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Spectroscopic properties of the reaction center and of the 47 kDa chlorophyll protein of Photosystem II

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The D1-D2-cytochrome *b*-559 reaction center complex and the 47 kDa antenna chlorophyll protein isolated from spinach Photosystem II were characterized by means of low temperature absorption and fluorescence spectroscopy. The low temperature absorption spectrum of the D1-D2-cytochrome *b*-559 complex showed two bands in the Q_y region located at 670 and 680 nm. On the basis of its absorption maximum and orientation the latter component may be attributed at least in part to P-680, the primary electron donor of Photosystem II. The 47 kDa antenna complex showed absorption bands at 660, 668 and 677 nm and a minor component at 690 nm. The latter transition appeared to be associated with the characteristic low temperature 695 nm fluorescence band of Photosystem II. The 695 nm emission band was absent in the D1-D2 complex, which indicates that it does not originate from the reaction center pheophytin, as earlier proposed. The transition dipole responsible for the main fluorescence at 684 nm from this complex had a parallel orientation with respect to the membrane plane in the native structure. The reaction center preparation contains two spectrally distinct carotenoids with different orientations.

Introduction

Although there are indications that the reaction center of Photosystem II is in many respects similar to that of photosynthetic purple bacteria, much less is known about the structural and functional organization of the pigments in the reaction center of PS II than of its bacterial counterpart. This is mainly due to the fact that until very recently the smallest PS II complex with photochemical activity which could be isolated still retained a large number of antenna chlorophylls. After selective removal of the light-harvesting Chl *a*/*b*-protein complex a reaction center core complex remains which contains approximately 50 Chl *a* molecules per reaction center [1]. This core complex contains six intrinsic polypeptides with apparent molecular weights of approx. 47 (CP47 or CPa-1; Ref. 2), 43 (CP43 or CPa-2), 30–34 (D1 and D2), 9 and 4 kDa and extrinsic proteins which are associated with the oxygen evolving complex [1,3]. The major fraction of the Chl *a* molecules is bound to the two larger polypeptides.

The location of the reaction center in the core

Abbreviations: Chl, chlorophyll; LD, linear dichroism; PS, Photosystem; P-680, primary electron donor of Photosystem II.

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complex has been a matter of much debate. It has been previously assumed that CP47 would contain the reaction center, but the homology between the primary structure of the D1 and D2 peptides, on the one hand, and of the L and M subunits of the reaction center of purple bacteria, on the other hand, appeared to contradict this notion and suggested that the reaction center would be associated with the D1 and D2 peptides [3]. Recently, the latter hypothesis has been proven correct by the isolation of a photoactive D1-D2-cytochrome *b*-559 complex [4,5] which did not contain CP47 or CP43. It was therefore of interest to study the spectroscopic characteristics of this complex in more detail in order to obtain information about its structural properties. The present paper reports the results of such a study, together with measurements on the isolated CP47 subunit.

Materials and Methods

Photosystem II membrane fragments were prepared from spinach chloroplasts according to the method of Berthold et al. [6], with modifications as described in Ref. 7. This preparation was used as starting material for the isolation of the D1-D2-cytochrome *b*-559 complex, henceforth to be called the D1-D2 complex, as described in Ref. 5, except that NaCl was added to a final concentration of 30 mM to the supernatant of the ultracentrifugation step to reduce the binding of other components than the D1-D2 complex to the column. After elution as described in Ref. 5 the fractions containing the D1-D2 complex were concentrated in an Amicon ultrafiltration cell with a PM 10 Diaflo membrane. Before measurement the complex was diluted to an absorbance of 3.0 A/cm at 673 nm in a 50 mM Tris (pH 7.2) buffer containing 66% (v/v) glycerol and 0.05% Triton X-100. The CP47 complex was prepared from the purified digitonin PS II core complex by a newly developed method (Fujitani, M. and Satoh, K., unpublished results) which utilizes heptyl-thioglucoside as solubilizing agent and DEAE-Toyopearl 650S chromatography for separation. The purified material consisted entirely of a polypeptide of about 47 kDa. This polypeptide was cross-reactive with antiserum against CP47 prepared by SDS-polyacrylamide gel electrophoresis. It was diluted to the same absorbance as the D1-D2 complex.

