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Minireview

A molecular understanding of complementary chromatic adaptation

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Abstract

Photosynthetic activity and the composition of the photosynthetic apparatus are strongly regulated by environmental conditions. Some visually dramatic changes in pigmentation of cyanobacterial cells that occur during changing nutrient and light conditions reflect marked alterations in components of the major light-harvesting complex in these organisms, the phycobilisome. As noted well over 100 years ago, the pigment composition of some cyanobacteria is very sensitive to ambient wavelengths of light; this sensitivity reflects molecular changes in polypeptide constituents of the phycobilisome. The levels of different pigmented polypeptides or phycobiliproteins that become associated with the phycobilisome are adjusted to optimize absorption of excitation energy present in the environment. This process, called complementary chromatic adaptation, is controlled by a bilin-binding photoreceptor related to phytochrome of vascular plants; however, many other regulatory elements also play a role in chromatic adaptation. My perspectives and biases on the history and significance of this process are presented in this essay.

Abbreviations: AP – allophycocyanin; CCA – complementary chromatic adaptation; FdB – *Fremyella diplosiphon* blue mutant; FdBk – *Fremyella diplosiphon* black mutant; FdG – *Fremyella diplosiphon* green mutant; FdR – *Fremyella diplosiphon* red mutant; FdTq – *Fremyella diplosiphon* turquoise mutant; GL – green light; GUS – β-glucoronidase PBS, phycobilisomes; PCc – constitutive PC; PC – phycocyanin; PCi – red light inducible PC; PCs – sulfur stress-induced PC; PE – phycoerythrin; RL – red light

Introduction

The vivid pigmentation of cyanobacteria and red algae is mostly a consequence of the presence of the phycobilisome (PBS), an abundant major light harvesting complex that under some conditions can account for 30% of total cellular protein (Tandeau de Marsac and Houmard 1993; Grossman et al. 1995). This peripheral membrane complex associates with the outer surface of photosynthetic membranes, absorbing and efficiently transferring excitation energy to the photosynthetic reaction centers (Porter et al. 1978; Searle et al. 1978). In working with cyanobacteria for the past 20 years, I have been continually impressed with the extent to which PBS levels in the cell may vary and curious about how environment conditions, and especially light intensity, light quality and nutrient levels control PBS biogenesis. Therefore, a substantial part of my scientific efforts have been oriented toward unraveling processes that govern PBS accumulation in cyanobacteria, especially as a consequence of changing light quality.

A description of the PBS was first reported in the pioneering work of Gantt and Conti (1966a, b). Elisabeth Gantt demonstrated that the knob-like structures that line the surface of the intracellular membranes

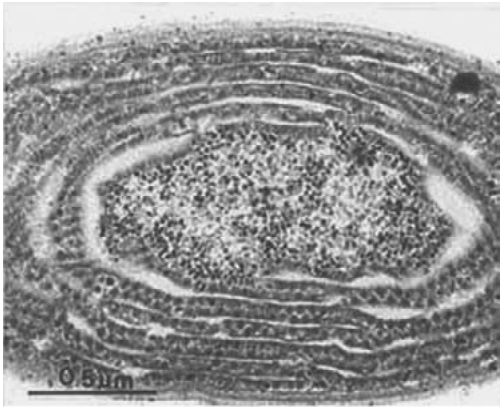

Figure 1. Electron micrograph showing PBS lining the surfaces of the thylakoid membranes of the unicellular cyanobacterium *Synechococcus*. The image was kindly provided by Elisabeth Gantt.

Figure 2. Don Bryant (Pennsylvania State University) and Alex Glazer (University of California, Berkeley), two prominent researchers who pioneered work on PBS function, structure and regulation.

in cyanobacteria and red algae were composed of the pigmented phycobiliproteins and were responsible for harvesting excitation energy. This work led to the isolation of PBS and some of the clearest micrographs of these light harvesting structures, both attached to and stripped from thylakoid membranes. It also opened the door for detailed analyses of PBS structure, protein and pigment composition and the mechanisms by which energy is transferred from the PBS to the photosynthetic reaction centers. Figure 1 presents an electron micrograph of the unicellular cyanobacterium *Synechococcus* in which the PBS can be seen lining the surface of the thylakoid membranes (especially in the lower half of the picture).

The PBS is composed of two domains, the rods and core, each containing both pigmented and non-pigmented polypeptides. The predominant pigmented

Figure 3. F. diplosipon grown on solid agar medium in red light, (RL) (left) and green light (GL) (right). For a color version of this figure, see color section in the front of the issue.

proteins in the rods are phycocyanin (PC) and phycoerythrin (PE) while the core contains allophycocyanin (AP). The chromophores that covalently bind to the apo-phycobiliproteins are the linear tetrapyrroles phycocyanobilin, phycourobilin or phycoerythrobilin. Each phycobiliprotein is composed of a specific α and β subunit that associate into heterodimers and subsequently aggregate into trimers and hexamers. Non-pigmented or linker polypeptides serve as structural elements involved in the biosynthesis and stabilization of PBS (Glazer 1982, 1985), but also facilitate efficient flow of excitation energy to the photosynthetic reactions centers. Specific lyases catalyze the attachment of the chromophore to the apo-phycobiliprotein (Fairchild et al. 1992; Fairchild and Glazer 1994; Kahn et al. 1997). A number of investigators have done marvelous work that has helped elucidate the structure and function of PBS; these include Elizabeth Gantt (Gantt 1981), Alex Glazer (Glazer and Cohen-Bazire 1971; Glazer 1982; Glazer et al. 1983; Glazer 1985), Herbert Zuber (Glauser et al. 1992, 1993) and Robert Huber (Schirmer et al. 1986), and a detailed description of PBS structure can be found in a number of review articles (Gantt 1981; Glazer et al. 1983; Glazer 1985; Sidler 1994). Figure 2 shows Alex Glazer (right) along with former student Don Bryant (left). Don also contributed considerably to our understanding of PBS structure and regulation (some relevant references with respect to the subject of this article are Bryant 1981; Bryant and Cohen-Bazire 1981), but has recently devoted much of his time to elucidating Photosystem I structure and function.

