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Review article

STRUCTURAL ORGANIZATION AND FUNCTIONS OF PHYCOBILIPROTEINS IN CYANOBACTERIA

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ABSTRACT: In this review an attempt has been made to explain the various types of phycobiliproteins and their functions in cyanobacteria. These phycobiliproteins contain linear tetrapyrrole rings attached to apoprotein through thioether linkage. They are involved in the transfer of light energy from phycobiliproteins to chlorophyll a of photosystem II. In addition, they vary the pigment content in response to variation in light quality. Phycobilisomes also act as nitrogen reservoir and help the organism to meet stress conditions.

Key words: Allophycocyanin, Chromatic adaptation, Energy transfer, Phycobilisomes, Phycocyanin, Phycoerythrin, Nitrogen reservoir.

Abbreviations: APC – Allophycocyanin; Chl *a*- Chlorophyll a; PBP- Phycobiliprotein; PC – phycocyanin; PS-Photosystem.

Cyanobacterial photosynthesis

Cyanobacteria are oxygenic photosynthetic prokaryotes whose photosynthetic apparatus shows resemblance to those of higher plants. Plants and cyanobacteria contain similar photosystem (PS) II and photosystem I reaction center complex. Phycobilisomes (PBsomes) are major light harvesting complex (LHC) proteins in PS II of cyanobacteria and transfer the energy to photochemical reaction center to perform photosynthesis. In addition to this, some of the cyanobacteria are able to fix nitrogen. Hence they are known as 'Biofertilizers'.

Cyanobacterial photosynthetic pigments:

Chlorophyll a:

All cyanobacteria possess Chl *a* (chlorophyll) as the major pigment. It is believed that Chl *a* occurs in vivo in several spectroscopic forms. Chl *a* 660, Chl *a* 670, Chl *a* 680, Chl *a* 685, Chl *a* 690 and Chl *a* 700-720 nm. The number indicates their red absorption maximum of each of the spectral forms [1 and 2]. The strongly fluorescing short wavelength forms of Chl *a* are mainly present in PS II. The weakly fluorescing long wavelengths forms are mostly present in PS I. In cyanobacteria Chl *b* is absent.

Carotenoids and Xanthophylls:

Almost all cyanobacteria contain the yellow and orange pigments called carotenoids and xanthophylls respectively, which act as accessory pigments in photosynthesis. The action spectrum of photosynthesis demonstrates that light energy absorbed by carotenoids is utilized with varying degrees of efficiency in photosynthesis. The light energy absorbed by the carotenoids is not used directly but transferred to Chl *a* where it is efficiently used in the photosynthetic process [3 and 4].

Phycobilins:

In cyanobacteria, the PS II contains only small fraction of Chl *a*. The major light harvesting pigments are phycobilins. There are three types of phycobilins e.g phycocyanobilin and phycoerythrobilin. The structures of these chromophores are shown in Fig.1. These are linear tetra pyrrolo rings which are attached to the cysteine amino acid of the apoprotein by thioether linkages. In cyanobacteria only phycoerythrobilin and phycocyanobilin are present. In red algae in addition to phycoerythrobilin, a second chromophores group is present which is known as phycourobilin.

