteria and higher plants. For example, PsaF, together with PsaJ, in cyanobacteria is mainly involved in the function and organization of the PSI complex, while PsaF is involved in plastocyanin docking in green algae and higher plants [41,53,66,67]. PsaL together with PsaI and PsaM is involved in linking PSI monomers to oligomers in cyanobacteria [68] while the role of PsaL in higher plants is to stabilize the binding of PsaH and PsaO [37,69]. In addition, the eukaryotic organisms have evolved some PSI subunits which may perform new functions (Table 1). PsaG, PsaH, PsaN and PsaO are unique to green algae and higher plants. PsaG participates in the regulation of electron transport by stabilizing the PSI core complex in *Arabidopsis* [44,70]. PsaH and PsaO, together with PsaL, are involved in forming a domain in PSI that associates with LHCII to participate in state transitions [37,69,71]. PsaN was identified in the lumenal side of PSI and was necessary for interactions between plastocyanin and PSI during photosynthetic electron transport [3,41].

The recently characterized PSI structures from *P. patens* provide valuable insights into the evolution of mosses during the adaptation to a terrestrial environment. While still containing the cyanobacterial PsaM subunit, it also evolved the plant-specific PsaG, PsaH, and PsaO subunits but the plant-specific PsaN subunit was not identified [65] (Table 1). The PsaF subunit contains a C-terminal extension that is present in cyanobacteria, red and green algae, but not in higher plants. The PSI subunit composition and the protein sequence of PsaF in *P. patens* reflect it as the ancient ancestor of terrestrial organisms.

The originally identified PsaP subunit in higher plants by biochemical method is not present in the crystal structure of PSI [3,72], suggesting that PsaP might not be a component of PSI. Indeed, recent study has clearly shown that PsaP is not considered as a PSI subunit but is a protein factor involved in the thylakoid membrane curvature at grana margins and thus is renamed as CURT1B in *Arabidopsis* [73].

2.2. Evolution of functional PSI from oligomer to monomer

The most dramatic aspect of PSI evolution is the oligomeric state design from trimer to monomer (Table 1). In cyanobacterium *Thermosynechococcus elongatus*, PSI forms trimeric complexes with a 3-fold rotational symmetry [38]. Recently the tetrameric and dimeric forms of PSI in thermophilic cyanobacterium *Chroococcidiopsis* sp. TS-821 have been discovered and PsaL may be responsible for the formation of tetrameric PSI, which is more readily able to dissociate into monomers to respond to the changing environment [74]. According to phylogenetic analysis, the tetrameric PSI may stand for a transition form during the evolution from cyanobacterial trimeric PSI to plant monomeric PSI. In eukaryotic photosynthetic organisms, such as green algae and plants, it is widely accepted that the PSI complex exists as a monomer [3]. Although there have been reports about dimeric and trimeric PSI forms in higher plants [75,76], it is still unclear whether oligomeric PSI unambiguously exists in plants or whether it can be an artifact of the detergent solubilization [76]. The newly evolved PsaH subunit and the structural modification of the PsaL subunit may prevent the trimer formation [3,4,62]. It is noticeable that the *Arabidopsis* mutants devoid of PsaH or PsaL subunit show no visible phenotype and all grow autophototrophically [37,69,77]. Although the oligomeric states of PSI in the mutants were not analyzed, it seems that loss of PsaL or PsaH could not result in the changes in PSI oligomeric state. It is possible that some newly evolved protein factors or PSI subunits are responsible for the transitions of oligomeric state. Further genetics and biochemical data are needed to determine which subunits and/or auxiliary proteins are responsible for plant monomeric PSI formation.

The functional significance of the PSI oligomeric state from trimeric form in cyanobacteria to monomeric forms in higher plants has been deeply discussed [4]. It seems that the trimeric PSI has a higher cross-section and is more efficient in capturing photons under low light conditions while the PSI monomer is more favored for state transitions under natural fluctuating environmental conditions [4]. In green algae and plants, the peripheral interfaces of monomeric PSI provide a vital interface for interactions between PSI and a mobile LHCII, which switches back and forth between PSII and PSI to balance the excitation of the two photosystems. The light harvesting proteins, core subunit composition and the oligomeric state of PSI in various photosynthetic organisms are summarized in Table 1.

3. Assembly factors for PSI subunits and cofactors

The biogenesis of the thylakoid membrane is a complex process including the synthesis and maintenance of proteins, lipids and pigments. Genetic and biochemical studies have identified many factors in protein sorting, insertion and assembly of the photosynthetic complexes [52,78,79]. In the case of PSI assembly, a set of facilitating factors has been found to help the proper folding of the newly synthesized PSI subunits, integration of the many cofactors into PSI and incorporation of the light harvesting antenna with the core complex (Table 2). Unlike the known PSII assembly factors, which are all encoded by nuclear genome and then transported to the plastids, the identified PSI assembly factors are encoded both by plastid and nuclear genes. The molecular functions and interrelationships of the auxiliary factors imply that a network of regulators monitors the rapid PSI assembly process.

