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Minireview

Dynamics of the cyanobacterial photosynthetic network: Communication and modification of membrane protein complexes

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ABSTRACT

Cyanobacterial photosystem 2 and cytochrome b_6f complexes have been structurally resolved up to the molecular level while the adjustment of their function in response to environmental and intracellular parameters is based on various modifications of these complexes which have not yet been resolved in detail. This minireview summarizes recent results on two central modifications for each complex: (a) for the cytochrome b_6f complex the implication of PetP, a new subunit, and of three copies of PetC, the Rieske protein, for the fine-tuning of the photosynthetic electron transport is evaluated; (b) for photosystem 2, the heterogeneity of the D1 subunit and the role of subunit Psb27 is discussed in relation to stress response and the biogenesis/repair cycle. The presented "dynamic" models for both complexes should illustrate the need to complement structural by more extensive functional models which consider the flexibility of individual complexes in the physiological context – beyond structure.

Introduction

All major membrane protein complexes of the cyanobacterial electron transport (ET) network (Fig. 1), i.e. photosystem 2 (PS2), cytochrome b_6f complex (Cyt b_6f) and photosystem 1 (PS1), have been structurally well characterized (Baniulis et al., 2009; Ferreira et al., 2004; Guskov et al., 2009; Jordan et al., 2001; Kamiya and Shen, 2003; Kurisu et al., 2003; Loll et al., 2005; Stroebel et al., 2003; Yamashita et al., 2007). However, substantial information on the dynamics and on modifications of these complexes in their native environment, i.e. the thylakoid membrane (TM), is still missing. This includes the regulation of their biogenesis and degradation as well as the "communication" (crosstalk) of these complexes within their membrane or between membranes, i.e. the cytoplasmic membrane (CM) and the thylakoid membrane.

After all, the available 3D structures of the isolated complexes represent only a "snapshot", i.e. one dominating complex which has been isolated and purified under certain conditions from the (native) membrane, while several other, less prominent modifications of these complexes co-existing at the same time in the membrane, are missing: due to lower abundance and/or instability they may be more difficult to find, isolate and characterize. Also, components which are attached to these complexes which may represent important intermediates in biogenesis, degradation or adaptation to environmental conditions may have been lost in the course of (harsh) purification procedures which are required for crystallization purposes. For this reason it may be worthwhile to focus on such complexes which may also be important for the communication within the components of the ET chain by providing a quick response towards internal and external changes.

Starting from a gallery of co-existing intermediate complexes, which may be found adjacent to routine preparation procedures, their quantity may be increased by choosing either milder isolation procedures or by exposing the cells to various stress conditions. Structural and functional characterization of these new complexes may then be combined with the creation of deletion mutants, heterologous overexpression, and also with pulse labeling studies to find out about the sequence of events in correlation with the appearance and disappearance of these components.

In this contribution we focus on heterogeneity of PS2- and Cyt b_6f complexes in cyanobacteria, namely in the mesophile *Synechocystis* sp. PCC 6803 (*S.*6803) and the thermophile *Thermosynechococcus elongatus* (*T. elongatus*) which are both well characterized in respect of their genomic sequence and the structure of their intrinsic photosynthetic membrane proteins, respectively.

New structure–function relationships of cyanobacterial Cyt b_6f (beyond the crystal structure)

3D structures of the Cyt b_6f complex from the green algae *Chlamydomonas reinhardtii* and two cyanobacteria, *Mastigocladus*

