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Adaptation and Regulation of Photosynthetic Apparatus in Response to Light

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3 Adaptation and Regulation of Photosynthetic Apparatus in Response to Light

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Solar light can be efficiently captured and converted into chemical energy by all phototrophs, including photosynthetic bacteria, cyanobacteria, algae, and vascular plants, through their specific photosynthetic machinery. The major environmental challenge to photosynthetic organisms is the variability in the light. To cope with the rapidly fluctuating light environment (specifically in intensity and wavelength distribution), the phototrophs have evolved complex regulatory systems to adapt to changing light conditions. Advanced understanding of the adaptive mechanisms developed by photosynthetic organisms will inform the bioengineering of phototrophs to enhance the utilization of solar energy, for the production of biofuel and commodity products from light, CO₂, and water. In this chapter, we will summarize recent studies on the molecular basis underlying the physiological adaptation and regulation of photosynthetic machinery, in particular, in cyanobacteria, toward irradiance variation.

3.1 PHOTOSYNTHETIC APPARATUS: COMPOSITION AND ORGANIZATION

The primary reactions of photosynthesis are mediated by a series of photosynthetic complexes associated with or embedded in the photosynthetic membranes. These pigment–protein complexes can be classified into several groups according to their functions: light-harvesting antenna complexes, photosynthetic reaction centers (RCs), the cytochrome (Cyt) complex, and ATP synthase (ATPase). They are structurally and functionally linked in order through the photosynthetic electron transport chain (Figure 3.1). Light energy captured by the light-harvesting antenna is rapidly and efficiently transferred to the RCs to drive the transmembrane charge separation. The electrons are then transferred to the (plasto)quinone pool and subsequently to the Cyt enzymes. The electron transfer reactions are coupled to the formation of an electrochemical gradient across the photosynthetic membranes, which is essential for driving the ATP synthesis.
3.1.1 Light-Harvesting Complexes

The first step in the process of photosynthesis is the absorption of light photons by an array of antenna pigment–protein complexes, termed light-harvesting complexes (LHCs). The spectral properties and macromolecular conformations of photosynthetic antenna complexes vary dramatically depending on the different origins. The photosynthetic apparatus of the anoxygenic purple bacteria presents the simplest configurations (Cogdell et al. 2006; Liu et al. 2011; Liu and Scheuring 2013). Most purple photosynthetic bacteria synthesize two types of LHCs classified according to their in vivo absorbance, B875 (LH1) and B800-850 (LH2) complexes. Such antenna complexes are generally composed of two polypeptides (α and β subunits), two or three bacteriochlorophyll (BChl) molecules, and some carotenoids. Green algae and higher plants contain integral LHCI and LHClII as the peripheral antenna proteins associated with photosystem I (PSI) and photosystem II (PSII) supercomplexes, respectively (Croce and van Amerongen 2014). The migration of LHCs between PSII and PSI in the thylakoid membrane is essential to balancing the excitation energy between the two photosystems during state transitions (Minagawa 2013).

Phycobilisomes (PBsomes) are the major light-harvesting antenna complexes in cyanobacteria and red algae (Adir 2005; Liu et al. 2005b; Watanabe and Ikeuchi 2013). They are aggregations of water-soluble phycobiliproteins (PBPs) and linker polypeptides (Liu et al. 2005b), and serve as external antenna macrocomplexes associated with the stromal surfaces of thylakoid membranes (Arteni et al. 2008; Liu et al. 2008a). Red algae also have an intrinsic antenna LHCl-like complex, functionally associated with PSI (Wolfe et al. 1994). PBsomes consist of two structural domains: the inner domain contains three cylinders that are arranged in a triangular PBsome core, and the peripheral domain contains six rodlike structures that radiate from the core. Both the core and the rods of the PBsome are composed of stacked PBP hexamers. This domain is composed predominantly of allophycocyanins (APCs), whereas the peripheral rods are mainly composed of phycocyanins (PCs) and phycoerythrins (PEs). Energy transfer in PBsomes is expected to progress from PE (λ_{max} = 545 – 565 nm) (Liu et al. 2005a) stepwise to PC (λ_{max} = 620 nm), APC (λ_{max} = 650 nm), and eventually, chlorophylls (Chls). It is evident that the presence of PBsomes extends the absorbance range covered by PSII and PSI. The stepwise energy transfer within the PBsomes may probably also play a photoprotective role (Liu et al. 2008b). A key physiological importance of PBsomes is reflected in light-state transitions, which will be discussed in detail below.