3.1. Assembly factors for PSI subunits

3.1.1. Alb3

Alb3 (Albino3) belongs to the membrane insertases YidC–Oxa1–Alb3 family and is highly conserved in bacteria, mitochondria, and chloroplasts [80–82]. Alb3 was first found as a component of the machinery for post-translational insertion of the LHC proteins into the thylakoid membrane [83,84]. Alb3 is also required for the co-translational

Table 2
Summary of functionally identified PSI assembly factors in oxygenic organisms. The conserved PSI assembly factors from cyanobacteria to higher plants are listed together with locus tag for the coding genes. Indicated are also the protein domains, localization and proposed functions of the assembly factors.

Assembly factors	*Synechocystis*	*C. reinhardtii*	*P. patens*	*A. thaliana*	Protein domain	Localization	Proposed functions	Refs
Subunit assembly factors								
Alb3	*Slr1471*	CHLREDRAFT_187295	PHYPADRAFT_13532	AT2G28800	OxaA/YidC	Intrinsic, PDM, TM	Integration, folding, and/or assembly of PsaA/B, pD1 and LHC	[85,90,91]
VIPP1	*sll0617*	CHLREDRAFT_134824	PHYPADRAFT_117800	AT1G65260	PspA	TM, chloroplast envelope	PSI assembly, thylakoid biogenesis, chloroplast envelope maintenance	[95–98]
Ycf3	*Slr0823*	ChreCp037	PhpapaCp038	ATCG00360	TPR	TM	Later steps of PSI assembly and/or stromal ridge formation	[99–102]
Ycf4	*Sll0226*	ChreCp038	PhpapaCp028	ATCG00520	No	TM	Scaffold for PSI assembly and/or stromal ridge formation	[99,103–105]
Ycf37/Pyg7	*Slr0171*	CHLREDRAFT_184916	PHYPADRAFT_148653	AT1G22700	TPR	TM	Formation of PSI trimers, later steps of PSI assembly	[106–109]
Y3IP1	*No*	CHLREDRAFT_158401	PHYPADRAFT_142249	AT5G44650	No	TM	PSI assembly by interacting with Ycf3	[102]
PPD1	*No*	CHLREDRAFT_205916	PHYPADRAFT_131430	AT4G15510	PsbP	Extrinsic, L	Early steps of PSI assembly by integrating with specific domains of PsaA/B	[112]
Psa2	*No*	CHLREDRAFT_160591	PHYPADRAFT_167917	AT2G34860	DnaJ-type zinc finger	L	Early and/or later steps of PSI assembly	[114]
Cofactor assembly factors								
RubA	*Slr2033*	CHLREDRAFT_182463	PHYPADRAFT_163749	AT1g54500	Rubredoxin	TM	Integration of Fx in PSI assembly, PSII accumulation	[117–119]
Hcf101	*Slr0067*	CHLREDRAFT_102098	PHYPADRAFT_227402	AT3G24430	MRP-like, Fer4_NifH	S	Scaffold for [4Fe–4S] cluster assembly	[123,124]
CnfU	*Sll2667*	CHLREDRAFT_104310	PHYPADRAFT_26756	AT4G01940 AT5G49940	NifU	S	Scaffolds for iron–sulfur cluster assembly and delivery	[48,122]

L, lumen; PDM, PratA-defined membrane; S, stroma; TM, thylakoid membrane.

membrane insertion of the reaction centers of PSII in *Synechocystis* and *Chlamydomonas* [85,86]. Recent studies in *Arabidopsis* demonstrate that Alb3 is involved in PSII assembly via its interaction with other PSII assembly factors, such as LPA2, LPA3, or AtTerC [87–89]. In addition, Alb3 may mediate PSI assembly by assisting the insertion of the reaction center protein, PsaA and PsaB, as well as the LHCI proteins into the thylakoid membrane. One member of Alb3, Alb3.1, was mainly responsible for the assembly of the LHC complex, and another member Alb3.2 was mainly involved in the assembly of PSI reaction center complex [85,90,91]. Recently, a complex containing chlorophyll synthase (ChlG), the high-light-inducible protein HliD, the Ycf39 protein, and the YidC/Alb3 insertase has been isolated in the cyanobacterium *Synechocystis* PCC 6803. The complex also contains chlorophyll, chlorophyllide, and carotenoid pigments. The physical linkage between ChlG and YidC/Alb3 suggests that YidC/Alb3 may assist in loading of chlorophylls into nascent apoproteins [92]. Taken together, Alb3 is an essential general assembly factor for the biogenesis of the photosynthetic membrane complexes.

Alb3's homologous proteins YidC in *Escherichia coli* and OxaI in mitochondria function in the co-translational and post-translational insertion of membrane proteins [80]. The crystal structure of YidC from *Bacillus halodurans* at 2.4 Å resolutions has revealed a hydrophilic groove, which generates a hydrophilic environment to recruit the extracellular part of the substrates into the low-dielectric environment of the membrane. This work provides the structural basis of Sec-independent membrane protein insertion by YidC [93].

