J. Mol. Microbiol. Biotechnol. (2002) 4(3): 249–253.

Oxygen-Regulated Expression of Genes for Pigment Binding Proteins in *Rhodobacter capsulatus*

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Abstract

Oxygen is the major external factor affecting the expression of photosynthesis genes in facultatively photosynthetic bacteria. Many investigations over the last years mainly carried out on the closely related species *Rhodobacter capsulatus* and *Rhodobacter sphaeroides* have identified a number of proteins involved in the oxygen-regulated signal pathway, in which the RegB/RegA two component system plays a central role. While the RegB/RegA system activates photosynthesis genes under low oxygen tension other proteins like CrtJ and PPBP have a repressing function under high oxygen tension. Additional DNA binding proteins like the integration host factor can modulate the expression of photosynthesis genes. The role of alternative sigma factors in this signal pathway is still unclear.

Introduction

Facultatively phototrophic bacteria like *Rhodobacter capsulatus* can adapt quickly to changing environmental conditions by using different pathways for energy conversion. If high levels of oxygen are present, *Rhodobacter* gains energy by aerobic respiration and synthesizes only low amounts of photosynthetic complexes. If, however, the oxygen tension drops below a threshold value, the synthesis of pigments and pigment binding proteins is strongly increased and photosynthetic complexes are assembled into a newly formed intracytoplasmic membrane system. This process of bacterial differentiation is independent of light. As long as some oxygen is available the cells still perform aerobic respiration. This allows the investigation of mutant strains unable to perform photosynthesis under conditions inducing the formation of photosynthetic components. Under anaerobic conditions *Rhodobacter* can use light energy for anoxygenic photosynthesis.

The influence of oxygen on the formation of the photosynthetic apparatus in *R. capsulatus* has been known for many years. However, the molecular mechanisms for sensing the oxygen signal, for signal transmission within the cell and for regulation of gene expression could not be studied until genetic tools became available for this organism and the genes encoding the components of the photosynthetic apparatus were identified and sequenced. The genes for the pigment binding proteins of the reaction center and the light harvesting I complex are organized in the polycistronic *puf* operon which is part of a 44 kb photosynthesis gene cluster that also harbours genes for the non pigment binding protein of the reaction center, for pigment synthesis and for regulatory proteins. The *puc* operon which is localized elsewhere on the chromosome encodes the proteins of the light harvesting II complex. Over the last years many factors involved in the oxygen-regulated expression of photosynthesis genes in *Rhodobacter* have been identified and characterized (Bauer, 1995; Gregor and Klug, 1999).

The RegB/RegA Two Component System

A central regulator in the oxygen-dependent signal transduction in *R. capsulatus* is the RegB/RegA two component system. RegB is a membrane bound histidine kinase which can transfer a phosphatidyl residue *in vitro* to the response regulator RegA in a redox-dependent manner (Mosley *et al.*, 1994; Inoue *et al.*, 1995). It is, however, not clear what signal is sensed by RegB *in vivo* and which domains of RegB contribute to signal sensing. For PrrB, the homologue of RegB in *R. sphaeroides*, evidence was provided that it receives a signal from PrrC which depends on the electron flow through the *cbb3* cytochrome c oxidase (Oh and Kaplan, 2000).

In order to define the RegB domains which are involved in redox sensing, it is important to know the topology of this membrane protein. Mosley *et al.* (1994) suggested a model with five membrane spanning regions of RegB on the basis of computer prediction, with the N-terminus extending into the periplasm. More recent analysis of the *regB* sequence revealed that a C nucleotide was missing in the original sequence. Correction of the sequence resulted in an extension of the deduced amino acid sequence at the N-terminus and added an extra membrane spanning domain (Chen *et al.*, 2000). A model with six trans membrane domains was confirmed for RegB by analyzing RegB-LacZ and RegB-PhoA fusion proteins (Chen *et al.*, 2000). This model is in agreement with a topology model published on the basis of similar experiments for PrrB of *R. sphaeroides* (Ouchane and Kaplan, 1999).