3.1.2 Reaction Centers

Photosynthetic RCs are pigment–protein complexes that convert the excitation energy from antenna complexes into chemical potential energy (Olson and Blankenship 2004). The key reactions of photosynthesis occur in two homologous types of RCs: (1) RC1 type in some anoxygenic photosynthetic bacteria, such as green sulfur bacteria and heliobacteria, and (2) RC2 type in other anoxygenic photosynthetic bacteria, for instance, purple bacteria and green filamentous bacteria; RC1 and RC2 coexist in all oxygenic photosynthetic organisms,
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i.e., cyanobacteria, algae, and plants (Hohmann-Marriott and Blankenship 2011). These two types of RCs probably share a common evolutionary ancestor because of their similar structures and cofactor arrangements of the electron transfer domains (Schubert et al. 1998). The cyanobacterial PSI complex presents a trimeric structure, and PSII complexes exist as dimers (Mazor et al. 2014; Suga et al. 2015).

### 3.1.3 Cytochrome and ATP Synthase

Various cytochromes are mainly responsible for the electron transfer released from the primary processes of charge separation in RCs. The Cyt b₆f complex is a dimeric membrane-intrinsic complex located in the thylakoid membranes. It is essential for both photosynthetic and respiratory electron transfer chains (Berry et al. 2009). In the linear electron transfer scheme of oxygenic photosynthesis, Cyt b₆f receives electrons from PSII by plastoquinol and passes them to PSI by reducing plastocyanin or Cyt c₆. This results in proton release in the lumen, generating a proton electrochemical gradient across the membrane. Cyt b₆f can switch from linear electron transfer between both PSs to a cyclic mode of electron transfer around PSI (Shikanai 2014). The cytochrome c oxidoreductases (Cyt bc₁) are multisubunit enzymes existing in a broad variety of organisms, including the purple nonsulfur photosynthetic bacteria (Berry et al. 2009). They are components of both cyclic photosynthetic and mitochondria-like linear respiratory electron transport chains.

ATPase is a large protein complex, catalyzing the synthesis of ATP from ADP and inorganic phosphate driven by a flux of protons across the membrane down the proton gradient generated by electron transfer. ATPases are located in the plasma membrane and photosynthetic membrane of bacteria, the chloroplast thylakoid membrane in algae and plants, and the mitochondrial inner membrane in plants and animals.

### 3.1.4 Diversity of Photosynthetic Apparatus Organization

The physiological arrangement and functional coordination of these photosynthetic constituents are fundamental to efficient light capture and energy transfer mechanisms. In order to adapt to diverse habitats, photosynthetic organisms have developed distinct photosynthetic machinery to regulate energy conversion, as shown in Figure 3.1. Purple photosynthetic bacteria contain one type of RC and two types of LHCs, LH1 and LH2. Cyanobacteria, red algae, green algae, and higher plants consist of PSI, PSII, and various membrane or extramembrane light-harvesting antenna complexes. Distinct from green algae and higher plants, cyanobacteria and red algae utilize PBsomes to capture light for PSI and PSII. In addition, cyanobacterial thylakoid membranes house both photosynthetic and respiratory electron transport chains (Liu et al. 2012), and some complexes are shared by the two electron transport pathways.

### 3.2 Light Effects on the Photosynthetic Stoichiometry

#### 3.2.1 Light Intensity

The ratio of antenna quantity to photosynthetic RCs has been demonstrated to depend on light intensity during cell growth. To retain efficient light absorbance to RCs, additional 30% PBsome antenna complexes are synthesized under low-light conditions compared to high-light conditions (Figure 3.2).

