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Chromatic Acclimation in Cyanobacteria: A Diverse and Widespread Process for Optimizing Photosynthesis

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Abstract

Chromatic acclimation (CA) encompasses a diverse set of molecular processes that involve the ability of cyanobacterial cells to sense ambient light colors and use this information to optimize photosynthetic light harvesting. The six known types of CA, which we propose naming CA1 through CA6, use a range of molecular mechanisms that likely evolved independently in distantly related lineages of the *Cyanobacteria* phylum. Together, these processes sense and respond to the majority of the photosynthetically relevant solar spectrum, suggesting that CA provides fitness advantages across a broad range of light color niches. The recent discoveries of several new CA types suggest that additional CA systems involving additional light colors and molecular mechanisms will be revealed in coming years. Here we provide a comprehensive overview of the currently known types of CA and summarize the molecular details that underpin CA regulation.

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INTRODUCTION

Photosynthetic organisms achieve optimum levels of photosynthetic activity by adjusting their photosynthetic machinery to changes in the amount and color of light in the environment. Chromatic acclimation (CA) is a process that modifies the composition of the light-harvesting structures of many photosynthetic microbes as the ambient light color changes. CA was first described over 100 years ago (24, 33, 34), when blue-green filamentous cyanobacteria collected in a European lake gradually changed color several days after being placed in the window of a laboratory. This led to the surprising discovery that the color of light to which these cyanobacteria are exposed determines their color phenotype, with red light causing the cells to turn blue-green and green light making them brick red, and that this process is reversible. This serendipitous finding set into motion research over the past century that has revealed the molecular mechanisms underpinning CA as well as leading to discoveries that have contributed to our understanding of photosynthesis, signal transduction, bacterial evolution, and global ecology. In recent years, there has been an explosion of interest in the study of CA, led by the identification of new types of CA that allow photosynthetic organisms around the world to acclimate to a diverse array of light wavelengths. Here, we blend the rich historical understanding of CA with exciting new findings while providing perspective on the shared principles between different types of CA. We also propose a newly modified naming system to classify and organize the currently known forms of CA as well as those that are likely to be discovered in the future.

The six types of CA that have been discovered to date are presented in **Figure 1** and are more fully described below. The central theme in all types of CA is the selective use of a variety of chromophores, including open-chain tetrapyrroles (or bilins), to maximize photon capture and thus the light reactions of photosynthesis. Bilin chromophores are covalently attached to specific cysteine residues of phycobiliproteins, proteins that are part of cyanobacterial photosynthetic light-harvesting antennae called phycobilisomes (PBS). In general, PBS capture light wavelengths that are poorly absorbed by chlorophylls and funnel this energy into photosynthetic reaction centers. During CA, only a subset of the chromophores in PBS change. CA has most likely evolved because the absorption bandwidth of each of the different bilin chromophores used in PBS is narrow relative to the width of the irradiance spectrum used for photosynthesis and because the spectral distribution of ambient light can vary tremendously, particularly in aquatic environments (**Figure 2**) and microbial mats (79, 112). Thus, CA-regulated PBS changes lead to the selective use of chromophore types that maximize the absorbance of the predominant colors (wavelengths) of

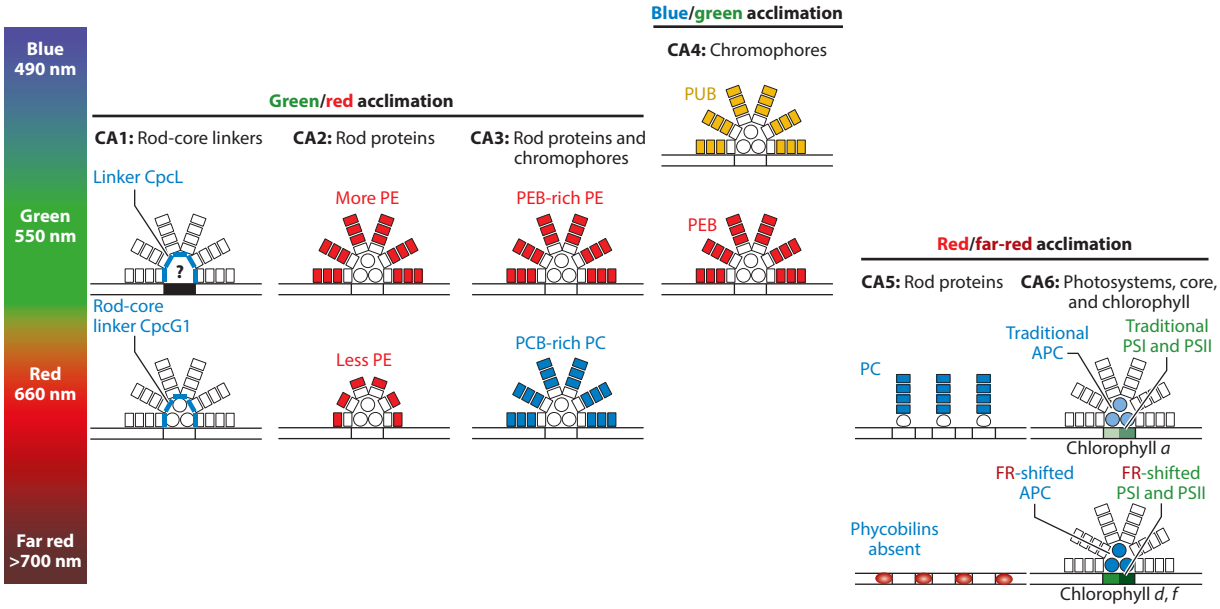


Figure 1

Summary of the changes in the light-harvesting structures that occur during the six known types of chromatic acclimation. Portions of the light-harvesting structures that change during CA are shown in color, while all other aspects are shown in white for simplicity. Additionally, all of the PBS antennae are shown with the same architecture, although some small differences in protein stoichiometry and PBS rod and core size may exist. Parallel horizontal black lines represent the photosynthetic (thylakoid) membranes with photosynthetic reaction centers demarked by two black vertical lines within thylakoid membranes. CA1, CA2, and CA3 are different forms of green/red acclimation. During CA1, red light leads to the production of canonical PBS that contain the rod-core linker CpcG1, which binds the rods to the allophycocyanin core, while growth in green light induces the linker CpcL, which appears to lead to formation of PBS without core components that preferentially associate with Photosystem I (*black rectangle*). It is not clear how the rods are linked to the reaction centers in this situation (*question mark*). CA2 induces phycoerythrin production in green light, which leads to longer PBS rods. CA3 has complementary roles by inducing phycocyanin production in red light and phycoerythrin production in green light. CA3 also regulates production of the bilin chromophores PCB and PEB, which leads to changes in the color of the PBS rods. Blue/green acclimation type CA4 changes the relative amounts of the bilin chromophores PUB and PEB, while not affecting the PBS proteins. This also leads to a change in the color of the rods. CA5 leads to a loss of PC-containing phycobilins in far-red light, which are replaced by chlorophyll *d*–based light-harvesting antennae in the membrane (*dark red ovals*). CA6 (also called FaRLiP) causes large changes in the photosynthetic apparatus in far-red light, inducing far-red-shifted allophycocyanin, alternate photosystem proteins, and chlorophylls *d* and *f*. Abbreviations: APC, allophycocyanin; FaRLiP, far-red-light photoacclimation; FR, far red; PC, phycocyanin; PCB, phycocyanobilin; PBS, phycobilisome; PE, phycoerythrin; PEB, phycoerythrobilin; PSI, Photosystem I; PSII, Photosystem II; PUB, phycourobilin.

the surrounding light. Under conditions of changing light colors, this strategy can capture much more photon energy to power photosynthesis than can be harvested by producing PBS with fixed chromophore types, whose absorption properties may not match the predominant ambient light colors as they vary.

The substantial contribution of CA to global photosynthetic activity is becoming increasingly clear. For example, one type of CA, CA4, has been estimated to operate in about 40% of the 7×10^{26} marine *Synechococcus* cells, the second-most abundant photosynthetic microorganism within the world's oceans (28, 42). CA is predicted to increase fitness in a wide range of ecological niches, including those in terrestrial, freshwater, and marine environments (**Figure 2**), with CA-capable and CA-incapable species or populations often coexisting (1, 23, 36, 42, 92, 97, 117). CA would appear to be an overwhelmingly beneficial trait to possess since it allows a portion of the

