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ORGANIZATION OF CHLOROPHYLL-PROTEIN COMPLEXES OF PHOTOSYSTEM I IN *CHLAMYDOMONAS REINHARDII*

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The polypeptide pattern, chlorophyll-protein complexes, fluorescence emission spectra and light intensity required for saturation of electron flow via Photosystem (PS) II and PS I in a pale-green photoautotrophic mutant, y-lp, were compared to those of the parent strain, *Chlamydomonas reinhardii* y-1 cells. The mutant exhibits a 686 nm fluorescence yield at 25°C and 77 K 2–6-fold higher than that of the parent strain cells, and is deficient in thylakoid polypeptides 14, 17.2, 18 and 22 according to the nomenclature of Chua (Chua, N.-H. (1980) Methods Enzymol. 60C, 434–446). All chlorophyll-protein complexes ascribed to PS II and the CP I complex were present in both type of cells. However, a chlorophyll-protein complex CP Ia containing – in the parent strain – the 66–68 kDa polypeptides of CP I and the four above-mentioned polypeptides, was absent in the mutant. It was previously reported that a chlorophyll-protein complex, CP O, obtained from *C. reinhardii* contains five polypeptides, namely, 14, 15, 17.2, 18 and 22 (Wollman, F.A. and Bennoun, P. (1982) Biochim. Biophys. Acta 680, 352–360). A CP O-like complex was present also in the mutant y-lp cells but it contains only one polypeptide, 15. Energy transfer from PS II to PS I was not impaired in the mutant, although a 4-fold higher light intensity was required for the saturation of PS I electron flow in the y-lp cells as compared with the parent strain. No difference was found in the light saturation curves for PS II activity between the mutant and parent strain cells. Based on these and additional data (Gershoni, J.M., Shochat, S., Malkin, S. and Ohad, I. (1982) Plant Physiol. 70, 637–644), it is concluded that the chlorophyll-protein complexes of PS I in *Chlamydomonas* comprise a reaction center-core antenna complex containing the 66–68 kDa polypeptides (CP I), a connecting antenna consisting of four polypeptides (14, 17.2, 18 and 22), and a light-harvesting antenna containing one polypeptide, 15. These appear to be organized as a complex, CP Ia. The interconnecting antenna is deficient in the y-lp mutant and thus the CP Ia complex is unstable and energy is not transferred from CP O to CP I. The effective cross-section of PS I antenna is thus reduced and a high fluorescence is emitted at 686 nm.

Introduction

Following development of improved procedures for the isolation of PS I enriched or purified preparations [1–3] and electrophoretic separation of chlorophyll-protein complexes [4–6], it became evident that the PS I chlorophyll-proteins contain, in addition to the P-700 apoprotein (66–68 kDa) participating in the formation of the Chl *a*-protein complex I (CP-I), several additional chlorophyll-binding polypeptides [1,7,8]. The detailed organization of the PS I antenna appears to be rather

Abbreviations: CP, chlorophyll-protein complex; DCIP, 2,6-dichlorophenolindophenol; LDS, lithium dodceyl sulfate; PS, photosystem; Chl, chlorophyll.

complex [1,7–9]. Based on previous results obtained with *Chlamydomonas reinhardii* y-1 mutant in which the greening process was modulated by alternate use of protein-synthesis inhibitors and light-dark exposures [10], it was postulated that the PS I antennae system contains, in addition to the CP I complex, a light-harvesting (LHCI) antenna which fluoresces at 705–708 nm at 77 K. This emission could be detected in intact cells only if the synthesis and assembly of the reaction center I and core antenna (CP I) were inhibited during the growth or greening process. The 708 nm fluorescence was partially quenched when the synthesis and assembly of CP I complex was resumed by cells already containing the putative LHCI antenna [10].

Examination of the electrophoretic polypeptide pattern of a *C. reinhardii* fluorescent mutant y-lp, derived from the y-1 mutant [11], revealed a lack or substantial reduction of four thylakoid polypeptides in the molecular mass range of 20.5–27 kDa [12]. Since the y-lp cells could grow photoautotrophically, we assumed that the lacking polypeptides could not be involved in electron-carrier or ATP-synthesis activities. However, it might be possible that these polypeptides could be connected to the chlorophyll-antennae system. Thus, a detailed analysis of the chlorophyll-protein complexes of this mutant and the parent strain was undertaken. While our work was in progress, a mutant of *Chlamydomonas* lacking five thylakoid polypeptides, including the four missing in our y-lp mutant, was described by Wollman and Bennoun [8]. According to these authors, all five polypeptides were required to form a PS I antenna component, CP O [8]. The results of our work describe the electrophoretic isolation of the LHCI antenna responsible for the 708 nm fluorescence emission from both the parent strain and y-lp mutant cells, as well as of a complex CP Ia containing all the PS I chlorophyll-protein complexes. Comparison of the polypeptide composition of these antennae permitted the assignment of possible roles to the various polypeptides participating in the formation of the chlorophyll-protein complexes of PS I in *Chlamydomonas* cells.

