Light regulation of pigment and photosystem biosynthesis in cyanobacteria

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Abstract:

Most cyanobacteria are obligate oxygenic photoautotrophs, and thus their growth and survival is highly dependent on effective utilization of incident light. Cyanobacteria have evolved a diverse set of phytochromes and cyanobacteriochromes (CBCRs) that allow cells to respond to light in the range from ~300 nm to ~750 nm. Together with associated response regulators, these photosensory proteins control many aspects of cyanobacterial physiology and metabolism. These include far-red light photoacclimation (FaRLiP), complementary chromatic acclimation (CCA), low-light photoacclimation (LoLiP), photosystem content and stoichiometry, short-term acclimation (state transitions), circadian rhythm, phototaxis, photomorphogenesis/development, and cellular aggregation. This minireview highlights some discoveries concerning phytochromes and CBCRs as well as two acclimation processes that improve light harvesting and energy conversion under specific irradiance conditions: FaRLiP and CCA.

Introduction

Members of the phylum *Cyanobacteria* are unique among prokaryotic chlorophototrophs (i.e., chlorophyll-based phototrophs): nearly all are oxygen-evolving, obligate photoautotrophs, and they often fix dinitrogen as well. The cyanobacterial photosynthetic apparatus comprises three principal energy transducing and light-harvesting complexes: Photosystem I (PSI; plastocyanin/cytochrome c_6: ferredoxin photooxidoreductase) [1,2], Photosystem II (PSII, water:plastoquinone photooxidoreductase) [3], and phycobilisomes (PBS) [4]. PSII and PSI are interconnected by electron shuttles plastoquinone and cytochrome c_6 (or plastocyanin) and the cytochrome b_6f complex, which acts as a plastoquinol:cytochrome c_6/plastocyanin oxidoreductase [5]. Acting together, these complexes allow cells to photooxidze water and reduce ferredoxin (and ultimately $NADP^+$ via ferredoxin:$NADP^+$ oxidoreductase) [6]. The proton gradient produced by this electron transport chain is used by ATP synthase to generate ATP for carbon fixation and cell growth [7].

As might be expected for organisms whose existence depends upon light, cyanobacteria have evolved a complex set of photoreceptors that control many aspects of their physiology and metabolism. For example, the genome of *Fremyella diplosiphon* PCC 7601, also known as *Tolypothrix tenuis* PCC 7601, encodes 27 different phytochrome or cyanobacteriochrome (CBCR) photoreceptors, some of which are predicted to contain multiple light-sensing domains [8]. Similarly, the genome of *Nostoc punctiforme* PCC 73102 encodes more than 30 putative photoreceptors; 21 of these proteins have been shown to bind bilin chromphores [9,10]. A recent comparative genomic analysis of 44 cyanobacterial genomes showed that, in general, the number of photoreceptors encoded within cyanobacterial genomes increases with genome size and with developmental complexity [10].

By shuffling and combining different protein domains, chromophore types, the number of covalent linkages between cysteines and the chromophore, and the chromophore environment, evolution has created proteins with a remarkable capacity to sense light wavelengths (colors) from 300 nm to >740 nm [11-14], which can influence cellular physiology and metabolism by coupling to various output domains (see Figure S1 in [9] for examples). In general, cyanobacteria can sense ten different wavelength ranges (light colors): near-ultraviolet (NUV, 300–395 nm), violet (VL, 395–410 nm), blue (BL, 410–485 nm), teal (TL, 485–515 nm), green (GL, 515–570 nm), yellow (YL, 570–590 nm), orange (OL, 590–615 nm), red (RL, 615–675 nm), far-red (FRL, 675–740 nm), and near-infrared (NIR, >740 nm) [11-14]. Members of the phytochrome/CBCR superfamily characteristically contain bilin-binding GAF (cGMP phosphodiesterase/Adenylate cyclase/FhlA), PAS (Per/Arnt/Sim), and PHY (Phytochrome) domains. These sensory elements are most commonly associated with phosphoacceptor/histidine kinase output domains, although methyl-accepting chemotaxis, GGDEF (cyclic-di-GMP synthase), and some other types of output domains also occur [9,15,16]. When compared across different cyanobacteria, similar light-sensing modules can be coupled to different output domains [9-11,16].

This diversity of photosensors and mechanisms of light perception is matched by the variety of physiological responses that cells exhibit in response to light. As summarized in **Figure 1** and as discussed below, these may include but are not limited to Far-Red Light Photoacclimation (FaRLiP), Complementary Chromatic Acclimation (CCA), Low-Light Photoacclimation (LoLiP), photosystem content and stoichiometry, short-term acclimation (state transitions), circadian rhythm, phototaxis, photomorphogenesis/development, and cellular aggregation. This minireview will highlight recent developments in defining the roles of light in

the sensing and control of some of these processes that affect pigment biosynthesis and the photosynthetic apparatus.

Phytochrome and cyanobacteriochrome photosensors: modular sensor design leads to remarkable diversity for sensing and responding to light

Phytochromes are photoreceptors that use cysteinyl thioether-linked, bilin chromophores to regulate biological responses to RL/FRL. They have a conserved, knotted PAS-GAF-PHY photosensory module, in which a bilin chromophore is bound to a conserved cysteine residue in the GAF domain [11,16-18]. Cyanobacteria also produce knotless phytochromes, in which a GAF-PHY photosensory module also senses RL/FRL (e.g., RfpA) [17–19••]. Isomerization of the 15,16 double bond of the chromophore photoconverts the RL-absorbing, 15*Z* (P_r) form into the FRL-absorbing 15*E* (P_{fr}) form. Reversion of the metastable P_{fr} state can also occur thermally in the dark. In general, proteins with chromophores that exhibit slow dark reversion rates and faster photoconversion rates are suitable for sensing different light wavelengths/colors. Conversely, proteins that exhibit rapid dark reversion rates probably function as power sensors and are best suited to sense light quantity/irradiance [20].