3.1.2. VIPP1

VIPP1 (vesical-inducing protein in plastids 1) has been suggested to play important roles in thylakoid biogenesis from cyanobacteria to higher plants although the proposed roles of this protein are multiple in different studies. Null mutations of VIPP1 could not be obtained in *Synechocystis* sp. PCC 6803. The mutant strains with significant reduced levels of VIPP1 (about 20% of the wild type) showed a comparable loss of thylakoid membrane content and reduced PSI and PSII activities, indicating that VIPP1 is essential for thylakoid biogenesis in *Synechocystis* sp. PCC 6803 [94]. Recently, the function of VIPP1 in another cyanobacterium *Synechococcus* sp. PCC 7002 has been investigated in a null mutant depleted of VIPP1 by using a smart indirect route in which the deletion of VIPP1 was obtained in a PSI-less strain [95]. The resulting mutant could not grow photoautotrophically but could grow photoheterotrophically under low light conditions. Thylakoids were present in *vipp1* mutant but no PSI was assembled and PSI activity was abolished, while the PSII was still assembled and active, suggesting that VIPP1 is essential for the biogenesis of PSI but not for the thylakoid membrane in cyanobacteria.

The VIPP1 may evolve new functions in eukaryotic species. The *VIPP1*-RNAi strains of *C. reinhardtii* showed no obvious phenotypes under low light conditions. However, thylakoid swelling and loss of photosynthetic activity were observed when the mutants grew under high light conditions. The contents of PSII, Cyt b_6f, ATPase, and PSI in the mutants were universally decreased while the lipid composition was comparable with the wild type. These results suggest a role of VIPP1 in the biogenesis/assembly of thylakoid membrane core complexes rather than the formation of the thylakoid membrane [96]. The molecular function of VIPP1 in thylakoid assembly may be mediated by the interaction with Alb3 as described above [85]. However, how these two factors cooperate in the assembly of thylakoids in *C. reinhardtii* needs to be studied further.

Accumulating evidence has shown that the function of VIPP1 in higher plants is pleiotropic. VIPP1 was firstly reported as an essential factor in the thylakoid maintenance by vesicle transport in *Arabidopsis* due to its dual targeting in thylakoid membrane [97]. The *vipp1* T-DNA insertion mutant displayed high chlorophyll fluorescence phenotype and was unable to grow photoautotrophically on soil. The electron transport was impaired and the thylakoid membrane was degraded in the mutant [97]. In addition, balloon chloroplasts in *Arabidopsis vipp1* mutants were observed. VIPP1 forms a large complex at envelopes to maintain the membrane potential. Thus, VIPP1 is also critically important for maintenance of the chloroplast envelope [98].

3.1.3. Ycf3

Ycf3 is a plastid-encoded protein associated with the thylakoid membrane. The function of Ycf3 as an essential PSI assembly factor was well characterized in tobacco and *C. reinhardtii* by chloroplast transformation [99,100]. Loss of Ycf3 leads to complete loss of the PSI core complex and photoautotrophic growth in tobacco plants and *C. reinhardtii*. Interactions of Ycf3 with PsaA and PsaD and the weak association of Ycf3 with the stromal surface of the thylakoids suggest that Ycf3 is involved in the formation of the stromal ridge [101,102].

3.1.4. Ycf4

Ycf4 is another plastid-encoded assembly factor. It is an extrinsic membrane protein and associated with the thylakoid membrane. Inactivation of *Ycf4* in *C. reinhardtii* resulted in complete loss of PSI [99]. Furthermore, Ycf4 was detected in a large intermediate complex containing PSI subunits from PsaA to PsaF in *C. reinhardtii* [103]. These studies suggest that Ycf4 is essential for PSI assembly and that Ycf4 plays a role either during the formation of the stromal ridge or in the subsequent assembly of the intermediate complex in *C. reinhardtii*.

However, the studies on the role of Ycf4 in tobacco and cyanobacteria suggest that Ycf4 may act as a non-essential factor for PSI assembly. Its knockout mutants are capable of accumulating sufficient amount of PSI for autotrophic growth, although the accumulation of PSI in the mutant lines was only about 10% of the wild type [104,105]. Apparently, the role of Ycf4 in PSI assembly has been changed during evolution in different species, which implies that different molecular mechanisms of PSI assembly exist in cyanobacteria, green algae and higher plants.

3.1.5. Ycf37/Pyg7

Inactivation of *Ycf37* in *Synechocystis* sp. PCC 6803 resulted in about 30% decrease in PSI content but did not significantly influence photosynthetic growth under standard conditions [106], suggesting that Ycf37 has an accessory function in PSI biogenesis in cyanobacteria. Further studies have shown that Ycf37 plays important roles in the formation of PSI trimers and the late steps of PSI assembly in cyanobacteria [107,108].

The *Pyg7* (*pale yellow green7*) in *Arabidopsis* nuclear genome is a homologous gene with *Ycf37*. The *Arabidopsis pyg7* mutant completely and specifically lacks PSI and abolishes photoautotrophic growth [109], suggesting that Pyg7 is essential for PSI assembly in higher plants. Since PSI in photosynthetic eukaryotes does not form trimers, Pyg7 may adopt a function that is different from that of its cyanobacterial homolog. In view of the essential role of Pyg7 in PSI assembly, it is expected that it may be involved in a later stage of PSI assembly.

