The Location of Plastocyanin in Vascular Plant Photosystem I*

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Stuart V. Ruffle‡, Aziz O. Mustafa§, Ashraf Kitmitto§, Andreas Holzenburg¶, and Robert C. Ford§

From the ‡School of Biological Sciences, University of Exeter, Exeter, EX4 4PS, United Kingdom, the §Department of Biomolecular Sciences, University of Manchester Institute of Science and Technology, Manchester, M60 1QD, United Kingdom, and ¶Microscopy and Imaging Center, Department of Biology, Department of Biochemistry and Biophysics, Texas A&M University, College Station, Texas 77843-2257

We have studied the binding sites of the electron donor and acceptor proteins of vascular plant photosystem I by electron microscopy/crystallography. Previously, we identified the binding site for the electron acceptor (ferredoxin). In this paper we complete these studies with the characterization of the electron donor (plastocyanin) binding site. After cross-linking, plastocyanin is detected using Fourier difference analysis of two dimensionally ordered arrays of photosystem I located at the periphery of chloroplast grana. Plastocyanin binds in a small cavity on the luminal surface of photosystem I, close to the center and with a slight bias toward the Psal subunit of the complex. The recent release of the full coordinates for the cyanobacterial photosystem I reaction center has allowed a detailed comparison between the structures of the eukaryotic and prokaryotic systems. This reveals a very close homology, which is particularly striking for the luminal side of photosystem I.

The multisubunit protein complexes responsible for the light reactions of photosynthesis are found in the thylakoid membranes within the chloroplasts of vascular plants. Photosystem I (PS-I) is found at the edges of the granal stacks and in the stromal lamellae of these thylakoid membranes (1, 2). PS-I catalyzes the part of the light reactions responsible for the absorption of light energy and generating reduced ferredoxin (Fd, ferredoxin; MOPS, 4-morpholinepropanesulfonic acid). The three-dimensional structure of a cyanobacterial PS-I reaction center has been described for Synechococcus elongatus (4–8) to a current resolution better than 3 Å resolution. This recent release of the full coordinates for the cyanobacterial photosystem I reaction center has allowed a detailed comparison between the structures of the eukaryotic and prokaryotic systems. This reveals a very close homology, which is particularly striking for the luminal side of PS-I.

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Two-dimensional crystals of a P22,2, plane group occurring at the edges of grana in spinach thylakoids have been shown to contain PS-I and have yielded structural data to 2.7 nm (2) and refined three-dimensional data to 2.5 nm resolution (9). Unlike cyanobacteria, spinach PS-I does not appear to form trimers but does show many common structural features (2, 9). In neither of the studies on spinach (2, 9) were the mobile electron carriers Pc and Fd retained. However, studies on the binding site for Fd, the terminal mobile electron acceptor in PS-I, have recently been possible (10) using a cross-linking and image analysis approach.

In-vivo, cyanobacterial and algal PS-I can be reduced by either Pc or the alternative electron donor cytochrome c₆, whereas vascular plant PS-I is reduced only by Pc. Structural insight into Pc binding in cyanobacteria has been derived from modeling studies using PS-I from the cyanobacterium Synechococcus elongatus and Pc from Enteromorpha prolifera (a green alga) (7). This study concluded that the likely Pc binding site was in an indentation on the luminal surface of the PS-I complex. In this article we present data concerning the location of the vascular plant Pc binding site following chemical cross-linking of the native subunit to two-dimensional crystalline arrays of spinach PS-I.

EXPERIMENTAL PROCEDURES

Thylakoid membranes were prepared from market spinach (Spinacia oleracea). A two-step incubation procedure was used to prepare PS-I crystal-containing grana membranes as previously described (2, 10). Samples were prepared for electron microscopy as in (2, 10). Crystalline areas were selected using CRISP (11) and then processed using the lattice unbending procedures in the Medical Research Council Laboratory of Molecular Biology suite of programs (12). The final data set of 450 structure factors were merged from 3209 observations extracted from 12 crystals. Structure factors were calculated using vector summation and with amplitude weighting using the program TRIMERGE (11). Fourier vector difference maps were calculated using the CCP4 suite of programs (13).

