Three-dimensional Structure of *Chlamydomonas reinhardtii* and *Synechococcus elongatus* Photosystem II Complexes Allows for Comparison of Their Oxygen-evolving Complex Organization*

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Electron microscopy and single-particle analyses have been carried out on negatively stained photosystem II (PSII) complexes isolated from the green alga *Chlamydomonas reinhardtii* and the thermophilic cyanobacterium *Synechococcus elongatus*. The analyses have yielded three-dimensional structures at 30-Å resolution. Biochemical analysis of the *C. reinhardtii* particle suggested it to be very similar to the light-harvesting complex II (LHCII)-PSII supercomplex of spinach, a conclusion borne out by its three-dimensional structure. Not only was the *C. reinhardtii* LHCII-PSII supercomplex dimeric and of comparable size and shape to that of spinach, but the structural features for the extrinsic OEC subunits bound to the lumenal surface were also similar thus allowing identification of the PsbO, PsbP, and PsbQ OEC proteins. The particle isolated from *S. elongatus* was also dimeric and retained its OEC proteins, PsbO, PsbP, and PsbV (cytochrome c550), which were again visualized as protrusions on the lumenal surface of the complex. The overall size and shape of the cyanobacterial particle was similar to that of a PSII dimeric core complex isolated from spinach for which higher resolution structural data are known from electron crystallography. By building the higher resolution structural model into the projection maps it has been possible to relate the positioning of the OEC proteins of *C. reinhardtii* and *S. elongatus* with the underlying transmembrane helices of other major intrinsic subunits of the core complex, D1, D2, CP47, and CP43 proteins. It is concluded that the PsbO protein is located over the CP47 and D2 side of the reaction center core complex, whereas the PsbP/PsbQ and PsbV/PsbU are positioned over the luminal surface of the N-terminal region of the D1 protein. However, the mass attributed to PsbV/PsbU seems to bridge across to the PsbO, whereas the PsbP/PsbQ proteins protrude out more from the luminal surface. Nevertheless, within the resolution and quality of the data, the relative positions of the center of masses for OEC proteins of *C. reinhardtii* and *S. elongatus* are similar and consistent with those determined previously for the OEC proteins of spinach.

Photosystem II (PSII) is a large multisubunit protein complex that utilizes light energy to split water into molecular oxygen and reducing equivalents. It is located in thylakoid membranes of plants, algae, and cyanobacteria. To understand the molecular mechanisms of PSII requires knowledge of its 3D structure and particularly of the catalytic center, which is responsible for bringing about the thermodynamically difficult reactions of water oxidation and oxygen evolution.

In its complete form the PSII complex is composed of over 25 different proteins (1). At the heart of this multisubunit complex is the reaction center composed of the D1 and D2 proteins, which are encoded by the *psbA* and *psbD* genes. These proteins each consist of five transmembrane helices and bind the redox-active cofactors responsible for the primary and secondary electron transfer processes that occur following the absorption of a photon (1, 2). It is also likely that the manganese cluster, which catalyzes the oxidation of water, is ligated to the luminal side of the D1 protein (3). Surrounding the D1 and D2 proteins are the other PSII subunits. These include the chlorophyll a binding proteins CP47 and CP43 that transfer excitation energy to the reaction center (4). They are encoded by the *psbB* and *psbC* genes, respectively, and both proteins have six transmembrane helices characterized by very large loops joining the luminal ends of helices five and six. A structural model for the organization of the transmembrane helices of these PSII subunits has been deduced from electron crystallography (5–7), which also revealed the transmembrane helices of other low molecular weight subunits of the PSII core. Higher plants and green algae have an additional outer light-harvesting system composed of proteins that bind both chlorophyll a and b, of which there are six types (Lhcb proteins) (8). The majority of the light-harvesting systems are made up of Lhcbl–3 and are known as light-harvesting complex II (LHCII). LHCII is organized as trimers, the structure of which has been determined to 3.4 Å (9). The other chlorophyll a/b-binding proteins, Lhcb4, Lhcb5, and Lhcb6, also known as CP29, CP26, and CP24, respectively, bind less chlorophyll b than LHCII and are thought to exist as monomers. In cyanobacteria and red algae the outer light-harvesting system is contained in phycobilisomes attached to the stromal surface of the core complex. They consist of phycobiliproteins, such as allophycocyanin, phycocyanin, and phycoerythrin, which are encoded by *apc* and *cpc* genes (10).