![Figure 3.2](See color insert.) (a) Room-temperature absorption spectra of whole cells and isolated PBsome thylakoid membranes from the unicellular red alga *Porphyridium cruentum* grown under low light (LL, 6 W/m²) and moderate light (ML, 15 W/m²). (From Liu, L.N. et al., *J. Biol. Chem.*, 283, 34946–34953, 2008.) Spectra were normalized to the chlorophyll absorption band at 682 nm. Results showed that the amount of PBsomes (500–650 nm) is dependent upon the light intensity. (b) The absorption spectrum of purple photosynthetic membranes adapted to high light (HL), ML, and LL. The absorption ratios of LH2 (845 nm) to the core complex (LH1, 880 nm) are 1.16, 1.86, and 2.6, respectively. (From Liu, L.N. et al., *J. Mol. Biol.*, 393, 27–35, 2009; Scheuring, S., and J.N. Sturgis, *Science*, 309, 484–487, 2005.) Results indicated that the ratio of antenna to RC varies according to the light intensity.
(Liu et al. 2008a). Similarly, in the photosynthetic membranes from the purple photosynthetic bacterium *Rhodopseudomonas photometricum* adapted to high light, ~3.5 LH2s are present per core complex, whereas under low-light conditions, ~7 LH2s per core were observed, and the moderate-light-adapted membranes have an intermediate LH2/core ratio of 4.8 (Liu et al. 2009b; Scheuring and Sturgis 2005).

In cyanobacteria, the ratio of PSII to PSI is variable according to the light intensity and spectral quality. The switch from low light to high light suppresses the PSI biosynthesis, resulting in an increase of the PSII/PSI ratio. This responsive effect has been shown to be triggered by the redox state of the electron transport chain (Murakami and Fujita 1991). Furthermore, two genes have been implicated in the regulation of the PSII/PSI ratio. Inactivation of a gene encoding for a putative sensory histidine kinase, *rppA*, leads to phenotypic changes consistent with a role in transducing redox signals to changes in PSII and PSI gene expression (Li and Sherman 2000). Inactivation of *pmgA* specifically abolishes the PSII/PSI ratio change in response to high light (Hihara et al. 1998). Both RppA and PmgA are excellent candidates for redox signal transduction proteins.

### 3.2.2 Light Quality

The acclimation of photosynthetic organisms to changes in light wavelength is ubiquitous and may be best characterized by the complex process of complementary chromatic adaptation (CCA) (Grossman et al. 1993; Kehoe and Gutu 2006). In many freshwater, marine, and soil cyanobacterial species whose PBsomes contain both PE and PC, the ratio of PC to PE in PBsomes varies in response to light spectra (Figure 3.3). Green light (optimally 540 nm) promotes PE biosynthesis, whereas red light (optimally 650 nm) elevates PC biosynthesis. CCA leads to the optimized absorbance of PBsomes to capture the most abundant wavelength of light in the green-to-red spectral region.

CCA regulation of PC and PE synthesis is predominantly at the transcriptional level for PE and PC genes (*cpeBA* and *cpc2*). The β and α subunits of PE are encoded by the *cpeBA* operon, which is highly upregulated by green light (Federspiel and Grossman 1990). The β and α subunits of “inducible PC” as well as three corresponding linker proteins are encoded by a large transcription unit, *cpc2* (*cpcB2A2H2I2D2*) (Conley et al. 1988). Its expression is highly upregulated by red light. Maintaining the expression of these operons is not essential once steady-state CCA is obtained (Oelmuller et al. 1989). The changes in RNA levels of PBsome components after an inductive light treatment are relatively rapid (Oelmuller et al. 1988). *cpc2* RNA reaches a maximum level 2 h after a shift from green to red light and drops to undetectable levels 2 h after a shift from red to green light, while *cpeBA* RNA reaches a maximum level 8 h after a shift from red to green light and drops to undetectable levels more than 14 h after a shift from green to red light. In contrast to the rapid response at the transcriptional level, PE and PC protein levels altered more slowly, requiring a few days to fully shift between the red- and green-light steady states. The regulatory mechanisms governing these responses are different for *cpc2* versus *cpeBA*. Two light-response pathways controlling the PBsome biosynthesis during CCA, an Rca system and a Cgi system, have been identified (Kehoe and Gutu 2006).

