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REACTION CENTER TRIPLET STATES IN PHOTOSYSTEM I AND PHOTOSYSTEM II

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Summary

A photosystem I (PS I) particle has been prepared by lithium dodecyl sulfate digestion which lacks the acceptor X, and iron-sulfur centers B and A.

Illumination of these particles at liquid helium temperature results in the appearance of a light-induced spin-polarized triplet signal observed by EPR. This signal is attributed to the triplet state of P-700, the primary donor, formed by recombination of the light induced radical pair $P\text{-}700^{+}A_1^{-}$ (where A_1 is the intermediate acceptor). Formation of the triplet does not occur if P-700 is oxidized or if A_1 is reduced, prior to the illumination.

A comparison of the P-700 triplet with that of P-680, the primary donor of Photosystem II, shows several differences. (1) The P-680 triplet is 1.5 mT (15 G) wider than the P-700 triplet. This is reflected by the zero-field splitting parameters, which indicate that P-700 is a slightly larger species than P-680. The zero-field splitting parameters do not indicate that either P-700 or P-680 are dimeric. (2) The P-700 triplet is induced by red and far-red light, while the P-680 triplet is induced only by red light. (3) The temperature dependences of the P-700 triplet and the P-680 triplet are different.

Introduction

Recently EPR signals attributed to light-induced spin-polarized triplet states of P-700 [1], the primary donor chlorophyll of Photosystem I (PS I) and P-680 [2], the primary donor chlorophyll of Photosystem II (PS II), have been reported. These triplet signals exhibit the same unusual electron spin polariza-

Abbreviations: PS, photosystem; ENDOR, electron nuclear double resonance.

tion pattern as the primary donor (P-870) triplet in photosynthetic bacteria [3—5]. This is taken as an indication that the triplet is formed by radical pair recombination between the photo-oxidized primary donor and the photo-reduced intermediate electron acceptor when electron transport to the first stable primary acceptor is blocked by prior reduction [5]. In PS II, reduction of the primary acceptor can be achieved chemically or by electron donation from endogenous donors [2]. Illumination under these conditions results in charge separation between P-680 and a pheophytin intermediate (Ph) [2,6,7]. Decay of the $P\text{-}680^+ Ph^-$ radical pair results in the formation of the triplet state of P-680 [2]. Trapping of the pheophytin in the reduced form prevents charge separation and thus triplet formation does not occur [2]. Similarly, in PS I, P-700 triplet formation is thought to occur by recombination of the light-induced radical pair, $P\text{-}700^+A_1^-$, (where A_1 is the intermediate electron acceptor [8—15]) when the stable primary acceptor, X [16,17] (sometimes termed A_2 [8]), is reduced [1]. Since X has a very low midpoint potential (approx. —730 mV [18]), reduction had to be achieved photochemically by freezing under illumination [1] as demonstrated in Ref. 11. The difficulties in reducing X, and the presence of relatively large EPR signals from X and the iron-sulfur centers B and A [19,20] (sometimes termed P-430 [21]) prevented previous workers from obtaining good triplet spectra [1]. In this work these difficulties have been overcome by preparing a PS I particle which is depleted of the acceptors X, center B and center A. A triplet signal attributed to the triplet state of P-700 is reported in this preparation.

The relationship between the triplet state of P-700 and the redox state of A_1 is demonstrated, confirming that the formation of the triplet is due to a primary photochemical process. A comparison of the P-700 triplet with the P-680 triplet is made and several differences are reported.

Materials and Methods

PS I photoreactive complexes containing 110 Chl per P-700 were isolated from pea chloroplasts as previously described [22]. These particles (0.5 mg Chl/ml) were treated with lithium dodecyl sulfate (0.75%) for 45 min at 4°C. The solubilized particles (4 ml) were loaded on 36 ml sucrose gradients (0.1 M—1.0 M sucrose containing 0.1% sodium cholate) and centrifuged for 15 h at 100 000 × *g*, 4°C. After centrifugation the sucrose gradients were fractionated (from the top) into 2-ml samples. PS I particles which lacked iron-sulfur centers (assayed by EPR in Fig. 2) were collected from chlorophyll-containing fractions (6—8) and concentrated by lyophilization. Gel electrophoresis was done on slab gels as previously described [22]. Chlorophyll determinations were done according to Arnon [23]. Absorption spectra were acquired using an Aminco DW-2 spectrophotometer (American Instruments Co., Silver Springs, MD).

