**Seeing New Light: Recent Insights into the Occurrence and Regulation of Chromatic
Acclimation in Cyanobacteria**

Short title: Regulation of Chromatic Acclimation in Cyanobacteria

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23 **Abstract**

24 Cyanobacteria exhibit a form of photomorphogenesis termed chromatic acclimation (CA), which
25 involves tuning metabolism and physiology to external light cues, with the most readily
26 recognized acclimation being the alteration of pigmentation. Historically, CA has been
27 represented by three types that occur in organisms which synthesize green-light-absorbing
28 phycoerythrin (PE) and red-light-absorbing phycocyanin (PC). The distinct CA types depend
29 upon whether organisms adjust levels of PE (type II), both PE and PC (type III, also
30 complementary chromatic acclimation), or neither (type I) in response to red or green
31 wavelengths. Recently new forms of CA have been described which include responses to blue
32 and green light (type IV) or far-red-light light (FaRLiP). Here, the molecular bases of distinct
33 forms of CA are discussed.

Introduction

Photomorphogenesis is a process by which organisms perceive external light cues, including wavelengths (or colors) of light available and light intensity, and subsequently adjust cellular metabolism, organismal growth, and development to optimize survival in response to a dynamic photoenvironment. This process is particularly critical for photosynthetic organisms, which depend upon light for driving photosynthesis, or the conversion of light energy to chemical energy. In cyanobacteria, microbes which exhibit oxygenic photosynthesis similar to higher plants, photomorphogenesis is used to tune physiology and photosynthetic efficiency for promoting productivity in response to external light cues, while limiting the potential for light-associated cellular damage. The most widely recognized form of photomorphogenesis occurring in cyanobacteria is chromatic acclimation, a process enabling these organisms to tune the protein or pigment content of phycobilisomes (PBSs), or the accessory light-harvesting complexes linked to photosystems that contribute to photosynthesis, to external light cues to maximize productivity and survival (recently reviewed [1]).

The occurrence of chromatic acclimation (CA), historically referred to as chromatic adaptation, has been long known in cyanobacteria and was primarily associated with cyanobacterial responses to the relative abundance of red or green wavelengths of light [2,3]. In early characterization of CA reported ~40 years ago, Tandeau de Marsac [3] classified three types of chromatic acclimation occurring in cyanobacteria that contain two types of phycobiliproteins, green-light-absorbing phycoerythrin (PE) and red-light-absorbing phycocyanin (PC), in the rods of PBSs: type I, organisms fail to exhibit a change in either PE or PC content in response to changes in external light; type II, organisms alter PE levels in

responses to changes in available green or red light, whereas PC levels remain unchanged; and type III, organisms increase PE content in green-enriched light and preferentially accumulate PC in red-enriched light. This latter form of CA is commonly referred to as complementary chromatic acclimation or CCA [3]. After decades of operating in a framework of these three recognized types of CA, additional forms of chromatic acclimation have been reported recently, including type IV CA in which marine cyanobacteria adjust the chromophore composition of phycobiliproteins in response to the prevalence of blue vs. green wavelengths of light [4-6] and Far-Red Light Photoacclimation (FaRLiP) that involves cellular responses to far-red and red light [7-12].

As indicated above, our early understanding of CA was based primarily on organisms that respond to red and green light to adjust levels of the PE and PC phycobiliproteins found in the rods of PBSs [2,3]. The primary models for understanding chromatic acclimation have been a relatively limited number of genetic systems, including type III chromatically-acclimating filamentous freshwater cyanobacterium *Fremyella diplosiphon* (for reviews see [1,5,13-15]). However, knowledge regarding the range of wavelengths of light associated with CA in cyanobacteria and the associated molecular mechanisms of regulation have expanded significantly, as represented by the aforementioned type IV CA and FaRLiP. Simultaneous advancements in molecular tools for sequencing genomes and abilities to analyze a broader range of organisms have led to greater insights into the molecular bases of CA regulation for both established and new forms of CA. These advances have resulted in a more complex understanding of the range of wavelengths of light and biochemical mechanisms involved in CA across a variety of organisms. Here, I discuss the distinct forms of CA for which molecular

insights have been described, including types II [3], III (CCA) [3], and IV [4,6] CA, as well as the most recently described FaRLiP [9,10].

