

## Minireview

## Structure and functional role of supercomplexes of IsiA and Photosystem I in cyanobacterial photosynthesis

Roman Kouřil<sup>a</sup>, Ana A. Arteni<sup>a</sup>, Julia Lax<sup>b</sup>, Nataliya Yeremenko<sup>c</sup>, Sandrine D'Haene<sup>d</sup>, Matthias Rögner<sup>b</sup>, Hans C.P. Matthijs<sup>c</sup>, Jan P. Dekker<sup>d</sup>, Egbert J. Boekema<sup>a,\*</sup><sup>a</sup> Department of Biophysical Chemistry, Groningen Biomolecular Sciences and Biotechnology Institute, University of Groningen, Nijenborgh 4, 9747 AG Groningen, The Netherlands<sup>b</sup> Lehrstuhl für Biochemie der Pflanzen, Fakultät für Biologie, Ruhr-Universität Bochum, 44780 Bochum, Germany<sup>c</sup> Aquatic Microbiology, Institute of Biodiversity and Ecosystem Dynamics, Universiteit van Amsterdam, Nieuwe Achtergracht 127, 1018 WS Amsterdam, The Netherlands<sup>d</sup> Division of Physics and Astronomy, Faculty of Sciences, Vrije Universiteit, De Boelelaan 1081, 1081 HV Amsterdam, The Netherlands

Accepted 29 March 2005

Available online 7 April 2005

Edited by Gáspár Jékely

**Abstract** Cyanobacteria express large quantities of the iron stress-inducible protein IsiA under iron deficiency. IsiA can assemble into numerous types of single or double rings surrounding Photosystem I. These supercomplexes are functional in light-harvesting, empty IsiA rings are effective energy dissipaters. Electron microscopy studies of these supercomplexes show that Photosystem I trimers bind 18 IsiA copies in a single ring, whereas monomers may bind up to 35 copies in two rings. Work on mutants indicates that the PsaF/J and PsaL subunits facilitate the formation of closed rings around Photosystem I monomers but are not obligatory components in the formation of Photosystem I–IsiA supercomplexes.

© 2005 Federation of European Biochemical Societies. Published by Elsevier B.V. All rights reserved.

**Keywords:** Photosystem I; IsiA; PsaF/J; PsaL; Electron microscopy

## 1. Introduction

More than half of the total primary production on Earth is provided by cyanobacteria, which are abundant in most marine and freshwater habitats. As environmental conditions vary constantly in time (e.g., light intensity, nutrient content), there are effective regulatory mechanisms, which allow cyanobacteria to cope with unfavorable conditions and maintain their photosynthetic production at the same time. The effect of a low iron content on the photosynthetic machinery is particularly interesting since the amount of iron can considerably fluctuate in aquatic ecosystems and because iron is essential for a number of enzymes and proteins involved in the photosynthetic light reactions (see [1,2] for reviews).

Pioneering studies with the cyanobacterium *Anacystis nidulans* grown under conditions of iron deficiency revealed significant alterations in the photosynthetic apparatus such as a loss of pigments and phycobilisomes, which was accompanied by

spectral changes [3–6]. Later on detailed biochemical analysis of thylakoid membranes isolated from iron-deficient cells identified the presence of a new 36kDa chlorophyll (Chl) *a* binding complex, designated CPVI-4 [7]. Afterwards, it was found that iron deficiency leads to the induction of an iron stress-inducible *isiAB* operon, which actually expresses two proteins, named IsiA and IsiB. It was proven that the CPVI-4 complex was encoded by the *isiA* gene [8,9]. Due to the strong sequence homology of this complex to the CP43 core antenna of PSII the IsiA protein was referred to CP43'. IsiB, flavodoxin, encoded by the *isiB* gene replaces the iron-rich soluble electron transfer protein ferredoxin [10,11]. Recently, taking advantage of DNA microarray technology, an analysis of a full-genome microarray of the cyanobacterium *Synechocystis* sp. PCC 6803 revealed that iron deficiency triggers a whole cascade of regulations of gene transcription [12]. Regulation of photosynthesis genes resulted in both reduction and specific downregulation of major iron-containing complexes involved in electron transport, like Photosystem I (PSI), the cytochrome *b<sub>6</sub>f* complex and Photosystem II (PSII) [12].