The initial light signaling for CCA is not well characterized. A phytochrome would be a potential candidate for a red-light sensor. However, the phytochrome responding to green light has not been found. If CCA is controlled by a single photoreceptor, it should contain a novel pigment or another green-absorbing chromophore. There is a precedent in the purple photosynthetic bacterium *R. centenum* for a

![FIGURE 3.3](See color insert.) (a) Whole-cell absorption spectra of the cyanobacterium *Fremyella diplosiphon* cells grown in green and red light. The phycoerythrin (PE) and phycocyanin (PC) absorption peaks are indicated. (From Kehoe, D.M., and A. Gutu, *Annu. Rev. Plant Biol.*, 57, 127–150, 2006.) (b) Changes of *F. diplosiphon* PBsomes in composition and structure induced by green and red light.
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phytochrome-like protein that binds a second pigment (Jiang et al. 1999). Alternatively, a second photoreceptor, possibly a rhodopsin, could be involved (Hoff et al. 1995).

3.2.3 Light–Dark Cycle

The daily light–dark cycle controls rhythmic changes in the behavior and physiology of most species, such as cyanobacteria, plants, animals, and fungi. The so-called circadian rhythm displays an endogenous and entrainable oscillation of about 24 h. Cyanobacteria exhibit a self-sustained circadian rhythm that results in temporal changes in gene expression patterns, even in the absence of environmental cues (Dong and Golden 2008; Dong et al. 2010; Golden 1995). Correct circadian regulation maximizes photosynthesis, which is carried out specifically in plant chloroplasts, and productivity, by increasing Chl content, modifying the stoichiometry of photosynthetic complexes, and enhancing photosynthetic carbon fixation (Dodd et al. 2005). A recent study has described how the nuclear-encoded clock regulates the expression of key chloroplast-associated genes (Noordally et al. 2013). Based on observations of rhythms in delayed fluorescence (Gould et al. 2009), with a readout of the chemical state of PSII, the clock is likely to have profound effects on the structure and function of thylakoid membranes. However, how the circadian clock controls the photosynthetic performance at the biochemical and structural levels remains uncharacterized.

3.3 LIGHT EFFECTS ON THE ORGANIZATION OF PHOTOSYNTHETIC MACHINERY

Light variability not only determines the optimization of photosynthetic stoichiometry but also results in, inevitably, the reconfiguration of photosynthetic apparatus organization, for regulating the energy transduction under diverse light conditions.

3.3.1 Photoadaptation of the Photosynthetic Apparatus

To understand the dynamic organization of photosynthetic complexes and the mechanisms of photosynthetic processes, it is essential to assess the in situ assembly and distribution of membrane proteins in native photosynthetic membranes under their physiological conditions. Recently, atomic force microscopy (AFM) has matured as a unique and powerful tool for directly assessing the supramolecular organization of photosynthetic complexes in their native environment at submolecular resolution (Liu and Scheuring 2013). The tight arrangement of LHCs has been observed in AFM topographs of the photosynthetic membranes in a unicellular red alga, Porphyridium cruentum (Figure 3.4) (Liu et al. 2008a). Under moderate light, PBsomes are randomly distributed and tightly clustered on photosynthetic membranes. In contrast, under low light, increasing amounts of PBsomes form densely packed rows on the membrane surface. The presence of dense...
antenna domains might be a general regulatory mechanism for light trapping when photons are relatively rare. Such structural constraints would enhance photosynthetic electron transfer under diverse light conditions (Liu et al. 2009b).

A similar response has also been recorded in the thylakoid membrane of higher plants (Dekker and Boekema 2005; Kirchhoff 2014). Electron microscopy data on the dark- and light-adapted Arabidopsis thaliana thylakoids indicated that the granal thylakoid lumen significantly expands under light stress (Kirchhoff et al. 2011). This light-induced expansion may moderate the restrictions imposed on protein diffusion in the lumen in the dark.

AFM imaging has also characterized comprehensively how the organization of the Rsp. photometricum photosynthetic membrane is modulated toward light variation (Liu et al. 2009b; Scheuring and Sturgis 2005). In high-light-adapted membranes, ~3.5 LH2s are present per core complex, whereas after low-light growth, ~7 LH2s per core were recorded. Two different types of protein assemblies in the bacterial photosynthetic membranes were identified: core–LH2 domains and paracrystalline LH2-rich domains (Figure 3.4). Additional LH2 incorporated into the membrane segregated in paracrystalline antenna domains, whereas the domains with core complexes seemed architecturally unaffected. The two domains have distinct roles to optimize the photosynthetic activity during light intensity change: core–LH2 domains maintain efficient harvesting, trapping, and transmission of solar energy; LH2-rich domains enhance light capture when only few photons are available but do not perturb the photosynthetically active core assemblies. The membrane adapted to medium-light conditions exhibited the intermediate composition and organization of the photosynthetic apparatus (Liu et al. 2009b). Similar protein assembly patterns have been found in other species, for instance, Phaeospirillum molischianum (Gonçalves et al. 2005), Rhodopseudomonas palustris (Scheuring et al. 2006), and Rhodobacter sphaeroides (Adams and Hunter 2012). In Rps. palustris photosynthetic membranes of high-light-adapted cells, the core complexes also segregate into hexagonally packed paracrystalline domains, reminiscent of the assembly found in Blastochloris viridis (Scheuring et al. 2004). The dense packing of the large paracrystalline LH2 domains may limit quinone diffusion and, therefore, favor quinone distribution in the proximity of the cores.