The largest and most diverse group of cyanobacterial photoreceptors are the CBCRs, which extend the range of light wavelengths perceived to shorter wavelengths of visible light or even NUV [11,18]. At least eight subfamilies of CBCRs are known, many of which contain a second cysteine motif (e.g., DXCF, DXCIP, insert-Cys, etc.) in the GAF domain; this allows the formation of a thioether linkage to position C-10 of the chromophore (see **Figure 2**) [12, 15, 21•-25••]. Unlike most phytochromes, the GAF domains of CBCRs are usually able to bind a chromophore and are photoactive in the absence of PAS and/or PHY domains [11, 25••]. CBCR diversity is partly achieved by varying the bound bilin, which can be phycocyanobilin,

phycoviolobilin or biliverdin. Diverse spectral-tuning mechanisms, including dual-cysteinyl thioether linkages and specific arrangements of aromatic residues surrounding the chromophore [9, 11-25••], further enhance photosensor diversity. Photosensors of FRL or NIR can be associated with a biliverdin chromophore instead of phycocyanobilin [14,18]. The blue/green photocycles in some DXCF CBCRs are due to reversible thioether bond formation to carbon C-10 of the chromophore (**Figure 2**), and in some GAF domains, phycoviolobilin or mixtures of this chromophore and phycocyanobilin occur [9,15,21•,24,25••]. Recent studies of CBCR proteins, which have GAF domains lacking the canonical cysteine demonstrated that a second cysteine ligates an unidentified chromophore that unidirectionally photoconverts in response to GL [21•]. Protonation of the isomerized chromophore can also play an important role in defining the spectroscopic properties of CBCRs [26•].

The remarkable diversity of phytochrome-like and CBCR photoreceptors allows organisms to regulate many physiological processes in response to the incident light. For example, *N. punctiforme* PCC 73102 has 21 phytochrome and CBCR photoreceptors that collectively contain 41 biochemically validated, bilin-binding GAF domains [9]. This indicates that many of these proteins are able to integrate information about multiple wavelengths of light to formulate a more precise output signal. In one extreme example in photoreceptor NpF2164, seven GAF domains, six of which bind phycocyanobilin covalently, are fused to a methyl-accepting chemotaxis protein output domain. Two of the GAF domains contain a DXCF motif containing an additional cysteine residue that forms a second covalent linkage to C-10 of phycocyanobilin [12, 15, 22-25••]. This reduces the number of conjugated double bonds in the chromophore and produces domains that can respond to shorter wavelengths of light [21•,24]. Collectively, the six GAF domains in NpF2164 allow this protein to integrate information about

incident radiation over the range from ~300 to 700 nm—nearly the entire spectral region covered by all CBCR photosensors.

These flexible changes, coupled to different types of output modules, allow cells to sense light and control diverse biological processes (**Figure 1**) [9,11,16–19••,27–30]. In the following sections, we describe some recent advances in defining the roles of phytochromes and CBCRs in light control of photosynthesis in cyanobacteria **(Figure 1)**. We will principally focus on two processes, FaRLiP and CCA. Other processes, including circadian rhythm, long-term adaptation (photosystem content and ratio) and short-term acclimation (state transitions) to light intensity, and LoLiP, will not be discussed in detail. It should be noted that not all light-regulated processes affect the photosynthetic apparatus. For example, CBCRs can also regulate phototaxis [11,28,29], cellular morphology and development [30] and cellular aggregation [27]. In the latter process, three CBCRs cooperatively produce a light-color-sensitive input system for cyclic-di-GMP signaling that leads to cell aggregation [27].

Far-red light photoacclimation (FaRLiP)

FaRLiP is a newly discovered type of photoregulation, which controls the biosynthesis of specialized chlorophylls (Chls) and photosystems in terrestrial cyanobacteria. This photoacclimation response allows cyanobacteria capable of FaRLiP to utilize FRL ($\lambda > 700$ nm) for oxygenic photosynthesis and growth [19••,31–35]. FaRLiP was initially identified in *Leptolyngbya* sp. JSC-1 and has subsequently been experimentally verified in several other species distributed across nearly the full taxonomic diversity of cyanobacteria [19••,32,36]. Under FRL-enriched conditions, which can be produced by filtering of light by Chl *a*, canopy effects or by scattering in soil, cyanobacteria that can perform FaRLiP (hereafter FaRLiP strains)

synthesize Chl *d*, Chl *f*, long-wavelength-absorbing forms of allophycocyanin (AP), and they use these unusual pigments to extensively remodel PSI, PSII, and PBS (**Figures 3, 4**) [19••,31–34••]. Comparative genomic analyses have shown that thirteen cyanobacteria have a conserved cluster of 20 genes, denoted as the FaRLiP cluster. This cluster encodes Chl *f* synthase (ChlF), transcriptional activators RfpA, RfpB, and RfpC, and paralogous copies of pigment-binding core subunits of PSI, PSII, and PBS [19••,32–35,37•]. RfpA is a RL/FRL-responsive, knotless phytochrome that covalently binds a single phycocyanobilin chromophore that interconverts between its P_r and P_{fr} forms in response to RL and FRL, respectively (**Figure 4A,B**) [19••]. RfpA contains a histidine kinase, auto-phosphorylation domain. RfpC, an essential CheY-like response regulator, is thought to act as a phosphate shuttle between RfpA and RfpB. RfpB, a response regulator that contains two CheY-like phosphorylation domains and a DNA-binding domain, is the transcriptional activator that ultimately controls the expression of the genes in the FaRLiP gene cluster in response to FRL (**Figure 4**) [19••,35,37•].

