INTERNATIONAL JOURNAL OF PLANT, ANIMAL AND ENVIRONMENTAL SCIENCES
IJPAES
VOLUME-2, ISSUE-2 APRIL-JUNE-2012 ISSN 2231-4490

Coden : IJPAES www.ijpaes.com

Received: 4th Feb-2012 *Revised: 9th Feb-2012* *Accepted: 12th Feb-2012*

Review article

STRUCTURAL ORGANIZATION AND FUNCTIONS OF PHYCOBILIPROTEINS IN CYANOBACTERIA

Ayyaraju Middepogu[1]. Murthy S.D.S[1]* and Prasanna Reddy.B[2]

[*1]Department of Biochemistry, Sri Venkateswara University, Tirupati -517 502, A.P. India.
[2]Department of Quality Control, Nosch labs Pvt Ltd, Hyderabad, India

Corresponding author : E-mail: sdsmurthy@rediffmail.com

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 pyrrolerings 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.

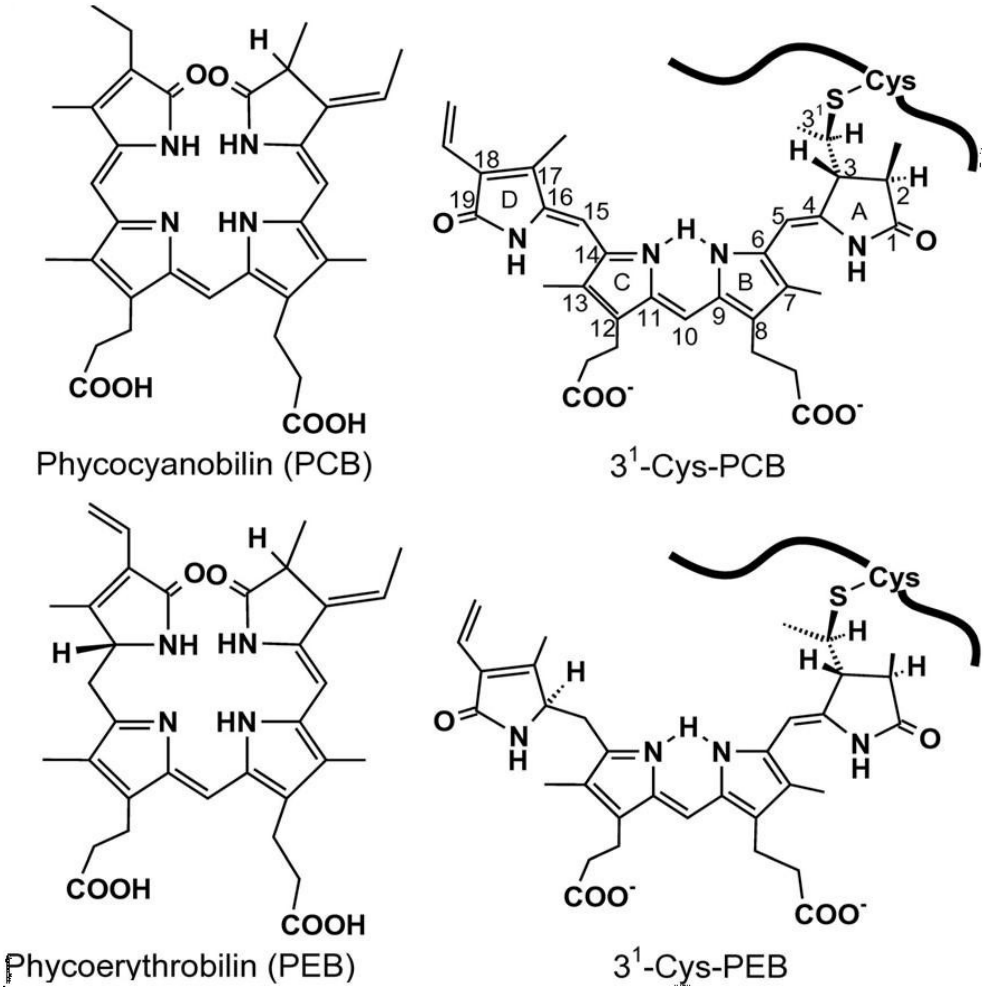

Fig 1: Structures of free (Left) and bound (Right) PCB and PEB. (Complied by Zhao et al., 2007 [23])

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 1and 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: l ratio in all PBPs [19]. Additional polypeptides are also present B-PE and R-PE [20]. The building block for PBPs is the monomer (αβ). It generally exists either as trimer $(\alpha\beta)_3$ or hexamer $(\alpha\beta)_6$ which are common aggregation states. Aminoacid sequences for the α and β subunits of biliproteins from the cyanobacterium Mastigocladus Iaminosus 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 submit		
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].