Materials and Methods

Two *C. reinhardii* mutants have been used: y-1 which has been described before in detail [13] and y-lp, a fluorescent mutant derived from the y-1 strain [11]. Both mutants were grown on a mineral medium containing acetate as the sole carbon source [14].

Chloroplast membranes for electrophoretic analysis and for measurements of photosynthetic activity were prepared as described before [15]. For measurements of Mg^{2+}-induced fluorescence rise, membranes were prepared as described by De Petrocellis et al. [16]. Fluorescence emission spectra at room temperature were recorded using a Perkin-Elmer spectrofluorimeter, model MPF4. Excitation was a 430 nm. Fluorescence emission and excitation spectra at 77 K were carried out as described by Gershoni and Ohad [17]. Measurements of variable fluorescence at 77 K [18] were carried out using a home-made attachment mounted on the apparatus previously described [11]. The emitted light was filtered through a Schott RG-665 cutoff filter and through a Balzers 680 interference filter for PS II, or through a Baird-Atomic 730 interference filter (20 nm half-band width) for PS I. Measurements of photosynthetic activities were carried out spectrophotometrically or polarographically using H_2O as an electron donor and DCIP as an electron acceptor for PS II [15] and reduced DCIP and methyl viologen as electron donor and acceptor for PS I, respectively [19].

LDS-polyacrylamide gel electrophoresis was carried out at 4°C using 7.5–15% acrylamide gradient gels [20]. Samples for chlorophyll-protein complex separation were prepared as described by Delepelaire and Chua [21] and were run in the electrophoretic system described by Chua [20]. Resolution of thylakoid polypeptides was carried out using the modification to the procedure of Laemmli [33] as described by Delepelaire and Chua [21]. For estimation of molecular mass values, the following markers were used: phosphorylase *b*, 94000 kDa; bovine serum albumin, 67000 kDa; ovalbumin, 43000 kDa; carbonic anhydrase, 30000 kDa; soybean trypsin inhibitor, 20100 kDa; and α-lactalbumin, 14400 kDa (all from Pharmacia Fine Chemicals).

Results

Fluorescence properties and thylakoid polypeptide pattern of the y-lp mutant

Both parent strain and the y-lp mutant cells exhibit a single fluorescent emission peak (685 nm) at room temperature. However, on a chlorophyll basis, the fluorescence yield of the mutant is 1.7–2.5-times higher than that of the parent strain in various cultures (Fig. 1). The fluorescence emission spectrum at 77 K, normalized to the chlorophyll content of the sample, showed even a higher ratio of the 686 nm emission band of the y-lp mutant relative to that of the parent strain (3.5–5-fold) (Fig. 2). As shown in Fig. 2, a 2.5-fold increase in the 696 nm emission peak and a 1.7-fold increase in the 714 nm peak of the mutant cells were observed relative to that of the parent strain cells. This could be due to the contribution of the large 686 nm emission band which renders the two other peaks to appear merely as broad shoulders in the mutant. Examination of the 77 K fluorescence emission spectra from a number of cultures showed always a lesser increase (1.3–1.73) in the 714 fluorescence band, ascribed to the PS I antenna, while the increase in the 686 nm emission varied between 2.5- and 4-fold. Thus, one can conclude that the main difference between the mutant and the parent strain resides in the fluorescence emission at 686 nm, usually ascribed to the light harvesting Chl *a*/*b*-protein complex (LHC) [22].

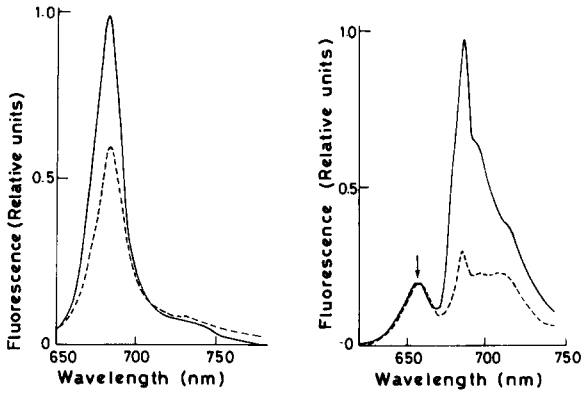


Fig. 1. Fluoresence emission spectra at 25°C of parent strain y-l (- - - - - -) and mutant y-lp (———) cells. The chlorophyll concentration for each sample was 5 μg Chl/ml; the maximal emission was at 685 nm.

Fig. 2. Fluorescence emission spectra at 77 K of parent y-l (- - - - - -) and y-lp (———) mutant cells normalized to the chlorophyll concentration of the sample. Arrow indicates fluorescence of phycocyanine used as an internal standard [7]. The chlorophyll emission peaks are at 686, 696–697 and 714 nm. Note the high fluorescence yield of the y-lp cells at 686 nm.

