Three-dimensional Model and Characterization of the Iron Stress-induced CP43'-Photosystem I Supercomplex Isolated from the Cyanobacterium Synechocystis PCC 6803*

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The cyanobacterium Synechocystis PCC 6803 has been subjected to growth under iron-deficient conditions. As a consequence, the isiA gene is expressed, and its product, the chlorophyll a-binding protein CP43', accumulates in the cell. Recently, we have shown for the first time that 18 copies of this photosystem II (PSII)-like chlorophyll a-binding protein forms a ring around the trimeric photosystem I (PSI) reaction center (Bibby, T. S., Nield, J., and Barber, J. (2001) Nature, 412, 743–745). Here we further characterize the biochemical and structural properties of this novel CP43'-PSI supercomplex confirming that it is a functional unit of approximately 1900 kDa where the antenna size of PSI is increased by 70% or more. Using electron microscopy and single particle analysis, we have constructed a preliminary three-dimensional model of the CP43'-PSI supercomplex and used it as a framework to incorporate higher resolution structures of PSI and CP43 recently derived from x-ray crystallography. Not only does this work emphasize the flexibility of cyanobacterial light-harvesting systems in response to the lowering of phycobilisome and PSI levels under iron-deficient conditions, but it also has implications for understanding the organization of the related chlorophyll a/b-binding Pcb proteins of oxychlorobacteria, formerly known as prochlorophytes.

Iron is the most abundant transition metal in the crust of the earth and is an absolute requirement for photosynthetic organisms such as cyanobacteria, because it is needed for many of the redox reactions of the photosynthetic electron transport system. However, in most aquatic ecosystems it can be sufficiently low to limit photosynthetic activity (1, 2). This finding is attributed mainly to the low solubility of Fe$^{3+}$ above neutral pH in oxygenic ecosystems (3). As a result, cyanobacteria and other microorganisms have evolved a number of responses to cope with frequently occurring conditions of iron deficiency (4). One such response is to express two iron stress-induced genes, isiA and isiB (5, 6), which are located on the same operon. The isiB gene encodes for flavodoxin, which can functionally replace the iron containing ferredoxin (7). The isiA gene encodes for a protein called CP43', because it has an amino acid sequence homologous to that of the chlorophyll a-binding protein, CP43 of photosystem II (PSII) (8, 9). Like CP43, CP43' is predicted to have six transmembrane helices, and judged by the conservation of histidine residues, it is likely to bind the same number of chlorophyll a molecules. The major difference is that CP43' lacks the large hydrophilic loop that joins the luminal ends of helices V and VI of CP43. For this reason, it has 342 amino acids rather than 472 (see Fig. 1).

Under iron stress, the isiA gene is transcribed into two messages, a monocistronic message containing only isiA and a dicistronic message that also contains the isiB gene (10). Although the discovery of the CP43-like iron stress-induced protein was made some time ago (11), its precise function has not been elucidated. There have been at least four postulates. (i) CP43' aids the recovery of cells by acting as a chlorophyll store so that PSII and photosystem I (PSI) complexes can be quickly synthesized when iron becomes readily available in the environment (12). (ii) CP43' protects PSII from photo-induced damage by acting as a dissipater of excitation energy (13). (iii) CP43' is a functional replacement for CP43 in PSI during iron starvation (8). (iv) CP43' acts as a light-harvesting complex under iron stress conditions, mainly for PSI (5) but perhaps also for PSI (16). Recently we showed for the first time that a CP43'-PSI trimer supercomplex can be isolated from the cyanobacterium Synechocystis PCC 6803 when grown under iron-stressed conditions (17). Here we report a more detailed description of this supercomplex and present a preliminary three-dimensional model of its structure.