When the response regulator RegA was identified (Sganga and Bauer, 1992) it was suggested that it indirectly acts on the transcription of photosynthesis

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genes since the authors did not detect a known DNA binding motif. It was shown later that RegA harbours a helix-turn-helix motif at its C-terminus and that it binds to the *puf* and *puc* promoter regions (Kirndörfer *et al*., 1997; Du *et al*., 1998; Kirndörfer *et al.*, 1998; Hemschemeier *et al*., 1999; Hemschemeier *et al*., 2000a). Although it is now generally accepted that RegA is a DNA binding protein, there is still a controversy about the role of its phosphorylation. Bird *et al*. (1999) observed that phosphorylation enhances binding of RegA to its target DNA. On the other hand it was reported that unphosphorylated RegA and phosphorylated RegA show similar DNA binding affinity *in vitro* (Hemschemeier *et al*., 2000a). There is evidence from several investigations that a conformational change of RegA after phosphorylation leads to activation of photosynthesis genes. Du *et al*. (1998) isolated a constitutively active RegA protein with an amino acid exchange in near proximity to the region linking the N-terminal receiver domain and the C-terminal DNA binding domain. A truncated RegA protein which contains only the C-terminal activation domain still leads to oxygen-regulated activation of *puf* and *puc* transcription, although to a lesser extent than wild type RegA (Hemschemeier *et al.*, 2000b). Mutant RegA protein which can not be phosphorylated due to an exchange of aspartate 63 can still bind to the *puf* and *puc* promoter regions *in vitro* but is unable to activate transcription of these genes *in vivo* (Hemschemeier *et al*., 2000b).

As mentioned above, an *R. capsulatus* mutant strain harbouring the truncated RegA protein consisting of the activaton domain only, still showed oxygen-regulated expression of the *puf* and *puc* genes (Hemschemeier *et al.*, 2000b). This result clearly shows that mechanisms independent of RegA contribute to this oxygen-regulated process. The CrtJ protein (PpsR in *R. sphaeroides*) has been shown to repress *puc* expression at high oxygen tension (Ponnampalam *et al*., 1995) by redox-dependent, co-operative binding to distant sites in the *puc* promoter region (Ponnampalam *et al*., 1997; Elsen *et al*., 1998). Binding of CrtJ to the *puf* promoter was not reported, but a mutant strain lacking this protein shows altered oxygen-regulated *puf* expression (unpublished results). The PPBP (*puf* promoter binding protein) has been shown to bind to the *puf* promoter region and was suggested to repress *puf* expression under high oxygen tension (Klug, 1991). Isolation and sequence analysis of this protein or the identification of the corresponding gene, however, were unsuccessful. Analysis of different mutant strains revealed that PPBP is not identical to RegA or CrtJ (unpublished results). Since the binding sites of CrtJ and PPBP in part overlap the binding sites of RegA, it is conceivable that RegA can only bind to the *puf* and *puc* promoter regions, when CrtJ and PPBP no longer bind to these targets at low oxygen tension. This model is in agreement with the observation of an oxygen-regulated activation of photosynthesis genes by the isolated RegA activator domain which can not be phosphorylated in a redox-dependent manner by RegB.

Mutant strains lacking RegB or RegA show almost no increase of *puc* expression after reduction of oxygen tension, whereas *puf* operon expression shows a significant increase after change of growth conditions (Hemschemeier *et al*., 2000a). Indeed the *puf* operon is part of a large cluster of genes which are partially cotranscribed and have been named “super-operon” (Young *et al*., 1989; Wellington and Beatty, 1991). The *puf* operon is localized within the coding region of the *bchZ* gene. A low level of *puf* transcription occurs from promoters of upstream bacteriochlorophyll and carotenoid genes (Wellington *et al*., 1991). It has been proposed that this type of gene organization guarantees low level of *puf* transcription in *R. capsulatus* at high oxygen tension and allows a faster adaptation to changes in growth conditions.