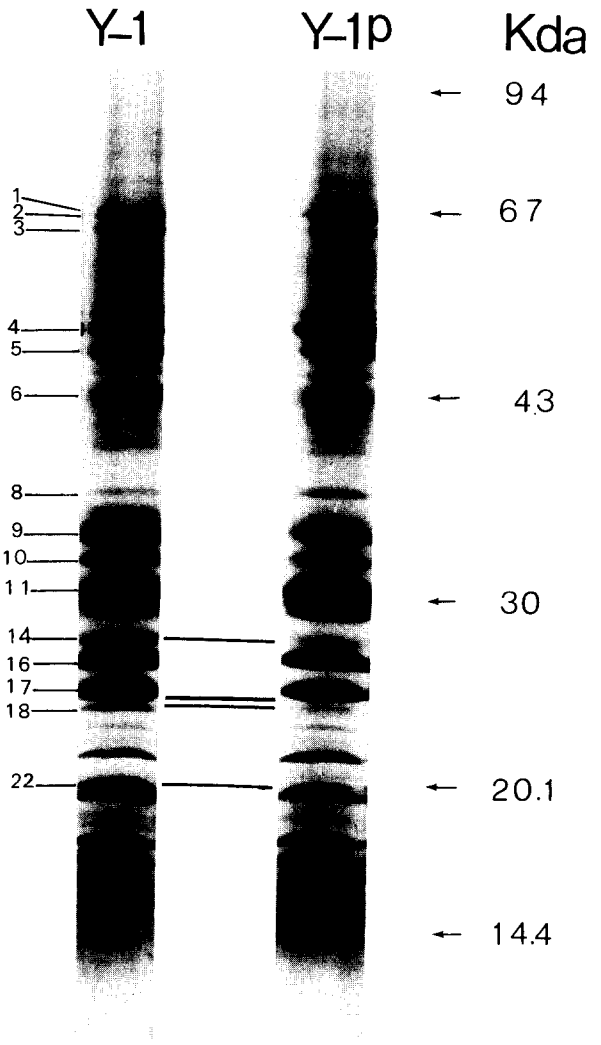


Fig. 3. Polypeptide pattern of the parent strain (y-l) and y-lp mutant cells. Membranes from both types of cells were prepared and separated by LDS-polyacrylamide gel electrophoresis, after heat denaturation, as described in Materials and Methods. Numbers on the left represent the polypeptide nomenclature according to Chua [20]. Lines represent the polypeptides missing in the mutant cells. Polypeptide 17.2 is not always well separated and appears as a heavy band together with polypeptide 17.

Examination of the thylakoid polypeptide pattern following heat denaturation of the solubilized samples in LDS showed that in the y-lp mutant, polypeptides 14, 15, 17.2, 18 and 22, according to the nomenclature of Chua [20] (26.5, 26, 24, 23 and 20.5 kDa, respectively) are missing or largely depleted relative to the parent strain (Fig. 3). To establish whether a correlation exists between the lack of these polypeptides and the high fluorescence emission at 686 nm, the parent and mutant strains' chlorophyll-protein complexes as well as their polypeptide components were analyzed.

Chlorophyll-protein complexes and their polypeptide composition in the parent and mutant strains

Electrophoretic separation of chloropyll-protein complexes, solubilized in LDS in the cold, showed the presence of CP I, CP III–CP IV, CP V and CP II complexes in relatively comparable amounts in both types of cells (Fig. 4). The gel system used in these experiments does not resolve the CP Ia complex previously described by Anderson et al. [7]. Thus, while apparently only minor differences could be detected in the PS II chlorophyll-protein complexes (CP II–CP V, CP III–CP IV [21] between the mutant and the parent strain, the possibility remained that differences migh exist in the PS I related complexes.

Electrophoretic separation of chlorophyll-protein complexes, according to Wollman and Bennoun, whereby an additional complex CP O [8] was detected, allowed us to resolve the CP I from the CP O and CP Ia complexes in thylakoids of the parent strain cells. However, under similar conditions, only the CP I and CP O complexes could be detected in thylakoids of the y-lp mutant. Furthermore, the CP O complex of the mutant was unstable and faded away with increasing electrophoresis time (Fig. 5). These results indicated that all or at least part of the polypeptides missing in the y-lp mutant might participate in the formation of the CP O–CP Ia complexes. Analysis of the CP

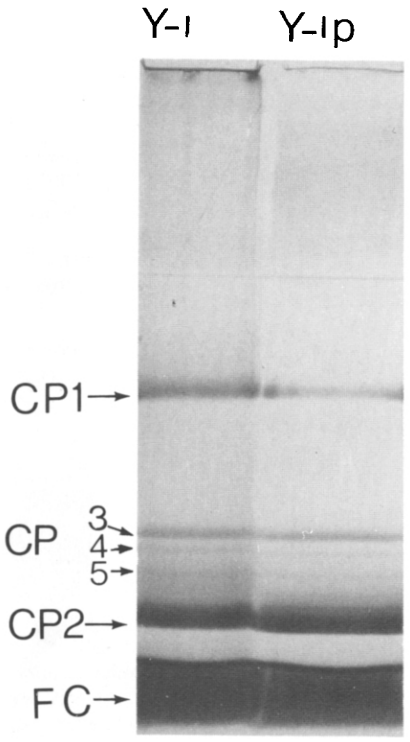


Fig. 4. Chlorophyll-protein complexes of y-I and y-lp cells separated LDS-polyacrylamide gel electrophoresis in the cold [21]. CP, chlorophyll-protein complexes; FC, free chlorophyll. The gels were photographed without staining.

