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Research article

The PsbP and PsbQ family proteins in the photosynthetic machinery of chloroplasts

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ABSTRACT

The PsbP and PsbQ proteins are extrinsic subunits of the photosystem II in eukaryotic photosynthetic organisms including higher plants, green algae and euglena. It has been suggested that PsbP and PsbQ have evolved from their cyanobacterial homologs, while considerable genetic and functional modifications have occurred to generate the eukaryote-type proteins. In addition, number of PsbP and PsbQ homologs exist in the thylakoid lumen of chloroplasts. These homologs are nuclear-encoded and likely diverged by gene duplication, and recent studies have elucidated their various functions in the photosynthetic machinery. In this short review, recent findings and new idea about these components will be discussed.

1. Introduction

In eukaryotic photosynthetic organisms, oxygenic photosynthesis takes place in chloroplasts, in which protein complexes involved in the light-harvesting and photosynthetic electron transport are located in thylakoid membranes. Photosynthetic electron transport machinery is composed of two light-energy driven photosystems (PS), PSI and PSII, the cytochrome (Cyt) b_6f, and the ATP synthase. In linear electron transport (LET), electrons extracted from water in PSII are transported to PSI through Cyt b_6f and eventually produce NADPH. During this process, PSII oxidizes water thereby producing molecular oxygen and protons in the thylakoid luminal space. In addition, protons are concomitantly transferred from the stroma to the lumen and the resulting ΔpH is used to drive ATP production in the ATP synthase. Furthermore, ΔpH is additionally formed by cyclic electron transport around PSI (PSI-CEF), which recycles electrons from ferredoxin (Fd) or NADPH to the plastoquinone pool. In PSI-CEF, the existence of two different electron transport pathways has been demonstrated; One is an antimycin-sensitive complex including PGR5 and PGRL1 proteins (Hertle et al., 2013; Leister and Shikanai, 2013) and the other is the NAD(P)H dehydrogenase-like (NDH-like) complex (Peng et al., 2009, 2011; Ifuku et al., 2011a), both of which are suggested to interacts with PSI.

The biogenesis and regulation of the multi-subunits complexes in thylakoid membranes have been intensively studied, and recent studies suggest the importance of the proteins accumulated in thylakoid luminal space. Proteomic and genomic studies have identified up to 80 proteins in Arabidopsis to be localized in the lumen (Peltier et al., 2002; Schubert et al., 2002; Kieselbach and Schröder, 2003). Since recent review article has already described known and proposed functions of thylakoid luminal proteins in photosynthesis regulation (Järvi et al., 2013), only a brief summary on the functional category of luminal proteins is shown in Fig. 1. In addition to the major luminal proteins, such as PSI and PSII extrinsic subunits, the electron carrier plastcyanin (PC), and violaxanthin deepoxigenase (VDE), a number of proteins involved in protein folding and quality control, such as immunophilins (CYP- and FKBP-types) and Deg proteases have been identified (Schuhmann and Adamska, 2012; Gollan et al., 2012). Furthermore, several enzymes involved in the thiol/disulphide modulation has been identified, suggesting the importance of redox regulation and sensing in thylakoid lumen (Hall et al., 2010; Järvi et al., 2013); Lumen Thiol Oxidoreductase1 (LTO1) catalyzes disulphide bond formation of the PsbO subunit in PSII (Karamoko et al., 2011), and CS26 was proposed to regulate thiol oxidation by production of S-sulphocysteine in the

Abbreviation: Cyt, cytochrome; Fd, ferredoxin; FTIR, Fourier transform infrared; LHCII, light-harvesting complex II; NDH, NAD(P)H dehydrogenase; OEC, oxygen-evolving complex; PSII, photosystem II; PPD, PsbP-domain; PPL, PsbP-like; PQL, PsbQ-like.

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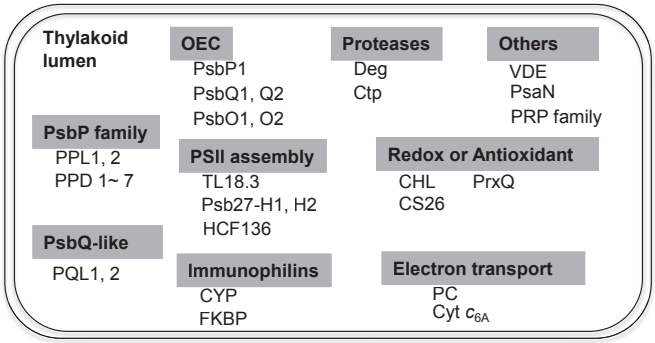

Fig. 1. Functional categories of thylakoid luminal proteins in Arabidopsis chloroplasts. Only known and proposed functions of the lumen proteins experimentally identified by proteome studies are shown. Each protein name is described in the text or as in Järvi et al. (2013).

lumen (Bermúdez et al., 2012). These facts indicate the protein interactive network in thylakoid lumen that supports functions of the photosynthetic electron transfer machinery.

