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DICHROISM OF TRANSIENT ABSORBANCE CHANGES IN THE RED SPECTRAL REGION USING ORIENTED CHLOROPLASTS

II. *P*-700 ABSORBANCE CHANGES*

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SUMMARY

The light induced transient absorbance changes associated with the trap of photosystem I have been studied using magnetically oriented spinach chloroplasts and a polarized measuring beam. The ΔA spectra for the two polarizations parallel and perpendicular to the plane of the photosynthetic membranes have been recorded in the spectral range 630–850 nm.

A dichroic ratio greater than two is observed both in the main band around 700 nm and in the radical cation band around 810 nm, leading to the conclusion that the far-red transition moment of the *P*-700 dimeric species is lying almost parallel to the membrane plane.

Dichroic ratios smaller than one are reported in the 650–670 nm band of the ΔA spectrum. The possible attribution of this band to excitonic interactions in the dimer favors the hypothesis of a tilting out of the membrane plane of this transition. This finding ruled out an orientation parallel to the membrane plane of the two chlorophyll molecules constituting the *P*-700 phototrap.

A small residual transient absorbance change is observed in the absence of artificial electron acceptor. Its spectrum shows significant differences as compared to the normal *P*-700 spectrum: the magnitude of the signal at 700 nm is only 15–25 % of the normal signal, the half-band width of the band around 700 nm is nearly twice as large and the dichroic ratio in the band is only 1.5 ± 0.1. In the presence of ferricyanide, this signal is still observed both for intact and osmotically broken chloroplasts, suggesting a heterogeneity in the population of traps in Photosystem I.

INTRODUCTION

The photosynthetic apparatus of green plants consists of a lipoprotein mem-

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brane in which the various photosynthetic pigments are embedded. The function of most of these pigments (antenna) is to collect the light quantum and funnel its energy towards a special type of molecule (trap) where the separation of charges can occur. The trap of Photosystem I is characterized by specific absorption changes (bleaching) that have been attributed [1–3] to the photooxidation of a particular chlorophyll *a*, named *P*-700 (or chlorophyll a_1). From ESR spectroscopy, it has been concluded [4] that *P*-700 is probably a hydrated dimer, although a higher polymerized form cannot be excluded.

Recent work in this and other laboratories has involved the use of polarized light spectroscopy on oriented chloroplasts to determine the orientation of the antenna molecules with respect to the plane of the photosynthetic membrane [5–8]. These measurements are of interest for a better knowledge of the structure of membranes at the molecular level and for the understanding of the mechanisms of energy transfer in photosynthesis, but they do not provide information on the reaction centers. Such information can be obtained from the study of the dichroism of the transient absorbance changes that reflect the photooxidation of the traps using a polarized measuring beam and an anisotropic suspension of chloroplasts.

Junge and Eckhof [9, 10] used a photoselection technique to determine the dichroism of *P*-700 on an unoriented suspension of chloroplasts that was rendered anisotropic by the exciting flash itself. Making assumptions about the arrangement of the Photosystem I antenna molecules, they concluded that *P*-700 was oriented at a rather flat inclination with respect to the photosynthetic membrane. However the technique of photoselection, although very elegant in its principle [11], is not the most appropriate method for this type of study. Besides the specific need for assumptions concerning the orientation of the antenna, this method is intrinsically much less sensitive than a technique involving the measurement of the dichroism of absorbance changes using oriented chloroplasts [12]. Moreover, possible artifacts [10, 12] are very similar for these two methods, because the membranes which are giving the polarized component of the ΔA signal in photoselection experiments are oriented with the same geometry as the ones we are analyzing by our technique.

Using spinach chloroplasts oriented by a magnetic field we have recently measured [13] a very high dichroism in the main band of the Photosystem I trap at 700 nm, indicating an orientation almost parallel to the membrane plane of the corresponding transition moment. In the present report, we extend our measurements in the spectral region of 630–850 nm to the various absorbance changes linked to the activity of Photosystem I.

MATERIALS AND METHODS

The experimental arrangement and the preparation of chloroplasts are described in the preceding paper [14].