The amount of P-700 was determined by difference spectra. After a baseline was recorded on the spectrophotometer, one of two samples was treated with 1 mM $K_3Fe(CN)_6$ and the other with 2 mM sodium ascorbate. The samples were allowed to equilibrate prior to recording a difference spectrum. Reversible absorbance changes were then obtained by rereducing the oxidized sample with ascorbate. Reversible absorption changes peaked at 699 nm in PS I samples;

these changes were used to calculate the amount of P-700 present using a millimolar extinction coefficient of 65 [24].

PS II particles were prepared by the procedure of Mullett and Arntzen [25]. EPR samples were prepared as described in Ref. 2. EPR measurements were carried out at liquid helium temperatures using a Varian E9 spectrometer and an Oxford Instruments cryostat and temperature monitoring system. Accurate microwave frequency measurements were made using a Varian digital frequency meter 5240A. Accurate magnetic field measurements were made using a Bruker NMR oscillator B-NM20 and probe.

Illumination in the EPR cavity was provided by a 500 W projector. Light intensity at the cavity window was 0.35 $J \cdot cm^{-2} \cdot s^{-1}$. Illumination while freezing was provided by a 300 W projector and a Fibrox 150 W fiber-optic light source.

Interference filters were purchased from Pomfret Research Optics Inc. filter Model numbers 302201-2 and 3-22032 were used.

Neutral red was purchased from British Drug Houses, Poole, Dorset, U.K. and phenazine methosulfate and methyl viologen from Sigma Chemical Co., St. Louis.

Results

A. Preparation of electron acceptor-depleted PS I

PS I particles were prepared which retained characteristics attributed to PS I in vivo. For example, the PS I particles contained 110 Chl/P-700, exhibited a 77 K fluorescence emission maximum at 736 nm and mediated high rates of electron transport from plastocyanin to NADP [22]. The polypeptide composition of this preparation of PS I, shown in Fig. 1, lane A, consists of the apoprotein of P-700 (66 000—68 000 daltons) [26], polypeptides involved in forming the peripheral light-harvesting complex of PS I (19 000—24 000 daltons) [22] and several lower molecular weight polypeptides (9000—19 000 daltons). The PS I particles, when examined by EPR, were found to exhibit EPR signals attributed to the iron-sulfur centers A and B (Fig. 2A, see Refs. 19, 20).

The PSI particles described above were treated with lithium dodecyl sulfate is an attempt to deplete the complexes of electron acceptors. Detergent-treated P-700-containing fractions were separated from solubilized material by sucrose gradient centrifugation and examined for polypeptide content and for the presence of the electron acceptors. Fig. 1, lane B, shows the polypeptide composition of lithium dodecyl sulfate-treated PS I particles. These PS I particles contain 30 Chl per P-700 and polypeptides of 66 000—68 000, 22 000 and 10 000 daltons. Similar PS I particles used for the study of PS I photochemistry have been previously prepared by treatment of PS I with sodium dodecyl sulfate [9,15,27,29]. These preparations were reported to contain only polypeptides of 66 000—68 000 daltons, although low molecular weight polypeptides may not have been resolved (see, for examples, Refs. 20, 28). The lithium dodecyl sulfate-treated PS I particles, shown in Fig. 1, lane B, hereafter are termed the core complexes of PS I. Examination of the PS I core complexes by EPR techniques revealed that EPR signals due to the iron-sulfur centers A and B are lacking in this preparation (Fig. 2B). In addition, the light-induced reversible signals attributed to $P\text{-}700^+$ and X^- were not observed in the PS I core complex.