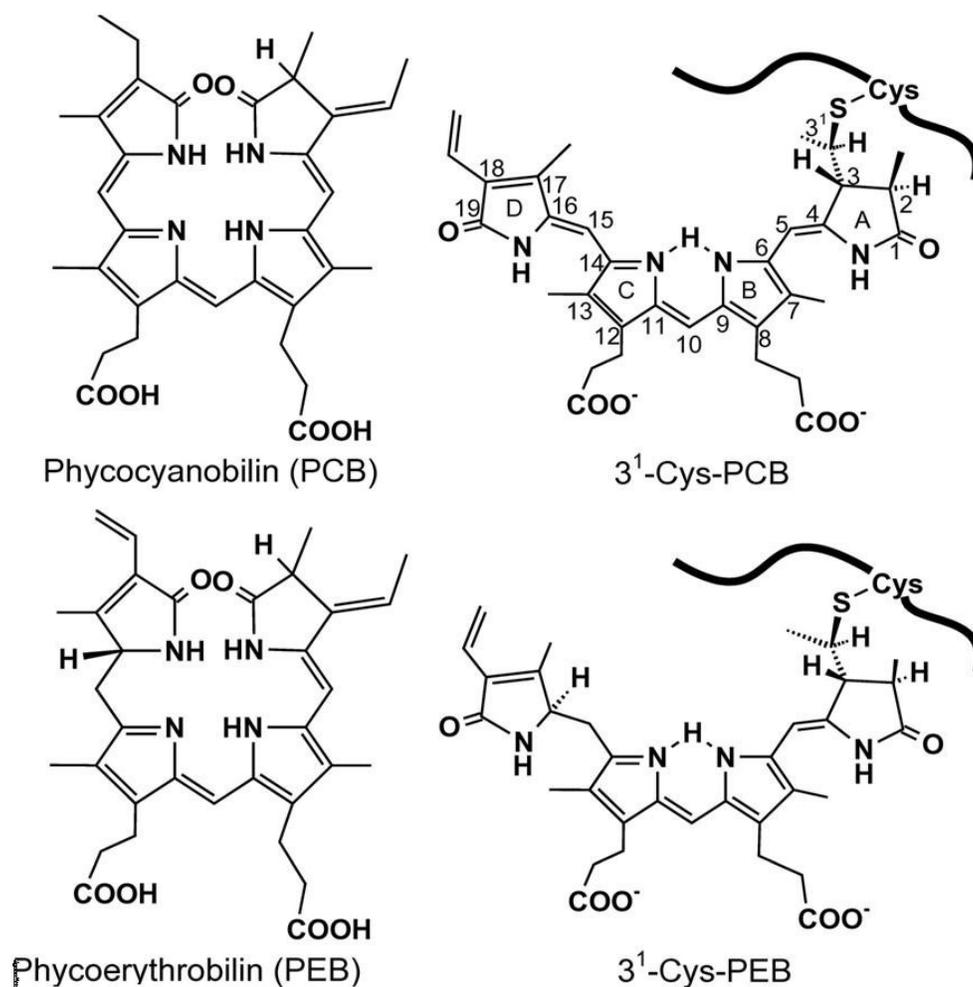


Fig 1: Structures of free (Left) and bound (Right) PCB and PEB. (Compiled by Zhao et al., 2007 [23])

Phycobiliproteins-subunit composition and spectral characteristics:

Cyanobacteria, red algae and cryptomonads contains unique light harvesting pigment proteins called phycobiliproteins (PBP) which are absent in higher plants. Unlike higher plant light harvesting chlorophyll proteins, these PBPs are packed in multimeric pigment protein complexes called PBsomes located on the stromal surface of the thylakoid membrane. Several workers have reviewed the various aspects of PBsome structure and function [5, 6, 7, 8,9,10, and 11].

Types of biliproteins and their occurrence:

The major components of PBsomes are the bilin-containing proteins: Phycoerythrin (PE), phycocyanin (PC) and allophycocyanin (APC). The last two pigment proteins are universally present in all cyanobacteria and red algae [12], while PE is a variable component and its presence is regulated by the available quality of light [13 and 14]. In cyanobacteria another pigment protein called phycoerythrocyanin (PEC) replaces the PE whose synthesis is regulated only by light quantity not by quality [14 and 15]. These phycobiliproteins collectively absorb light in green, orange and red region of the spectrum allowing these organisms, which contain them to carry out photosynthesis.

Structure and spectral properties of the Biliproteins:

All the biliproteins are composed of an apoprotein portion to which linear tetrapyrrole structures are linked by cysteine thioether bonds [16]. The spectral properties and subunit composition of the individual phycobiliproteins are listed in Table 1 and 2. The diversity of spectral properties of PBPs results largely from the environment of chromophore conferred by the apoprotein rather than the structural properties of the chromophore itself. In addition to this, spectral properties of the biliproteins will be determined by the participation of the specific polypeptides in the formation of higher aggregate state [17 and 18]. The protein portion of the PBPs consists of two dissimilar polypeptides designated as α , β which occur in 1:1 ratio in all PBPs [19]. Additional polypeptides are also present B-PE and R-PE [20]. The building block for PBPs is the monomer ($\alpha\beta$). It generally exists either as trimer ($\alpha\beta$)₃ or hexamer ($\alpha\beta$)₆ which are common aggregation states. Amino acid sequences for the α and β subunits of biliproteins from the cyanobacterium *Mastigocladus laminosus* revealed that there is a 64% homology between subunits of PC whereas it shows 26% homology with α subunit of APC. The β subunit of PEC exhibits 67% homology with this in C-PC and only 37% homology with the β subunit of APC [21 and 22]. These results suggest that the degree of sequence conservation strongly control the functional properties of these biliprotein subunits.

