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A NEW CHLOROPHYLL-PROTEIN COMPLEX RELATED TO PHOTOSYSTEM I IN *CHLAMYDOMONAS REINHARDII*

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A new chlorophyll-protein complex, CP O, was isolated from *Chlamydomonas reinhardii* using lithium dodecyl sulfate polyacrylamide gel electrophoresis run at 4°C. A similar complex is recovered using Triton/digitonin solubilization of thylakoid membranes of the F54-14 mutant lacking in CP I and ATPase. CP O is enriched in long-wavelength chlorophyll *a* and contains five polypeptides (27.5, 27, 25, 23 and 19 kDa). Its 77 K fluorescence emission spectrum peaks at 705 nm while CP II have an emission maximum at 682 and 720 nm, respectively. Comparison of the polypeptide pattern of the wild type and AC40 mutant of *C. reinhardii* shows that the five CP O polypeptides are specifically lacking in the mutant. Although the 77 K emission originating from the Photosystem (PS) I pigments is lower in the mutant than in the wild type, the two spectra show the same peaks at 686, 694 and 717 nm. However, comparison of the 77 K emission spectrum of the F14 mutant lacking in CP I with that of the double mutant AC40-14 lacking in CP I and CP O shows the absence in the latter of the large emission band peaking at 707 nm. The 707 nm emission is thought to arise from some PS I antennae and is quenched in the wild type by the presence of PS I traps located in CP I. We conclude that CP O is a part of the PS I antenna in *C. reinhardii* which controls the 707 nm fluorescence emission.

Introduction

Most of our knowledge of chlorophyll-protein complexes has come from polyacrylamide gel electrophoresis of thylakoid membranes solubilized with anionic detergents. In addition to the finding of CP I and CP II [1,2] a number of workers have detected new chlorophyll-protein complexes by improving the techniques or studying new photosynthetic organisms [3].

Furthermore, greening experiments and fractionation of the thylakoid membranes using neutral detergents have provided information on the organization of the light-harvesting antenna. However, the relationship that exists between spectrally identified pigment beds 'in vivo' and the chlorophyll-protein complexes isolated by different techniques remains unsatisfactory in most cases.

The assignment of CP I to the PS I reaction center is the most reliable correlation established thus far. This arises from the ability of the isolated CP I to perform the primary PS I photoreaction [4,5]. A good correlation also exists in *Chlamydomonas reinhardii* between CP III and CP IV isolated by polyacrylamide gel electrophoresis in the presence of LDS at 4°C [6] and PS II reaction centers [7,8]. However, we still do not know

Abbreviations: CP, chlorophyll-protein complex; LDS, lithium dodecyl sulfate; PS, photosystem; Chl, chlorophyll; LHC, light harvesting chlorophyll-protein complex, Mes, 4-morpholineethanesulfonic acid.

whether both complexes or one only constitute the reaction center.

Most unsatisfactory is our understanding of the organization of the light-harvesting antenna. A number of complexes binding Chl *a* and *b* have been isolated by different techniques, but their relation to one another has not been established. For instance, the number of polypeptides claimed to be associated with the light-harvesting Chl *a*/*b*-protein complex varies from one to six [3,9]. The assumption that PS I and PS II have structurally independent antenna, although postulated by several groups [10,11], still has little solid support. Some Chl *a*/*b*-protein complexes with higher Chl *a*/Chl *b* ratios than the main Chl *a*/*b*-protein complex (also termed LHCP, LHC, CP II) have been described by Machold et al. [12,13] and Camm and Green [14]. These are candidates for a part of the PS I antenna located outside CP I. Mullet et al. have recently shown, both by greening experiments [15] and Triton fractionation of the thylakoid membranes in pea [16], that at least three polypeptides, different from the apoprotein of CP I, control the long-wavelength fluorescence emission (736 nm) at 77 K and are involved in the organization of the PS I antenna.

We have isolated a new chlorophyll-protein complex, CP O, in *C. reinhardii* by polyacrylamide gel electrophoresis in the presence of LDS at 4°C. This complex, although it differs from an LHC fraction obtained by Triton-digitonin solubilization of the thylakoid membranes, shares some polypeptides with the CP II isolated on LDS-polyacrylamide gel electrophoresis. Study of a pigment mutant lacking in CP O provides supporting evidence that this complex corresponds to a part of the PS I antenna.

Material and Methods

The wild-type strain of *C. reinhardii* and the F14, AC40, AC40-14 and F54-14 mutants were grown in Tris-acetate/phosphate medium [17] at 25°C under an illumination of 150 lx.