Chls *d* and *f* are FRL-absorbing Chls that have thus far only been identified in some cyanobacteria [19••,31,38••–40]. The Q_y absorbance maxima in methanol for Chls *d* and *f* are 697 and 707 nm, respectively [41]. Six FaRLiP strains have been experimentally verified to synthesize Chl *a*, Chl *d* and Chl *f* when cells are grown in FRL (>700 nm); however, these strains only synthesize Chl *a* when cells are grown in visible light wavelengths (~400 to 700 nm) [19••,32,34••,35,37•]. In addition to the thirteen FaRLiP strains identified by comparative genomics, a few other cyanobacterial strains also synthesize Chl *d* and/or Chl *f* [38••,39,42–49]. Chl *d* is the major pigment (>95%) synthesized by *Acaryochloris marina*, but there is no evidence so far that its synthesis is regulated by FRL [39,45,50,51]. However, studies in other cyanobacterial species show that the synthesis of Chl *d* or Chl *f* occurs when cells are grown in

FRL [19••,32,34••,35,37•,42,44,45,52]. Although some candidates for enzymes involved in the synthesis of Chl *d* have been proposed [53], the enzyme(s) responsible for its synthesis are currently unknown. Interestingly, small amounts of Chl *d* can be produced non-enzymatically from Chl *a* in the presence of thiol compounds and oxygen ([54–56]; M-Y Ho and DA Bryant, unpublished observations). This surprising observation suggests that a thiol ligase or protein cysteinyl lyase might be involved in Chl *d* synthesis. The enzyme for the synthesis of Chl *f* was also unknown until its recent identification as ChlF, formerly PsbA4, a protein encoded in all FaRLiP gene clusters [34••]. ChlF is an ancestral form of the PsbA core subunit of PSII, so-called super-rogue PsbA, which lacks the amino acid residues for binding a $Mn_4Ca_1O_5$ cluster [57]. Instead of oxidizing water to produce dioxygen, ChlF apparently produces Chl *f* (or chlorophyllide *f*) by photooxidation of Chl *a* (or chlorophyllide *a*) [34••]. RfpA, RfpB, and RfpC strongly activate the transcription of *chlF*/*psbA4*, which explains the induction of Chl *f* synthesis when FaRLiP strains are grown in FRL [19••,34••,35,37•] (see **Figure 4C**). The *chlF* and *rfpABC* genes are universally present in the genomes of FaRLiP strains, and it seems likely that the genomes of other Chl *f*-producing cyanobacteria will have similar FaRLiP gene clusters.

Chl *d* and Chl *f* must associate with PSI and PSII to harvest FRL for photosynthesis. Paralogous copies of genes encoding pigment-binding, core subunits of PSI and PSII facilitate Chl *d* or Chl *f* binding and the harvesting of FRL (see **Figure 4C**) [19••; M-Y Ho *et al.*, unpublished results]. Similarly, the core subunits of the PBS are also replaced by FRL-absorbing AP subunits encoded in the FaRLiP cluster [19••,33,36,58,59]. Notably, AP subunits synthesized in white light (WL) and AP subunits encoded in the FaRLiP cluster both bind phycocyanobilin, although ApcE2 produced in FRL does so non-covalently, which leads to a red-shift of the absorption because of the presence of one additional conjugated double bond in the chromophore

[19••,36,58]. To harvest FRL efficiently, PBS are either remodeled by forming complexes with bicylindrical cores and peripheral rods, by solely forming bicylindrical cores, or by retaining a combination of bicylindrical cores and RL-absorbing PBS in three different cyanobacterial species [19••,33,36]. Like Chl *f* synthesis, the expression of genes required for remodeling of PSI, PSII, and PBS is regulated by RfpA, RfpB, and RfpC [35,37•]. In summary, in FaRLiP strains, RfpA, RfpB and RfpC regulate the syntheses of Chl *f* as well as the structural remodeling of PSI, PSII, and PBS; these changes optimize the photosynthetic apparatus for harvesting FRL for oxygenic photosynthesis and growth (**Figures 3, 4) [**19••].

Complementary Chromatic Acclimation (CCA)

CCA refers to the light wavelength (color)-dependent alteration of phycobiliproteins that occur in the peripheral rods of PBS, the light-harvesting antenna complexes of cyanobacteria (**Figure 3**). In these cyanobacteria light wavelength controls the expression of the genes encoding phycoerythrin (PE) and phycocyanin (PC) that make up the peripheral rods of PBSs, as well as the bilin chromophores that are bound to these phycobiliproteins and assembly-related proteins. These changes improve cellular light harvesting by increasing the overlap between the incident light and the absorption cross-section of PBS [60]. As noted above, the discovery of numerous CBCRs has revealed that cyanobacteria have the potential to regulate gene expression in response to light spanning the range from the NUV to the NIR (see Introduction). In CCA, this capability is applied to the production of bilins and phycobiliproteins. Because of the powerful selective advantage gained by improvements in light harvesting for organisms that are strictly phototrophic, it is not surprising that diverse members of the phytochrome/CBCR superfamily have been recruited to regulate this process.

The various CCA strategies employed by cyanobacteria are broadly grouped into four categories, denoted Types I-IV CCA [60,61••]. In Type I organisms, the expression of PC and PE is not regulated by light wavelength. In Type II organisms, PE synthesis occurs in GL or WL but not in RL, and PC synthesis is not regulated. In Type III organisms, the synthesis of both PE and PC are regulated in response to GL and RL, respectively. In Type IV organisms, the chromophore content of phycoerythrin II (PE-II) is modified to harvest BL or GL better. Recent studies of Types III and IV CCA have revealed new complexity in their photoregulation.

