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Variability of Light-Induced Circular Dichroism Spectra of Photosystem I Complexes of Cyanobacteria[1]

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Abstract—Circular dichroism (CD) spectra of photosystem I (PSI) complexes of the cyanobacteria *Thermosynechococcus elongatus*, *Arthrospira platensis* and *Synechocystis* sp. PCC 6803 were studied. CD spectra of dark-adapted PSI trimers and monomers, measured at 77 K, show common bands at 669-670(+), 673(+), 680(−), 683–685(−), 696–697(−), 702(−) and 711(−) nm. The intensities of these bands are species specific. In addition, bands at 683–685(−) and 673(+) nm differ in intensity for trimeric and monomeric PSI complexes. CD difference spectra ($P700^+$−P700) of PSI complexes at 283 K exhibit conservative bands at 701(−) and 691(+) nm due to changes in resonance interaction of chlorophylls in the reaction center upon oxidation of P700. Additional bands are observed at 671(−), 678(+), 685(−), 693(−) nm and in the region 720–725 nm those intensities correlate with intensities of analogous bands of antenna chlorophylls in dark-adapted CD spectra. It is suggested that the variability of CD difference spectra of PSI complexes is determined by changes in resonance interaction of reaction center chlorophylls with closely located antenna chlorophylls.

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It may be proposed that photosystem I (**PSI**) reaction centers of various cyanobacteria are organized in similar way that will result in identical (or similar) excitonic couplings of six chlorophylls (**Chls**) in the PSI reaction center: Chls of the primary electron donor (**P700**) and the primary electron acceptor ($\mathbf{A_0}$), and the pair of accessory Chls [1]. Circular dichroism (**CD**) spectra provide the evidence for excitonic interactions of antenna Chls in PSI complex [2, 3]; light-induced CD spectra yield additional information since they may indicate also the excitonic interaction of P700 with the nearest Chls [4–6]. Both dark-adapted and light-induced CD (P700 oxidized minus reduced) spectra of PSI complexes of *Arthrospira platensis* show, in addition to bands of the dimer splitting of P700 at 691(+) and 701(−) nm, also some minor components at 672(−), 678(+), and 685(+) nm. These bands have previously been attributed to antenna Chls [4, 5]. It was suggested that about 6–8 Chl molecules (including Chls of P700) may form a special aggregate [6]. Based on the molecular structure of the PSI reaction center, some bands in light-induced CD spectra of PSI complexes have been attributed to Chls located in close proximity to P700.

Studies of femtosecond transient hole-burning have provided experimental support for the hypothesis of excitonic coupling between Chls in PSI reaction center of the cyanobacterium *Synechocystis* sp. [7] or green alga *Chlamydomonas reinhardtii* [8]. Bands at 695 and 675 nm have been attributed to dimers of A_0 and accessory Chls, and a band at 683 nm – to connecting Chls. It was concluded that Chl with absorption at 691 nm (C691), attributed to primary electron acceptor A_0 [9], is an obligatory component of the PSI reaction center. Some discrepancy in light-induced CD and absorption transient bands of PSI complexes from pro- and eukaryotes may be caused by differences in spectral characteristics of antenna Chls [10]. It was concluded that all excitonic interactions between six Chls in reaction center have to be taken into consideration for the interpretation of "P700 reduced-minus-oxidized" CD difference spectra [10, 11].

Strong exciton coupling of Chls may be responsible for the long-wavelength antenna states [12, 13]. X-ray structure of the trimer PSI complex from *Thermosynechococcus elongates* allows the calculation of excitonic interactions between Chls within that complex [14]. The mean center-to-center distance between the neighboring Chls in PSI of cyanobacteria is 9.9 Å

[1] The article was translated by the authors.

which is only slightly above the diameter of the chlorin ring. From the mean nearest neighbor an average interaction energy between neighboring Chls of 70 cm^{-1} is calculated which corresponds to ~6 nm splitting between the upper and lower excitonic bands. The oscillator strength of the coupled Chls in the PSI reaction center is more equally distributed between upper and lower exciton states. For two Chl pairs (A38–A39 and B37–B38, according to nomenclature of [1]) the upper exciton state carries most of the oscillator strength; the ratio between the oscillator strengths of the lower and upper exciton states is of about 0.2 [15]. But excitonic interactions alone cannot explain the strong red shift of long-wavelength Chls. Most probably differences in van der Waals interactions between Chls in excited and ground states contribute to the red shift [16].