The calculated projection maps of cyanobacterial PS-I and the docking models were generated using SPIDER (14) from the protein data bank coordinates of the relevant proteins and protein complexes. Three-dimensional coulomb density maps were calculated from the coordinates, and a voxel size of 3 Å was applied with e.g. 64 × 64 × 64 voxels for a PS-I monomer. The resolution of the map was then curtailed to 25 Å using a three-dimensional Fourier low-pass filter. Sections (slices) through the density map were taken parallel to the putative membrane plane, and luminal and stromal slices were identified. Stromal and luminal projection maps were then calculated by averaging the luminal or stromal slices. Finally, to allow comparison with the experimental data with the P22,2, unit cell, the stromal map was flipped, simulating the screw axis.

Chemical cross-linking between PS-I from crystals and spinach Pc was essentially an adaptation of the method described by Lelong et al. (15). Pc, (a kind gift of Dr. K. Oleson, Goteborg University, Goteborg, Sweden) was cross-linked to PS-I crystal-containing samples at 4 mg/ml chlorophyll by incubating for 30 min at room temperature with 5 µM Pc, 2 mM N-ethyl-3-(3-dimethylaminopropyl) carbodiimide, 2 mM sulfo-N-hydroxysulfosuccinimide in 20 mM Hepes-NaOH, pH 7.5, and 5 mM MgCl₂. The cross-linking was stopped by addition of an equal volume of 0.2 M ammonium acetate. The crystals were then washed twice with 20 mM Tricine-NaOH, pH 7.8, and then resuspended in 20 mM Tricine-NaOH.
NaOH, pH 8.0, and 20% v/v glycerol before storage at −80 °C. Samples were mounted for electron microscopy at a chlorophyll concentration of 30–60 μg ml⁻¹.

Functional Pc binding was detected using an assay that monitors P700⁺ re-reduction as a percentage of control levels during illumination. The open symbols represent the percent additional reduction of P700⁺ that takes place after addition of excess Pc (an indication of the number of free, uncross-linked PS-I sites remaining). The data showed that functional binding of Pc occurs in the presence of cross-linked Pc and comparing those rates with the side of the crystal in contact with the specimen support film, then the up complexes give rise to a distinctively different appearance in projection from the down complexes.

RESULTS

Pc Binding Site—Cross-linking of Pc to PS-I was checked by monitoring the levels of free Pc in the supernatant after centrifugation of the cross-linker-treated membranes. This showed cross-linking of Pc over the 0–20 μm range, with little additional cross-linking above 20 μm Pc (data not shown). Whether the cross-linked Pc was functionally bound to PS-I was established by monitoring the rate of re-reduction of P700⁺ in the presence of cross-linked Pc and comparing those rates with maximal rates achieved after the addition of excess free Pc (Fig. 1). The data showed that functional binding of Pc occurs in the micromolar range, and saturation seems to occur at concentrations >25 μm with an apparent Kᵦ in the region of 10 μm. These levels are consistent with reported binding in this range (16). At least 80% of the binding sites appear to be available for functional Pc cross-linking. Electron microscopy of Pc-cross-linked thylakoids containing ordered arrays of PS-I revealed that the treatment did not alter the unit cell parameters of the crystals (Table I). Moreover the different crystals were sufficiently well ordered as judged by low inter-image phase residuals (Table I) to permit a Fourier difference analysis to be carried out. Fig. 2 shows the projection maps of control (Fig. 2a) and Pc cross-linked (Fig. 2b) PS-I crystals showing four complete PS-I complexes in the unit cell. As frequently encountered for negatively stained crystals, there was differential staining of the two sides of the crystal (2, 17). Because two PS-I complexes are oriented “up” and two are oriented “down” in the p22,2 unit cell, and because stain associates preferentially with the side of the crystal in contact with the specimen support film, then the up complexes give rise to a distinctively different appearance in projection from the down complexes.

