*Photosynthesis Research* **80:** 353–360, 2004.



*Minireview*

# Regulation of photosystem synthesis in *Rhodobacter capsulatus*

Carl Bauer
*Department of Biology, Indiana University, Bloomington, IN 47405, USA (e-mail: cbauer@bio.indiana.edu; fax: +1-812-855-6705)*

Received 6 April 2003; accepted in revised form 11 August 2003

*Key words:* AerR, AppA, crtJ, Howard Gest, Barry Marrs, regA, regB

**Abstract**

Control of the synthesis of the purple bacterial photosystem has been an active area of research for many decades. The period of the 1960s involved physiological characterization of photosystem synthesis under different growth conditions. In the 1970s Barry Marrs and coworkers developed genetic tools that were used to define and map genes needed for synthesis of photopigments. The 1980s was a period of cloning and physical mapping of photosynthesis genes onto the chromosome, the demonstration that regulation of photosystem synthesis involved transcriptional control of gene expression, and sequence analysis of photosynthesis genes. The 1990s was a period of the discovery and characterization of regulatory genes that control synthesis of the photosystem in response to alterations in oxygen tension and light intensity. Although several photosynthetic organisms are mentioned for comparison and contrast, the focus of this minireview is on *Rhodobacter capsulatus*.

*Abbreviations:* kb – kilobase(s); kbp – kilobasepair(s)

## Early history in the regulation of photosynthesis

In many purple bacterial species, synthesis of the photosystem is influenced by environmental factors such as oxygen tension and light intensity. The first detailed analysis of the regulation of pigment biosynthesis was a study by Cohen-Bazire et al. (1957). Their work was the first to clearly establish that pigment biosynthesis in photosynthetically growing *Rhodobacter sphaeroides* cells is rapidly inhibited by the addition of molecular oxygen or by an increase in light intensity. This work was followed by a number of physiological studies which demonstrated the effect of oxygen and light on synthesis of the photosystem in a number of purple photosynthetic bacteria (reviewed by Drews 1985).

The first genetic studies to probe the regulation of photosystem synthesis involved the isolation of arsenate resistant mutants of *Rhodobacter capsulatus* by Lien et al. (1971), which overproduced large amounts of the photosynthetic apparatus. This was followed by a study by Lascelles and Wertlieb (1971) that resulted in the isolation of a mutant of *R. sphaeroides* (TA-R) that aerobically produced photopigments. Neither of these mutants was characterized at a molecular level, and so it is unclear as to what genetic defects lead to the reported phenotype. Although the arsenate resistant strains appear to have been lost, the TA-R isolate is present in the Barry Marrs strain collection that is currently housed in the author's (Carl Bauer's) laboratory. It would be of interest to someday determine if known regulatory genes such as *regA* or *crtJ* are disrupted in TA-R.

## The early years of modern genetics

The era of more current genetic studies on the regulation of the bacterial photosystem began when Barry Marrs developed sophisticated genetic tools for *R. capsulatus* (reviewed by Marrs 2002). The research

*Figure 1.* Barry Marrs' research group in 1987 at Dupont Corp. *Left to right*: Carl Bauer, Tim Reed, Barry Marrs, Marrianne Eleuterio and Debra Young.

from his group resulted in the isolation of numerous pigmentation mutations that were mapped to a ~45 kbp region of the *R. capsulatus* genome called the photosynthesis gene cluster (Marrs 1974, 1981; Yen and Marrs 1976). This region contained virtually all of the bacteriochlorophyll and carotenoid biosynthesis genes, as well as the photosystem structural genes (Marrs 1981). A similar photosynthesis gene cluster has been found in most other characterized purple bacterial species. There is also a 'photosynthesis gene cluster' present in the gram-positive bacterium *Heliobacillus mobilus* which is closely related to cyanobacteria (Xiong et al. 1998). Curiously, no photosynthesis gene cluster exists in sequenced genomes of the (oxygenic) cyanobacterium *Synechocystis* sp. PCC 6803 (Kaneko et al. 1996), the green sulfur bacterium *Chlorobium tepidum* (Xiong et al. 2000) or the green non-sulfur bacterium *Chloroflexus aurantiacus* (Xiong et al. 2000). Thus, only three of the five photosynthetic bacterial lineages contain a tight clustering of photosynthesis genes.

