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Mini Review Article

Role of Phycobiliprotein Antenna of Cyanobacteria, Red and Cryptophyte Algae in Association with Photosystems I and II

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ABSTRACT

Phycobiliproteins are photosynthetic antenna pigments of cyanobacteria and red algae, where they are assembled in macromolecular supercomplexes of phycobilisomes (PBS)s, as well as of cryptophyte algae, where they exist in the form of dimers. The absorbed light energy transfer from phycobiliprotein antenna to the photosystem II (PS II) is well known since the first studies in this field and is highly effective reaching 95-100%. However, interaction of phycobiliproteins with the photosystem I (PS I) is subject for discussion. Here, various data on energetic coupling of PBSs and phycobiliproteins with the PS II and PS I in photosynthetic organisms are discussed.

Keywords: Cryptophyte algae; Cyanobacteria; Energy transfer; Photosystem I; Photosystem II; Phycobilisome; Phycobiliproteins; Red algae

INTRODUCTION

All oxygenic photosynthetics have three types of pigment-protein complexes in their photosynthetic apparatus. First and foremost come complexes of photosystem I (PS I) and photosystem II (PS II) with reaction centers; second, there are various kinds of antennae fulfilling the role of light energy absorption and its subsequent transfer to photoactive complexes. Three groups of photosynthetics, cyanobacteria, red and cryptophyte algae possess the water-soluble phycobiliprotein antennae. In cyanobacteria and red algae, phycobiliproteins are organized in giant macrocomplexes of phycobilisomes (PBS)s , while in chloroplasts of cryptophyte algae the bphycobiliproteins are present in the form of relatively small protein dimers. To ensure the effective energy transfer, phycoiliproteins are attached to the thylakoid membrane in regions of intra-membrane PS I and PS II arrangement. PBSs are localized on the cytoplasmic side of the membrane; phycobiliprotein dimers of cryptophytes are revealed to be inside the chloroplast lumen.

ENERGY TRANSFER FROM PBS TO PS II

PBS is unconditionally considered to be an external antenna of PSII, which was demonstrated several times by different spectral methods in cyanobacteria and red algae. The energy transfer was demonstrated in vivo by: i) the action spectra of photoreaction II revealing PBS activity, ii) the low temperature fluorescence emission spectra containing PS II-chlorophyll bands under excitation in the PBS absorption region, iii) the fluorescence excitation spectra of PSII antennal chlorophyll dominated by PBS-belonging bands. It was also revealed for various species of cyanobacteria by the time-resolved fluorescence spectroscopy [1-4].

The hemidiscoidal cyanobacterial PBS and PS II interact within the flat cytoplasmic surface of PS II dimer and the bottom surface of the PBS core [1,5,6]. Only the dimeric form of PS II being equal to PBS surface guaranties a stable binding, whereas monomeric PS II is not able to bind PBS properly [1,7]. A supercomplex of the PBS core and PS II can be isolated by mild detergent treatment [8], although its fine structure has not been determined experimentally, as well as the molecular structure of the PBS core remains not fully elucidated [5,8]. Some structural details of PBS-PS II megacomplex were revealed by cryo-EM and cross-linking/mass-spectrometry techniques [3,6,7]. Two long-wavelength chromophorylated ApcD and ApcE polypeptides present in bottom allophycocyanin cylinders of the PBS core are known as the terminal emitters functioning as the final steps of energy transfer from PBS to PS II [3,4]. Besides that, ApcE, also known as LCM or anchor protein, forms a special docking site in PBS attachment to the PS II dimer [9]. At present, determining the docking sites between PBS and PSII and the energy transfer calculations are limited to spatial modeling based

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on the existing crystallographic data of PS II dimers and high-resolution EM data of hemidiscoidal PBS structure [6,10,11].

ENERGY TRANSFER FROM PBS TO PS I

Earlier assumptions of the PBS role as an external antenna of PS II were based on the putative compensation that antennal pigments provide for both relatively high PS I/PS II ratio in the cyanobacterial and red algal cells and on the shortage in chlorophyll content of PSII [12]. Later, this opinion changed when it became to reveal photooxydation P700 being the exceptional for PS I in the light absorbed by PBSs [13,14]. These results were supplemented as well by measuring the action spectra of PS I-dependent reversible photoinhibition of respiration in cells of cyanobateria irrefutably proving the energy transfer PBS → PS I [2]. All other spectral methods used in studies of PBS-PS II interaction turned out to be useful in case of PS I and had also shown, that PBSs transfer the absorbed energy to PS I. 77 K emission spectra of chlorophyll measured under the excitation of PBSs, in addition to fluorescence peaks of PS II, usually reveal a distinct peak at 715-730 nm belonging to PS I, while the long-wavelength PS I fluorescence excitation spectra exhibit maxima attributed to phycobiliproteins. Time-resolved 77 K fluorescence emission spectra of cyanobacteria measured under excitation of PBSs show an increase of PS I and PS II chlorophyll emissions developed in parallel [2,15]. Efficient energy transfer from PBSs to chlorophyll has been found in cyanobacterial heterocysts that lack PS II and possess PS I [16]. In the obtained PS II-less mutants of cyanobacteria PBSs stay bound in the intact form to the photosynthetic membrane [17]. Besides, the purified PBS samples incorporate significant amounts of ferredoxin: $NADP^+$ reductase, an extrinsic membrane protein functionally connected to PS I [18].