MATERIALS AND METHODS

Growth Conditions—All studies were conducted on preparations isolated from Synechocystis sp. PCC 6803 having a histidine tag attached to the C terminus of the PSII protein, CP47 (18). Cells were grown phototrophically in mineral medium BG-11 (19), containing kanamycin and glucose at 30 °C and 70 microeinstein m$^{-2}$ s$^{-1}$ illumination. Iron-stressed cultures were obtained by growing cells in the same BG-11 medium but lacking iron-containing compounds. Cultures were harvested after 3 days, and in the case of the iron-starved culture, the cells had a blue shift in their long wavelength absorption band of approximately 7 nm compared with that of normal cells. Thylakoid membranes were isolated using a procedure similar to that described by Tang and Diner (20). The isolated membranes (1 mg chlorophyll ml$^{-1}$) were solubilized with 1% β-D-dodecyl maltoside at 4 °C for 10 min and centrifuged at 45,000 rpm using a Beckman Ti70 rotor. The supernatant was then passed through a Ni$^{2+}$ affinity column. Given that CP47 had a histidine tag, PSI was selectively bound to the column while the non-bound fraction containing PSI was collected. Continuous sucrose density gradients were prepared according to the freeze-thaw method provided by Hankamer et al. (21). The PSI-enriched fraction eluted from the affinity column was layered on top of the gradient and subjected to...

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1 The abbreviations used are: PSI, photosystem II; PSI, photosystem I.
12 h of centrifugation in a SW28 rotor at 26,000 rpm. The resulting bands were independently removed for biochemical and structural characterization. The separation of the PSI fraction into discrete populations for estimating molecular masses was also accomplished by size exclusion high performance liquid chromatography using a Phenomenex BioSep SEC S3000 column coupled to a Kontron high performance liquid chromatography system. Elution profiles were monitored at 670 nm and 280 nm to detect chlorophyll protein-containing fractions.

Biochemical Characterization—SDS-polyacrylamide gel electrophoresis and Western blotting were performed as described in Hanka-mer et al. (21). Optical absorption spectra were measured at room temperature using a Shimadzu MPS 2000 spectrometer. Steady-state fluorescence spectra were obtained using a Perkin Elmer LS50 at 77 K and measured with an excitation wavelength of 440 nm. To record fluorescence excitation spectra, the sample was excited between 650 and 700 nm, and the emission was detected at 720 nm.

Electron Microscopy and Image Processing—Preparations were negatively stained with 2% uranyl acetate on glow-discharged carbon-evaporated grids and imaged using a Philips CM 100 electron microscope at 80 kV. The magnification was calibrated at × 51,500. Twenty electron micrographs were taken for each preparation and subsequently calculated to have the first minima of their contrast transfer functions to be in the range of 17–23 Å. Electron micrographs were digitized using a Leafscan 45 densitometer set at a step size of 10 μm. Single particle data sets of ~3000 (CP43-PSI supercomplex) and 4200 (PSI trimer) were obtained by interactively selecting all possible particles from the micrographs. All subsequent processing was performed within the IMAGIC-5 software environment (22, 23). The single particle images were coarsened by a factor of 2, resulting in a sampling frequency of 3.88 Å/pixel on the specimen scale. Reference-free alignment coupled with multi-variate statistical analysis was used to classify each data set to identify initial class averages. These data were then used for iterative refinement, resulting in the improved class averages. The relative orientations of the improved class averages were determined by

FIG. 1. Comparison of the folding diagrams of CP43 and CP43' based on the sequencing of the psbC and isiA gene of Synechocystis 6803 and hydropathy analyses. The predicted amino acid sequences are given with the position of the histidines highlighted. Note that the E-loop joining the 2-transmembrane helices V and VI of CP43 is significantly more extensive than the corresponding loop of CP43'.
the angular reconstitution technique (24), allowing for an initial three-dimensional reconstruction to be obtained by exact-back projection (25). Reprojections were taken from this initial three-dimensional map to further refine the class averages and identify any atypical views present within the data set. The data converged after several rounds of iterative refinement in this manner, whereby roughly 40% of the class averages were discarded after assessment through cross-correlation functions. The resolution of the final three-dimensional map was determined by Fourier shell correlation (FCS) between two independent three-dimensional reconstructions (26) compensated for the C3 symmetry used (27).