3.1.6. Y3IP1

Although the process of PSI biogenesis is conserved from cyanobacteria to higher plants with regard to the sequence of subunit assembly and many conserved auxiliary proteins, some new protein factors appeared in plants during evolution. Y3IP1 (Ycf3-interacting protein 1) is a newly evolved nuclear-encoded protein conserved in photosynthetic eukaryotes that participate in PSI assembly by interacting with Ycf3 [102]. It was identified by Ycf3-tagged immunoaffinity purification method in transplastomic tobacco and its function was subsequently studied by reverse genetics in tobacco and *Arabidopsis*. The RNAi mutants are specifically impaired in PSI accumulation. Considering Y3IP1 as an interaction partner of Ycf3, it may also be involved in the formation of stromal ridge during PSI assembly although the precise molecular function is unknown yet.

3.1.7. PPD1

More recently, several lumenal protein factors have been found to play important roles in the assembly and function of PSII and NAD(P)H dehydrogenase-like complexes while the functions of the majority of lumenal proteins are still unknown [110,111]. Because PSI is a large protein complex that induces the translocation of electrons from plastocyanin at the lumenal side of the membrane to ferredoxin on the stromal side, its assembly factors should exist not only in the stromal side but also in the lumenal side of the thylakoid membrane.

PPD1 (PSBP-domain protein1) has been identified as a first thylakoid lumenal protein that is essential for PSI assembly in higher plants, as deletion of PPD1 results in a specific loss of stable PSI complex and the inability of photoautotrophic growth [112]. PPD1 is encoded by a nuclear gene and conserved in eukaryotic organisms but its homologs are not found in the prokaryotes. PPD1 interacts directly and specifically with distinct loops of PsaA and PsaB subunits in the lumenal sides of the thylakoid membrane. This indicates that PPD1 may participate in PSI assembly by assisting the proper folding and integration of PsaA and PsaB into the thylakoid membrane. Recently, the PPD1 RNAi lines displaying a range of phenotypes with respect to PSI accumulation were obtained and the role of PPD1 in PSI assembly was further characterized. It is confirmed that decreased amounts of PPD1 in the RNAi mutants resulted in gradient defects in PSI accumulation [113].

3.1.8. Psa2

Psa2, a DnaJ-type zinc finger protein, is another thylakoid lumenal protein that has been found to be specifically required for PSI accumulation via interaction with a PsaG-containing subcomplex in maize and *Arabidopsis* [114]. Psa2 is essential for PSI assembly since the *psa2* mutants die shortly after germination on soil. Psa2 may promote PSI assembly in a later stage as PsaG is a peripheral subunit assembled in the later stage. The phenotype of the *psa2* mutant is more severe than that of the *psaG* mutant, thus, the role of Psa2 goes beyond assisting PsaG assembly into PSI. The implicated interaction of Psa2 with PPD1 suggests that these two factors may cooperatively play important roles in PSI assembly in the lumen. The exact role of Psa2 in PSI assembly remains to be investigated.

3.2. Assembly factors for PSI cofactors

The functional PSI complex contains many cofactors, nearly 200 cofactors including chlorophylls, carotenoids, phylloquinone and [4Fe–4S] clusters. How and when these inorganic and organic cofactors are assembled into the PSI complex remains largely unclear. It seems likely that integration of chlorophylls and carotenoids accompanies protein translation and assembly processes by increasing apoprotein stability [115,116]. Genetic studies have discovered that some auxiliary proteins are involved in the incorporation of iron–sulfur cluster into the newly synthesized apo-proteins (Table 2).

3.2.1. Rubredoxin (RubA)

Previously, it has been shown that RubA is specifically required for the insertion of iron–sulfur cluster Fx into the PsaA/B heterodimer and is essential for PSI assembly but has little or no effect on the PSII function in the cyanobacterium *Synechococcus* sp. PCC 7002 [117,118]. However, studies on the function of homologous genes of *rubA* in diverse oxygenic organisms including *Synechocystis*, *Chlamydomonas*, and *Arabidopsis* have demonstrated that rubredoxins have no effects on the PSI function but play a specific role in PSII accumulation [119], suggesting that a conserved rubredoxin is necessary for PSII accumulation in diverse oxygenic photoautotrophs. This discrepancy may indicate a difference in RubA function in different cyanobacterial species. In *Chlamydomonas* and *Arabidopsis*, there appear to be multiple chloroplast-localized rubredoxins. Thus, it is possible that one of these other homologs may function in PSI assembly, which needs to be analyzed.

3.2.2. CnfU/Nfu2

The iron–sulfur cluster assembly machinery responsible for iron–sulfur cluster biosynthesis is present in most bacteria, and eukaryotic organelles, chloroplasts and mitochondria [120,121]. The *Arabidopsis CnfU–V/Nfu2* mutant exhibited a dwarf and faint pale-green phenotype

with reduced protein levels of PSI and ferredoxin. The stromal iron–sulfur cluster insertion activity was severely impaired in chloroplasts. CnfU/Nfu2 in *Arabidopsis* may act as an iron–sulfur cluster scaffold protein that is required for the biogenesis of PSI and ferredoxin [48,122].

3.2.3. Hcf101

Hcf101 belongs to the [4Fe–4S]-cluster-containing P-loop NTPase superfamily, of which the bacterial, cytosolic and mitochondrial members have been described as biogenesis of Fe/S clusters [120,123]. In *Arabidopsis hcf101* mutant, the accumulation of the proteins that contain [4Fe–4S] clusters, such as the PSI complex and the ferredoxin–thioredoxin reductase complex, is specifically impaired while the proteins containing [2Fe–2S] are not affected. Hcf101 functions as a scaffold for [4Fe–4S] cluster assembly [49,123,124].

