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Development of the bacterial photosynthetic apparatus

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Abstract

Anoxygenic photosynthetic bacteria have provided us with crucial insights into the process of solar energy capture, pathways of metabolic and societal importance, specialized differentiation of membrane domains, function or assembly of bioenergetic enzymes, and into the genetic control of these and other activities. Recent insights into the organization of this bioenergetic membrane system, the genetic control of this specialized domain of the inner membrane and the process by which potentially photosynthetic and non-photosynthetic cells protect themselves from an important class of reactive oxygen species will provide an unparalleled understanding of solar energy capture and facilitate the design of solar-powered microbial biorefineries.

Introduction

The capture of solar energy by photosynthetic organisms is at the foundation of almost all life on Earth. Photosynthesis conserves the energy within sunlight by transforming it into either chemical bond energy or a transmembrane electrochemical gradient. Photosynthetic activity generates atmospheric O₂, which supports the respiration of heterotrophs, and provides reducing power to assimilate most of the CO₂ that is sequestered in the biosphere. Consequently, there has been considerable interest in studying capture of light energy by plants and photosynthetic microbes.

Anoxygenic photosynthetic bacteria were historically classified by their ability to use sulfide as an electron donor for CO₂ fixation, resulting in the terms purple sulfur bacteria (*Chromatiaceae*) and purple non-sulfur bacteria (*Rhodospirillaceae*) [1]. Photochemistry in anoxygenic photosynthetic bacteria is dependent on enzymes that are ancestors of plant photosystems [1]. The presence of anoxygenic photosynthesis in bacterial groups that occupy different niches suggests that this capacity evolved either in independent events or as an early event that spread horizontally [2]. Among the *Rhodospirillaceae*, *Rhodobacter* species are often the best understood when one considers properties of the photosynthetic apparatus [3], the use of reducing power derived from solar energy [4-6], control of photosynthetic gene expression [7,8,9] or genomic perspectives [10-13]. Here we summarize new advances in these fields over the past two years.

The photosynthetic apparatus

In *Rhodobacter sphaeroides* and related bacteria, solar energy is conserved by linking light-driven oxidation of a pair of bacteriochlorophyll molecules in a reaction center (RC) complex to electron transfer through membrane-bound bioenergetic enzymes (Figure 1). In this pathway, a periplasmically-positioned electron carrier (e.g. cytochrome cyt *c*₂) reduces the

photo-oxidized RC using electrons derived from quinone oxidation in the cyt *bc*₁ complex [14,15]. The resulting formation of a proton gradient supports ATP synthesis.

The other and most abundant proteins within the *R. sphaeroides* photosynthetic apparatus are bacteriochlorophyll-containing and carotenoid-containing complexes, named B875 and B800-850 according to their absorption maxima [16], which harvest solar energy and funnel it to the RC. Approximately 14 B875 complexes surround and contact the RC, whereas the B800-850 complexes are positioned around the B875-RC complex [16,17]. It was believed that *R. sphaeroides* contained a single set of B800-850 polypeptides, but a second B800-850 complex has been discovered that can aid light-energy capture in this [18] and other photosynthetic bacteria [19].

Analysis of purified *R. sphaeroides* photosynthetic membranes by atomic force microscopy (Figure 2) reveals an ordered array of particles with dimensions predicted from structural models of B875-RC and B800-850 complexes [20]. It is proposed that this supramolecular organization increases energy transfer efficiency from the B800-850 complexes to the B875-RC complexes [21,22].

The *Rhodobacter* photosynthetic apparatus is housed in the intracytoplasmic membrane (ICM) vesicles, a region of the cytoplasmic membrane that protrudes from the cytoplasmic membrane into the cytoplasm (Figure 3). The cellular abundance of the ICM, as well as its pigment-protein composition, changes as a function of light intensity [21,23]; therefore there must be a mechanism to control formation of these invaginations and alter their pigment-protein composition. It is also possible that cellular factors help generate the ordered arrays of pigment-protein complexes within purified ICM vesicles. However, the cellular organization of the photosynthetic membrane and the structure of these arrays are altered in mutants lacking either carotenoids or B800-850 complexes [21], and so the pigment-protein complexes themselves might play a role in these aspects of photosynthetic membrane development.

The ICM is physically connected to, but functionally distinct from, the cytoplasmic membrane (Figure 3) [23]. For example, the pigment-protein complexes are enriched in the ICM whereas phospholipid biosynthetic enzymes and penicillin-binding proteins are localized to the cytoplasmic membrane [23]. By contrast, ATPase and the cyt *bc*₁ complex are found in both the cytoplasmic membrane and the ICM [23]. Having identified ~2000 proteins in whole photosynthetic cells [24], the protein blueprint of the ICM can now be mapped [25]. This will help to identify uncharacterized ICM proteins, define how the ICM is formed, determine how lipids or proteins are moved into this specialized membrane domain and understand how pigment-protein complexes are assembled.