Especially PSI, the most iron-rich complex of the photosynthetic apparatus, is highly vulnerable to iron limitation stress and its content decreases more dramatically compared to PSII under stress conditions [4,5,13,14]. Further, it was found that the well-known reduction of phycobilisome content in iron-deficient cells is caused by a decreased rate of synthesis rather than an increased degradation [12,14]. On the other hand, the *isiA* gene was upregulated with highest extent [12]. Recent studies with iron replete cells revealed that IsiA is also synthesized under conditions of oxidative stress [2,15–17]. It was concluded that either there are more input signals inducing synthesis of IsiA, or that all stress conditions lead to oxidative stress, which would be the superior trigger for the induction of *isiAB* operon [2].

The exact role of IsiA in iron-deficient cells was the subject of discussion for many years. Originally, a function of IsiA as an alternative light-harvesting complex for PSII was suggested. Because of its high homology with the core antenna subunit CP43 of PSII, it was considered to replace either phycobilisomes or CP43 under condition of iron deficiency [7,9]. Secondly, an alternative function of the IsiA protein as a Chl

\*Corresponding author. Fax: +31 50 3634800.

E-mail address: [e.j.boekema@rug.nl](mailto:e.j.boekema@rug.nl) (E.J. Boekema).

storage protein, which can provide chlorophylls for the synthesis of chlorophyll-binding proteins during recovery from iron stress, was proposed [9]. However, further experiments questioned the above suggested roles of IsiA [11,18]. A strong quenching of Chl *a* fluorescence at various light intensities at room temperature and a higher resistance of iron-deficient cells to photoinhibition was attributed to the IsiA, which would function as a non-radiative dissipator of light energy protecting PSII against photo-oxidative stress [18–20]. However, the exact mechanism of quenching and also the way of interaction between the IsiA and PSII is not known yet. In addition, until now there is no evidence for the formation of specific complexes between IsiA and PSII.

Some years ago, two electron microscopy (EM) studies simultaneously revealed a surprising association of the IsiA–PSI [21,22]. Supercomplexes consisting of a ring of 18 IsiA proteins encircling a PSI trimer were found after short-term iron deficiency in two different cyanobacteria. Spectroscopic measurements indicated that IsiA can increase the light-harvesting capacity of the remaining PSI between 70% [23] and 100% [24] with a rapid and efficient energy transfer to PSI [25–27]. The increase in the antenna size of PSI is probably a response to the decrease in phycobilisome level and a decrease in the PSI to PSII ratio [4,5,13,14].

In this paper we summarize results of extensive EM studies of the wild-type (WT) cyanobacterium *Synechocystis* PCC 6803 and selected mutants lacking small peripheral PSI subunits under conditions of short and prolonged iron deficiency. In total, over 100 000 single particle projections were processed and single particle averaging revealed multiple types of interaction between PSI and IsiA. We describe the remarkable ability of IsiA to form variable ring-shaped structures with or without PSI and also discuss the role of the PsaF/J and PsaL subunits in binding of IsiA–PSI.

## 2. PSI–IsiA supercomplexes formed during short and long-term iron deficiency

EM analysis of single particles from WT *Synechocystis* grown at different periods in the absence of iron revealed a highly flexible interaction between IsiA proteins and both trimeric and monomeric PSI (Fig. 1). It is well documented that in the WT cells cultivated for 3–4 days in iron-free medium, a typical supercomplex of a PSI trimer surrounded by a ring of 18 IsiA proteins is exclusively formed [21,22]. But our data show that only a few additional days of iron deficiency can affect the stability of the  $\text{PSI}_3\text{IsiA}_{18}$  complexes and smaller complexes with incomplete rings of IsiA units around a PSI trimer can be formed, such as a complex with 13 IsiA copies (Fig. 1C; see also below). A further prolongation of iron stress up to 3 weeks gradually leads to decomposition of PSI trimers into monomers, which can be surrounded by variable single or double rings of IsiA (Fig. 1D,E,G–I) [28]. Nevertheless, the typical  $\text{PSI}_3\text{IsiA}_{18}$  complex can be still present in significant numbers, even after growth in iron free medium for 3 weeks. However, the projection maps of the supercomplexes consisting of PSI monomers and double IsiA rings always appeared rather fuzzy in comparison to those of the trimers. Analysis indicated that this was caused by flexibility in the binding of the monomers within the single double rings.