In all types of oxygenic photosynthetic organisms the manganese cluster is stabilized by an extrinsic OEC protein en-
coded by the psbO gene, having an apparent molecular mass of 33 kDa. There is no evidence to suggest that the manganese cluster is directly ligated to this protein and, indeed, it can be removed without inhibiting the water oxidation process (11, 12). In plants and algae, two other OEC extrinsic proteins are found, PsbP (23 kDa) and PsbQ (17 kDa). These two proteins play a role in optimizing the levels of Ca$^{2+}$ and Cl$^{-}$, which are required for the water-splitting reaction (13). In cyanobacteria, however, these proteins are replaced by PsbU (12 kDa) and PsbV (15 kDa), where the latter is cytochrome c$\delta$_{550} (Cyt c$\delta$_{550}) (14). It seems that these two cyanobacterial proteins also function to create the correct Ca$^{2+}$ and Cl$^{-}$ environment for the water-oxidation process although the presence of a redox-active cytochrome suggests some other additional function.

In this paper we report 3D structural maps of PSII complexes isolated from the green alga Chlamydomonas reinhardtii and the cyanobacterium Synechococcus elongatus. The structures have been obtained by electron microscopy and single-particle analyses of negatively stained preparations and reveal the location of the extrinsic OEC proteins on the lumenal surface of the two types of PSII complex. By incorporating the higher-resolution structure of the underlying intrinsic proteins derived from electron crystallography (5–7) into the 3D models we have been able to compare the organization of the OEC proteins for algal and cyanobacterial PSII.

MATERIALS AND METHODS

Isolation of Oxygen-evolving PSII Supercomplexes from C. reinhardtii—The C. reinhardtii mutant Xba9, deficient in photosystem I, was grown in Tris acetate phosphate medium (15), including 25 μg ml$^{-1}$ spectinomycin, 100 μg ml$^{-1}$ ampicillin, and 10 μg ml$^{-1}$ 3,4-dichlorophenyl)-1,1-dimethyl urea (16). The cells were washed and broken by French press (4,000 p.s.i.), and the thylakoid membranes were collected by sucrose density cushion centrifugation according to the method described by Diner and Wollman (17). LHCII PSII supercomplexes were purified from the thylakoids by continuous sucrose density gradient centrifugation, modified from that previously described (18) at the final solubilization step, where 50 mM instead of 20 mM. The LHCII PSII supercomplexes corresponded to the densest fraction of the gradient.

Purification of Oxygen-evolving PSII Cores from S. elongatus—S. elongatus cells were grown as a 30-liter culture in an airlift fermentor through which 5% carbon dioxide in air was bubbled. The culture was using medium D as described by Castenholz (19), at pH 7.5, 56 °C, and emphasize that the PsbP (23 kDa) and PsbQ (17 kDa) of the algal and cyanobacterial PSII complexes retain their OEC proteins by guest on March 24, 2020http://www.jbc.org/Downloaded from

RESULTS

Characterization of Isolated PSII Complexes from C. reinhardtii and S. elongatus—The isolation and purification procedures as described under "Materials and Methods" gave rise to PSII preparations from C. reinhardtii and S. elongatus that retained their OEC proteins. The C. reinhardtii complex contained chlorophyll b, as well as chlorophyll a, and its room-temperature absorption spectrum (Fig. 1a) was identical to that of the LHClI-II supercomplex previously isolated from spinach (18). Moreover, its protein composition, as determined by SDS-PAGE (Fig. 1a), is very similar to that of the spinach LHCCI-II supercomplex (18).

The room-temperature absorption spectrum of the S. elongatus PSII preparation shown in Fig. 1b contrasts with that of the isolated C. reinhardtii supercomplex, as it does not have chlorophyll b absorption bands.

The SDS polyacrylamide gel electrophoresis gel of the S. elongatus preparation is also shown in Fig. 1b. The SDS-PAGE profile shows that the algal and cyanobacterial PSII complexes retain their OEC proteins and emphasize that the PsbP (23 kDa) and PsbQ (17 kDa) of C. reinhardtii are replaced by PsbU (12 kDa) and PsbV (Cyt c$\delta$_{550} 15 kDa) in S. elongatus, whereas the PsbO (33 kDa) protein is common to both.

Image Analysis

C. reinhardtii Supercomplex—The C. reinhardtii supercomplexes were negatively stained and imaged using a Philips CM100 electron microscope. Using a data set of ~2,500 randomly ordered particles, 192 class averages were initially identified by reference free alignment and classification. After multireference alignment to improve their signal to noise ratio, 47 averages were selected, and their relative orientations were determined by the angular reconstitution technique. Fig. 2s shows five algal PSII supercomplex averages, characteristic of the 47 used in total for the final 3D map, which is shown in Fig. 2c with its corresponding reprojections (Fig. 2b).