The fact that RegB mutants still show some oxygen-regulated expression of photosynthesis genes also proves that other components beside the histidine kinase RegB are involved in oxygen or redox sensing. One of these additional sensing molecules is thioredoxin, an ubiquitous protein which undergoes a redox-dependent disulfid / dithiol exchange and affects the function of many cellular proteins. An *R. sphaeroides* strain with altered levels of reduced thioredoxin also shows altered expression of the *puf* and *puc* genes (Pasternak *et al*., 1999). Results from a yeast two hybrid screen suggest the interaction of thioredoxin A from *R. sphaeroides*, thioredoxin A and thioredoxin C from *R. capsulatus* with FnrL and gyrase (Härtig *et al*., 2000). An involvement of gyrase in oxygen-regulated expression of photosynthesis genes has been described before in *R. capsulatus* (Zhu and Hearst, 1988). FnrL was shown to participate in photosynthesis gene regulation in *R. sphaeroides* (Zeilstra-Ryalls and Kaplan, 1995). FnrL mutants of *R. capsulatus* however show similar expression of photosynthesis genes as wild type cells (Zeilstra-Ryalls *et al*., 1997). The exact signaling pathway from thioredoxin to photosynthesis gene expression is currently under investigation.

It is now well established that the RegB/RegA two component system does not only control the expression of photosynthesis genes but is also involved in oxygen-regulated expression of genes for nitrogen fixation, carbon dioxide assimilation and hydrogenase synthesis (Joshi and Tabita, 1996; Elsen *et al*., 2000). The constitutively active RegA protein RegA* has been shown to bind to the promoters of the *cbbI* and *cbbII* operons encoding components for the Calvin cycle (Dubbs *et al*., 2000; Vivhivanives *et al*., 2000), to the promoter of the *nifA2* gene encoding a *nif*-specific transcriptional activator, and to the promoter of the hydrogenase gene operon (Elsen *et al*., 2000).

Since binding of wild type RegA protein to DNA *in vitro* is weak it was postulated that additional factors are involved in facilitating DNA binding and activation of transcription by RegA. Results from a yeast two hybrid screen for proteins interacting with RegA suggest an interaction of RegA with proteins involved

in nitrogen fixation and an enzyme of the bacteriochlorophyll biosynthesis pathway (unpublished). It has been known for many years that mutants with defects in bacteriochlorophyll synthesis are affected in oxygen-regulated transcription of *puf* and *puc* operon (i.e. Klug *et al.*, 1986; Rödig *et al.*, 1999). Interaction of RegA with enzymes of the bacteriochlorophyll synthesis is an attractive model to explain this coregulation which needs further studies for confirmation.

Involvement of Integration Host Factor (IHF) in the Expression of Photosynthesis Genes

It has been shown for many bacterial response regulators that other proteins bind in close proximity to their DNA targets (i.e. Zhang and DeMoss, 1996; Charlton *et al.*, 1993). One of these proteins is the integration host factor (IHF) which induces a bending of the DNA after binding (Rice *et al.*, 1996). An *R. capsulatus* strain which carries a mutation in the *himA* gene encoding one of the subunits of IHF shows altered oxygen-regulated expression of some photosynthesis genes. After lowering of oxygen tension *pufQ-lacZ* and *pucB-lacZ* gene fusions show lower expression in the *himA* mutant compared to the wild type. The expression of a *bchD-lacZ* gene fusion, however, is not affected by the mutation (Kirndörfer *et al.*, 1998). When *puf* and *puc* expression was monitored by Northern blot analysis the maximal mRNA levels were similar in mutant and wild type strains. The increase of *puf* and *puc* mRNA levels after a shift of cultures from high to low oxygen tension was clearly delayed in the mutant strain. Purified IHF protein from *R. capsulatus* was shown to bind to the *puf* and *puc* promoter regions close to the RegA binding sites (Kirndörfer *et al.*, 1998). A typical consensus sequence for IHF binding as reported for *E. coli* and also described for the *puc* promoter region of *R. sphaeroides*, however, is not present in this region (Lee *et al.*, 1993).