In all cases, valinomycin (10^{-6} M) was added to the chloroplast suspension. Potassium ferricyanide (10^{-3} M) was used as an oxidant to slow down the otherwise very rapid reduction of *P*-700$^+$ [15].

RESULTS

For each polarization of the measuring beam, 400 transients were averaged at

every wavelength. A measurement at any particular wavelength was always compared to a reference measurement at 702.5 nm on the same sample. Four to eight measurements were taken on a given sample until a modification in the amplitudes and/or in the dichroic ratio would indicate the sample has to be changed. At the rather high concentration (10^{-6} M) of valinomycin used in this study, the field-indicating absorbance changes are accelerated so that they are no longer resolved on the time-scale of our measurements [14]. At every wavelength, we checked that the decay kinetics of the transients ($t_{\frac{1}{2}}$, 30–60 ms) were the same for the two polarizations and identical to the ones observed at 702.5 nm. The ΔA spectra for the two polarizations of the measuring beam are plotted versus wavelength in fig. 1.

In the absence of ferricyanide a residual transient absorbance change has been detected; the spectra for both polarizations are shown in Fig. 2.

DISCUSSION

The ΔA spectrum for unoriented chloroplasts can be estimated from data presented in Fig. 1 by summing $2\Delta A_{\parallel}+\Delta A_{\perp}$ [7]. Such a calculated spectrum resembles the one obtained with small particles enriched in Photosystem I activity by digitonin treatment of spinach chloroplasts [3]. Furthermore, the similarity of the kinetics observed at 702.5 nm and at the other wavelengths indicates that the transients described here correspond to the reversible photobleaching of *P*-700.

The simplest model for the *P*-700 chemical species which is compatible with available experimental results is a hydrated chlorophyll *a* dimer (chlorophyll *a*-$H_2O)_2$ [3, 4, 16]. Even with this model, there are two major problems that need to be solved in order to interpret the polarization data presented in this study. The first problem deals with the significance of the absorbance changes themselves, the second one is related to the excitonic coupling of the two chlorophylls in a dimer.

Significance of the P-700 absorbance changes

These changes are a consequence of the difference in absorption between the oxidized (*P*-700^+) and the reduced state of the dimer. It is not clear at present whether the *P*-700^+ species has the spectrum of a monomeric chlorophyll species in the region 650–700 nm or has nearly no absorption bands in this spectral range. Several interpretations have been proposed to account for the ΔA spectrum in the red [17–20]. The most classical ones consider a bleaching at 700 nm and either a red shift of another band around 685 nm [18–19] or the disappearance of a band at 683 nm plus the appearance of a new band at 686 nm [17] (due to the remaining unoxidized chlorophyll molecule in *P*-700^+). A very different model has also been proposed in which the bleaching of the band of the dimer at 680 nm is accompanied by a very large shift giving peaks at 685 and 700 nm [20]. Even by studying the evolution of the dichroism of the different bands of the ΔA spectrum at low temperatures [21] we have not been able to discriminate between these various hypotheses. Such discrepancies in the interpretations will preclude an unambiguous explanation of the polarization data presented in this study.

Excitonic coupling of transition dipole moments in a chlorophyll dimer

In a dimer, the electronic interactions between the transition moments of the

two parent molecules become so strong that it is only possible to excite the two interacting molecules collectively. The energy levels of the monomers being degenerate, this interaction results in a splitting of the energy levels in the dimer. Such interactions have been observed for bacteriochlorophylls in purified reaction centers from photosynthetic bacteria [22, 23]. There is some evidence of an excitonic splitting of the energy levels in the light minus dark circular dichroism of Photosystem I enriched particles which results in absorption bands at 683 and 700 nm [17]. In a study of the (chlorophyll *a*-H_2O)$_2$ adduct in vitro, excitonic splitting has been reported with components at 700 and 715 nm [16].

For the chlorophyll *a* molecules, the transition moments are lying in the tetrapyrrolic ring along two mutually perpendicular directions X and Y [24]. In the red part of the absorption spectrum only the Q_y transition is strongly allowed. Let us first consider a chlorophyll *a* dimer in which the planes of the monomers are stacked parallel to each other. According to Kasha [25, 26], if the two Q_y dipoles of the monomers are also parallel, excitonic coupling in the dimer produce only one allowed transition that keeps the same polarization as the transitions of the monomers. However, if the two transitions are at an angle with respect to each other, the excitonic interaction produces a splitting into two new transitions. These new transitions can be estimated by making the sum and the difference of the vectors representing the transition dipole moments of the monomers [25]. As a consequence the new transitions of the dimer are both lying in a plane (parallel to the planes of the monomers) but are polarized at 90° from each other.