3.2.4. Phylloquinone (PhQ) synthesis and PSI accumulation

Phylloquinone (PhQ) serves as specific cofactors mediating PSI electron transport in all oxygenic organisms. Therefore, inhibition of PhQ biosynthesis results in a specific loss of PSI and thereby leads to a phenotype similar to that of PSI assembly mutants. How and when PhQ are integrated into PSI by any carriers remains largely unknown. In *Synechocystis* PhQ-deficient mutants, the ratio of PSI/PSII is reduced compared to the wild type. The mutants can grow photoautotrophically under low light conditions probably because the deficient PhQ in PSI is functionally replaced by plastoquinone [125]. In *C. reinhardtii*, PhQ biosynthesis is impaired in the *menD1* mutant. The mutant grows as well as wild type in acetate medium under low light conditions but photosynthesis is impaired under high light conditions or on minimal medium. The level of PSII declines but the PSI function is not affected in this mutant. The function of PhQ in PSI may be replaced by plastoquinone in the mutant [126]. On the other hand, the absence of PhQ in higher plants seems to specifically affect the PSI function. In the mutant affected at the *PHYLLO* locus (a fusion of four individual eubacterial genes, *menF*, *menD*, *menC*, and *menH*) with impaired PhQ biosynthesis, there are a small amount of PSI accumulation (5–15% of wild type) and nearly normal PSII accumulation [127]. Mutation of *Arabidopsis* gene, *AEE14*, which encodes *o*-succinylbenzoyl-CoA ligase that is essential for PhQ biosynthesis, leads to PSI dysfunction and seedling lethal [128].

3.2.5. Carotenoid synthesis and PSI accumulation

Carotenoids are essential components of photosynthetic apparatus participating light absorption and chloroplast protection. There are two major groups of carotenoids, carotenes and their oxygenated derivatives, the xanthophylls, which are involved in LHC assembly and photoprotection. Although xanthophylls are not cofactors of PSI, the *Arabidopsis nox* mutant devoid of xanthophylls shows decreased accumulation of PSI due to impaired PSI core subunit translation and stability [129]. The exact role of xanthophylls in PSI accumulation is not clear.

3.3. Evolution of PSI assembly factors

Although the PSI subunits and the assembly factors for PSI are encoded both by nuclear and plastid genes in photosynthetic eukaryotic organisms, the assembly process of PSI in eukaryotic organisms occurs in a similar way as that in cyanobacteria. Some assembly factors that are required for or facilitate PSI assembly are also conserved among cyanobacteria, algae and plants during evolution (Table 2). However, these assembly factors may have evolved new functions in PSI assembly in algae and plants. For instance, Ycf4 is essential for PSI assembly in *C. reinhardtii* but not in cyanobacteria and plants [99–101,105]. Ycf37 has accessory functions in PSI assembly in cyanobacteria but its homolog Pyg7 is essential for PSI assembly in plants [106,107,109]. In addition, some assembly factors, such as Y3IP1, PPD1 and Psa2, are evolved in algae and plants probably to adapt a more complicated PSI assembly process in chloroplasts [102,112,114].

4. Cooperation of assembly factors for PSI assembly

The assembly of PSI is such a highly ordered process. Undoubtedly a network of assembly factors might cooperate closely to guarantee the proper folding and formation of a functional PSI.

In eukaryotic cells, the assembly of the PSI complex seems to require the cooperation of different assembly factors (Fig. 1). VIPP1 can be coimmunoprecipitated with Alb3.2 in *Chlamydomonas*. The interaction of Alb3.2 with VIPP1 suggests that Alb3.2 may be required for VIPP1 insertion in the thylakoid membrane, or the reverse may be true [85]. As mentioned above, Y3IP1, a newly evolved PSI assembly factor found only in eukaryotic organisms, interacts stably with Ycf3 to assist the assembly of PSI subunits [102]. How these two assembly factors encoded by two different genetic systems cooperate together at the same time and in the right space is unknown. In the maize mutants lacking PSI, Psa2 accumulates to normal levels. However, Psa2 is absent in *Arabidopsis apo1* mutant lacking PSI due to impaired splicing of *Ycf3-2* intron. It is thus suggested that Ycf3 may functionally relate to Psa2 in PSI assembly [114]. In addition, Psa2 and PPD1 co-migrated in a complex and the content of PPD1 markedly increased in the *psa2* mutant, indicating PPD1 and Psa2 function in a same biochemical process during PSI assembly [114].

In cyanobacteria, no evidence has shown that the interaction or the cooperation between the known identified PSI assembly factors exists during PSI assembly. Ycf3 and Ycf4 participate in the later steps of the PSI assembly process and probably act as chaperones for the PSI subunit assembly [101]. Ycf37 is required for the formation of the PSI trimer [107]. Whether or how these factors cooperate during PSI assembly remain to be investigated.