The apparatus used to measure absorption and fluorescence emission and excitation spectra and fluorescence polarization is described in Ref. 8. Linear dichroism was measured as described in Ref. 9. The samples were oriented by pressing them uniaxially in a polyacrylamide gel [9].

Results

Purification of the D1-D2 complex

As starting material for the preparation of the D1-D2 complex we used a grana fraction prepared according to the method of Berthold et al. [6] ('BBY particles') instead of one prepared according to Kuwabara and Murata [10], as in earlier work [5]. Chemical analysis indicated a lower Chl *a* content in our preparation: starting from the same batch of chloroplasts the Chl/pheophytin ratios were 4.1 : 2 and 6.2 : 2, respectively, for D1-D2 complexes obtained by the two methods (see also Ref. 5). By means of flash spectroscopy it has been shown that D1-D2 prepared by the second method contained some Chl *a* which does not transfer excitation energy to the reaction center [11]. Nevertheless, different batches of our D1-D2 preparations had different fluorescence yields when measured at room temperature, suggesting the presence of some unconnected Chl. The preparation with the lowest fluorescence yield (about two-thirds of that of BBY particles) was used for the measurements described below, on the assumption that this would represent the purest preparation.

Absorption and circular dichroism

Fig. 1 shows the low temperature absorption spectra of the D1-D2 (Fig. 1A) and of the CP47 (Fig. 1B) complex. The room temperature absorption spectrum of the D1-D2 preparation (data not shown) was very similar to that published earlier [5]. The spectrum of D1-D2 measured at 4 K shows a fairly simple structure in the Q_y region, with a maximum at 670 and a shoulder at 680 nm. The band at 539 nm can be attributed to pheophytin *a*. In the blue region bands of carotenoid at 467, 489 and 503 nm, and of cytochrome *b*-559 at 417 nm can be seen. The band at 436 nm

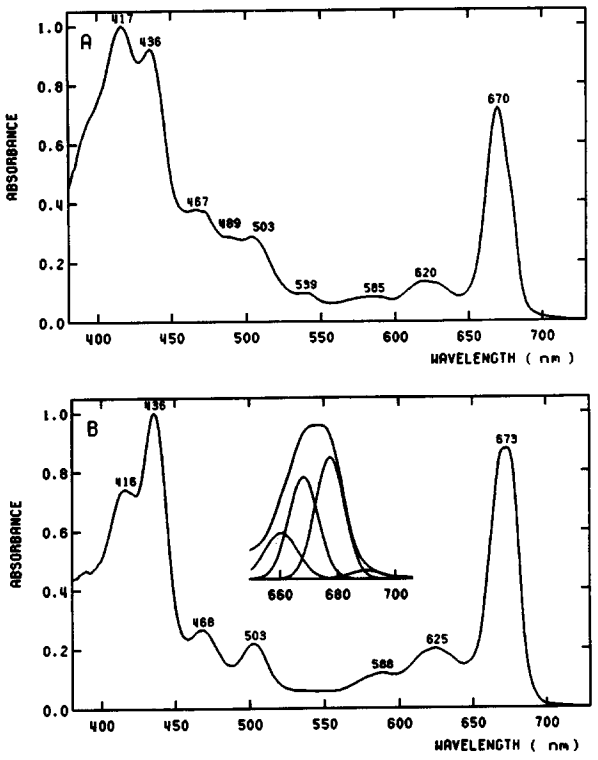

Fig. 1. Absorbance spectra of the D1-D2 complex (A) and of the CP47 complex (B) at 4 K. The inset of Fig. 1B shows the Gaussian deconvolution for the region between 650 and 705 nm.