If now we consider such a stacked dimer oriented with respect to the photosynthetic membrane, a linear dichroism measurement with oriented membranes will give a dichroic ratio greater than unity only if each of the transitions of the dimer is oriented at less than 35° of the membrane plane [7]. If a band is found with a dichroic ratio smaller than 1, the corresponding transition dipole of the dimer must be tilted by more than 35° out of the membrane plane and consequently at least one of the monomer transition moments must be tilted out of the membrane.

More generally, one has to consider also the tilt angle between the two planes of the monomers that constitute the dimer. This tilt angle is not known in vivo, and consequently, we will not consider at present all the possible configurations that could be achieved by the two monomers. We will however use the arguments mentioned above to determine if the dimer is parallel to or tilted out of the membrane plane.

Interpretation of the dichroism of the absorbance changes

Assuming the in vivo spectrum represents essentially the bleaching of a chloro-

TABLE I

DEPENDENCE OF THE DICHROIC RATIO $\Delta A_{\parallel}/\Delta A_{\perp}$ ON THE MEASURING WAVELENGTH

	820 nm	727.5 nm	702.5 nm	685 nm	660 nm
With ferricyanide	2.4±0.1	1.5±0.1	2.5±0.1	2.3±0.1	0.4±0.1
Without ferricyanide		1.5±0.1	1.5±0.1	1.4±0.1	

phyll *a* dimer, it is possible to discuss these results in terms of the orientation with respect to the membrane plane of the new transitions of the dimeric species without referring to the orientation of the transitions of the parent molecules in the framework of the dimer.

The dichroic ratio $\Delta A_{\parallel}/\Delta A_{\perp}$ measured at 702.5 nm for well-oriented spinach chloroplasts is always greater than 2 (Table I). The maximum value that we have reproducibly observed on several preparations was 2.5 ± 0.1. The dichroic ratio remains constant, within the accuracy of the measurement, in the spectral range 697.5–710 nm. This very high dichroism is an agreement with previous studies [10, 13] and indicates an orientation almost parallel to the photosynthetic membrane of the transition moment responsible for this absorption band of the dimer.

The *P*-700 spectrum shows a broad positive band peaking around 810 nm. By analogy with the in vitro spectrum of chlorophyll a^+ [27, 28] this absorbance increase has been attributed to the radical cation *P*-700$^+$ [29, 30]. A Y polarization of the infrared transition in the cation has been determined for bacteriochlorophyll *a* by molecular orbital calculations [31]. If this result can be extrapolated to chlorophyll *a*, the identical dichroic ratios found at 702.5 nm and at 810 nm in this study (Table I) and also at low temperatures [21] indicate that the 700 nm band of the *P*-700 dimer originates from mixing of Q_y transitions in the monomers. Consequently such an indication favors a *P*-700 model in which the 700 nm band is arising from a transition of the dimer itself [17–19].

Around 660 nm a broad negative band is apparent in the Fig. 1 spectrum.