**RESULTS**

**Isolation of the CP43'-PSI Supercomplex**—To isolate the CP43'-PSI supercomplex from *Synechocystis* PCC6803, we used a mutant that had a His tag attached to the C terminus of CP47, kindly provided by Dr. T. Bricker (Louisiana State University, Baton Rouge) (18). The mutant was grown photoheterotrophically in the presence and absence of iron in the culture medium. Thylakoid membranes were isolated, and after solubilization with 1% D-dodecyl maltoside, were passed through an Ni²⁺ affinity column. PSII was selectively bound to the column via the His tag, whereas the non-bound fraction containing PSI was collected and subjected to sucrose density gradient centrifugation. Fig. 2a shows that in the case of normal cells (Gradient A) two main chlorophyll-containing bands were observed corresponding to monomeric (band 2) and trimeric (band 3) PSI, whereas iron-stressed cells (Gradient B) gave two additional green bands (bands 1 and 4). The SDS-polyacrylamide gel electrophoresis analysis shown in Fig. 2b characterized the various bands and revealed that bands 1 and 4 contained free CP43 and CP43' plus PSI respectively. Size exclusion high performance liquid chromatography analysis of the solubilized PSI fractions presented in Fig. 3a indicated that the two PSI bands obtained with normal cells corresponded to the approximate molecular masses expected for a monomeric (∼356 kDa) and trimeric (1068 kDa) PSI complex (32) with the trimer being the dominant species. The additional peaks observed after iron stress correspond to native chlorophyll-binding CP43' (∼47 kDa) and a high molecular mass chlorophyll-containing species of approximately 1900 kDa, indicative of a CP43' and PSI supercomplex. Also of importance is that the level of the PSI trimer in iron-stressed cells was significantly lower than in normal cells.
reduced compared with that of normal cells when normalized against the monomeric level of PSI.

Spectral Characterization—The room temperature optical absorption spectra of the isolated PSI trimer, CP43', and the CP43'-PSI supercomplex are shown in Fig. 4. The PSI trimer has a long wavelength absorption maximum at 680 nm as compared with 670 nm for isolated free CP43'. As expected, the CP43'-PSI band has a maximum absorption at the intermediate wavelength of 673 nm. The high level of absorption in the 450–500-nm region in the case of CP43'/H11032 is because of its copurification with free carotenoid in the sucrose density gradients (see asterisk in Fig. 2a).

Fluorescence measured at 77 K showed that the PSI trimer had an emission maximum at 720 nm, whereas CP43' fluorescence maximally at 685 nm (Fig. 5a). However, in the case of the CP43'-PSI supercomplex, the emission profile was similar to that of PSI with the exception of some weak emission at approximately 685 nm. Upon the addition of 0.1% Triton X-100, this weak signal at 685 nm changed to the dominant emission (Fig. 5b), indicating that the detergent had uncoupled CP43' from PSI and therefore suggesting that in the untreated sample, energy is efficiently transferred from CP43' to PSI. Sucrose density gradient analyses showed that indeed the Triton X-100 treatment converted the CP43'-PSI band into trimeric PSI and free CP43' (data not shown). Further confirmation that CP43' within the CP43'-PSI supercomplex was functionally coupled to PSI was made by measuring excitation spectra for 77-K fluorescence emission at 720 nm (data not shown).

Structure of the CP43'-PSI Supercomplex—We have shown previously by electron microscopy and single particle analysis that the CP43'-PSI supercomplex is composed of a PSI trimer surrounded by a ring of 18 subunits of CP43' (17). The structural model presented in this initial report (17) was obtained by analyzing top views only, but other views were also observed in the electron micrographs including side elevations and views attributed to tilting particles. We have, therefore, taken advantage of these other views to obtain a range of class averages of the supercomplex, and a three-dimensional model has been calculated. Fig. 6a shows nine typical class averages taken from 76 class averages that shows a range of orientations as derived from a 3000-particle data set. All 76 class averages were used to construct the three-dimensional model representing ~2200 single particles. This three-dimensional model is shown in Fig. 6b as surface-rendered views and at the same orientation as the class averages given in Fig. 6a. It clearly indicates that the central PSI trimer is surrounded by 18 CP43' subunits. According to Fourier shell correlation analysis (Fig. 6c), the three-dimensional model has a resolution of approximately 24 Å. It is quite apparent from the comparison of the class averages that both stromal and luminal views were incorporated into the three-dimensional model. For example, the feature marked with an arrow in the class average numbered 1 in Fig. 6a is displaced to the right within each of the PSI

![Fig. 5](image-url) 77-K fluorescence emission spectra for PSI-fractions of *Synechocystis*. a, a comparison of spectra for free CP43', PSI trimers, and CP43'-PSI supercomplex as marked. b, fluorescence emission before (trace A) and after (trace B) adding 0.1% Triton X-100 to the CP43'-PSI supercomplex.