5. Dynamic regulations of PSI biogenesis

5.1. Expressions of assembly factors parallel the PSI assembly

A special feature of PSI compared with PSII is its very high stability during the leaf ontogenesis and in response to changing environmental conditions [53]. It was found that PSI content remains constant with increasing leaf age while the amount of Ycf4, Y3IP1, and PPD1 accumulated mainly in the young leaf and decreased with leaf aging [105,112]. These results suggest that the expression of Ycf4, Y3IP1, and PPD1 is dynamically regulated to participate in the PSI assembly process. It is noticeable that the content of Ycf3 remains stable with increasing leaf age, although the amount of Ycf3 is at least one order of magnitude lower than that of PSI, indicating that Ycf3 may also be involved in maintaining the PSI stability besides acting as an essential PSI assembly factor [99,105].

5.2. Regulation of expressions of PSI subunits

It is widely assumed that most membrane proteins encoded by chloroplast genes are synthesized and assembled by co-translational membrane insertion although the co-translational membrane insertion has been experimentally demonstrated only in Cyt *f* and D1 [130,131]. It has been suggested that regulation of the PSI complex accumulation involves a network of assembly-depended translational autoregulation of the plastid encoded subunits. The presence of PsaB is required for the translation of PsaA and the presence of PsaA is required for efficient PsaC translation in *C. reinhardtii* [132]. However, this control by epistasy of synthesis (CES) processes during the PSI biogenesis in *Chlamydomonas* has not been experimentally demonstrated in plants. On the other hand, PsaG, PsaH and PsaL are not required for the PSI accumulation since the mutants lacking these subunits show no visible phenotype and grow photoautotrophically, indicating that the PSI accumulation is not regulated by these PSI subunits in *Arabidopsis* [53]. Molecular genetic studies have also identified some nuclear encoded factors that are essential for post-transcriptional regulation of PSI gene

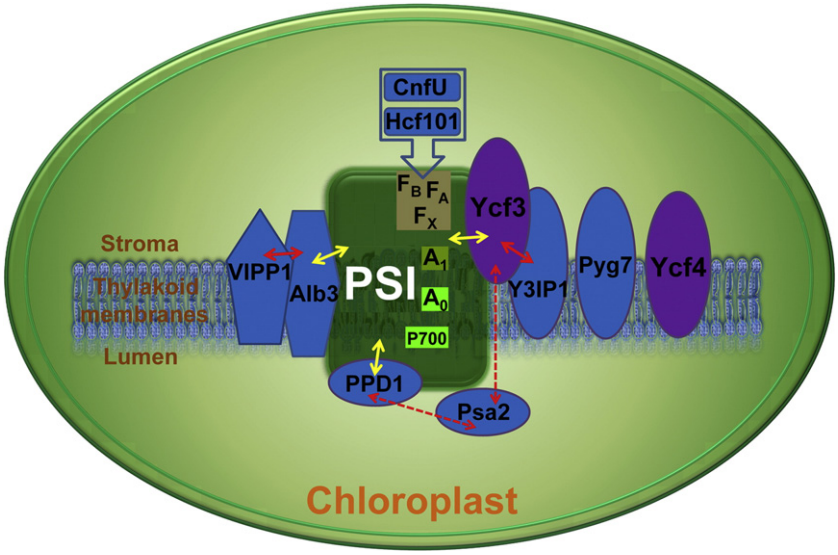

Fig. 1. Cooperation of a suite of assembly factors during PSI assembly in eukaryotic organisms. These assembly factors include both nuclear-encoded (blue) and plastid-encoded protein factors (purple). Experimentally verified interactions between assembly factors are indicated with red solid arrowheads and potential interactions with red dashed arrowheads and interactions between assembly factors and PSI subunits with yellow solid arrowheads. Thylakoid membrane proteins VIPP1 and Alb3 mediate the very first step of PSI biogenesis and also the initial stage formation of photosynthetic membrane complexes. Interactions between VIPP1 and Alb3 facilitate the execution of their regulatory roles in thylakoid biogenesis. Y3IPI interacts and cooperates with Ycf3 acting in the later step of PSI assembly. Pyg7 participates in the later stage of PSI biogenesis in higher plants. PPD1 interacts with distinct lumenal loops of PsaA and PsaB in the early step of PSI assembly. Psa2 mediates thiol transactions in the thylakoid lumen crucial for the stable accumulation of PSI complexes. Stromal proteins CnfU and Hcf101 regulate the assembly of iron–sulfur clusters for the PSI complex.

expression [52,133]. In *C. reinhardtii*, the regulated expressions of the *PsaA* and *PsaB* by trans-acting factors at different post-transcription levels have been summarized [52]. Among the trans-acting regulatory factors, Tab2 is highly conserved from cyanobacteria to higher plants. The Tab2 protein is specifically required for translation of *PsaB* mRNA by binding to *PsaB* 5′UTR in *C. reinhardtii* [134]. The ATAB2 protein is required for synthesis of both PSI and PSII by activating the translation of at least one target of each photosystem in *Arabidopsis* [135]. In cyanobacteria, the small RNA PsrR1 is recently found to regulate the expression of PsaL at the post-transcriptional level and is involved in the regulation of the PSI function at various environmental conditions [136].