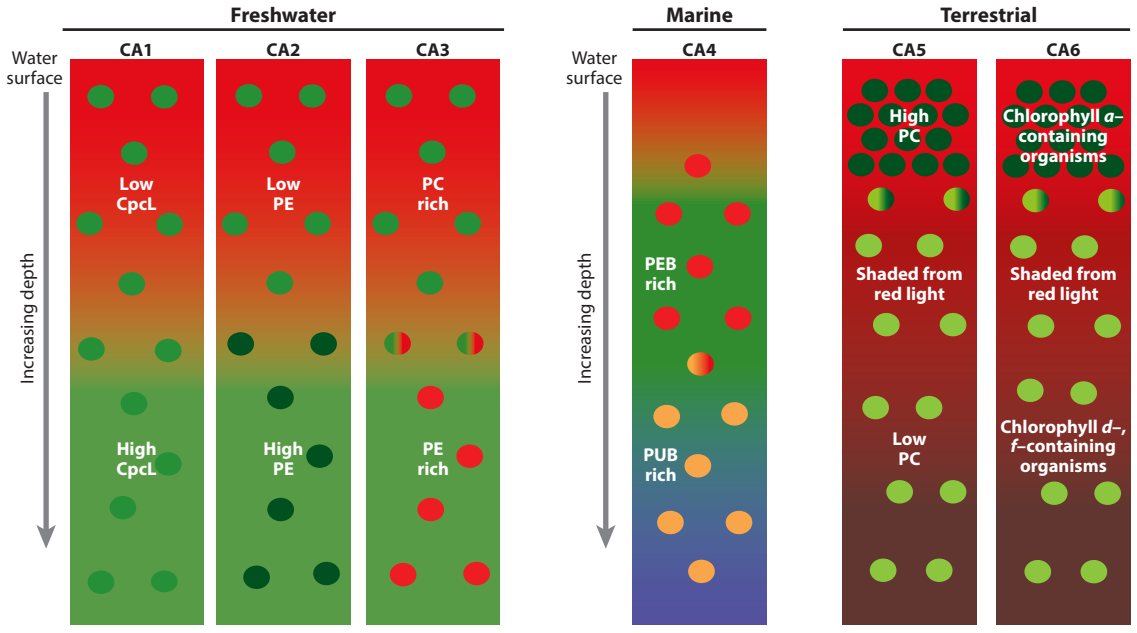


Figure 2

Chromatic acclimation is predicted to function across diverse ecological niches. Green/red acclimation types CA1, CA2, and CA3 likely are maximally useful in environments where red and green wavelengths predominate. CA1 induces the linker CpcL in green light, while CA2 and CA3 induce phycoerythrin in green light. CA3 has an additional, complementary role by inducing phycocyanin in red light. Blue/green acclimation type CA4 changes the relative amounts of the bilin chromophores PUB and PEB in marine environments where natural gradients of green and blue light occur between coastal and offshore environments or between surface and deep waters. Red/far-red acclimation types CA5 and CA6 (also called FaRLiP) likely are frequently useful in terrestrial environments, where dense surface populations of chlorophyll *a*–containing organisms create shaded conditions with little to no available red light below them. CA5 reduces expression of phycocyanin in far-red light, while CA6/FaRLiP leads to the induction of far-red-optimized core proteins, photosystems, and chlorophylls. Some marine cyanobacteria are also capable of CA3 or CA5. Abbreviations: FaRLiP, far-red-light photoacclimation; PC, phycocyanin; PE, phycoerythrin; PEB, phycoerythrobilin; PUB, phycourobilin.

PBS chromophore content to be adjusted to maximize energy collection for photosynthesis. This view is supported by evidence, presented below, that CA has evolved more than once. In addition, it exists in all of the major cyanobacterial lineages. However, while many cyanobacterial species are CA capable, there are also many that are not, likely because CA is a strategy that provides a fitness advantage predominantly under fluctuating light conditions (113).

The ability of CA-capable organisms to sense specific light colors and respond by producing PBS that are optimized to collect those wavelengths of light suggests that they possess sophisticated light-color-sensing and signal-transduction systems. In this review, we address the mechanisms and regulation of the types of CA that have been discovered thus far and examine what is known about the physiology, ecology, and evolution of these processes. Because this review is an update of a previous review on CA published in the *Annual Review of Plant Biology* (64), we only briefly review CA from a historical perspective.

Phycobilisome Biogenesis and the Discovery of Different CA Types

PBS are macromolecular light-capturing complexes that reside on the surface of the photosynthetic or thylakoid membranes. PBS structures have been extensively reviewed (43, 75, 124) and so are only summarized here. The most common PBS form is fan shaped or hemidiscoidal

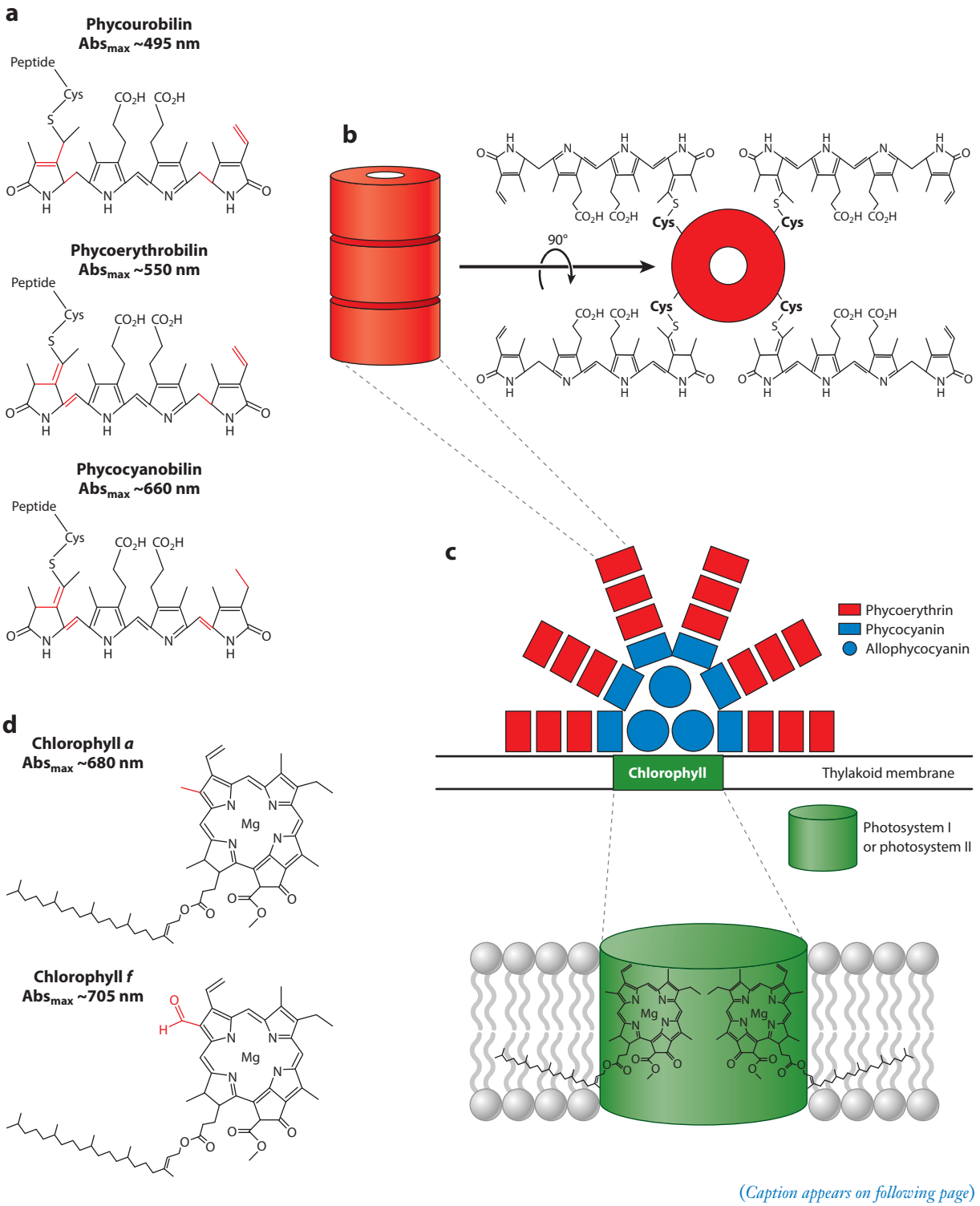
(**Figure 3**), with a central core and rods radiating from the core. Both the core and the rods are built of cylinders that contain phycobiliproteins and linker proteins. Phycobiliproteins are responsible for photon capture and possess one to three covalently attached chromophores that absorb specific wavelengths of light (39), while linkers predominantly lack chromophores and play structural and energy transfer roles (72, 118). Evolution has selected the type and local environment of each chromophore within a PBS to create an energy trap, with virtually unidirectional energy transfer through the PBS into photosynthetic reaction centers achieved by chromophores capturing higher-energy, shorter-wavelength photons in the outer rod regions and progressively lower-energy, longer-wavelength photons further down the rods and into the core (39). For every type of CA known, all chromophore substitutions maintain this energy trap.

In both the core and the rods, phycobiliproteins exist as α/β heterodimers. These must be correctly chromophorylated by enzymes called phycobilin lyases, which catalyze the covalent attachment of chromophores to specific cysteines of either the α or β subunit of a particular phycobiliprotein. These chromophorylation events allow the formation of the stable heterodimers that are used to build a PBS (103, 126). Three such heterodimers form a ring-like structure, and two rings are layered together to form a disc (**Figure 3**). These hexameric discs, which are hollow in their centers, are then stacked to form cylinders. There is a unique type of linker protein inserted into the centers of each specific pair of discs to be joined. As described in the sections below, various types of CA have been found to involve the light color regulation of almost all of the above processes, including the biosynthesis of specific bilin chromophores, lyases, phycobiliproteins, and linkers. In some types of CA, regulation is via a single photoreceptor that acts through its cognate transcription factor, while in others, posttranscriptional regulation, multiple photoreceptors, interplay between lyases, and as-yet-undescribed mechanisms are involved.