Complementary chromatic adaptation from way back

Reports in the late 1800s noted that certain cyanobacteria could change their pigmentation in response to the wavelengths of light in the environment (Engelmann 1883a, b, 1884). This control of pigmentation

in cyanobacteria by light was termed complementary chromatic adaptation (CCA) (Gaidukov 1903) because the pigmentation in the cell was modulated in a way that was complementary to the wavelengths of light in the environment; this process enables some cyanobacteria to efficiently absorb prevalent wavelengths of light in the environment. CCA is observed in a number of cyanobacteria examined in the natural environment (Tandeau de Marsac 1977). A visually dramatic representation of the process of chromatic adaptation is presented in Figure 3, which shows *F. diplosiphon* filaments after growth on solid medium in red light (RL) and green light (GL). Following the initial observation of CCA, 90 years passed before the biochemical analyses from Lawrence Bogorad's laboratory demonstrated that the phenomenon of CCA was a consequence of changes in the PBS pigment-protein composition (Bennett and Bogorad 1971, 1973; Bogorad 1975). The development of molecular tools in the 1970 and 1980s created new opportunities for elucidating the regulation of PBS biosynthesis. By the latter part of the 1980s, most genes encoding PBS structural polypeptides were cloned, sequenced and their expression characterized (summarized in Tandeau de Marsac et al. 1988; Tandeau de Marsac and Houmard 1993; Grossman et al. 1994). Researchers who contributed very significantly to isolating and characterizing genes encoding structural components of the PBS were Don Bryant, Nicole Tandeau de Marsac and members of my own group such as Peggy Lemaux and Pamela Conley. The initial molecular characterizations provided us with amino acid sequences of numerous phycobiliproteins and linker polypeptides, yielded a picture of the organization of phycobiliprotein and linker polypeptide genes on cyanobacterial genomes (e.g., many of the genes are clustered and some are co-transcribed), and provided the molecular foundation for probing the control of PBS composition by light quality.

The photobiology of complementary chromatic adaptation

Action spectra for PC and PE synthesis during CCA have been measured for both *T. tenuis* and *F. diplosiphon* by quantifying PE to PC ratios following exposure of these cyanobacteria to narrow bands of light wavelengths (Diakov and Scheibe 1973; Haury and Bogorad 1977; Vogelmann and Scheibe 1978). Maximal PE synthesis and minimal PC synthesis occurred at 550 nm GL, while maximal PC synthesis and minimal PE synthesis occurred at 640 nm RL. These data suggested that the photoreceptor(s) controlling CCA absorbed GL and RL (either through one or multiple chromophores), but elicited different responses in the two light qualities. PC synthesis and assembly into PBS dominate in RL while PE synthesis and assembly into PBS dominate in GL. The mixture of RL and GL in natural sunlight results in a PBS with intermediate levels of PC and PE.

In *F. diplosiphon* a single gene set, designated *cpeBA*, was shown to encode PE while three distinct gene sets encode PC; these have been designated *cpcB1A1* for the constitutively expressed PC_c, *cpcB2A2* for the red light inducible PC_i and *cpcB3A3* for PC_s, which is only expressed during sulfur deprivation conditions (Conley et al. 1985, 1986, 1988; Mazel et al. 1986, 1988; Mazel and Marliere 1989). Changes in phycobiliprotein content during CCA are due to changes in levels of transcripts from both *cpeBA* and *cpcB2A2* (Conley et al. 1985; Mazel et al. 1986; Oelmüller et al. 1988a, b). Since there is little change in the half-lives of mRNAs encoding the phycobiliproteins in RL and GL (Oelmüller et al. 1988a), levels of PE and PC_i appear to be primarily regulated by changes in rates of transcription of the *cpeBA* and *cpcB2A2* operons, respectively. Furthermore, genes encoding the linker polypeptides associated with PC_i, *cpcHID*, are RL-inducible and co-transcribed with *cpcB2A2* (Lomax et al. 1987). And while genes encoding the linker polypeptides associated with PE, *cpeCDE*, are also under the control of RL and GL, they are not in the same operon as *cpeBA* (Federspiel and Grossman 1990; Federspiel and Scott 1992). My laboratory was most interested in understanding the mechanisms controlling PBS gene expression and there were two viable approaches for defining regulators of this process; one approach involved using biochemical techniques to identify factors that associate with promoters of phycobiliprotein genes, whereas the other involved generating mutants with aberrant CCA and identifying genes altered in the mutant strains. We chose to concentrate on mutant generation and analysis while much of the work in Tandeau de Marsac's laboratory was focused on using biochemical approaches to identify regulatory elements.