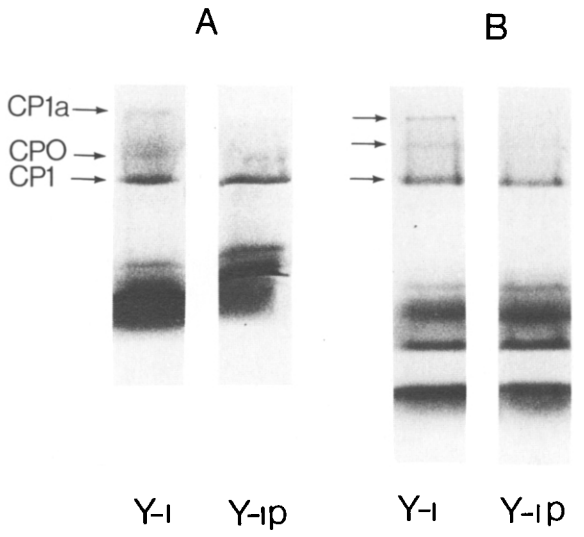


Fig. 5. Chlorophyll-protein complex separation according to the method of Wollman and Bennoun [8]. Membranes were solubilized in LDS in the cold and run for 2 h (A) or 3 h (B). Note the absence of the CP Ia complex and the lower intensity of the CP O complex in the y-lp mutant membranes (A); the CP O complex in the y-lp membranes disappears after 3 h of electrophoresis (B). Due to the short running time the other chlorophyll-protein complexes (CP III–CP IV, CPI, CP II and the free pigment (lower bands in both A and B)) are not well resolved and thus are not identified.

O complex polypeptides was carried out by excising the complex and reelectrophoresis after heat denaturation. The results of such an experiment (Fig. 6) show that CP O contains five polypeptides (cf. also Ref. 8) in the parent strain, including those absent in the y-lp mutant. the CP O complex of the mutant was isolated following short electrophoresis and analyzed for polypeptide composition as above. It was found that this complex contained mainly one polypeptide, 15 (26 kDa), out of the five present in the parent strain (Fig. 6). Analysis of the polypeptide composition of the CP

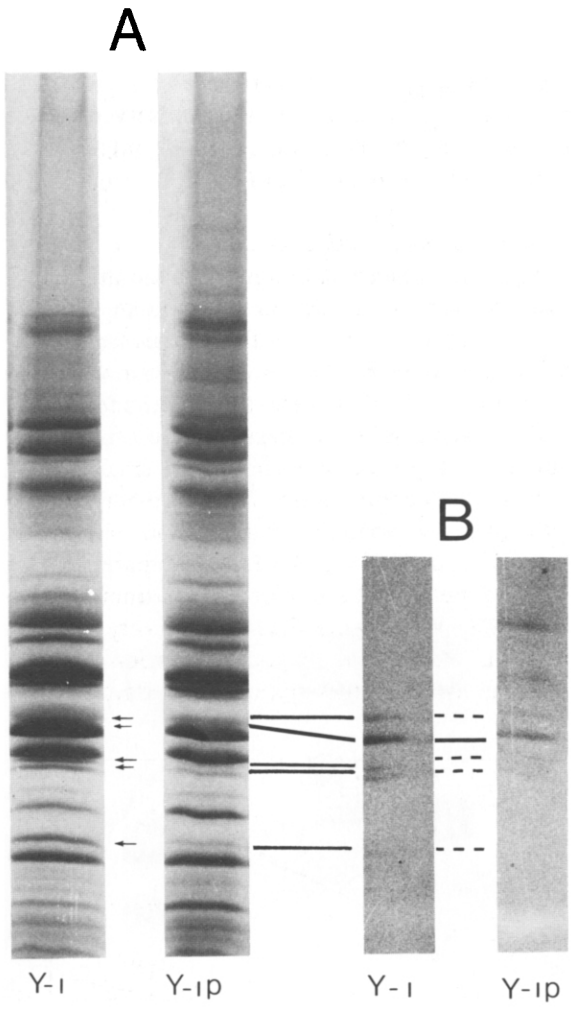


Fig. 6. Polypeptide composition of the CP O complex of y-l and y-lp membranes. The complexes obtained as in Fig. 5A were excised, heat denatured in the sample buffer, and reelectrophoresis was carried out using LDS in the cold. A, polypeptide pattern of the y-l and y-lp membranes. B, CP O complexes; dashed lines, polypeptides missing or present in reduced amounts in the y-lp membranes and CP O complex; the unmarked polypeptide bands present in the y-lp CP O complex might be contaminants, since a larger region of the first gel was removed in order to collect sample material for the second run.