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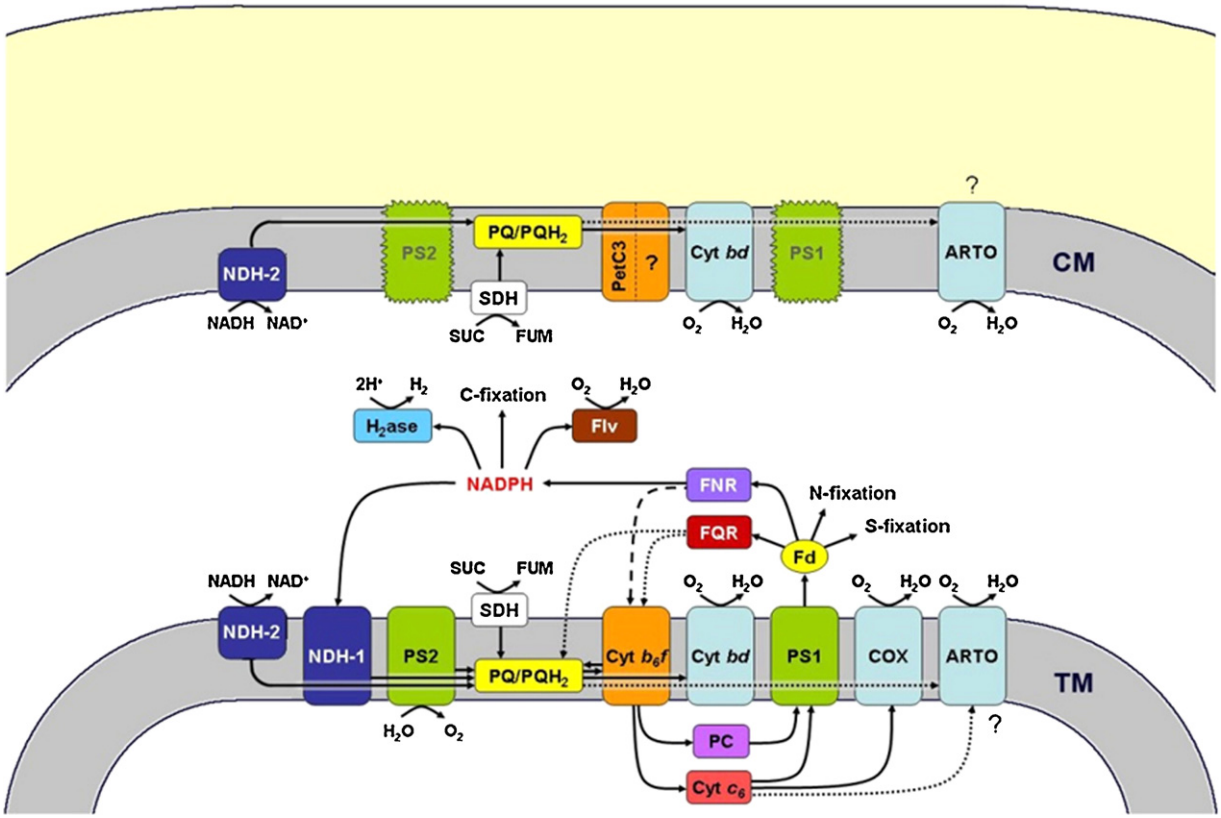

Fig. 1. Major components and routes of the cyanobacterial ET network in the CM and TM of *Synechocystis* sp. PCC 6803. ET processes in the CM (upper part) must be limited due to incomplete or missing components. Question marks and dotted lines indicate that localization and substrate of the alternative terminal oxidase (ARTO) as well as the ET route of plastoquinol (PQH_2) reduction *via* ferredoxin:plastoquinone (Fd:PQ) oxidoreductase (FQR) are still to be identified. The dashed line shows the proposed direct Cyt b_6f-reduction *via* Fd/FNR. COX, cytochrome *c* oxidase; Cyt *bd*, cytochrome *bd* oxidase; H_2ase, hydrogenase; Flv, flavoprotein-1 and -3 (Helman et al., 2003), Allakhverdieva et al., manuscript in preparation; FNR, Fd:$NADP^+$ oxidoreductase; NDH-1 and -2, type I and II NADPH dehydrogenase, respectively; PC, plastocyanin; SDH, succinate dehydrogenase. For further details and references, see Bernát and Rögner (in press).