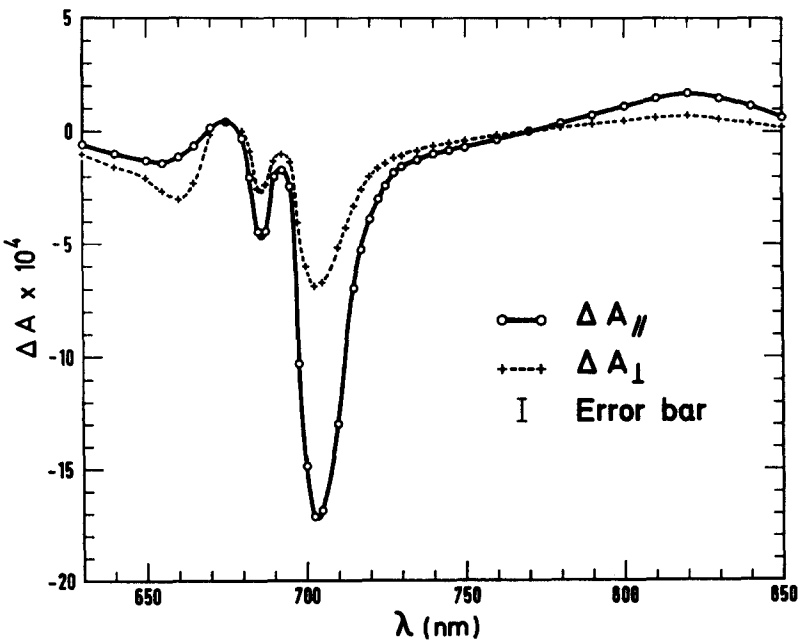

Fig. 1. Wavelength dependence of the *P*-700 absorbance changes on magnetically oriented spinach chloroplasts for the two polarizations of the measuring beam. Valinomycin, 10^{-6} M and ferricyanide, 10^{-3} M were added. Negative values for ΔA correspond to a decrease in absorbance.

This signal which has been observed with Photosystem I particles [3, 29] has not been described in the photoselection study [9, 10, 32], probably because of the already mentioned lack of sensitivity of this technique. In view of the small (0.40) dichroic ratio that we observed for this band, a finding that could have pertinent implications for the orientation of the *P*-700 dimer, it is important to know if this absorbance change has to be attributed to a transition in the dimer itself or to other effects.

The appearance of localized charges in the primary photochemical act could induce band shifts in the pigments close to the reaction center. These shifts which would be of the same nature (Stark effect) as the field indicating absorbance changes studied in the preceding paper [14] are usually a few nanometers in magnitude. As a consequence, the ΔA spectrum of these changes are characterized by sharp positive and negative peaks and small half-band width of the bands. This is different from what is observed in our case (Fig. 1) where the band at 650–670 nm is broad.

It has been demonstrated [21] that the Q_y transition moment of chlorophyll *b* molecules, which also absorb in this region, are tilted out of the membrane plane by an angle greater than 35°. The small dichroic ratio observed in this region could be explained by this species. However it is generally accepted that chlorophyll *b* is not present in Photosystem I reaction centers [33, 34].

Finally we note that both in the absorption spectrum and the fluorescence excitation spectrum of the (chlorophyll *a*-H_2O)$_2$ adduct a broad band peaking around 655 nm is observed [16]. Its amplitude relative to the 700 nm band compares well with the corresponding feature of the *P*-700 spectrum.

Considering the three arguments mentioned above we attribute the broad signal with a dichroic ratio of 0.40 at 660 nm to an optical transition of the *P*-700 dimer. One possible explanation would consider the 660 and the 700 nm bands as the two excitonic components of the dimer. The two new transitions observed upon excitonic coupling in a dimer being polarized at 90° from each other [25], it can be easily pictured that one of these transitions (the one responsible for the 700 nm band) is lying close to the plane of the photosynthetic membrane, the other one being tilted out of this plane by an angle of about 50° (to explain the dichroic ratio of 0.40 observed at 660 nm). In this case the corresponding energy of interaction would be quite large (about 900 cm^{-1}), a fact that can be accounted for by a small spacing of the two monomers in the *P*-700 dimer.

An alternative hypothesis would involve excitonic coupling of the Q_x transitions of the monomers. Such transitions, although slightly allowed, are known to occur at 580 and possibly at 620 nm [24] in monomeric chlorophyll *a*. As the result of excitonic interaction in the dimer these transitions will give new absorption bands which could be shifted and possibly enhanced. One of these bands absorbing in the range 640–660 nm would correspond to a transition dipole tilted out of the membrane plane by an angle of about 50°.

Orientation of P-700

The dichroic ratio of 2.5 that has been observed at 702.5 nm in this study indicates an orientation almost planar of the corresponding transition moments with respect to the photosynthetic membrane, knowing that such measurement always represents a minimum estimate of the intrinsic orientation [13]. Such a high orientation has never been measured for any of the antenna pigments of the chloroplasts [7].