## Molecular biology approaches to the analysis of photosynthesis genes

The use of modern molecular biology approaches to the analysis of photosynthesis gene expression began when Barry Marrs (Figure 1) teamed with Stanley N. Cohen to undertake physical mapping of photosynthesis genes in *R. capsulatus* by complementation of mutants using subcloned restriction fragments (Taylor et al. 1983). This work was followed by transposon mapping of the *R. capsulatus* photosynthesis gene cluster by Zsebo and Hearst (1984). The DNA sequence of the entire 45 kb photosynthesis gene cluster was obtained by Hearst and coworkers (Youvan et al. 1984; Armstrong et al. 1989; Burke et al. 1993; Alberti et al. 1995). Analysis of the functions of individual loci was accomplished by the construction of interposon mutations within each of the identified open reading frames (Giuliano et al. 1988; Young et al. 1989, 1992; Yang and Bauer 1990; Bollivar et al. 1994a, b). This provided the first understanding of the polypeptide composition of the reaction center and light harvesting structural genes (Youvan et al. 1984) as well as the first comprehensive understanding of genes involved in carotenoid and Mg-tetrapyrrole (chlorophyll and bacteriochlorophyll) biosynthesis in photosynthetic organisms (Bauer et al. 1993). Indeed, the information of pigment biosynthesis genes in *R. capsulatus* was a 'guiding light' for the characterization of (bacterio)chlorophyll and carotenoid biosynthesis genes in a variety of diverse experimental systems ranging from photosynthetic bacteria to plants (reviewed by Bauer et al. 1993; Suzuki et al. 1997).

The first experimental evidence for the regulation of photosynthesis gene expression in *R. capsulatus* was a study by Biel and Marrs (1983) who used bacteriophage Mud1-based *lacZ* fusions to demonstrate that the bacteriochlorophyll genes were transcriptionally regulated in response to alterations in oxygen tension. This work was followed by a number of RNA hybridization experiments which revealed that light harvesting and reaction center operons were transcribed at much higher levels than the bacteriochlorophyll or carotenoid genes (Clark et al. 1984; Klug et al. 1985; Zhu and Kaplan 1985; Donahue et al. 1986; Zhu and Hearst 1986; Zhu et al. 1986; Kiley and Kaplan 1987). These studies indicated that photosynthesis genes were regulated from 2- to 100-fold in response to changes in oxygen tension or light intensity. The results of these hybridization studies were confirmed by numerous transcription studies that used plasmid based transcriptional and translational fusions to *lacZ* (Bauer and Marrs 1988; Bauer et al. 1988, 1991; Young et al. 1989; Sganga and Bauer 1992; Buggy et al. 1994; Mosley et al. 1994; Ponnampalam et al. 1995). Posttransciptional regulation involving mRNA processing events was also discovered during this period (Belasco et al. 1985; Adams et al. 1989).

## Personal travels with photosynthetic bacteria

My doctoral thesis work from 1980 to 1986 was on the mechanism of bacteriophage lambda integration. Sam Kaplan's laboratory, which was studying the expression patterns of several *R. sphaeroides* photosynthesis genes, was in the same department (Department of Microbiology, University of Illinois, Urbana, Illinois) as that of my thesis advisor (Jeffrey Gardner). [For Kaplan's story, see Kaplan (2002).] Consequently, I became aware of the emerging field of molecular genetic analysis of photosynthesis genes (discussed above) from members of the Kaplan group. After completing my thesis, I decided to work with Barry Marrs who was arguably one of the best geneticists to work with photosynthetic bacteria. Barry was in the process of moving from academia to Exxon Corp where he was setting up a team of scientists to study bacterial photosynthesis. Barry arranged for laboratory space at the Cold Spring Harbor Laboratory for several Exxon investigators such as Fevzi Daldal, Doug Youvan and Pablo Scolnik. [Daldal et al. (2003) have written their story on their work on membrane-anchored cytochrome *c*, also in these history issues.] The initial plan was for me to work with Barry Marrs using space in Fevzi Daldal's laboratory. However, just before I was to leave for Cold Spring Harbor, Barry announced that he was leaving Exxon and going to Dupont Corp. Since the positions at Cold Spring Harbor were destined to vanish, I had little choice but to follow Barry to Dupont. In hindsight, doing a postdoctoral position at Dupont was a good move because it allowed me to experience industrial research in a way that still allowed me to freely move back into academia.

While working with Barry Marrs at Dupont (Figure 1), I undertook the first detailed promoter mapping studies of a photosynthesis promoter (the *puf* promoter) (Bauer et al. 1988). In collaboration with Debra Young (Figure 1), we observed that the *R. capsulatus* photosynthesis gene cluster contains several large 'superoperons' such that transcripts originating from upstream pigment biosynthesis operons often include the downstream *puf* and *puh* coding regions for reaction center and light harvesting I apoproteins (Young et al. 1989; Bauer et al. 1991). Similar results were also reported by Tom Beatty's laboratory (Wellington and Beatty 1991; Wellington et al. 1991, 1992; Beatty 1995). The coupling of pigment and pigment-binding protein transcripts was shown to be important in maintaining a basal level of photosystem synthesis, which is needed during transitions between aerobic and anaerobic growth (Young et al. 1989; Wellington et al. 1991).