5.3. Regulation of expressions of PSI assembly factors

Previous studies have shown that the PSI assembly process is regulated by both nuclear- and plastid-encoded assembly factors (Fig. 2). However, more evidence indicates that some nuclear encoded factors play an important role in regulating the expression of genes encoding the PSI assembly factors, which in turn regulates the assembly and accumulation of PSI (Fig. 2). For example, expression of the chloroplast gene *ycf3*, which encodes PSI essential assembly factor, is intricately regulated by several nuclear encoded factors. The open reading frame of *ycf3* contains three exons and two type-two introns. The first intron was implicated in the regulation of the expression of *ycf3* by other regulating factors in response to environmental changes. The barley mutant CL3 showed a PSI-deficient phenotype under higher temperature. The assembly of PSI is impaired due to a temperature-sensitive defect in splicing of *ycf3* first intron [137]. APO1, which was previously found to facilitate the incorporation of [4Fe–4S] clusters into PSI and NADH dehydrogenase complexes, was found to be absolutely required for splicing of the second intron in *ycf3*, as well as promoting the splicing of several chloroplast group II introns [138,139]. In *Arabidopsis apo1* mutant, the second intron of *ycf3* remained completely unspliced and the accumulation of PSI was severely impaired [139]. Like APO1, OTP51 is also essential for intron splicing of the second intron in *ycf3* and promoting the splicing of some other introns. There is no detectable PSI in the *otp51*

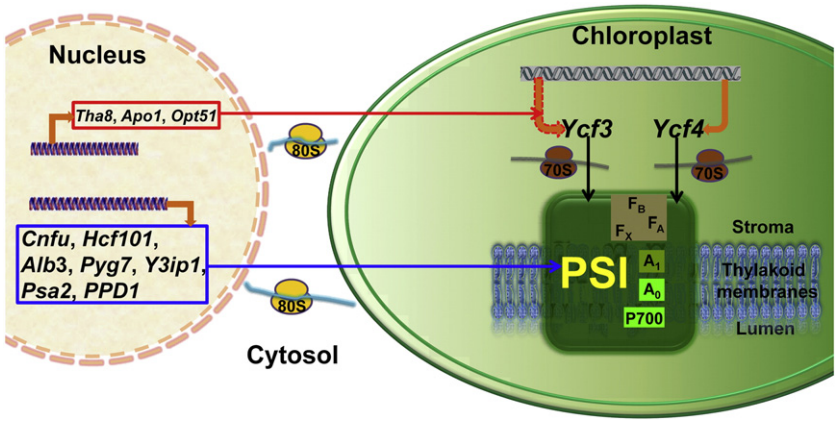

Fig. 2. Both nuclear- and plastid-encoded regulatory factors are required for the concerted assembly of the PSI complex in eukaryotic organisms. Nuclear gene-encoded assembly factors and plastid gene-encoded assembly factors collaboratively regulate the assembly of the PSI complex. In addition, nuclear gene-encoded auxiliary proteins THA8, APO1, and OPT51 orchestrate the stable accumulation of PSI via post-transcriptionally modulating the level of Ycf3 protein.

mutant because of the absent splicing of the *ycf3* second intron [140]. THA8 (thylakoid assembly 8) was identified as a nuclear encoded PPR protein that is required for the specific splicing of the *ycf3* second intron and *trnA* introns in maize and *Arabidopsis* [141]. Null alleles of maize *tha8* have a pale-green and seedling-lethal phenotype with decreased levels of thylakoid membrane complexes while the *Arabidopsis* mutant is embryo-lethal [141]. The crystal structure of THA8 binding with RNA was determined, and the binding sites of THA8 in *ycf3* second intron have also been identified [142]. Taken together, the intricate regulation of *ycf3* expression suggests a regulatory role of Ycf3 in PSI assembly and a key strategy of higher plants for adapting to the changing environment.

5.4. Regulation of PSI stability

PSI is prone to photoinhibitory damage under relatively weak light and chilling temperature conditions [143]. The entire PSI core complex is degraded during low temperature photoinhibition although the turn-over or repair processes are largely unknown. The BtpA protein, an extrinsic thylakoid membrane protein, was found to stabilize the reaction center proteins of PSI in *Synechocystis* 6803. Under normal temperature, the point mutation of *btpA* in the BP26 mutant line resulted in a decrease in PSI accumulation but the steady levels of transcripts of PSI genes were not changed in the BP26 mutant [50]. The *btpA* deletion mutant strain could not grow photoautotrophically under low temperature conditions because the stability of the reaction center complex of PSI was impaired [51]. Although the homologs of BtpA are present in Archaebacteria, Eubacteria and Animalia, no BtpA-like protein was found in algae and higher plants.

6. Concluding remarks and future perspectives

Considerable progress has been made in recent years in regard to the structure, function, assembly and regulatory factors of the PSI complex. Detailed dissection of molecular organization of PSI in cyanobacteria, moss, algae, and higher plants has provided important insights into the evolution of this complex. Studies on the rapid and highly ordered PSI assembly process, during which so many subunits and cofactors are integrated into a functionally complex assisted by many assembly factors, have yielded a preliminary scenario for the process (see a review [45]).

