CHAPTER 9

Transcriptional Response to Low O_2 Conditions in *Synechocystis* sp. Strain PCC 6803 Includes Induction of a Gene Cluster Containing *psbA* and *petC2*

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ABSTRACT

Microarray analysis indicated that low O_2 conditions resulted in up-regulation of *psbA1*, the normally low abundance transcript that encodes the D1' protein of photosystem II in *Synechocystis* sp. PCC 6803. Using a *ΔpsbA2*:Δ*psbA3* strain, we show that the *psbA1* transcript is translated and the resultant D1' is inserted into functional PSII complexes. Two other cyanobacterial strains have *psbA* genes that were induced by low O_2. In two of the three strains examined, *psbA* was part of an up-regulated gene cluster including an alternative Rieske iron-sulfur protein. We conclude that this cluster may represent an important adaptation to changing O_2 levels that cyanobacteria experience.

Keywords : Mutagens, Prochlorophytes, Rieske Fe-S protein

INTRODUCTION

It has become clear that the evolution of oxygenic photosynthesis and cyanobacteria took place primarily in an anaerobic environment. The sequencing of genomes of numerous photosynthetic bacteria has led to the proposal that the first phototrophs were procyanobacteria (anoxygenic ancestors of the extant cyanobacteria) (Berman-Frank *et al.* 2003; Mulkidjanian *et al.* 2006). Since these cyanobacterial ancestors were responsible for adding oxygen to the environment, the external environment was still low in oxygen until around 2 billion years ago (Bya). In addition, the level of O_2 in the atmosphere has varied during

this time period to a high of nearly 30%, but often closer to 10%, especially during the past 400 million years (Ward *et al.* 2006). Thus, it would seem likely that cyanobacteria had developed a regulatory system capable of inducing important genes under low oxygen and/or anaerobic conditions. Despite the importance of understanding this situation, very little information is available for the way in which cyanobacteria respond to low oxygen conditions. We have recently presented the first solid evidence in this area and shown that a series of important gene clusters were induced in a series of cyanobacteria, both diazotrophic and nondiazotrophic (Summerfield *et al.* 2008).

Before the development of oxygenic photosynthesis in cyanobacteria, the atmosphere was much more reducing in nature. Indeed, there was a glut of reducing equivalents on Earth's surface (Falkowski *et al.* 2006). During this period, electrons were made available from copious quantities of donors such as H_2, H_2S and CH_4. The electrons could be donated easily, because of a relatively small energy differential, to acceptors such as CO_2 and, to a lesser extent, SO_4. Since a relatively high amount of energy was needed to oxidize water, the biggest electron donor pool, H_2O, remained inaccessible until the advent of oxygenic photosynthesis. Although the exact date for the development of oxygenic photosynthesis and the cyanobacteria is somewhat elusive, the dates from different types of evidence are reaching some congruence. It is very likely that the evolution of cyanobacteria occurred prior to 2.4 Bya because their metabolism is required, at least in part, to explain the appearance and the rise of environmental oxygen at that time. The most recent evidence indicates the period for the rise of atmospheric O_2 to be between approximately 2.4 and 2.3 Bya and that this was followed by the onset of an extreme ice age (Rasmussen *et al.* 2008; Fisher *et al.* 2008). Indeed, others have argued the case for a late origin of photosystem II (PSII) evolution and suggested that oxygenic photosynthesis could have evolved close in geological time to the Makganyene Snowball Earth Event and suggest a causal link between these two important events (Kirschvink *et al.* 2008). Based on this analysis, higher levels of oxygen began to pollute the atmosphere approximately 2.2 Bya. Although our work does not directly impinge on such dates, we are comfortable with the situation in which atmospheric O_2 increased rather substantially soon after the development of water splitting function.

We have recently studied the impact of low-O_2 growth on global transcription in the unicellular, nondiazotrophic cyanobacterium *Synechocystis* sp. PCC 6803 (hereafter *Synechocystis*) (Summerfield *et al.* 2008). We used our *Synechocystis* microarray system to compare gene expression between aerobically grown and these low-O_2 incubated cells. These experiments led to some surprising findings, not the least of which was the induction of *psbA1*, the third copy of the gene encoding the main Photosystem II reaction center protein. In addition, an alternative Rieske iron-sulfur protein (*petC2*) was located in the same gene cluster, suggesting that changes in the cytochrome b6f complex might also occur during low-O_2 growth. We will discuss the implications of these results and reflect on the reasons why the cell might need to make changes in key proteins within these photosynthetic complexes.