Type II CA

Although the occurrence of type II CA was reported early [3], only of late has insight emerged about the specific regulators used by cells to control photomorphogenesis during this process. PE levels increase in green light and are repressed in response to red light during type II CA (Figure 1), whereas PC levels remain unchanged. This process is regulated by the cyanobacteriochrome photoreceptor CcaS and its cognate response regulator CcaR [16,17]. CcaS is a green- and red-light responsive photoreceptor with green-light-induced kinase activity that initiates a transcriptional cascade resulting in induction of PE in *Nostoc punctiforme* in green light [16]. Specifically, accumulation of phosphorylated CcaS in green light results in activation of CcaR through phosphorelay, which results in binding of CcaR-P to the promoter of *cpeC-cpcG2-cpeR1* and GL-induced expression of this operon including the PE linker gene (*cpeC*) and a PE regulatory gene (*cpeR1*). Expression of *cpeR1* is correlated with subsequent upregulation of the *cpeB-cpeA* operon which encodes PE apoproteins [16]. In red light, accumulation of unphosphorylated CcaR results in repression of *cpeC-cpcG2-cpeR1* expression, and a corresponding lack of PE induction [16].

Type III CA (Complementary Chromatic Acclimation or CCA)

CCA is the form of chromatic acclimation that has been mostly widely examined. This form of CA involves adjustments in pigmentation in response to external cues, i.e., PE accumulation is induced in response to green light and conversely PC accumulation is induced

and PE is repressed in red light, as well as changes in cellular and filament morphologies that also occur during CCA (for recent review see [1,5,13-15,18]). The primary model organism that has been used for these studies is *F. diplosiphon* (also referred to as *Tolypothrix* sp. PCC 7601; [19]). The tuning of pigmentation to external cues has been linked to optimization of photosynthetic efficiency in this organism [20].

RcaE-dependent regulation of CCA. Genetic approaches were used to identify molecular components responsible for CCA in *F. diplosiphon* (e.g., see [21-23]). Such studies led to the identification of a photoreceptor RcaE (regulator of chromatic acclimation E) largely responsible for the regulation of pigment levels during CCA [24,25] (Figure 1). RcaE, the founding member of the cyanobacteriochrome family of proteins, was later shown to work together with two response regulators, RcaF and RcaC, the latter of which is a DNA-binding transcriptional regulator directly responsible for regulating expression of phycobiliprotein-encoding genes [26-28]. In addition to pigment regulation, it was shown that RcaE was also the photoreceptor responsible for the regulation of cellular morphology, which is also a central part of CCA [29]. Apart from pigmentation and cellular and filament morphologies, additional RcaE-dependent cellular responses occurring during CCA have been described. RcaE has been recently shown to control expression of genes encoding inorganic carbon transporters, which function as a critical part of the carbon-concentrating mechanism linked to increasing photosynthetic efficiency and limiting photorespiration [30]. Together with the regulation of the accumulation of photosynthetic pigments, RcaE is thus proposed to be involved in the integrated coordination of modules critical for photosynthesis. RcaE also regulates a tetrapyrrole-binding protein that is implicated in multiple light-regulated responses in *F. diplosiphon*, including mediating cellular responses to oxidative stress [31,32]. Thus, critical advances have been made in understanding

the role of RcaE in both promoting photosynthetic efficiency and limiting light-associated cellular damage.

Although RcaE and its effectors are essential for regulating pigmentation and morphology, genome-wide studies of gene expression indicated that the signal components involved in cellular responses during CCA are much more numerous and complicated than had been previously recognized [33,34]. These results and others led to continued investigation into regulatory and structural factors critical for CCA. More than 20 years after identifying a single photoreceptor RcaE as fundamental for regulating CCA, there has recently been a rapid expansion of our understanding of additional photoreceptors involved in tuning CCA in *F. diplosiphon* beyond the simple response to red and green wavelengths for which it is most widely known. In these studies, photoreceptors have been identified that extend the wavelengths of light used to tune PE and PC content.