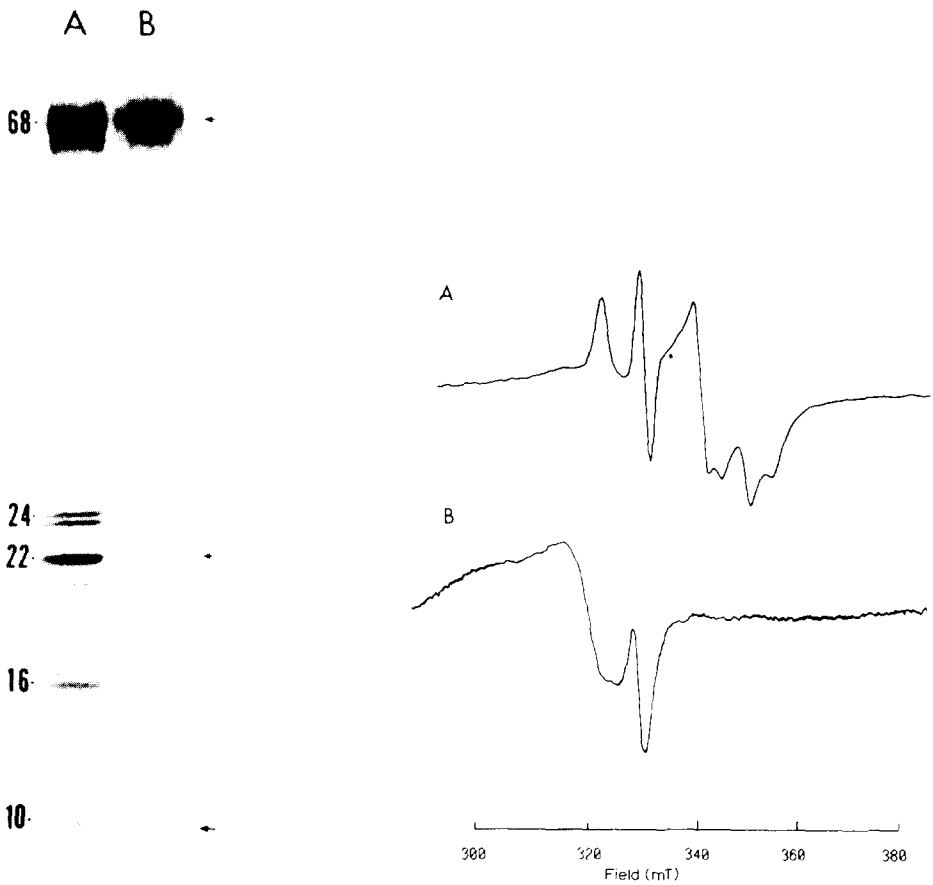


Fig. 1. Sodium dodecyl sulfate polyacrylamide slab gel (7.5—15%) electrophoresis of Photosystem I particles (A) and the core complex of Photosystem I (B) obtained from PS I particles after depletion of polypeptides by lithium dodecyl sulfate treatment. Molecular weight markers are indicated at the left of the figure.

Fig. 2. EPR spectra from the PS I preparations showing the effect of lithium dodecyl sulfate upon the iron-sulfur centers B and A. The spectra shown are of samples in the presence of sodium dithionite after illumination at 16 K in the EPR cavity. (A) An EPR spectrum of particles before treatment with lithium dodecyl sulfate. (B) An EPR spectrum of a sample after depletion of polypeptides by lithium dodecyl sulfate treatment. EPR conditions were as follows: temperature, 16 K; microwave power, 10 mW; modulation amplitude 1.0 mT (10 G); frequency, 9.267 GHz. The gain for (A) was 500 and the P-700 concentration was 15 nM while the gain for (B) was 2000 and the P-700 concentration was 7 nM.

However, an EPR signal at g 2.07 was observed (Fig. 2). This signal may be due to residual iron-sulfur centers or X which have been altered by the detergent treatment.

B. Spin-polarized triplet signal in PS I

Illumination of PS I core complex at liquid helium temperature induced the formation of a spin-polarized triplet signal (Fig. 3a). The triplet signal could be observed in the PS I core complex in the presence of sodium dithionite, sodium ascorbate or in anaerobic samples with no addition. One feature of the triplet signal, which has a g value of approx. 2.06, was obscured by the signal at g