## Isolation of regulatory mutants

After my stay at Dupont, I was offered a tenure track faculty position at Indiana University (Bloomington) which was actually a position that was vacated by the retirement of Howard Gest; see Figure 2). The intriguing part of the offer was the opportunity to form a combined joint laboratory with Howard who was still active in the isolation, cultivation and physiology of photosynthetic prokaryotes. This led to a fruitful collaboration that resulted in several joint publications (Yildez et al. 1991a, b, 1992a, b) and grants that supported members of our joint research groups.

Soon after my arrival at Indiana University, one of my first graduate students Mike Sganga and I undertook a screen for mutations that exhibited reduced pigmentation coupled with a reduction in β-galactosidase activity derived from a *puf::lacZ* translational fusion. This screen resulted in the first of several 'modern' isolates of *trans*-acting regulatory mutations that exhibited defects in anaerobic induction of photosynthesis gene expression (Sganga and Bauer 1992). Several mutants were mapped to a single locus, designated *regA*, that was found to encode a response regulator class of DNA-binding protein (Sganga and Bauer

*Figure 2.* Carl Bauer and Howard Gest in 1989 on an outing to look for photosynthetic bacteria specimens in sulfur-rich springs in southern Indiana.

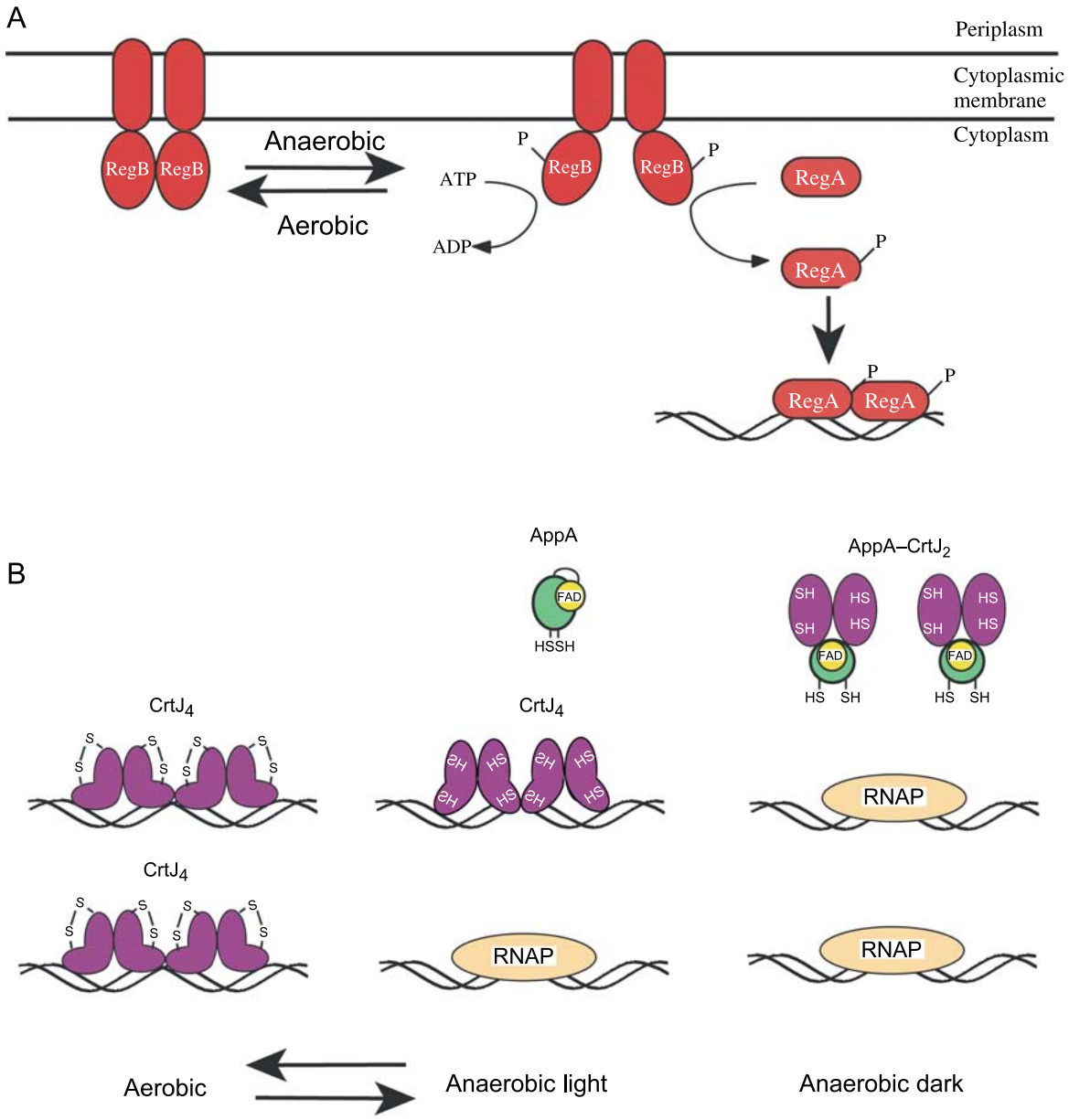


*Figure 3.* A diagram of several redox (oxygen) and light responding regulatory factors. (A) A depiction of the RegB–RegA two component system that controls anaerobic physiology of many α-proteobacteria. RegB is inactive under aerobic conditions; however, under aerobic conditions, RegB autophosphorylates and subsequently passes a phosphate to RegA. In most cases, phosphorylated RegA is active as an anaerobic repressor where it binds to promoter regions stimulating RNA polymerase activity. In some cases, dephosphorylated RegA can also act as a transcriptional activator/repressor. (B) CrtJ (also called PpsR in *R. sphaeroides*) is controlled at one level by the formation and breakage of a disulfide bond. Under aerobic growth conditions the disulfide bond-containing form of CrtJ tightly binds to DNA. Under anaerobic conditions the disulfide bond is reduced, which weakens interactions of CrtJ with the repressor binding site. In *R. sphaeroides*, a second protein known as AppA functions as a light inactivated antirepressor of CrtJ. Under dark conditions AppA binds to CrtJ, converting CrtJ from a tetramer into an inactive dimer. Excitation of the flavin by blue light inhibits AppA activity. For a color version of this figure, see http://www.kluweronline.com/issn/0166-8595.

1992) (Figure 3A). Response regulators are the DNA-binding component of a two-component signal transduction system, the other member being a histidine sensor/kinase that activates the response regulator by phosphorylation of a conserved aspartate (Volz 1995).

Disruption of the *regA* gene severely inhibits photosynthetic growth, particularly under low light intensities, but has no observable effect on the growth of aerobic cultures (Sganga and Bauer 1992). Fusions of *lacZ* to various photosynthesis genes demonstrated that *regA* strains fail to anaerobically induce light harvesting and reaction center gene expression (*puf*, *puc* and *puh*) above the basal levels observed under aerobic conditions (Sganga and Bauer 1992). In contrast, the expression of bacteriochlorophyll and carotenoid (*bch* and *crt*) genes are essentially identical in *regA* and wild type backgrounds, indicating that these loci are excluded from the RegA regulon (Sganga and Bauer 1992).