The AC40 mutant was provided by courtesy of Dr. Chua. This strain does not synthesize chlorophyll in the dark, and is not distinguishable from the wild type when grown under bright light (2000 lx or more). Under moderate illumination (150 lx) AC40 displays a reduced amount of chlorophyll per cell and distinct thylakoid polypeptides deficiencies.

The procedure for the isolation of chlorophyll-protein complexes from F54-14 using Triton and digitonin is similar to that described by Diner and Wollman [7] for the isolation of PS II particles.

LDS gels were made using 12% acrylamide and run at 4°C; SDS gels were made using a 7.5–15% acrylamide gradient and run at room temperature. Two-dimensional gels were obtained using slab gels in the two dimensions. An unstained gel strip showing the chlorophyll-protein complexes separated in the first dimension (LDS gel at 4°C using 12% acrylamide) was inserted into the stacking gel of the second dimension (SDS gel using a 7.5–15% acrylamide gradient) and run at room temperature. The resulting gel was stained with Coomassie brilliant blue. All types of gels were run in the system described by Laemmli [19] except that SDS or LDS was omitted from the stacking and resolving gels. 1 mM EDTA was added to the upper reservoir buffer only when gels were run at room temperature. Samples for electrophoresis, were prepared according to Ref. 9 using 1% SDS or LDS at a detergent/chlorophyll ratio of 10 (w/w) except when otherwise indicated. Prior to solubilization, thylakoid membranes were resuspended in 0.1 M dithiothreitol and 0.1 M Na_2CO_3 for SDS gels or in 0.4 M Tris-HCl, pH 8.8, for LDS gels.

Chl *a*/Chl *b* ratios were calculated according to the procedure of Ogawa and Shibata [20]. Absorption spectra were recorded using a Cary 118 spectrophotometer. Fluorescence emission spectra at 77 K were recorded using a device built by Jupin and described in Ref. 21. Corrections have been made for the response of the photomultiplier and the transmission of the monochromator using a standard ISCO lamp No. 413.

Results

Fig. 1a depicts a 12% acrylamide gel loaded with LDS-solubilized thylakoid membranes of the wild type of *C. reinhardii* and of the F14 mutant lacking CP I [22]. The gel was run at 4°C to stabilize chlorophyll-protein association. The electrophoresis pattern of the wild type shows, in