### 3.3.2 Light-State Transitions

State transitions are rapid adaptive responses to changes in light quality. Illumination conditions that lead to excess excitation energy of PSII compared to PSI induce a transition to state 2, in which more absorbed excitation energy is diverted to PSI. When PSI is overexcited relative to PSII, it induces a transition to state 1, in which more energy is transferred to PSII. Thus, state transitions act as a mechanism to balance excitation of the two photosystems under changing light regimes. State transitions have been extensively characterized in green alga Chlamydomonas reinhardtii and higher plant Arabidopsis thaliana. The processes of the state transitions involve the LHClI migration, the molecular reorganization of photosystem supercomplexes, the identification of LHClI kinase, the mapping of phosphorylated residues in LHClI, and the involvement of Cyt b,f in the control of LHClI phosphorylation (Minagawa 2013). It has been shown that the state transitions are regulated by the redox state of plastoquinone (PQ), an electron carrier located between two photosystems (Mullineaux and Allen 1990), and involve posttranslational modifications by phosphorylation of LHClI. Under different light conditions, for example, when PSI is excited, the redox state of the PQ pool is more reduced. The more reduced PQ pool induces the activation of an LHClI kinase and LHClI phosphorylation, resulting in the LHClI movement from PSI to PSI (state 2). Conversely, when the PQ pool is oxidized, the LHClI kinase is inactive, and LHClI is dephosphorylated by phosphatase and moves back from PSI to PSI (state 1). Thus, the PQ redox-regulated reversible phosphorylation of LHClI promotes state transitions and acts to redistribute absorbed excitation energy in response to different light conditions.

In cyanobacteria, there is no specific light-harvesting antenna for PSI, and the PBsomes serve as the major antenna for both photosystems. State transitions regulate the excitation energy transfer from the PBsomes to PSII or PSI. The structural basis of state transitions in cyanobacteria is still controversial (Figure 3.5). One hypothesis is that of mobile PBsomes, which suggests that state transitions may involve the physical association and disassociation of PBsomes between PSII and PSI, and thus, the energy redistribution between PSI and PSI (Allen and Holmes 1986). About 80% of all PBsomes were found to connect with PSI, and energy is transferred via PBsomes independently to PSI and PSI (Rakhimberdieva et al. 2001). Another model is that of energy spillover, which proposes that PBsomes can only associate with PSI and that excess Chl α-absorbed excitation energy may be redistributed from PSI to PSI (Biggins and Bruce 1989; Bruce et al. 1989). The redistribution of excitation energy absorbed by Chl is independent of the redistribution of excitation energy absorbed by the PBsomes. Both changes are triggered by the same environmental light conditions. An updated model states that PBsomes are capable of physically interacting with both PSI and PSI. Instead of the long-range movement, redistribution of PBsomes between PSI and PSI in the local membrane region might be essential to the state transitions (McConnell et al. 2002).