A second oxygen regulator of photosynthesis gene expression, designated *regB*, was discovered using a modified version of the procedure used to isolate *regA* mutants (Mosley et al. 1994). The *regB* gene mapped to a region upstream and in opposite orientation of the operon containing *regA*. The deduced amino acid sequence established RegB as a histidine sensor/kinase with six hydrophobic regions near the amino-terminus that anchor the protein to the cytoplasmic membrane (Chen et al. 2000) (Figure 3A). As is the case for *regA*, disruptions in *regB* reduce the level of *puf, puc* and *puh* expression but do not affect the expression of pigment biosynthesis genes (Mosley et al. 1994). Genetic analyses of the phenotypes associated with *regA* and *regB* mutants have been interpreted as evidence that RegA and RegB constitute a signal transduction system that regulates photosynthesis gene expression in response to alterations in oxygen tension (Mosley et al. 1994).

Although originally described as 'regulators of photosynthesis,' RegB and RegA are now known to be global redox-responding transcription factors that are responsible for controlling numerous, diverse energy-generating and energy-utilizing processes such as photosynthesis, carbon fixation, nitrogen fixation, hydrogen utilization, aerobic and anaerobic respiration, denitrification, electron transport and aerotaxis (reviewed by Elsen et al. 2004). The redox signal that is detected by the membrane bound sensor kinase, RegB, seems to originate from the aerobic respiratory chain because mutations in cytochrome *c* oxidase result in constitutive RegB autophosphorylation (Buggy and Bauer 1995; O'Gara et al. 1998; Oh et al. 2000). Highly conserved homologous of RegB and RegA have been found in a large number of photosynthetic as well as many non-photosynthetic bacteria (Elsen et al. 2004).

In addition to the isolation of RegA and RegB mutants, mutational analyses of the *R. capsulatus* and *R. sphaeroides* photosynthesis gene cluster suggested that an open reading frame termed *crtJ* codes for a *trans*-acting repressor of photopigment biosynthesis genes (Penfold and Pemberton 1991, 1994; Bollivar et al. 1994a). Spectral analyses of aerobically grown cultures demonstrated that the steady-state level of bacteriochlorophyll is elevated 2.6-fold in a *crtJ* mutant as compared to wild type cells (Bollivar et al. 1994a). The aerobic expression of various photopigment biosynthesis genes is also elevated 2-fold in a *crtJ* mutant strain, suggesting that CrtJ functions as an aerobic repressor of *bch* and *crt* genes (Gomelsky and Kaplan 1995a; Ponnampalam et al. 1995). Interestingly, the effect of CrtJ is not limited to the pigment biosynthesis genes. Aerobic expression of the *puc* operon, which codes for the light harvesting II structural apoproteins, is also 2-fold higher in a *crtJ* mutant despite the fact that *puf* and *puh* expression levels are essentially the same as in the wild type (Ponnampalam et al. 1995). Thus, *puc* operon expression is subject to repression by CrtJ as well as activation by RegB/RegA.

