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### Functional flexibility of photosystem I in cyanobacteria

Yeremenko, N.

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## Chapter 9

### Summary and Discussion

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## ***Synechocystis* sp. PCC 6803: a model organism in photosynthesis**

In the last 15 years, the cyanobacterium *Synechocystis* sp. PCC 6803 has developed into a favorite organism for scientists around the world. The strain was isolated from a freshwater lake, and was deposited in the Pasteur Culture Collection (PCC; Paris, France) in 1968 (Stanier *et al.*, 1971). Due to the work of Prof. Sergey Shestakov and coworkers in Moscow and Dr. John Williams (Michigan State University and Du Pont) in the early 1980s the strain was recognized to be spontaneously transformable (Grigorieva and Shestakov, 1982). This organism is capable to integrate foreign DNA into its genome by homologous recombination (allowing targeted gene replacement), which makes it suitable for many genetic manipulations. Furthermore, it is able to survive and grow under a wide range of conditions. This cyanobacterium has served as a model system in elucidating functional relationships for the Photosystem I (PSI) complex of oxygenic photosynthesis, which is structurally equivalent to the PSI core complex of higher plants. The greater stability of trimeric PSI complexes, genomic sequencing and the PSI X-ray structure provide other compelling reasons for using this cyanobacterial strain as model system for studies on PSI.

### **Cyclic electron flow**

Our primary aim was to investigate routes of PSI driven cyclic electron flow, one of the last unresolved phenomena in oxygenic photosynthesis. During oxygenic photosynthesis, photosystem II and I cooperate to achieve a linear electron flow from H<sub>2</sub>O to NADP<sup>+</sup> and, by that generate a trans-membrane proton gradient driving ATP synthesis. However, ATP can also be produced solely by PSI through cyclic electron transfer reactions. This mechanism enables the generation of a proton gradient across the thylakoid membrane without NADP<sup>+</sup> reduction by rerouting electrons of reduced PSI acceptors back toward the intersystem carriers. Cyclic and linear electron transfer share a common sequence of electron carriers, namely the plastoquinone (PQ) pool, cytochrome *b<sub>6</sub>f* complex, and plastocyanin. Hence, by adjusting the relative contribution of linear electron flow versus cyclic electron flow, photosynthetic organisms can tune energy generation (by ATP synthesis) and reducing power (by NADP<sup>+</sup> reduction) to their needs. Acceleration of PSI cyclic electron transfer has been observed previously in cyanobacteria exposed to salt stress (Jeanjean *et al.*, 1993; van Thor *et al.*, 2000). At that time, DNA array analysis attracted the attention of many scientists, as a powerful method to monitor expression of a whole genome. This approach could be applied only to organisms with a fully sequenced genome. *Synechocystis* sp. PCC 6803 was the first photosynthetic organism for which the entire genome sequence was determined. In 1996, Dr. Satoshi Tabata and coworkers at the Kazusa DNA Research Institute finished the

genomic sequence of this organism and made the information available in very useful format on a website named CyanoBase. Despite of a relatively small genome size (*Synechocystis* was predicted to have 3 264 open reading frames [ORFs]), more than 50% of all ORFs of *Synechocystis* have been characterized as hypothetical or having no similarity to known sequences. Thus, investigation of differential gene expression via microarray analysis may represent an important functional genomics approach. Nevertheless, at the time when the study described in this thesis started (2000) commercially available DNA microarrays for *Synechocystis* did not exist. A DNA array library of M13 clones directly acquired from a sequencing project and covering all *Synechocystis* genes (kindly provided by Dr. Tabata, Kasuza Laboratories Japan) was chosen to start whole transcriptome analyses of cells exposed to salt stress (0.5 M NaCl). We optimized methods that highly reduce experimental background in hybridisation by purification of the cDNA probe through removal of cDNA generated from rRNA (*chapter 2, this thesis*). A special approach for statistical data evaluation, which allows confident prediction of differentially expressed genes from sets of data with a small number of replicates, was established. The results obtained suggest that DNA arrays acquired from genome-sequencing projects may be successfully applied for initial determination of gene expression patterns, though we encountered a substantial problem in retrieval of information on individual genes from spots with altered signals.