Several additional aspects of CA physiology should be noted. First, all known forms of CA are reversible, and in those that have been investigated, the most recently provided color of light determines the composition of the PBS. Second, the time required for a CA-mediated shift in PBS structure is dependent on the growth rate of the cells, and for the types of CA thus far tested, at least several days are required for a complete CA response to occur. In addition, there is no evidence that phycobiliprotein turnover rates change during CA (8), suggesting that PBS structural changes occurring during this process are the result of dilution of the previously existing PBS forms during cell growth and division rather than their active removal via proteolysis (8, 38, 86).

In laboratories, narrow bandwidths of light are often used to determine the approximate wavelengths that are the most effective in eliciting the most extreme two states of a particular CA response. These states occur when PBS are the most optimally structured to absorb one or the other of two light colors. As described in this review, these light colors are often different for distinct types of CA, likely reflecting the different spectral niches in which various CA-capable cyanobacterial species live. Also, although all forms of CA can exist in two extreme states, if the two colors that lead to those states are both present, the PBS are composed of a mixture of the chromophores (and proteins, if applicable) from both states. However, it is not clear whether such heterogeneity exists within individual PBS, whether there are multiple PBS types within a single cell, or whether there is a mixture of cells with all of the PBS in any given cell being locked in one or the other CA state. Finally, evidence is accumulating that suggests that some cyanobacteria are capable of more than one type of CA simultaneously (11, 37, 49). In such cases, complex networks of photoreceptors and signaling pathways are certainly involved.

In 1902, Gaidukov (33) used the term complementary chromatic adaptation to describe CA since the cyanobacterial filament colors were complementary to the ambient light colors: red in green light and blue-green in red light. Seventy-five years later, Tandeau de Marsac (117) placed cyanobacteria containing the abundant phycobiliproteins phycocyanin and phycoerythrin into



(*Caption appears on following page*)

Figure 3 (*Figure appears on preceding page*)

Light-harvesting molecules involved in chromatic acclimation. (*a*) Chemical structures of the bilin chromophores phycourobilin, phycoerythrobilin, and phycocyanobilin, with differences between these isomers denoted in red. (*b*) Bilin chromophores are attached to cysteine residues on phycobiliproteins through thioether linkages. (*c*) Detail of the spatial arrangement between a phycobilisome and a photosynthetic reaction center. (*d*) Chemical structures of chlorophylls *a* and *f* found in photosynthetic reaction centers, with differences between the structures denoted in red. Chlorophyll is associated with Photosystem II or I proteins and is embedded in the thylakoid membrane by a large hydrophobic tail. Abbreviation: Abs_{max}, maximum absorbance.

three groups. In group 1 species, the abundance of these phycobiliproteins remained the same in red and green light, so this group did not carry out CA. Group 2 species had higher levels of phycoerythrin in green light than in red, while phycocyanin levels remained constant. Group 3 species displayed the phenotype described by Gaidukov for complementary chromatic adaptation: phycocyanin levels were high in red light and low in green light, while phycoerythrin levels were low in red light and high in green light. As described in this review, many other forms of CA have been discovered recently, but in none of these are the cell colors complementary to the eliciting light colors. Therefore, for clarity and simplicity, the word complementary is no longer used to describe CA.

Also, historically, group 1 cyanobacteria were designated as those that do not undergo CA, leading to confusion about the nature of type 1 CA (CA1). In this review, we propose that a recently discovered form of CA be given the CA1 designation. Additionally, group 2 is now called type 2 CA (CA2), group 3 is type 3 (CA3), and all other forms of CA have been named in the chronological order of their discovery. Finally, the word acclimation has replaced adaptation in the name CA because adaptation requires a genetic change in an organism while acclimation does not, and no genetic change occurs during any known type of CA.

The initial description of CA3 in the early 1900s was followed by further study, mainly in the 1960s and 1970s, of CA3 photobiology. Action spectra were used to identify the wavelengths that maximally elicited CA3 (green light, approximately 541 nm, and red light, approximately 641 nm) (21, 30, 31, 46, 47, 87, 122). The green-red photoreversibility of CA3 was noted to have intriguing similarity to plant red/far-red light responses controlled by phytochrome photoreceptors discovered in the late 1950s (13). Indeed, several decades later, a phytochrome-like histidine kinase called RcaE was identified as a green-red photoreceptor controlling the CA3 response (52, 62, 119). RcaE was the first of a new class of cyanobacterial photoreceptors named cyanobacteriochromes (CBCRs) (59) that control light responsiveness for many, but not all, types of CA through two-component phosphorelay systems.

THE PHYSIOLOGY AND REGULATION OF CA SYSTEMS IDENTIFIED TO DATE

There has been a significant increase in our awareness and understanding of many types of CA since last addressed in the *Annual Review of Plant Biology* (64). In this review, we examine the six distinct types of CA that have been identified thus far, including the between-species variation that exists for several of these types. Undoubtedly, many additional types and variations of CA remain to be discovered, underscoring the fitness benefits of tuning PBS absorption characteristics to the ambient light color environment in a wide variety of light niches and the overall importance of CA to cyanobacteria. The first three types of CA primarily respond to green and red light, the fourth to green and blue light, and the fifth and sixth to red and far-red light.

CA1

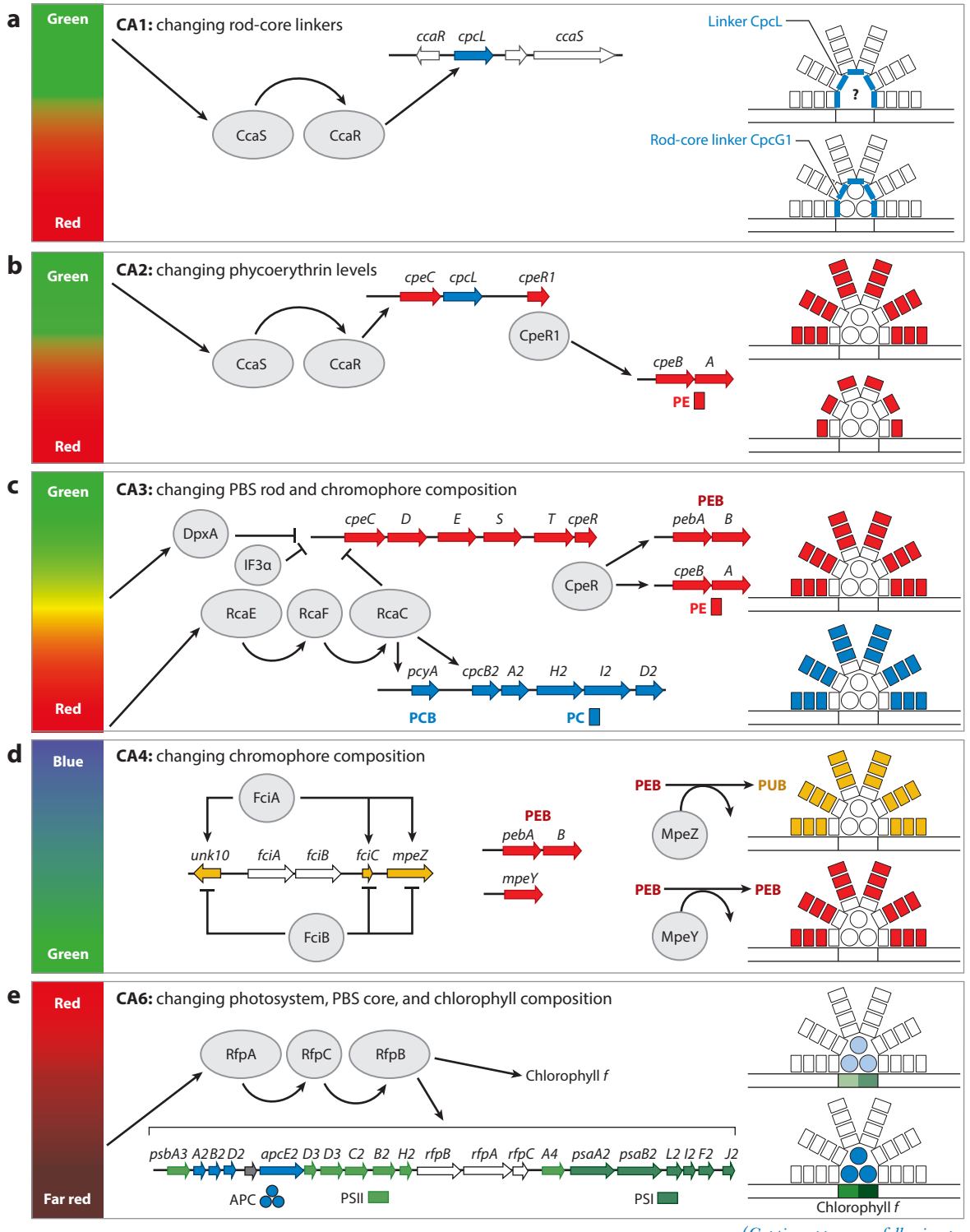
CA1 is the simplest and most recently discovered form of green/red CA. CA1 was originally identified by Ikeuchi's group in *Synechocystis* sp. PCC 6803, which neither produces phycoerythrin nor

undergoes the historically better-known processes of CA2 or CA3 (65, 117). It was identified by the discovery of a photoreceptor called CcaS, which had sequence similarity to RcaE (53, 62). CcaS maximally absorbed green [wavelength $(\lambda)_{max} = 535$ nm] and red ($\lambda_{max} = 672$ nm) light and was encoded near the gene encoding its cognate response regulator, CcaR. These components were reported to be responsible for the red-green-light-mediated twofold change in RNA levels of *cpcG2*, which has since been renamed *cpcL* (125) (**Figure 4*a***). CpcL encodes a linker that links PBS to Photosystem I and leads to a redistribution of energy between the two photosystems (20, 53, 65, 66). Since this change is occurring within the PBS, but not to either a phycobiliprotein or a chromophore, the type of CA being regulated by CcaS and CcaR in *Synechocystis* sp. PCC 6803 is truly a unique process compared to all other forms of CA that have been described. Although "CA0" was proposed for this form of CA (50), we suggest that this name is inaccurate because the zero incorrectly implies that there is no CA occurring. At the same time, we note that CA1 historically refers to the absence of CA, as defined by Tandeau de Marsac (117). Thus, these names are reversed from the processes they actually designate. For this reason, we propose that the form of CA described here for *Synechocystis* sp. PCC 6803 be designated CA1. Because linker-based CA is likely to be a major new form of CA, we also recommend that this designation be used for all subsequently discovered forms of CA that involve changes in linker abundance but not in phycobiliprotein or chromophore abundances.