is mainly due to the Soret transitions of Chl *a*. As was concluded from the linear dichroism spectrum of the core complex of *Synechococcus* sp. and of its two major constituents [12], the bands in the region 560–650 nm are presumably composed of a mixture of the $Q_{x\ 0\text{-}0}$ (around 630 nm) and the vibrational transitions $Q_{y\ 0\text{-}1}$ (around 620 nm) and $Q_{x\ 0\text{-}1}$ (around 585 nm) of Chl *a*. The spectrum of the D1-D2 complex confirms that it is highly enriched in pheophytin *a* and cytochrome *b*-559 relative to Chl *a* as compared with a PS II core complex containing 45 Chl *a* per reaction center [7].

The 4 K spectrum of CP47 (Fig. 1B) is very similar to that of CP2-b, a chlorophyll protein complex of the blue green alga *Synechococcus*, which contains the 47 kDa polypeptide and a fraction of the 30–34 and 9 kDa polypeptides [12]. In the second derivative spectrum the positions of at least three spectrally distinct Chl *a* transitions could be discerned in the Q_y region, with maxima at 660, 668 and 677 nm. A fourth component, located at 690 nm, was observed in the fourth derivative spectrum. By means of a Gaussian deconvolution program the spectrum in the region 650–710 nm was fitted with these four components (inset, Fig. 1B). The halfwidth of all four bands varied between 12 and 14 nm and the relative intensities of the 660, 668, 677 and 690 nm components were 0.18, 0.36, 0.43 and 0.03, respectively. In addition, the spectrum of CP47 shows bands of carotenoid at 468 and 503 nm and of the Soret transitions of Chl *a* at 416 and 436 nm. No evidence was found for the presence of pheophytin *a*, as reflected by the absence of a band at 540 nm, in consistence with the chemical analysis (Fujitani, M. and Satoh, K., unpublished results).

The circular dichroism spectrum of the D1-D2 complex measured at 77 K is shown in Fig. 2. It is characterized by a strong negative signal at 682 nm and a smaller positive band at 669 nm.

Fluorescence

Upon excitation at 430 nm the D1-D2 complex showed a main emission at 679 nm when measured at room temperature. Upon cooling to 4 K this band shifted to 684 nm (Fig. 3). A minor band at 739 nm presumably reflects a vibrational subband of the main emission. The emission spectrum of CP47 showed a maximum at 681 nm at room temperature which shifted to 693 nm at 4 K. In the case of CP47 the vibrational subband is

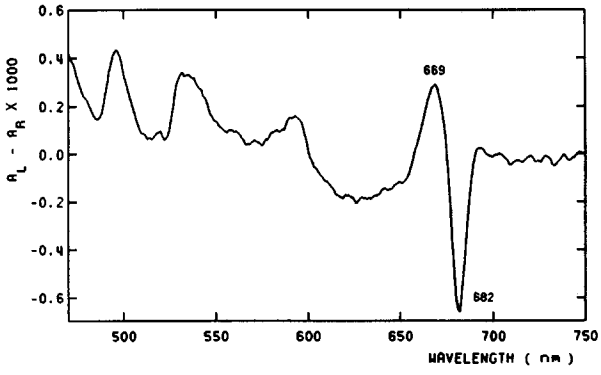

Fig. 2. Circular dichroism spectrum of the D1-D2 complex measured at 77 K. The absorbance at the Q_y maximum was 0.30 at 293 K.

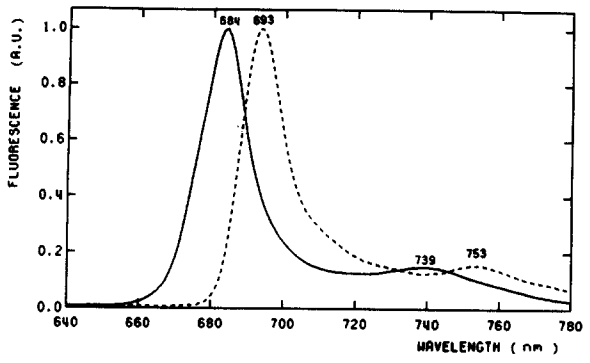

Fig. 3. Emission spectra of the D1-D2 complex (———) and of the CP47 complex (- - - - - -) at 4 K excited at 430 nm.