In vivo and *in vitro* promoter analysis

Three polypeptides interact with the *cpeBA* promoter

at the position −110 to +81 relative to the transcription start site (Sobczyk et al. 1993). One binding protein was RNA polymerase, which bound to sequences from −40 to +15. Two other polypeptides, RcaA and RcaB, also interacted with the *cpeBA* promoter and were only detected in extracts of cells maintained in GL. RcaA bound the sequence between −67 and −45 (which contains a tandem 5′-TTGTTA-3′ repeat separated by 4 bp). The exact position of the binding site for RcaB was not clear.

Protein-DNA interactions with the sequence of the *cpeBA* operon extending from −67 to −44 were also observed by Schmidt-Goff and Federspiel (1993) and a protein designated PepB bound to the 5′-TTGTTA-3′ direct repeat. Since RcaA and PepB appear to bind the same sequences, they are likely to be identical proteins. However, in the studies of Sobczyk et al. (1993) the RcaA/PepB binding activity was only detected in protein extracts from GL-grown cells while in the studies of Schmidt-Goff and Federspiel (1993) this activity was detected in extracts from both RL- and GL-grown cells. These contradictory findings may reflect different physiological states of the cells used in the two studies.

Interactions of the *cpcB2A2* promoter with soluble *F. diplosiphon* proteins have also been examined. Proteins from RL- and GL-grown *F. diplosiphon* cells bind to the −298 to +25 region of the *cpcB2A2* operon (Casey and Grossman 1994). The major binding region was associated with sequences between −162 and −126 from the *cpcB2A2* transcription start site. To determine if this region of the promoter was critical for CCA, the *cpcB2A2* promoter region was fused to the reporter gene β-glucuronidase (*GUS*) and analyzed for activity *in vivo*. This study demonstrated that prominent binding at −162 to −126 was not critical for CCA, but that a sequence extending from −76 to +25 conferred RL/GL responsiveness to GUS expression. Furthermore, a protein only present in extracts of RL-grown cells was shown to specifically bind this region of the *cpcB2A2* promoter, and a DNA fragment from −37 to +25 was able to specifically compete for this binding activity (Casey and Grossman 1994). The −37 to +25 fragment contains the direct repeat 5′-AAATTTGCACAAA-3′. All of these results suggest that the sequence from −37 to +25 is involved in binding a protein present in RL-grown cells, and that this binding may be critical for RL-specific transcription from *cpcB2A2*.

Use of mutants and genetic techniques to dissect complementary chromatic adaptation

My laboratory became very interested in using CCA mutants to elucidate the mechanism of photoregulation. A variety of CCA mutants were identified in several laboratories (Cobley and Miranda 1983; Tandeau de Marsac 1983; Bruns et al. 1989; Chiang et al. 1992; Casey et al. 1997; Kehoe and Grossman 1996) and categorized into red (FdR), blue (FdB), green (FdG) and black (FdBk) mutant classes. The FdR mutants appear red under all conditions of illumination and they constitutively synthesize PE while PC is never synthesized. The FdB strains are bluer than wild-type cells in RL and require more GL to suppress PC synthesis than wild-type cells. The FdG strains exhibit normal PC_i expression, but the genes encoding PE never become active. In the FdBk mutants there are moderate levels of both PE and PC, however, these levels remain the same in RL and GL.

At the time when we initiated work on these mutants, critical resources became available that allowed for successful genetic analysis of CCA. John Cobley had generated an *F. diplosiphon* mutant that grew as short filaments such that the colonies formed by the cells remained discrete (the filaments did not quickly spread over the entire plate). Furthermore, John constructed a plasmid that could autonomously replicate in *F. diplosiphon*, facilitating the stable introduction of DNA into the organism (Cobley et al. 1993). We used these tools to complement the FdR mutant and identified the gene *rcaC* (Chiang et al. 1992). The *rcaC* gene encodes a polypeptide of 651 amino acids with sequence similarity to response regulators of two component regulatory systems (for reviews see Parkinson and Kofoid 1992; Appleby et al. 1996). Often, response regulators are transcription factors that bind specific promoter sequences and alter the transcriptional activity of target genes; promoter-binding activity may be regulated by the reversible phosphorylation at a specific aspartate residue in the receiver domain. Typically, perception of an enviromental signal (such as light) by a specific sensor polypeptide would trigger a phosphorelay that results in the activation of genes via the phosphorylation of a response regulator. At this stage it is not clear if RcaC directly interacts with the promoters of the phycobiliprotein operons or if its effect on CCA is indirect. Furthermore, RcaC has several domains that may be phosphorylated including an amino terminal aspartate (D51), a carboxy-terminal aspartate (D576) and a

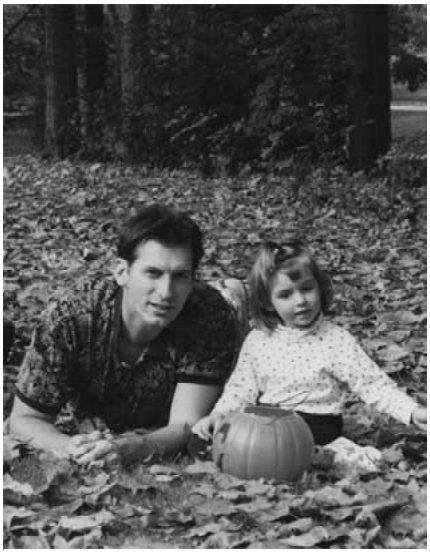

Figure 4. David Kehoe (left), who identified the gene encoding a phytochrome-like photoreceptor that controls complementary chromatic adaptation, and his daughter Ivy celebrating the colors of fall. David is an Assistant Professor in the Biology Department at Indiana University.

histidine residue present in an H block domain (often present in sensor polypeptides); while D51 appears to be critical for CCA, the role of D576 and H block histidine are not clear (Kehoe and Grossman 1995).