CA2

CA2 is a form of green/red CA identified by Tandeau de Marsac in 1977 (117). Although phycoerythrin levels were elevated in green light, compared to red light, there was no light color regulation of phycocyanin levels. Because of this, the cellular color phenotypes of CA2 are more subtle than those described above for CA3 (51). The first CA2-capable cyanobacterium examined at the molecular level was *Nostoc punctiforme* PCC 73102 (51). Its genome was found to contain a cluster of genes, one of which encoded a protein that was highly similar in sequence and photochemistry to the green/red-sensing CBCR called CcaS, which controls *cpcL* expression during CA1 in *Synechocystis* sp. PCC 6803. Other genes in this cluster encoded CcaR, a response regulator similar to that found to regulate CA1, the phycoerythrin linker CpeC, a rod-core linker of phycocyanin called CpcG2 or CpcL (125), and a protein called CpeR1 that had been previously identified as an activator of phycoerythrin expression in the CA3 species *Fremyella diplosiphon* UTEX 481 (16, 105). Deletion of the *N. punctiforme ccaS* gene led to the loss of CA2 regulation of phycoerythrin accumulation, measured as absorbance, although substantial amounts of phycoerythrin were still produced. Similarly, deletion of the *N. punctiforme ccaR* gene eliminated CA2-mediated phycoerythrin changes. In addition, phycoerythrin was reduced to almost undetectable levels, unlike for the *ccaS* mutant. Based on these results, it was proposed that CcaS acts as a phosphatase of CcaR under the noninducing light color (51), as had been previously proposed for RcaE during CA3 (63). RNA blot analyses were used to show that the deletion of *ccaS* and *ccaR* also eliminated CA2 regulation of the RNA abundance of *cpeBA*, the genes encoding the α and β subunits of phycoerythrin.

Overall, it was proposed that in *N. punctiforme*, CcaS autophosphorylated in green light and subsequently phosphorylated CcaR, which was found to bind a region of DNA upstream of the area of the genome encoding *cpeC*, *cpcG2* or *cpcL* (125), and *cpeR1*, triggering the CpeR1-mediated activation of *cpeBA* operon expression (51) (**Figure 4*b***). For CA2-capable species, the CcaS/R regulators and general features of CA2 systems used in *N. punctiforme* appear to be widespread, having been found in other CA2-capable *Geminocystis* cyanobacteria (50) and in *Gloeotrichia* UTEX 583, which also shows some features of CA3-capable species (114). It was also proposed that CcaS and CcaR might make up the second system that had been identified (3, 61, 68, 85, 105) as one



(Caption appears on following page)

Figure 4 (*Figure appears on preceding page*)

Regulatory mechanisms controlling CA. (*a*,*b*) Signaling pathways controlling CA1 in *Synechocystis* sp. PCC 6803 and CA2 in *Nostoc punctiforme* sp. PCC 73102 both involve the CBCR CcaS and response regulator CcaR but regulate different physiological responses (see **Figure 1**). (*c*) Red/green CA3 in *Fremyella diplosiphon* UTEX 481 uses the CBCR RcaE and two response regulators, RcaF and RcaC, to regulate the composition of the rod proteins and chromophore composition (PEB or PCB). The Cgi pathway also represses production of phycoerythrin-containing rods and involves repression by an IF3 translation initiation factor. A candidate CBCR for the Cgi photosensor is DpxA, a histidine kinase that represses phycoerythrin expression in yellow light. (*d*) The blue-green CA4 system (CA4-A is shown) in *Synechococcus* sp. RS9916 regulates PUB and PEB levels in the rods and is inversely regulated by FciA and FciB, two proteins with similarity to AraC-class transcription factors. Genes such as *pebAB* and *mpeY* are not CA4 regulated, while some in the genomic island (*gold arrows*) are upregulated in blue light. (*e*) During CA6 (also called FaRLiP) in *Leptolyngbya* sp. JSC-1, variation in expression of a cluster of genes changes the chlorophyll content (chlorophyll *a* or chlorophyll *d*/*f*) in Photosystems II and I and the type of allophycocyanin present in the PBS core. These changes are regulated by the phytochrome superfamily member RfpA and two response regulators, RfpB and RfpC. The light-color responses during CA1, CA2, CA3, and CA6/FaRLiP have all been shown to involve photoreceptors with histidine kinase activity through two-component systems or phosphorelay. Abbreviations: APC, allophycocyanin; CBCR, cyanobacteriochrome; FaRLiP, far-red-light photoacclimation; PC, phycocyanin; PCB, phycocyanobilin; PBS, phycobilisome; PE, phycoerythrin; PEB, phycoerythrobilin; PSI, Photosystem I; PSII, Photosystem II; PUB, phycourobilin.

of the two CA3 regulatory pathways in *F. diplosiphon*, although this possibility was later negated by the discovery that this second system was regulated after transcription initiation (9) (see the section titled CA3).

CA3

CA3 has been the subject of photobiology research for many decades. These studies began with measuring changes in light absorption by cells, and as more sophisticated analytical tools became available, they extended into the physiology and molecular biology of this process and its regulation.

Discovery and initial characterization. Because of the dramatic shifts between green and red cell coloration, CA3 was the first type of CA to be discovered (33). It is the most complex form of green/red CA known, and there is evidence that it is also responsive to teal (λ_{max} = 494 nm) and yellow (λ_{max} = 568 nm) light (127). The initial studies of CA3 established that green and red light were the most efficient elicitors of this response (see the section titled Phycobilisome Biogenesis and the Discovery of Different CA Types) and led to the proposal that either one or two photoreceptors controlled this response (85). A single photoreceptor was expected to control both green and red light responses. If two photoreceptors were involved, one was expected to respond to green light and the other to red. Surprisingly, although current evidence suggests that two photoreceptors control CA3 (see below), these sense four different light colors and operate through different signal-transduction pathways, making this response more complex and novel than originally predicted.

The physiology and molecular basis of the CA3 response in different cyanobacterial species have been defined in the 1970s through the 2000s and have been previously reviewed (44, 64). Thus, in this section we only summarize the information pertinent to the CA3 model organism *F. diplosiphon* UTEX 481 (also known as *Calothrix* sp. PCC 7601 or *Tolypothrix* sp. PCC 7601) and necessary to provide context for the latest findings, which are discussed in the subsequent two sections.

In *F. diplosiphon*, the differential accumulation of PBS containing phycoerythrin in green light and phycocyanin in red light, which leads to the striking changes in cell color during CA3, is due to changes in the expression of many genes. Those that are the most critical for CA3 are shown in **Figure 4*c***. The *cpeCDESTR* (hereafter *cpeC*) operon is more highly expressed in green light than red light (9, 26, 27), with the first three genes encoding phycoerythrin-associated

linkers. *cpeR* encodes an activator (16, 105) whose accumulation leads to increased expression of *cpeBA*, which encodes the α and β subunits of phycoerythrin (78), and *pebAB*, which encodes the oxidoreductases required to produce phycoerythrobilin (PEB), the green-light-absorbing phycoerythrin chromophore (3, 29). Therefore, the *cpeC* operon has a central role in coordinating green-light-activated gene expression during CA3. In red light, the expression of the above genes is strongly (but not completely) reduced and the *cpcB2A2H2I2D2* (hereafter *cpc2*) operon, encoding a CA3-specific set of α and β subunits of phycocyanin and phycocyanin-associated linkers, is highly upregulated (18, 19, 73). Red light also upregulates the expression of *pcyA*, which encodes the oxidoreductase that produces phycocyanobilin, the red-light-absorbing phycocyanin chromophore (2, 29).