A similar in plane orientation has been found for the 810 nm transition of $P\text{-}700^+$ in this study and also for the 820 radical cation band of the photooxidized trap of Photosystem II at low temperature [35]. These observations suggest that the red transition moments in the reaction centers chlorophylls are the most in plane among the transitions of the photosynthetic pigments. However, in the hypothesis of a dimeric structure for *P*-700, the dichroic ratio of 0.40 observed at 660 nm is not reconcilable with a model where the two chlorophyll *a* tetrapyrrolic rings are parallel to the membrane plane.

More information is needed on the nature of the *P*-700 absorbance changes, on the internal structure of this species and on the polarization of the transitions in this dimer in order to interpret our data in terms of the angles of the transition moments of the parent molecules with respect both to each other and to the plane of the photosynthetic membrane. In this respect, the study of model systems [16] and of oriented reaction centers from photosynthetic bacteria [36] where the absorbance changes are already better characterized [22, 23] might be very fruitful.

Heterogeneity of Photosystem I reaction centers

When analyzing the spectral dependence of the dichroic ratio in the main red band of *P*-700 we observed a decrease of this ratio in the red edge of the 700 nm band. At 727.5 nm the dichroic ratio was only 1.5 instead of 2.5 at 702.5 nm (Table I). We have ruled out experimentally the possible contribution from artifacts: anisotropic light scattering effects, fluorescence effects on the phototube response, possible luminescence from the filters were eliminated by proper modifications of the experimental arrangement.

Differences in the dichroic ratios at 702.5 and 727.5 nm are not expected if the main band of *P*-700 arises from a single transition and could indicate either the presence around 727.5 nm of the second excitonic component of the dimer, as suggested for in vitro systems [16], or a heterogeneity in the population of Photosystem I reaction centers.

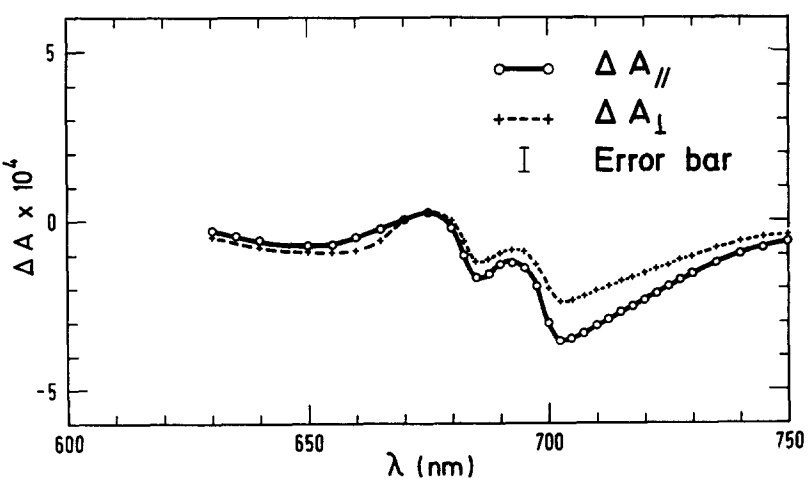

Fig. 2. Wavelength dependence of the residual absorbance changes on magnetically oriented spinach chloroplasts for the two polarizations of the measuring beam. Valinomycin, 10^{-6} M; no ferricyanide.

In the absence of ferricyanide we observed that the signal at 727.5 nm was still present and practically unchanged in its amplitude, kinetic and polarization as compared to a control in the presence of the oxidant. The spectra of $\Delta A_{\parallel}$ and $\Delta A_{\perp}$ in the absence of external electron acceptor are depicted in Fig. 2. The overall shape of these spectra resembles quite closely the ones of Fig. 1 specially in the positions and the relative amplitudes of the peaks. However significant differences are observed specially in the half-band width of the 700 nm band and in the ratio of the amplitudes at 685 and 692.5 nm. Without addition of ferricyanide, the signal is considerably smaller (by a factor of 4 to 7, depending on the preparation) and shows a lower polarization for all the bands as compared to the control (Fig. 2).