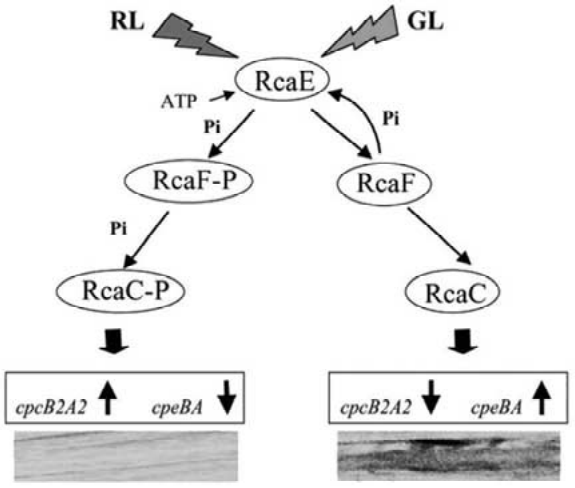

Figure 5. Model showing some aspects of the phosphorelay control of *cpcB2A2* and *cpeBA* during complementary chromatic adaptation in *F. diplosiphon*. The pigmented cells on solid medium are shown at the bottom of the figure. Permission to use the figure was kindly provided by the Journal of Biological Chemistry. RL – red light; GL – green light.

Complemention of the FdBk class of mutants, first achieved by David Kehoe, whose picture is shown in Figure 4, led to identification of *rcaE*, a gene encoding a protein of molecular mass of 74 kDa (Kehoe and Grossman 1996). David worked in a concentrated manner to make transformation of *F. diplosiphon* highly efficient, which facilitated identification of the genes that complemented our mutant strains. RcaE has the four motifs at its carboxy terminus typical of sensor polypeptides that are required for histidine kinase activity (N, G1, F and G2) as well as an H block. Surprisingly, the amino-terminal half of the protein has a domain of approximately 140 amino acids that is similar to the tetrapyrrole chromophore attachment domain of phytochromes; it appears to contain the cysteine residue that covalently binds to the tetrapyrrole chromophore. Recent biochemical studies have demonstrated that RcaE covalently binds a linear tetrapyrrole chromophore, that the cysteine is required for the covalent attachment of the chromophore to the protein, and that the protein isolated from the cyanobacterium exhibits a RL-GL chromogenic shift (K. Terauchi, B.L. Montgomery, A.R. Grossman, J.C. Lagarias, D.M. Kehoe, submitted). These results suggest that RcaE is a phytochrome-like sensor protein that serves as the major photoreceptor for controlling CCA.

Phytochrome-like photoreceptors have now been identified in a number of different organisms. The sequence of the entire *Synechocystis* sp. Strain PCC 6803 genome (cyanobase) revealed several deduced polypeptides related to both RcaE and eukaryotic phytochromes. One of the genes encoding a phytochrome-like protein, designated *cph1*, has been expressed *in vitro* and is capable of binding a chromophore and undergoing a photochromic shift in absorbance (Yeh et al. 1997; Yeh and Lagarias 1998). These results suggest that there are several phytochrome-related polypeptides in cyanobacteria that act as photoreceptors and that probably govern gene expression via a phosphorylation cascade. Phytochromes in plants may also function by modulating the phosphorylation of regulatory proteins. Lagarias and colleagues have demonstrated that plant phytochrome synthesized in yeast can undergo autophosphorylation, although this protein appears to have serine/threonine kinase rather than histidine kinase activity (Yeh and Lagarias 1998). Other phytochrome-like proteins in bacteria appear to control growth under certain light conditions (Wilde et al. 1997), carotenoid synthesis (Davis et al. 1999) and phototactic move-

ment (Bhaya et al. 2001; Wilde et al. 2002). Defining the signal transduction processes that are triggered by phytochrome-like photoreceptors in prokaryotes is providing us with new insights into mechanisms involved in light-regulated gene expression and the evolution of phytochrome structure and function in plants.

Interestingly, a number of the FdR mutants could not be complemented by *rcaC* (Kehoe and Grossman 1997). Some of these were complemented by *rcaF*, the gene immediately downstream of *rcaE* on the cyanobacterial genome. Translation of the RcaF protein, which is homologous to response regulators, initiates 12 bp downstream of the translation termination site of *rcaE*. However, like CheY and Spo0F, response regulators involved in flagellar movement in *E. coli* and sporulation in *Bacillus subtilis*, respectively (Clegg and Koshland 1984; Ravid et al. 1986; Yamaguchi et al. 1986; Wolfe et al. 1987; Perego and Hoch 1996), RcaF is very small (124 amino acids) and does not contain an identifiable output domain (it only has a putative receiver domain). RcaF may act as an intermediate in the phosphorelay pathway controlling CCA and transfer phosphate groups from its cognate sensor (presumably RcaE) to other response regulators such as RcaC.