Since its discovery, there has been widespread interest in how CA3 is regulated. The first CA3 signal-transduction system identified was the Rca pathway (**Figure 4*c***). It is a complex type of two-component system called a phosphorelay (4) initiated by RcaE, which contains a domain with similarity to those of plant phytochromes and an output domain related to those found in histidine kinases (62). RcaE was proposed to more strongly autophosphorylate in red light than in green light, where it may have phosphatase activity (63, 119). RcaF is a single-domain response regulator that was initially proposed to be phosphorylated by RcaE (63). Genetic evidence indicates that RcaF then phosphorylates RcaC, another response regulator that contains two receiver domains (one at its N terminus and one at its C terminus), a histidine phosphotransfer domain, and an OmpR/PhoB-class DNA-binding domain (15, 63). In red light, RcaC directly controls the repression of the *cpeC* operon and activation of the *cpc2* operon and *pcyA* by binding to the L box, which is present upstream of the promoters of these genes (67). It was proposed that in green light, the reduced phosphorylation of RcaC decreases its binding to the L boxes, eliminating the activation of *cpc2* and *pcyA*. It also removes the repression of *cpeC* operon expression, increasing the production of CpeR and activating the expression of other green-light-expressed genes such as *cpeBA* and *pebAB* (3, 16, 105). While the Rca system at first appeared to be capable of providing complete regulation of CA3, genetic and molecular data suggested that an additional system called the control of green light induction (Cgi) pathway substantially contributes to the control of green-light-expressed genes during CA3 (3, 61, 68, 105).

In addition, in the 1970s it was noted that cell morphology, shape, and average filament length were also regulated by CA3 in *F. diplosiphon* (8). These observations led to the identification of several genes that were CA3 regulated yet predicted to encode non-PBS-associated proteins. These included *chlLN* and *chlB*, which are under the control of both RcaE and CpeR and encode subunits of the light-independent form of protochlorophyllide reductase, the enzyme that carries out the penultimate step in chlorophyll *a* biosynthesis (106, 115). Also, RcaE appears to regulate light-color-dependent changes in cell morphology (10), although the expression of the putative morphogene *tonB* increased in green light in an RcaE-independent manner (94).

Advances in understanding the signal transduction and photobiology of CA3 regulation. Recent work has led to a better mechanistic understanding of CA3 regulation, including the Rca and Cgi pathways. RcaE was directly shown to be a green light (λ_{max} = 540 nm)-red light (λ_{max} = 660 nm)-sensing photoreceptor that preferentially autophosphorylated in red light (52). Containing a single GAF domain as its photosensory module, it was the first identified member of the CBCR photoreceptors (59, 62), which are now known to control many forms of CA (128).

The Cgi system has also been further defined, with studies of the region upstream of *cpeC* demonstrating that it regulates *cpeC* RNA levels after transcription initiation, most likely through transcriptional attenuation in red light (9). In addition, this system represses *cpeC* expression in red light, so that the regulation of the *cpeC* operon by CA3 is via two repressing systems acting

in red light, the Rca system acting at the level of transcription and the Cgi pathway apparently operating by transcription attenuation. The Cgi system requires a region of the *cpeC* 5′ leader near the start codon that is predicted to form a 30-nucleotide-long stem-loop with a free energy of folding of −3.4 kcal/mol (9). Even single-nucleotide substitutions within this region resulted in the loss of red light repression of *cpeC* expression. Collectively, these data suggest that an RNA-binding protein may be interacting with this region, and perhaps components of the translation initiation complex, in a light-color-dependent fashion.

Support for this possibility has come from a genetic screen for Cgi components that uncovered several mutants with lesions in or near *infC*, which encodes a translation initiation factor called IF3 (45). An essential gene in other organisms, this *infC* gene is dispensable in *F. diplosiphon* due to the presence of a second, diverged *infC* gene in the genome. These were named *infCa* and *infCb*, respectively. The deletion of *infCa*, but not *infCb*, resulted in the loss of Cgi regulation of *cpeC*, suggesting that IF3α plays a role in the Cgi regulation of CA3 (45). The position of IF3 on the 30S subunit of the ribosome may allow interactions with the *cpeC* 5′ leader stem-loop region identified as critical for Cgi system function (84). Interestingly, many plant genomes appear to encode multiple chloroplast-specific IF3s, and two have been confirmed in the model plant *Arabidopsis* (84). The two genes encoding these IF3s are differentially expressed developmentally and under various environmental conditions. Because the regulation of chloroplast gene expression is commonly at the level of translation initiation and involves RNA-binding proteins and stem-loop structures within the RNA 5′ leader regions (96), related mechanisms could be at work in the regulation of the Cgi system in *F. diplosiphon* and chloroplast gene expression in plants. Many other cyanobacteria also possess multiple IF3-encoding genes, including strains that do not undergo CA (45). Thus, research on CA may have uncovered a novel form of gene regulation that is widespread throughout the *Cyanobacteria*.

The genetic screen that uncovered *infCa* also led to the identification of *dpxA*, encoding a CBCR with a GAF photosensory domain and histidine kinase output domain (127). The deletion of *dpxA* led to an increased level of phycoerythrin, but not phycocyanin, in white-light-grown cells, suggesting that DpxA might be part of the Cgi pathway (**Figure 4*c***). This was supported by the fact that DpxA operates through a system that is independent of the Rca pathway. The DpxA photosensory domain maximally absorbed teal and yellow light, and autophosphorylation of full-length DpxA was greater in yellow light than blue light (127). In vivo, the effect of deleting *dpxA* on increased phycoerythrin levels (measured as absorbance) was the greatest in yellow and red light, and the least in blue light. Overall, these results suggest that DpxA autophosphorylation in yellow and red light leads to the repression of phycoerythrin accumulation, and that this effect is absent in blue light. Taken together, these results make DpxA a viable candidate for the photoreceptor controlling the Cgi system, although this hypothesis has yet to be directly tested. In addition, the downstream signaling components through which DpxA acts are currently unknown. Interestingly, the DpxA absorption maxima are on the two sides of the RcaE green light absorption maximum, which is quite broad (52, 127), suggesting that the role of DpxA, and perhaps the Cgi system, is to fine-tune the levels of phycoerythrin in *F. diplosiphon* in the blue-green region of the spectrum. The discovery of DpxA suggests that the regulation of CA3 involves the integration of multiple light cues and likely involves networks of photoreceptor-driven signaling pathways.

Additional insights into CA3-regulated responses beyond the PBS. Recently, there has been additional progress in understanding how CA3 affects *F. diplosiphon* processes that are not related to PBS biogenesis (8, 95). These light-color-mediated changes in cell morphology and physiology have been found to be regulated by RcaE and include the expression of the morphogenes *bolA* and *mreB* (109, 110); a light-dependent iron limitation response (93); a reduction in the levels of

reactive oxygen species during growth in green light (108); changes in carboxysome number, size, and structure (100); and photorespiration (80). Intriguingly, RcaE also regulates the abundance of another *F. diplosiphon* photoreceptor, a CBCR named IflA (12). An L box with strong sequence identity to those found upstream of the *cpc2*, *pcyA*, and *cpeC* transcription start sites was found to overlap the *iflA* transcription start site. IflA contains two photosensory GAF domains. The N-terminal GAF domain senses red light (λ_{max} = 645 nm) and far-red light (λ_{max} = 688 nm), while the C-terminal GAF domain senses blue light (λ_{max} = 412 nm) and green light (λ_{max} = 525 nm). IflA also has a central, nonphotosensory PHY domain (12). One role of IflA is to increase growth when the ratio of red to far-red light in the environment is high, but because IflA has no identifiable signaling output domain, it is not clear how it transmits its information to other sensory components in the cell. Together, the study of CA3 has revealed a network of three spectrally diverse photoreceptors, RcaE, DpxA, and IflA, that integrate unique light color cues to optimize cell physiology and photosynthesis.

CA4

The most distinctive form of light color acclimation known, CA4 is a highly streamlined type of CA that has thus far only been found to occur in the marine environment, where it is a globally important form of phenotypic plasticity.

Discovery and characterization. In 2001, Palenik (92) discovered a completely new type of CA, which was subsequently named type 4 chromatic acclimation (CA4) (25). Unlike CA2 and CA3, it was maximally responsive to blue and green light and specifically occurred in the unicellular marine cyanobacterium *Synechococcus*. This organism is broadly distributed throughout the world's oceans and is considered to be the second-most abundant phototroph on Earth (28). The diversification of marine *Synechococcus* light-harvesting systems is likely an important component of their ecological success, and all known marine *Synechococcus* strains use PBS for photosynthetic light harvesting. Although some strains have phycocyanin-containing rods, most have rods with both phycocyanin and phycoerythrin, and the majority of these possess phycocyanin as well as two forms of phycoerythrin called phycoerythrin I (PE-I) and phycoerythrin II (PE-II) (90, 91, 111). These two phycobiliproteins are related at the structural and amino acid sequence levels, but they bind different chromophores and are encoded by different genes. PE-I α and β subunits are encoded by the *cpeBA* operon and are called CpeA and CpeB, while PE-II α and β subunits are encoded in the *mpeBA* operon and are called MpeA and MpeB. Discs made of MpeA/MpeB heterodimers are always located at the most core-distal positions of each rod, while discs of CpeA/CpeB heterodimers are contiguous with MpeA/MpeB discs and separated from the core by one basal phycocyanin disc. In marine *Synechococcus*, PE-I and PE-II often attach blue-light-absorbing phycourobilin (PUB) (λ_{max} = 495 nm) in addition to the green-absorbing PEB (λ_{max} = 550 nm) used in CA2- and CA3-capable cyanobacteria (58, 111).