Linked to CrtJ is another open reading frame termed AerR that also codes for an aerobic repressor of photosynthesis genes (Dong et al. 2002). Reporter studies showed that AerR functions as a repressor of bacteriochlorophyll genes as well as of the *puf* operon. Interestingly, AerR contains a vitamin $B_{12}$ binding domain indicating that it may use $B_{12}$ as a cofactor (Gomelsky et al. 2003). Alternatively, AerR may also regulate Mg-tetrapyrrole biosynthesis in response to the presence or absence of $B_{12}$, although this possibility has not been examined.

**Biochemical analysis of regulatory proteins**

The early 1990s, to the present day, was a period of discovery of *trans*-acting transcription factors coupled with analyses of target genes. From the mid 1990s, my laboratory and several others have undertaken extensive biochemical analyses of these transcription factors. These studies include analysis of autophosphorylation of RegB and phosphoryl group transfer to RegA, as well as the DNA binding activity of RegA (recently reviewed by Elsen et al. 2004) (Figure 3A). These studies suggest that RegB directly responds to alterations in cellular redox status, and that both phosphorylated and dephosphorylated RegA are important in controlling gene expression.

We also have undertaken biochemical analysis of CrtJ, which indicates that CrtJ directly responds to changes to oxygen tension through the formation and breakage of a disulfide bond which stimulates DNA binding activity (Masuda et al. 2002) (Figure 3B). Interestingly, the expression of a CrtJ homolog in *R. sphaeroides* is also known to be controlled by a flavin-containing antirepressor called AppA (Gomelsky and Kaplan 1995b, 1997, 1998). In a recent study, Masuda and Bauer (2002) demonstrated that AppA functions as a blue light-inhibited antirepressor of CrtJ. Light excitation of AppA appears to affect $\pi-\pi$ stacking interactions between FAD (flavin adenine dinucleotide) and a conserved tyrosine residue, which in turn causes a long-range conformational change in AppA (Kraft et al. 2003). The dark form of AppA is capable of interacting with CrtJ, converting CrtJ from an active tetramer into an inactive dimer, whereas the light excited form of AppA is incapable of interacting with the CrtJ tetramer (Masuda and Bauer 2002).

## Where we are going from here

In the decade of the 1990s we went from no identifiable photosystem transcription factors to a plethora of redox and light responding activators and repressors. Many of these transcription factors can now be isolated in pure forms that can be used for *in vitro* transcription studies. There are many questions outstanding as to the molecular mechanisms of repression and activation by these regulatory proteins. In the decades to come, we hope to enter a period where a detailed understanding of these factors, such as three-dimensional structural analysis can be used to further reveal how they function.

## Acknowledgments

I thank past and present members of my research group for the many insightful contributions that they have made to help unravel the regulation of photosynthesis gene expression. I also thank Barry Marrs and Howard Gest for their help in getting me established in this field. I apologise for not being able to cite all of the contributions from other laboratories due to space limitations. Research in my laboratory is supported by the National Institutes of Health and the National Science Foundation. This paper was edited by J. Thomas Beatty.

## References

Adams CW, Forrest ME, Cohen SN and Beatty JT (1989) Structural and functional analysis of transcriptional control of the *Rhodobacter capsulatus puf* operon. J Bacteriol 171: 473–482

Alberti M, Burke DH and Hearst JE (1995) Structure and sequence of the photosynthesis gene cluster. In: Blankenship RE, Madigan MT and Bauer CE (eds) Anoxygenic Photosynthetic Bacteria, pp 1083–1106. Kluwer Academic Publishers, Dordrecht, The Netherlands

Armstrong GA, Alberti M, Leach F and Hearst JE (1989) Nucleotide sequence, organization and nature of protein products of the carotenoid biosynthesis gene cluster of *Rhodobacter capsulatus*. Mol Gen Genet 216: 254–268

Bauer CE and Marrs BL (1988) *Rhodobacter capsulatus puf* operon encodes a regulatory protein (PufQ) for bacteriochlorophyll biosynthesis. Proc Natl Acad Sci USA 85: 7074–7078

Bauer CE, Young DY and Marrs BL (1988) Analysis of the *Rhodobacter capsulatus puf* operon: location of the oxygen-regulated promoter region and the identification of an additional *puf*-encoded gene. J Biol Chem 263: 4820–4827

Bauer CE, Buggy JJ, Yang Z and Marrs BL (1991) The superoperonal organization of genes for pigment biosynthesis and reaction center proteins is a conserved feature in *Rhodobacter capsulatus*: analysis of overlapping *bchB* and *puhA* transcripts. Mol Gen Genet 288: 433–444

Bauer CE, Bollivar DW and Suzuki JY (1993) Genetic analysis of photopigment biosynthesis in eubacteria: A guiding light for algae and plants. J Bacteriol 175: 3919–3925