Model for the control of complementary chromatic adaptation

As a consequence of the analysis of the *rcaC*, *rcaF* and *rcaE* genes and the physiology of the various mutant strains, we have proposed an initial model describing CCA control (Kehoe and Grossman 1997); a simple representation of this model is presented in Figure 5. While RcaE, RcaF and RcaC are members of bacterial two component regulatory systems and participate in a phosphorelay system, it is a complex phosphorelay that includes at least three proteins and at least five potential phosphoacceptor domains. As shown in the model, RL stimulates and GL inhibits the transfer of phosphoryl groups along the phosphorelay pathway. RcaE is a phytochrome-like photoreceptor that perceives the light signal. We propose that RL triggers autophosphorylation of RcaE followed by transfer of the phosphoryl group to the response regulator RcaF (which may also serve as an entrance point for phosphoryl donors other than RcaE). Phosphorylated RcaF then transfers the phosphoryl group to the H block (histidine phosphotransfer domain) of RcaC, which can then pass the phosphoryl group to either the amino or (perhaps) carboxy terminal aspartate of the receiver domain. While the amino terminal receiver domain of RcaC is critical for CCA (Kehoe and Grossman 1995), the role of the carboxy terminal receiver domain is unclear, although it may help fine tune the system with respect to other environmental conditions.

But there is much more to the CCA story, which is being actively pursued by a number of investigators including David Kehoe and John Cobley. There appears to be some form of control exerted on *cpcB1A1* (Kahn and Schaefer 1997; Manna et al. 2000); thus the constitutive PC_c gene may also be modulated by specific environmental conditions. Furthermore, a regulatory factor has been identified that is specifically involved in the control of *cpeBA*. Mutants that exhibit normal regulation of *cpcB2A2* and *cpeCDE*, but fail to accumulate *cpeBA* mRNA in GL, have been identified and designated turquoise (FdTq) mutants (Seib and Kehoe 2002). Genetic complementation of these mutants resulted in the isolation of *cpeR*, which encodes a protein with limited sequence similarity to the PP2C class of protein serine/threonine phosphatases. The *cpeR* gene is located downstream of and perhaps cotranscribed with *cpeCDE* (Cobley et al. 2002), which has interesting implications with respect to regulation. Furthermore, there is still a low level of increased transcription in GL from the *cpeCDE* and *cpeBA* operons in a *rcaE* null mutant, suggesting that a photoreceptor in addition to RcaE may play a role in modulating expression of genes encoding PBS polypeptides with respect to light quality (Seib and Kehoe 2002). The identification of regulatory elements and how they interact to yield a PBS structure that is tailored to light conditions is still a very fertile field of investigation.

Concluding remarks

While I have focused this essay on the role that light quality plays in the biosynthesis of PBS, both light intensity and nutrient levels also regulate PBS biosynthesis, as well as the biosynthesis of other photosynthetic complexes (Fujita et al. 1994; Grossman et al. 2001). Furthermore, there appear to be regulatory elements that integrate the effects of light and nutrient availability (especially nutrient limitation) on photosynthetic activity, possibly by the generation of redox signals (Fujita et al. 1987; Escoubas et al. 1995; Durnford and Falkowski 1997; Alfonso et al. 1999; Li and Sherman 2000; van Waasbergen et al. 2002) that enable cell survival during adverse environmental

Figure 6. Arthur Grossman (author) during a recent visit (July 2002) to the hot springs of Yellowstone National Park.

conditions (Schwarz and Grossman 1998; van Waasbergen et al. 2002). I have enjoyed analyzing the responses of photosynthetic microbes to harsh environments and recently visited hot springs in Yellowstone National Park (as seen in Figure 6) to puzzle over the resilience of the photosynthetic apparatus under near boiling conditions. I believe that as our understanding of the dynamic control of photosynthetic function and flexibility increase, we will be able to explore possibilities for using molecular technologies to engineer the photosynthetic apparatus for better performance under specific environmental conditions, which can have significant social and economic impacts.

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References

Alfonso M, Perewoska I, Constant S and Kirilovsky D (1999) Redox control of *psbA* expression in cyanobacteria *Synechocystis* strains. J Photochem Photobiol 48: 104–113

Appleby JL, Parkinson JS and Bourret RB (1996) The multi-step phosphorelay: not necessarily a road less traveled. Cell 86: 845–848

Bennett A and Bogorad L (1971) Properties of subunits and aggregates of blue-green algal biliproteins. Biochemistry 10: 3625–3634

Bennett A and Bogorad L (1973) Complementary chromatic adaptation in a filamentous blue-green alga. J Cell Biol 58: 419–435

Bhaya D, Takahashi A and Grossman AR (2001) Light regulation of Type IV pilus-dependent motility by chemosensor-like elements in *Synechocystis* PCC6803. Proc Natl Acad Sci USA 13: 7540–7545

Bogorad L (1975) Phycobiliproteins and complementary chromatic adaptation. Annu Rev Plant Physiol 26: 369–401

Bruns B, Briggs WR and Grossman AR (1989) Molecular characterization of phycobilisome regulatory mutants in *Fremyella diplosiphon*. J Bacteriol 171: 901–908