RESULTS AND DISCUSSION

Low-Oxygen Induction of Cryptic psbA Genes in Cyanobacteria

Cultures were grown in a 6 L bioreactor illuminated with 100 μmoles photons/m^2/s and bubbled with air for 3 days (Summerfield *et al.* 2008;.Toepel *et al.* 2008). RNA was harvested from cells grown aerobically (t=0), and after that the cells were bubbled with 99.9% N_2 and 0.1% CO_2 to produce low O_2 conditions for 1, 2 and 6 h. Microarrays were used to compare gene expression between aerobically grown and low O_2 bubbled cells. A major surprise from the microarray data was that a cluster of genes (slr1181-slr1185) containing *psbA1* and *petC2* (genes encoding alternative isoforms of the Photosystem II protein,

D1, and the Cytochrome b6f Rieske iron-sulfur center protein, PetC, respectively) was up-regulated during growth under low O_2. For verification of these results, we used semiquantitative RT-PCR as shown in Fig. 9.1E. The *Synechocystis psbA2* and *psbA3* genes encode the same D1 protein with *psbA2* transcribed at high levels constitutively and *psbA3* being stress induced. Due to the similarity of their nucleotide sequences, the *psbA2* and *psbA3* transcripts could not be distinguished in this experiment. The *psbA2*/*psbA3* transcripts were present at high levels under aerobic and low O_2 conditions, whereas the *psbA1* transcript was not detected under aerobic conditions, but was strongly induced by 6 h under low O_2 (Fig. 9.1E).

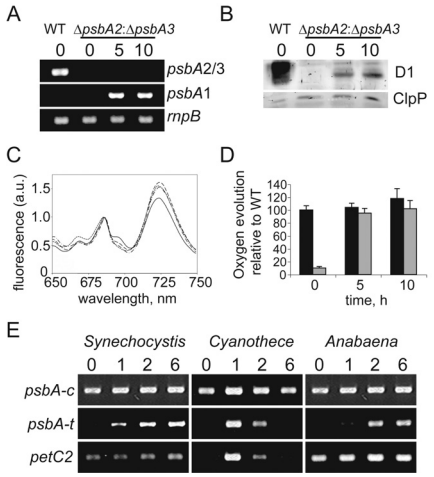

Fig. 9.1 Increased abundance of *psbA* transcript and D1 protein under low O_2 conditions. (A)-(D) *Synechocystis* sp. PCC 6803 wild type and a Δ*psbA2*:Δ*psbA3* mutant. (A) Semi-quantitative RT-PCR using primers to *psbA2/A3*, *psbA1* and *rnpB*; (B) Western blot using antibody to D1 and ClpP. (A), (B) The number above each lane represents time, h under low O_2 conditions. (C) 77K fluorescence after excitation at 435 nm WT cells grown in air (____) and the Δ*psbA2*:Δ*psbA3* mutant after growth in air (.....), and after low O_2 induction for 5h (_._._) and 10 h (- - - -). (D) O_2 evolution for wild-type cells (black bars) and the Δ*psbA2*:Δ*psbA3* mutant (grey bars) under aerobic (0 h) and low O_2 conditions (5, 10 h). Oxygen evolution was normalized to wild type at 0 h (423 µmol O2 evolved/mg Chl/h). (E) The transcript levels of *psbA* and *petC2* were shown by semi-quantitative RTPCR for cells grown in air (0 h) and then bubbled with 99.9% N_2 plus 0.1% CO_2 for 1, 2 and 6 h. *psbA*-c represents the consitutively expressed gene for each strain: *Synechocystis* (*psbA2*, *psbA3*); *Cyanothece* (*psbA1*, *psbA5*) and *Anabaena* (*psbA1*). *psbA*-t represents the low O_2 induced genes: *Synechocystis* (*psbA1*), *Cyanothece* (*psbA2*) and *Anabaena* (*psbA0*). *petC* gene in *Anabaena* (*all4511*) (as first described in 4).