located at 753 nm. To obtain information about the efficiency of energy transfer to the emitting dipoles the excitation spectra for both complexes were measured at 4 K (Fig. 4). A comparison with the absorption spectrum shows that the most conspicuous feature of the excitation spectrum of the D1-D2 complex (Fig. 4A) is the low contribution of the carotenoid bands, resulting in a value of less than 20% for their efficiency of energy transfer to Chl *a*. A value of about 50% is found in the band of pheophytin *a* at 540 nm.

The excitation spectrum of CP47 (Fig. 4B) shows a fairly low efficiency of 40% for the carotenoid bands. The slight but distinct blue-shift of the excitation spectra of D1-D2 and CP47 in the Q_y region relative to their corresponding absorption spectra indicates that excitation in the short wavelength forms of Chl *a* leads to a higher fluorescence yield than excitation in the longer wavelength forms.

Polarized excitation spectra were also measured and the results are given in Fig. 5. The degree of polarization $(I_{\parallel} - I_{\perp})/(I_{\parallel} + I_{\perp})$ of the D1-D2 complex had a value of 0.02 and 660 nm, but rose upon excitation at longer wavelengths to 0.3 at 689 nm. A negative value of -0.02 was observed at 590 nm. The polarization of the CP47 complex was slightly negative in the region between 655 to 680 nm and then rose steeply to a value of approximately 0.4 at 694 nm.

Linear dichroism and polarized emission

The linear dichroism (LD) and anisotropy ratio (LD/A) spectra measured at 4 K are given in Fig. 6. The preparations were oriented by means of uniaxial squeezing in polyacrylamide gel [9]. In the Q_y region the LD spectrum of D1-D2 (Fig. 6A) shows a maximum at 681 nm and a minimum at 666 nm. A shoulder is observed at 675 nm and a

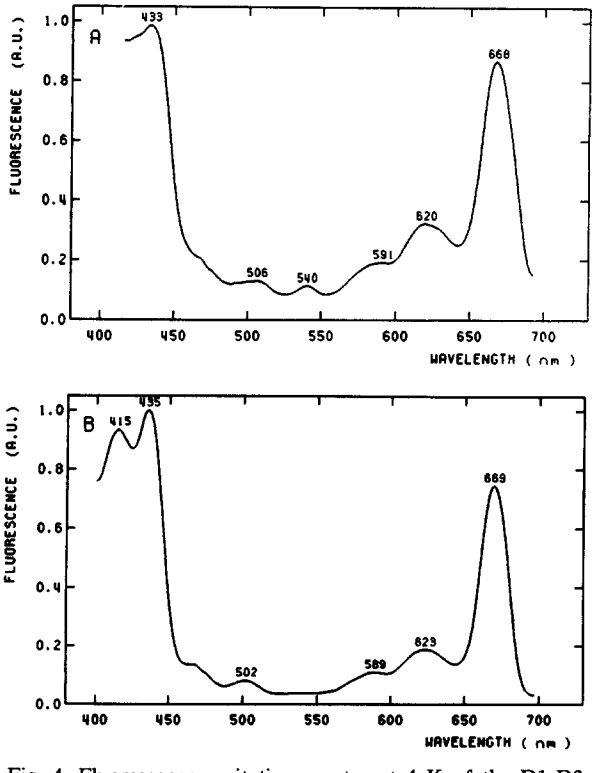

Fig. 4. Fluorescence excitation spectra at 4 K of the D1-D2 complex (A) and of the CP47 complex (B) detected at 700 and 710 nm, respectively. The absorbances of the samples were the same as in Fig. 1.