S. elongatus Dimeric Core—Negatively stained S. elongatus PSII dimeric core particles were also imaged using a Philips CM100 electron microscope, and an initial data set of about 13,000 single-particle images was collected. Unlike with C. reinhardtii, the images of the S. elongatus particles were dominated by two preferential orientations, described as top and side views. This feature was found to be dependent on whether the electron microscopy grids were glow discharged, and the total data set used was reduced to 2,500 images after iterative refinement procedures due to the similarity of the views. For the final 3D reconstruction, 67 class averages were used that

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Fig. 1. Absorption spectra and protein composition of (a) C. reinhardtii LHCII-PSII supercomplex and (b) S. elongatus dimeric core complex. The protein composition was obtained by SDS-PAGE and visualized by silver staining for C. reinhardtii and Coomassie Blue for S. elongatus.

showed the broadest range of orientations. Five examples of these characteristic class-average views are given in Fig. 3a, and the corresponding surface-rendered views from the final calculated 3D map are shown in Fig. 3c. Lane b of Fig. 3 shows the reprojections for comparison.

Characteristics of the 3D Maps

An oblique surface-rendered view of the 3D structure of the C. reinhardtii supercomplex is shown in Fig. 4. In its general appearance it is remarkably similar to that reported for the isolated spinach LHCII-PSII supercomplex, except that in the latter case the 3D model was obtained by cryoelectron microscopy at a resolution of 24 Å (29). The model for the C. reinhardtii supercomplex is at a lower resolution (low pass filtered to 30 Å) and is slightly larger, attributed to the presence of negative stain and its interaction with detergent (30). The supercomplex is dimeric, having been found to be C2 point-group symmetric, thus containing two sets of subunits. The protrusions observed on the luminal surface, marked A/A and B/B in Fig. 4, are the OEC proteins based on their similarity with those observed on the luminal surface of the spinach PSII supercomplex (29). Protrusions A/A have been identified in the spinach complex as the extrinsic PsbO (33 kDa) protein, whereas the larger protrusions B/B have been thought to contain both the PsbP (23 kDa) and PsbQ (17 kDa) proteins (29).

The C. reinhardtii supercomplex has dimensions of 350 Å × 175 Å × 135 Å overall length (x), width (y), and height (z), which compare with 330 Å × 165 Å × 110 Å, respectively, for the spinach LHCII-PSII supercomplex deduced from cryoelectron microscopy (29). The distance between the peaks of A/B and A'/B' is 72 Å, and between A'/A and B'/B it is 60 and 100 Å, respectively. These values are very similar to those of spinach, calculated to be 68 Å for both A/B and A'/B', with A/A' and B/B' giving 68 and 109 Å, respectively (29).

The 3D structure of the S. elongatus core low pass filtered to 30 Å is shown in Fig. 5 and is also a dimer with C2 point-group symmetry. Distinct protrusions are observed on the one surface (also see Fig. 3c, side views), which we attribute to the OEC proteins. Their organization differs from that observed for C. reinhardtii and spinach. For example, the bulky protrusion due to PsbP and PsbQ proteins seen in spinach and C. reinhardtii are absent and are replaced by a less extensive protein mass labeled D/D'. In contrast, the region marked C/C', attributed to the PsbO protein (see below), is more comparable with the A/A' densities in the supercomplex structure. The complex has overall dimensions of 220 Å × 150 Å × 95 Å overall length (x), width (y), and height (z), and the distance between peaks CD and C'D' is 60 Å, and between C/C' and D/D' the distances are 64 and 92 Å, respectively.

Comparison of C. reinhardtii and S. elongatus Structures with Those of Spinach

Fig. 6, a and b compares top view projection maps of the membrane region of C. reinhardtii and spinach supercomplexes, the latter taken from Ref. 29. Despite the fact that images were obtained after different treatments (negatively stained at room temperature for C. reinhardtii, compared with vitrified, non-stained samples for spinach), they are remarkably similar in shape and size. Similarly, a projection map of the membrane region of S. elongatus dimeric core (Fig. 6c) matches closely with that of the spinach core dimer complex (Fig. 6d) also obtained from negatively stained samples (31).

The similarity between the dimer core complexes of S. elongatus and spinach is more clearly seen in Fig. 7, where the two projection maps of the membrane regions have been overlaid. Also included in Fig. 7 is the positioning of the major transmembrane helices derived from recent electron crystallography studies on the spinach dimeric core complex (7). Given that the latter was obtained from cryoelectron microscopy and at a resolution of 8 to 9 Å, the fit into the low resolution negative stain core dimer maps is remarkably good and consistent with previous modelling (29, 32).