Under our experimental conditions (repetitive flashes, spectral range, time-resolution, presence of valinomycin) the only known absorbance changes that can be observed are linked to Photosystem I activity. Without addition of ferricyanide, the 20 μs and 200 μs components of the reduction of $P\text{-}700^{+}$ observed by Haehnel [37] escape our detection system and only a slow phase of smaller amplitude is observed. Consequently the existence, in the absence of ferricyanide, of a signal at 700 nm spectrally different from the usual *P*-700 indicates a heterogeneity of the Photosystem I reaction centers. However, it is important to determine whether this heterogeneity arises from the sample itself or is an intrinsic feature of the photosynthetic apparatus.

These experiments were repeated using osmotically broken chloroplasts (90 min in distilled water at 4 °C); the valinomycin concentration had to be increased (up to $5 \cdot 10^{-6}$ M) in order to accelerate sufficiently the decay of the signal at 650 nm [14],

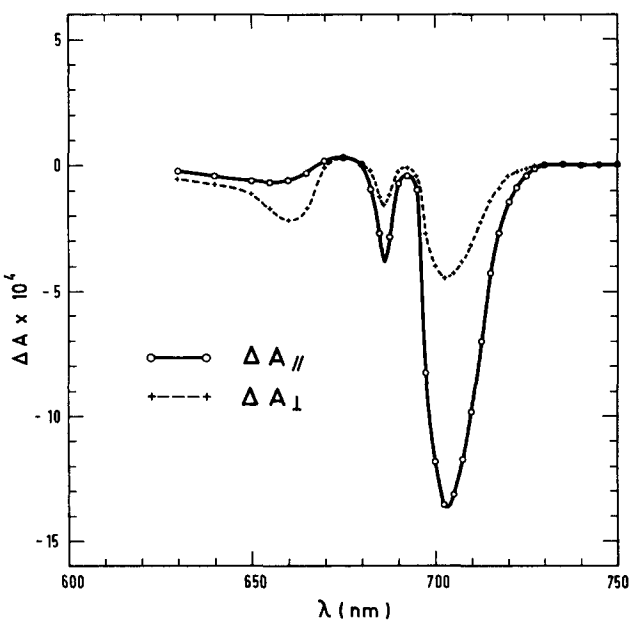

Fig. 3. Spectrum obtained by plotting the difference between the spectra of Figs. 1 and 2 for each polarization of the measuring beam.

and the magnetic field was not used. Upon addition of ferricyanide (10^{-3} M), the signal at 702.5 nm was increased by a factor of about 4 and the kinetic of decay was slowed down by a factor of 3 ($t_{\frac{1}{2}}$, 120 ms instead of 40 ms) as compared to the control without ferricyanide. Under the same circumstances, the signal at 727.5 nm remained unchanged in amplitude and kinetic. This similitude of behaviour for broken and unbroken chloroplasts strongly suggests that the signal described in Fig. 2 is an intrinsic property of functional chloroplasts and represents the photooxidation of a new type of reaction center from Photosystem I.

It is clear from the experiments described above that the spectrum shown in Fig. 1 represents the sum of absorbance changes in the absence of ferricyanide (Fig. 2) plus another absorbance change that is only revealed in the presence of the oxidant. The spectrum of this last absorbance change which can be obtained by substracting the spectra of Figs. 1 and 2 for each polarization is depicted in Fig. 3. In the same manner as the dichroic ratio of 1.5 ± 0.1 measured at 702.5 nm for the signal observed in the absence of ferricyanide (Fig. 2) remains constant over the whole red band, the dichroic ratio of the signal depicted in Fig. 3 stays constant (3 ± 0.1) in the region 697.5–725 nm. Furthermore, the half-band widths for the two spectra are different by a factor of 2.

The similarities between the spectra of these two types of signal suggest that they both represent aggregated chlorophyll *a* (the difference in half-band width could possibly be accounted for by different states of aggregation). It is known that Photosystem I is distributed between two different types of structures: grana and stroma membranes [38]; it is possible that the two types of reaction centers that are indicated by our experiments represent the two possible locations of these phototraps. Finally, we note that similar conclusions concerning the heterogeneity of Photosystem I reaction centers have been reached recently by Haehnel [39] who found that 75 % of the chlorophyll a_I were coupled to chlorophyll a_{II} and that the remaining 25 % were functionally isolated.

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