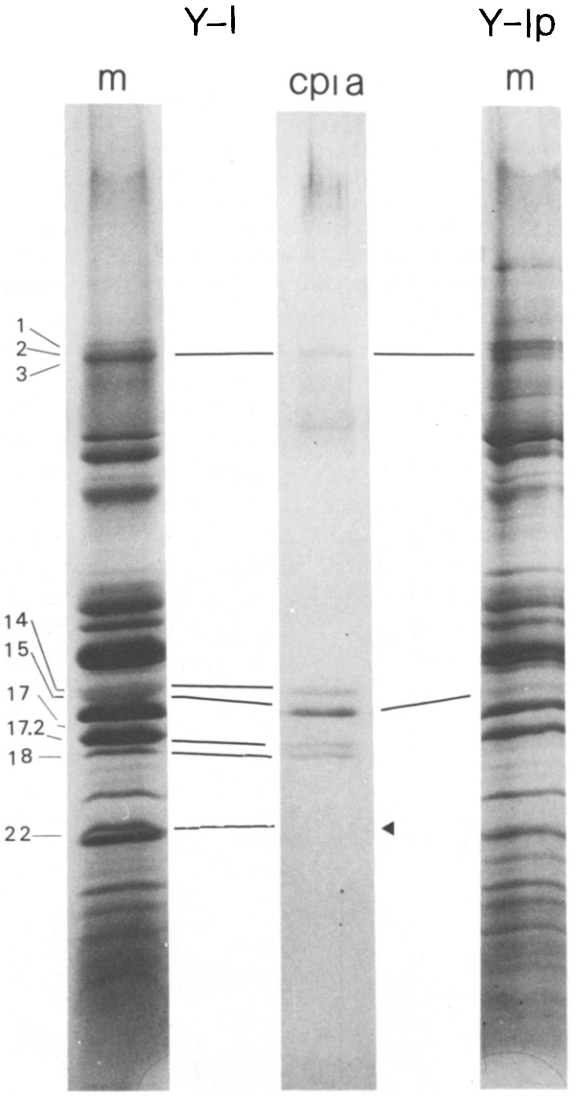


Fig. 7. Polypeptide composition of the CP Ia complex of the y-1 cells. The CP Ia complex obtained as in Fig. 5A was excised, denatured by heating in the sample buffer, and electrophoresis was carried out in the presence of LDS in the cold. m, membranes; polypeptide 2 is usually present in the CP I complex; the arrowhead indicates location of polypeptide 22 present in the CP Ia complex as a vary faint band detectable on the gels but difficult to reproduce in photographs.

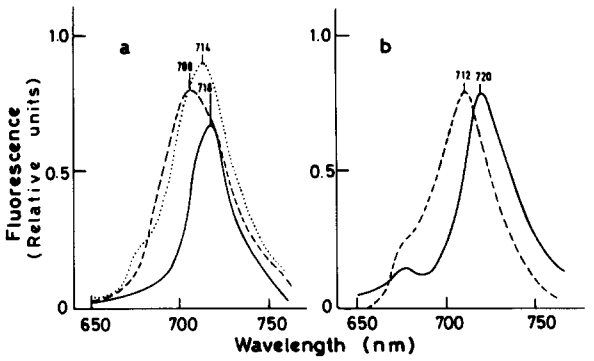


Fig. 8. Low-temperature (77 K) fluorescence emission spectra of the CP Ia (·····), CP O (- - - - - -) and CP I (———) complexes of the parent strain (A) and of mutant cells (B). The numbers indicate the fluorescence maxima of each complex (nm). Chlorophyll-protein complexes were separated as in Fig. 5A; the green bands were excised, frozen in liquid nitrogen and spectra recorded as in Materials and Methods.

Ia complex of the parent strain showed the presence of the polypeptides of CP O as well as the apoprotein of PS I or CP I polypeptides (66–68 kDa) (Fig. 7). Thus, one can conclude that CP Ia contains both the CP I and CP O complexes, and its formation and/or stability requires the presence of all five polypeptides, whereas polypeptide 15 of 26 kDa present in the y-lp mutant is sufficient to bind chlorophyll and form a CP O-like antenna.

The fluorescence emission spectra at 77 K of the chlorophyll-protein complexes separated by LDS-polyacrylamide gel electrophoresis are shown in Fig. 8. The CP I and CP Ia complexes exhibit longer wavelength emission bands than CP O in the parent strain cells. The same situation is found when one compares the CP O and CP I complexes in the y-lp mutant cells. The emission maxima of CP I and CP Ia varied in different preparations between 714 and 720 nm, while that of the CP O complex was found to be between 708 nm and 712 nm. Such variations were never observed in the long-wavelength emission peak of intact cells, which is always at 714–715 nm.