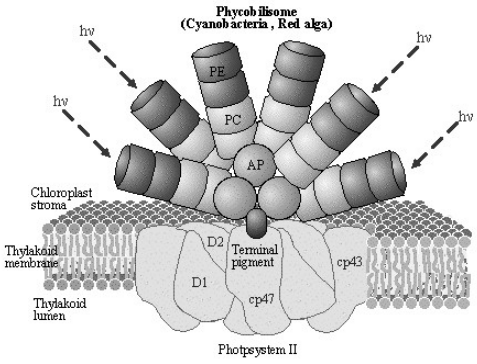

Fig 2: Hemidiscoidal Structure of phycobilisome in cyanobacteria (Modified from Bryant *et al*., 1979 [25])

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 exists 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].

Acknowledgments:

S D S. Murthy is thankful to UGC-MRP 2011-14 for financial support

REFERENCES

[1] Govindjee R. and Rabinowitch, E. 1961. Studies on the second Emerson effect in the Hill reaction in algal cells. J. Biophys 1:377-388.

[2] French, G.S. 1966. In: Biochemistry of Plants (Goodvin, T. W. ed.) Vol, pp. 377-386, Academic Press, London.

[3] Cogdell, R.J. and Gardiner, A.T. 1991. Functions of carotenoids in photosynthesis. Metabolism, Academic Press, pp. 185-193.

[4] Wilson A, Ajlani G, Verbavatz J, Vass I C, Kerfeld C A, Kirilovsky D 2006. A Soluble Carotenoid Protein Involved in Phycobilisome-Related Energy Dissipation in Cyanobacteria. The Plant Cell. 18:992-1007.

[5] Gantt, E. 1981. Phycobilisomes. Annu. Rev. Plant Physiol 32: 327-347.

[6] Cohcn-Bazire, G. and Bryant, D.A. 1982. Phycobilisomes: composition and structure. In: The Biology of Cyanobacteria (Edited by Carr, N. G. and Whitton, B. A. eds.) pp.143-190, Blackwell Sci. Publishers, Oxford.

[7] MacColl, R.1982. Phycobilisomes and Biliproteins. Photochem. Photobiol. 35: 899-904.

[8] Glazer, A., 1984. Phycobilisome: a macromolecular complex specialized for light energy transfer. Biochim. Biophys. Acta.768:29-51.

[9] Zilinskas, B. A. and Greenwald, L. S. 1986. Phycobilisome structure and function. Photosynth. Res. 10:7-35

[10] Sidler W A 1994. Phycobilisome and phycobiliproteins structures, In: Molecular Biology of the cyanobacteria, (Bryant, D. A. eds.) pp: 139-216, Kluwer Academic Publishers, Dordrecht, The Netherlands.

[11] Mullineaux C W 2008. Phycobilisome-reaction centre interaction in cyanobacteria. Photosynth. Res. 95: 175-182.