As shown in an earlier study using a PSII preparation isolated from spinach (30), the core dimer complex is located centrally in the supercomplex so that the LHCII/CP29/CP26 subunits are restricted to the tip region (18). In Fig. 7 we have incorporated the overlaid projection maps of the core dimers of S. elongatus and spinach into the projection map of C. reinhardtii taken from Fig. 6a. The relative positioning of these negatively stained images is based on the structural model derived from spinach (32). As can be seen, the core complexes are adequately accommodated into the C. reinhardtii supercomplex projection.

The incorporation of the core dimer projection into the C. reinhardtii structure also allows for the positioning of the transmembrane helices within the supercomplex and therefore gives a framework to determine the relative location of the algal OEC proteins.

Relative Positioning of the OEC Proteins

Fig. 8, a, b, and c are projection maps of the protrusions attributed to the OEC proteins of C. reinhardtii, S. elongatus, and spinach (from Ref. 29), respectively. These have been obtained by removing the membrane portion of the complete 3D map thus revealing the masses of the OEC proteins. The similarity of the tetrameric organization of these proteins for C. reinhardtii (Fig. 8a) and spinach (Fig. 8c) is clearly seen where A/A' are attributed to the PsbO protein and B/B' to the PsbP and PsbQ proteins of the OEC. The organization of the OEC proteins of S. elongatus is somewhat different (Fig. 8b). The denser region, C'/C', attributed to the PsbO protein (see below)
and the less dense region D/D, seems to be bridged, a feature also recently reported by Kuhl et al. (33).

By accepting the model for the positioning of the underlying transmembrane helices in this way it is possible to make a more complete comparison of the organization of the OEC proteins for the three systems. In Fig. 8, d, e, and f, the transmembrane helices have been incorporated based on Fig. 7 with...
The lumenal surface of the N-terminal region of the D1 protein and included the two unknown transmembrane helices in the same region (29). These relative positions are shown for the spinach model in Fig. 8 but are also appropriate for *C. reinhardtii* (see Fig. 8d). The situation with *S. elongatus* is similar in that the density designated C/C' is located toward the CP47/D2 side of the complex and is therefore likely to be the 33-kDa protein. On the other hand the remaining portion of the density D/D' is significantly less than the B/B' region observed in spinach and *C. reinhardtii* and tends to be continuous with the C/C' region. Nevertheless, this density also stretches toward the lumenal surface of the N-terminal end of the cyanobacterial D1 protein also incorporating the region occupied by the two helices of unknown origin and in that way shows a similarity to the algal and higher plant systems. This similarity, and also that of the regions designated to the PsbO protein, is clearly seen when all three OEC 3D map portions are overlaid on top of the modelled cylinders representing the underlying transmembrane helices (see Fig. 9).

**Fig. 6.** Various top views of the membrane portion (i.e. with the projections of the OEC proteins removed) of (a) LHCII-PSII supercomplex of *C. reinhardtii*, (b) LHCII-PSII supercomplex of spinach, (c) dimeric core of *S. elongatus*, and (d) dimeric core of spinach. The projection maps are based on negatively stained data except for the vitrified, non-stained LHCII-PSII supercomplex data from spinach, taken from Nield et al. (29). The negatively stained spinach dimeric core data are taken from Nield et al. (31).

**Fig. 7.** Overlay of projection map of the membrane regions of the dimeric core of *S. elongatus* (red) and spinach (yellow) taken from Fig. 6, c and d and the incorporation of transmembrane helices obtained by electron crystallography (7). The helices are shown as rods where green and red are CP43 and CP47, respectively. The yellow and brown are attributed to the D1 and D2 proteins, respectively. The blue helices are of unknown low molecular weight proteins. The projections of dimeric cores have been placed into the central region of the LHCII-PSII projection map of *C. reinhardtii* based on previous identification of the spinach dimeric core within the spinach supercomplex (30).

**Fig. 8.** Projection map of the OEC extrinsic proteins of (a) *C. reinhardtii*, (b) *S. elongatus*, and (c) spinach. The spinach map is derived from Nield et al. (29). A/A' and B/B' are attributed to the PsbO (33 kDa) and PsbP/PsbQ (23/17 kDa) proteins, respectively, of the OEC of *C. reinhardtii* and spinach. C/C' and D/D' are attributed to the PsbO (33 kDa) and PsbV/PsbU (15/12 kDa), respectively, of the OEC of *S. elongatus*. The bottom panels, d, e, and f, indicate the position of the extrinsic OEC proteins of (d) *C. reinhardtii* (shaded blue), (e) *S. elongatus* (shaded red), and (f) spinach (shaded green), relative to the underlying transmembrane helices based on the models given in Fig. 7. The bar represents 5 nm.
FIG. 9. Comparison of the OEC positioning relative to the underlying transmembrane helices based on Fig. 8. C. reinhardtii (blue hatch), S. elongatus (red hatch), and spinach (green hatch) are shown. Coloring of the helices is as given in Fig. 7.