We were most interested to determine whether or not these *psbA1* transcripts were translated into protein, and if the protein could be inserted into productive PSII complexes. Since *psbA2/3* transcripts are very abundant in *Synechocystis* wild type, we used the double knockout mutant Δ*psbA2:*Δ*psbA3*. This strain cannot normally grow under photoautotrophic conditions, and any D1 protein or PSII activity would have to come from PSII complexes produced after transition to low O_2 conditions i.e., after insertion of the *psbA1* gene product D1′. As expected, semiquantitative RT-PCR showed that the wild type transcribed *psbA2/3* under aerobic conditions, whereas no *psbA2/3* transcripts were detected in the Δ*psbA2:*Δ*psbA3* strain (Fig. 9.1A). Western blot analysis demonstrated clearly that there was no D1 protein in the double mutant under aerobic conditions, but significant D1′ protein was detected by 5 h (Fig. 9.1B). The 77K fluorescence spectra of the mutant strain indicated that intact complexes were present under low-O_2 conditions (Fig. 9.1C). In particular, the 695 nm peak, corresponding to excitation

of Chl a associated with CP47 and indicative of assembled PSII centers, was at a significant level by 10 h under low-O_2 conditions. All this was accompanied by dramatic increase in PSII O_2 evolving activity by 5 and 10 h after growth under low-O_2 conditions (Fig. 9.1D). We conclude from these experiments that the *psbA1* gene was transcribed and translated under low-O_2 conditions and that D1′ was inserted to produce functional PSII complexes.

We next determined if similar low-O_2 induction occurred in other cyanobacterial strains, including those capable of N_2 fixation. Therefore, we examined the unicellular, N_2-fixing strain *Cyanothece* sp. ATCC 51142 (hereafter *Cyanothece*), a filamentous heterocystous strain *Anabaena* sp. PCC 7120 (hereafter *Anabaena*) and the ancient and divergent strain *Gloeobacter violaceus* sp. PCC 7421 (hereafter *Gloeobacter*). The semiquantitative RT-PCR results for *Cyanothece*, *Anabaena* and *Synechocystis psbA* genes are compared in Fig. 9.1E. For the sake of simplicity, we call the normal constitutive and highly expressed genes *psbA-c* and the genes normally transcribed in only trace amounts under aerobic conditions *psbA-t* (trace). Both *Cyanothece* and *Anabaena* strains showed an increase in *psbA-t* transcript level under low-O_2 growth, but with differing kinetics (Fig. 9.1E). *Cyanothece* demonstrated a rapid induction that peaked around 1 h and then subsequently declined. *Anabaena* kinetics resembled those of *Synechocystis* and increased around 2 h and stayed high through 6 h. *Cyanothece* resembles *Synechocystis* in that both have a *psbA* gene that is clustered near *petC2*. In *Cyanothece*, the levels of both transcripts were strongly increased by 1 h under low-O_2 conditions followed by an fairly rapid decline. In *Anabaena*, there was no *petC* gene close to *psbA-t* and none of the 4 *petC* genes showed induction similar to that of *Synechocystis* or *Cyanothece* (Summerfield *et al.* 2008). However, the *Anabaena petC2* gene *all4511* (transcribed under aerobic conditions) did show increased transcript levels under low-O_2 conditions (Fig. 9.1E). In low-O_2 incubated *Gloeobacter*, there was no specific gene induction of any of the 5 copies of *psbA*, (including the 2 genes expressed at trace levels under normal aerobic conditions) or the single copy of *petC* (Summerfield *et al.* 2008). The upregulation of a *psbA* gene normally transcribed at low levels has recently been reported for *Thermosynechococcus elongatus* BP-1 (hereafter *Thermosynechococcus*) under similar low oxygen conditions (Sicora *et al.* 2009).