[12] Gantt E, Lipschutz C A, Grabowski J, Zimmerman B K 1979. Phycobilisomes from blue-green and red algae. Isolation criteria and dissociation characteristics. Plant Physiol 63: 615-620.
[13] Bogorad L 1975. Phycobiliproteins and complementary chromatic adaptation. Annu. Rev. Plant Physiol 26: 369-401.
[14] Bryant D A 1982. Phycoerythrocyanin and phycoerythrin: properties and occurrence in cyanobacteria. J. Gen. Microbiol 128: 835-844.
[15] Sarah J, Shaun B, Nicholas H M, Conrad W M 2005. Involvement of phycobilisome diffusion in energy quenching in cyanobacteria. Plant Physiol 138: 1577-1585.
[16] Brown, A.S., Offner, G.D., Ehrhardt, M.M. and Troxler, R.F. 1979. Phycobilin-apoprotein linkages in the α and β subunits of phycocyanin from the unicellular rhodnphyte Cyanidium caldarium. Amino acid sequence of 35S-labelled chromopeptides. J. Biol. Chem 254: 7803-7811.
[17] Lundell D J, Glazer A N 1981. Allophycocyanin B: a common subunit in Synechococcus allophycocyanin B (max 670 nm) and al1ophycocyanin (max 650 nm). J. Biol. Chem 256: 12600-12606.
[18] Yamazaki I, Mimuro M, Murao T, Yamazaki T, Yoshihara K, Fujita Y 1984. Excitation energy transfer in the light harvesting antenna system of the red alga: Porphyridiutn cruentum and the blue reen alga Anacystis nidulans: Analysis of time-resolved fluorescence spectra. Photochem. Photobiol. 39: 233-240.
[19] Liu L N, Chen X L, Zhang Y Z, Zhou B C 2005. Characterization, structure and function of linker polypeptides in phycobilisomes of cyanobacteria and red algae: Biochim.Biophys.Acta 1708: 133-142.
[20] Glazer A N 1980. Structure and evolution of photosynthetic accessory pigment systems with special reference to phycobiliproteins. In: The Evolution of Protein Structure and Function, (Sigman, D. S. and Brazier, M. A. eds.) pp.221-244, Academic Press, New York.
[21] Frank G, Sidler U, Widmer H, Zuber H 1978. Complete amino acid sequenccs of both subunits of phycocyanin from the cyanobacterium Mtastigocladus laminosus. Hoppe-Seylers, Z. Physiol. Chem 359: 1491-1507.
[22] Anderson L K, Toole C M 1998. A model for early events in the assembly pathway of cyanobacterial phycobilisomes. Mol. Microbiol 30: 467-474.
[23] Zhao K H, Su P, Tu J M, Wang X, Liu H, Scher M P, Eichacker L, Yang B, Zhou M, Scheer H 2007. Phycobilin:cystein-84 biliprotein lyase, a near universal lyase for cysteine-84-binding sites in cyanobacterial phycobiliproteins. Proc. Natl. Acad. Sci 104:14300-14305.
[24] Bryant, D. A. 1991. In Cell culture and somatic cell genetics of plants, (Bogorad, L. and Vasil, K., eds) vol. 7 B, pp. 255-298, Academic Press, Inc. New York.
[25] Bryant D A, Grglielimi G, Tanduau de Marsac N, Castets A M, Cohen-Bazire G 1979. The structure of cyanobacterial phycobilisomes. A Model. Arch. Microbiol 123: 113-127.
[26] Koller K P, Wehrmeyer W, Morschel E 1979. Stabilization of photosystem two dimmers by phosphorylation: implication for the regulation of the turnover of D1 protein, FEBS Lett 408: 276-280.
[27] Glazer A N, Williams R C, Yamanaka G, Schachman H K 1979. Characterization of cyanobacterial phycobilisomes in zwitterionic detergents. Proc. Natl. Acad. Sci USA, 76: 6162-6166.
[28] Tandeau de Marsac N. and Cohen-Bazire G 1977. Molecular composition of cyanobacterial phycobilisomes. Proc. Natl. Acad. Sci. 74: 1635-1639.
[29] Li D H, Xie J, Zhao Y W, Zhao J Q 2003. Probing connection of PBS with the photosystem in intact cells of Spirulina platensis by temperature induced fluorescence fluctuation. Biochim. Biophys. Acta 1557: 40-45.
[30] Zilinskas B A 1982. Isolation and characterization of the central component of the phycobilisome core of Nostoc. sp. Plant Physiol. 70: 1060-1065.

[31] Xiangyu G, Song Q, Fangqing Z, Xiaowen Z. Xuexi T 2007. Phycobilisomes linker family in cyanobacterial genomes: divergence and evolution Int. J. Biol.Sci. 3:434-445.
[32] Redlinger T, Gantt E 1981. Phycobilisome structure of Porphyridium cruentum. Polypeptide composition. Plant Physiol 68: 1373-1379.
[33] Murthy S D S, Mohanty P 1991. Mercury induced alteration of energy transfer in phycobilisome by selectively affecting the pigment protein, phycocyanin in the cyanobacterium, Spirulina platensis. Plant Cell Physiol. 32: 231-237.
[34] Cohen-Bazire G, Beguin S, Rimon S, Galzer A N, Brown D M 1977. Physiochemical and immunological properties of allophycocyanins. Arch. Microbiol 111: 225-238.
[35] Grossman A R, Schaefer M R, Chiang G G, Collier J L 1993a. The phycobilisomes, a light harvesting complex responsive to environmental conditions. Microbiol. Rev 57: 725-749.
[36] Dagen A J, Alfano R R, Zilinskas B A, Swenberg C E 1986. Analysis of fluorescence kinetics and energy transfer in isolated subunits of phycoerythrin from Nostoc sp. Photochem. Photobiol 43: 71-79.
[37] Yamanaka G, Glazer A N, Williams R C 1978. Cyanobacterial phycobi1isomes. Characterization of the phycobilisomes of Synechococcus sp 6301. J. Biol. Chem. 253: 8303-8310.
[38] Gingrich J C, Blaha L K, Galzer A N 1982. Rod structure in cyanobacterial phycobilisomes. Analysis of Synechocystis 6701 mutants low in phycoerythin. J. Cell Biol 92: 261-268.
[39] Zilinskas B A, Howell D A 1983. Role of the colorless polypeptides in phycobilisome assembly in Nostoc Sp. Plant Physiol. 71: 379-387.
[40] Glazer A N 1982. Phycobilisomes: structure and dynamics. Ann. Rev. Microbiol. 36:173-198.
[41] Glick R E, Zilinskas B A 1983. Role of colorless polypeptides in phycobilisomes, reconstitution from separated phycobiliproteins. Plant Physiol 69: 991-997.
[42] Glazer, A. N 1989. Light guides. Directional energy transfer in a photosynthetic antenna. J. Biol. Chem 264: 1-4.
[43] Li Y, Wang B, Ai X C, Zhang X K, Zhao J Q, Jiang LJ 2004. Spectroscopic investigation on the energy transfer process in Photosynthetic apparatus of cyanobacteria, Spectrochim Acta A Mol biomol Specgtrosc 60:1543-1547.
[44] Brecht M, Radics, V.J, Nieder B, Bittl R 2009. Protein dynamics-induced variation of excitation energy transfer pathways. Proc Natl Acad Sci. 106:11857-11861.
[45] Yokono M, Murakami A, Akimoto S 2011. Excitation energy transfer between photosystem II and Photosystem I in red algae: Larger amounts of phycobellisome enhance spillover. Biochem. Biophys Acta. 1807 : 847-853.
[46] Tredwell C J, Synoweic J A, Searle G F W, Porter G, Barber J 1978. Picosecond time- resolved fluorescence of chlorophyll in vivo. Photochem. Photobiol 28: 1013-1020.
[47] Porter G Tredwell C J Searle G F W and Barber J 1978. Picosecond time-resolved energy transfer in porphyridium cruentum. Part I. In the intact alga. Biochim. Biophys. Acta 501: 232-245.
[48] Wendler J, Holzworth A R, Wehrmeyer W 1984. Picosecond time resolved energy transfer in phycobilisomes isolated from the red alga Porphyridium cruentum. Biochim. Biophys. Acta 765: 58-67.
[49] Glazer A N 1985. Light harvesting by phycobilisomes. Ann. Rev. Biophys. Biophys. Chem 14: 47-77.
[50] Mimuro M, Yamazaki I, Yamazaki T, Fujita Y 1985. Excitation energy transfer in the chromatically adapted phycobilisomes systems of blue-green algae: difference in the energy transfer kinetics at phycocyanin level. Photochem. Photobiol 41: 597-603.
[51] Bruce D, Biggins J, Stenier T, Thelwalt M 1985. Mechanism of light state transition in photosynthesis.IV. Picosecond fluorescence spectroscopy of Anacystis nidulans and Porphyridium cruentum in state 1 and state 2 at 77 k. Biochim. Biophys. Acta. 806: 237-246.