Are Alternative Sigma Factors Involved in Oxygen-Regulated Expression of Photosynthesis Genes ?

As soon as the DNA sequences for photosynthesis genes in *R. capsulatus* were identified they were analyzed for homology to typical bacterial promoter regions. While some photosynthesis genes are preceeded by promoters showing a typical sigma-70 consensus sequence, other promoters lack such homologies. Thus, the involvement of alternative sigma factors in the transcription of photosynthesis genes had to be considered. The vegetative sigma factor gene of *R. capsulatus rpoD* was not analyzed until 1996 (Pasternak *et al.*). For many years the only alternative sigma factor known in *R. capsulatus* was RpoN (sigma 54) which is required for transcription of certain genes involved in nitrogen fixation (Cannon *et al.*, 1996). More recently the *rpoH* gene of *R. capsulatus* was cloned and characterized (Emetz and Klug, 1998). The amount of the 5′ ends of the *rpoH* transcript increased in *R. capsulatus* after a shift to high temperature but was independent of oxygen tension (Emetz and Klug, 1998).

Decreasing oxygen tension in cultures of *R. capsulatus* leads to increased amounts of a 34 kD protein which cross-reacts with antibodies raised against a bacterial sigma factor (Emetz and Klug, 1998). However, final proof is lacking that this protein is indeed sigma-32 and that the *rpoH* gene product is involved in transcription of photosynthesis genes. Using an *in vitro* transcription system with purified RNA polymerase from *R. capsulatus* it was shown that the *puf* and *puc* promoters can be activated by RegA in the presence of the housekeeping sigma factor (Bowman *et al.*, 1999). These results suggest that no alternative sigma factor may be required for the oxygen-regulated transcription of photosynthesis genes, but no *in vivo* data confirming this assumption are available.

Conclusion

Much effort has been taken over the last years to elucidate the mechanisms of oxygen-regulated gene expression in *Rhodobacter*. One of the remarkable discoveries was the fact that the RegB/RegA two component system is a global regulator for many metabolic pathways which are directly or indirectly affected by oxygen. As for most bacterial two component systems the mechanism of signal sensing is not clear. Evidence was presented that the RegB homologue PrrB in *R. sphaeroides* is indirectly affected by the electron flow through the Cbb3 terminal oxidase (Oh and Kaplan, 2000). Although *R. capsulatus* and *R. sphaeroides* are closely related, they differ significantly in regard to the organization of their electron transport chains. While *R. sphaeroides* contains a branched aerobic electron transport chain that is terminated with two functional cytochrome c oxidases (*cbb3* and *aa3*), *R. capsulatus* does not contain the *aa3* cytochrome c oxidase. Experimental proof for a similar mechanism of redox sensing in *R. capsulatus* is lacking to date.

Although the central role of RegB/RegA in the oxygen-dependent signal pathway has been proven, the exact molecular mechanisms of signaling need further investigation. The role of phosphorylation of RegA is discussed controversially, and the exact mechanism of activation of RNA polymerase by RegA is not known. The domains of RegB and RegA which are involved in signal recognition and signal transmission need to be determined. Despite the central function of RegB/RegA many other factors have been shown to be involved in the redox-dependent signal pathways, and the picture of a complex regulatory network has emerged. The knowledge of the complete genome sequences of *R. capsulatus* and *R. sphaeroides* makes it possible to apply DNA chip technologies and proteomics which may be the tools to better understand this regulatory network and to asign the functions for individual components in the future.