![Fig. 6](image-url) Image processing of various two-dimensional views of the CP43'-PSI supercomplex. a, a selection of nine typical class averages taken from 76 different class averages used for the three-dimensional reconstruction. b, surface-rendered views of the final three-dimensional map calculated by angular reconstitution viewed from the same angles presented in a. c, Fourier-shell correlation at 3σ/√3 gives a resolution of 24 Å for the three-dimensional model. Bar represents 20 nm.
monomers, whereas in class average numbered 4 it is displaced to the left. This finding indicates that these 2 two-dimensional class averages are derived from particles imaged from different sides of the supercomplex. Thus, the relative orientations of these two averages differ by $-180^\circ$. This difference is present in the three-dimensional model and therefore is a reliable feature within all the class averages used. From this observation, we conclude that the supercomplex can orientate itself with its luminal or stromal surface toward the carbon grid and that the three-dimensional model reflects this fact.

Although the present three-dimensional model of the CP43'-PSI supercomplex has potential for further refinement by electron cryomicroscopy of non-stained vitrified samples, it does provide a framework in which to model the structures of PSI (28) and CP43 (29) obtained by x-ray crystallography of complexes isolated from the thermophilic cyanobacteria *Synechococcus elongatus*. The structure of the PSI trimer is now at a resolution of 2.5 Å (32), but at the time of submitting this paper only the 4-Å model of Kraus et al. (28) was available in the data base. In the case of CP43, the 3.8-Å data are available (29) and have been used to model the 6-transmembrane helices and the positioning of the tetrapyrrole headgroups of chlorophyll a. We have taken the models of the PSI trimer and CP43 derived by x-ray crystallography and built them into the three-dimensional electron microscopy map of the CP43'-PSI supercomplex as shown in Figs. 7 and 8.

**Discussion**

As a consequence of iron starvation, *Synechocystis* PCC 6803 expresses its *isiA* and *isiB* genes. Concomitant with this gene expression is a drop in the level of PSI (33) and phycobiliproteins (5). We have found that in addition to these well recognized responses to iron limitation, *Synechocystis* forms a supercomplex composed of a ring of 18 copies of the CP43' protein surrounding a PSI trimer. The CP43'-PSI supercomplex was isolated by sucrose density centrifugation, and size exclusion chromatography estimated its molecular mass to be approximately 1900 kDa. This mass is consistent with that predicted by the calculation for a PSI trimer (1068 kDa) plus 18 copies of the CP43' protein (846 kDa).

Assuming that each CP43' subunit binds at least 12 chlorophylls as does CP43 (29), the CP43' antenna ring of the PSI supercomplex would contain 216 or more chlorophylls. It is for this reason that the optical absorption spectrum of this supercomplex is significantly different from that of the PSI trimer alone. The chlorophyll a molecules bound within the CP43' protein have a long wavelength absorption maximum at approximately 670 nm. Therefore, the long wavelength absorption peak shifts from 680 nm for PSI to 673 nm for the CP43'-PSI supercomplex. Some free CP43' in the supercomplex preparation could also contribute to this blue shift, but fluorescence measurements suggest that this contamination is not
significant. When isolated, the CP43' protein has a relatively high fluorescence yield at 77 K peaking at 685 nm. Although some emission at this wavelength was detected from the CP43'/H11032-PSI supercomplex, the PSI low temperature fluorescence peaking at 720 nm was the dominating emission. Only after the addition of 0.1% Triton X-100 to dissociate the CP43'/H11032-protein from the PSI trimer was a large fluorescence emission seen at 685 nm from the supercomplex. Therefore, we conclude that the chlorophylls within the CP43'/H11032-ring are excitonically coupled to those within the PSI trimer core. Given that the PSI trimer binds almost 300 chlorophyll a molecules (32), we can conclude that the additional 216 chlorophylls in the CP43'/H11032-ring increases the light-harvesting capacity of the PSI reaction centers within the supercomplex by at least 70%. It has previously been suggested that CP43' could act as an additional antenna of PSI (16).