The PSI long-wavelengths antenna states are characterized by a large Stokes shift of about 200 cm^{-1} due to strong electron-phonon coupling and by a large inhomogeneous broadening of 200–400 cm^{-1} [17, 18]. The full width of half maximum (FWHM) of absorption and fluorescence bands of the extreme red Chls is about 20–25 nm in PSI trimers of *A. platensis* at 77 K [19, 20] as compared to 7–8 nm for that of bulk Chls. Stark spectroscopy revealed that the changes of permanent dipole moments between the ground and excited state are 3–5 times higher for long-wavelength Chls than those for monomeric Chls [21, 22]. These unusual spectroscopic properties give evidence that strongly excitonic coupled Chls are responsible for the red absorption and emission bands, respectively. The narrow band at 711 nm observed in CD spectra of PSI monomer and trimer complexes from *A. platensis* is formed by excitonically coupled Chls [12, 17, 18]. The 77 K CD spectra of the trimeric PSI complexes exhibit also low amplitude components around 736 nm for *A. platensis* and 720 nm for *T. elongates* attributed to red-most chlorophylls [11]. No CD signals at 77 K have been resolved so far for C708 of PSI complexes of *Synechocystis* [22, 23]. Small CD signals might be explained by small rotational strength of the lower energy exciton band of excitonically coupled Chls.

Thus although the position and orientation of all reaction center cofactors and antenna Chls in the PSI complex of the cyanobacterium *T. elongates* [1] as well as that in PSI core complex of higher plant [24] have been determined, the spectral properties of the densely packed Chl molecules as well as the functional coupling of P700 with linker and some antenna Chls, especially with long-wavelength Chls, remains unclear. Main goal of this study was to identify the contribution of different spectral forms of antenna Chls in light-induced CD spectra of PSI complexes of cyanobacteria *A. platensis*, *T. elongates* and *Synechocystis* sp. PCC 6803.

METHODS

PSI complexes. PSI trimers and monomers of *A. platensis* have been isolated with n-dodecyl-β-d-maltoside (**DM**) (detergent: Chl ~15) as described [25]; samples in 50 mM Tris-HCl buffer (pH 8) containing 0.04% DM were stored in dark at –70°C. Before measurements the defrozen samples have been kept in the dark at 4°C for 24 h, then diluted to a final Chl concentration of about 15–20 μM with a buffer 0.05 M Tris-HCl (pH 8.0) containing 0.02% DM, 100 mM NaCl and 25 mM $MgCl_2$. The PSI trimers and monomers of *T. elongatus* and *Synechocystis* sp. were isolated as described [25] and stored in 20 mM Hepes-buffer (pH 7.5) with 10 mM $MgCl_2$, 10 mM $CaCl_2$, 500 mM mannitol and 0.03% DM. The same buffer was used for dilution samples to final Chl concentration of about 15–20 μM. Chl : P700 ratio of all used complexes varied between 95 and 110.

Absorption spectra. 77 K absorption spectra of oriented PSI complexes prepared according to [11] have been recorded with spectrophotometers 1E-UV/VIS, Cary (USA) and Hitachi-557 (Japan). Difference (light- and chemo-induced) absorption spectra were recorded on the spectropolarimeter JASCO-715 (Japan) simultaneously with CD spectra. The procedure of PSI complexes orientation is described in [11].

Circular dichroism spectra. CD spectra were recorded on spectropolarimeter JASCO-715. The measurements at 283 K have been done in 1 cm rectangular quartz cell; Peltier thermostat was used to hold temperature. Measurements at 77 K were performed in 0.2 cm Plexiglas cells with 65% (v/v) glycerol. Spectral band width was 3 nm for measurements at 283 K and 2 nm for measurements at 77 K. The intensity of the measuring beam determined with Light Meter Model LI-250 (USA) instrument in the region 660–690 nm was about 0.05–0.08 μE m^{-2} s^{-1}. The level of noise of spectropolarimeter was of about 0.3–0.4 mdegr (sampling time 2 s). To improve signal/noise ratio, accumulation of several CD spectra (typical number 20) and Fourier filtration and smoothing have been used. Second derivative spectra were obtained by using JASCO software programs and Origin 6.1.