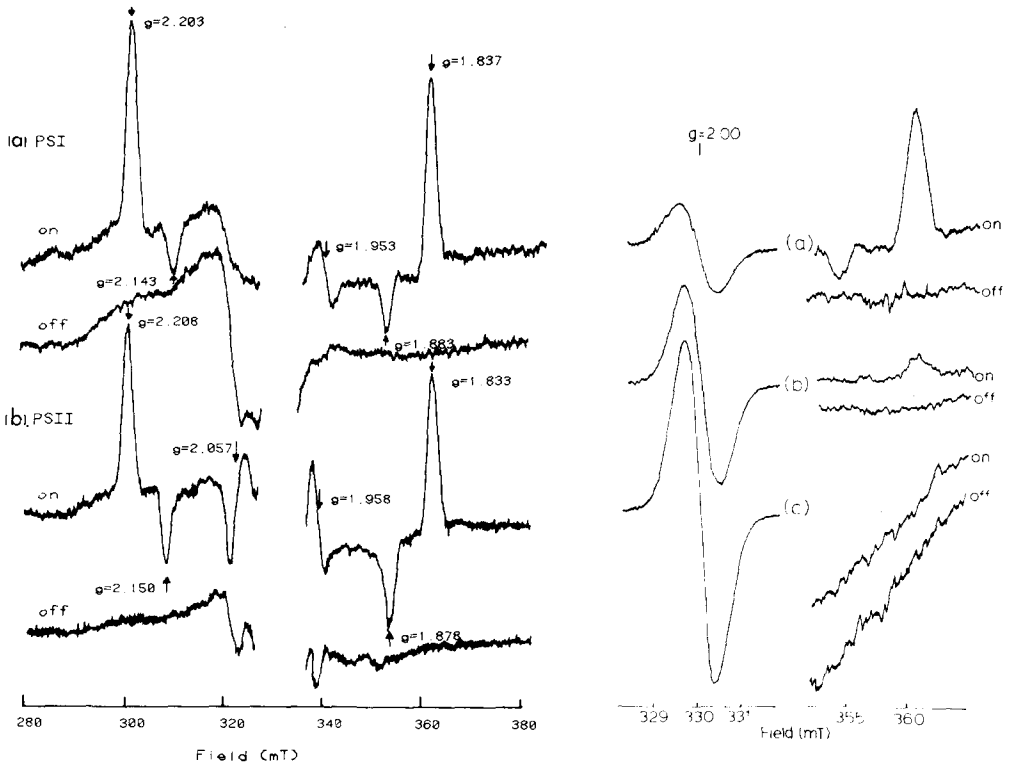


Fig. 3. EPR signals from light-induced spin-polarized triplet signals in PS I and PS II showing accurate g values. The top two spectra (a) show the effect of illumination at 3.5 K upon the PS I core complex prepared with lithium dodecyl sulfate. The sample (0.3 mg Chl/ml) contained sodium dithionite and had been frozen anaerobically in the dark. The lower two spectra (b) show the effect of illumination at 3.5 K upon PS II particles. The sample (1.0 mg Chl/ml) contained sodium dithionite and had been frozen in the dark. EPR conditions were as follows: temperature, 3.5 K, microwave power, 0.05 mW; modulation amplitude, 1.0 mT (10 G); frequency, 9.2679 GHz; instrument gain, 20 000; sweep time, 1 h; time constant, 3 s.

Fig. 4. The effect of chemical and photochemical oxidation of P-700 upon the ability to photoinduce the PS I triplet. All spectra are of PS I particle (1 mg Chl/ml) prepared by digestion with lithium dodecyl sulfate. (a) Spectra in a sample frozen in the dark in the presence of 100 μM methyl viologen as a control. (b) Spectra in a sample containing 100 μM methyl viologen whch was frozen in liquid N_2 while under illumination. (c) A sample frozen in the dark in the presence of (5 mM) $K_3Fe(CN)_6$. Under each set of conditions the high field features of the light-induced triplet signal are shown (right-hand side) and the radical signal around g 2 is shown on the left-hand side. The EPR conditions for measurement of the triplet signal were as described in the legend to Fig. 3 except that the sweep time was 16 min. The radical spectra were taken at 50 K; microwave power, 0.05 mW; modulation amplitude, 0.2 mT (2 G); frequency, 9.2601 GHz; instrument gain, 2000; sweep time, 8 min/400 G; time constant, 0.3 s.

2.07. This feature could be clearly delineated in spectra obtained by light modulation (Rutherford, A.W. and Norris, J.R., unpublished data).

The electron spin polarization pattern of the triplet signal indicates that the triplet is formed by recombination of a radical pair [5] (presumably $P\text{-}700^+A_1^-$. Trapping of the PS I reaction centers in the state $P\text{-}700^+A_1$ or $P\text{-}700A_1^-$ prior to illumination at low temperature should result in loss of the ability to photo-induce the triplet state.