Control of photosynthetic membrane development

Like other facultative anaerobes, many purple photosynthetic bacteria switch their mode of energy metabolism in response to changes in O₂ tension. Pioneering studies by Cohen-Bazire [26] and Lascelles [27] showed that O₂ negatively regulated ICM development because *R. sphaeroides* contained photosynthetic membranes under anaerobic conditions in the presence or absence of light. Transcription of so-called photosynthesis genes is now known to be positively and negatively regulated by O₂ (for reviews, see [7,8 •,9,28,29]).

PrrBA (RegBA) is a master global regulator in *Rhodobacter*, related photosynthetic bacteria and other species [7,9]. PrrBA was discovered as an activator of photosynthesis genes, but it also directly controls genes involved in pigment synthesis, CO₂ fixation, N₂ fixation and H₂ metabolism [4,7,30]. The emerging picture predicts that the PrrBA functions in a homeostatic feedback loop to balance the production of reducing power from light or other resources (when O₂ is limiting) with induction of synthesis pathways that recycle excess reductant. The

transcription factor in this pathway (PrrA/RegA) binds numerous promoters and activates transcription *in vitro* [4], its C-terminus contains a DNA binding motif from the Fis family of transcription factors [31,32], and target sites for this protein are predicted to exist upstream of numerous other, uncharacterized genes [7,8•]. Like many response regulators, PrrA activity increases upon phosphorylation [33], presumably because this stimulates PrrA dimerization [34], which is needed to activate transcription [35]. The ability of PrrA and its homologs [36] to weakly activate transcription in the absence of phosphorylation [30,33] could possibly explain expression of target genes in the presence of O₂ (Figure 4).

PrrA phosphorylation is proposed to respond to changes in the oxidation/reduction state of the aerobic electron transport chain, because removing the cyt *cbb*₃ terminal oxidase or blocking its activity increases expression of target genes in the presence of O₂ [37]. The cognate histidine kinase of PrrA, PrrB/RegB, has been analyzed both as a full-length membrane protein [38] and as a C-terminal soluble domain [33,39]. When this and other features of PrrB are considered, it appears that its N-terminal membrane-spanning domain lowers the steady-state level of phosphorylated PrrA, possibly by stimulating PrrB phosphatase activity [38-40]. Precisely how activity of the aerobic electron transport chain controls function of the PrrBA pathway is not clear. However, purified cyt *cbb*₃ oxidase can both transfer electrons to O₂ (its traditional role) and alter the kinase and phosphatase activity of full-length PrrB *in vitro* [39]. PrrB also contains a quinone binding site [41], and so this kinase could receive multiple inputs from the respiratory chain as a way to control development or the composition of the photosynthetic apparatus.

Photosynthesis also requires a system(s) for recycling excess reducing power. This process is especially crucial for heterotrophic phototrophs (photoheterotrophs) that use organic carbon as a source of electrons in order to reduce light-oxidized RC complexes. For example, during photoheterotrophic growth at saturating light intensities, *R. sphaeroides* and other purple bacteria induce expression of the Calvin-Benson-Bassham cycle, and use CO₂ as an electron acceptor for excess reducing power, even when a fixed carbon source is present [4]. Likewise, the nitrogenase-dependent production of H₂ by photoheterotrophic cultures grown in the presence of NH₄⁺ (first observed by Gest and Kamen [42]) recycles excess reducing power [5]. *R. sphaeroides* and related bacteria also accumulate poly-hydroxybutyrate when supplied with excess carbon and reductant [6]. Global gene expression profiles and mutant analysis suggests that the *R. sphaeroides* RSP4157 gene cluster plays a heretofore unrecognized role in the recycling of reducing power under photoheterotrophic conditions [43]. It is not surprising to find that anoxygenic phototrophs are able to use a variety of pathways to recycle excess reducing power when one considers the myriad of electron donors and acceptors that these organisms are likely to encounter in nature. An additional link in the cycle of reducing power is seen by the ability of added electron acceptors to alter photosynthetic gene expression, and development of the photosynthetic apparatus [35,44-46].

The stress of solar energy generation

There are also deleterious consequences associated with converting light into biological energy. During solar energy capture, the excited chlorophyll pigments of the light-harvesting complexes can transfer their energy to O₂, which generates the powerful oxidant singlet oxygen, ¹O₂ [47,48]. Carotenoids within pigment-protein complexes are one line of defense against ¹O₂ [47-49], but toxicity of this reactive oxygen species to photosynthetic cells means that carotenoid quenching does not provide total protection. The *R. sphaeroides* photosynthetic apparatus does not possess a water-splitting activity with which to evolve O₂ but, if O₂ is present, ¹O₂ is formed by energy transfer from excited, triplet-state chlorophyll pigments, to molecular oxygen and is bacteriocidal to these cells [47,50•]. Anoxygenic photosynthetic bacteria can probably form ¹O₂ in nature because the photosynthetic apparatus is synthesized at the low O₂ tensions present in the habitats that they inhabit [23].