Difference (P700 oxidized-minus-reduced) CD spectra. These spectra were obtained by three different approaches.

(1) Alternative accumulation of light-induced difference spectra. P700 was photooxidized by blue light illumination from LED LDB13633 (Ligitek, Taiwan). LED was placed directly in standard optical cell (10 × 10 × 42 mm) and the sample was illuminated top-down. The intensity of actinic light was about 100 μE m^{-2} s^{-1}. The red glas filter with transmission above 620 nm was used to protect the photomultiplier against scattered actinic light. To keep P700 in reduced state at the absence of actinic illumination,

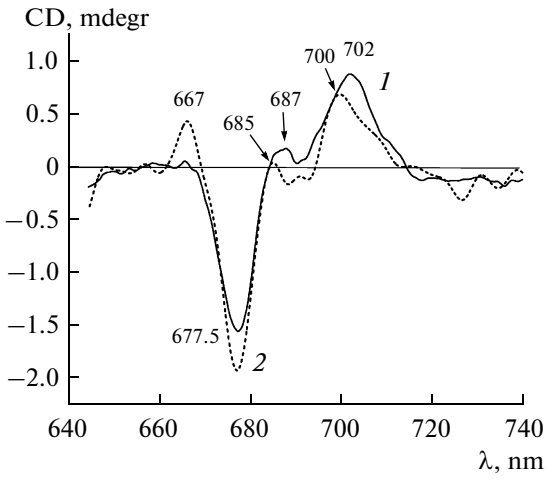

Fig. 1. Light-induced CD spectra of PSI trimers of *T. elongatus* measured under alternate (*1*) or constant (*2*) accumulation of signal; $D_{680} = 1$.

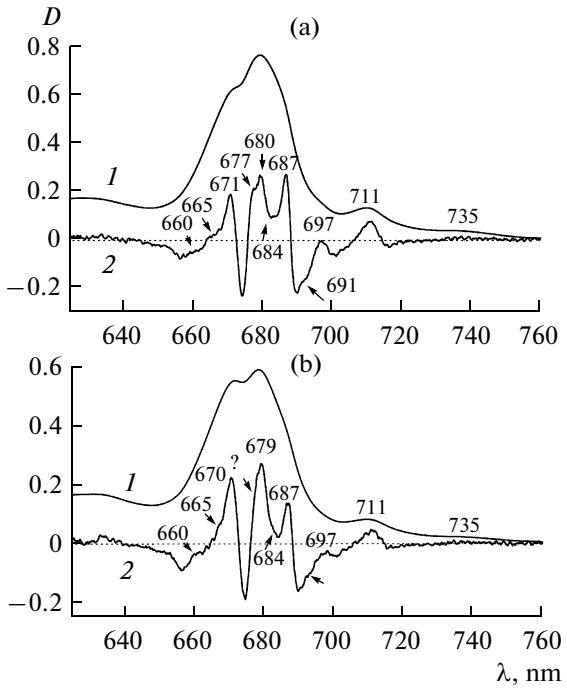

Fig. 2. 77 K absorption spectra (*1*) and their second derivatives inverted by sign (*2*) of PSI trimers of *A. platensis*. Complexes were oriented parallel (a) or rectangular (b) to polarization of measuring beam; 2 is the second derivative x (−20), differentiation step 1.8 nm.

2 mM of sodium ascorbate and 0.2–0.4 μM phenazinmetosulphate (**PMS**) were added to sample; half-life of $P700^+$ dark reduction was 4–5 s. To diminish the influence of irreversible degradation of the sample on CD spectra, the measurements in the light have been alternated with measurements in the dark. The calculated difference spectra have been averaged.

(2) Constant accumulation of light-induced difference spectra. The stock solution of PSI complex was separated on two parts. In one part (without reducing agent) P700 was oxidized by measuring beam in course of spectra accumulation. This is possible because half-life of $P700^+$ dark reduction is about 30 min and the intensity of the measuring beam is significant. In second part 1 mM of ascorbate and 1 μM PMS were added to the sample, and several CD spectra were recorded.