This has the advantage that luminal and stromal surfaces of the PS-I complex are readily differentiated, with the stromal surface represented top right and bottom left in the map, while the luminal surface is bottom left and top right (Fig. 2, a and b). Cross-linking with Pc (Fig. 2b) results in increased density on the luminal side of the complex in a central position. The binding also results in an extension of the differential staining effect with the luminal surface deviating more greatly from the stromal surface in its overall shape and appearance. Fourier difference analysis results in a difference map (Fig. 2c) that shows a very strong peak centered on the luminal surface. A much weaker difference peak at the edge of the stromal PS-I surface is also present but is of less significance. This is partly because of its weaker character but also because of its presence at the periphery of the stromal surface, where small differences due to stain penetration may be exaggerated.

Structural Comparison of Cyanobacterial and Plant PS-I Complexes—The full coordinates of the cyanobacterial PS-I reaction center have recently been released (8) (Protein data bank ID 1JB0). A comparison of the structures of the plant and cyanobacterial PS-I reaction centers at low (∼25 Å) resolution has therefore become possible for the first time. Fig. 3 compares the luminal (I) and stromal (II) surfaces of plant PS-I with corresponding surfaces of cyanobacterial PS-I (III, IV, respectively). A very strong resemblance is noticeable between the luminal surfaces of the plant (I) and cyanobacterial (III) complexes. Densities due to the subunits PsaF/J and PsaL are readily identifiable. Of interest is the more protruding PsaL density in the cyanobacterial structure. This subunit has been associated with trimer production in cyanobacterial preparations (18), while trimers have not been observed with plant material. The location of the main peak in the Fourier differ-

| Number of processed images | 12   | 12   |
|----------------------------|------|------|
| Unit cell dimensions:      |      |      |
| a (nm)                     | 28.4 ± 0.9 | 28.7 ± 0.5 |
| b (nm)                     | 27.6 ± 0.7 | 27.8 ± 0.7 |
| γ (°)                      | 90   | 90   |
| Two-dimensional space group| p22,2 | p22,2 |
| Average inter-image phase residual (°) | 24.7 | 25.3 |
| No. of structure factors   | 467  | 450  |
| No. of observations        | 2862 | 3209 |
| Approximate resolution limit (nm) | 1.8 | 1.8 |
| a:b axis ratio             | 0.96 | 0.96 |
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The location of plastocyanin in vascular plant photosystem I is superimposed on the plant luminal surface (thick contour, I), indicating that Pc binding occurs at a roughly central location equidistant between the PsaA and B subunits and with a slight bias toward the PsaL side. In both complexes, the putative binding site sits over a shallow depression.

The stromal surfaces of cyanobacterial (IV) and plant (II) PS-I complexes are also similar in overall shape. Again, the PsaL subunit protrudes more from the cyanobacterial complex. The stromal ridge, identified as the location of the PsaC, D, and E subunits in cyanobacterial PS-I is prominent in both structures, although the plant stromal ridge is broader with additional density close to PsaL. It is feasible that this extra stromal density could represent the plant-specific PsaH subunit, which has been associated with the PsaL subunit (19, 20) as well as with the docking of LHClII during state transitions (21).

The thick contour shows the position of the main peak in the Fourier difference analysis of Fd cross-linked PS-I crystals. The peak lies over the stromal ridge, with a bias toward the PsaE-end of the ridge. A thin ridge of density on the stromal surface is detected in both low resolution maps, (asterisk, II and IV). Examination of the cyanobacterial structure shows that this feature is partly formed by N-terminal residues 14–40 of the PsaA subunit (see “Discussion”).