In this review, I would like to focus on the PsbP and PsbQ family, one of the major protein families in the thylakoid lumen. The PsbP and PsbQ proteins are extrinsic subunits of the photosystem II in green plants including higher plants and green algae (Enami et al., 2008). It is known that the PSII extrinsic proteins have undergone quite drastic changes during the evolution of oxyphototrophs from cyanobacteria to higher plants (De Las Rivas et al., 2004; Roose et al., 2007; Enami et al., 2008). The origins of PsbP and PsbQ are thought to be their cyanobacterial homologs CyanoP and CyanoQ, respectively (Kashino et al., 2002; Thornton et al., 2004); however, it has been suggested that the molecular functions of CyanoP and CyanoQ in the oxygen-evolving complex (OEC) are largely different from PsbP and PsbQ. In red algae and diatoms, PsbQ', a 20 kDa homologue of PsbQ, is bound to PSII as an extrinsic subunits (Okumura et al., 2008; Nagao et al., 2010). In addition, diatoms have specific extrinsic subunit, Psb31, and recent structural analysis suggests that Psb31 might be a homolog of PsbQ (Nagao et al., 2013). Furthermore, genomic and proteomic studies have identified a number of PsbP and PsbQ homologs in chloroplasts. All PsbP and PsbQ homologs are nuclear-encoded and likely result from gene duplication (Roose et al., 2007). This review summarizes recent findings and new idea about their function and molecular evolution in the photosynthetic electron machinery.

2. Members of the PsbP and PsbQ family in Arabidopsis

2.1. Members of the PsbP family

The structure and function of the PsbP family proteins have recently been thoroughly reviewed (Bricker et al., 2013), and only the essence will be descried here. In Arabidopsis, at least nine members of PsbP family proteins, PsbP and eight PsbP homologs, are accumulated in thylakoid lumen (Table 1) (Roose et al., 2007; Ishihara et al., 2007; Ifuku et al., 2010). Based on the amino-acid sequence similarity with PsbP, PsbP homologs are classified into two PsbP-like proteins (PPL) and six PsbP-domain proteins (PPD) (Ishihara et al., 2007). The presence of additional members of the PsbP family, which are named as PPD7 or PPD8 have been suggested, but they have not been detected by proteome studies (Sato, 2010; Järvi et al., 2013).

Comparison of amino-acid sequences suggests that PPL1 is most closely related to CyanoP, while PsbP and the other PsbP homologs are paralogs of PPL1 (Ishihara et al., 2007; Sato, 2010; Jackson et al., 2012). Structural modeling *in silico* (Sato, 2010) suggests that all members of the PsbP family have a similar αβα structure, called a Mog1p/PsbP-like fold in SCOP: a structural classification of proteins database (Ifuku et al., 2004). On the other hand, the N- or C- terminal sequence as well as the loop region connected to the central β−sheets differ among the members (Sato, 2010). It has been suggested that this structural difference among PsbP family proteins should be related to their functional difference in the thylakoid lumen (Sato, 2010; Bricker et al., 2013). In particular, the N-terminal extension specifically found in PsbP is required for its stable interaction with PSII and for its function to retain essential Ca^{2+} and Cl^- ions in PSII (Ifuku and Sato, 2002, 2008; Tomita et al., 2009).

2.2. Members of the PsbQ family

In addition to two authentic PsbQs in PSII, Arabidopsis has three PsbQ-like (PQL) homologs (Table 1). All five PsbQ family proteins have an obvious thylakoid lumen-targeting signal, consistent with previous proteomic studies which suggested their localization in the thylakoid lumen, except for PQL3 (Peltier et al., 2002; Schubert et al., 2002; Zybailov et al., 2008). It should be noted that three PQL proteins were given different names by different groups (Peng et al., 2009; Suorsa et al., 2010; Yabuta et al., 2010), and unified names have been proposed (Ifuku et al., 2011a), which will be described in the following section. Comparison of amino-acid sequences suggests that the PQL proteins are more similar to plant PsbQ than CyanoQ, indicating the possibility that PQLs may have been differentiated from PsbQ after PsbQ had evolved from CyanoQ (Yabuta et al., 2010).

A phylogenetic analysis has investigated the evolutional relationship among PsbQ family proteins (Yabuta et al., 2010). Structural modeling indicates that all of the PQL proteins are predicted to have the four-helix bundle structure similar to PsbQ and CyanoQ (Calderone et al., 2003; Balsera et al., 2005), and only this sequence region was used to construct a reliable tree. The obtained tree

Table 1
The PsbP and PsbQ family proteins in Arabidopsis.

Protein name	Other name	Gene locus (TAIR)	Proposed function	References
PsbP1		At1g06680	OEC	Yi et al., 2007; Allahverdiyeva et al., 2013
PPL1		At3g55330	PSII repair	Ishihara et al., 2007
PPL2	PnsL1	At2g39470	NDH-like subunit	Ishihara et al., 2007
PPD1		At4g15510	PSI assembly	Liu et al., 2012
PPD2		At2g28605	Singlet-oxygen signaling (*Chlamydomonas*)	Brzezowski et al., 2012
PPD3		At1g76450		Ifuku et al., 2010
PPD4		At1g77090		Ifuku et al., 2010
PPD5		At5g11450	Strigolactone biosynthesis	Roose et al., 2011
PPD6		At3g56650		Ifuku et al., 2010
PPD7[a]		At3g05410		Sato, 2010
PPD8[a]		At5g27390		Järvi et al., 2013
PsbQ1		At4g21280	OEC	Yi et al., 2006; Allahverdiyeva et al., 2013
PsbQ2		At4g05180	OEC	Yi et al., 2006; Allahverdiyeva et al., 2013
PQL1/2	PnsL2	At1g14150	NDH-like subunit	Suorsa et al., 2010; Yabuta et al., 2010
PQL2/1	PnsL3	At3g01440	NDH-like subunit	Suorsa et al., 2010; Yabuta et al., 2010
PQL3[a]		At2g01918	NDH-like activity	Yabuta et al., 2010

[a] Protein expression in the thylakoid lumen was not confirmed by the proteome studies.