**Table: 1 Spectral properties of various phycobiliproteins in cyanobacteria
(Adopted from Bryant, 1991 [24])**

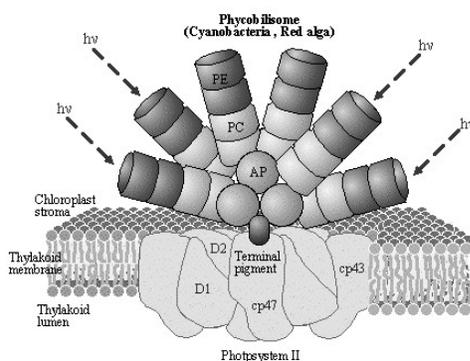
Biliproteins	Source	Absorption peak / shoulders (nm)	Fluorescence maxima (nm)
C – PE	Cyanobacteria	540,575	577
R – PE	Red algae	567,538,498	578
b – PE	Red algae	545,563	570
B – PE	Red algae	545,563,498	575
PEC	Cyanobacteria	568,590	610
C – PC	Cyanobacteria	620	642
R – PC	Red algae	617,555	636
APC	Cyanobacteria Red algae	650,620	660
APC	Cyanobacteria Red algae	654,610	680
APC B	Cyanobacteria Red algae	671,618	680

**Table 2: Polypeptide composition of phycobiliproteins in cyanobacteria
(Adopted from Bryant, 1991[24])**

Biliproteins	Source	Subunit composition and possible aggregation stages	Phycobilin chromophore type and number per subunit		
			α	β	γ
C – PE	Cyanobacteria	$(\alpha\beta)_3 (\alpha\beta)_6$	α	β	γ
R – PE	Red algae	$(\alpha\beta)_6 \gamma$	2 PEB	3 PEB	-
b – PE	Red algae	$(\alpha\beta)_n$	2 PEB	2 PEB & 1 PUB	1 PUB & 1 PUB
B – PE	Red algae	$(\alpha\beta)_6 \gamma$	2 PEB	3 PEB	-
PEC	Cyanobacteria	$(\alpha\beta)_3$	2 PCB	3 PEB	2 PUB & 2 PUB
C – PC	Cyanobacteria	$(\alpha\beta)_3 (\alpha\beta)_6$	2 PEB	2 PCB	-
R – PC	Red algae	$(\alpha\beta)_3$	1 PCB & PEB	2 PEB	-
APC	Cyanobacteria Red algae	$(\alpha\beta)_3$	1 PCB	1 PCB & 1 PCB	-
APC	Cyanobacteria Red algae	$(\alpha\beta)_3 \gamma$	1 PCB	1 PCB	-
APC B	Cyanobacteria Red algae	$(\alpha\beta)_2 (\alpha\beta)^*$	1 PCB	1 PCB	1 PCB

The molecular architecture of cyanobacterial phycobilisomes:

The most commonly occurring structure called hemidiscoidal is found in both red algae [26] and cyanobacteria [25]. The model for this type of PBsomes is made of two distinct domains; a core made up of in *Synechococcus* 6301; [26] or three (all other cyanobacteria) cylindrical objects which contain APC from which six rods made up of stacked discs. Other phycobiliproteins extend in a hemidiscoidal array (Fig. 2). The discs proximal to core contain PC, whereas discs distal to the core contain PE. The structure and intactness of the PBsome will be maintained by certain colourless polypeptides which are known as linker polypeptides in addition to the phycobiliproteins [28, 29 and 19].



**Fig 2: Hemidiscoidal Structure of phycobilisome in cyanobacteria
(Modified from Bryant et al., 1979 [25])**

Linker polypeptides - their role in structural organization:

The structure of PBsome is maintained both by hydrophobic interactions between components in this biliprotein aggregate [30 and 31] and by several linker polypeptides which are first described by Tandeau de Marsac and Cohen- Bazire (1977) [28]. The linker polypeptides have been divided into three groups depending on their functions and molecular weights (Tandeau de Marsac and Cohen-Bazire, 1977) [28]. The group I polypeptides vary in the molecular weights depending on the organism used and isolation procedure followed. These types of polypeptides are involved in the attachment of PBsomes to the thylakoid membrane. The group I polypeptides from three organisms: *Synechococcus* 6301 [17] *Prophyridium cruentum* [32] *Nostoc* sp [30] *Spirulina platensis* [33] has molecular weights 75, 95 and 95 kDa respectively.

