



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 -glucuronidase; 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

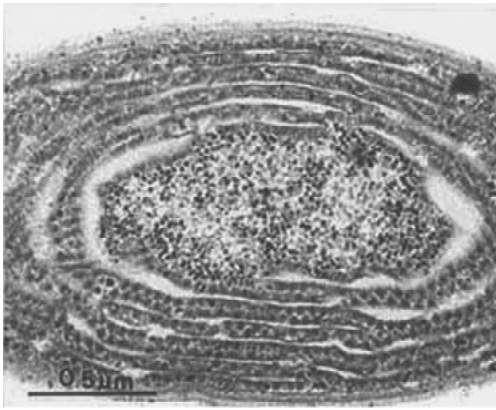


Figure 1. Electron micrograph showing PBS lining the surfaces of the thylakoid membranes of the unicellular cyanobacterium *Synechococcus*. The image was kindly provided by Elisabeth Gantt.



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 Elisabeth 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 oc-

curred 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 environmental 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 phycobili-protein 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

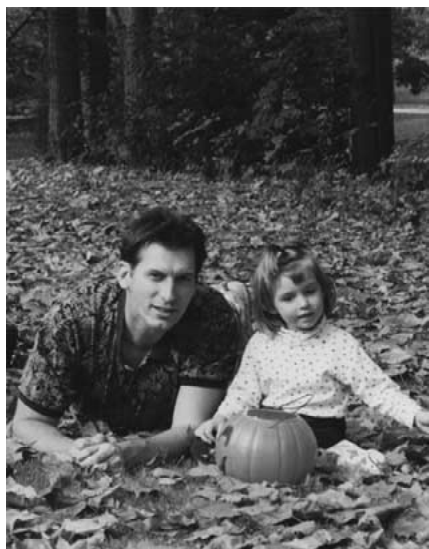


Figure 4. David Kehoe (left), who identified the gene encoding a phytochrome-like photoreceptor that controls complementary chromatic adaptation, and his daughter Ivy celebrating the colors of fall. David is an Assistant Professor in the Biology Department at Indiana University.

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).

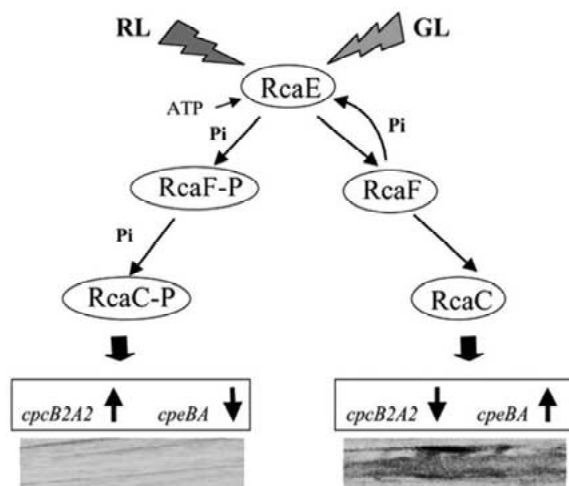


Figure 5. Model showing some aspects of the phosphorelay control of *cpcB2A2* and *cpeBA* during complementary chromatic adaptation in *F. diplosiphon*. The pigmented cells on solid medium are shown at the bottom of the figure. Permission to use the figure was kindly provided by the Journal of Biological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

Complementation 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 Copley. 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 co-transcribed with *cpeCDE* (Copley 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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