D1 Structure

What would be the purpose of an alternative D1 in PS II under low-O2 conditions? The potential involvement of this D1′ has been studied extensively for over a decade, but with no satisfactory answer (Sicora *et al.* 2004; Sicora *et al.* 2006; Kos *et al.* 2008; Sicora *et al.* 2008). When *psbA1* was expressed under the control of the *psbA2* promoter in cells lacking *psbA2* and *psbA3*, the modified strain could grow photoautotrophically (Salih *et al.* 1997). In addition, D1′ centers were found to be functional but less efficient than normal PSII centers (Funk *et al.* 2001). A number of hypotheses that might explain the need for D1′ were proposed, but could not be verified experimentally. We suggest that one reason for the change can be found in the structure shown in Fig. 9.2. This model represents two of the D1 helices (C and CD) and depicts three amino acids that are changed in *Synechocystis* D1′. As indicated in Fig. 9.2, F 158 L (on helix C) and T 268 A (on helix E, the rest of helix is omitted for clarity) are altered in all of the low-O_2 inducible *psbA* genes identified to date (as was G 80 A which is located on the lumen loop between helices A and B and is not shown in Fig. 9.2); in addition, residue F 186 L (on helix CD) is altered in *Synechocystis*. In a thorough review of the crystal structure of cyanobacterial PSII that included a close look at the antenna system, (Muh *et al.* 2008) discussed the relevant interactions of the chlorin molecules with amino acid side chains as portrayed by the 3.0 Å structure. F 158 is an aromatic residue and T 286 is a polar, non-aromatic residue, both of which are within 6.0 Å of the π-system. Thus, it is possible that changes in these amino acids slightly alter the binding of the chlorophylls to D1. Whether

or not that is an important aspect for the construction or function of new PSII centers under low-O_2 conditions is something that must await future research. It should be noted that after the induction of *psbA1*, these transcripts represent about 15% of the total *psbA* transcripts that were made during the 6 h of low-O_2 growth for *Synechocystis*. Thus, this fraction is not large in total, but may represent a larger proportion of those transcripts translated into D1 protein and inserted into the complex.

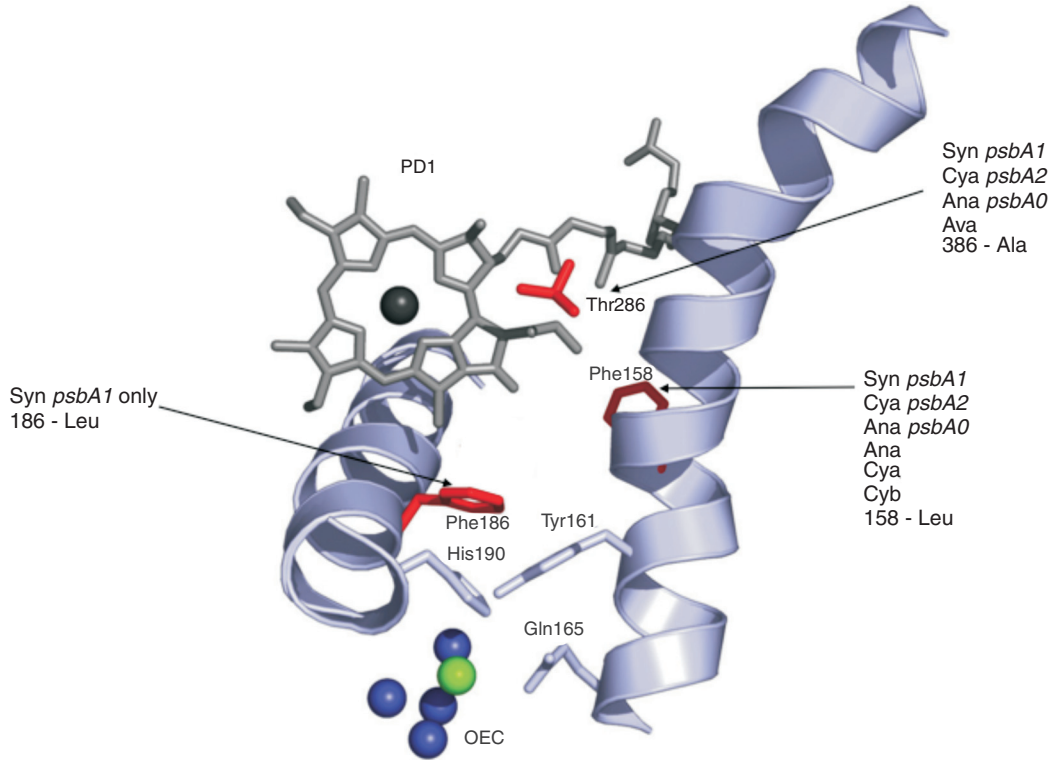

Fig. 9.2 Crystal structure D1 helices C and CD and Thr 286 of helix E. Residues highlighted in red are altered in the low oxygen-induced D1′ proteins of *Synechocystis*, *Cyanothece*, *Anabaena* and *Thermosynechococcus*.