Studies using fluorescence recovery after photobleaching (FRAP) based on live-cell imaging using a confocal fluorescence microscope have indicated that the PBsomes are mobile along the surface of a thylakoid membrane (Mullineaux et al. 1997) and that the diffusion of PBsomes from RC to RC is required for state transitions (Joshua and Mullineaux 2004) and nonphotochemical quenching (NPQ) (Joshua et al. 2005). A recent study further demonstrated that state transitions have an important regulatory function in mesophilic red algae, but this process is replaced by NPQ in thermophilic red algae (Kana et al. 2014). However, FRAP experiments have revealed a partial fluorescence recovery in wholly bleached cells of the red alga Phaeodactylum tricornutum and, more interestingly,
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FIGURE 3.5 Models of the association between PBsome and PSI and PSII. (a) Mobile PBsomes, suggesting that PBsomes have a loose association with PSI and PSII and that the movement of PBsomes between the two photosystems is essential to state transitions. (From Mullineaux, C.W. et al., Nature, 390, 421–424, 1997; Bald, D. et al., Photosynth. Res., 49, 103–118, 1996.) (b) Possible coupling of PBsome with PSI and PSII. The PBsome core can come into contact with a PSI dimer. Tilted packing of PBsomes and PSII is essential to driving the connection. PBsomes can also interact with PSI trimers through the rods, to form a PSI–PBsome supercomplex under the state 2 condition. (The model is adapted from Bald, D. et al., Photosynth. Res., 49, 103–118, 1996. From McConnell, M.D. et al., Plant Physiol., 130, 1201–1212, 2002.) (c) A schematic model showing the organization of a cyanobacterial thylakoid membrane, showing possible associations between the PBsome core and PSI and PSII complexes in states 1 and 2. (From McConnell, M.D. et al., Plant Physiol., 130, 1201–1212, 2002; Liu, H. et al., Science, 342, 1104–1107, 2013.) Energy transfer from the core to PSI occurs from the ApcE subunit to D1/D2. Energy transfer from the core to PSI is via the ApcD subunit. Energy “spillover” from PSI to PSII is assumed to occur from CP47 to PSI. APC core cylinders are associated with PSII dimers, and PC rods interact with PSI trimers. In state 2, trimeric PSI is in close contact with both the PsbB (CP47) protein of PSII and the ApcD subunits of the core. In state 1, the PBsome–PSII supercomplexes are organized into rows. One PBsome–PSII supercomplex is shown to remain, coupling with one PSI trimer via ApcD, to form the PBsome–PSII–PSI supercomplex. (d) A structural model of the PBsome–PSII–PSI photosynthetic megacomplex, depicting that the PBsome core fully covers and close-couples with the PSII dimer, whereas the PSI is associated with ApcD through a side-on orientation. (From Liu, H. et al., Science, 342, 1104–1107, 2013; Watanabe, M. et al., PNAS, 11, 2512–2517, 2014.) (e) A structural model of the PBsome–CpcL–PSI supercomplex isolated from the cyanobacterium Anabaena (Watanabe et al. 2014), describing the CpcL–PBsome rods, which specifically bind at the periphery of the PSI tetramers. FNR, ferredoxin; PBS, PBsome.
immobilized PBsome complexes in vitro (Liu et al. 2009a). The observations might suggest that the fluorescence recovery recorded during FRAP experiments could be ascribed to the intrinsic photophysics of the bleached PBsomes in situ, rather than the diffusion of PBsome complexes on the thylakoid membranes. Furthermore, AFM images on the native thylakoid membrane of P. cruentum showed significant crowding of PBsome complexes (Figure 3.4) (Liu et al. 2008a). Under such a crowd circumstance, the rapid and long-range movement of PBsomes may be significantly restricted by steric hindrance, taking into account the large size of individual PBsomes, their dense lateral packing membrane surface, as well as the limited free vertical spacing between opposite thylakoid layers. In addition, given the fact that PSII and PSI are mixed in the thylakoid membrane (Mustardy et al. 1992), the dense coverage of PBsomes on the thylakoid membranes may denote the structural association between the PBsomes and both photosystems underneath.

Recently, the existence of PBsome–photosystem supercomplexes has been proved (Figure 3.5). Using a chemical cross-linking strategy, a protein megacomplex composed of a PBsome, PSII, and PSI from a cyanobacterium, Synechocystis sp. PCC6803, has been isolated (Liu et al. 2013). This provided evidence about the presence of PBsome–PSII–PSI supercomplexes in vivo. Time-resolved fluorescence spectroscopy further demonstrated that the PBsome could deliver excitations to the RCs of either PSI or PSII, although the energy transfer from the PBsome to PSI is efficient, rather than that from the PBsome to PSII is slow. Another work characterized a supercomplex PBsome–CpcL–PSI isolated from a cyanobacterium, Anabaena (Watanabe et al. 2014). Within the supercomplex, PSI is organized into tetramers (a dimer of dimers). The PBsome subcomplex, CpcL–PBsome rods, specifically binds at the periphery of the PSI pseudotetramers.