(3) CD spectra of complexes with chemically oxidized P700. The stock solution of PSI complexes was also separated on two parts. In one part P700 was oxidized by 1 mM ferricyanide and several CD spectra have been measured immediately without change of the sample. The accumulation of spectra of PSI complexes with P700 in the reduced state (with 1 mM ascorbate and 1 μM PMS) was carried out in second part. Difference spectrum was calculated from accumulated and smoothed spectra with P700 reduced and oxidized.

Comparison of different methods to measure difference CD spectra ($P700^+$ – P700) shows that shape of spectra depends on the type of measurement. Difference spectra of samples with chemically oxidized P700 are similar to spectra measured using constant accumulation (data not shown). According to Fig. 1, 667 nm band found in CD spectra that have been registered using methods (2) and (3), is absent in CD spectra obtained using alternative accumulation (method 1). This difference could be determined by accumulation of irreversible changes in CD spectra of antenna Chls in course of long-term illumination of sample by actinic light. Therefore the method (1) was chosen as for main measurements.

RESULTS AND DISCUSSION

Absorption spectra of antenna Chls. The possible appearance of antenna Chl bands in P700 difference spectra requires the simultaneous measurement of low temperature absorption and CD spectra of the same samples for that the difference spectra are registered. Figure 2 shows the typical 77 K absorption spectrum and their second derivative inverted by sign. Nine narrow spectral bands with full width at half maximum (**FWHM**) of about 7–12 nm are revealed for PSI samples oriented relatively to polarization plane of measuring beam. Because the studied PSI complexes are characterized by similar antenna Chl bands in spectral region up to 700 nm, only data for PSI complexes of *A. platensis* are presented in Table 1.

Second derivatives of low temperature CD spectra. The position of maxima in absorption and CD spectra coincide but some spectral bands in CD spectra made their identification more complicated because of superposition of positive and negative spectral bands.

Table 1. Spectral bands of antenna Chls (nm) in 77 K absorption and CD spectra as compared with P700 bands in light-induced CD spectra (ΔACD) of PSI complexes of various cyanobacteria

Abs. 77 K *A. platensis*	CD, 77 K *A. platensis* trimer	CD, 77 K *A. platensis* monomer	CD, 77 K *Synechocystis* sp.	CD, 77 K *T. elongates* trimer	CD, 77 K *T. elongates* monomer	ΔCD* 283 K
661	–	–	+662	–	+662	–
665	+664	–	–	+663	–	–
–	669	**+669**	+ 670	–	**+669**	–
671	**+672.5**	**+673**	**+ 672.5**	**+672**	**+673**	+671**
677	–	–677	–	–	–678	**–677**
680	**–681**	**+680**	–	(–681)	–	–
(684)	–	–	**–683**	–	**-685**	–
687	**–686**	**–684**	–686	**–685**	–	+685
691	–	–	–691	–690	–	**–691**
						+692**
697	**–696**	**–696**	–	(–695)	**-697**	–
–	–	–	**–702**	–701.5	**–702**	**+701**
708	–	–	–	–	**–**	–
711	**–713**	–	–	**–711**	**–711**	–
735	–735	–	–	–	**–**	–720

Notes: * Light-induced CD bands ($P700^+ - P700$) – averaged values; **Observed only for PSI of *Synechocystis* sp. Bold – main bands.

"Wrong" bands in derivative spectra may be excluded by deconvolution of measured CD spectra on Gaussian components and their subsequent differentiation of simulated spectra. Figure 3a shows CD spectrum and its inverted second derivative of PSI complexes of *A. platensis*. Positive bands at 664, 667 and 671 nm (FWHM is 7–8 nm) are identified with high probability as well as negative bands at 681 and 685 nm (FWHM is 6–7 nm), at 696 nm (FWHM is 8–10 nm), and at 713 nm (FWHM is 12–14 nm).

The CD spectrum deconvoluted into 7 Gaussian components at 664(+), 667(+), 671(+), 681(–), 685(–), 696(–), and 713(–) nm is presented in Fig. 3b. Bands at 675, 678, and 690 nm in the second derivative spectrum of the original CD spectrum of the PSI trimers of *A. platensis* may be identified as wrong ones since they are present also in simulated CD spectrum after differentiation (Fig. 3c) while corresponding Gaussian bands are absent. Perhaps these spectral Chl forms observed in absorption spectra do not appear in CD spectra because of the lower rotational strength and superposition with more intense bands. Indeed the remarkable optical activity of Chl 677–678 and Chl 690–691 appears in difference CD spectrum (PSI trimer minus monomer).