Alternative Rieske Fe-S Protein of Cytochrome b6f Complex

The Rieske Fe-S protein is involved in quinol binding and electron transfer, making it an essential component of the cytochrome b6f complex. *Synechocystis*, *Cyanothece* and *Anabaena* have multiple copies of the *petC* gene that encode alternative copies of this Rieske Fe-S protein of the cytochrome b6f complex (Table 9.1). PetC1 is the major Rieske protein in *Synechocystis*. However, in *Synechocystis, Cyanothece* and *Anabaena,* the *petC2* gene is up regulated under low oxygen conditions. Overlapping functions of PetC1 and PetC2 in *Synechocystis* were demonstrated by photoautotrophic growth of *ΔpetC1* and *ΔpetC2* strains, but not the strain lacking both *petC1* and *petC2* (Schneider *et al.* 2004). However, aerobic growth of the *ΔpetC1* strain was retarded compared with wild type and the *ΔpetC2* strain, indicating that PetC2 did not fully replace PetC1 under these conditions. PetC2 has the conserved cysteines and histidines of a Rieske protein and a high midpoint potential similar to PetC1, but amino acid differences at the "hinge region" may affect quinol oxidation (Fig. 9.3). For example, changes in the hinge region may account for slowing of electrons through cytochrome b6f complex in the absence

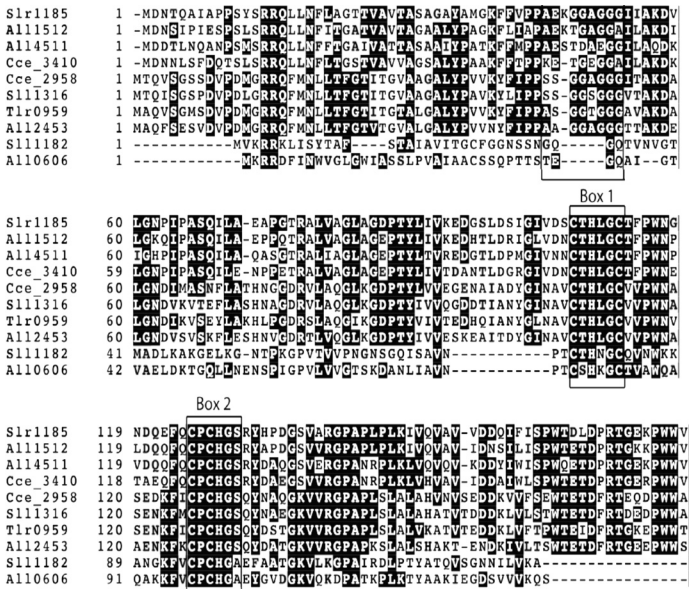

Fig. 9.3 Alignment of PetC proteins of *Synechocystis*, *Cyanothece*, *Anabaena* and *Thermosynechococcus*. PetC1 proteins are sll1316, cce_2958, all2453, and tlr0959, PetC2 proteins are slr1185, cce_3410, all1512, and all4511. PetC3 proteins are sll1182, all0606.

of PetC1 under aerobic conditions (Schneider *et al.* 2004). In contrast, PetC3 has conserved cysteines and histidines of a Rieske protein, but exhibits amino acid variation in these regions (Box 1 and Box 2 in Fig. 9.3) and has shortened N and C termini. The lower midpoint potential of PetC3 makes its function unclear; however, PetC3 is associated with the cytochrome b6f complex and the Δ*petC1: ΔpetC3* strain had a more severe phenotype than the Δ*petC1* strain. These data have been interpreted to mean that during aerobic growth there is a heterologous population of cytochrome b6f complexes. Under low oxygen conditions, we suggest that this population includes more PetC2-containing complexes as the *petC2* gene is upregulated but the *petC3* gene is not. The PetC2 containing cytochrome b6f complexes may play a specific role under these conditions. The up-regulated *petC2* genes of *Synechocystis*, *Cyanothece* and *Anabaena* encode PetC2 proteins that have similar protein sequences (as determined by per cent identity). The exception is *Thermosynechococcus* that has only one copy of *petC*. In *Synechocystis* and *Cyanothece,* but not *Anabaena,* the induced *petC* copy is located in a cluster with the low oxygen induced *psbA* gene (Fig. 9.3 a-c).