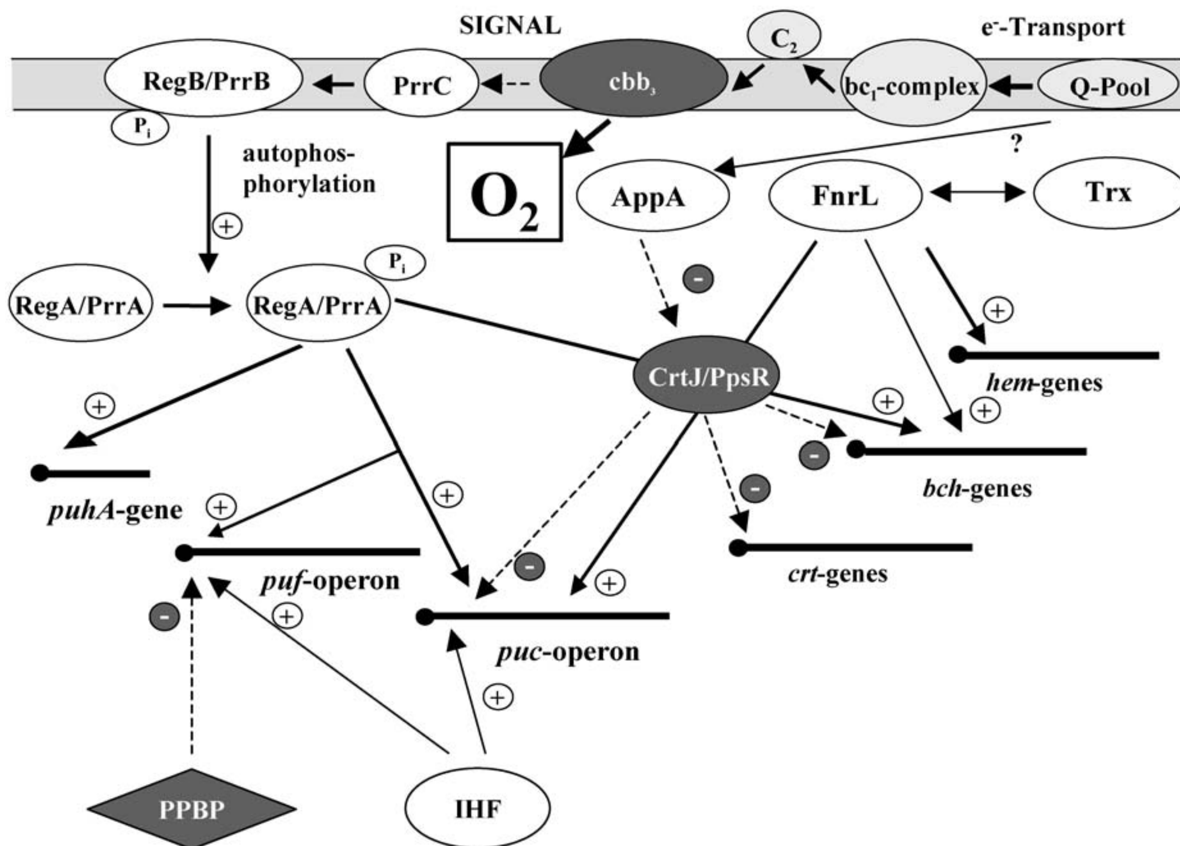

Figure 1. Schematic overview of proteins which are involved in the transcriptional regulation of photosynthesis genes in *Rhodobacter*. Proteins which activate transcription are shown in white, proteins which negatively affect tramscription in black. Proteins which are found only in *Rhodobacter capsulatus* are shown in rectangles, proteins which are known for both organisms, *R. capsulatus* and *R. sphaeroides,* are surrounded with circles. Negative action of proteins on other proteins are indicated by broken arrows, stimulating effects by solid arrows. Thioredoxin (*trxA*) has been shown to affect the *puf*-operon transcription, but the mechanism of signal transmission has not been elucidated so far. Not all proteins which act on transcription of photosynthesis genes are included for reason of clarity; *hem*: genes for heme synthesis; *bch*: genes for bacteriochlorophyll synthesis; *crt*: genes for carotenoid synthesis; *puc*-operon: encodes structural and regulatory proteins for the formation of the LHII antenna complex; *puf*-operon: encodes structural proteins of the LHI antenna complex, the reaction center proteins and proteins involved in the assembly of these complexes; *puhA* gene: encodes the non-pigment-binding subunit of the reaction center.

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