The difference CD spectra "PSI trimers minus monomers". Spectral bands may be expected in difference CD spectra "PSI trimers minus monomers" that appear as a result of resonance interaction of Chls localized on different PSI monomers. However no new bands have been revealed in CD spectra of PSI trimers; difference between CD spectra of PSI trimers and monomers is only due to changes in the intensity of CD bands, caused by differences of the rotational strength of Chls. According to Fig. 4, the bands at 664, 672–673, 678, 682–684 and 687–689 nm are observed in difference spectrum. A negative band at 677 nm is present in CD spectra of PSI monomers that could not be identified in second derivative CD spectra (Fig. 3).

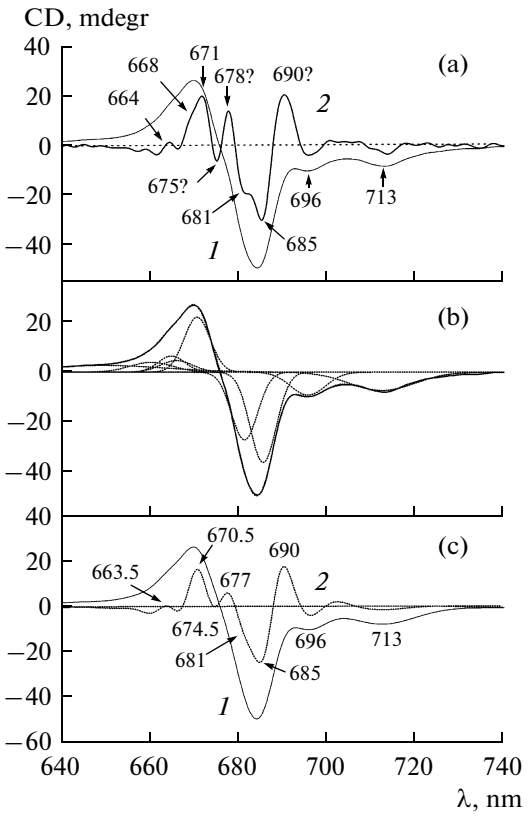

Fig. 3. Second derivative of CD spectra of *A. platensis* PSI trimers at 77 K: (a) – CD spectrum (*1*) and its second derivative (*2*), (b) – deconvolution of measured spectrum (solid) into the Gaussian bands at 661(+), 664(+), 667(+), 671(+), 680(–), 685(–), 696(–) and 713(–) nm (dotted), (c) – CD spectrum as a sum of 8 Gaussian bands (*1*) and its second derivative (*2*). Bands at 674.5, 677 and 690 nm may be wrong since they absent as corresponding Gaussian bands.

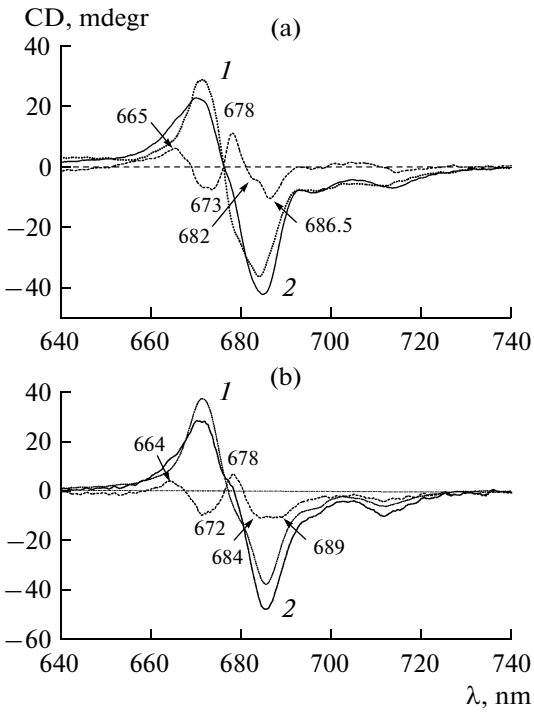

Fig. 4. 77 K Difference CD spectra "trimer minus monomer" of PSI complexes of *A. platensis* (a) and *T. elongatus* (b) obtained by subtraction of monomer spectrum (*1*) from that of trimer (*2*). Spectra have been normalized to $D_{680} = 1$ prior to subtraction.