New photoreceptors regulating gene expression and pigmentation during CCA. IflA, an RcaE-dependent photoreceptor, carries two chromophores in two separate GAF domains [35]. IflA functions in response to blue, green, red and far-red light [35]. Genetic analysis indicated that IflA functions during growth at low cell density [35]. As its abundance is regulated directly by RcaE, which itself is a light-activated kinase [36], the photoregulation that occurs during CCA is indeed more complex than had been previously appreciated (Figure 1). In addition to IflA, other RcaE-independent photoreceptors that function during CCA have been identified. DpxA is a photoreceptor that responds to teal and yellow wavelengths of light to impact PE levels [37]. DpxA is a light-regulated kinase involved in tuning PE levels [37]. Thus, the regulation of PE levels in *F. diplosiphon* occurs through coordinate regulation by multiple photoreceptors (Figure 1).

Cgi pathway. Of note, it had been previously recognized that additional factors in *F. diplosiphon* contribute to the regulation of PE levels. This observation was initially primarily identified through the recognition that minor differences in PE levels persist in response to green light in a mutant lacking RcaE [38]. This finding suggested another green-light dependent system for regulating PE levels in *F. diplosiphon*, which would contribute to CCA in response to green light through a previously uncharacterized mechanism for green light-induced control of PE accumulation. The system was named the control of green light induction (Cgi) pathway [39,40]. As described above, the primary means for regulating CCA appear to be via photoreceptor-dependent signaling linked to transcriptional regulation; however, the Cgi pathway represents an independent mechanism for posttranscriptional regulation, occurring primarily through a factor associated with control of translation initiation [39,40]. Translation initiation factor α (IF3 α) encoded by gene *infC* is a central component in the Cgi pathway, wherein IF3 α exhibits a novel gene expression function resulting in repression of *cpeC* operon expression and thus repression of PE accumulation in red light in *F. diplosiphon* [40] (Figure 1).

Type IV CA

This form of CA has been recognized for marine cyanobacteria and the molecular basis of regulation has begun to be elucidated [4,6,41-43]. During type IV CA, the chromophore content of phycobiliproteins is controlled rather than the apoprotein content which is the target of types II and III CA described above [4,6]. This regulation of chromophore contained in PBSs involves a PE-specific bilin lyase, i.e., MpeZ, which is found in many strains capable of type IV CA and which is responsible for converting green-light-absorbing chromophore phycoerythrobilin (PEB) to blue-light-absorbing chromophore phycourobilin (PUB) in response

to shifts in green and blue light [41,43]. Key regulators of the process have been described and named FciA (type four chromatic acclimation island) and FciB, which impact expression of three genes found in the same genetic operon as FciA and FciB [42] (Figure 1). Notably, among these Fci-regulated genes is MpeZ, which is induced by FciA in blue light and repressed by FciB in green light [42]. This light-dependent regulation of MpeZ through the FciA and FciB system results in PUB accumulation in blue light and PEB in green light [42] (Figure 1).

FaRLiP

This mostly recently reported form of CA occurs in cyanobacteria which synthesize distinct red-shifted PBSs which allow cells to grow in far-red enriched light. Such PBSs have been reported for strains including chlorophyll *d*-containing *Acaryochloris marina* [8], chlorophyll *f*-containing cyanobacterium *Halomicronema hongdechloris* [44], and *Chlorogloeopsis fritschii*, *Leptolyngbya* sp. strain JSC-1 and other cyanobacteria containing both chl *d* and chl *f* [7,10,11]. Initial insights into the molecular regulation of the far-red induced acclimation response, which has been named Far-Red Light Photoacclimation (FaRLiP) have been reported [7-12]. A red- and far-red responsive cyanobacteriochrome RfpA works together with response regulators RfpB and RfpC to control transcriptional regulation of genes needed to build the characteristic red-shifted photosystems and far-red-absorbing PBSs found in FaRLiP-capable cells [10-12]. Recent studies with the marine cyanobacterium *Synechococcus* sp. PCC 7335 indicated that slight variations in Rfp-dependent regulation of FaRLiP exist, as this strain showed regulation of PC and photosystem II in addition to the *rfp* cluster and production of red-shifted PBSs typical of other FaRLiP-capable strains mentioned above [45,46].