Fig. 4 shows the effect of oxidizing P-700 upon the ability to photo-induce

the triplet signal. Fig. 4c shows a sample frozen in the dark in the presence of $K_3Fe(CN)_6$ (approx. 10 mM). Under these conditions P-700 is oxidized and a large radical signal at g 2.0 is present. No triplet can be photo-induced under these conditions. The sloping baseline is due to an effect of potassium ferricyanide. To show that the loss of the triplet signal is not simply due to a broadening effect of Fe^{3+} upon the spectrum, P-700 was photochemically oxidized by freezing under illumination in the presence of methyl viologen (100 μM) (Fig. 4b). It can be seen that P-700 oxidation occurs (i.e., at g 2.00 a radical with a peak to peak width of 0.75—0.8 mT (7.5—7.0 G) is generated) and at the same time the ability to photo-induce the triplet signal is lost. Fig. 4a is a control experiment showing a sample frozen in the dark in the presence of methyl viologen.

Fig. 5 shows that under conditions where A_1 is trapped in the reduced form (Fig. 5b) (i.e., strong illumination while freezing in the presence of sodium dithionite [11]) the triplet signal significantly diminished in size and a large radical signal attributed to A_1^- was stably generated. The radical signal attributed to A_1^-, when measured at 50 K with a microwave power of 0.05 mW and a modulation amplitude of 0.32 mT, had a peak-to-peak width of approx. 1.4 mT (14 G). This linewidth is in agreement with that reported for A_1 [11,14].

It was necessary to carry out the freezing under illumination in the presence of an exogenous donor in order to trap a significant amount of centers in the state P-700 A_1^-. The spectra shown in Fig. 5 were obtained in the presence of 200 μM neutral red, but phenazine methosulfate at a similar concentration could also be used. This experiment has been carried out seven times on two different preparations of PS I core complexes. The results of these experiments and those done with phenazine methosulfate were all essentially similar and, although some variation in the extent of the effect was observed, the relationship between the triplet signal and the radical signal is clear in every case. If samples containing reduced A_1^- were thawed in the dark, A_1^- became oxidized and the triplet state could again be photo-induced (Fig. 5c). These results demonstrate that trapping PS I in the state P-700A_1^- blocks the formation of the spin polarized triplet signal.

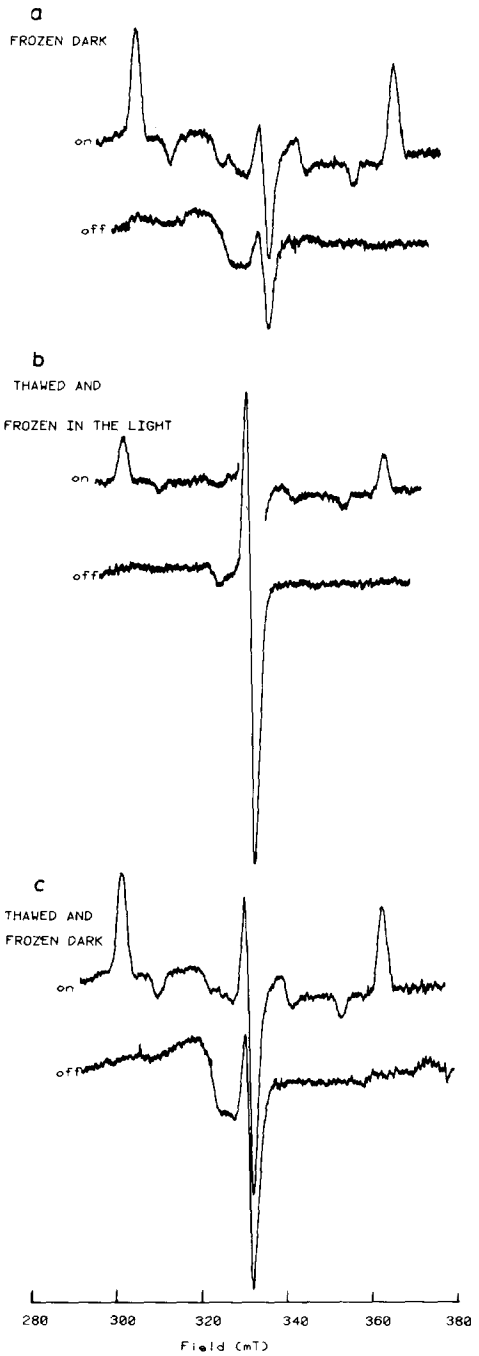
Also of note in Fig. 5 is that the dark g 2.07 signal (see Fig. 2) disappeared when A_1 was reduced. This may be due to a paramagnetic interaction like that reported between A_1^- and X^- [15].