CD spectra of PSI trimers of *A. platensis* and *T. elongates* are very similar; therefore the difference spectra "trimers minus monomers" for both PSI complexes are similar also. Bands at 672(+) and 676–677(–) nm are more intense in CD spectrum of PSI monomers while the bands at 665(+), 682(–) and 686(–) nm are more intense in CD spectrum of PSI trimers. High intensity of band at 677–678 nm in CD spectra of PSI monomers correlates with high intensity of 677(–) nm band in light-induced spectra of P700 (Figs. 4 and 5). It may be proposed that formation of trimer as well as P700 photooxidation is accompanied by decrease of the rotational strength of band at 677(–) nm that leads to the appearance of a negative band in the difference spectrum "P700 oxidized minus reduced" as well as in the difference spectrum "trimers minus monomers".

Similarity of CD spectra of PSI trimers from various cyanobacteria is especially visible in spectral region of the carotenoid absorption; rotational strength of carotenoids in PSI trimers is about 2–3 times higher as compared with monomers [12]. In combination with derivative spectra, the difference CD spectra indicate that main part of spectral Chl forms show significant optical activity and therefore are visible in CD spectra.

Light-induced CD spectra of PSI complexes. Light-induced CD spectra of PSI complexes from different cyanobacteria measured by alternate accumulation are characterized by similar set of spectral bands (Fig. 5). All spectra (except the spectra of monomers from *T. elongatus*) show a positive band around 702 nm and a negative band at 692–694 nm that have been interpreted as a dimeric exciton splitting of P700 [2, 3, 11, 27]. The shift of position of the negative band to 694 nm observed for PSI monomers of *A. platensis* and *Synechocystis* is the result of red shift because of superposition with very intense positive band at 685 nm. Bands at 692(–) and 701(+) nm ascribed to the conservative dimer splitting are predominant for PSI complexes enriched with P700 [4–6, 27] and may be caused by photobleaching of the special pair of dimer (P700) of the reaction center. PSI monomers of *T. elongatus* are the only exclusion. They show a positive 692 nm band (Fig. 5b).

The amplitude of the negative band at 676–677 nm is maximum in all studied PSI complexes and correlates with maximum amplitude of this band in low temperature absorption spectra. Band at 685(+), most

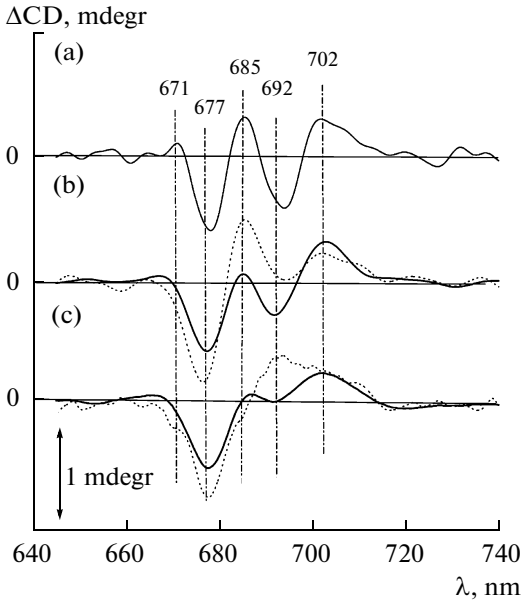

Fig. 5. Light-induced CD (ACD) spectra of PSI complexes of *Synechocystis* (a), *A. platensis* (b) and *T. elongatus* (c); solid – trimers, dashed – monomers. Spectra have been measured upon alternate accumulation of signal, $D_{680} = 1$.