Coordinately Regulated Gene Clusters

A clue to this low-O_2 induction of *psbA* and *petC* genes may be found in the genome organization of these clusters (Fig. 9.4). Figures 9.4a and b highlight the clusters in *Synechocystis* and *Cyanothece* that we have studied by microarray and RT-PCR analysis. It is evident that both clusters contain a series of genes that are annotated as hypothetical or unknown and the entire cluster is up-regulated under low-O_2 conditions. Figure 9.4C represents the two gene clusters on separate parts of the *Anabaena* genome with the inducible *psbA* gene (alr3742) and *petC2* (all4511). In addition, we provide similar information for *Thermosynechococcus* in Fig. 9.4d. Note that *Cyanothece* and *Anabaena* have an *sqr* gene located close to a low oxygen induced *petC2* gene. *Synechocystis* and *Thermosynechococcus* also contain *sqr*

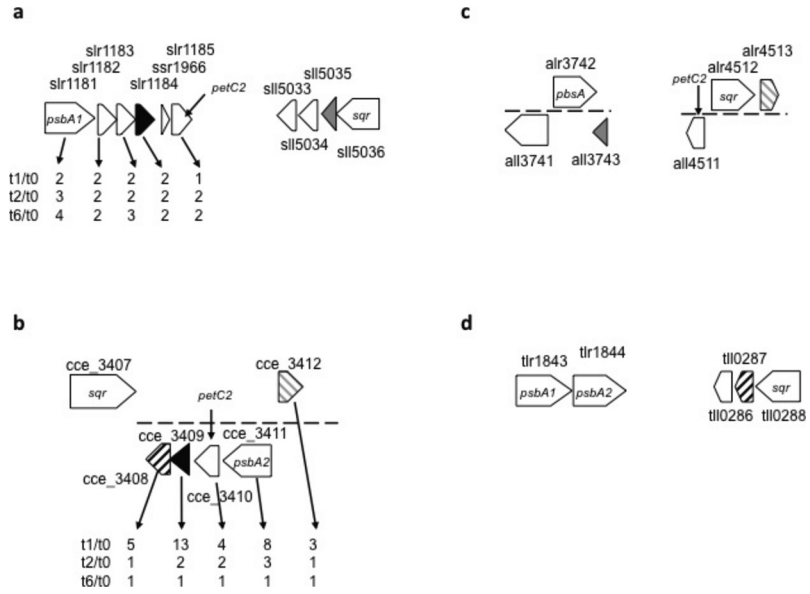

Fig. 9.4 Gene clusters co-ordinately regulated under low oxygen conditions containing the *psbA* gene that encodes the alternative D1′ polypeptide: (a) *Synechocystis* sp. PCC 6803 and (b) *Cyanothece* sp. ATCC 51142. Numbers represent fold change of transcript abundance on transition from aerobic to low oxygen conditions. Genes neighboring low oxygen induced *psbA* genes and *petC* gene in (c) *Anabaena* sp. PCC 7120 and (d) *Thermosynechococcus elongatus* BP-1. Genes with sequence similarity in two or more strains have the same shading. Both slr1184 and cce_3409 (shaded black) encode proteins containing rhodanese-like domains. The predicted proteins encoded by cce_3412 and alr4513 share 60% identity. The sulfide quinine reductase (*sqr*) proteins of *Cyanothece* sp. ATCC 51142 and *Anabaena* sp. PCC 7120 share 61% identity. There is only one copy of *petC* in *Thermosynechococcus elongatus* BP-1 (not shown).