In this preparation, no light-induced reversible signals attributable to P-700$^+$-A_1^- could be detected using our conditions of illumination. This is in contrast to the results obtained in a sodium dodecyl sulfate preparation of PS I which was also deficient in acceptors [15].

A broad triplet signal, thought to be an antenna carotenoid triplet, has been previously reported in PS I [1]. This triplet could only be detected in the PS I core complex using a light-modulated EPR technique (Rutherford, A.W. and Norris, J.R., unpublished data).

C. A comparison of triplet signals in PS I and PS II

Fig. 3b shows the light induced triplet signal observed in PS II particles and attributed to the triplet state of P-680 [2]. It can be seen from the g values that the P-680 triplet has a broader splitting than the P-700 triplet. This is reflected



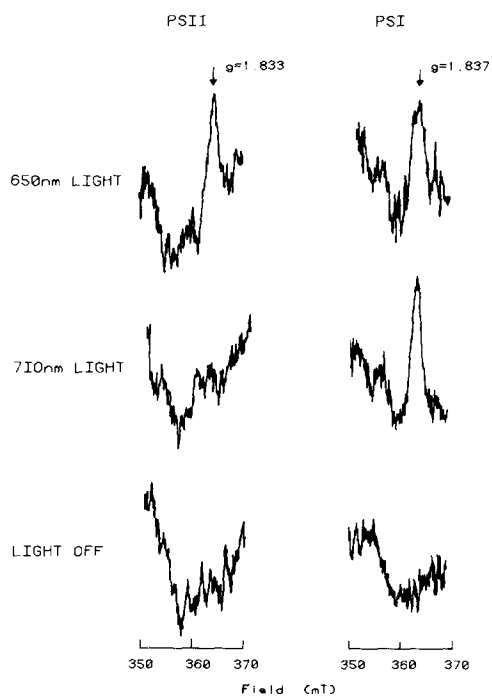


Fig. 5. The effect of freezing under illumination in the presence of 200 μM neutral red and sodium dithionite. All spectra are of the same sample. (a) Frozen in the dark, (b) Thawed and illuminated while freezing in liquid nitrogen. (c) Thawed and frozen in the dark. Thawing and freezing was carried out under oxygen free nitrogen. Illumination in the EPR cavity was as described in Methods. EPR conditions were as described in the legend to Fig. 3 except that the instrument gain was 10 000, the sweep time 30 min and the time constant 1 s.

Fig. 6. The efficiency of red and far-red light to induce the triplet signal in PS I and PS II particles. Samples were frozen anaerobically in the dark. Samples were illuminated in the cavity with red and far-red light. Interference filters passing 650 nm and 710 nm light were used. The light intensity at the cavity window was 0.01 $J \cdot cm^{-2} \cdot s^{-1}$ and 0.0085 $J \cdot cm^{2} \cdot s^{-1}$ for 650 and 710 nm light, respectively. Sample concentration and EPR conditions were as described in the legend to Fig. 3 except that the instrument gain was 100 000, the sweep time was 2 h and the response time was 10 s.

TABLE I

THE ZERO-FIELD SPLITTING PARAMETERS OF PS I AND PS II REACTION CENTER TRIPLETS COMPARED TO MONOMERIC CHLOROPHYLL *a*

	$\|D\|$ (cm^{-1})	$\|E\|$ (cm^{-1})
PS I	0.0283	0.0040
PS II	0.0290	0.0044
Chl *a*	0.0273 *	0.0040 *

* Values are taken from Ref. 30.

in the $|D|$ zero-field splitting parameter (Table I). This suggests that the P-680 triplet is delocalized over a smaller area than is the triplet of P-700. Neither signal, however, is significantly narrower than that of monomeric chlorophyll *a*