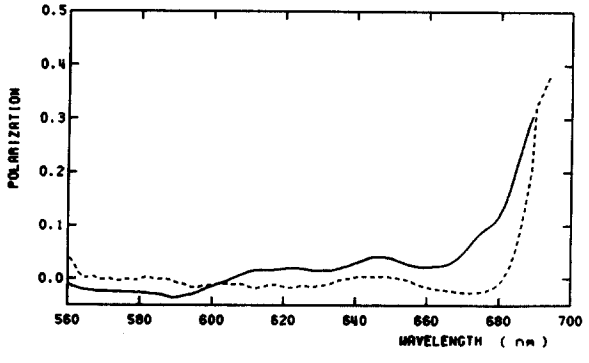

Fig. 5. Fluorescence polarization spectra of the D1-D2 (———) and of the CP47 complex (- - - - -) detected at 705 and 715 nm, respectively, and measured at 4 K.

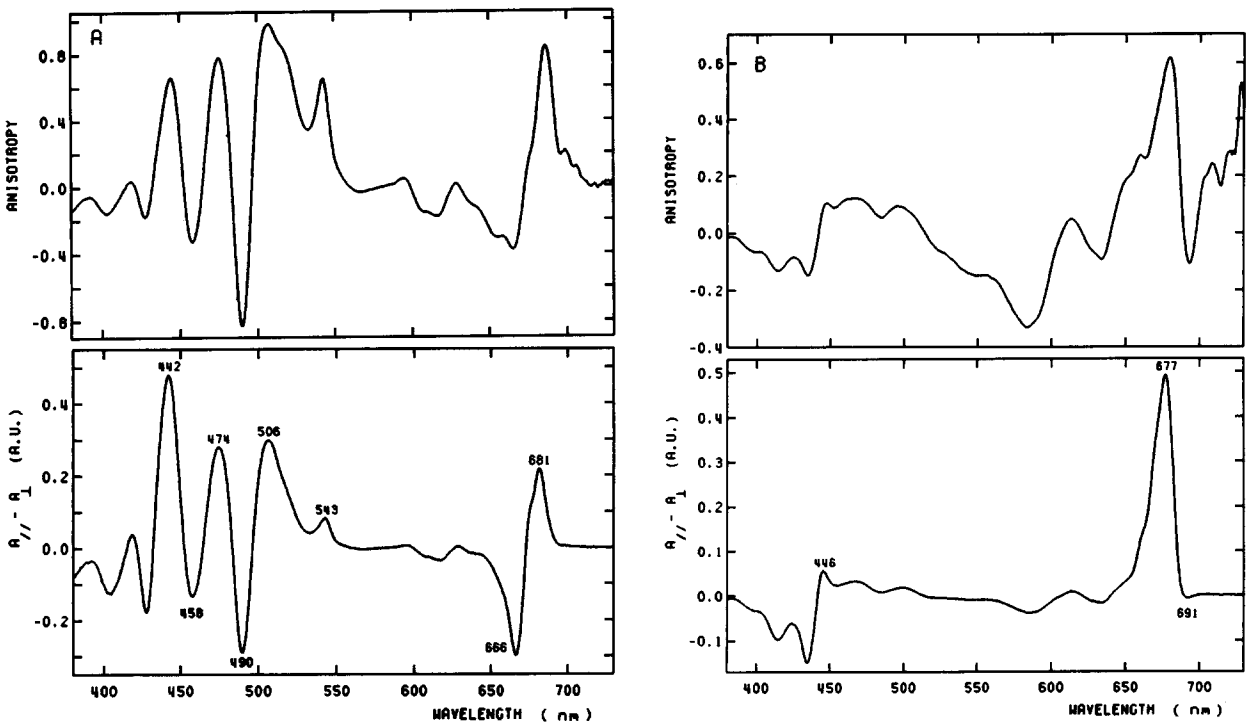

Fig. 6. Linear dichroism ($A_{\parallel} - A_{\perp}$) and anisotropy ($\Delta A/A$) spectra (4 K) of the D1-D2 complex (A) and of the CP47 complex (B).

broad negative LD component is present around 610 nm. The Q_x transition of pheophytin *a* gives rise to a positive LD at 543 nm. A shoulder at 515 nm in the LD/A spectrum is also assigned to pheophytin *a*. In the blue region two populations of carotenoid with different orientations can be seen resulting in marked oscillations of the LD signal with maxima at 442, 474 and 506 nm and minima at 427, 458 and 490 nm. The same features can be observed in the LD/A spectrum.