genes. In *Synechocystis*, the *sqr* gene is located on its largest plasmid, pSYSM. Neighbouring the *sqr* genes of *Synechocystis*, *Cyanothece* and *Thermosynechococcus* are hypothetical genes that share more than 50% identity. Similarity between other genes in these clusters is shown by the use of shading in Fig. 9.4. Could the fact that all these strains contain *sqr* genes be significant? It should be noted that the up-regulation of *psbA* under low-O_2 conditions may help maintain internal aerobic cellular environment: the importance of this aspect will vary between strains as cyanobacteria differ in their sensitivity to O_2 levels. Furthermore, low-O_2 conditions are often associated with an increased level of H_2S that can damage PSII. Importantly, O_2 can inactivate H_2S. Increasing D1′ levels could accelerate the replacement of damaged D1, both increasing the rate of oxygenic photosynthesis, but also limiting further damage to PSII. The SQR protein, encoded by *sqr*, transfers electrons from H_2S to the quinone pool and is present in many anoxygenic phototrophs, as well as *Aphanothece halophytica*, where it may have a role in detoxification of sulfide. Alternatively, low-O_2 conditions on earth, when oxygenic photosynthesis arose, raises the possibility that these low-O_2 induced *psbA* genes, as well as PetC and SQR, represent ancient genes that were important metabolically prior to the huge increase of O_2 in the atmosphere approximately, 2.5 bya.

Cyanobacteria: *psbA* and *petC* Gene Families

What are the implications of these findings in cyanobacterial physiology? Many cyanobacteria contain *psbA* gene families (Table 9.1). These frequently encode two D1 isoforms, D1:1 and D1:2, with the D1:2

isoform being more abundant under stress conditions such as high light. This is not always the case; in *Synechocystis,* there is no D1:2 isoform and stress conditions increase the transcription of *psbA3* (which encodes the same D1:1 as the constitutively expressed *psbA2*). In all four strains with low O_2 induced *psbA* genes, these encoded a distinct D1 isoform, called D1′, and phylogenetic analyses indicated that these genes were divergent from the other copies of *psbA* within three of the four strains. In addition, all four of these low O_2 induced *psbA* genes were expressed at only trace amounts under normal growth conditions. Do many cyanobacteria have low O_2 induced *psbA* genes? Table 9.1 presents an analysis of most of the cyanobacteria for which complete genome sequences are now available. This indicates that all strains, except *Prochlorococcus* strains, *Microcystis aeruginosa* NIES-843, and *Trichodesmium erythraeum* IMS101 contain multiple *psbA* genes that encode for two or more versions of D1. *Microcystis aeruginosa* NIES-843, *Trichodesmium erythraeum* IMS101a and several *Prochlorococcus* strains have multiple copies of *psbA,* but these encode the same D1 isoform. In these *Prochlorococcus* strains, multiple *psbA* genes are predicted to have arisen from recent gene duplications, and these are found in both high (e.g., *Prochlorococcus marinus* str. MIT 9312) and low light ecotypes (e.g., *Prochlorococcus* marinus str. MIT 9313) (Kettler *et al.* 2007). The marine *Synechococcus* strains contained 3 or 4 copies of *psbA* that encode two D1 isoforms for each strain. Overall these data are consistent with the reduced genome sizes observed in the marine cyanobacteria with *Prochlorococcus* strains containing fewer *psbA* genes than *Synechococcus* strains (Table 9.1). The nitrogen-fixing strains *Nostoc punctiforme* and *Anabaena variabilis* ATCC 29413 contain multiple copies of *psbA* encoding 3 and 4 D1 isoforms, respectively. There is no data to indicate whether increased transcription of any of these genes forms part of the response to low oxygen conditions. Based on the presence of the three conserved amino acid substitutions, we could predict the *Anabaena variabilis* ATCC 29413 gene Ava_1583, but not the *Nostoc punctiforme psbA* genes, to be up-regulated under low oxygen conditions. The extent of low O_2 induction of *psbA* genes in cyanobacteria remains to be determined and these data would provide insight into the role of these alternative D1 proteins.

There are fewer *petC* genes than *psbA* genes in each strain with the majority of strains having only one *petC* gene. In fact only 8 of the 35 strains had more than one *petC* copy. However, having only one *petC* copy does not rule out having a low oxygen induced *psbA* gene as has already been reported in the case of *Thermosynechococcus* (Sicora *et al.* 2009).