### 3.4 Regulation of Electron Transport Pathways

The organization of photosynthetic complexes regulates the electron transport pathway and efficiency. All photosynthetic membranes that have been analyzed exhibit a dense packing of multicomponent photosynthetic complexes (Liu and Scheuring 2013). On the one hand, protein crowding is favorable for excitation energy transfer between complexes; on the other hand, it significantly reduces the lipid content and space between protein complexes and, as a consequence, probably membrane fluidity, which is required for the diffusion of hydrophobic electron/proton transport carriers (i.e., quinone molecules). Therefore, it represents an obstacle for efficient cyclic electron transduction between RCs and Cyt bc1 complexes in membranes. Analysis of the molecular environment and long-range protein organization proposed a continuous “lipid area network” for long-range quinone diffusion throughout the photosynthetic membrane of the purple photosynthetic bacterium R. photometricum (Liu et al. 2009b). Recent studies on the distribution and dynamics of respiratory components in the plasma membrane of Escherichia coli revealed that respiratory complexes are concentrated in mobile domains in the membrane (Llorente-Garcia et al. 2014). Different complexes are concentrated in separate domains, with no significant colocalization and, therefore, no supercomplexes. This is another indication of a rapid and long-range quinone diffusion that serves to shuttle electrons between islands of distinct electron transport complexes in the membrane.

Photosynthetic electron transfer induced by light excitation modulates the redox state of electron transport components. A number of cyanobacterial responses are known to be triggered by changes in the redox state of PQ or the Cyt b6f complex, and thioredoxin, which accepts electrons from PSI. Light-harvesting regulation can act to control the balance of linear and cyclic electron transport, and therefore, the balance of proton-motive force and reducing power as photosynthetic outputs. Switches that remove electrons from the photosynthetic electron transport chain are also known as electron valves: they serve to prevent dangerous overreduction of the electron transport chain (Liu et al. 2012). There is scope for short-scale posttranslational mechanisms to switch between cyclic and linear electron transport. One example is the regulation of the cyclic electron transport pathway involving complex I under different light intensities (Liu et al. 2012). Fluorescence microscopy images of the fluorescently tagged complex I in Synechococcus elongatus PCC7942 showed that the larger-scale distribution of complex I in the thylakoid membrane is controlled in response to a redox switch triggered by light intensity changes. Oxidation of the PQ pool induces the clustering of complex I in segregated thylakoid membrane zones, whereas reduction of the PQ pool induces a posttranslational switch in the distribution of respiratory complexes to a state in which it is more evenly dispersed in the membrane. Complex II (succinate dehydrogenase) showed a similar change in distribution under the same conditions. This switch in the distribution of respiratory complexes correlates with a major change in the probability that electrons from the respiratory complexes are transferred to a PSI rather than to a terminal oxidase (Liu et al. 2012). The switch provides a mechanism to promote cyclic electron transport when the reduction of the PQ pool indicates an adequate supply of electrons in the cell. Although many questions about the mechanism remain to be addressed, the observation indicates that the distribution of electron transport complexes in the membrane at the submicron scale is under physiological control and plays a crucial role in controlling pathways of electron flux.

Another example of cyanobacterial electron valves is the flavodiiron (Flv) proteins Flv1–4: they are cytoplasmic proteins that take electrons from the photosynthetic electron transport chain and divert them to alternative acceptors. Flv1 and Flv3 form a heterodimer that takes electrons from the acceptor side of PSI and uses them to reduce oxygen (Allahverdiyeva et al. 2013). An Flv2/Flv4 heterodimer takes electrons from the acceptor side of PSII, passing them to an unknown acceptor (Zhang et al. 2012). The regulation of the activities of Flv proteins is not known, and they presumably act only as an electron transport switch on slow timescales.
3.5 PHOTOPRODUCTION

Light not only is the basic driving force for photosynthesis but can also be destructive, particularly when the light-harvesting antennae capture excess photons after photosynthetic electron transport saturation. The photosynthetic apparatus has developed appropriate physiological mechanisms to modulate the absorbance of excitation energy while avoiding the potentially phototoxic effects of excess photons (Bailey and Grossman 2008).