In the Q_y region the LD and LD/A spectra of CP47 (Fig. 6B) are very similar to the corresponding spectra of the CP2-b Chl *a*-protein complex of *Synechococcus* sp. [12], with a maximum at 677 nm, shoulders at 668 and 660 nm and a well-resolved component at 691 nm. The latter is most clearly observed in the LD/A spectrum (Fig. 6B). This negative LD signal was also observed in PS II membrane fractions [7] and in 'core' PS II preparations from *Chlamydomonas* [13] and *Synechococcus* [12] as wel as in CP2-b [12]. The main differences between the LD and LD/A spectra of CP47 and CP2-b concern the positive pheophytin *a* band at 543 nm and the negative carotenoid signals at 490 and 458 nm which are present in CP2-b [12] and absent in CP47 (Fig. 6B). As shown in Fig. 6, these signals are characteristic of the presence of an oriented D1-D2 component. In CP47 the rather flat LD/A signal in the 460–510

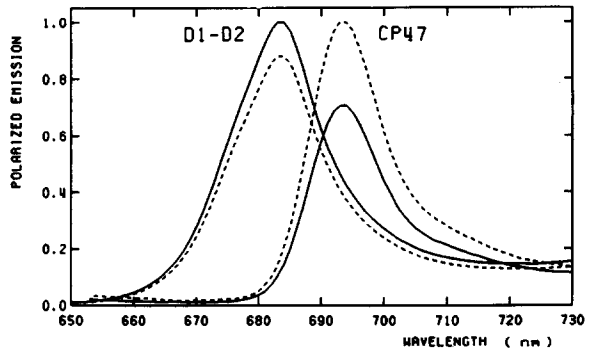

Fig. 7. Polarized fluorescence emission spectra (normalized) of the same samples as in Fig. 6. $F_{\parallel}$ (———) and $F_{\perp}$ (------) are recorded parallel and perpendicular to the plane of orientation. The excitation beam (430 nm) was parallel to this plane. Temperature, 4 K.

nm spectral range suggests an homogeneous orientation of the carotenoid molecules at less than 35° from the plane of orientation. In the 580–630 nm region the CP47 and CP2-b particles exhibit very similar LD and LD/A spectra.

Using the same oriented samples the polarized emission spectra were measured at 4 K (FIg. 7). The emission of the D1-D2 complex was polarized parallel to the plane of orientation, whereas the fluorescence emitted from CP47 had a perpendicular polarization.

Discussion

The results presented here give a characterization of the spectroscopic properties of the D1-D2-cytochrome *b*-559 complex and of the 47 kDa Chl *a*-protein complex. There is convincing evidence now [4,5,11,14] that the D1-D2 complex contains the reaction center, while the amino acid sequences and the pigment composition with two pheophytins and presumably four Chls per complex are similar to those of reaction center preparations of purple bacteria.