Cyanobacteria capable of Type III CCA synthesize more PE in GL compared to RL, and more PC in RL compared to GL (**Figure 3**) [60]. When organized in the peripheral rods of PBSs, these phycobiliproteins specifically increase light harvesting of the complementary light colors, GL and OL/RL, respectively. The master-regulator of Type III CCA in *F. diplosiphon* is a GL/RL-responsive CBCR, RcaE, which modulates expression of the genes encoding PE (*cpeBA*) and PC-2 (*cpcB2A2*) and their associated linker polypeptides [62]. A similar photoreceptor, CcaS, controls PE synthesis in GL in Type II chromatic acclimation in *N. punctiforme* [26•,63]. RcaE also increases the expression of another CBCR, IflA, in GL [64]. IflA contains two chromophorylated GAF domains that together allow this photoreceptor to integrate information concerning four colors of light: BL, GL, RL and FRL. Deletion of *iflA* reduced the growth rates of low-density cultures of *F. diplosiphon*, suggesting that its role is to sense the RL:FRL ratio in the environment and accelerate growth at low cell density. These observations suggest a new role for RcaE beyond its role in regulating Type III CCA and that a complex network of CBCRs regulates CCA [64].

The concept of a regulatory CBCR network for CCA was further expanded with the discovery of the TL/YL-responsive protein, DpxA, in *F. diplosiphon* [65•]. DpxA represses PE

accumulation in YL but not in TL, adding a finer layer of control over the RcaE-mediated repression of PE in GL and preventing the deterioration of Type III CCA at near-green wavelengths, to which RcaE does not respond optimally [65•]. The discovery of IflA and DpxA reveal a higher level of complexity for the regulation of Type III CCA by light. Similar to phototaxis [11,29] and cell aggregation [27], multiple CBCR photoreceptors are employed to achieve optimal control.

Type IV CCA remains the least characterized CCA mechanism. Marine *Synechococcus* species that can perform Type IV CCA alter the bilin chromophore(s) that are attached to PE-II [61••]. When cells are grown in BL, PE-II is predominantly chromophorylated with phycourobilin (PUB), while phycoerythrobilin (PEB) is the predominant chromophore attached to PE-II when cells are grown in GL [60,61••]. The changes in chromophore content optimize the light-harvesting capacity of PE-II for each condition. The transcriptional regulators responsible for tuning the PUB:PEB ratio in response to BL and GL were recently identified as FciA and FciB. Inactivation of either *fciA* or *fciB* caused cells to adopt permanently a GL- or BL-phenotype, respectively [61••]. FciA activates the expression of three genes in BL, including the gene encoding the lyase/isomerase, MpeZ, which attaches PUB to the alpha subunit of PE-II. FciB represses the transcription of these three genes in GL. This co-regulated genomic island was likely acquired by various marine *Synechococcus* spp. through horizontal gene transfer. Surprisingly, none of the genes in this operon encodes a protein with a known photosensing domain, so the connection between light color and gene expression in Type IV CCA is still a mystery, as are the functions of the other two co-regulated genes, *fciC* and *unk10* [61••].

Other light-regulated processes affecting the photosynthetic apparatus in cyanobacteria

LoLiP describes the ability of some *Synechococcus* strains to alter their photosynthetic apparatus in order to absorb far-red light after growth at low irradiance [31,66•] (**Figure 1**). Low-light (LL)-adapted and high-light (HL)-adapted ecotypes of *Synechococcus* species from hot spring microbial mats exhibited different responses to HL and LL [66•]. Comparative genomics of HL- and LL-adapted strains revealed an operon containing four genes that is exclusively found in the genomes of the LL-ecotypes. The genes are predicted to encode a putative CBCR, the alpha and beta subunits of an AP variant (*apcD4* and *apcB3*, respectively) and *isiX*, a homolog of the iron-stress-inducible, chlorophyll-binding IsiA protein [67•]. The AP genes in this operon produce a FRL-absorbing AP variant and contribute to the FRL absorbance observed in LL-adapted *Synechococcus* sp. cells after growth at low irradiances, but how these proteins are assembled into the photosynthetic apparatus is still not established (NT Soulier and DA Bryant, unpublished results).

The cyanobacterial circadian clock rhythmically controls gene expression patterns governing cellular physiology, allowing cells to adapt to predictable environmental fluctuations occurring on a daily basis—most notably changes in temperature and light—in a manner that is independent of cell cycle phase [for a recent review, see 68]. This clock is controlled by phosphorylation of oscillator proteins, encoded by the *kaiABC* genes, which receive signals indicating a change in external environmental conditions via regulatory information transmission from light- and redox-sensitive proteins such as CikA and LdpA [68]. The Kai complex/circadian clock appears to affect transcription globally by rhythmically compacting the chromosomal DNA in cells [68]. In one half of the diel cycle, the compacted chromosome is transcriptionally inaccessible, while in the following half this compaction is reversed, allowing the transcriptional machinery to function. A CBCR protein, CikA in some cyanobacteria has a

GAF domain that binds phycocyanobilin via two thioether linkages and absorbs maximally ~415 to 420 nm [9,11,15,21•,24]. Recently, reconstruction of the circadian oscillator in a non-circadian model organism, *Escherichia coli,* demonstrated oscillations in KaiC phosphorylation and in a synthetic transcriptional reporter. This achievement establishes the minimally sufficient set of proteins required for circadian control of transcriptional output, which opens up the possibility for introduction of circadian control into heterologous systems [69••].

Other processes, such as the overall cellular content of components of the photosynthetic apparatus and adjustments to the PSI:PSII ratio, also respond to light color and intensity [70•-73]. Although it is known that sensor kinases for stresses affect these adjustments, it is not known whether specific photoreceptors are involved in the long-term adaptation/acclimation of the photosynthetic apparatus. Similarly, short-term acclimation of the photosynthetic apparatus (state transitions) involves rapid changes in the specific associations of PSI, PSII, and PBS [74,75••]. Similarly, short-term acclimation of the photosynthetic apparatus, i.e. state transitions, induced by changes in light color/wavelength, involve relative movements of PBS and/or photosystems that modify the contacts between PBS and the two photosystems as well as between PSII and PSI [76,77]. Although these processes are believed to be regulated by the redox state of the plastoquinone pool, a CBCR photoreceptor similar to CcaS is involved in controlling the synthesis of a membrane-anchored PC-CpcG2 rod complex that associates with PSI [78•].