[52] Searle G F W, Barber J, Porter G, Tredwell C J 1978. Picosecond time resolved energy transfer in Porphpyridium cruentum. Part II. In the isolated light harvesting complex. (Phycobilisomes). Biochim. Biophys. Acta. 501: 246-256.

[53] Holzworth A R, Wendler J, Wehrmeyer W 1983. Studies on chromophore coupling in isolated phycobiliproteins. I. Picosecond fluorescence kinetics and energy transfer in phycocyanin from Chroomonas sp. Biochim. Biophys. Acta. 724: 388-395.

[54] Dale R E, Teale F W J 1970. Number and distribution of chromophore types in native phycobiliproteins. Photochem. Photobiol 12: 99-117.

[55] Clement-Metral D J, Gantt E 1983. Isolation of oxygen evolving phycobilisomes photo system I particles from Porphyridium cruentum. FEBS Lett 156: 185-188.

[56] Fork D C, Mohanty P 1986. Fluorescence and other characteristics of blue-green algae (Cyanobacteria), red algae and cryptomonads. In: Light Emission by Plants and Bacteria (Govindjee, Amsez, I. and Fork, D.C., eds.) pp. 451-496, Academic Press, New York.

[57] Singhal G S, Mohanty P, Govindjee 1981. Effect of preheating intact cells on pigments revealed by absorption and fluorescence spectra. Z. Pflanzen. physiol. 103: 217-228.

[58] Yamanaka G, Glazer A N 1980. Dynamic aspects of phycobilisome structure. Phycobilisome turn over during nitrogen starvation in Synechococcus Sp. Arch. Microbiol 124: 39-47.

[59] Schreiber U 1979. Cold induced uncoupling of energy transfer between phycobilins and chlorophyll in Anacystis nidulans. Antagonistic effects of monovalent and divalent cations and of high and low pH. FEBS. Lett 107: 4-9.

[60] Sacina M, Tobin M J, Mullineaux C W 2001. Diffusion of phycobilisomes on the thylakoid membranes of the cyanobacterium Synechococcus 7942; effect of phycobilisomes size, temperature and membrane lipid composition. J. Biol. Chem. 276: 46830-46834.

[61] Belmore SC. and Shevell S.K. 2011. Very-long-term and short-term chromatic adaptation: are their influences cumulative? Vision Res. 51:362-366.

[62] Schwarz R, and Forchhammer K 2005. Acclimation of unicellular cyanobacteria to macronutrient deficiency: emergence of a complex network of cellular responses. Microbiol 151: 2503-2514.