To assess whether the observed gene responses were unique to NaCl stress or whether these were rather general stress responses, we also applied other types of stresses like nitrogen and phosphorus starvation. After overlay of data we found up-regulation to be very common between all stresses applied. Nevertheless, responses unique to NaCl stress were obtained as well (*chapter 3, this thesis*). Regulation was characterized as an inventory of the metabolic category to which the regulated genes belong. Most prominent in salt stress were regulated genes that belonged to the category 'photosynthesis and respiration' and 'regulatory functions'. A pattern of genes with induced level of expression during adaptation to salt stress was obtained and candidates for mutagenesis were chosen for investigation of PSI functioning. A particular up-regulated clone containing two genes for hypothetical proteins drew our interest. One of them, *slr1208*, was suggested from sequence homology analysis to be an oxido-reductase with a function in 'photosynthetic organisms' (Raymond *et al.*, 2002). The other one, *ssr2016*, was homologous to an ORF for a hypothetical protein in *Arabidopsis* that was recently annotated as involved in photosynthetic proton gradient formation and in loss of sensitivity for the classical PSI cyclic inhibitor antimycin A upon its mutation (Munekage *et al.*, 2002). In order to investigate the potential role of *ssr2016*

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and *slr1208* in cyclic electron flow in cyanobacteria single and double knockout mutants were created in *Synechocystis*. Double (or even triple) mutants are required because cyclic electron flow generated by PSI generally consists of several electron flow pathways that act in parallel. Accordingly, mutagenesis of only one pathway by a single knockout may not be informative when a remaining pathway takes over the function. The stromal oxidation of NADPH constitutes a large contribution to PSI-dependent cyclic electron transfer in cyanobacteria (this route, also known from chlororespiration is referred to as indirect PSI cyclic flow). Therefore disrupted *ssr2016* and *slr1208* genes were also transformed into the NDH-1 deficient M55 mutant (Ogawa, 1991). The phenotypes of mutants obtained in this work and the previously described mutants M55 (*ndhB* knockout), SM8 (truncated FNR) (van Thor *et al.*, 2000), and M55-SM8 were studied for PSI cyclic capacity in the normal and high salt conditions in presence of selected inhibitors. Analysis was performed by pulse amplitude modulation (PAM) reflectance spectroscopy to estimate  $P700^+$ , by the photoacoustic energy storage technique (PAS), and by measurement of light-induced pH changes with fluorescent acridine dye (*chapter 4, this thesis*). The kinetics of  $P700^+$  reduction of all mutants was significantly slower than in the wild type. Results in PAS largely confirmed the PAM, in those cases that higher energy storage was observed, while anaerobiosis abolished it. The relation of the state of reduction of the ferredoxin pool and the interfering Mehler reaction rendered ideas about the possible function of *slr1208*. The phenotype of the *ssr2016* mutant was confirmed, knockout of this hypothetical gene product rendered insensitivity for antimycin A. By overall interpretation of the experimental data, a potential role for *slr1208* in ferredoxin oxidation has been put forward as a working hypothesis for future research. The latter includes the question whether the product of *slr1208* functionally interacts with the product of *ssr2016*. A potential scheme of electron transfer pathways and functional accommodation of those inside the cyanobacterial cell was deduced from the results.

### **Iron limitation or oxidative stress**

Another mutant of *Synechocystis*, which attracted our attention through its altered kinetic performance in PSI cyclic electron flow, was a mutant lacking the F and J subunits of PSI. There is a striking contrast between the function of the PsaF and PsaJ subunits in chloroplasts of plants and algae on the one hand and cyanobacteria on the other hand. In chloroplasts, PsaF plays an important role in facilitating electron transfer from plastocyanin or Cyt  $c_6$  to  $P_{700}$ . In cyanobacteria, PsaF is not needed for efficient reduction of  $P700^+$ , neither in linear nor in cyclic electron transfer, and therefore was proposed to have a different function.

In our studies, we have observed a difference in phenotype of the *psaFJ* mutant and the wild type that resulted in a longer adaptation period after transfer of cells in the exponential phase of growth from standard to a high salt medium (0.5 M NaCl) (*chapter 5, this thesis*). Studies on the photosynthetic performance of the mutant have led us to the observation of impaired PSI functionality. During measurement of P700 oxidation/reduction kinetics we noticed some conflicting phenomena: directly after switching on white actinic light, P700 oxidation started, after which a rapid transient reduction was observed within about 200 ms. This transient reduction was fully abolished after addition of DCMU. Next to the transient, the subsequent approach to full oxidation was slower and led to a less oxidised state in the mutant than in the wild type. Suppression of PSI in the *psaFJ* mutant is accompanied by impaired electron flux from the acceptor site of PSI to the PQ-cytochrome *b<sub>6</sub>f* complex (cyclic flow), and is going hand in hand with the de-repression of the *isiAB* operon. The latter encodes the iron-starvation- inducible proteins IsiA (or CP43') and IsiB (flavodoxin). Presence of IsiA in the mutant was also suggested from the 77K fluorescence emission spectrum.