It was also shown that phycocyanobilin chromophore is presenting these polypeptides. The structural properties of these pigments suggested that they act as terminal acceptor of excitation energy transfer in the PBsome [34, 35 and 36]. Group II polypeptides have the molecular weights ranging from 30 to 70 kDa. It varies in different organisms from two in *Synechococcus* 6301 [37] to six in *Prophyridium cruentum* [32]. The function of these polypeptides is to maintain rod structures in both PE-PC rods. The number of the group II polypeptides varies depending on the light under which the organisms are grown [38 and 39]. Glazer (1982) [40] has suggested that group II polypeptides have dual functions of linking' two trimers to form hexamers and joining separate hexamers to form rods. Group III polypeptides which are having molecular weights of 25 to 30 kDa [28] are involved in attaching rods to the APC core. They may also join two trimers of PC to form hexamer which is directly linked to the APC core [40]. Reconstitution studies in *Nostoc* sp provided the direct evidence for the involvement of group III polypeptides to attach PC hexamers to APC core [41]. In addition to the above mentioned linker polypeptides (10 and 19 kDa) have been isolated from the PBsomes of *Nostoc* sp [39]. They are most likely to be the core components of APC which are isolated with APC.

Functional aspects of the phycobilisomes:**Energy transfer:**

The molecular architecture of the PBsome is such that the excitation energy absorbed by these phycobiliproteins is transferred to the PS II reaction center with an efficiency of approximately 80-90%. In earlier studies to deduce the sequence of the energy transfer, the controlled dissociation in reduced ionic strength buffer was used. These studies indicated that there is a stepwise energy transfer of excitation energy as shown in the following sequence [42, 43, 44 and 45].

Later Porter's group have applied pico second time-resolved spectroscopy to study the sequential energy transfer in higher plant Chl antenna [46] as well as in PBsome containing organisms [47]. These studies allowed direct measurement and confirmation of proposed sequential energy transfer. Picosecond (ps) time-resolved energy transfer studies by Wendler et al., (1984) [48] using a laser dye are also in agreement with the findings of Porter's group supporting the fact that the energy transfer occurs from PE to PC to APC. Since the initial studies of Porter's group with red algae, These picosecond time-resolved measurements have been extended to several related systems such as the intact cells of several species of cyanobacteria [49 and 50], red algae [47 and 51], isolated PBsomes [52 and 49] and PBsome components [53 and 36]

The data obtained through the use of time-resolved fluorescence and absorption spectroscopy supports an arrangement of chromophores ordered within the PBsome such that homo transfer is minimized and the flow of energy is polar, directed towards the PBsome terminal emitter. This directional energy transfer in PBsome is possible by several structural features 1). The biliproteins of each type contains both s and f (sensitizing and fluorescing) chromophores [54]. The f chromophores of PE become sensitizers in the transfer of excitation energy to PC in PE-PC hetero aggregates or PBsomes.

Transfer is more rapid among hetero aggregates than among homo aggregates [18 and 50]. Glazer et al., (1985) [49] suggested that rate limiting step in PBsome is the transfer of excitation energy from one disc to new disc within the PBsome rod; 2). The rod sub-structure of PBsome creates six separate domains so that inter-rod transfer of energy is prohibited by distance constraints; 3) Transfer within the rod is directional. Energy difference between different rod elements and the core minimize reverse energy transfer and allow the long wavelength absorbing core to serve as efficient traps. This molecular architecture of PBsome described ensures that random walking is minimized and they exist the directional energy transfer to the final emitter in the core of the PBsome. Environmental factors affect the energy transfer (phycocyanin to chlorophyll a) in cyanobacteria:

The light energy absorbed by PBsome is transferred to the reaction centre (RC) of PS II through the antenna chlorophylls [55 and 56]. A variety of environment factors are known to affect the efficiency of energy transfer from PC to Chl a by affecting the pigment protein interaction i.e. heat treatment [57], nitrogen stress [58], low temperature [59] and mercury (heavy metal) stress [60].

Chromatic adaptation:

Variations in the pigmentation of cyanobacteria, that result from different illumination conditions is known as complementary chromatic adaptation [13 and 61]. Cells grown in red light appear to be blue green in colour due the presence of only PC in their PBsome rods. Transfer of these cells to green or cool white fluorescent light leads to the development of a brown pigmentation indicating the presence of both PE and PC. Thus, PBsomes are helpful to the organism to adapt to different qualities of light.

Nitrogen reservoir:

The PBsomes are made up of PBPs which rich in nitrogen content. During stress conditions, cyanobacteria degrade PBPs to release essential amino acids to synthesize proteins to support the metabolic activity. Thus PBsomes play the role as nitrogen reservoirs [62].

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