In summary, the contribution of PBSs feeding energy to PS I is considered to be proved giving rise to three models of energy transfer from PBS to PS I, reviewed in [14]: i) “spillover” model; ii) ternary PBS-PSII-PS I complex formation; iii) direct energy migration from the PBS to PS I without PS II being involved. It should be specified that, in red algae thylakoids, the PS I exists in a monomeric form [19] and, in cyanobacteria, PS I mainly forms trimers with a certain share of monomers [20]. Computer modeling demonstrated the docking of PBS to PS I monomer only, corresponding to a realization of energy transfer between these two pigment-protein complexes [10]. In contrast to the PSII dimers [1], the surface of the PSI shows a major protrusion of three hydrophilic polypeptide subunits (PsaC, PsaD, and PsaE), which extends into the cytoplasm [21] and prevents a tight binding of PBS to PS I trimer due to its threefold symmetry [10].

ApcD is necessary for efficient energy transfer from PBSs to PS I [22]. PS I is highly sensitive to any shortcomings in PBS functioning. When, for some reason, altered conventional PBSs in the mutant cyanobacterial cells cannot properly attach to the thylakoid membrane the energy feeding of PS I is realized by small cylindrical PBS anchored to PS I by the synthesized special linker CpcG2 polypeptide [23-27].

ENERGY TRANSFER FROM PHYCOBILIPROTEINS TO PS II IN CRYPTOPHYTES ALGAE

Unlike cyanobacteria or red algae, the phycobiliproteins of cryptophytes do not assemble in PBS megacomplexes with the mass of several million Daltons but form ($\alpha 1 \beta \alpha 2 \beta$)-polypeptide heterodimers with the relatively small mass of ~60 kDa [11]. Each species possess one of seven unique for cryptophyte algae phycobiliproteins that complement in antenna function the Chl a/c-protein also present in chloroplasts, like in all other representatives of Chromophyta [3]. In contrast to PBSs, the heterodimers are not localized on the stromal surface of the thylakoid membrane but occupy the entire space of the lumen and are most likely assembled into cylindrical structures oriented perpendicular to the thylakoid membrane [16,17]. Isolation of the thylakoid membrane fragments followed by cryo-EM microscopy demonstrated that antennal chlorophyll a/c-proteins are connected in thylakoids with the PSI monomers and PS II dimers [28]. Unfortunately, simultaneous isolation of water-soluble phycobiliproteins and membrane proteins (the PS II, PS I, or Chl a/c-protein) is challenging [29]. Thus, further studies are required to find an answer to this conundrum.

Migration of energy from phycobiliproteins to total chlorophyll a in the cell was revealed using steady state spectroscopy [30]. Stationary fluorescence emission and excitation spectra of cells were recorded at room and low temperature, when the fluorescence was associated either predominantly with chlorophyll a of the PS II or with chlorophyll of both photosystems [31,32]. The energy transfer pathways either direct or mediated through chlorophyll a/c-protein were suggested but the possibility of energy migration exclusively to the PS II or also to the PS I remained under examination [33]. Superfast fluorescence measurements and global spectral analysis of the fluorescence emission were performed in a wide spectral range [34] that allowed the possible distribution of the absorbed energy between the photosystems.

Therefore, several factors did not allow to draw the definite conclusions about the possible association between phycobiliproteins and photosystems. First, the presence of two antennae, Chl a/c-protein and phycobiproteins, is unique for chloroplasts and provide for their hinder overlapping absorption and fluorescence spectral bands. Second, standard for many cryptophyte algae species absence of long-wavelength chlorophyll a forms in PS I does not allow to discriminate between PS I and PS II. Therefore, the stationary fluorescence emission spectra, the degree of photooxidation of the reaction center P700, and the action spectra of both photosystems were measured simultaneously and compared in one species, *Rhodomonas salina* [35].

Only in the third case, recording of the action spectra of photosynthetic activities, which has not been used earlier for investigating the pigment apparatus in cryptophytes, finally yielded conclusive evidence (Figure 1).

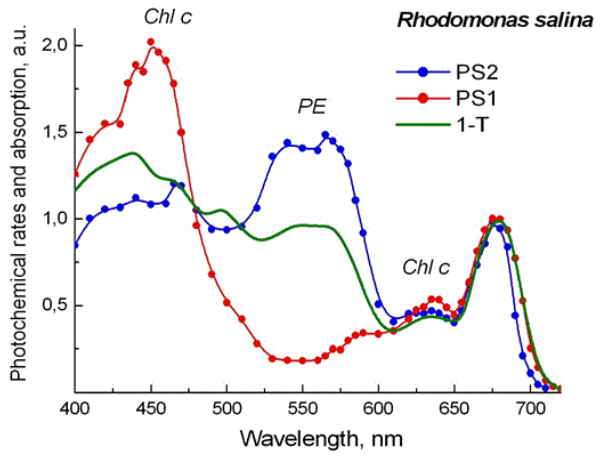

Figure 1: Action spectra for photoreactions I (PS1, red) and II (PS2, blue) normalized to the red chlorophyll a peak of the *Rhodomonas salina* absorption spectrum (1-T, green). Bands belonged to phycobiliprotein (PE - phycoerythrin) and chlorophyll c (Chl c) of chlorophyll a/c-protein are designated. Absence of phycobiliprotein association with PS1 is seen clearly. The figure taken from [35] with alteration. For details of measurements see [35,36].

An advantage of this method over the others, is that the pattern of the action spectrum containing all pigment bands of each photosystem repeats the spectrum of its absorption *in vivo* not influenced by the presence of the other photosystem [2,36]. As a result, it was established that the exceptional association of phycobiliproteins with the PS II is the defying difference from PBSs, present in cyanobacteria and red algae [37].

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