Beatty JT (1995) Organization of photosynthesis gene transcripts. In: Blankenship RE, Madigan M and Bauer CE (eds) Anoxygenic Photosynthetic Bacteria, pp 1209–1219. Kluwer Academic Publishers, Dordrecht, The Netherlands

Belasco JG, Beatty JT, Adams CW, von Gabain A and Cohen SN (1985) Differential expression of photosynthesis genes in *R. capsulata* results from segmental differences in stability within the polycistronic *rxcA* transcript. Cell 40: 171–181

Biel AJ and Marrs BL (1983) Transcriptional regulation of several genes for bacteriochlorophyll synthesis in *Rhodopseudomonas capsulata* in response to oxygen. J Bacteriol 156: 686–694

Bollivar DW, Suzuki JY, Beatty JT, Dobrowlski J and Bauer CE (1994a) Directed mutational analysis of bacteriochlorophyll *a* biosynthesis in *Rhodobacter capsulatus*. J Mol Biol 237: 622–640

Bollivar DW, Wang S, Allen JP and Bauer CE (1994b) Molecular genetic analysis of terminal steps in bacteriochlorophyll a biosynthesis: characterization of a *Rhodobacter capsulatus* strain that synthesizes geranylgeraniol esterified bacteriochlorophyll *a*. Biochemistry 33: 12763–12768

Buggy JJ and Bauer CE (1995) SenC, a homolog of the yeast cytochrome *c* oxidase assembly factor SCO1, is involved in both aerobic respiration and anaerobic photosynthesis gene expression in *Rhodobacter capsulatus*. J Bacteriol 177: 6958–6965

Buggy JJ, Sganga MW and Bauer CE (1994) Characterization of a light responding *trans*-activator responsible for differentially controlling reaction center and light harvesting-I gene expression in *R. capsulatus*. J Bacteriol 176: 6936–6943

Burke D, Alberti M and Hearst JE (1993) The *Rhodobacter capsulatus* chlorin reductase encoding locus, *bchA*, consists of three genes, *bchX, bchY, and bchZ*. J Bacteriol 175: 2407–2413

Chen W, Jager A and Klug G (2000) Correction of the DNA sequence of the *regB* gene of *Rhodobacter capsulatus* with

implications for the membrane topology of the sensor kinase RegB. J Bacteriol 182: 818–820

Clark WG, Davidson E and Marrs BL (1984) Variation of levels of mRNA coding for antenna and reaction center polypeptides in *Rhodopseudomonas capsulata* in response to changes in $O_2$ concentration. J Bacteriol 157: 945–948

Cohen-Bazire GW, Sistrom WR and Stanier RY (1957) Kinetic studies of pigment synthesis by non-sulfur purple bacteria. J Cell Comp Physiol 49: 25–68

Daldal F, Deshmukh M and Prince RC (2003) Membrane-anchored cytochrome *c* as an electron carrier in photosynthesis and respiration: past, present and future of an unexpected discovery. Photosynth Res 76: 127–134

Dong C, Elsen S, Swem L and Bauer CE (2002) AerR, a second aerobic repressor of photosynthesis gene expression in *Rhodobacter capsulatus.* J Bacteriol 184: 2805–2814

Donohue TJ, Hoger JH and Kaplan S (1986) Cloning and expression of the *Rhodobacter sphaeroides* reaction center H gene. J Bacteriol 168: 953–961

Drews G (1985) Structure and functional organization of light-harvesting complexes and photochemical reaction centers in membranes of phototrophic bacteria. Microbiol Rev 49: 59–70

Elsen S, Swem L, Swem D and Bauer CE (2004) RegB/RegA, a highly conserved redox-responding global regulatory system. Microbiol Mol Biol Rev (in press)

Giuliano G, Pollock D, Stapp H and Scolnik PA (1988) A genetic–physical map of the *Rhodobacter capsulatus* carotenoid biosynthesis cluster. Mol Gen Genet 213: 78–83

Gomelsky M and Kaplan S (1995a) Genetic evidence that PpsR from *Rhodobacter sphaeroides* 2.4.1 functions as a repressor of *puc* and *bch*F expression. J Bacteriol 177: 1634–1637

Gomelsky M and Kaplan S (1995b) *appA*, a novel gene encoding a *trans*-acting factor involved in the regulation of photosynthesis gene expression in *Rhodobacter sphaeroides.* J Bacteriol 177: 4609–4618

Gomelsky M and Kaplan S (1997) Molecular genetic analysis suggesting interaction between AppA and PpsR in regulation of photosynthesis gene expression in *Rhodobacter sphaeroides*. J Bacteriol 179: 128–134

Gomelsky M and Kaplan S (1998) AppA, a redox regulator of photosystem formation in *Rhodobacter sphaeroides* 2.4.1, is a flavoprotein. J Biol Chem 273: 35319–35325