Modeling of Plastocyanin and Ferredoxin Binding—Modeling of reduced Pc (from Synechococcus sp. PCC 7942) at the luminal surface of PS-I was performed using x-ray crystallographic structures of the cyanobacterial PS-I complex (8) and Pc (Protein data bank ID 1BXV) (22). Similar studies were carried out for Fd binding on the stromal PS-I surface. Modeling was performed with the aim of optimizing for four constraints: a) compatibility with the position and shape of the difference peaks in the low resolution electron crystallography maps of plant PS-I, b) avoidance of steric clashes between docking partners, c) minimization of distances for electron transfer, and d) fine tuning to include any positional data from cross-linking and to avoid of any obvious unfavorable conformations such as mismatching of hydrophobic and polar regions and close proximity of similarly charged residues. The models were then assessed by generating stromal and luminal surfaces at low resolution that could be directly compared with the results obtained for Pc and Fd cross-linked PS-I complexes. Fig. 4 shows a model with both Pc and Fd bound to the PS-I complex, and Fig. 5 compares the surfaces generated from models with the low resolution plant PS-I data.

Pc docking was assisted by the elongated shape of the molecule. It was clear that the end-on docking of a single Pc molecule as shown in Fig. 4 was compatible with the electron crystallography data (see Fig. 5, I and III). In contrast, a side-on docking produced an elongated density on the luminal surface, which was quite different from the shape of the density observed in the plant studies. Distances between the copper atom of Pc and P700 were also optimized in the end-on configuration with typical distance of 15 Å from the copper atom to the edges of the chlorophyll tetrapyrrole rings. The additional density due to Pc in the model drastically alters the profile of the simulated luminal surface of PS-I (Fig. 5, III), with weaker features becoming camouflaged by the intense Pc peak. A similar effect is observed for the experimental data (Fig. 5, I), e.g. the weak PsaL density disappears in both maps. As in Fig. 3, the luminal surface for the experimentally derived plant PS-I-Pc map corresponds quite closely to the simulation with cyanobacterial PS-I-Pc.
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The LHCI polypeptides are estimated to be present with the LHCII protein plus pigments (~30–40 kDa), a complement of eight LHCI proteins should represent the major proportion of the density in the unit cell, and the presence of even one LHCI protein ought to be detectable at 25 Å resolution. It could be argued that connections between LHCI and PS-I are weak because they are apparently disrupted by the crystallization process employed here, which includes a mild detergent treatment; but this is hard to reconcile with the observation of detergent-solubilized particles (19) where LHCI and PS-I co-purify. Cross-linking studies of detergent-solubilized and purified spinach PS-I/LHCI (19) demonstrated considerable cross-linkage between the four LHCI polypeptides but did not detect extensive association of LHCI with PS-I core polypeptides except PsaK and possibly PsaG. Thus there is still much to be understood about the association of PS-I with its light-harvesting antennae proteins.

Site-directed mutagenesis has shown that a hydrophobic patch containing Leu, Gly, and Ala on Pc is crucial for binding and electron transfer to PS-I. This patch is close to the copper atom binding site in Pc (24). Surface-charged residues in Pc and PsaF have also been implicated in docking of Pc in plants, in particular acidic Glu and Asp residues on Pc and Lys and Arg residues on the N-terminal region of PsaF (25–28). This electrostatic interaction may be required for initial attraction to and/or stabilization of Pc on the luminal surface of PS-I rather than in a lock-and-key type of docking. The oxidation kinetics of Pc have been measured under many conditions, with electron transfer usually at least biphasic in plants. A fast phase of around 10–20 µs and a slower phase of around 200 µs have been observed (29–30). The fast electron transfer step has been associated with tightly bound Pc, while the slower phase may be due to loosely associated Pc or due to inter-Pc transfer (29–32). In this study, we find evidence for a single Pc molecule bound to PS-I, which is presumably the Pc associated with the fast electron transfer event. The distance (~15 Å) between the copper atom of Pc and the edges of the special pair (P700) of PS-I in the model is consistent with the fast electron transfer. The modeled Pc is close (18 Å) to the N terminus of the cyanobacterial PsaF subunit. Higher plant PsaF, which has an N-terminal extension that has been implicated in Pc binding should be able to interact more intimately with plant Pc (28). At the bottom and center of the shallow luminal depression is the pseudo-2-fold symmetry axis of the heterodimeric reaction center. Two surface helices provided by the PsaA and B subunits are related by the pseudo-symmetry, and they are situated between the special pair of chlorophylls (P700) and the luminal surface in contact with the aqueous phase. Mutation of these helices is known to affect electron transfer (33). Two highly conserved tryptophan residues exactly straddle the 2-fold axis with their aromatic rings facing into the aqueous medium. In the model these are in close proximity to the hydrophobic patch on the surface of Pc.