There are three major pigment types of marine *Synechococcus* that contain both PE-I and PE-II. The first two are blue light specialists, which have a high PUB:PEB ratio and capture blue light effectively, and green light specialists, which have a low PUB:PEB ratio and effectively absorb green light. For each of these two types, the PUB:PEB ratio is not influenced by ambient light color changes, and therefore these do not undergo CA. The third pigment type is made up of blue-green generalists, also called the CA4 strains, which are capable of modifying their PUB:PEB ratio in response to the ambient blue-light-to-green-light ratio (25, 92).

The first step in understanding the mechanism and regulation of CA4 was the identification of the changes occurring in the PBS during growth in blue versus green light. Two initial discoveries

made it clear that the structural basis for CA4 was different from CA1, CA2, and CA3. First, there were no detectable changes in PBS protein composition in green versus blue light during CA4. Second, it was shown in two different marine *Synechococcus* strains, M16.7 and RS9916 (hereafter 9916), that CA4 involves chromophorylation changes at three cysteines (C), two in MpeA (C83 and C140) and one in CpeA (C139), where PEB was attached in green light and PUB was attached in blue light (25, 107). Therefore, CA4 specifically involves changes in PBS-bound chromophores, rather than changes in PBS protein subunits.

Molecular characterization of the genes and proteins involved in CA4. Comparative genomic analyses of marine *Synechococcus* isolates from around the world provided important early insights into the process of CA4 (58, 111). These studies found that the presence of a 4–6 kb genomic region with the hallmarks of a genomic island (GI) was highly correlated with CA4 capability. They also identified two phylogenetically distinct groups of CA4-capable strains with slightly different genes and gene organization within their CA4 GIs (**Figure 5*a***). The first identified group was named CA4-A and the second CA4-B, based on the hypothesis that these would control two different but related forms of CA4.

The CA4-A-specific gene *mpeZ* encoded a protein with similarity to phycobilin lyases and to the CA4-B-specific *mpeW* gene product. Both GIs contained the genes *fciA* and *fciB*, which are similar in sequence to AraC family transcription factors in their C-terminal regions. The small open reading frame *fciC* is present in all CA4-A GIs and encodes a protein related to the ribbon-helix-helix domain of some phage repressors (5). All CA4-A and CA4-B GIs contain *unk10*, while *unk14* is only present in some CA4-A GIs. InterPro searches show that Unk10 has a nif-11-like signature (IPR02903) found in all cyanobacteria and Unk14 belongs to the DUF2237 family of proteins of unknown function, present in all marine picocyanobacteria.

While comparative genomics approaches provided a number of hypotheses regarding CA4 regulation, the development of methods for culturing, plating, and genetically modifying marine

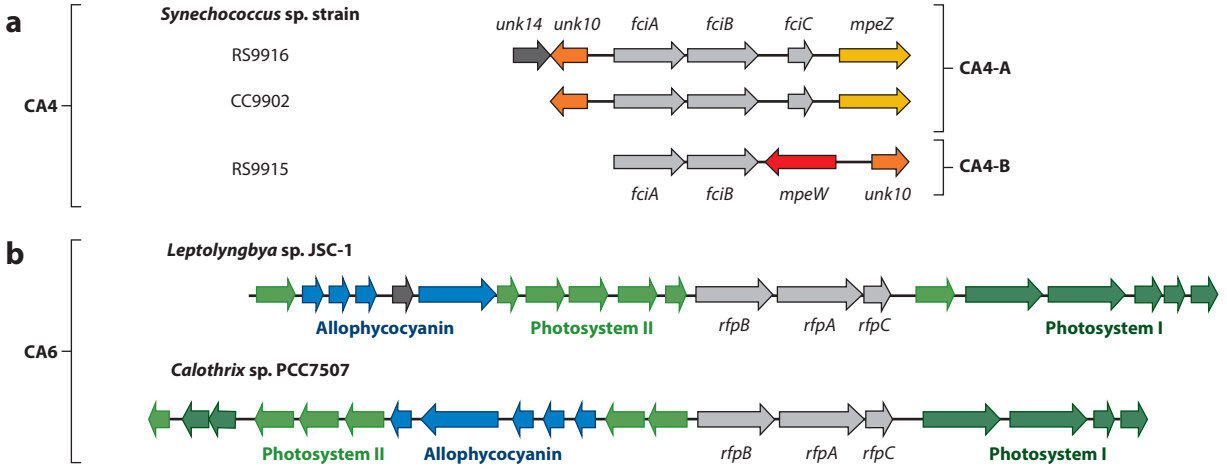


Figure 5

Genomic localization of genes involved in CA. Genomic diversity of exemplar strains capable of (*a*) CA4 and (*b*) CA6 (also called FaRLiP). All strains capable of CA4 contain a small genomic island with *fciA*, *fciB*, *unk10*, and either *mpeZ* or *mpeW*. All strains that contain *mpeZ* also contain *fciC*. Strains capable of CA6/FaRLiP have a large genomic region containing *rfpA*, *rfpB*, *rfpC*, and genes encoding far-red-specific allophycocyanin subunits, Photosystem II, and Photosystem I. Abbreviation: FaRLiP, far-red-light photoacclimation.

Synechococcus has allowed the direct testing of these hypotheses as well as the development of new ones. Specifically, genetic manipulations such as the disruption and overexpression of some of the abovementioned genes have helped define their roles in CA4. Thus far, genetic analyses of CA4 have been conducted using the CA4-A model strain 9916, isolated from the Gulf of Aqaba in the Red Sea (32). Additionally, various RNA-seq, RT-PCR, and RNA blot analyses have identified CA4-responsive genes in both CA4-A and CA4-B strains, demonstrating that CA4 is regulated at least in part by mRNA abundance changes (58, 102, 107). Interestingly, in 9916, expression of only the three genes *fciC*, *unk10*, and *mpeZ* was strongly upregulated by blue light, and all three were located within the CA4-A GI (102). None was strongly upregulated in green light. Another intriguing result was that the blue-light-induced increase in *mpeZ* expression in a CA4-A strain was the opposite of the green-light-induced increase in *mpeW* expression found in a CA4-B strain (58, 102, 107). This information provides an important foundation for understanding CA4 regulation and evolution, as discussed below.

CA4-A involves chromophore changes at three phycobiliprotein residues: CpeA-C139, MpeA-C83, and MpeA-C140. This suggested the involvement of a phycobilin lyase, and because *mpeZ* appeared to encode such a lyase and its expression was upregulated in blue light during CA4, it was the first gene disrupted in 9916 (58, 107). MpeZ was shown to be a PEB lyase-isomerase, attaching PEB to MpeA-C83 and isomerizing it to PUB (107). In a *mpeZ* mutant, PEB is attached to MpeA-C83 in blue light, and subsequent work has shown that the lyase MpeY is responsible for this attachment (101). In wild-type cells, RNA-seq data showed that although *mpeY* RNA levels are not regulated by CA4, in green light they are higher than *mpeZ* RNA levels, while in blue light, CA4 drives the level of *mpeZ* RNA above the *mpeY* RNA level. Thus, it is likely that changes in the relative levels of MpeZ and MpeY determine which chromophore is attached to MpeA-C83.

The mechanisms underpinning the CA4-mediated chromophore changes at CpeA-139 and MpeA-C140 are not yet clear. In 9916, there are no other CA4-regulated genes that encode putative lyases, so additional systems similar to MpeZ/MpeY are unlikely to control the other CA4-driven chromophore changes. It is possible that CA4 regulation is also occurring posttranslationally, or involves the small protein encoded by the CA4-regulated gene *unk10*. It is also possible that Unk14 is involved, although many CA4-A-capable strains do not appear to contain *unk14* in the CA4 GI, making it unlikely to be an essential component of CA4-A.

Two genes within the 9916 GI that are not differentially expressed during CA4 are *fciA* and *fciB*. Diametric phenotypes were obtained after interruption of each. An *fciA* mutant displayed a green light phenotype during growth in blue or green light, while an *fciB* mutant exhibited a blue light phenotype in either light condition (102). Because the CA4-A response upregulates three GI genes in blue light, FciA was proposed to act as an activator when the blue-to-green light ratio is high and FciB as a repressor when the blue-to-green ratio is low. FciA and FciB are clearly the master regulators of CA4-A in 9916, since all CA4-based chromophorylation and gene expression phenotypes were affected in these mutants (102) (**Figure 4*d***). Both FciA and FciB have C-terminal regions that suggest that they belong to the AraC family of transcription factors (35, 104, 121), but no DNA-binding sites have been characterized to date. In addition, the mechanism(s) through which the relative amounts of blue and green light are being sensed during CA4 remains unknown. Unlike the cyanobacteria that carry out CA2 and CA3, marine *Synechococcus* is unlikely to use CBCRs for light color sensing since no genes encoding such proteins have been identified in the genomes of these organisms.

Why are there two types of CA4? The existence of two related but different CA4 GIs is intriguing. The presence of *fciA*, *fciB*, and *unk10* on both GIs and the similarity of the proteins encoded by *mpeZ* and *mpeW* suggest that these arose from a common ancestor. However, CA4-A causes

the upregulation of *mpeZ*, *unk10*, and *fciC* RNA levels in blue light while CA4-B causes the upregulation of at least *mpeW* RNA in green light. An interesting possibility is that the CA4-A GI has evolved to confer green light specialists with the capacity to use blue light more effectively and that the CA4-B GI has evolved to confer blue light specialists with the ability to more effectively use green light. This hypothesis could be tested by transforming a series of green light specialists and blue light specialists with either the CA4-A GI or the CA4-B GI and testing for acquisition of CA4 capability. Such experiments would provide important insights into the evolution and acquisition of this globally important trait.