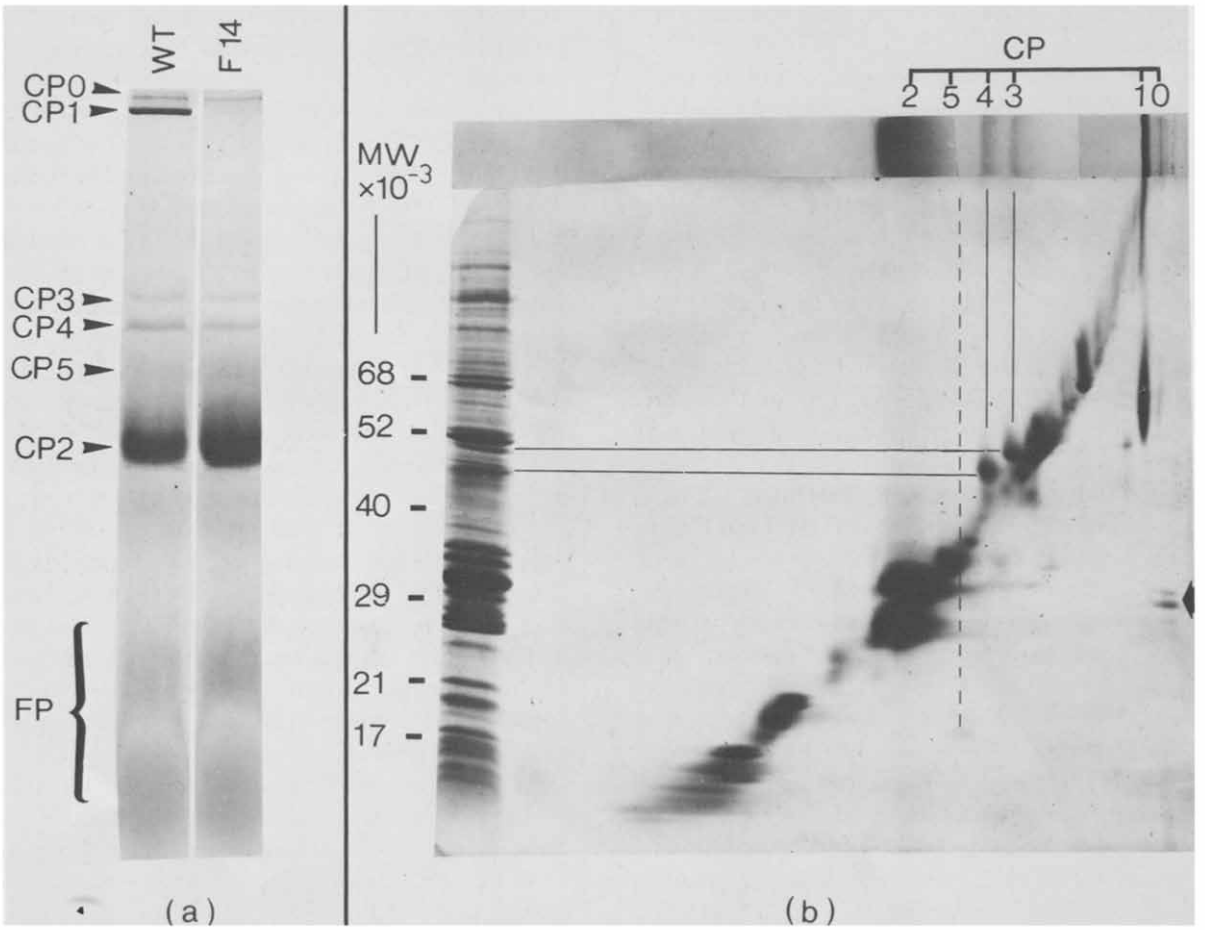

Fig. 1. (a) LDS gels (12% acrylamide) at 4°C of thylakoid membranes from the wild type (WT) and F14 strains of *C. reinhardii*. The gel is unstained. Only the chlorophyll-protein complexes are visible (FP, free pigment). (b) Electrophoretic pattern of wild-type thylakoid membranes in a two-dimensional gel. First dimension: LDS, 12% acrylamide, 4°C. Second dimension: SDS, 7.5% acrylamide gradient, room temperature. A gel strip showing the chlorophyll-protein complexes (CP) resolved in the first dimension is mounted on top of the figure. A gel run at room temperature of nonheated wild-type thylakoid membranes shows the polypeptides resolved in the second dimension on the left of the figure. ➡: polypeptides released from CP O (25–30 kDa region); (- - - - - -) polypeptides released from CP V; (———) polypeptides released from CP III and CP IV.

order of decreasing mobility, free pigments, CP II, CP V already described by Delepelaire and Chua [6], CP IV and CP III associated with PS II reaction centers [6], CP I associated with PS I reaction centers [2] and a faint band hereafter referred to as CP O. Chlorophyll-protein complexes of lower mobility than CP I have already been found in higher plants [12,23,24]. All of these were described as oligomeric forms of CP I. In the present case, however, the CP O band remains in the F14 mutant lacking CP I.

We then performed two-dimensional gel electrophoresis of the wild-type membranes (Fig. 1b) in order to determine the polypeptide composition of this complex. A number of off-diagonal spots appear and correspond to complexes that have been dissociated in the second dimension. Indicated on the figure are the polypeptides released from CP V (band 11, 30.5 kDa; and band 23, 18.5 kDa) and those corresponding to the apoproteins of CP III and CP IV (band 5, 50 kDa; and band 6, 48 kDa). The poorly resolved spot at the top of the