The modeled Fd is close to PsaC and PsaE subunits and on top of the stromal ridge. The docking configuration also allows contact between PsaD and Fd via a long C-terminal arm (residues 100–138 in S. elongatus) that winds over and around the PsaC subunit. The interaction of Fd with PS-I has been studied by cross-linking, and PsaD has been identified as being of crucial importance in Fd binding (19, 34–37). Studies with Synechocystis sp. PCC 6803 have shown that Lys-106 on PsaD can be cross-linked to Glu-93 on Fd (19). In the S. elongatus PS-I structure, the equivalent Lys-104 of PsaD extends from the top of the stromal ridge. A lysine residue, Lys-34 in PsaC, has been identified as strongly influencing Fd binding and electron transfer. This residue also lies toward the top of the stromal ridge.

**DISCUSSION**

The data shown in this paper, when compared with the recently released coordinates for the cyanobacterial PS-I reaction center (8), demonstrate that cyanobacterial and plant PS-I reaction center complexes are very similar in shape and dimensions at ~25 Å resolution. Only minor differences are observed such as the slightly different protrusion of the PsaL subunit from the main body of the complex and the small additional domain in the plant stromal ridge. A conclusion that follows from this close similarity is that there is no significant density in the maps of the plant PS-I crystals for the peripheral light harvesting antennae (LHCl) proteins of PS-I. The location of these plant-specific proteins therefore remains unresolved. This is an interesting but somewhat perplexing outcome because the LHCII polypeptides are estimated to be present with a stoichiometry of about eight proteins per PS-I complex (19) in plant chloroplasts. Given the approximate mass of a single
The location of Fd as discussed in this paper is different from the location identified in studies of cyanobacterial PS-I using electron microscopy and single particle analysis (38). In the latter studies, a location off to the side of the stromal ridge was suggested with contact to PsaC, D, and E subunits as well as with the stromal surface of the PsAA subunit. A small density (marked with an asterisk in Fig. 3, II and IV), which is formed by the N-terminal residues 14–40 of PsAA, would be predicted to be involved in such contacts. Two positively charged arginine residues (Arg-40 and Arg-36) project upwards from this region and hence could provide some electrostatic interactions with Fd.

The kinetics of Fd reduction are complex, with phases in the 0.5–100 μs range (39). These studies place broad limits on the possible electron transfer distance between the iron-sulfur center of PsaC and Fd and could be taken as indicating that alternative docking configurations might exist as discussed in a recent review (39). In the model shown in this report, a distance of about 18 Å for electron transfer is implied, which is slightly longer than the distance (14 Å) reported for a location to the side of the stromal ridge (7).

In conclusion, information on the binding of mobile water-soluble electron carriers to PS-I has been obtained in low resolution electron crystallographic studies. These data allow the positioning of Pc and Fd with reasonable accuracy, and when combined with high resolution data for cyanobacterial PS-I, as well as cross-linking and mutagenesis data, they now form the basis for the generation of testable models of functional PS-I-Pc and PS-I-Fd complexes. These models should be refined using molecular dynamics simulations and energy minimization and tested using site-directed mutagenesis.

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