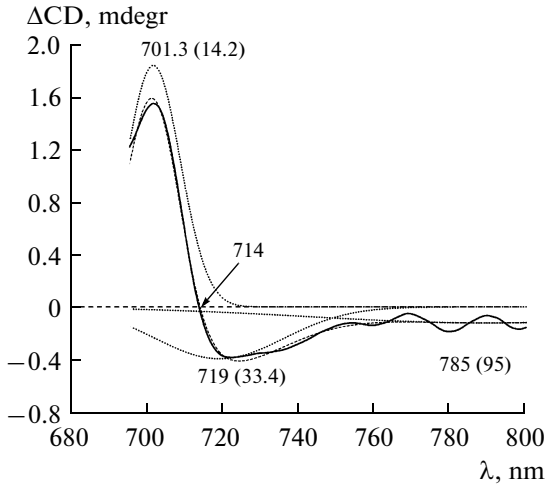

Fig. 6. Light-induced CD spectrum of *A. platensis* in far-red region (solid) and its deconvolution into three Gaussian bands (dashed). 20 accumulations, $D_{700} = 0.98$, $D_{702} = 0.03$.

intense in PSI monomers of *A. platensis*, is extremely low for complexes of *T. elongatus*. It is interesting to note that both bands at 677(–) and 685(+) nm are revealed as minor components in PSI complexes enriched with P700 [4–6, 27]. The narrow band at 671 nm found for PSI complexes from Synechocystis (Fig. 5a), was observed earlier only for complexes enriched with P700.

To reveal the minor components in light-induced spectra the PSI trimers of *A. platensis*, samples with high optical density have been used (Fig. 6). Band at 711–713 nm of antenna Chl characterized by relatively low FWHM and significant rotational strength, is absent [17]. However the wide (FWHM 33 nm) negative band at 720 nm is revealed that is overlapped with very wide absorption band of P700 cation radical. It is obvious that the observed wide band at 720 nm cannot be ascribed to pigments of the universally organized reaction center since it is specific only for PSI of some cyanobacteria. It is difficult to explain such strong variability of the difference CD spectra by suggestion that only excitonic interactions of 6 Chls in reaction center are responsible for those spectra.

Light-induced CD spectra ($P700^+ - P700$) presented in this study differ significantly from spectra reported earlier for samples with lower (40–60) Chl : P700 ratio [4, 5]. Intense bands at 677 and 685 nm observed earlier as minor ones with amplitude that did not exceed 30% of that of symmetric bands at 690–691 and 700–701 nm (Table 2). The variability of light-induced CD spectra of PSI complexes was interpreted as the result of changes in rotational strengths of Chl molecules in PSI reaction center upon oxidation of P700. It obvious that such interpretation is not complete since the variability of CD spectra is dependent on: Chl : P700 ratio of PSI complexes, type of cyanobacteria from what PSI complexes have been isolated, and from tertiary structure of PSI complexes (trimer or monomer). Each of these factors may effect much stronger the organization of antenna Chls than that of the reaction center.

Taking into account the highly conservative organization of Chls in the reaction center of PSI [1, 24], two types of spectral bands in difference CD spectrum "P700 oxidized minus reduced" may be expected. First type – bands caused by changes in excitonic interaction between molecules of six Chl in the reaction center that have to be identical (or very similar) for different PSI complexes. Second type – bands caused by changes in resonance interaction of the reaction center Chls with antenna Chls. To reveal these bands we did the Gaussian deconvolution of difference CD spectra using standard program Origin 6.1. Following limitations have been used: (1) the amount of the Gaussian bands (seven) has to be similar for all spectra, (2) variability of maximum position has to be about 2 nm for six main CD bands and about 10 nm for long-wavelength band at 720 nm, (3) variability of FWHM are between 9–15 nm and for 720 nm band 15–40 nm, (4) sign of rotation was fixed only for two very closely positioned bands at 691 and 693 nm. No limitations were used for the intensity of bands. Results of deconvolution of CD spectra of PSI trimers and monomers of *A. platensis* and *T. elongatus* are presented on Table 3.

Table 2. Position of maxima and the relative intensity of bands (italic) in light-induced CD spectra of P700 (P700–P700$^+$) in PSI complexes from various cyanobacteria; bold – main bands