Ecological significance of CA4. One feature of CA4 that sets it apart from all other known types of CA is its clear global ecological importance, although initially its prevalence in the environment was not clear. After the discovery of CA4, phenotypic screening of culture collections and analyses of published PUB:PEB ratios from the literature initially suggested that CA4-capable strains accounted for up to 20% of all isolated *Synechococcus* strains (42; see also **http://roscoff-culture-collection.org**). However, reliably extrapolating this estimate in the field to obtain a more accurate global estimate of CA4-capable cells was problematic because of the challenge of discriminating them from other *Synechococcus* pigment types using a fluorescence-based approach such as flow cytometry (17, 89, 120, 129). Although distinguishing high-PUB from low-PUB cells was possible, discriminating between blue light specialists and CA4 cells that were acclimated to blue light was impossible, as was distinguishing between green light specialists and green-light-acclimated CA4 cells. Progress began to be made in overcoming this hurdle in the last few years, when the pigment diversity of natural *Synechococcus* populations started to be assessed by sequencing amplicons of either the phycocyanin operon *cpcBA* or the PE-I operon *cpeBA* (130). However, while the *cpcBA* genetic marker could discriminate *Synechococcus* cells containing only phycocyanin from those containing both phycocyanin and phycoerythrin (either PE-I only or both PE-I and PE-II), it could not distinguish populations with different PUB:PEB ratios. Sequence information from the *cpeBA* marker, in contrast, allowed discrimination between green light specialists containing only PE-I and those containing both PE-I and PE-II, as well as CA4-A cells. Unfortunately, blue light specialists are phylogenetically indistinguishable from CA4-B cells using sequence information obtained with this marker (57, 71, 130).

Some interesting initial findings concerning the distribution of CA4 were obtained with these markers. In the vicinity of Hong Kong, Liu et al. (71) were able to detect *cpeBA* sequences related to that of the CA4-A strain 9916 both in January and in July at an oceanic-influenced mesotrophic coastal station (PM7) located off Port Shelter, whereas there were no CA4 cells at the eutrophic estuarine station NM3. Similarly, Humily et al. (57) found that about 28% of the *Synechococcus cpeBA* reads retrieved from a site off the northwest French coast were from CA4-A strains, although that population was dominated by green light specialists (63% of total reads). Xia et al. (130) also analyzed surface samples from multiple cruises in the northwestern Pacific Ocean using the same primers and discovered that CA4-A cells constituted up to 100% of the *Synechococcus* population in subpolar waters, while green light specialists dominated in warm coastal waters.

Grébert et al. (42) successfully constructed a global distribution map of all *Synechococcus* pigment types by using three different genetic markers, the *cpcBA* and *mpeBA* operons and the CA4-B-specific *mpeW* gene. Sequencing reads for these markers were recruited from the extensive metagenomic data set collected during the *Tara* Oceans circumnavigation (116). For the first time, strains capable of CA4-A and CA4-B were reliably identified in field data. Globally, CA4-A strains represented 22.6% of all *Synechococcus* reads and CA4-B strains represented 18.9% of all *Synechococcus* reads, and these two pigment types exhibited very complementary geographic distributions (42) (**Figure 6*a***). CA4-A cells predominated in the nutrient-rich, temperate or cold waters found at

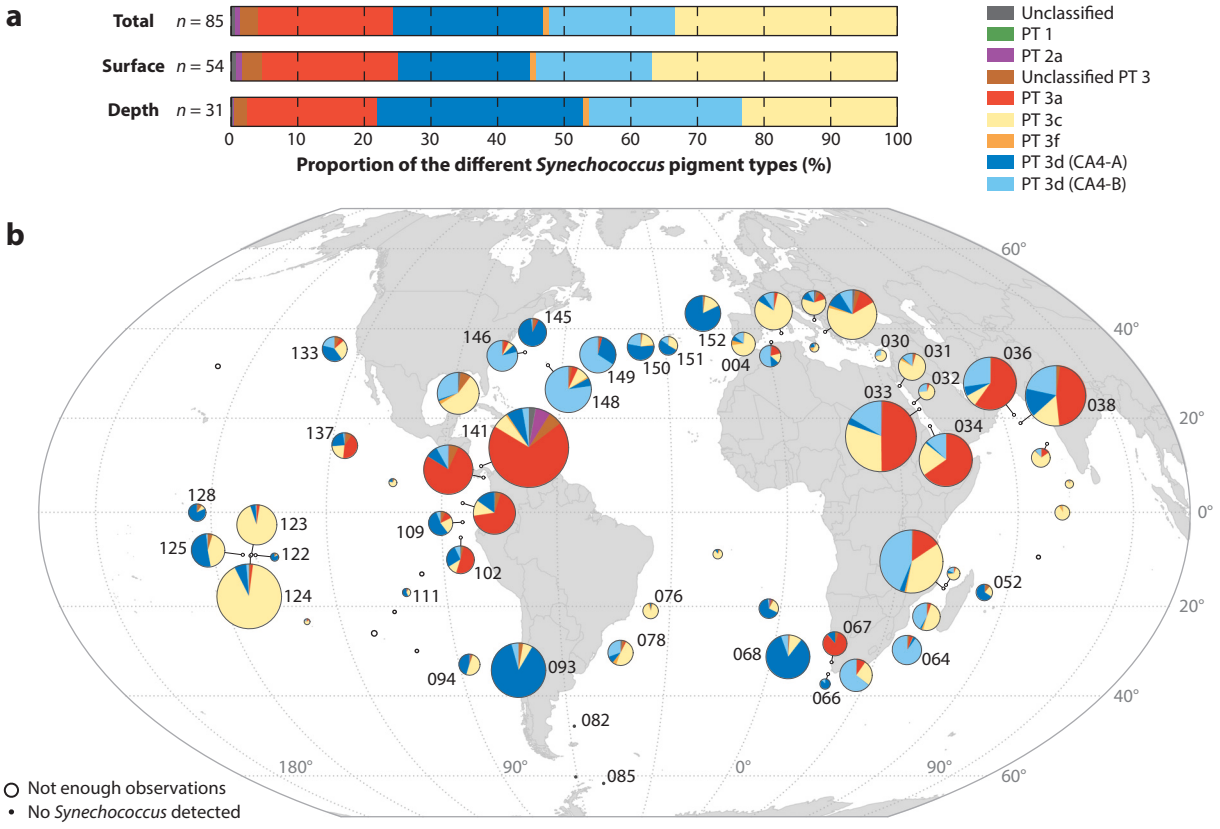


Figure 6

Ecological importance of *Synechococcus* capable of CA4. (*a*) Relative abundance of each *Synechococcus* pigment type (PT) in the whole *Tara* Oceans dataset (*Total*), at the surface, and at the deep chlorophyll maximum, as assessed by recruiting reads of three distinct marker genes (*cpcBA*, *mpeBA*, and *mpeW*). (*b*) Map showing the global distribution of all *Synechococcus* PTs, including CA4-A (*dark blue*) and CA4-B (*light blue*), in surface waters along the *Tara* Oceans circumnavigation transect (see Reference 42 for details on the other PTs). Diameters of pie charts are proportional to the number of *cpcBA* reads normalized by the sequencing effort. Stations with less than 30 *cpcBA* or *mpeBA* reads are indicated by open circles, and those with no *cpcBA* reads by black dots. Numbers next to pie charts correspond to the numbers of the *Tara* Oceans stations. Only those stations that were specifically discussed in Reference 42 have a station number. Adapted with permission from Reference 42.

high latitudes and in upwelling areas, while CA4-B cells were most abundant in warm, nutrient-poor waters (**Figure 6*b***). The CA4-A phenotype was consistently strongly correlated with low temperature, high chlorophyll, and high nitrate and phosphate concentrations, while the CA4-B phenotype was associated with low concentrations of these two nutrients. Both forms of CA4 appeared to be globally more abundant at depth than at the surface, suggesting that CA4 provides a fitness advantage during growth at low irradiances. This finding correlates well with the previous observation that CA4-A predominates in subpolar waters (130), where irradiance levels are low throughout most of the year. The *Tara* Oceans data were also analyzed for the presence of other PBS biosynthesis genes (42). Surprisingly, some *Synechococcus* populations inhabiting the vast iron-poor areas of the Pacific Ocean that had been genetically assigned to the CA4-A group were found to possess *mpeZ*, encoding a PEB lyase-isomerase, but lacked *fciA* and *fciB*, which encode the master regulators of CA4. Also missing was *mpeY*, encoding a PEB lyase (101). The phenotype of such

cells would be that of a blue light specialist, a conclusion confirmed by the finding of an identical genomic arrangement in BIOS-E4-1, a strain isolated from iron-poor waters of the southern Pacific Ocean that exhibits a blue light specialist phenotype. Thus, these naturally occurring CA4-A mutants appear to constitute a second type of blue light specialists, having adapted to blue, iron-depleted, ultraoligotrophic waters by inactivating CA4, which is likely to be an energetically costly acclimation mechanism. Overall, it appears that CA4 confers a fitness benefit to *Synechococcus* cells in many but not all ecological niches colonized by this ubiquitous organism.