Bryant DA (1981) The photoregulated expression of multiple phycocyanin species: general mechanism for control of phycocyanin synthesis in chromatically adapting cyanobacteria. Eur J Biochem 119: 425–429

Bryant DA and Cohen-Bazire G (1981) Effects of chromatic illumination on cyanobacterial phycobilisomes: evidence for the specific induction of a second pair of phycocyanin subunits in *Pseudanabaena* 7409 grown in red light. Eur J Biochem 119: 415–424

Casey ES and Grossman AR (1994) *In vivo* and *in vitro* characterization of the light-regulated *cpcB2A2* promoter of *Fremyella diplosiphon*. J Bacteriol 176: 6362–6374

Casey ES, Kehoe DM and Grossman AR (1997) Suppression of mutants aberrant in light intensity responses of complementary chromatic adaptation. J Bacteriol 179: 4599–4606

Chiang GG, Schaefer MR and Grossman AR (1992) Complementation of a red-light indifferent cyanobacterial mutant. Proc Natl Acad Sci USA 89: 9415–9419

Clegg D and Koshland D (1984) The role of a signaling protein in bacterial sensing: behavioral effects of increased gene expression. Proc Natl Acad Sci USA 81: 5056–5060

Cobley JG and Miranda RD (1983) Mutations affecting chromatic adaptation in the cyanobacteirum *Fremyella diplosiphon*. J Bacteriol 153: 1486–1492

Cobley JG, Zerweck E, Reyes R, Mody A, Seludo-Unson JR, Jaeger H, Weerasuriya S and Navankasattusas S (1993) Construction of shuttle plasmids which can be efficiently mobilized from *Escherichia coli* into the chromatically adapting cyanobacterium, *Fremyella diplosiphon*. Plasmid 30: 90–105

Cobley JG, Clark AC, Weerasurya S, Queseda FA, Xiao JY, Bandrapali N, D'Silva I, Thounaojam M, Oda JF, Sumiyoshi T and Chu MH (2002) CpeR is an activator required for expression of the phycoerythrin operon (*cpeBA*) in the cyanobacterium *Fremyella diplosiphon* and is encoded in the phycoerythrin linker-polypeptide operon (*cpeCDESTR*). Mol Microbiol 44: 1517–1531

Conley PB, Lemaux PG and Grossman AR (1985) Cyanobacterial light-harvesting complex subunits encoded in two red light-induced transcripts. Science 230: 550–553

Conley PB, Lemaux PG, Lomax TL and Grossman AR (1986) Genes encoding major light-harvesting polypeptides are clustered on the genome of the cyanobacteirum *Fremyella diplosiphon*. Proc Natl Acad Sci USA 83: 3924–3928

Conley PB, Lemaux PG and Grossman AR (1988) Molecular characterization and evolution of sequences encoding light-harvesting components in the chromatically adapting cyanobacterium *Fremyella diplosiphon*. J Mol Biol 199: 447–465

Davis SJ, Vener AV and Vierstra RD (1999) Bacteriophytochromes: phytochrome-like photoreceptors from nonphotosynthetic eubacteria. Science 286: 2517–2520

Diakoff S and Scheibe S (1973) Action spectra for chromatic adaptation in *Tolypothrix tenuis*. Plant Physiol 51: 382–385

Durnford DG and Falkowski PG (1997) Chloroplast redox regulation of nuclear gene transcription during photoacclimation. Photosynth Res 53: 229–241

Engelmann TW (1883a) Farbe und Assimilation. Assimilation findet nur in den farbstoffhaltigen Plasmathielchen statt. II. Näherer Zusamennhang zwischen Lichtabsorption und Assimilation. Bot Z 41: 1–13

Engelmann TW (1883b) Farbe und Assimilation. III. Weitere Folgerungen. Bot Z 41: 17–29

Engelmann TW (1884) Untersuchungen über die qualitativen Beziehungen zwischen Absorption des Lichtes und Assimilation in Planzenzellen. I. Das Mikrospectrophotometer ein Apparat zur quantitativen Mikrospectralanalyse. II. Experimentelle Grundlagen zur Ermittlung der quantitativen Beziehungen zwischen Assimilationsenergie und Absorptionsgrösse. Bot Z 42: 97–105

Escoubas J-M, Lomas M, LaRoche J and Falkowski PG (1995) Light intensity regulation of *cab* gene transcription is signaled by the redox state of the plastoquinone pool. Proc Natl Acad Sci USA 92: 10237–10241

Fairchild CD and Glazer AN (1994) Oligomeric structure, enzyme kinetics, and substrate specificity of the phycocyanin a subunit phycocyanobilin lyase. J Biol Chem 269: 8686–8694

Fairchild CD, Zhao J, Zhou J, Colson SE, Bryant DA and Glazer AN (1992) Phycocyanin a-subunit phycocyanobilin lyase. Proc Natl Acad Sci USA 89: 7017–7021

Federspiel NA and Grossman AR (1990) Characterization of the light-regulated operon encoding the phycoerythrin-associated linker proteins from the cyanobacterium *Fremyella diplosiphon*. J Bacteriol 172: 4072–4081

Federspiel NA and Scott L (1992) Characterization of a light-regulated gene encoding a new phycoerythrin-associated linker protein from the cyanobacterium *Fremyella diplosiphon*. J Bacteriol 179: 5994–5998