Possible role of the CP O complex

The results presented above indicate that CP O is a component of the PS I antennae complex which might be impaired in the y-lp mutant due to lack or reduction in the amount of four thylakoid polypeptides. If this were the case, one should expect that the effective cross-section of the PS I antennae of the mutant should be smaller than that of the parent strain. Measurements of the light intensity required for saturation of electron flow, via both PS II and PS I, in both parent strain and y-lp mutant cells support this assumption. No difference was found in the light intensity required to obtain 50% of the maximal electron-flow rate, via PS II, between these types of cells. However, a

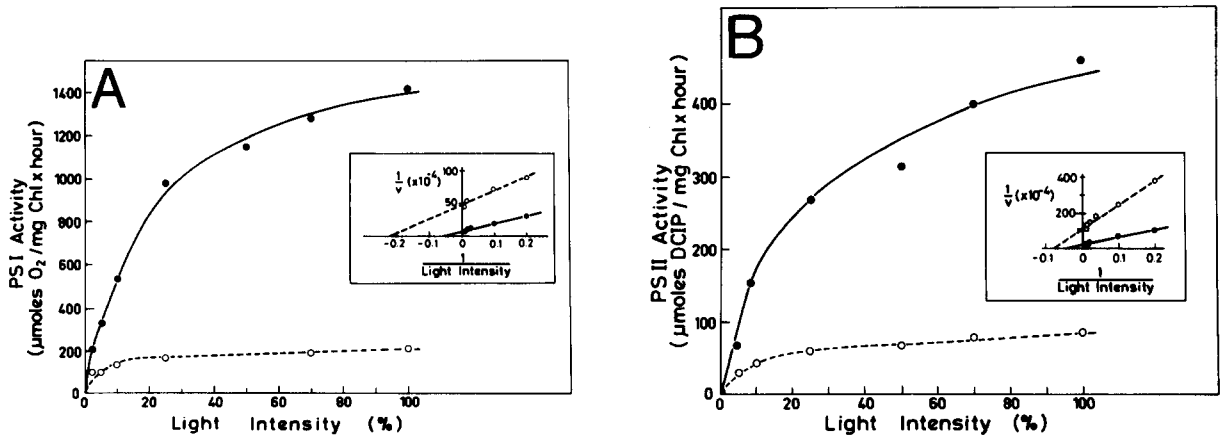


Fig. 9. Photosynthetic electron-flow rates as a function of light intensity in isolated membranes of the y-l (O- - - - - -O) and mutant (●———●) cells PS I (A) and PS II (B) activities were measured as described in Materials and Methods. The maximal (100%) light intensity was 175 $W \cdot m^{-2}$ (Corning 6-65 cutoff filter) for PS II and $1.1 \cdot 10^3$ $W \cdot m^{-2}$ (unfiltered light) for PS I. Inserts, double-reciprocal plots of activity vs light intensity.

4-fold increase in the light intensity required for half saturation of PS I was observed in the y-lp mutant as compared with the parent strain (Fig. 9, inset). One should also note that the electron-flow rates on a chlorophyll basis for both PS II and PS I obtained for the y-lp mutant are several times higher than those of the parent strain (Fig. 9). This could be expected, since the total amount of chlorophyll present in the mutant membranes is lower, i.e., the mutant has a higher ratio of reaction centers/chlorophyll.

Energy transfer and spillover

The data presented above demonstrate a defect in the organization of PS I antennae complex correlated with the lack of four thylakoid polypeptides in the y-lp mutant. However, no explanation has yet been offered for the high fluorescence yield at 686 nm observed in the mutant cells at both 25°C and 77 K. Assuming that this emission band originates in the PS II light-harvesting antenna [22], one could expect this situation to occur if spillover from PS II to PS I were impaired.

No difference was found between the parent strain and the y-lp mutant cells in the Mg^{2+}-induced fluorescence rise in isolated thylakoids [23], and the kinetics of fluorescence rise in whole cells at 77 K [24] for both PS II and PS I (686 and 714 nm, respectively). The 77 K emission at 714 nm was excited by the 651 nm (Chl *b*) and 683 nm (Chl *a*) absorbing bands of PS II and PS I in both types of cells in a similar way (Fig. 10). Furthermore, State 1–State 2 transition in intact cells [23,24] could be demonstrated in both parent strain and y-lp mutant by measuring flurescence changes following transfer of cells from red light (650 nm) to far-red light (730 nm).

These results indicate that energy transfer between the photosystems is not significantly altered in the mutant cells. One possible explanation for this phenomenon is that energy transfer can occur directly from LHC to the PS I reaction center core antenna. Measurements of the excitation bands of the 686 nm fluorescence emission at 77 K showed a significant difference between the y-lp mutant and the parent strain. In the former, a higher ratio of the 668 nm/651 nm excitation was found as compared to the parent strain. This could indicate either a higher ratio of Chl *a*/CHl *b* in the light-harvesting complex of the mutant or that part of the 686 nm fluorescence does not originate in this complex in *Chlamydomonas* fluorescing at 708 nm PS I antennae complex. Comparison of the absorption spectra of the CP II (LHC) complex obtained as in Fig. 4, showed the same ratio of Chl *a*/Chl *b* in this complex from both the y-l and y-lp mutant cells.