Conclusions

One of the central features of CA is the tuning of the pigment composition and/or size of phycobilisomes to optimize light absorption for photosynthesis, while limiting overexcitation of photosynthetic pigments, the latter of which is associated with cellular damage. This feature results in organisms possessing tunable or flexible PBSs. For example, it has been long known that the widely studied *F. diplosiphon* tunes both protein composition and size of PBSs in response to external light cues [2,3,47]. Although there are potential costs to maintaining a tunable PBS for organisms in dynamic environments over the short-term [48], complementary chromatic acclimation has been shown to yield fitness advantages over long-term environmental acclimations in natural contexts [49,50].

Although studies of type III CA or CCA in *F. diplosiphon* have spanned decades, recent insights supported by genome sequence availability and genome-wide transcriptional analyses have resulted in a more complete and nuanced understanding of the multiple layers of regulation that allow CCA-capable cells to maintain optimized photosynthetic efficiency and photoprotection. Furthermore, breakthroughs based on studies with additional genetic systems have resulted in significant advancements in our understanding of the occurrence and molecular bases of regulation of additional forms of CA, including type II CA, type IV CA and the emergent FaRLiP. Together with the large number of photoreceptors known to exist in cyanobacteria for which no distinct phenotypes have been ascribed (e.g., see references [1,19]), these recent developments in our understanding of CA indicate that new light on photoacclimation in cyanobacteria may continue to shine for years to come.

Acknowledgements

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218 Funding: The work in the author’s laboratory on photomorphogenesis and chromatic acclimation
219 of cyanobacteria is supported by the National Science Foundation [grant no. MCB-1243983 to
220 B.L.M.], whereas work on biotechnological adaptations with cyanobacteria based on light-
221 responses is supported by the U.S. Department of Energy, Chemical Sciences, Geosciences and
222 Biosciences Division, Office of Basic Energy Sciences, Office of Science [grant no. DE-FG02-
223 91ER20021 to B.L.M.].

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Figure Legend

Figure 1. Photoreceptor-dependent signaling associated with the regulation of distinct types of chromatic acclimation (CA) in cyanobacteria. Four types of chromatic acclimation for which insights into the molecular pathways involved in regulation have been elucidated are depicted (type I CA which does not involve acclimation of phycoerythrin [PE] and phycocyanin [PC] in response to changes in external cues is not shown). Shown are specific photoreceptors, photoreceptor-dependent effectors or response regulators (RR), and cellular outputs associated with each type of CA. Type II CA involves regulation of PE levels in response to changes in green vs. red light availability, but no effect on PC levels. Type III, also known as complementary CA [CCA], involves green-light upregulation of PE levels and red-light-dependent induction of PC and repression of PE. Type IV CA includes perception of blue and green light and subsequent regulation of the chromophore content of cells, with phycoerythrobilin (PEB) produced in green light and phycourobilin (PUB) produced in blue light. FaRLiP is a form of photoacclimation which occurs in response to red and far-red light and includes far-red-dependent synthesis of distinct photosystem and phycobilisome components that confer on cells the ability to grow in far-red light conditions. –P indicates phosphorylation of a photoreceptor or effector/RR in response to a specific color of light.

CA type	photoreceptor (color detected)	effector(s)	output
Type II	CcaS (green [G], red [R])	CcaR	PE
Type III/ CCA	RcaE (G, R)	RcaF, RcaC	PE, PC
	IfIA (blue [B], G, R, far-red [FR])	?	PE
	DpxA (teal [T], yellow [Y])	WP_045867495	PE
	? (R)	IF3α	PE
Type IV	FciA, FciB (B, G)	MpeZ	PEB → PUB
FaRLiP	RfpA (R, FR)	RfpB, RfpC	PE, PC