Concluding Remarks

Genome sequencing and bioinformatic analyses have led to a rapid expansion of our knowledge of photoreceptors in cyanobacteria. Coupled with insightful functional and structural studies, rapid progress is now being made in elucidating their roles in diverse photoreceptors in various

physiological and metabolic processes. It is important that cyanobacteria that have not been used traditionally as laboratory model organisms among cyanobacteria receive adequate study. Filamentous cyanobacteria are physiologically and developmentally complex and tend to have much larger genomes than unicellular cyanobacteria, and correspondingly they have greater numbers of uncharacterized photoreceptor. It is possible to apply genetic methods, especially conjugation, to the study of some of these organisms [35,37•,60]. Another approach that can now be used, but that has been underutilized, is to study the ecophysiological role of light in natural cyanobacterial communities (e.g., hot spring mat or hypersaline mat communities). It should be possible to manipulate the incident light in ways that can reveal the roles of photoreceptors in diverse processes *in situ*, and thereby gain insights into the light niches and selective pressures that led to the evolution of various photoadaptive and photoacclimation process as described above. The FaRLiP and LoLiP processes described here were discovered through a combination of *in situ* and *ex situ* studies. An especially powerful approach is to combine field studies using –omic methods with *ex situ* studies of truly representative organisms isolated from the same microbial community. As collaborator Dr. David M. Ward at Montana State University, often remarks, it is always a good idea to "let Nature be your guide."

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This study showed that a specialized rod-core linker, CpcG3/CpcL, assembled phycocyanin rods that associate with PSI complexes to form a phycobiliprotein/PSI supercomplex.

Figure Legends

Figure 1. Network of light regulation and its impact on photosynthetic components in cyanobacteria. Far-red light photoacclimation (FaRLiP), complementary chromatic acclimation (CCA), low-light photoacclimation (LoLiP), circadian rhythm, PSI and PSII content and ratio, and state transitions affect the biosynthesis, biogenesis and functionality of different photosynthetic components and complexes. Solid lines represent verified connections. Dashed-lines indicate uncertain relationships.

Figure 2. Chromophore structure of the GAF domain of PixJ1 from *Thermosynechococcus elongatus* BP-1, a BL/GL photoreceptor [25••]. **A.** Phycoviolobilin structure with thioether linkages at carbons C-3^1 and C-10. **B.** Details of the binding pocket for phycoviolobilin showing the thioether linkages provided by cysteines 522 and 494 of PixJ. **C.** Structure of the phycoviolobilin binding pocket of PixJ1 (for additional details, see [25••]. The structures in panels **B** and **C** were modified from RSCB PDB accession number 4FOF (for additional details, see [25••]). **D**. Appearance of the GAF domain of PixJ1 in solution in its Pb and Pg forms (top), and absorbance spectra of the two forms of the protein (below). Panel D is adapted from [11].

Figure 3. Acclimation of *Synechococcus* sp. PCC 7335 to different light conditions. *Synechococcus* sp. PCC 7335 is a cyanobacterium that performs both complementary chromatic acclimation (CCA) and far-red light photoacclimation (FaRLiP). The absorbance spectra were taken for *Synechococcus* sp. PCC 7335 cultured in white light (WL), red light (RL), green light (GL), and far-red light (FRL) and were normalized at 750 nm. Production of phycoerythrin (PE) is induced in WL and GL, while the synthesis of PC is reduced in GL. In RL, more phycocyanin (PC) is produced, and synthesis of PE is downregulated. FRL induces syntheses of Chl *d*, Chl *f*, and FRL-absorbing allophycocyanin subunits (AP). Please see references [33–35] and the text for additional details.

Figure 4. Far-red light (FRL, $\lambda > 700$ nm) regulates far-red light photoacclimation (FaRLiP) through RfpABC-dependent and independent pathways. **(A)**. Recombinant RfpA in its P_r and P_{fr} forms. **(B)**. Absorbance spectra of recombinant GAF domain of RfpA after 700 nm or 645 nm illumination (very similar results were obtained with the ful-length protein). **(C)**. Scheme of FRL-regulated pigment biosynthesis and remodeling of the photosynthetic apparatus. FRL

photoconverts RfpA from P_{fr} form to P_r form, activating its histidine kinase, which then activates RfpC through phosphorylation. Activated RfpC, acting as a phosphate shuttle, phosphorylates the response regulator/transcriptional activator, RfpB. Genes involved in chlorophyll (Chl) biosynthesis and remodeling of PSI, PSII, and phycobilisome (PBS) are induced in RfpABC-dependent (black arrows) and RfpABC-independent (white arrows) pathways. Note that although it shows the active form of RfpB is phosphorylated in this figure, the active form could also be dephosphorylated. Panel B is modified from [19]. Panel C is modified from [37•] with updated results from [34••].