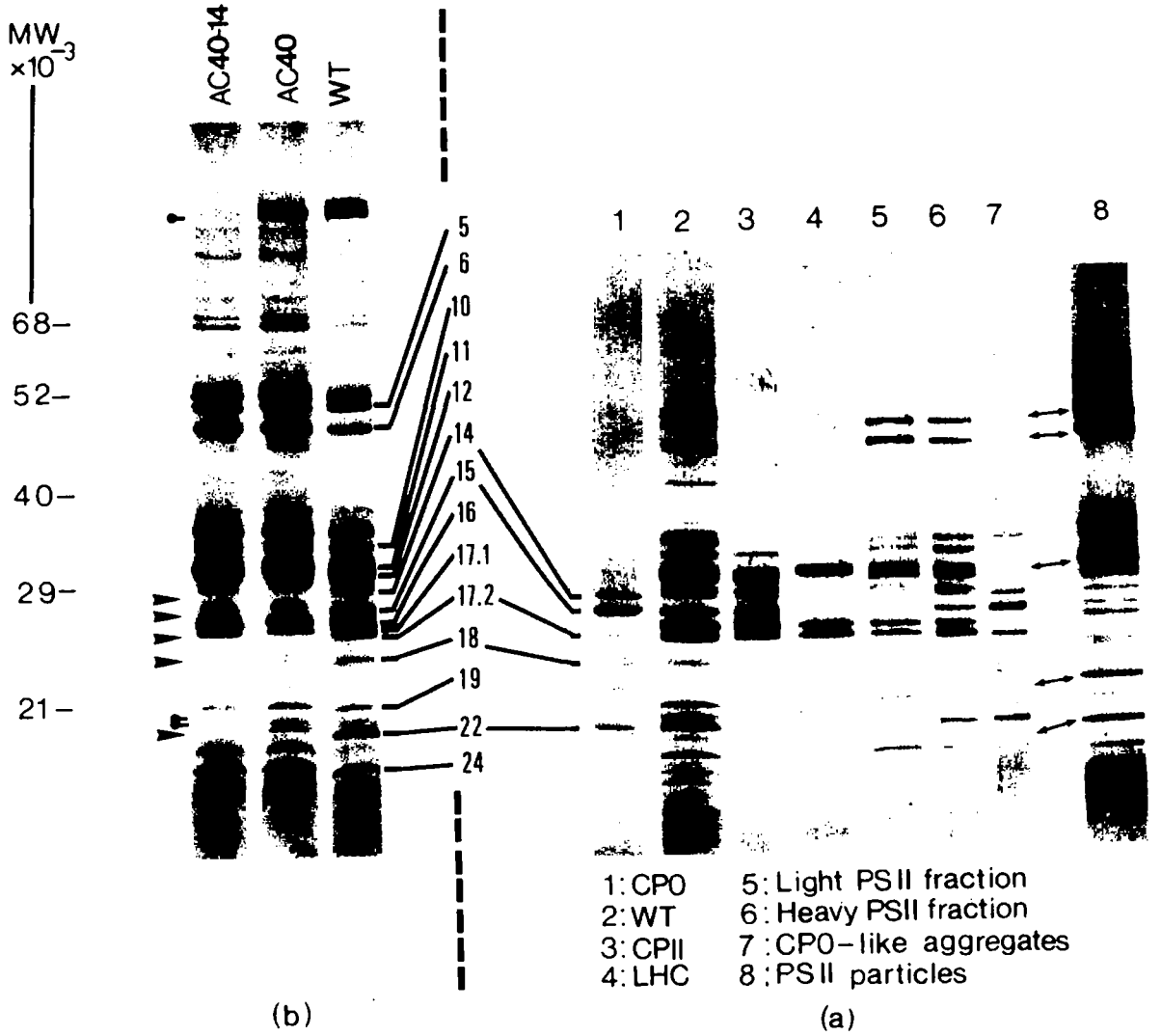

Fig. 2. SDS gels at room temperature of thylakoid polypeptides using a 7.5–15% acrylamide gradient. (a) CP O and CP II bands were cut out from an LDS gel at 4°C, inserted in slots 1 and 3 and run at room temperature in the presence of SDS. Slots 4–8 correspond to several sucrose gradient fractions obtained after Triton-digitonin solubilization of thylakoid membranes from the F54-14 mutant. (b) Polypeptide pattern of thylakoid membranes from the wild type (WT), AC40 and AC40-14 strains. The five CP O polypeptides lacking in the AC40 and AC40-14 mutants are indicated by arrows. The latter is also lacking in the three bands (indicated by ●—) usually missing in PS I-deficient mutants [22]. Polypeptides are described by their number according to Chua and Bennoun [25] except for 17.1 and 17.2 (see text). Polypeptide 14 in the wild-type pattern is better resolved in a, slot 2, than in b.

two-dimensional gel on the right corresponds to the apoprotein of CP I (band 2, 66 kDa). Further to the right are seen at least two spots in the 25–30 kDa region which correspond to the dissociation of CP O. The detection of these polypeptides is, however, limited by the small proportion of non-dissociated CP O in the first dimension.

We then cut directly the CP O band from an LDS gel run at 4°C using F14 thylakoid membranes and reran it at room temperature. Starting with more material, satisfactory concentrations of the individual polypeptides were obtained (Fig. 2a, slot 1). Five major polypeptides are resolved. The main one corresponds to polypeptide 15 (27 kDa).