Based on recent findings in the PSI assembly process, we propose a working model of the PSI assembly process (Fig. 3). The first step begins with the co-translational integration of PsaB into the thylakoid membrane, which is essential for translation and integration of PsaA, subsequently these two subunits form a huge heterodimer [46,132]. The PsaA/B heterodimer serves as a platform for the assembly of remaining subunits and the cofactors. Several assembly factors, such as Alb3, VIPP1, and PPD1, are involved in this early step to assist the proper integration of the PsaA/B subunit [85,95,112]. Phylloquinone and 4Fe–4S cluster (Fx) are integrated into the heterodimer [118,144]. The integration of Fx into the heterodimer is assisted by RubA, Hcf101, and CnfU [119,122,123]. The assembly of Fx is required for the subsequent integration of PsaC, PsaD, and PsaE on the stromal side [118]. Ycf3 and Y3IP1 may assist the assembly of the heterodimer and probably three subunits PsaC, PsaD, and PsaE on the stromal side since Ycf3 interacts with PsaA and PsaD and Y3IP1. Ycf4 may be involved in the assembly of PsaC, PsaD, and PsaE on the stromal side or the subsequent assembly of the intermediate complex since the intermediate complex Ycf4 was detected in a large complex containing PSI subunits from PsaA to PsaF and COP2 [103]. It is interesting to note that a dramatic decrease in COP2 as low as 10% of wild-type did not affect the accumulation of PSI, suggesting that COP2 is not essential for PSI assembly. It is probably involved in stabilizing the Ycf4 complex [103]. The Ycf4 complex was destabilized in the absence of PsaF, which is specifically localized on the Ycf4 complex before being assembled into the PSI assembly intermediate subcomplex [103]. Pyg7 is involved in the later steps of PSI assembly since it is essential for PSI assembly in higher plants [109]. In subsequent steps, PsaJ, PsaH, PsaL, PsaG, PsaK, PsaN, and LHCI, are assembled. However, how and when these subunits are integrated remains unknown. Alb3 may assist the integration of LHCI as Alb3 is a component of the machinery for post-translation insertion of LHC proteins into the thylakoid membrane [84,90]. Psa2 may promote PSI assembly in a later stage since it is required for PSI accumulation via interaction with a PsaG-containing subcomplex in maize and *Arabidopsis* [114].

Despite these advances, many questions remain to be resolved regarding the regulation of PSI function, assembly and turnover processes. A major task in the future is to identify novel factors for PSI assembly. Genetic approaches to screen for PSI deficient mutants have been proven successfully to identify important assembly factors, such as Ycf3, Ycf4, Ycf37, PPD1, Pyg7, and Psa2. Biochemical approach has been performed successfully to identify assembly factor Y3IP1, the Ycf3 interaction partner, using co-immunoprecipitation with FLAG-tagged Ycf3 [102]. The combination of genetic and biochemical approaches should be instrumental in identifying new PSI assembly factors in the future.

The step-by-step assembly process of PSI remains largely unknown. This is because PSI assembly is a very rapid process. In addition, the mutation of the known genes encoding for essential PSI assembly factors leads to complete loss of the PSI complex, which makes it very difficult to identify the intermediate complex. Using partially-complemented transgenic mutants that accumulate certain levels of PSI but still can

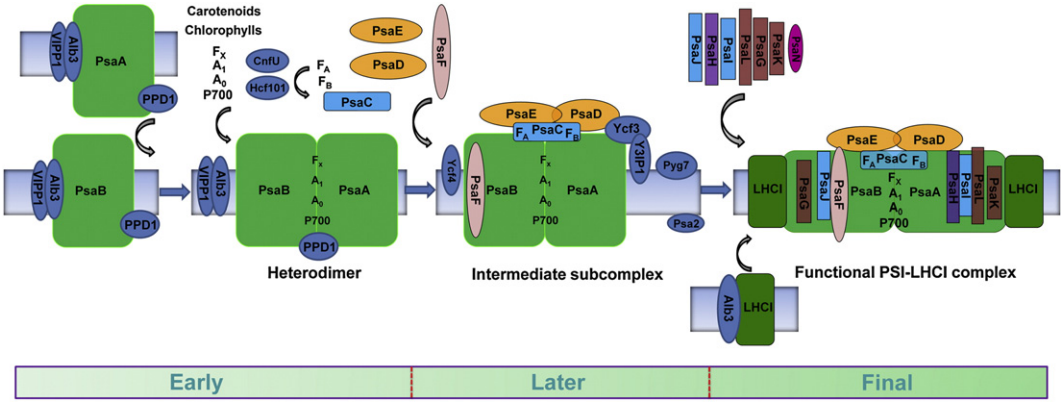

Fig. 3. A model for the assembly process of the functional PSI complex and the role of regulatory factors in PSI assembly. Ycf4 in cyanobacteria is important but not essential for PSI complex assembly while Ycf4 is essential for PSI assembly in *Chlamydomonas reinhardtii*. In cyanobacteria, Ycf37 is important but not essential for PSI assembly whereas Pyg7 is essential for PSI assembly in higher plants. RubA is essential for PSI assembly which is probably specific for the cyanobacterium *Synechococcus* sp. PCC 7002. PPD1, Y3IP1 and Psa2 are exclusive to eukaryotic organisms. See text for details. This schematic diagram for PSI assembly is according to Ozawa et al. [103] and Nickelsen and Rengstl [79].

photoautotrophically grow may allow us to isolate possible PSI assembly intermediates. Also, tag-based purification, which has been successfully used in *C. reinhardtii* to identify Ycf4-containing complex [103], may be applicable for other known assembly factors to separate discrete intermediate complexes of PSI.

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