Summary Figure

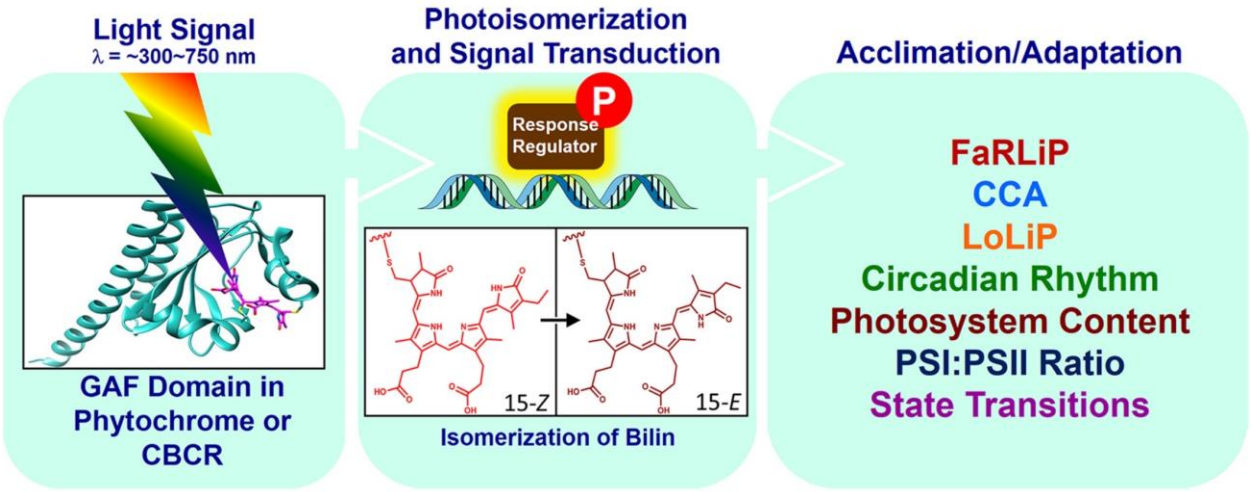


Figure 1

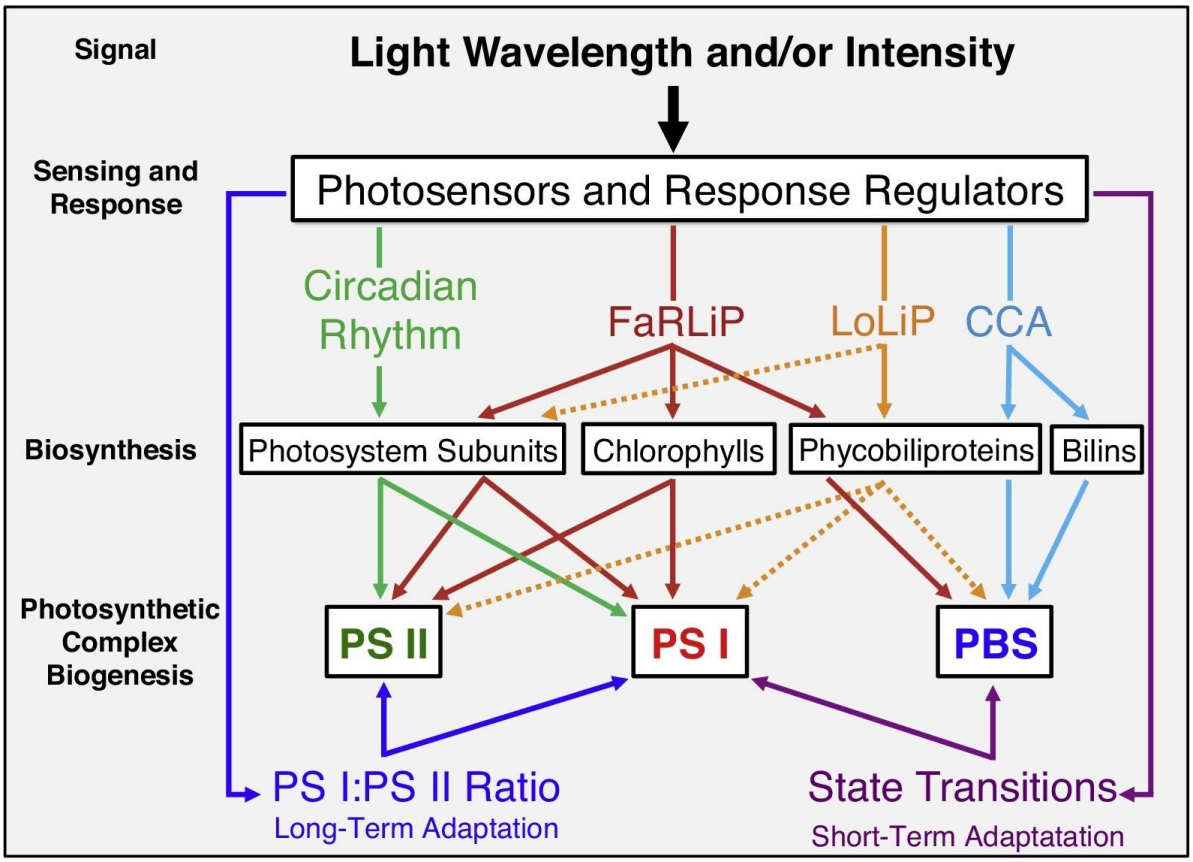

Signal
Light Wavelength and/or Intensity
Sensing and Response
Photosensors and Response Regulators
Circadian Rhythm
FaRLiP
LoLiP
CCA
Biosynthesis
Photosystem Subunits
Chlorophylls
Phycobiliproteins
Bilins
Photosynthetic Complex Biogenesis
PS II
PS I
PBS
PS I:PS II Ratio
Long-Term Adaptation
State Transitions
Short-Term Adaptatation