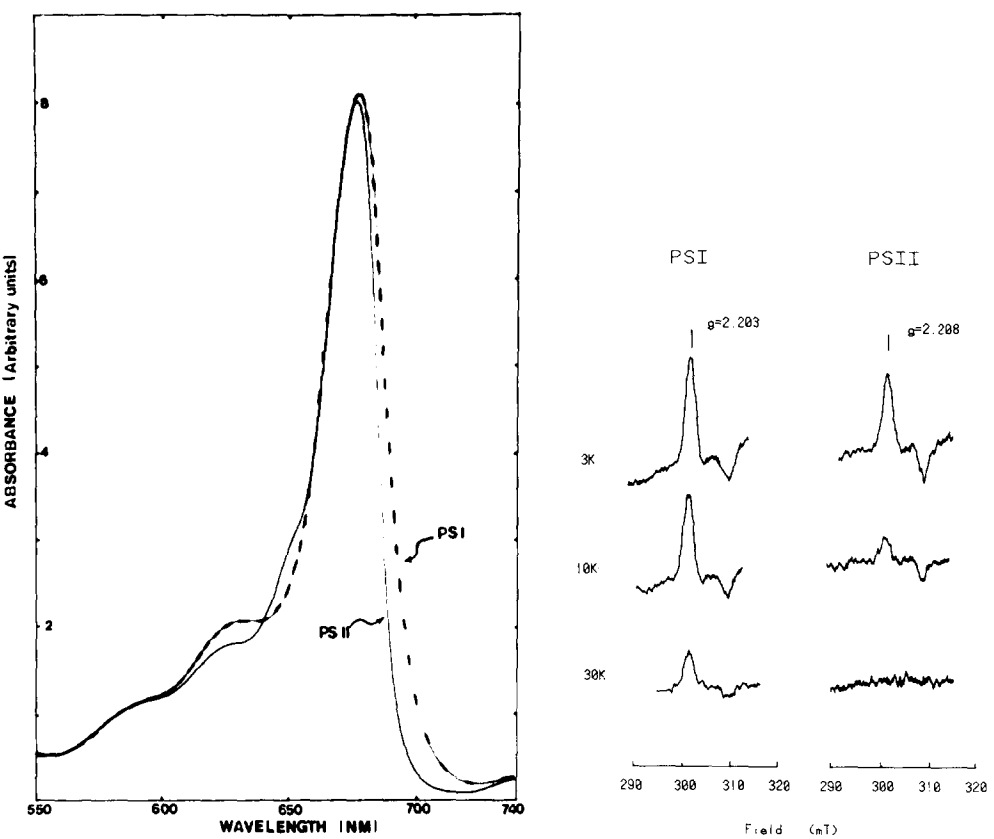


Fig. 7. Absorption spectra at 20°C of PS I (- - - - - -) which had been depleted of the acceptors X, B and A by lithium dodecyl sulfate treatment, and PS II particles (———). The absorption maximum of the PS I preparation is at 678 nm. The absorption maximum of the PS II preparation occurs at 676.5 nm. The PS II also has a shoulder at 650 nm, probably due to residual Chl *b* in the preparation. Samples were resuspended in 50 mM Tricine-NaOH, pH .78, at 10—15 mg Chl/ml for the measurements.

Fig. 8. The effect of temperature upon the light induced triplet signals of PS I and PS II. The conditions of helium flow, vacuum pressure and heater settings were identical at comparable temperatures, although actual temperature values are only approximate. EPR conditions and illumination in the cavity were the same as described in the legend to Fig. 5.

and, unlike photosynthetic bacteria, a special chlorophyll pair arrangement of P-700 or P-680 is not indicated from these results.

The triplet signals in PS I and PS II can be further differentiated by the wavelength dependence of excitation (Fig. 6). It can be seen that 650 nm light is relatively more effective than 710 nm light at inducing the P-680 triplet in PS II particles, while 710 nm light is more effective at inducing the P-700 triplet in PS I particles than is 650 nm light. This experiment has been carried out three times in two separate preparations of PS I and PS II. This result is consistent with the fact that PS II particles retain a portion of the Chl *b*-containing light-harvesting complex which absorbs at 650 nm and can excite PS II photochemistry (see absorption spectrum, Fig. 7). The Photosystem I core complex, on the other hand, is depleted of Chl *b* and shows greater absorption at 710 nm (Fig. 7). The wavelength dependence of excitation shown in Fig. 6 is consistent with the identification of triplet signals in PS I and PS II.

The microwave power dependence of the P-700 triplet is similar to that described for the P-680 triplet [2]. Increasing the microwave power results in a marked decrease in signal size until the triplet is absent in PS I particles at powers above 5—10 mW. This is probably due to depolarization of the signal due to the measuring microwaves as described in [31].