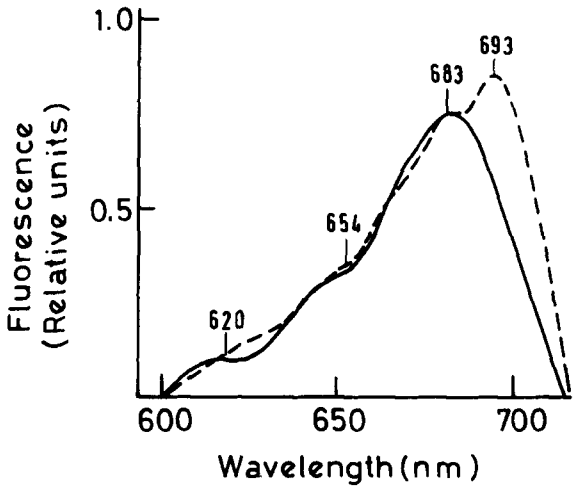


Fig. 10. Low-temperature (77 K) fluorescence excitation spectra of the 714 nm emission band of intact cells of y-l (- - - - - -) and of y-lp mutant (———).

Discussion

In a previous publication, we presented indirect evidence for the existence of a LHCI antenna complex in *Chlamydomonas* fluorescing at 708 nm at 77 K when disconnected from the reaction center-core antenna complex of PS I [10]. Wollman and Bennoun [8] have recently reported the presence of a chlorophyll-protein complex CP O associated with the PS I complex of *Chlamydomonas*. The complex was detected by SDS polyacrylamide gel electrophoresis and consisted of five polypeptides, namely 14, 15, 17.2, 18 and 22, according to the nomenclature of Chua [20]. The isolated complex fluoresces at 77 K at 708 nm and was absent in a *Chlamydomonas* mutant lacking the above polypeptides.

The results presented in this work demonstrate that a CP O-like complex, identified by gel electrophoresis in the presence of LDS and by its fluores-

cence properties, can be detected containing only the polypeptide 15. However, the presence of the other polypeptides (14, 17.2, 18 and 22, according to Chua [20]), which are missing or drastically reduced in the y-lp mutant, appears to be necessary for the organization of the LHCI together with the other components of PS I chlorophyll-protein complexes (reaction center I, CP I).

It should be noted that these PS I components can be resolved by LDS-polyacrylamide gel electrophoresis as an aggregate, defined here as CP Ia. The presence and optical properties of a complex of an apparent molecular mass higher than that of CP I have been reported by Anderson et al. [7]. This complex was considered to be an oligomer of CP I [7, 26–28] and it was demonstrated that its appearance coincides with the formation of the PS I antenna systems following continuous illumination of developing bean leaves previously exposed to alternate light-dark cycles [26,28]. The exact polypeptide composition of this complex in high plants is not yet well established. Nevertheless, it was reported by Argiroudi-Akoyunoglou [28] that in addition to the 66–68 kDa polypeptides of the P-700 complex, the CP Ia complex contains also polypeptides of 25 and 17 kDa. More recently, Anderson [29] has shown that CP Ia has six polypeptide and this might not be an oligomer of CP I.

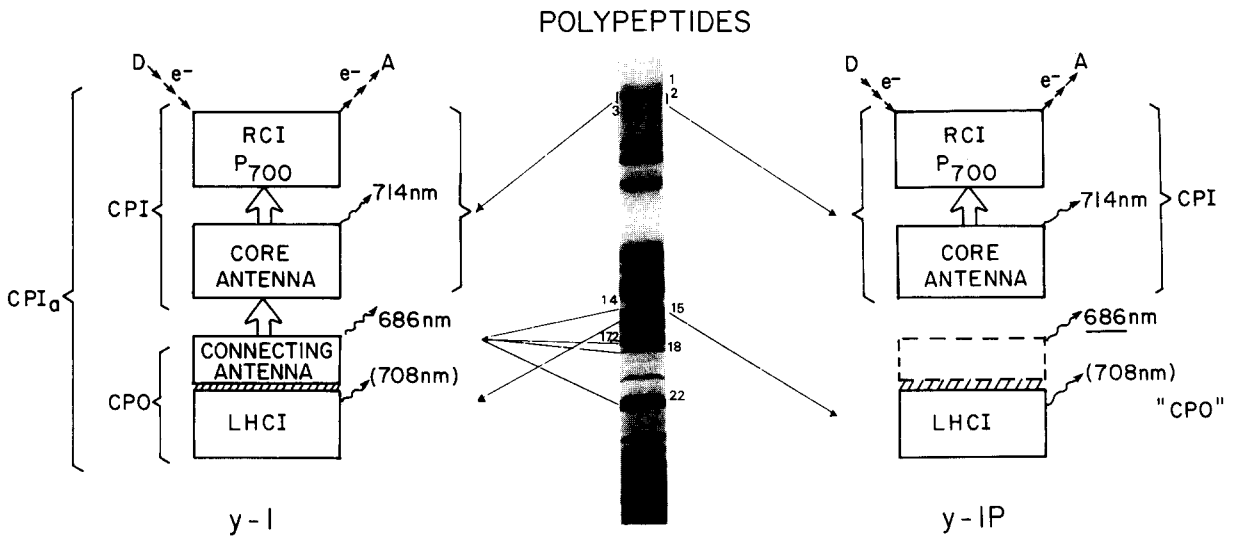
The polypeptide composition of the CP Ia complex in *Chlamydomonas*, as shown in this work, appears to comprise the apoprotein of P-700 (66–68 kDa) which also participates in the formation of the CP I complex [2,15] as well as the five polypeptides found in the CP O complex. The absence or reduction in the amount of four of these polypeptides in the y-lp mutant results in the loss or instability of the CP Ia complex.