CA5

In 2009, Chen's group (14) identified type 5 chromatic acclimation (CA5) in *Acaryochloris marina*, which in addition to chlorophyll *d*–based light harvesting complexes possesses noncanonical phycobiliprotein-containing light-harvesting antennae that are rod shaped and contain phycocyanin and, at their base, allophycocyanin (56, 77) (**Figure 1**). CA5 appears to be maximally responsive to far-red light (~720 nm), which in the strain MBIC11017 led to a loss of phycobiliproteins while growth in red light (~625 nm) resulted in a large increase in phycobiliprotein abundance (23, 40). Thus, these cells appear to shift from using light-harvesting antennae that are phycobiliprotein-based to using chlorophyll *d*–based antennae when light conditions are shifted from red to far-red light. Additional studies have shown that the expression of nearly 25% of the genes in this organism's genome are differentially expressed during these light color shifts, and that far-red light also promotes biofilm formation, with genes encoding proteins involved in cell wall and membrane biosynthesis being upregulated while many genes encoding components related to photosynthesis are downregulated (48).

Since a directed genetic system does not yet exist for *A. marina*, although transposon mutagenesis is possible (123), the signal-transduction pathway(s) controlling the CA5 response have not yet been identified. One phytochrome superfamily member, AM1_5894, has been characterized from strain MBIC11017 with absorption properties in the far-red and infrared regions of the spectrum. It is a cyanobacterial member of the bacteriophytochrome family that possesses both a histidine kinase output domain and a response regulator receiver module (74). Its role, if any, in controlling CA5 remains unknown. Several CBCRs from *A. marina* have been characterized spectrally, but these do not appear to be likely candidates for CA5 photoreceptors since their in vitro reconstituted forms maximally absorb in the blue, green, and red regions of the spectrum (81–83).

CA6 (FaRLiP)

CA6 [also known as far-red-light photoacclimation (FaRLiP)] is the most recently identified form of CA. CA6/FaRLiP was first characterized by Bryant's group and also operates in the far-red light range (37). However, because the physiological responses of this form of CA are quite different from those of CA5, it is considered to be a separate form of CA, just as CA2 and CA3 both respond to green light but are considered to be separate processes because of their different cellular responses. CA6/FaRLiP is best understood in *Leptolyngbya* sp. JSC-1, a filamentous cyanobacterium found within a floating mat in a hot spring (11). A process that enhances the use of far-red light for oxygenic photosynthesis and growth in diverse cyanobacterial species from many different environments (6, 7, 36, 37, 41, 60, 76, 88, 132), CA6/FaRLiP has generated strong interest, in part due to the potential biotechnological applications of this process (22, 128). This response operates by controlling the biosynthesis of both the photosynthetic apparatus and the light-harvesting antennae. This includes a shift in the use of different types of chlorophylls, from chlorophyll *a* in red light to chlorophylls *f* and *d* in far-red light, and the replacement of the core subunits of both

Photosystems I and II as well as the PBS (131). Additionally, the overall CA6/FaRLiP cellular response is extensive, with the expression of nearly 3,000 genes changing twofold or more after a shift to far-red light (37). These components are encoded within a cluster of 21 genes in the genome, a genomic region that also contains genes encoding a photoreceptor and signal-transduction proteins (**Figure 5*b***).

The photoreceptor RfpA, which belongs to a distinct subgroup of knotless phytochromes (37, 98, 99) and maximally absorbs red light ($\lambda_{max} \sim 645$ nm) and far-red light ($\lambda_{max} \sim 695$ nm), was initially implicated in CA6/FaRLiP light sensing (37). Due to the absence of genetic tools for *Leptolyngbya* sp. JSC-1, several other CA6/FaRLiP-capable cyanobacterial species were used to investigate the roles of RfpA and two response regulators called RfpB and RfpC, encoded adjacent to *rfpA* within the far-red-induced photosynthetic light-harvesting complex and reaction center gene cluster, in CA6/FaRLiP (54, 132). In *Chlorogloeopsis fritschii* sp. PCC 9212, *Chroococcidiopsis thermalis* sp. PCC 7203, and *Synechococcus* sp. PCC 7335, all three of these proteins appear to facilitate the process of far-red light acclimation (**Figure 4*e***). RfpB has been proposed to act as a transcription factor, based on the similarity of one of its domains to winged-helix domains of known transcription factors (132). RfpC is a single-domain response regulator and thus is likely functioning as a phosphoryl group shuttle, although its role is unknown. The gene cluster implicated in conferring CA6/FaRLiP is conserved in thirteen cyanobacterial species (36). A CA6/FaRLiP-like gene cluster is also present in the cyanobacterium *Halomicronema hongdechloris*, which produces chlorophylls *a* and *f* but not chlorophyll *d*. After a shift to far-red light, this species loses its PBS rods and remodels the PBS core to contain variants of allophycocyanin that have red-shifted absorption characteristics, matching the absorption features of the chlorophyll *f* produced in far-red light (70). Also, after shifts from white to far-red light, the chlorophyll composition of Photosystem I changes from all chlorophyll *a* to 92% chlorophyll *a* and approximately 8% chlorophyll *f* (69).

Interestingly, both *Leptolyngbya* sp. JSC-1 and *Synechococcus* sp. PCC 7335 also carry out CA3 (49). In *Synechococcus* sp. PCC 7335, loss of FaRLiP regulators affects the amount and ratios of phycocyanin and phycoerythrin (55), raising the possibility that the CA6/FaRLiP and CA3 regulatory pathways are intertwined. Further complexity is suggested by the finding that in *Leptolyngbya* sp. JSC-1, *rfpA* transcripts are most abundant in cells grown in far-red light, suggesting that either RfpA autoregulates its expression or another photoreceptor regulates *rfpA* gene expression (37). CA6/FaRLiP might provide a selective light absorption advantage in far-red-light-enriched environments found beneath vegetation canopies, within microbial mats, or in soil environments. The influence of CA6/FaRLiP is extensive in *Leptolyngbya* sp. JSC-1, leading to at least twofold changes in expression of greater than 40% of genes in this organism (37). Notably, there are many differences in the downstream responses controlled by CA6/FaRLiP between *Leptolyngbya* sp. JSC-1 and *Synechococcus* sp. PCC 7335, including major differences in PBS structures (54, 55), perhaps because they live in different environments.

CONCLUDING REMARKS AND PERSPECTIVES

In the last few decades, there has been a dramatic increase in our knowledge of the types of CA occurring in the natural environment and how they operate. We have progressed from investigating the nature of the phenotypically dramatic green-red color changes occurring during CA3 to studying processes such as CA1, which is only detectable using sophisticated molecular tools; the dual systems regulating CA3; and CA6/FaRLiP, which is useful for efficiently harvesting light for photosynthesis in the far-red region of the spectrum, colors which are beyond the ability of humans to see.

With this new knowledge has also come an expanded awareness of the diversity of the ecological niches in which the various forms of CA can be found. Free-living cells, symbionts, or epiphytes in marine, freshwater, or terrestrial environments—it is now almost easier to list the types of environments in which CA-capable cyanobacteria are not known to inhabit than to name those where CA occurs. In addition, it is becoming increasingly clear that CA is a widespread mechanism for optimizing the efficiency of photon capture for photosynthesis in cyanobacteria that play important roles in the Earth's carbon and oxygen cycles. Because CA2 and CA3 were the first forms of CA to be identified and both involve the adjustment of phycoerythrin levels, the initial estimate of CA frequency was made only for phycoerythrin-containing cyanobacteria (117). Approximately 27% of the strains examined from the Pasteur Culture Collection did not undergo CA2 or CA3; 16% were CA2 strains; and 57% were CA3 strains. While these data convincingly show the high frequency of CA in phycoerythrin-containing strains, the impact of this finding is tempered by the fact that a large but undefined percentage of cyanobacterial species do not contain phycoerythrin. The overwhelming importance and prevalence of CA in the natural environment has been brought into sharp focus recently by the discovery of CA4 (25, 92) and the estimate that strains capable of this process make up about 40% of the 7×10^{26} marine *Synechococcus* cells in the world's oceans (28, 42). It will be important to take into account the increased effectiveness of photosynthesis that CA provides to cyanobacteria as we continue to refine global estimates of primary productivity.

Given the discoveries of several entirely novel CA types in the last decade, it is reasonable to expect continued growth in the number of new types of CA that are discovered in the coming years. This increase will almost certainly be accompanied by the identification of ever more nuanced variations of CA between species, even for a specific type of CA. Such variations will have almost certainly arisen due to a combination of chance and selection for features of CA that are the most beneficial for that organism's photosynthetic capabilities and the specific light color environment in which it resides. What we have learned about CA thus far clearly shows that its various forms have predominantly evolved independently in distantly related lineages of the *Cyanobacteria* phylum. Yet the phenotypic plasticities provided by the many processes that we call CA have all led to the same outcome: the evolution of photosynthetic light-harvesting antennae that effectively utilize the various colors of ambient light.

As progress continues to be made in deciphering the molecular mechanisms and regulation of the different forms of CA, the next and perhaps greatest challenge will be to better understand both the fitness costs and benefits for CA-capable cyanobacteria in their natural environments. Only then will we truly understand the biology of CA.

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Errata

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