The others are, respectively, polypeptide 14 (27.5 kDa), 18 (23 kDa), 22 (19 kDa) and a polypeptide migrating at the front of 17 that we have numbered 17.2 (25 kDa). A contamination by CP I is currently found when wild-type membranes are used in the same procedure (data not shown).

The absorption spectrum at room temperature and the fluorescence emission spectrum at 77 K of CP O were compared with those of CP II and CP I isolated under the same conditions (Fig. 3). CP O is enriched in long-wavelength Chl *a* and has a red absorption maximum close to that of CP I. Examination of the blue region of the spectrum shows that CP O contains some carotenoids and Chl *b*. However, the Chl *a*/Chl *b* ratio is significantly higher than that in CP II (6.3 vs. 0.86). The latter complex has its main 77 K emission band at 682 nm and a long-wavelength emission in the 740 nm region. The emission of CP O peaks at 705 nm while that of CP I is at a still longer wavelength, 720 nm. The 720 nm emission is an order of magnitude lower due to the quenching by PS I centers. Both CP I and CP O have a short-wavelength emission, probably due to free chlorophyll released from the complexes during freeze-thawing of the gel bands.

We then looked among pigment-deficient mutants of *C. reinhardii* for a strain lacking specifically CP O. Two strains which are yellow in the dark display such a deficiency when grown under suitable illumination. We chose one of them, AC40, that we analyzed in detail. Fig. 2b shows the thylakoid polypeptide pattern of wild-type and AC40 strains. We observe that AC40 is depleted in the polypeptides of CP O (bands 14, 15, 17.2, 18 and 22, indicated by arrows).

We therefore expected significant modifications of the spectral characteristics of the AC40 mutant with respect to that in the wild type.

The 77 K emission spectra of both strains are shown in Fig. 4a. The same three emission peaks are visible: 696 and 694 nm originating from PS II and 717 nm which corresponds to some PS I antenna disconnected from PS I centers during freezing [26–28]. The 717 nm/686 nm emission ratio is smaller in the mutant, but it strongly depends on the state of illumination of the cells during freezing [29] as well as on the state of PS II → PS I energy transfer in each strain [30]. Therefore, we

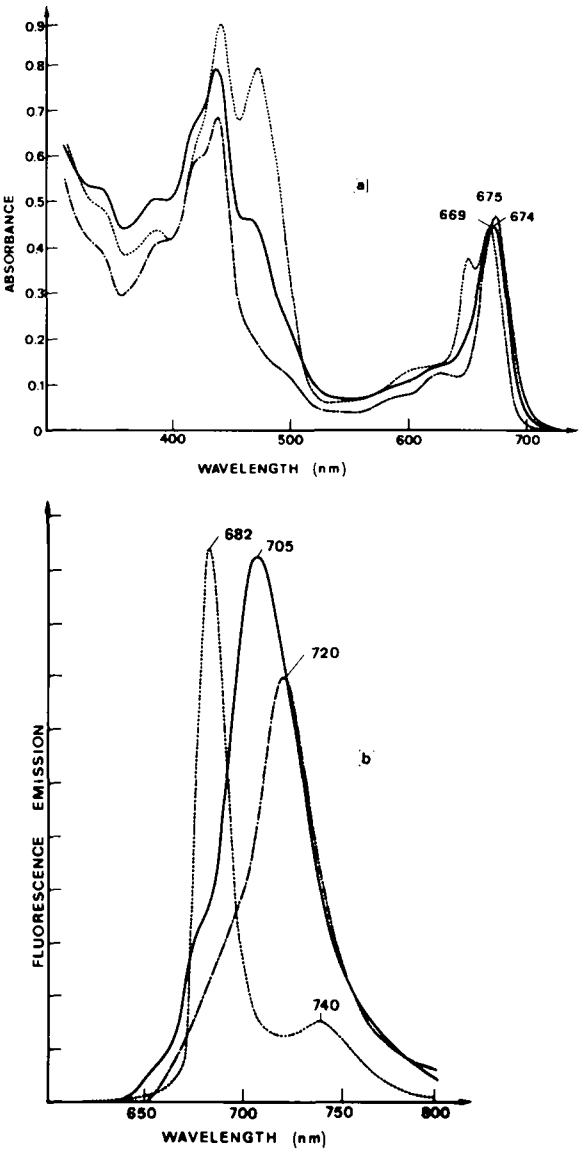

Fig. 3. Spectral characteristics of CP O, CP I and CP II isolated on LDS gels at 4°C. (a) Absorption spectrum at room temperature. (b) Fluorescence emission spectrum at 77 K. The scale of sensitivity is an order of magnitude higher for the CP I spectrum. (———) CP O, (– – – –) CP I, (· · · · · ·) CP II.

conclude that no major change occurs in the 77 K emission spectrum when only CP O is missing from the thylakoid membranes.