One possible expression of the misassembly of the PS I antenna complex in the y-lp mutant might be the high fluorescence yield at 686 nm observed at both 25°C and 77 K. The presence of a short-wavelength fluorescence (673–687 nm) emission band originating in the PS I complex was reported before [1,9].

The characteristic properties of the y-lp mutant reported here could be explained, if one assumes that the ligh-harvesting antenna of PS I in this mutant is incomplete. Chl *a* binds to the polypeptide of 26 kDa and can be isoalted as an unstable chlorophyll-protein CP O. However, due to the lack or reduction in content of the other four polypeptides, this complex does not seem to be able to transfer energy efficiently to the PS I reaction center and, therefore, the requirement for high light intensity in order to saturate electron flow via PS I described here for this mutant.

Based on the data presented here and previously [10,30], one might represent the structural organization and energy flow in the PS I complex of *Chlamydomonas* according to a linear scheme in which LHCI is linked and transfers energy via an interconnecting complex to the core antenna, the latter forming, together with the reaction center I, the CP I complex. The connection between the LHCI (or CP O) and the core antenna might contain additional chlorophyll, possibly Chl *b* [8], and the missing polypeptides of the y-lp mutant. In this mutant this interconnecting complex seems to be incomplete and thus gives rise to the 686 nm fluorescence which under normal conditions is absent or quenched (Scheme I). According to this scheme, energy absorbed by the light-harvesting complex of PS I (CP O) is transferred via the interconnecting antenna to the reaction center-core complex (CP I). In the absence of a reaction center complex or of the core antenna [10,30], this energy is emitted as fluorescence at 708 nm. In the y-lp mutant, the interconnecting antenna is deficient and this energy is not transferred to PS I but emitted as fluorescence at 686 nm. However, y-lp cells grown in the presence of chloramphenicol, which lack the reaction center-core complex and interconnecting antenna, fluoresce intensely at 708 nm and have a CP O complex (Ish-Shalom, D. and Ohad, I., unpublished data).

The above model differs from that described by Mullet et al. [1] for the organization of higher plants' PS I complex as well as for that proposed by Brinkman and Senger [9] for *Scenedesmus*. One should note that a CP O complex has not yet been detected in higher plants' thylakoids and that the fluorescence emission at 77 K was not altered in *Scenedesmus* lacking the reaction center of PS I [9]. Apparently, the organization of the PS I antenna in various organisms is different and one should consider with care the tendency to apply a general model obtained from the study of one organism to other unrelated species.



SCHEME I

SCHEMATIC REPRESENTATION OF THE PS I CHLOROPHYLL-PROTEIN COMPLEXES IN THE *CHLAMYDOMONAS* PARENT STRAIN AND y-lp MUTANT CELLS

The organization of the antennae is represented as a linear array (axial asymmetry), allowing contact between reaction center I and electron donors (D) and acceptors (A). Open arrows indicate energy transfer; CP, chlorophyll protein complexes identified by LDS-polyacrylamide gel electrophoresis; ⇝, fluorescence emitted at 77 K; ( ), fluorescence emitted when connecting core antenna or reaction center are missing [10,28]. The main emission band at 77 K in the y-lp mutant is at 686 nm (underlined); nomenclature of polypeptides is according to Chua [20].

Wollman and Bennoun [8] presented indirect evidence suggesting that the CP O complex might be involved in the process of energy spillover between PS II and PS I. Apparently, energy transfer between PS II and PS I is not significantly altered in the y-lp mutant, as indicated in this work. Thus, one might conclude that either the LHCI does not participate in this process or, alternatively, that connection between the two photosystems can occur in more than one way. One should mention, however, that fluorescence quenching in intact cells might not necessarily indicate State 1—State 2 transition and spillover of energy from PS II to PS I [31]. Preliminary results obtained using SDS-polyacrylamide gel electrophoresis described by Bennet et al. [32] indicated that a complex having the same fluorescence emission bands at 77 K and polypeptide composition as the CP Ia can be obtained from the parent strain *Chlamydomonas* but not from the y-lp mutant (Thornber and Ohad, unpublished data). Furthermore, greening experiments carried out with the y-lp mutant demonstrated that the CP O polypeptides are synthesized late in the process, after the formation of the CP I complex (Ish-Shalom and Ohad, upublished data). These and previously published data [10] lend support to the tentative model of PS I chlorophyll-protein organization of *Chlamydomonas* presented here.

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