The orientation of the D1-D2 particles in the squeezed gel must be compared to the geometry of this complex when it is still embedded in the photosynthetic membrane. In this respect the 543 nm transition assigned to pheophytin *a* and the 490 nm carotenoid signal, which exhibit LD of opposite signs, can be used as specific markers for this particle. The 543 nm transition gives rise to a positive LD in thylakoids [15], grana membranes [7], the core PS II particle [13], the CP2-b complex [12] and D1-D2 (Fig. 6A). The 490 nm negative LD is clearly present in the core particle [13], the CP2-b complex [12] and D1-D2 (Fig. 6A). It has been previously demonstrated that the core and the CP2-b particles exhibit the same orientation with respect to the squeezing direction in the gel as they have with respect to the normal to the photosynthetic membrane in vivo [7,12,13,15]. The sign of the LD for the 543 nm and 490 nm transitions observed in the present study for the D1-D2 particle (Fig. 6A) thus unambiguously demonstrates the same behavior for the D1-D2 particle, i.e., the directions of the complex which are in vivo parallel to the membrane plane, orient in the gel perpendicular to the squeezing direction. The close resemblance between the LD and LD/A spectra of CP47 (Fig. 6B) and CP2-b [12], except for the contribution of D1-D2 pigments in the latter, demonstrates a similar orientation property also for the CP47 particle.

The spectra of the D1-D2 complex, especially in the Q_y region, are much less resolved than those of bacterial reaction center preparations where the absorption and LD measurements reveal well-separated bands of the bacteriopheophytin molecules, the accessory bacteriochlorophylls and the primary electron donor [16]. In contrast, the low temperature absorption spectrum of the D1-D2 complex shows only one band at 670 nm and a shoulder at 680 nm. Nevertheless, significant information can be obtained from the LD and the excitation spectra. In the LD spectrum a maximum is observed at 681 nm with a shoulder at 675 nm and a minimum at 666 nm. In addition, the second derivative of the excitation spectrum showed bands at 664, 670 and 681 nm. The transition at 681 nm may be ascribed, at least in part, to the primary donor P-680. The triplet-minus-singlet spectrum of PS II particles measured by means of absorption detected magnetic resonance at 1.2 K is dominated by a negative band at 682 nm, attributed to the disappearance of the ground state absorption of the P-680 dimer [17]. This indicates that, as at room temperature, the primary electron donor absorbs near 680 nm at 4 K. Moreover, the strong positive LD/A signal in this region is in agreement with the in plane orientation of the Q_y transition of P-680 [18,19]. It is of interest to note that the negative CD signal at 682 nm is conserved in all PS II preparations and in intact chloroplasts [7,20].

The assignment of the other transitions by analysis of the absorption, CD and LD spectra poses more difficulties. The negative LD band at 666 nm cannot be ascribed to the photoactive pheophytin *a*, the Q_y transition of which makes a large angle with the membrane [21], because the available evidence indicates that this transition, at least at room temperature, is at considerably higher wavelength, around 680 nm [21,22]. Furthermore, there is no evidence for a component with negative dichroism around 666 nm in the LD and LD/A spectra at 10 K of the core PS II [12,13] and of CP2-b [12]. It is thus possible that this

spectral component observed in D1-D2 represents chlorophyll molecules, the orientation of which has been disturbed during the isolation procedure, which involves high Triton X-100 concentrations. In this respect the negative LD and LD/A components seen around 610 nm in the spectra of the D1-D2 particles which have no counterparts in the spectra of the core and CP2-b complexes [12], could correspond to the vibrational $Q_{y\ 0\text{-}1}$ component of the main $Q_{y\ 0\text{-}0}$ transition at 666 nm. Such short wavelength negative LD components are commonly observed for a variety of PS I fractions which have received rather harsh treatments with detergents [23,24]. Also, the increased fluorescence yield noted upon excitation on the short wavelength side of the main Q_y band of D1-D2 (Fig. 4A) could be ascribed to some disconnected pigments absorbing in this region. With the exception of the Chl *a* band mentioned above, the LD and LD/A spectra of CP2-b [12] show the combined features of the corresponding spectra of D1-D2 and CP47. This extends the earlier observation that the spectra of the core particle could be constructed from those of CP2-b and CP2-c of *Synechococcus* [12]. It thus appears that the orientation of the chromophore pigments in PS II can be efficiently used to probe the integrity of the pigments during fractionation processes and may help in the development of more gentle isolation schemes.