Fujita Y, Murakami A and Ohki K (1987) Regulation of photosystem composition in the cyanobacterial photosynthetic system: the regulation occurs in response to the redox state of the electron pool located between the two photosystems. Plant Cell Physiol 28: 283–292

Fujita Y, Murakami A, Aizawa K and Ohki K (1994) Short-term and long-term adaptation of the photosynthetic apparatus: homeostatic properties of thylakoids. In: Bryant DA (ed) The Molecular Biology of Cyanobacteria, pp 677–692. Kluwer Academic Publishers, Dordrecht, The Netherlands

Gaidukov N (1903) Die Farbervänderung bei den Prozessen der Komplementären chromatischen Adaptation. Ber Deutsch Bot Ges 21: 517–522

Gantt E (1981) Phycobilisomes. Annu Rev Plant Physiol 32: 327–347

Gantt E and Conti SF (1966a) Phycobiliprotein localization in algae. Brookhaven Sym Biol 19: 393–405

Gantt E and Conti SF (1966b) Granules associated with the chloroplast lamellae of *Porphyridium cruentum*. J Cell Biol 29: 423–430

Glauser M, Bryant DA, Frank G, Wehrli E, Rusconi SS, Sindler W and Zuber H (1992) Phycobilisome structure in the cyanobacteria *Mastigocladus laminosus* and *Anabaena* sp. PCC 7120. Eur J Biochem 205: 907–915

Glauser M, Sidler W and Zuber H (1993) Isolation, characterization and reconstitution of phycobiliprotein rod-core linker polypeptide complexes from the phycobilisome of *Mastigocladus laminosus*. Photochem Photobiol 57: 344–351

Glazer AN (1982) Phycobilisomes: structure and dynamics. Annu Rev Microbiol 36: 173–198

Glazer AN (1985) Light harvesting by phycobilisomes. Annu Rev Biophys Chem 14: 47–77

Glazer AN and Cohen-Bazire G (1971) Subunit structure of the phycobiliproteins of blue-green algae. Proc Natl Acad Sci USA 68: 1398–1401

Glazer AN, Lundell DJ, Yamanaka G and Williams RC (1983) The structure of a 'simple' phycobilisome. Annals Institut Pasteur/Microbiol 134B: 159–180

Grossman AR, Schaefer M, Chiang G and Collier J (1994) The responses of cyanobacteria to environmental conditions: light and nutrients. In: Bryant D (ed) The Molecular Biology of Cyanobacteria, pp 641–675. Kluwer Academic Publishers, Dordrecht, The Netherlands

Grossman AR, Bhaya D, Apt KE and Kehoe DM (1995) Light-harvesting complexes in oxygenic photosynthesis: diversity, control and evolution. Annu Rev Genet 29: 231–287

Grossman AR, Bhaya D and He Q (2001) Tracking the light environment by cyanobacteria and the dynamic nature of light harvesting. J Biol Chem 276: 11449–52

Haury JF and Bogorad L (1977) Action spectra for phycobiliprotein synthesis in a chromatically adapting cyanophyte, *Fremyella diplosiphon*. Plant Physiol 60: 835–839

Kahn K and Schaefer MR (1997) *rpbA* controls transcription of the constitutive phycocyanin gene set in *Fremyella diplosiphon*. J Bacteriol 179: 7695–7704

Kahn K, Mazel D, Houmard J, Tandeau de Marsac N and Schaefer MR (1997) A role for CpeYZ in cyanobacterial phycoerythrin biosynthesis. J Bacteriol 179: 998–1006

Kehoe DM and Grossman AR (1995) The use of site directed mutagenesis in the analysis of complementary chromatic adaptation. In: Mathis P (ed.) Proceedings from the Xth International Photosynthesis Congress: Photosynthesis: from Light to Biosphere, pp 501–504. Kluwer Academic Publishers, Dordrecht, The Netherlands

Kehoe DM and Grossman AR (1996) Similarity of a chromatic adaptation sensor to phytochrome and ethylene receptors. Science 273: 1409–1412

Kehoe DM and Grossman AR (1997) New classes of mutants in complementary chromatic adaptation provide evidence for a novel four-step phosphorelay system. J Bacteriol 179: 3914–3921

Li H and Sherman LA (2000) A redox-responsive regulator of photosynthesis gene expression in the cyanobacterium *Synechocystis* sp. strain PCC 6803. J Bacteriol 182: 4268–4277

Lomax TL, Conley PB, Schilling J and Grossman AR (1987) Isolation and characterization of light-regulated phycobilisome linker polypeptide genes and their transcription as a polycistronic mRNA. J Bacteriol 169: 2675–2684

Manna P, Nieder RP and Schaefer MR (2000) DNA-binding properties of the *Fremyella diplosiphon* RpbA repressor. J Bacteriol 182: 51–56

Mazel D and Marliere P (1989) Adaptive eradication of methionine and cysteine from cyanobacterial light-harvesting proteins. Nature (London) 341: 245–248

Mazel D, Guglielmi G, Houmard H, Sidler W, Bryant DA and Tandeau de Marsac N (1986) Green light induces transcription of the phycoerythrin operon in the cyanobacterium *Calothrix* 7601. Nucleic Acids Res 14: 8279–8290

Mazel D, Houmard J and Tandeau de Marsac N (1988) A multigene family in *Calothrix* sp. PCC 7601 encodes phycocyanin, the

major component of the cyanobacterial light-harvesting antenna. Mol Gen Genet 211: 296–304