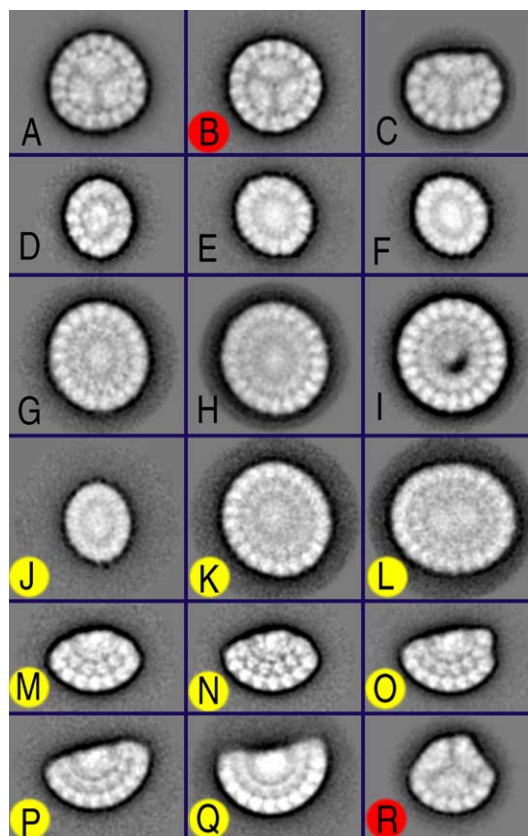


Fig. 1. An overview of the various types of PSI–IsiA supercomplexes obtained by single particle electron microscopy. Results of statistical analysis and classification of particles from WT *Synechocystis* PCC 6803 and PsaF/J and PsaL mutants of *Synechocystis* PCC 6803 under short- and long-term iron stress ([28,29,34] and Arteni, Lax, Rögner and Boekema, unpublished results). Projection maps marked in yellow are from the PsaL mutant; the ones in red from the PsaF/J mutant and the others from WT. (A) PSI trimer with a complete ring with 18 IsiA copies. (B) PSI trimer with a ring of 17 copies. (C) PSI trimer with an incomplete ring with 13 IsiA units. (D–F) PSI monomers with single rings of 12–13 copies of IsiA, respectively. (G–I) PSI monomers with closed double rings with 12, 13 and 14 copies in the inner ring and 19, 20 and 21 copies in the outer, respectively. (J,K) mutant PSI–IsiA complexes, similar to those of (D) and (H) from WT. (L) A dimeric PSI particle with 15 and 22–23 copies of IsiA in the inner and outer ring. (M–Q) PSI–IsiA particles with incomplete variable double rings of IsiA binding exclusively at the PsaF/J side. (R) Mutant trimers with an incomplete IsiA ring binding to one PSI monomers.

Recent data of DNA microarray analysis show that iron deficiency induces downregulation of both the PsaL subunit, which is required for trimerization of PSI, and the PsaI subunit, which is important for stability of PsaL [12]. Our data are in a good agreement with this observation, as we detected a more than two times higher amount of PSI in monomeric form compared to the level of PSI trimers under conditions of prolonged iron deficiency [28].

The physiological significance of formation of large PSI–IsiA supercomplexes is probably an increase of absorption cross-section of the remaining PSI, as spectroscopic measurements indicate a fast and efficient energy transfer from IsiA to PSI [25–27]. In the case of the largest PSI–IsiA supercomplex (Fig. 2I), the double ring of IsiA can give an almost 7-fold increase in the light-harvesting ability of PSI, assuming 16 Chl *a* molecules for each IsiA protein [24]. For efficient energy

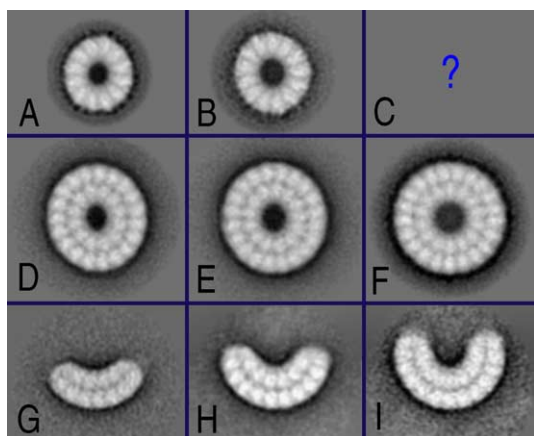


Fig. 2. An overview of the various types of IsiA supercomplexes obtained by single particle electron microscopy. Results of statistical analysis and classification of particles from WT *Synechocystis* PCC 6803 under long-term iron stress (from [28] and Kouřil, unpublished results). (A,B) Closed single rings with 12 and 13 IsiA copies. (C) Existence of single rings with 14 IsiA copies is possible, but particles not yet found. (D–F) closed double rings with 12, 13 and 14 copies in the inner ring and 19, 20 and 21 copies in the outer, similar to those of Fig. 1. (G–I) Open double rings with variable numbers of IsiA copies.

transfer, it is probably not relevant that the orientation of IsiA copies around the PSI monomers is somewhat flexible, because distance of pigments is the prime parameter in the rate of transfer of excitation energy.