It is well known that three low-temperature emission bands located at 680 (F_{680}), 685 (F_{685}) and 695 nm (F_{695}) are associated with PS II. F_{680}, which has been attributed to the light-harvesting Chl *a/b* protein [25], should be lacking in both the D1-D2 and CP47 complexes. The dipoles responsible for F_{695} are oriented more or less perpendicular to the membrane plane [8,26,27]. On the basis of this orientation, which is both atypical for Chl *a* in vivo [7,9,12] and comparable to that of the Q_y transition of the primary acceptor pheophytin *a*, it has been proposed that F_{695} originates directly from pheophytin [28]. Support for this hypothesis was obtained from measurements with core complexes of spinach [7] and *Chlamydomonas* [13]. A correlation was observed between the amplitude of F_{695} and that of the negative LD component at 691 nm [13]. Although F_{695} is emitted from CP2-b [29], which contains both CP47 and a fraction of the D1 and D2 polypeptides present in the core particle, the amplitude of the component at 691 nm in the LD spectrum of CP2-b is reduced compared to that observed in the spectrum of the core particle [12]. Thus, it could not be concluded whether F_{695} and the negative LD signal at 691 nm [12,13] were associated with D1-D2 or with CP47. With the present investigation of the two newly isolated particles, it becomes clear that F_{695} together with the LD band at 691 nm belongs to the photochemically inactive CP47, while D1-D2 which contains the photoactive pheophytin *a* does not fluoresce at 695 nm. Thus, the hypothesis on the pheophytin origin of F_{695}, which has been instrumental in developing the investigation of the structural and functional organization of the PS II pigments, has been essentially disproved. In view of the absence of a pheophytin *a* band in the absorption spectrum of CP47, it is reasonable to assume that the species responsible for both the LD signal at 691 nm and F_{695} is a Chl *a* molecule. The minor component at 690 nm which is observed in the Gaussian deconvolution of the absorption spectrum of CP47 may be attributed to this pigment. Its function, however, remains unknown.

The LD spectrum of the D1-D2 complex clearly indicates the presence of two spectrally distinct carotenoid molecules with different orientations. The blue region of the low temperature absorption and LD spectra could be fitted with two sets of carotenoid bands, as is shown for the absorption

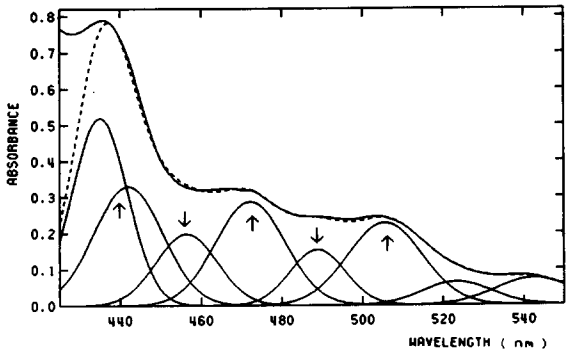

Fig. 8. Gaussian deconvolution of the blue region of the absorbance spectrum of the D1-D2 complex. The two sets of carotenoid transitions (see text) are indicated by upward and downward pointing arrows, respectively. The dashed line gives the sum of the Gaussian components.

spectrum in Fig. 8. The three bands of the first carotenoid are located at 506, 474 and 443 nm and the position of the maxima of the second one are blue shifted by 12–14 nm to 489 and 456 nm. The short-wave band of this second carotenoid cannot be resolved, due to the large overlap with other pigments below 440 nm. The band at 435 nm in the analysis of Fig. 8 is accounted for by the Soret transitions of Chl *a*, and two minor components around 520 and 540 nm represent bands of pheophytin *a*, respectively. Chemical analysis of the D1-D2 complex reveals the presence of 1.0 ± 0.3 β-carotene molecules per reaction center [5]. The observation that two spectrally different carotenoid species with different orientation can be distinguished suggests that two carotenoid molecules are associated with the PS II reaction center, in contrast to the bacterial reaction center which contains only one [16]. Part of the carotenoids, especially of the short-wave species, then would be solubilized and lost during the isolation of the D1-D2 complex.

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