The temperature dependence of the P-700 triplet is different from that of the P-680 triplet. Both signals are maximal at the lowest temperatures obtainable (ca. 3 K); however, as the temperature is raised, the P-700 triplet disappears at a higher temperature than does the P-680 triplet (Fig. 8).

Discussion

The removal of the iron-sulfur centers B and A and the primary acceptor, X, from PS I particles results in a PS I preparation which still undergoes charge separation as previously reported [9,15]. The radical pair produced, $P\text{-}700^{+}A_1^{-}$, decays by the formation of a spin-polarized triplet state of P-700. Prior oxidation of P-700 (Fig. 4) or reduction of A_1 (Fig. 5) prevents charge separation and consequently the triplet is not formed.

The $|D|$ zero field splitting parameter of the triplet signal in PS I, as noted by Frank et al. [1], is very similar to that of monomeric chlorophyll. This evidence alone cannot be taken as an indication of a monomeric structure of P-700 since a $|D|$ parameter identical to the monomeric value would be exhibited by a triplet on a dimer if all the axes of the two molecules were parallel [32]. It is generally accepted, from the EPR linewidth [33] and the ENDOR [34] spectrum of $P\text{-}700^{+}$, that P-700 is a special pair of chlorophyll molecules. Recently, however, it has become apparent that neither line of evidence is unequivocal (see Ref. 35 for discussion of environmental effects upon linewidth of chlorophyll cation radicals, and Ref. 36 for a discussion of the ENDOR spectra).

The triplet signal from P-700 was distinguished from that of P-680 in several ways. Firstly, the P-680 triplet signal is 1.5 mT (15 G) wider than the P-700 triplet and this results in slight differences in the *g* values of the features and in the zero-field splitting parameters. Secondly, the PS II triplet is produced by illumination with red but not far-red light, while the PS I triplet is induced by

both red and far-red light. This behavior is consistent with the formation of the triplet signals in PS I and PS II. Thirdly, the PS I triplet-signal is observable at higher temperatures than is the PS II triplet. Since increasing temperature could affect the triplet signal size in several different ways (i.e., a decrease in the spin-lattice relaxation time, the occurrence of another decay route, or an increase in the decay rate of the triplet to the ground state), no definite conclusions can be drawn from this observation, although it is useful as a means of differentiating the two triplets.

It must be kept in mind that the properties of the triplets in the two purified particles may be affected by the purification treatments and therefore may be different from those of the triplets observed in chloroplasts. However, in photosynthetic bacteria the characteristics of the analogous triplet signals are very similar in whole cells, chromatophores and reaction centers (for review see Ref. 30).

These EPR results showing decay of a light induced radical pair via a relatively long-lived triplet state in both PS I and PS II call for reassessment of kinetic optical data obtained previously (see, for example, Refs. 8—10, 12, 13, 15). By analogy with the bacterial system it seems likely that the back reaction via the triplet state is favored as the temperature is lowered [31]. It has been shown that in *Rhodopseudomonas sphaeroides* the quantum yield of triplet formation is 1 at liquid helium temperature [32]. Comparison of the EPR data reported here with the kinetic optical data should be made with caution, since different conditions of temperature and different kinds of preparations have been used. However, optical kinetic measurements at 5 K have been carried out on a comparable PS I preparation which lacked the acceptors X, center B and center A [9]. The monophasic kinetic changes observed were ascribed to $P\text{-}700^+$ and its re-reduction from A_1^- on the assumption that the following reaction occurred:

$$P\text{-}700A_1 \overset{h\nu}{\rightleftharpoons} P\text{-}700^+A_1^-$$

In the present work it is demonstrated that, in at least a proportion of the centers, the following reaction occurs:

$$\begin{array}{l} P\text{-}700A_1 \xrightarrow{h\nu} P\text{-}700^+A_1^- \\ \quad \nwarrow P\text{-}700^tA_1 \swarrow \\ \qquad \text{triplet} \end{array}$$

It therefore seems possible that the optical changes may reflect the decay of the P-700 triplet. A triplet decay mechanism was ruled out at the time because the presence of oxygen, which increases the decay kinetics of chlorophyll and carotenoid triplets in antenna complexes and in vitro [33,34], did not change the observed kinetics [9]. It is possible, however, that the triplet within the reaction center is inaccessible to oxygen.

Kinetic measurements of the decay rates of the EPR triplet signals are required before any firm conclusions can be drawn.

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