### 3. Role of the PsaF/J and PsaL subunits in binding of IsiA–PSI

To elucidate a role of small peripheral subunits in binding of IsiA proteins to PSI we performed an EM analysis of two mutants lacking PsaF/J and PsaL subunits grown in iron-free medium. Our results show that the PsaF/J subunits are not obligatory for IsiA binding to PSI because a ring of 17 IsiA units can be formed around the PSI trimer (Fig. 1B) [29]. However, the presence of a smaller complex consisting of an incomplete ring of IsiA associated to PSI trimers may indicate that the absence of PsaF/J subunits decreases the binding affinity of IsiA–PSI (Fig. 1R), because WT trimers with incomplete rings were hardly observed.

Based on a detailed analysis of the X-ray structure of PSI [30], the PsaF was assigned to be the major recognition and interaction site for IsiA proteins [31]. An important role of the PsaJ in energy transfer from IsiA ring to PSI reaction center was proposed from modeling of the high-resolution X-ray data into a low-resolution 3D-cryo-EM map of PSI–IsiA supercomplex. Three separate clusters of Chl *a* molecules at the periphery of the PSI core complex, comprising the PsaA, PsaB and PsaJ subunits, were suggested [23,26].

The importance of the PsaF/J subunits in mediation of the interaction between IsiA and PSI is also obvious from the presence of an interesting PSI–IsiA supercomplex in WT iron deficient cells, which consists of a PSI trimer with an incomplete ring of 13 IsiA units (Fig. 1C). Close inspection shows that the lower two PSI monomers have the PsaF/J a density at their periphery and are flanked by IsiA copies, but that this density and the IsiA copies are lacking in the upper PSI monomer. The susceptibility of the PsaF/J subunits to the iron deficiency is caused by downregulation of PsaJ [12]. This subunit is impor-

tant for stability and proper conformation of the PsaF [32] and both subunits together enhance binding of IsiA.

A decrease in binding affinity of IsiA–PSI was also observed in the case of a PsaL mutant, especially after short-term iron stress. All IsiA proteins were bound in variable partial double rings to PSI monomers, exclusively on the side of PsaF/J (Fig. 1M–Q). Supercomplexes with an inner ring of six IsiA copies have the sharpest features, suggesting a rather specific binding (Fig. 1M–N). A higher number of copies induces flexibilities between PSI and the rings, as can be seen from an increasing fuzziness, especially in the particle of Fig. 1Q. The exact number of the IsiA copies bound to PSI monomers lacking PsaL is variable and is not restricted to a double ring conformation, since the occurrence of single partial rings was demonstrated in an independent study [33]. Only conditions of prolonged iron deficiency led to the formation of variable single or double IsiA rings around PSI monomers (Fig. 1J and K). The PsaL mutant does not produce PSI trimers, but small numbers of particles were interpreted as a double IsiA ring around a unique PSI dimer (Fig. 1L). From the variation in shape and distribution we can conclude that the PsaL subunit is not an obligatory structural component for binding of IsiA–PSI [34].

### 4. PSI-free IsiA complexes formed during prolonged iron deficiency

The extensive EM study of WT cyanobacteria grown for 3 weeks under conditions of iron deficiency also revealed the capability of cyanobacteria to form highly diverse IsiA complexes, which do not require the presence of either PSI trimers or monomers for their assembly (Fig. 2). Two varieties of single IsiA rings consisting of either 12 or 13 IsiA units (Fig. 2A and B), different double IsiA rings with 12, 13 and 14 copies in the inner ring and 19, 20 and 21 copies in the outer, respectively (Fig. 2D–E), and fragments of double rings with variable number of IsiA units (Fig. 2G–I) were found. The exact match in numbers of IsiA units in inner ring of double rings and in single rings (Fig. 2D,E and A,B, respectively) can predict the existence of single ring of 14 IsiA units, even though we did not detect this type of complex in our data set (Fig. 2C). EM analysis of both PsaF/J and PsaL mutants showed that the formation of variable single or double IsiA rings is not restricted only to wild type cells, as small numbers of similar rings and fragments of IsiA were also observed in both types of mutants ([34], unpublished data). Since the period of iron deficiency was shorter in mutant cultures compared to WT, we suppose that the extent of iron stress itself is likely more crucial for synthesis of IsiA supercomplexes than the composition of PSI. On the other hand, the absence of small peripheral subunits of PSI can cause, e.g., oxidative stress [15], which can, in addition to iron deficiency stress, further enhance the synthesis of IsiA.