Oelmüller R, Conley PB, Federspiel N, Briggs WR and Grossman AR (1988a) Changes in accumulation and synthesis of transcripts encoding phycobilisome components during acclimation of *Fremyella diplosiphon* to different light qualities. Plant Physiol 88: 1077–1083

Oelmüller R, Grossman AR and Briggs WR (1988b) Photoreversibility of the effect of red and green light pulses on the accumulation in darkness of mRNAs coding for phycocyanin and phycoerythrin in *Fremyella diplosiphon*. Plant Physiol 88: 1084–1091

Parkinson JS and Kofoid EC (1992) Communication modules in bacterial signaling proteins. Annu Rev Genet 26: 71–112

Perego M and Hoch JA (1996) Protein aspartate phosphatases control the output of two-component signal transduction systems. Trends Genet 12: 97–101

Porter G, Tredwell CJ, Searle GFW and Barber J (1978) Picosecond time-resolved energy transfer in *Porphyridium cruentum*. Part I. In the intact alga. Biochim Biophys Acta 501: 232–245

Ravid S, Matsumura P and Eisenbach M (1986) Restoration of flagellar clockwise rotation in bacterial envelopes by insertion of the chemotaxis protein CheY. Proc Natl Acad Sci USA 83: 7157–7161

Schirmer T, Huber R, Schneider M, Bode W, Miller M and Hackert ML (1986) Crystal structure analysis and refinement at 2.5 A of hexameric C-phycocyanin from the cyanobacterium *Agmenellum quadruplicatum*. The molecular model and its implications for light-harvesting. J Mol Biol 188: 651–676

Schmitt-Goff CM and Federspeil NA (1993) *In vivo* and *in vitro* footprinting of a light-regulated promoter in the cyanobacterium *Fremyella diplosiphon*. J Bacteriol 175: 1806–1813

Schwarz R and Grossman AR (1998) A response regulator of cyanobacteria integrates diverse environmental signals and is critical for survival under extreme conditions. Proc Natl Acad Sci USA 95: 11008–11013

Searle GFW, Barber J, Porter G and Tredwell CJ (1978) Picosecond time-resolved energy transfer in *Porphyridium cruentum*. Part II. In the isolated light-harvesting complex (phycobilisomes). Biochim Biophys Acta 501: 246–256

Seib LO and Kehoe DM (2002) A turquoise mutant genetically separates expression of genes encoding phycoerythrin and its associated linker peptides. J Bacteriol 184: 962–970

Sidler WA (1994) Phycobilisome and phycobiliprotein structures. In: Bryant D (ed) The Molecular Biology of Cyanobacteria, pp 139–216. Kluwer Academic Publishers, Dordrecht, The Netherlands

Sobczyk A, Schyns G, Tandeau de Marsac N and Houmard J (1993) Transduction of the light signal during complementary chromatic adaptation in the cyanobacterium *Calothrix* sp. PCC 7601: DNA-binding proteins and modulation by phosphorylation. EMBO J 12: 997–1004

Tandeau de Marsac N (1977) Occurrence and nature of chromatic adaptation in cyanobacteria. J Bacteriol 130: 82–91

Tandeau de Marsac N (1983) Phycobilisomes and complementary adaptation in cyanobacteria. Bull Inst Pasteur 81: 201–254

Tandeau de Marsac N and Houmard J (1993) Adaptation of cyanobacteria to environmental stimuli: new steps towards molecular mechanisms. FEMS Microbiol Revi 104: 119–190

Tandeau de Marsac D, Mazel D, Damerval T, Guglielmi G, Capuano V and Houmard J (1988) Photoregulation of gene expression in the filamentous cyanobacterium *Calothrix* sp. PCC7601. Photosynth Res 18: 99–132

van Waasbergen LG, Dolganov N and Grossman AR (2002) Environmental control depends on PAS domain-bearing sensor protein. J Bacteriol 184: 2481–2490

Vogelmann TC and Scheibe J (1978) Action spectrum for chromatic adaptation in the blue-green alga *Fremyella diplosiphon*. Planta 143: 233–239

Wilde A, Churin Y, Schubert H and Borner T (1997) Disruption of a *Synechocystis* sp. PCC 6803 gene with partial similarity to phytochrome genes alters growth under changing light qualities. FEBS Lett 406: 89–92

Wilde A, Fiedler B and Borner T (2002) The cyanobacterial phytochrome Cph2 inhibits phototaxis towards blue light. Mol Microbiol 44: 981–988

Wolfe AJ, Conley P, Kramer TJ and Berg HC (1987) Reconstitution of signaling in bacterial chemotaxis. J Bacteriol 169: 1878–1885

Yamaguchi S, Aizawa S-I, Kihara M, Isomura M, Jones CJ and Macnab RM (1986) Genetic evidence for a switching and energy-transducing complex in the flagellar motor of *Salmonella typhimurium*. J Bacteriol 168: 1172–1179

Yeh KC and Lagarias JC (1998) Eukaryotic phytochromes: light-regulated serine/threonine protein-kinases with histidine kinase ancestry. Proc Natl Acad Sci USA 95: 13976–13981

Yeh KC, Wu S-H, Murphy JT and Lagarias JC (1997) A cyanobacterial phytochrome two-component light sensory system. Science 277: 1505–1508