3.5.1 NONPHOTOCHEMICAL QUENCHING AND ORANGE CAROTENOID PROTEIN

High levels of solar radiation can increase the production of reactive oxygen species and cause damage of photosynthetic membranes and pigment–protein complexes. Cyanobacteria have evolved a protective mechanism, NPQ, to dissipate excess PBsome-absorbed energy as heat (El Bissati et al. 2000). In contrast to plants and eukaryotes, cyanobacteria lack both pH-dependent quenching and the xanthophyll cycle (Gorbunov et al. 2011). NPQ in cyanobacteria is triggered by strong blue light, which excites both PBsomes and Chls. Recent studies have shown that the NPQ in cyanobacteria is mediated by a 35 kDa water-soluble orange carotenoid protein (OCP) (Kerfeld et al. 2003; Kirilovsky and Kerfeld 2013; Wilson et al. 2006). As a high-light sensor, OCP is directly involved in the fluorescence quenching of PBsomes and possibly in the regulation of energy transfer between the PBsomes and photosystems (Kerfeld et al. 2003; Kerfeld and Kerfeld 2013). OCP contains a single bound carotenoid (3′-hydroxyechinenone), which can change the conformation between its orange (OCP\textsuperscript{o}) and red forms (OCP\textsuperscript{r}) (Kirilovsky and Kerfeld 2013). The photoactivated OCP\textsuperscript{r} binds to the PBsome core, where it takes excitation energy from the phycobilins and converts it to heat in order to prevent photodamage of the RCs at high light. The reversal of OCP\textsuperscript{r}-induced energy quenching (conversion of OCP\textsuperscript{o} back to OCP\textsuperscript{o}) depends on a second cytoplasmic protein, the fluorescence recovery protein (FRP), which binds to the OCP and weakens its association with the PBsome (Gwizdala et al. 2013).

3.5.2 PHOTOPRODUCTION OF PBSome

The photoproduction of PBsomes from excess excitation energy remains poorly characterized. A study using single-molecule spectroscopy imaging on purified PBsomes from the red alga \textit{P. cruentum} elucidated an energetic decoupling in PBsomes with respect to intense light (Figure 3.6) (Liu et al. 2008b). Strong green light was able to induce the fluorescence decrease of PBsomes and the fluorescence increase of the peripheral PE in the PBsome at the first stage of photobleaching. This indicates that excess photon energy can be dissipated from the peripheral PE in the PBsome to minimize the photodamage of RCs. This process may serve as a photoprotective mechanism ascribed to the PBsomes under strong light illumination. It is corroborated with high-light-induced reorganization (Six et al. 2007; Stoitchkova et al. 2007) and photodegradation of PBsomes (Rinalducci et al. 2008). The photoprotective role of PE has also been characterized in marine cyanobacteria (Wyman et al. 1985). The chromophore variety and increasing abundance extend the absorbance spectrum and enhance the absorption capacity, enabling photosynthetic organisms to survive in various environments. The energetic decoupling of PBsomes occurring under high light indicates a novel physiological role of the chromophore variety: creating a multistep photoprotection mechanism to effectively prevent photodamage of photosynthetic RCs in response to excess excitation energy (Liu et al. 2008b).

![FIGURE 3.6](See color insert.) Schematic model of light-induced decoupling of PBsomes, indicating a possible photoprotective mechanism of the PBsome. Green open circles present the potential decoupling sites within the PBsome. B-PE, B-phycoerythrin; b-PE, b-phycoerythrin; RPC, R-phycocyanin.
3.6 SUMMARY

By harvesting solar energy and converting it into chemical energy, the phototrophs play essential roles in maintaining life on Earth. Variability in the light environment presents major challenges to photosynthetic organisms. To survive in such a fluctuating environment, the phototrophs have evolved regulatory and photoprotective mechanisms to optimize the organization and efficiency of the photosynthetic apparatus. Cyanobacteria are the most important contributors to the global energy production and carbon cycle. For a sustainable future of our society, cyanobacteria are also promising industrial organisms for the production of fuels and metabolic chemicals. Advanced understanding of the photoadaptation/photocaluclation process of cyanobacteria will be of fundamental necessity to the development of biotechnology and bioengineering of photosynthetic microorganisms.

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