Fig. 4b shows the 77 K emission spectra of a mutant lacking in CP I (F14) and of a double mutant lacking both CP I and CP O (AC40-14). The polypeptide pattern of the latter is shown in

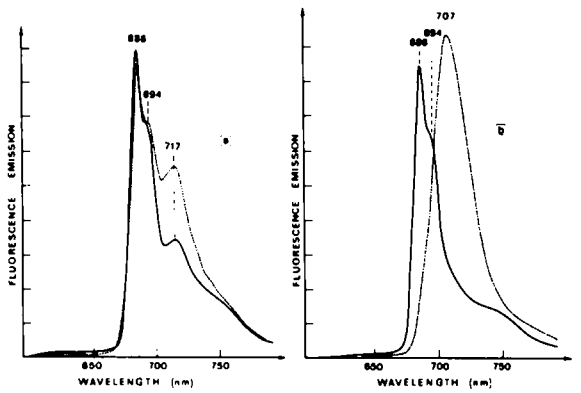

Fig. 4. Fluorescence emission spectrum at 77 K using whole cells of the: (a) wild type (·····) and AC40 (———) mutant lacking in CP O (scale: 1). (b) F14 (·····) and AC40-14 (———) mutants (scale 1/4 and 1/2, respectively).

Fig. 2b. The fluorescence emission intensity is drastically increased in the F14 mutant where PS I centers are missing from the thylakoid membranes. A large emission band peaking around 707 nm dominates every other band. Interestingly enough, the 707 nm emission band is lacking in the double mutant AC40-14. There remain only the PS II peaks at 686 and 694 nm with a shoulder at a longer wavelength, 740 nm. Thus, the absence of CP O is correlated with the lack of the pigments responsible for the 707 nm emission. This is further supported by the observation of the 77 K fluorescence emission spectrum of isolated CP O which peaks at 705 nm (Fig. 3b).

Whereas CP O and CP I are entirely distinct complexes, we mentioned that CP O and CP II which display markedly different pigment compositions both contain polypeptides migrating in the position of bands 14 and 15 (Fig. 2a, slots 1 and 3). We attempted to isolate a light-harvesting complex lacking bands 14 and 15 but containing the other polypeptides found in CP II. This was achieved by the analysis of the chlorophyll-protein complexes obtained in the course of the preparation of PS II particles using the F54-14 mutant of *C. reinhardii* lacking in ATPase and PS I centers. This preparation has been described previously [7] and can be summarized as follows: purified thylakoids [25] are solubilized in 1% Triton and 1.25% digitonin (2 h at 4°C). The $100000 \times g$ supernatant (solubilized membranes) is loaded on a 10–40% sucrose gradient containing 20 mM Mes, pH 5.9, 0.03% Triton. Two green PS II active fractions (termed 'light' and 'heavy') are recovered below a dark green LHC fraction.

These three fractions were run on SDS gels (Fig. 2a, slots 4–6). One observes the presence of three polypeptides in LHC (band 11, 30.5 kDa; 16, 26.5 kDa; 17, 25 kDa) and an association of these three with the five polypeptides currently found in purified PS II particles (band 5, 50 kDa; 6, 47 kDa; 12, 30 kDa; 19, 21 kDa; 24, 18 kDa: Fig. 2a, slot 8 and Refs. 7 and 8) in the 'light' PS II fraction. The 'heavy' PS II fraction contains the same polypeptides as the 'light' fraction plus the five CP O polypeptides described in this paper. Two additional polypeptides in the 33 kDa region are also present, one of which is currently found in CP II.