Gomelsky L, Sram J, Moskvin OV, Horne IM, Dodd HN, Pemberton JM, McEwan AG, Kaplan S and Gomelsky M (2003) Identification and *in vivo* characterization of PpaA, a regulator of photosystem formation in *Rhodobacter sphaeroides*. Microbiology 149: 377–388

Kaneko T, Sato S, Kotani H, Tanaka A, Asamizu E, Nakamura Y, Miyajima N, Hirosawa M, Sugiura M, Sasamoto S, Kimura T, Hosouchi T, Matsuno A, Muraki A, Nakazaki N, Naruo K, Okumura S, Shimpo S, Takeuchi C, Wada T, Watanabe A, Yamada M, Yasuda M and Tabata S (1996) Sequence analysis of the genome of the unicellular cyanobacterium *Synechocystis* sp. strain PCC6803. II. Sequence determination of the entire genome and assignment of potential protein-coding regions. DNA Res 3: 109–136

Kaplan S (2002) Photosynthesis genes and their expression in *Rhodobacter sphaeroides* 2.4.1: a tribute to my students and associates. Photosynth Res 73: 95–108

Kiley PJ and Kaplan S (1987) Cloning, DNA sequence, and expression of the *Rhodobacter sphaeroides* light-harvesting B800-850_ and B800-850ß genes. J Bacteriol 169: 3268–3275

Klug G, Kaufmann N and Drews G (1985) Gene expression of pigment-binding proteins of the bacterial photosynthetic apparatus: transcription and assembly in the membrane of *Rhodopseudomonas capsulata.* Proc Natl Acad Sci USA 82: 6485–6489

Kraft B, Kikuchi J, Masuda S, Dragnia V, Tollin G, Zaleski JM and Bauer CE (2003) Spectroscopic and mutational analysis of the blue-light photoreceptor, AppA: a novel photocycle involving flavin stacking with aromatic amino acids. Biochemistry 42: 6726–6734

Lascelles J and Wertlieb D (1971) Mutant strains of *Rhodopseudomonas sphaeroides* which form photosynthetic pigments aerobically in the dark. Biochem Biophys Acta 226: 328–340

Lien S, San Pietro A and Gest H (1971) Mutational and physiological enhancement of photosynthetic energy conversion in *Rhodopseudomonas capsulata*. Proc Natl Acad Sci 68: 1912–1915

Marrs BL (1974) Genetic recombination in *Rhodopseudomonas capsulata*. Proc Natl Acad Sci USA 71: 971–973

Marrs BL (1981) Mobilization of the genes for photosynthesis from *Rhodopseudomonas capsulata* by a promiscuous plasmid. J Bacteriol 146: 1003–1012

Marrs BL (2002) The early history of the genetics of photosynthetic bacteria: a personal account. Photosynth Res 73: 55–58

Masuda S and Bauer CE (2002) AppA is a blue-light photoreceptor that anti-represses photosynthesis gene expression in *Rhodobacter sphaeroides* Cell 110: 613–623

Masuda S, Dong C, Swem D, Setterdahl AT, Knaff DB and Bauer CE (2002) Aerobic repression of photosystem synthesis through formation of an intramolecular disulfide bond in CrtJ. Proc Natl Acad Sci USA 99: 7078–7083

Mosley C, Suzuki J and Bauer CE (1994) Identification and molecular genetic characterization of a sensor kinase responsible for coordinately regulating light harvesting and reaction center gene expression in response to anaerobiosis. J Bacteriol 176: 7566–7573

O'Gara JP, Eraso JM and Kaplan S (1998) A redox-responsive pathway for aerobic regulation of photosynthesis gene expression in *Rhodobacter sphaeroides* 2.4.1. J Bacteriol 175: 2292–2302

Oh J-H, Eraso JM and Kaplan S (2000) Interacting regulator circuits involved in orderly control of photosynthesis gene expression in *Rhodobacter sphaeroides* 2.4.1. J Bacteriol 182: 3081–3087

Penfold RJ and Pemberton JM (1991) A gene from the photosynthetic gene cluster of *Rhodobacter sphaeroides* induces *trans*-suppression of bacteriochlorophyll and carotenoid levels in *R. sphaeroides* and *R. capsulatus*. Curr Microbiol 23: 259–263

Penfold RJ and Pemberton JM (1994) Sequencing, chromosomal inactivation and functional expression in *E. coli* of *pps*, a gene which represses carotenoid and bacteriochlorophyll synthesis in *Rhodobacter sphaeroides*. J Bacteriol 176: 2869–2876

Ponnampalam S, Buggy JJ and Bauer CE (1995) Characterization of an aerobic repressor that coordinately regulates bacteriochlorophyll, carotenoid and light harvesting-II expression in *Rhodobacter capsulatus*. J Bacteriol 177: 2990–2997

Sganga MW and Bauer CE (1992) Regulatory factors controlling photosynthetic reaction center and light-harvesting gene expression in *Rhodobacter capsulatus*. Cell 68: 945–954