DISCUSSION

Here we report the first 3D structural models of a supercomplex isolated from the green alga Chlamydomonas reinhardtii and of a core dimer complex isolated from the thermophilic cyanobacterium Synechococcus elongatus. Although both structures have been calculated from data using negatively stained preparations and are limited to 30-Å resolution, they allow some important comparisons and conclusions to be made about the structure of PSII.

(i) The fact that a particle very similar to that isolated from spinach exists in C. reinhardtii suggests that the LHClI-PSII supercomplex may be a basic unit in chlorophyll-6-containing eukaryotic organisms. Based on studies with spinach, the LHClI-PSII supercomplex binds about 200 chlorophylls per particle and, therefore, 100 chlorophylls per reaction center, whereas the rest are chlorophyll a. The chlorophyll a/b ratio is consistent with each supercomplex containing one trimer of LHClI and a single copy each of CP26 and CP29 per reaction center (18). About 30% of these are chlorophyll b, whereas the rest are chlorophyll a. The chlorophyll a/b ratio is consistent with each supercomplex containing one trimer of LHClI and a single copy each of CP26 and CP29 per reaction center (18). The chlorophyll a/b ratio is consistent with each supercomplex containing one trimer of LHClI and a single copy each of CP26 and CP29 per reaction center (18).

(ii) The core dimer of S. elongatus has a structure remarkably similar to that of the core dimer of spinach with the exception of the OEC proteins. This similarity was noted earlier (30), but is further confirmed here by comparison of the top projections of the 3D structures (Fig. 7). Thus the basic structural features of the PSII core dimer seems to be conserved between higher plant, algal, and cyanobacterial systems.

(iii) Because of the structural similarities between the different photosynthetic systems, it is possible to incorporate a model of transmembrane helix organization obtained by electron cryoelectron microscopy for spinach PSII (5, 6). As a consequence, a comparison of the similarities and differences in the location and nature of the OEC proteins in the different systems can be made. We conclude that in all three cases the PsbO protein is positioned on the luminal surface above the CP47/D2 side of the core. In particular, helices 5 and 6 of CP47 are well covered by the PsbO protein, and therefore the large hydrophilic loop that joins them may be involved in docking this protein. The designation of the five helices adjacent to CP47 to those of the D2 protein is tentative and based on published cross-linking studies (32). If this assignment is correct then the PsbP and PsbQ proteins are located on the luminal surface at the N-terminal end of the D1 protein and also incorporate two helices of two low molecular weight proteins. This is also true for the densities of D/D’ in the structure of S. elongatus, which we attribute to PsbU and PsbV (Cyt c550). Because the combined molecular mass of PsbU and PsbV is 27 kDa then it is not surprising that they would appear to be reduced in size and have a smaller contact site with the surface of the core compared with the PsbP/PsbQ proteins, which have a combined real molecular mass of about 46 kDa.

Within the low resolution of the model, it is worthy of note that the position of the center of the mass attributed to the 33-kDa protein, relative to the underlying transmembrane helices, is conserved for all three structural models. Moreover it seems that the PsbP/PsbQ proteins of spinach C. reinhardtii and the PsbU/PsbV of S. elongatus are located over the same regions of the D1 protein and incorporate the two helices of unknown origin located at the N terminus of the D1 protein. Further details will almost certainly emerge from high resolution studies using non-stained complexes and cryoelectron microscopy.

(iv) Both structures presented indicate that the 17-kDa and PsbU extrinsic proteins are attached to the surfaces of the 23-kDa and PsbV (Cyt c550) extrinsic proteins, respectively, for algal/higher plants and cyanobacterial systems in line with previous binding and cross-linking studies (35, 36). However, our single-particle analyses indicate that the 23-kDa and PsbV (Cyt c550) extrinsic proteins are located adjacent to the 33-kDa protein. This arrangement is also consistent with published experiments (35–37), which indicate that the 33-kDa protein facilitates the binding of the 23-kDa/PsbV proteins, but its presence is not absolutely necessary for their attachment to the luminal surface. In fact, our structural models, derived from single-particle analyses, indicate that the densities assigned to the 33- and 23-kDa/PsbV proteins are in contact and that this contact could be even more extensive in regions closer to the luminal surfaces.

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