A transcriptional response to $^1\text{O}_2$ *in vivo* that requires the *R. sphaeroides* alternative sigma factor, σ^E has been described [50•]. *R. sphaeroides* σ^E activity is not increased by other reactive oxygen species (superoxide, hydrogen peroxide or hydroxyl radicals) [51,52], suggesting that this is a specific response to $^1\text{O}_2$ [50•]. In the absence of $^1\text{O}_2$, *R. sphaeroides* σ^E forms a complex with its cognate anti-sigma factor, ChrR [53], that prevents this sigma factor from forming a complex with RNA polymerase [54]. Thus, it is proposed that $^1\text{O}_2$ somehow alters the σ^E -ChrR complex, releasing σ^E in order that this sigma factor is able to bind RNA polymerase and activate gene expression [50•].

$^1\text{O}_2$ is able to oxidize unsaturated fatty acids, destroy the integrity of bioenergetic membranes, inactivate enzymes or abolish the function of other biomolecules [48]. $^1\text{O}_2$ is bacteriocidal to *R. sphaeroides* σ^E mutants when carotenoids are limiting [50•]; therefore, one or more σ^E -dependent gene products are required for viability under these conditions. Known σ^E target genes encode a periplasmic electron carrier (cyt c_2), which, as with electron donors to the RC, is near the site of $^1\text{O}_2$ formation, a putative cyclopropane fatty acid synthase, which could protect unsaturated fatty acids against peroxidation, and one of two σ^{32} homologs, RpoH_{II}, which could activate expression of gene products that repair damaged proteins or aid assembly of the photosynthetic apparatus, as well as previously uncharacterized proteins that could protect cells from, or repair damage caused by $^1\text{O}_2$ [50•]. Thus, phototrophs appear to have a dedicated stress-response that protects them from damage caused by $^1\text{O}_2$, as well as repairing it.

Conclusion

Analysis of photosynthetic bacteria have provided crucial insights into the light reactions of photosynthesis, the formation of chemiosmotic ion gradients across biological membranes, the assembly of specialized membrane domains, and into how cells use reducing power generated by solar energy capture [1-5,23,55]. The completed genome sequences for several genera and species of anoxygenic phototrophs [10-13] mean that whole-genome and comparative genomic approaches [24,25,43,45,46] can now provide new insight into functions that control ICM development, assembly of the supramolecular arrays of pigment-protein complexes, formation and removal of toxic byproducts like $^1\text{O}_2$, and into how cells partition reducing power derived from solar energy. This information will be crucial to tapping the ability of photosynthetic microbes to generate alternate energy supplies, to produce high-commodity carbon compounds, or to remove toxic compounds [6,9]. Finally, the microbial genome database predicts that many photosynthetic and non-photosynthetic bacteria contain homologs of pathways that have or are being analyzed in anoxygenic photosynthetic bacteria [7,53]. Thus, fundamental insights into other biological systems will be derived from continued analysis of these fascinating bacteria.

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Figure 1.

Cross-section of the *R. sphaeroides* ICM, illustrating the function of the major components of this bioenergetic membrane. The figure depicts the orientation of ICM components relative to the cytoplasmic and periplasmic compartments. Abbreviations: Bchl, bacteriochlorophyll; Bchl₂, bacteriochlorophyll special pair; ADP, adenosine diphosphate; ATP, adenosine triphosphate; P_i, phosphate; e⁻, electron; Q, ubiquinone; cyt c₂, cytochrome c₂; B800-850 & B875, light harvesting complexes, respectively.

Figure 2.

Supramolecular organization of ICM pigment-protein complexes. Sealed ICM vesicles (green) contain a high-density array of ordered pigment-protein complexes. In this array, each RC complex is surrounded by a series of B875 light harvesting complexes and are proposed to be coupled or linked with another B875-RC complex by the PufX protein. B875-RC pairs are arranged in a lattice, enabling tight ordered packing of ICM pigment-protein complexes. B800-850 light harvesting complexes are proposed to be arranged in pools two to three complexes wide between the B875-RC pairs. It is proposed that this ordered arrangement of pigment-protein complexes allows efficient energy transfer from B800-850 pigments to B875 pigments and to the RC special pair where photochemistry occurs.

Figure 3.

Cellular depiction of the *R. sphaeroides* ICM that houses the photosynthetic apparatus. This image shows the ICM (red spheres) protruding from the cytoplasmic membrane (purple) into the cytoplasm of this Gram-negative bacterium (outer membrane is green). Left panel: long-axis cross section of a cell. Right panel: short-axis cross section of a cell. These images were generated by digital reconstruction (Harold Trease, Pacific Northwest National Laboratory, US Department of Energy) of sequential thin-section electron micrographs of photosynthetically grown cells (Samuel Kaplan, University of Texas Medical School at Houston) and are reproduced here with permission.

Figure 4.

Homeostatic control of gene expression by the PrrBA pathway. The left panel depicts the state of PrrA-dependent gene expression in the presence of O₂. Under these conditions, the aerobic electron transport chain (ETC) is operative, the steady-state level of phosphorylated PrrA (PrrA-Pi) is low, and so there is a low basal level transcription of target genes (e.g. PS genes and electron sinks). The right panel depicts the state of PrrA-dependent gene expression under low O₂ or anaerobic conditions. In this case, the lack of aerobic electron transport chain activity increases the steady state level of PrrA-Pi, which activates transcription of photosynthesis genes and gene products that recycle excess reducing power under anaerobic conditions.