The *isiA* gene is widely distributed in cyanobacteria of marine ecosystems, where iron limitation has rendered the gene its name *isiA* (*iron stress inducible*). Due to the high amount of iron-containing proteins in the electron transport chain (Ferreira and Straus 1994) iron limitation greatly affects especially PSII and PSI, resulting in an increased production of reactive oxygen species (Aro et al., 1993; Asada, 1994). We therefore propose that oxidative stress, as a consequence of a decrease in electron flux from the stroma to PQ, acts as a trigger for induction of the *isiAB* operon. The conceptual connection between oxidative damage and *isiA* expression was strongly supported by our experiments, in which artificially provoked oxidative stress in iron- replete medium conditions showed abundant presence of *isiA* transcript. This observation demonstrated that the induction of *isiAB* expression likely occurred by oxidative stress as a secondary consequence of stresses like iron limitation and high salt or by absence of PsaF/J subunits. In the mutant, the binding pocket for ferredoxin (Fd) may lack the mechanical support of the little hook that extends from the C-terminal end of the PsaF protein in the PSI crystal structure (Jordan *et al.*, 2001). This altered geometry of the binding pocket may cause a less close positioning of Fd and its catalytic partners (PsaC, PsaD, PsaE) for electron acceptance from PSI in the mutant. Hence, oxidative stress may follow from oxygen acting as acceptor for the very reduced (low redox potential) FeS proteins at the 'top' of PSI. In this way, the trigger for induction of the *isiAB* gene should accordingly be defined broader than iron stress only; we propose oxidative stress rather than iron stress *per se*. Indeed, differential gene expression analysis revealed that *isiA* and *isiB*

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in *Synechocystis* sp. PCC 6803 (Li *et al.*, 2003; Murata, 2003) are highly expressed under peroxide stress. The strong interrelationship between iron limitation and oxidative stress in cyanobacteria as model oxygenic photosynthetic organisms is reviewed recently (Michel and Pistorius, 2003).

### Iron-starvation inducible proteins

The appearance of IsiA proteins in cells is a phenomenon by itself. The *isiA* gene (*sl10247*) encodes a hydrophobic protein of about 37 kDa that shares strong homology with the CP43 (PsbC) protein of PSII, and is therefore often called CP43'. Although IsiA has similarity to PsbC, evidence was provided that IsiA cannot compensate for the loss of PsbC in a PsbC-free *Synechocystis* sp. PCC 6803 mutant, even when this mutant was grown under iron limitation (Rögner *et al.*, 1991). Instead, recently it has been shown for *Synechocystis* sp. PCC 6803 (Bibby *et al.*, 2001) and for *Synechococcus elongatus* PCC 7942 (Boekema *et al.*, 2001) that under iron limitation the trimeric PSI complex is modified to a PSI-IsiA supercomplex. Electron microscopy and single particle analysis revealed that a closed ring of 18 IsiA proteins surrounds the trimeric PSI. Each IsiA subunit binds about 16-17 chlorophyll *a* molecules and serves as a rapid and efficient antenna for PSI in the supercomplex (Andrizhiyevskaya *et al.*, 2002; Melkozernov *et al.*, 2003). Spectroscopic characterization of PSI-IsiA supercomplexes from cyanobacteria grown under iron starvation further suggest that the IsiA ring increases the absorption cross-section of PSI by about 70-100% (Andrizhiyevskaya *et al.*, 2002; Melkozernov *et al.*, 2003). Chl *a* molecules bound to the low-molecular weight proteins of PSI have been suggested to play a role in the energy transfer from the outer IsiA ring towards the reaction center (Nield *et al.*, 2003). Three of these chlorophylls are bound to PsaJ, a subunit containing one transmembrane  $\alpha$ -helix (Fromme *et al.*, 2001). PsaF is in close contact to PsaJ, also contains one transmembrane helix, and forms hydrophobic interactions with several  $\beta$ -carotene molecules of the PSI core complex. In order to investigate the role of these small PSI subunits in the PSI-IsiA supercomplex formation we grew a *psaFJ* mutant under iron-depleted conditions. The electron microscopy analysis of the single particles revealed that circular PSI-IsiA complexes consisted of a central PSI trimer surrounded by a ring of seventeen IsiA units, one less than in the wild-type supercomplex (*chapter 6, this thesis*). This observation is intriguing, because the prime number 17 implies that in the mutant complex each PSI monomer has a different position to the IsiA ring. Nevertheless, a precise organization of PSI and IsiA is possible without PsaF and PsaJ. These results demonstrate that IsiA can associate to PSI in alternative arrangements and that the size of the PSI complex determines the number of IsiA units in the surrounding

ring. Iron-limitation was not obligatory to induce the formation of PSI-IsiA supercomplexes in the *psaFJ* mutant, but the highest yield in supercomplexes was after an iron-limitation of 48-64 hours. After prolonged growth under iron-free conditions the situation changes: PSI disappears nearly completely and IsiA protein becomes by far the most abundant chlorophyll-protein complex in the mutant. A partial purification and subsequent characterization by mass spectrometry, spectroscopy and electron microscopy revealed the presence of several types of IsiA aggregates, of which a 'doughnut'-like complex not associated with PSI is the most conspicuous (*chapter 7, this thesis*). This ring-shaped complex is smaller than the normal ring of eighteen IsiA proteins around a wild type trimeric PSI complex, or the 17-mer homologue that we observed in the *psaFJ* mutant, but large enough to encircle a monomeric PSI complex. We conclude that the combination of oxidative stress and iron limitation that is exerted on PSI in the *psaFJ* mutant results in the accumulation of IsiA in a form that does not contribute to light harvesting for PSI.