laminosus and *Nostoc* sp. PCC 7120, are available at 3.1 and 3.0 Å resolution, respectively (Baniulis et al., 2009; Kurisu et al., 2003; Stroebel et al., 2003; Yamashita et al., 2007). They all show a functional dimer of two monomers linked by domain swapping. Each monomer consists of four large (17.5–32 kDa) subunits [Cyt *f* (PetA), Cyt b_6 (PetB), the Rieske 2Fe–2S protein (PetC) and subunit IV (PetD)] and four small subunits (3.3–4.1 kDa; PetG, -L, -M and -N) at unit stoichiometry. While most of these subunits are encoded by single genes, the Rieske protein is encoded by a gene family in most cyanobacteria (Schneider et al., 2002, 2004a,b); for a review see (Schneider and Schmidt, 2005); besides, two putative b_6 polypeptides are reported in *Gloeobacter violaceus* (Dreher et al., 2010; Nakamura et al., 2003). Beyond the eight Cyt b_6f subunits which can be identified in all X-ray structures, there is evidence for additional protein components which may interact transiently with the Cyt b_6f complex: in higher plants, Cyt b_6f has been co-isolated with ferredoxin:$NADP^+$ oxidoreductase (FNR) (Zhang et al., 2001), and the functional coupling of a small phosphoprotein, PetO (Hamel et al., 2000) to Cyt b_6f has also been reported. In cyanobacteria, PetP has been proposed as a new cyanobacterial Cyt b_6f subunit (Gendrullis et al., 2008; Volkmer et al., 2007) which might be analogous to PetO. However, the role of PetC (and PetB) heterogeneity and the function of the weakly bound PetP in cyanobacteria are still unknown.

According to mutagenesis studies, the minimal functional Cyt b_6f should consist of six essential subunits: Cyt *f*, Cyt b_6, the Rieske 2Fe-2S protein, subunit IV, PetG, and PetN. It has been shown that deletion of PetP or two *bona fide* small subunits, PetL and PetM – although they have an impact on the ET properties – keep the Cyt b_6f complex functional (Schneider et al., 2001, 2007a,b; Volkmer et al., 2007), while deletion of any other subunit is lethal. Decreasing b_6f activity or a normal b_6f activity with inability to effectively oxidize an over-reduced PQ-pool seems to have a high impact on the activation/activity and abundance of the Cyt *bd* oxidase: this enzyme can partly take over the role of Cyt b_6f in PQH_2-reoxidation as could be shown by deletion of the subunits PetM and PetC1 from Cyt b_6f (Schneider et al., 2001, 2004a,b; Tsunoyama et al., 2009) and by stress conditions such as high light (HL) or glucose treatment (Berry et al., 2002; Gendrullis et al., 2008), respectively. In this section we shortly summarize the most prominent results on the new PetP subunit (in both *T. elongatus* and *S.*6803) and on the multiple Rieske proteins (in *S.*6803).

PetP as a new subunit of the meso- & thermophilic cytochrome b_6f complex

Highly purified Cyt b_6f complexes from *S.*6803 and *T. elongatus* contain a potential new Cyt b_6f subunit with a molecular mass of 7.2 and 7.1 kDa, respectively, coined PetP, i.e. the 9th Cyt b_6f subunit (Gendrullis et al., 2008; Volkmer et al., 2007). This polypeptide is highly conserved in cyanobacteria and encoded by the open reading frames (ORFs) *ssr2998* and *tsr0524* in *S.*6803 and *T. elongatus*, respectively (Volkmer et al., 2007). Sequence analysis predicted PetP as a cytoplasm-localized soluble protein. The absence of this subunit in all up to now published cyanobacterial structures suggests, that PetP is loosely/temporarily associated with the complex, similar to PetO of the plastid Cyt b_6f complex (Hamel et al., 2000). However, in contrast to PetO, PetP is apparently not a phosphopro-