An additional solubilization step can be provided by the addition of a 1% Triton layer on top of the gradient. One then recovers two main green bands corresponding respectively to an LHC fraction of the same composition as that in the first gradient type (Fig. 2a, slot 4) and to highly purified PS II particles (Fig. 2a, slot 8). There is in addition a particulate fraction at the bottom of the

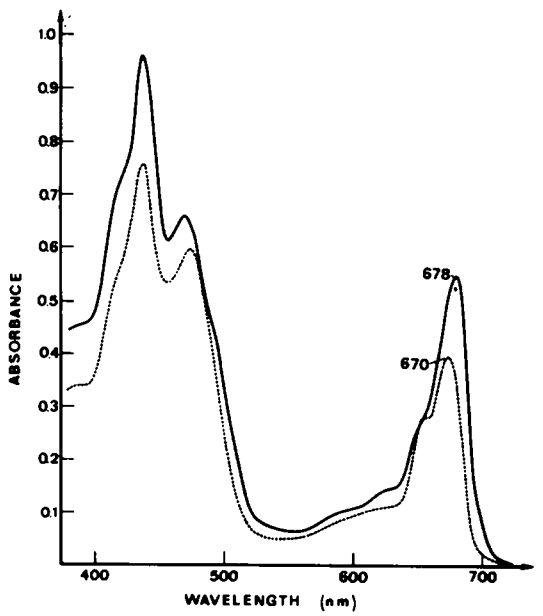

Fig. 5. Absorption spectrum at room temperature of CP O-like aggregates (———) and LHC (·····).

gradient. This high-density fraction consists mainly of the CP O polypeptides (Fig. 2a, slot 7). Its absorption spectrum shares many characteristics with that of CP O (Fig. 5): the same enrichment in long-wavelength Chl *a*, and the presence of some carotenoids and Chl *b*. The different detergent systems used for the preparation of CP O and CP O-like aggregates as well as some variations in the relative amounts of each polypeptides between the two may explain the shift observed in the red maximum of absorption.

The LHC fraction displays a higher Chl *a*/Chl *b* ratio than does CP II, 1.76 vs. 0.86. This is consistent with the fact that the free pigment zone observed after gel electrophoresis consists mainly of Chl *a*. Some of these free pigments must have been detached from CP II during the eletrophoretic migration, leaving an apparent excess of Chl *b* bound to the complex.

The above results show that most of the polypeptides found in CP II (Fig. 2a, slot 3) can be separated into two different complexes, LHC and CP O. Furthermore, we observe on the sucrose gradient a direct association between LHC and PS II particles. In contrast, CP O is found in association with the 'LHC-PS II center' complex, but not with the PS II particles alone.

Discussion

Since the observation of three green bands after polyacrylamide gel electrophoresis in the presence of SDS of thylakoid membranes, CP I, CP II and free pigments [1,2], considerable controversy has occurred concerning the actual composition of CP II. Focusing on *C. reinhardii* only, one notices an increasing complexity in the polypeptide composition of CP II as time passes: one polypeptide only in 1976 [31], three in 1977 [32] and six in 1981 [9]! Meanwhile, published works on CP II from higher plants also report from one to six polypeptides [3,9]. A recent procedure for the isolation of LHC using Triton X-100 developed by Burke et al. [33] has yielded three polypeptides in pea and barley [33,34]. We stress that the main Chl *a*/*b*-protein complex when isolated on gels in the presence of anionic detergent is referred to as CP II whereas it is refered to as LHC when obtained on a sucrose gradient after mild detergent treatment of the thylakoid membranes.

In the present work, we have extracted both the CP II on LDS gels at 4°C and obtained an LHCP gradient fraction after Triton-digitonin extraction of the thylakoid membranes of *C. reinhardii*. The latter fraction resembles that found in higher plants. It contains three polypeptides (30.5, 26.5 and 25 kDa in *C. reinhardii* vs. 30, 25 and 23 kDa in pea [33], has a Chl *a*/Chl *b* ratio of 1.75, but its maximum of absorption at room temperature in the red region is blue shifted (670 nm) as compared to that reported for the LHC in pea (676 nm). Such a difference can be accounted for by different amounts of Triton bound to the complex or by a different state of aggregation after its isolation by the two procedures. It is of interest to note that the three polypeptides that we find in the LHC cross-react immunologically among themselves [35], have similar amino acid composition and identical patterns of N-terminal amino acids [36].

On the other hand, the composition of the CP II band cut out from LDS gels which contains six polypeptides, three of which constitute our LHC fraction, confirms the results of Delepelaire and Chua [9]. The very careful analysis of CP II undertaken by these authors rules out the possibility that the three others are contaminants. The six polypeptides have an anomalous migration pattern with respect to the acrylamide concentration which is characteristic of their involvement in chlorophyll proteins. The marked difference in the polypeptide composition of the LHC and CP II isolated in *C. reinhardii* in the present work illustrates the dependence of the characterization of chlorophyll-binding complexes on the isolation procedure.