The number of bound IsiA proteins is tightly correlated with degree of iron stress (*chapter 8, this thesis*). In WT it may vary from 7 units per PSI trimer in short term iron stress up to 35 units in a double ring around a PSI monomer upon prolonged iron stress. This large antenna would contain about 560 chlorophylls and would give an almost seven-fold enlargement of the light-harvesting capacity of PSI. At the same time significant part of IsiA builds supercomplexes without PSI, possibly to provide photoprotection. This way, the IsiA protein is remarkably unique to form flexible supramolecular structures of variable size to optimally respond to the degree of iron stress.

In terms of functionality of IsiA, three options have been proposed:

- 1) ***A new chlorophyll a-containing membrane-integral light-harvesting antenna.*** Light saturation curves, fluorescence spectra, PSI kinetics, and time-resolved absorption and emission analysis provided evidence that IsiA is indeed a functional antenna for PSI (Andrizhiyevskaya *et al.*, 2002; Melkozernov *et al.*, 2003). The IsiA ring resembles multimers of the light-harvesting proteins (LH1 and LH2) found in anoxygenic bacteria (Karrasch *et al.*, 1995; McDermott *et al.*, 1995), and it was also recently shown that an antenna ring around PSI consisting of chlorophyll *a/b*-binding Pcb proteins is present in the *Prochlorococcus marinus* strain SS120 (Bibby *et al.*, 2001).
- 2) ***A reserve of chlorophyll*** for rapid biosynthesis of active photosynthetic complexes when there is relief from adverse conditions (Riethman and Sherman, 1988).

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3) **Photoprotection of PSII via light shielding.** On the basis of results with an IsiA-free *Synechococcus elongatus* PCC 7942 mutant and a mutant overproducing IsiA, a protective function of IsiA for PSII against photo-induced damage was postulated, and IsiA was supposed to act as a dissipator of excitation energy (Park *et al.*, 1999; Sandström *et al.*, 2001). The authors explained their finding as protection of PSII against photodamage in case PSI suffered impaired operation from lack of iron at its acceptor site.

We noticed that in a mutant without the PsaFJ transmembrane subunits of PSI, IsiA was expressed constitutively, while the acceptor site of PSI had sufficient iron. Very recently, we observed that the constitutively induced IsiA in the *psaFJ* mutant cells of *Synechocystis* protects those cells against photobleaching after transfer from low light conditions ( $50 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ ) to high light exposure ( $900 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ , for periods up to 24 h). The mutant contrasted dramatically in its insensitivity to high light with a mutant that lacked IsiA. The latter mutant grows perfectly in low light conditions, but it quickly (< 3 h) bleaches in high light. The wild type, and an *isiB*-deficient mutant proved more protected than the IsiA-deficient mutant, but less than the remarkably high light resistant *psaFJ* mutant (these new data are not presented in this thesis and will be published elsewhere).

The crystal structure of CP43 from *Synechococcus elongatus* has identified 13 Chl molecules (Vasil'ev *et al.*, 2001). IsiA is predicted to have six transmembrane helices as CP43, and since the chlorophyll binding sites are conserved, IsiA is assumed to bind 12-13 chlorophylls (Bricker and Frankel, 2002). Nevertheless, recent spectroscopic characterization of PSI-IsiA supercomplexes from cyanobacteria grown under iron starvation revealed that the IsiA ring increases the absorption cross-section of PSI by about 100% (Andrizhiyevskaya *et al.*, 2002). This means that IsiA should bind about 17 Chl molecules, assuming 96 Chl molecules in each PSI monomer. In reality, only a refined crystal structure of IsiA may determine the exact number of bound Chl molecules and may help to shed further light on the function of this protein.

## Conclusions

The observations in this thesis show a remarkable and unforeseen level of functional flexibility in cyanobacteria. Part of this flexibility stems from the presence of alternative pathways in cyclic electron transfer of Photosystem I. Furthermore, we have presented evidence that a particular molecule associated with Photosystem I, the iron-starvation-inducible protein IsiA, can adopt different roles depending on the environmental conditions.

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