Figure 2

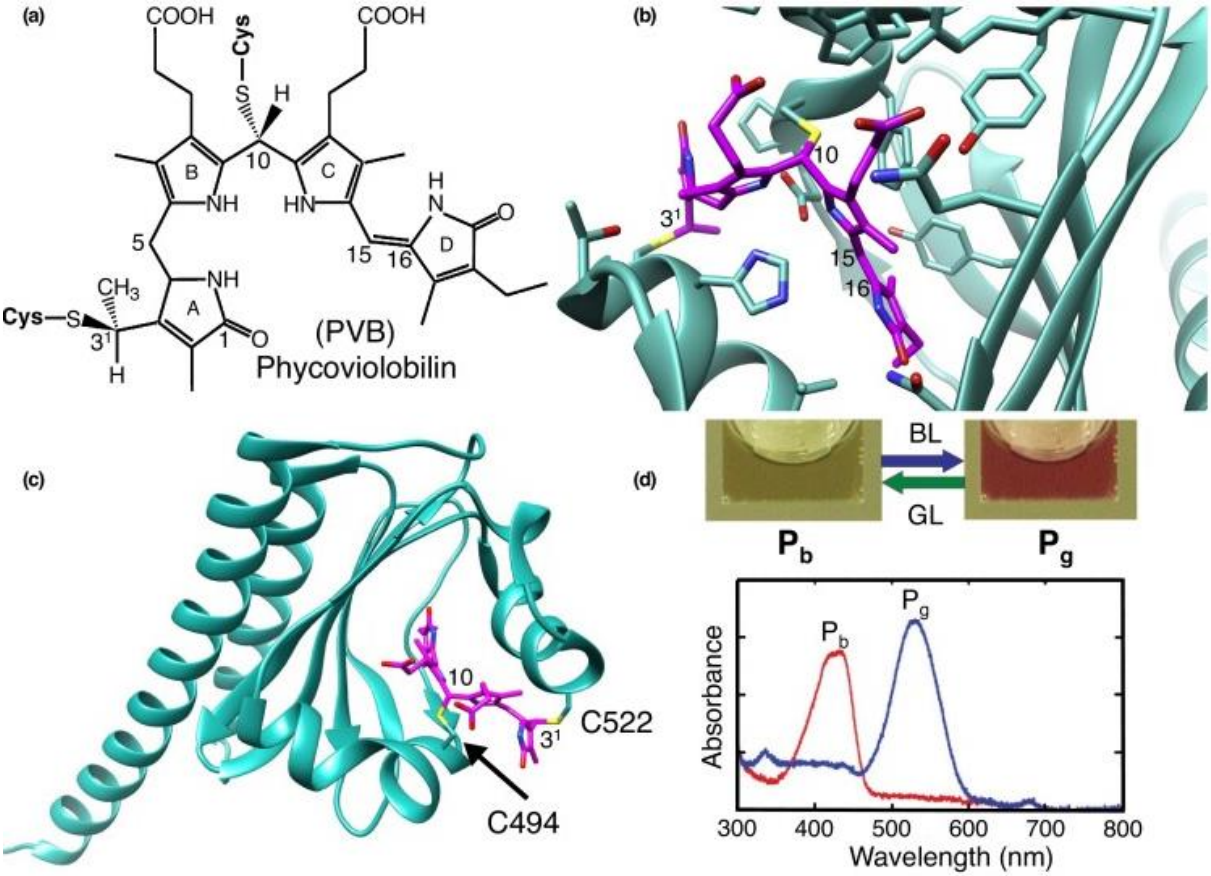

(a)
COOH
Cys
S
H
COOH
B
10
C
NH
HN
H
N
O
5
15
16
D
CH3
NH
A
Cys—S
3¹
1
O
H
(PVB)
Phycoviolobilin
(b)
10
3¹
15
16
(c)
10
3¹
C522
C494
(d)
BL
GL
Pb
Pg
Pg
Pb
Absorbance
300
400
500
600
700
800
Wavelength (nm)