Suzuki JY, Bollivar DW and Bauer CE (1997) Genetic analysis of chlorophyll biosynthesis. Ann Rev Genet 31: 61–89

Taylor DP, Cohen SN, Clark WG and Marrs BL (1983) Alignment of genetic and restriction maps of the photosynthesis region of the *Rhodopseudomonas capsulata* chromosome by a conjugation-mediated marker rescue technique. J Bacteriol 154: 580–590

Volz K (1995) Structural and functional conservation in response regulators. In: Hoch JA and Silhavy TJ (eds) Two-Component Signal Transduction, pp 53–64. ASM Press, Washington, DC

Wellington CL and Beatty JT (1991) Overlapping mRNA transcripts of photosynthesis gene operons in *Rhodobacter capsulatus*. J Bacteriol 173: 1432–1443

Wellington CL, Taggart AKP and Beatty JT (1991) Functional significance of overlapping transcripts of *crtEF*, *bchCA*, and *puf* photosynthesis gene operons in *Rhodobacter capsulatus*. J Bacteriol 173: 2954–2961

Wellington CL, Bauer CE and Beatty JT (1992) Superoperons in purple non-sulfur bacteria: the tip of the iceberg? Can J Microbiol 38: 20–27

Xiong J, Inoue K and Bauer CE (1998) Tracking molecular evolution of photosynthesis by characterization of a major photosynthesis gene cluster from *Heliobacillus mobilis*. Proc Natl Acad Sci USA 95: 14851–14856

Xiong J, Fisher WM, Inoue K, Nakahara M and Bauer CE (2000) Molecular evidence for the early evolution of photosynthesis. Science 289: 1724–1730

Yang ZY and Bauer CE (1990) *Rhodobacter capsulatus* genes involved in early steps of the bacteriochlorophyll biosynthetic pathway. J Bacteriol 126: 619–629

Yen H-C and Marrs BL (1976) Map of genes for carotenoid and bacteriochlorophyll biosynthesis in *Rhodopseudomonas capsulata*. J Bacteriol 126: 619–629

Yildiz FH, Gest H and Bauer CE (1991a) Genetic analysis of photosynthesis in *Rhodospirillum centenum*. J Bacteriol 173: 4163–4170

Yildiz FH, Gest H and Bauer CE (1991b) Attenuated effect of oxygen on photopigment synthesis in *Rhodospirillum centenum*. J Bacteriol 173: 5502–5506

Yildiz FH, Gest H and Bauer CE (1992a) Conservation of the photosynthesis gene cluster in *Rhodospirillum centenum*. Mol Microbiol 6: 2683–2691

Yildiz FH, Bauer CE and Gest H (1992b) Characterization of light harvesting and reaction center complexes from *Rhodosprillum centenum*. In: Murata N (ed) Research in Photosynthesis, Vol III, pp 19–26. Kluwer Academic Publishers, Dordrecht, The Netherlands

Young DA, Bauer CE, Williams JC and Marrs BL (1989) Genetic evidence for superoperonal organization of genes for photosynthetic pigments and pigment-binding proteins in *Rhodobacter capsulatus*. Mol Gen Genet 218: 1–12

Young DA, Rudzik MB and Marrs BL (1992) An overlap between operons involved in carotenoid and bacteriochlorophyll biosynthesis in *Rhodobacter capsulatus*. FEMS Microbiol Lett 95: 213–218

Youvan DC, Bylina EJ, Alberti M, Begusch H and Hearst JE (1984) Nucleotide and deduced polypeptide sequences of the photosynthetic reaction center, B870 antenna, and flanking polypeptides from *R. capsulata*. Cell 37: 949–957

Zhu YS and Hearst JE (1986) Regulation of expression of genes for light-harvesting antenna proteins LH-I and LH-II; reaction center for polypeptides R-L, RC-M, and RC-H; and enzymes of bacteriochlorophyll and carotenoid biosynthesis in *Rhodobacter capsulatus* by light and oxygen. Proc Natl Acad Sci USA 83: 7613–7617

Zhu YS and Kaplan S (1985) Effects of light, oxygen and substrates on steady-state levels of mRNA coding for ribulose-1,5-bisphosphate carboxylase and light-harvesting and reaction center polypeptides in *Rhodopseudomonas sphaeroides*. J Bacteriol 162: 925–932

Zhu YS, Cook DN, Leach F, Armstrong GA, Alberti M and Hearst JE (1986) Oxygen regulated mRNAs for light-harvesting and reaction center complexes and for bacteriochlorophyll and carotenoid biosynthesis in *Rhodobacter capsulatus* during shift from anaerobic to aerobic growth. J Bacteriol 168: 1180–1188

Zsebo KM and Hearst JE (1984) Genetic physical mapping of a photosynthetic gene cluster from *R. capsulata*. Cell 37: 937–947