Recent experiments show that the presence of IsiA in the cells causes a quenching of a room temperature Chl *a* fluorescence of PSII and increases the resistance of cells against a high-light stress (see Section 1). As we did not detect any particle resembling a potential PSII–IsiA complex in our data set, we assume that the PSI-free IsiA rings can be involved in quenching of light energy and protect PSII against photo-oxidative damage by shading it. A recently found mobility of IsiA proteins in the thylakoid membrane [35] can be important for a flexible interaction with PSII and a quenching regulation.

## 5. Conclusions

The summarized structural studies clearly show that the adaptation mechanism of cyanobacteria to conditions of iron deficiency leads to the assembly of PSI–IsiA and IsiA supercomplexes with an astonishing structural variation. In general the variation of the many structures that IsiA can form, with and without PSI, is rather unique. It is also remarkable that many types of single and double rings surrounding PSI have counterparts without PSI. The only other protein in photosynthesis that is capable to form highly variable ring structures is light-harvesting complex I (LH1) from purple bacteria [36]. On a different level structural variation is also present in green plants, in which PSII complexes bind a variable number of peripheral light-harvesting antenna complexes to form super and megacomplexes [37]. Thus the ability to form flexible protein structures is rather special for cyanobacteria. In this way, the cyanobacteria can cope with a different degree of iron deficiency in an optimal way and survive till the amount of iron in the environment will be restored. However, most of the variation of IsiA only appears in mutants, rather than in WT bacteria. It needs to be established how much of this variation is present under physiological conditions in salt and fresh water and in which species it will occur.

Although the structural organization of the IsiA under conditions of iron stress seems to be well characterized, the fate of IsiA supercomplexes after transition to iron replete conditions is still an interesting open question and remains to be answered. Future structural research should also concentrate on the question which PSI domains and subunits are crucial for IsiA binding. Furthermore it would be helpful to improve resolution in the existing 3D model for PSI<sub>3</sub>IsiA<sub>18</sub> complexes [26] to address questions about crucial chlorophylls in energy transfer.

**Acknowledgments:** R.K. was supported by the European Union, Grant HPRN-CT-2002-00248 (“PSICO network”). The work of J.P.D and E.J.B was supported by a grant from the Foundation of Life and Earth Sciences (ALW) of NWO. M.R. acknowledges support from the Deutsche Forschungsgemeinschaft (SFB 480) and the European Graduate College 795.