We conclusion, have identified a strategy used by many freshwater, as well as marine diazotrophic, cyanobacteria to respond to low ambient O_2 levels. The key feature to this response is the induction of a *psbA* gene that is normally transcribed at very low levels. This *psbA* gene is transcribed and a modified D1 protein, called D1′ in *Synechocystis,* is translated and inserted into functional PSII complexes. This response is often paralleled by the induction of a gene encoding an alternative Rieske iron-sulfur protein that also can be functionally inserted into complexes. Although the exact reason for these changes will require additional studies, it is clear that low-oxygen represents an important condition for many cyanobacteria. Ultimately, the main question is whether or not these environmental responses help the organism to grow under these low-oxygen conditions. In the case of *Synechocystis*, the cells do continue to grow and divide for about 18 h. We have also identified a mutant that grows even better under these conditions. The main gene clusters that are upregulated under these low-oxygen conditions included sll0789 and sll0790, a response regulator and histidine kinase, *hik31*, respectively. Experiments using an insertion mutant in *hik31* suggests that Hik31 is involved in regulation under low oxygen conditions. This gene and its involvement in regulation under low-O_2 conditions is currently being studied in our lab. Without question, this response is of sufficient evolutionary significance that it elicits a series of structural and regulatory changes that we are just beginning to identify and understand.

Table 9.1 Number of *psbA* genes, D1 isoforms and *petC* genes identified in different cyanobacteria

Cyanobacterial strain	*psbA genes*	*D1 isoforms*	*petC genes*	*genome size (Mb)*
Acaryochloris marina MBIC11017	3	2	2	8.36
Anabaena sp. PCC 7120	5	3	4	7.21
Anabaena variabilis ATCC 29413	6	4	3[c]	7.07
Arthrospira maxima CS-328[a]	2	2	1	~6.00
Crocosphaera watsonii WH8501[a]	2	2	1	4.92
Cyanothece sp. ATCC 51142	5	4	2	5.46
Gloeobacter violaceus PCC 7421	5	3	1	4.66
Microcystis aeruginosa NIES-843	5	1	2	5.84
Nostoc punctiforme ATCC 29133	5	3	3[c]	9.01
Prochlorococcus marinus MED4	1	1	1	1.66
Prochlorococcus marinus MIT9313	2	1	1	2.41
Prochlorococcus marinus SS120	1	1	1	1.75
Prochlorococcus marinus str. AS9601	2[b]	1	1	1.67
Prochlorococcus marinus str. MIT 9211	1	1	1	1.69
Prochlorococcus marinus str. MIT 9215	1	1	1	1.74
Prochlorococcus marinus str. MIT 9301	1	1	1	1.64
Prochlorococcus marinus str. MIT 9303	2[b]	1	1	2.68
Prochlorococcus marinus str. MIT 9312	2	1	1[d]	1.71
Prochlorococcus marinus str. MIT 9515	2[b]	1	1	1.70
Prochlorococcus marinus str. NATL1A	3	1	1	1.86
Prochlorococcus marinus str. NATL2A	3	1	1	1.84
Synechococcus elongatus PCC 6301	3	2	1	2.75
Synechococcus elongatus PCC 7942	3	2	1	2.74
Synechococcus sp. CC9311	4	2	1	2.61
Synechococcus sp. CC9902	4	2	1[d]	2.23
Synechococcus sp. JA-2-3B'a (2-13)	3	2	1	3.05
Synechococcus sp. JA-3-3Ab	4	2	1	2.93
Synechococcus sp. PCC 7002	3	2	3	3.41
Synechococcus sp. RCC307	4	2	1	2.22
Synechococcus sp. CC9605	3	2	1[d]	2.51
Synechococcus sp. WH7803	4	2	1	2.37
Synechococcus sp. WH8102	4	2	1	2.43
Synechococcus sp. PCC6803	3	2	3	3.96
Thermosynechococcus elongatus BP-1	3	3	1	2.59
Trichodesmium erythraeum IMS101[a]	3	1	1	7.75

TABLE LEGEND:

(*a*) draft assembly

(*b*) One *psbA* gene is labeled hypothetical.

(*c*) Identified as *petC* based on similarity to *petC* from *Anabaena*.

(*d*) Identified as *petC* based on similarity to *petC* from *Synechococcus* sp. WH 8102.

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ABBREVIATIONS

Chl a	Chlorophyll a	PSII	Photosystem II

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