Figure 3

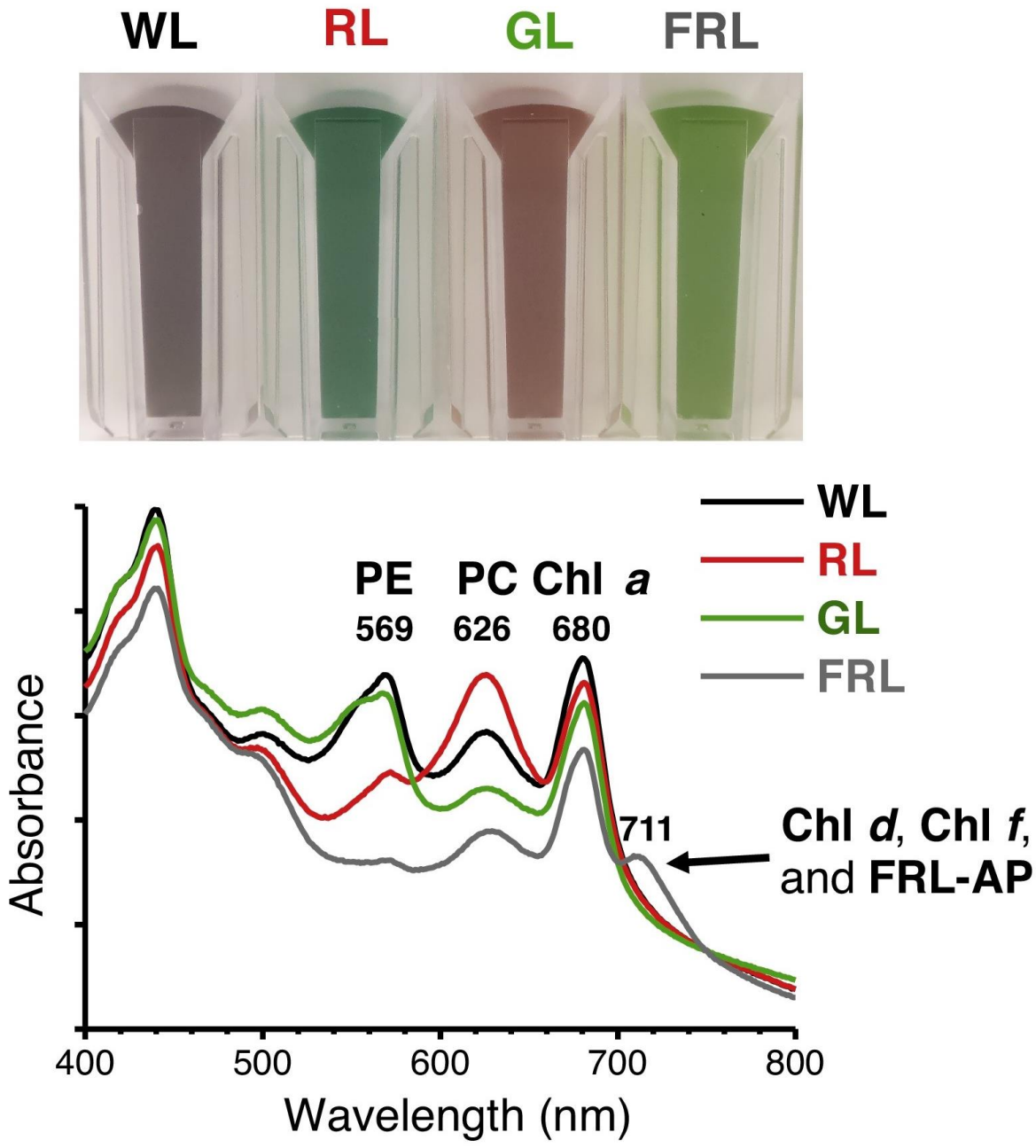
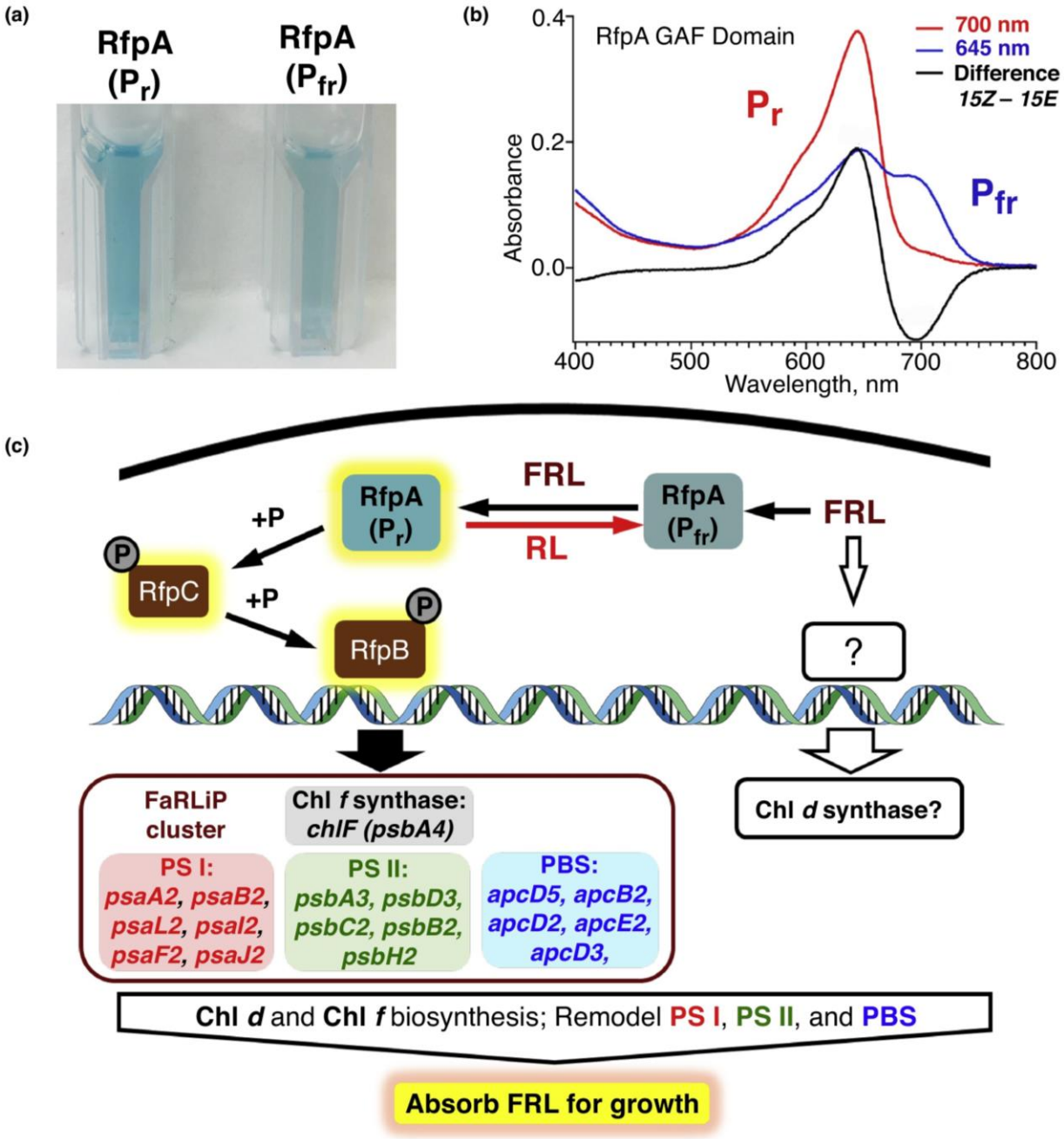

WL
RL
GL
FRL
PE
569
PC
626
Chl a
680
711
Chl d, Chl f,
and FRL-AP
Absorbance
400
500
600
700
800
Wavelength (nm)

Figure 4


(a)
RfpA (Pr)
RfpA (Pfr)
(b)
RfpA GAF Domain
700 nm
645 nm
Difference
15Z – 15E
Pr
Pfr
Absorbance
0.4
0.2
0.0
400
500
600
700
800
Wavelength, nm
(c)
RfpA (Pr)
FRL
RL
RfpA (Pfr)
FRL
+P
RfpC
+P
RfpB
?
FaRLiP cluster
Chl f synthase: chlF (psbA4)
PS I: psaA2, psaB2, psaL2, psaI2, psaF2, psaJ2
PS II: psbA3, psbD3, psbC2, psbB2, psbH2
PBS: apcD5, apcB2, apcD2, apcE2, apcD3,
Chl d synthase?
Chl d and Chl f biosynthesis; Remodel PS I, PS II, and PBS
Absorb FRL for growth