Sample (detergent)	Chl:P700	Spectral bands						Reference
		1	2	3	4	5	6	
Spinacea oleracea (Triton-X100)	60	**696.5** *−1*	**688** *+1.2*	–	–	–	–	[2]
Pisum sativum (Triton-X100)	50	**700** *−1.0*	**689** *+1.3*	–	–	678 *−0.6*	670 *+0.3*	[27]
Pisum sativum (Triton-X100)	40	**698** *−1.0*	**691** *+1.4*	**685** *+1.2*	–	–	671 *−0.28*	[4, 6]
Pisum sativum (DDS-Na)	50	**699** *−1.0*	**691** *+1.3*	–	–	678 *+0.2*	–	[4, 6]
Pisum sativum (Triton-X100)	65	**699** *−1.0*	**691** *+1.5*	–	680 *+0.4*	–	671 *−0.3*	[4, 6]
A. platensis (Triton-X100)	60	**701** *−1.0*	**701** *−1.0*	–	**681** *+1.1*	–	671 *−0.75*	[5]
*A. platensi*s, trimer (DM)	100	**702** *−1.0*	**692** *+0.8*	685 *−0.2*	–	**677** *+1.6*	–	This article
*A. platensi*s, monomer (DM)	100	**702** *−1.0*	?	**685** *−2.1*	–	**676.5** *+3.2*	–	This article
T. elongatus, trimer (DM)	100	**702** *−1.0*	?	686 *−0.3*	–	**677** *+1.7*	–	This article
T. elongatus, monomer (DM)	100	**702** *−1.0*	**692** *−1.1*	–	–	**678** *+2.5*	–	This article
Synechocystis sp. (DM)	100	**701** *−1.0*	**694** *+1.2*	**685** *−1.1*	**–**	**678** *+1.8*	671 *−0.3*	This article

Table 3. Components of the Gaussian deconvolution of light-induced CD spectra (P700–P700$^+$) of PSI complexes. λ – wavelength of maximum or minimum of bands; Δ – FWHM; amplitude (θ) is in units of ellipticity for samples with $D_{680} = 1$

Band parameters	*A. platensis* trimer	*A. platensis* monomer	*T. elongatus* trimer	*T. elongatus* monomer	*Synechocystis* sp.
λ, nm	672.3	672.1	670.0	670.4	672.5
Δ, nm	8.6	8.5	11	8.5	8.6
θ, mdegr	−1.9	−1.2	−1.5	+0.4	−3.9
λ, nm	**677.8**	**677.5**	**678.2**	**678.4**	**678.5**
Δ, nm	8.5	8.6	8.9	8.5	8.5
θ, mdegr	+11.8	+16.5	+10.1	+12.3	+13.2
λ, nm	684.6	684.7	685.1	684.0	686
Δ, nm	8.8	8.6	8.5	9.0	9.1
θ, mdegr	−6.9	−7.5	−5.3	−5.7	−14.0
λ, nm	**692.0**	**691.9**	**690.4**	**689.3**	**692.0**
Δ, nm	10.2	10.7	11.9	11.5	9.1
θ, mdegr	+11.7	+6.6	+10.5	+7.1	+15
λ, nm	694.0	692.0	692.7	692.0	–
Δ, nm	12.0	11.3	10.5	8.5	–
θ, mdegr	−1.1	−2.8	−2.8	−9.9	–
λ, nm	**700.0**	**701.5**	**702.0**	**701.9**	**700.0**
Δ, nm	13.0	14.6	13.1	13.6	12.6
θ, mdegr	−9.1	−6.8	−6.4	−6.9	−8.8
λ, nm	725	–	720	720	
Δ, nm	28	–	23	20	
θ, mdegr	+1.4	–	+2.4	+1.2	

The position and amplitude of 701(–) and 691 (+) nm bands are most stable and these bands predominate in light-induced CD spectra of all PSI complexes enriched with P700 (or with destroyed antenna). The position and amplitude of band at 678(+) nm that is weakly revealed in complexes, enriched with P700, and are also stable (Table 2). This band may be due to as the reaction center Chl as by their interaction with antenna Chls that are characterized with absorption band at 677 nm. Other bands are strongly variable by intensity for various PSI complexes, and their appearance in difference CD spectra is determined predominantly by changes of antenna Chls. It is interesting to note the unusually small FWHM of spectral bands in light-induced spectra at 77 K that is typical for antenna Chls (Table 3).

Thus the data described in this work indicate that the light-induced spectra induced by P700 oxidation reflect not only the excitonic interactions between six Chls in the reaction center but also the resonance interaction of P700 with antenna Chls. Significant differences in organization (orientation) of antenna Chls of PSI complexes of various cyanobacteria causes the variability of light-induced CD spectra.

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