## References

- [1] Raven, J.A., Evans, M.C.W. and Korb, R.E. (1999) The role of trace metals in photosynthetic electron transport in O<sub>2</sub>-evolving organisms. *Photosynth. Res.* 60, 111–149.
- [2] Michel, K.P. and Pistorius, E.K. (2004) Adaptation of the photosynthetic electron transport chain in cyanobacteria to iron deficiency: the function of IdiA and IsiA. *Physiol. Plant.* 120, 36–50.
- [3] Öquist, G. (1974) Iron deficiency in the blue-green algae *Anacystis nidulans*. *Physiol. Plant.* 30, 30–37.
- [4] Sherman, D.M. and Sherman, L.A. (1983) Effect of iron deficiency and iron restoration on ultrastructure of *Anacystis nidulans*. *J. Bacteriol.* 156, 393–401.
- [5] Guikema, J.A. and Sherman, L.A. (1983) Organization and function of chlorophyll in membranes of cyanobacteria during iron starvation. *Plant Physiol.* 73, 250–256.
- [6] Guikema, J.A. and Sherman, L.A. (1984) Influence of iron deprivation on the membrane composition of *Anacystis nidulans*. *Plant Physiol.* 74, 90–95.
- [7] Pakrasi, H.B., Riethman, H.C. and Sherman, L.A. (1985) Organization of pigment proteins in the photosystem II complex of the cyanobacterium *Anacystis nidulans* R2. *Proc. Natl. Acad. Sci. USA* 82, 6903–6907.
- [8] Laudenbach, D.E. and Straus, N.A. (1988) Characterization of a cyanobacterial iron stress-induced gene similar to *psbC*. *J. Bacteriol.* 170, 5018–5026.
- [9] Burnap, R.L., Troyan, T. and Sherman, L.A. (1993) The highly abundant chlorophyll–protein complex of iron-deficient *Synechococcus* sp. PCC 7942 (CP43′) is encoded by the *isiA* gene. *Plant Physiol.* 103, 893–902.
- [10] Sandmann, G. (1985) Consequences of iron deficiency on photosynthetic and respiratory electron transport in blue-green algae. *Photosynth. Res.* 6, 261–271.
- [11] Falk, S., Samson, G., Bruce, D. and Huner, N.P.A. (1995) Functional analysis of the iron-stress induced CP43′ polypeptide of PS II in the cyanobacterium *Synechococcus* sp. PCC 7942. *Photosynth. Res.* 45, 51–60.
- [12] Singh, A.K., McIntyre, L.M. and Sherman, L.A. (2003) Microarray analysis of the genome-wide response to iron deficiency and iron reconstitution in the cyanobacterium *Synechocystis* sp. PCC 6803. *Plant Physiol.* 132, 1825–1839.
- [13] Ivanov, A.G., Park, Y.I., Miskiewicz, E., Raven, J.A., Huner, N.P.A. and Öquist, G. (2000) Iron stress restricts photosynthetic intersystem electron transport in *Synechococcus* sp. PCC 7942. *FEBS Lett.* 485, 173–177.
- [14] Sandström, S., Ivanov, A.G., Park, Y.I., Öquist, G. and Gustafsson, P. (2002) Iron stress responses in the cyanobacterium *Synechococcus* sp. PCC 7942. *Physiol. Plant.* 116, 255–263.
- [15] Jeanjean, R., Zuther, E., Yermenko, N., Havaux, M., Matthijs, H.C.P. and Hagemann, M. (2003) A photosystem I *psaFJ*-null mutant of the cyanobacterium *Synechocystis* PCC 6803 expresses the *isiAB* operon under iron replete conditions. *FEBS Lett.* 549, 52–56.
- [16] Yousef, N., Pistorius, E.K. and Michel, K.P. (2003) Comparative analysis of *idiA* and *isiA* transcription under iron starvation and oxidative stress in *Synechococcus elongatus* PCC 7942 wild-type and selected mutants. *Arch. Microbiol.* 180, 471–483.
- [17] Singh, A.K., Li, H. and Sherman, A. (2004) Microarray analysis and redox control of gene expression in the cyanobacterium *Synechocystis* sp. PCC 6803. *Physiol. Plant.* 120, 27–35.
- [18] Park, Y.I., Sandström, S., Gustafsson, P. and Öquist, G. (1999) Expression of the *isiA* gene is essential for the survival of the cyanobacterium *Synechococcus* sp. PCC 7942 by protecting photosystem II from excess light under iron limitation. *Mol. Microbiol.* 32, 123–129.
- [19] Sandström, S., Park, Y.I., Öquist, G. and Gustafsson, P. (2001) CP43′, the *isiA* gene product, functions as an excitation energy dissipator in the cyanobacterium *Synechococcus* sp. PCC 7942. *Photochem. Photobiol.* 74, 431–437.
- [20] Cadoret, J.C., Demoulière, R., Lavaud, J., van Gorkom, H.J., Houmard, J. and Etienne, A.L. (2004) Dissipation of excess energy triggered by blue light in cyanobacteria with CP43′ (*isiA*). *Biochim. Biophys. Acta* 1659, 100–104.
- [21] Bibby, T.S., Nield, J. and Barber, J. (2001) Iron deficiency induces the formation of an antenna ring around trimeric photosystem I in cyanobacteria. *Nature* 412, 743–745.
- [22] Boekema, E.J., Hifney, A., Yakushevskaya, A.E., Piotrowski, M., Keegstra, W., Berry, S., Michel, K.P., Pistorius, E.K. and Kruij, J. (2001) A giant chlorophyll–protein complex induced by iron deficiency in cyanobacteria. *Nature* 412, 745–748.
- [23] Bibby, T.S., Nield, J. and Barber, J. (2001) Three-dimensional model and characterization of the iron stress-induced CP43′-Photosystem I supercomplex isolated from the cyanobacterium *Synechocystis* PCC 6803. *J. Biol. Chem.* 276, 43246–43252.
- [24] Andrizhivetskaya, E.G., Schwabe, T.M.E., Germano, M., D’Haene, S., Kruij, J., van Grondelle, R. and Dekker, J.P. (2002) Spectroscopic properties of PSI–IsiA supercomplexes from the cyanobacterium *Synechococcus* PCC 7942. *Biochim. Biophys. Acta* 1556, 265–272.
- [25] Melkozernov, A.N., Bibby, T.S., Lin, S. and Barber, J. (2003) Time-resolved absorption and emission show that the CP43′ antenna ring of iron-stressed *Synechocystis* sp. PCC6803 is efficiently coupled to the photosystem I reaction center core. *Biochemistry* 42, 3893–3903.
- [26] Nield, J., Morris, E.P., Bibby, T.S. and Barber, J. (2003) Structural analysis of the photosystem I supercomplex of cyanobacteria induced by iron deficiency. *Biochemistry* 42, 3180–3188.