The involvement of polypeptides 14 and 15 found in CP II in a new complex CP O isolated on LDS gels at 4°C should bring new insights into the organization of the light-harvesting antenna in *C. reinhardii*. CP O, which has a lower mobility than CP I, is different from CP Ia, an oligomeric form of CP I, previously observed in spinach [23], tobacco [24] and barley [12]. Firstly, it is still present in a mutant lacking CP I; secondly, its absorption spectrum at room temperature, although enriched in long-wavelength Chl *a*, shows a higher contribution of carotenoids and Chl *b* than

that of CP I (Chl *a*/Chl *b* ratio 6.3). Thirdly, the fluorescence yield of CP O at 77 K is higher than that of CP I which is quenched by PS I centers and peaks at a shorter wavelength, 705 nm vs. 720 nm. Fourthly, its polypeptide composition, although showing some CP I contamination when wild-type thylakoid membranes are used, consists mainly of two polypeptides also found in CP II (14/27.5 and 15/27 kDa) plus three minor ones (17.2/25, 18/23 and 22/19 kDa). This polypeptide composition is further confirmed by the analysis of the AC40 mutant lacking in CP O and that of Triton/digitonin-solubilized thylakoids of the F54-14 mutant, lacking in CP I and ATPase, after sucrose gradient centrifugation (CP O-like aggregates). The latter procedure shows that the polypeptides involved in LHC and CP O have different interactions with PS II centers. Therefore, it is possible to obtain the PS II centers in three states: (1) where they are associated with an oligomeric complex containing LHC and CP O polypeptides; (2) where they are associated with LHC only; (3) where they are detached from both the LHC and CP O. These two complexes are then found independently in two other fractions of the gradient.

At 77 K, an emission band of high intensity is observed at 707 nm in mutants of *C. reinhardii* lacking CP I [29]. This emission is attributed to non-CP I antenna which cannot transfer energy to PS I traps in such mutants. That CP O corresponds to this part of the PS I antenna is supported by the 705 nm emission of this isolated complex at 77 K. This is further confirmed by the absence of the 707 nm emission in the double mutant AC40-14 lacking both CP O and CP I. Consistent with this interpretation is the fact that CP O polypeptides are specifically recovered in purified PS I particles obtained by Triton solubilization of wild-type membranes (Ref. 37 and Delepelaire, P., unpublished data).

Mullet et al. [16] have isolated two types of PS I particles. PS I-65 particles, containing only Chl *a* bound to CP I, were obtained by Triton treatment of PS I-110 particles which released at least three polypeptides and 45 chlorophylls. Assuming their Chl *a*/Chl *b* ratio of 18 in PS I-110 particles, one obtains a Chl *a*/Chl *b* ratio of 6.5 in the PS I antenna located outside CP I. This is very consistent with the Chl *a*/Chl *b* ratio of 6.3 that we find in CP O.

In *C. reinhardii* the 77 K emission originating from CP I peaks in the 720 nm region. Then the non-CP I PS I antenna fluoresces at shorter wavelengths than CP I. This is at variance with the spectral characteristics of the corresponding PS I antenna in pea described by Mullet et al. [16]. It is however, consistent with the observed differences in the respective PS I emission peaks in whole cells of *C. reinhardii* and higher plants (717 vs. 730 nm) and indicates a different organization of the PS I antenna.

Thus, the light-harvesting antenna in *C. reinhardii* can be divided into two building blocks. One corresponds to the LHC, contains three polypeptides (39.5, 26.5 and 25 kDa) and a low Chl *a*/Chl *b* ratio; this fraction shows spectral characteristics of the PS II antenna. The other corresponds to CP O, contains two major polypeptides (27 and 27.5 kDa) and three minor ones (25, 23 and 19 kDa), and mainly long-wavelength Chl *a*; this fraction is part of the PS I antenna. Some interaction may occur between the two parts of the antenna, since we isolated a PS II heavy fraction from a mutant lacking CP I, which contains PS II centers associated with LHC and CP O. An increased PS II antenna size was indeed observed in CP I-deficient mutants which could indicate a connection between the PS II antenna and the non-CP I PS I antenna (Wollman, F.A., unpublished data).In these mutants, disconnection of long-wavelength pigments from the PS II antenna was observed upon Mg^{2+} addition [18]. Thus, CP O could be directly involved in Mg^{2+} regulation of energy distribution. Experiments are now in progress to ascertain this possibility.

Acknowledgements

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