The results presented here and elsewhere (17) clearly show that in response to iron deprivation, *Synechocystis* induces an additional antenna system for PSI. The processing of top views of the CP43'-PSI supercomplex indicate that the 18 CP43'-subunits do not form a perfect ring because of the fact that the PSI trimer is not circular. The three-dimensional model presented in Fig. 6b was constructed using a number of top, intermediate, and side views showing that the supercomplex has a diameter of approximately 330 Å and a thickness of ~80 Å in negative stain. Because the hydrophobic surfaces of the supercomplex must have a detergent layer, the true diameter is likely to be slightly less. The two-dimensional class averages (Fig. 6a) and three-dimensional reconstruction (Fig. 6b) reveal rather flat stromal and luminal surfaces that are not expected for the stromal surface since the PSI trimer normally binds extrinsic PsaC, PsaD, and PsaE proteins. However, we are confident that the three-dimensional model is composed of characteristic stromal and luminal views because differences can be observed in the internal density distribution of the PSI monomers within different two-dimensional class averages, indicative of different orientations on the carbon grid (see Fig. 6a).

The absence of the expected surface structural features attributed to PsaC, PsaD, and PsaE is emphasized when the x-ray structure of the PSI trimer is modeled into the three-dimensional model of the CP43'-PSI supercomplex (see Fig. 7). There is a possibility that the extrinsic proteins are dislodged by the uranyl acetate-staining procedure used before imaging in the electron microscope. It would be highly desirable to obtain a three-dimensional model for the supercomplex using non-stained samples and electron cryomicroscopy, which would remove any effects of uranyl acetate. However, there is the alternative possibility that the PSI reaction centers within the supercomplex do not bind all three extrinsic proteins. Under iron-stressed conditions flavodoxin replaces ferredoxin as the PSI electron acceptor. This may lead to modifications in the levels and binding affinities of the three extrinsic proteins. For example, flavodoxin can act as a PSI electron acceptor in the absence of PsaD and PsaE, whereas ferredoxin cannot (35).

The modeling of the CP43'-PSI supercomplex using the x-ray structures of the PSI trimer and of the PSII CP43, however, does provide a framework to start to understand how the chlorophylls of the CP43' ring transfer energy to those bound within the PSI trimer. In Fig. 8, we have modeled the position of the chlorophylls derived from the x-ray crystallography into the CP43'-PSI complex. For convenience, we have assumed that the transmembrane helix and chlorophyll organization is the same in CP43' and CP43, and that helices V and VI of...
CP43' are located closest to the reaction center core as they are in the case of CP43 within the PSII structure (36, 37). The resulting model is consistent with our finding that the chlorophyll molecules of the CP43’ ring and PSI trimer are sufficiently close to facilitate energy transfer to the PSI reaction centers. Of particular note is that there seems to be possible entry points for energy transfer (see asterisks in Fig. 8) corresponding to chlorophyll interdistances of 12–18 Å. The three entry points for each monomer seem to involve chlorophyll a molecules clustered close to helices c and d of the PsaB (single asterisk) and PsaA proteins (triple asterisk) and those probably associated with the PsaJ protein (double asterisk) (32). However, this modeling is preliminary and will be improved with a better resolution of the three-dimensional map of the CP43’-PSI supercomplex and by having access to the coordinates of the 2.5-Å x-ray model of PSI (32).

The results presented here raise the question of why do cyanobacteria increase the antenna size of PSI under iron-stressed conditions? One possibility is that it is a compensatory response to the lowering of the PSI and phycobiliprotein levels (4). With an extra antenna system, PSI can increase its rate of oxidation activity of PSII. In the absence of a high resolution structure of PSII, little is known about the location of these loops relative to the manganese cluster, which forms the catalytic center for the water-splitting reactions.

Finally it is worth noting that Prochlorophytes, like cyanobacteria, have trimeric PSI (15, 34), which would be a requirement for the formation of the antenna ring and, indeed, could be the functional significance of the trimerization of the PSI reaction center complex in prokaryotes in general.

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