- [27] Andrizhiyevskaya, E.G., Frolov, D., van Grondelle, R. and Dekker, J.P. (2004) Energy transfer and trapping in the Photosystem I complex of *Synechococcus* PCC 7942 and in its supercomplex with IsiA. *Biochim. Biophys. Acta* 1656, 104–113.
- [28] Yermenko, N., Kouřil, R., Ihalainen, J.A., D'Haene, S., van Oosterwijk, N., Andrizhiyevskaya, E.G., Keegstra, W., Dekker, H.L., Hagemann, M., Boekema, E.J., Matthijs, H.C.P. and Dekker, J.P. (2004) Supramolecular organization and dual function of the IsiA chlorophyll-binding protein in cyanobacteria. *Biochemistry* 43, 10308–10313.
- [29] Kouřil, R., Yermenko, N., D'Haene, S., Yakushevska, A.E., Keegstra, W., Matthijs, H.C.P., Dekker, J.P. and Boekema, E.J. (2003) Photosystem I trimers from *Synechococcus* sp. PCC6803 lacking the PsaF and PsaJ subunits bind an IsiA ring of 17 units. *Biochim. Biophys. Acta* 1607, 1–4.
- [30] Jordan, P., Fromme, P., Witt, H.T., Kuklas, O., Saenger, W. and Krauss, N. (2001) Three-dimensional structure of cyanobacterial photosystem I at 2.5 Å resolution. *Nature* 411, 909–917.
- [31] Fromme, P., Melkozernov, A., Jordan, J. and Krauss, N. (2003) Structure and function of photosystem I: interaction with its soluble electron carriers and external antenna systems. *FEBS Lett.* 555, 40–44.
- [32] Xu, W., Tang, H., Wang, Y. and Chitnis, P.R. (2001) Proteins of the cyanobacterial photosystem I. *Biochim. Biophys. Acta* 1507, 32–40.
- [33] Aspinwall, C.L., Duncan, J., Bibby, T., Mullineaux, C.W. and Barber, J. (2004) The trimeric organisation of photosystem I is not necessary for the iron-stress induced CP43' protein to functionally associate with this reaction centre. *FEBS Lett.* 574, 126–130.
- [34] Kouřil, R., Yermenko, N., D'Haene, S., Oostergetel, G.T., Matthijs, H.C.P., Dekker, J.P. and Boekema, E.J. (2005) Supercomplexes of IsiA and Photosystem I in a mutant lacking subunit PsaL. *Biochim. Biophys. Acta* 1706, 262–266.
- [35] Sarcina, M. and Mullineaux, C.W. (2004) Mobility of the IsiA chlorophyll-binding protein in cyanobacterial thylakoid membranes. *J. Biol. Chem.* 279, 36514–36518.
- [36] Bahatyrova, S., Frese, R.N., van der Werff, K.O., Otto, C., Hunter, C.N. and Olsen, J.D. (2004) Flexibility and size heterogeneity of the LH1 light harvesting complex revealed by atomic force microscopy – functional significance for bacterial photosynthesis. *J. Biol. Chem.* 279, 21327–21333.
- [37] Dekker, J.P. and Boekema, E.J. (2005) Supramolecular organization of thylakoid membrane proteins in green plants. *Biochim. Biophys. Acta* 1706, 12–39.