Biochimica et Biophysica Acta 850 (1986) 226–233
Elsevier

BBA 42011

EPR signal II in cyanobacterial Photosystem II reaction-center complexes with and without the 40 kDa chlorophyll-binding subunit

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(Received February 5th, 1986)

Key words: Electron transfer; ESR; Signal II; Photosystem II; Photosynthesis; (Cyanobacterium, *Synechococcus*)

The steady-state amplitude and flash-induced kinetics of EPR signal II in two Photosystem II (PS II) reaction center protein complexes from *Synechococcus* were measured to probe the organization of species involved in the PS II electron-transfer chain. A PS II reaction center complex (E-1) which has 47, 40, 31, 28 and 9 kDa subunits shows both fast decaying (signal II_f) and slowly decaying (signal II_{s+u}) EPR components. The amplitude of signal II_f, which represents Z (the donor to P-680), is about 1 spin per 30 Chl. This corresponds to one spin per reaction center in this preparation. Signal II_{s+u}, the slowly decaying component of signal II, reflects D, a donor to PS II on a side chain from the path of water oxidation in higher plants and algae. Signal II_{s+u} is present in the E-1 preparation in a ratio of about 1 spin per 40 Chl. Flash-induced signal II_f in E-1 shows biexponential decay with half-times of 20 ms and 300 ms. In a PS II reaction center complex (CP2b) which has 47, 31, 28 and 9 kDa subunits, but no 40 kDa subunit, an appreciable amount of signal II_f is observed (about 1 per 50 Chl). Less than 1 spin per 400 Chl of signal II_{s+u} is visible in this sample. The kinetics of Z^+ reduction (signal II_f) in CP2b is similar to that seen in E-1 preparations, indicating that CP2b contains all of the molecules necessary for primary charge separation and secondary electron donation from Z.

Introduction

Photosystem II reaction center complexes have been isolated from several organisms, including higher plants [1,2], *Chlamydomonas* [3] and *Synechococcus* [4]. These Photosystem II reaction center complexes have similar polypeptide compositions. They contain two large polypeptides between 40 and 50 kDa that are chlorophyll-binding proteins in PS II [4,5]. There are two or more proteins having a molecular weight around 30000. One of the 30 kDa proteins is assigned as a herbicide-binding protein in higher plants [1]. The PS II complex also contains a small polypeptide which is thought to be an apoprotein of cytochrome *b*-559 [2].

The primary reaction of PS II correlates with the presence of the large chlorophyll-binding protein; 47 kDa protein in higher plants [6–8] and *Synechococcus* [9,10] and 50 kDa protein in *Chlamydomonas* [5,11]. The *Synechococcus* chlorophyll protein complex called CP2b, which has 47, 31, 28 and 9 kDa subunits but no 40 kDa subunit [4,9], shows high electron-transport activity from

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Abbreviations: PS, Photosystem; P-680, primary donor of PS II; Q_A, primary electron acceptor of PS II; Q_B, secondary electron acceptor of PS II; Z, donor to P-680; Mes, 4-morpholineethanesulfonic acid; Chl, chlorophyll, DCBQ, 2,5-dichloro-*para*benzoquinone; DCMU, 3-(3,4-dichlorophenyl)-1,1-dimethylurea; PMSF, phenylmethylsulfonylfluoride.

diphenylcarbazide to dichlorophenolindophenol [9], and contains an appreciable amount of Q_A(X320), photoreducible pheophytin and cytochrome *b*-559 [10].

EPR signal II (signal II) originates from a radical species on the donor side of PS II [12,13], most likely a semiplastoquinone cation [14,15]. There are at least two different pools of this species with different roles in PS II. Half of the signal II is either stable in the dark or is formed upon first illumination and decays with a half-time of several hours in whole chloroplasts. The dark stable portion and the slowly decaying portion of the free radical species are designated signal II_u and signal II_s, respectively [12,16]. Quantitation of this persistent pool (D^+) of signal II in chloroplast thylakoid membranes shows one free radical formed per PS II reaction center [12,17]. The other half of the pool of signal II originates from Z^+, which is involved in the transfer of positive charge from the oxidized reaction center of PS II, P-680$^+$, to the oxygen-evolving enzyme. This portion of signal II reflects the direct donation of electrons to P-680$^+$ in Tris-treated PS II preparations [18] and possibly also in O_2-evolving preparations from spinach [19]. In samples competent in O_2 evolution the observed signal II transient is referred to as signal II_{vf} [20–22]. In samples completely devoid of O_2-evolution capability, the rise and decay kinetics of signal II are slower than in O_2-evolving samples [18,19], and the transient signal observed is referred to as signal II_f [23]. The lineshapes of signal II_f, signal II_s and signal II_u are identical [23]. Due to the rapid reduction kinetics the steady-state light-induced signal II_{vf} is not normally observed [20,21], although a rough field-position profile has been reported based on flash-induced transients [20].

Signal II has been observed in various PS II reaction center preparations [17,24], and in some cases signal II amplitudes were measured. Babcock et al. reported 1 Z^+ per P-680 in Tris-treated chloroplasts, but only 0.6 Z^+ per P-680 in several PS II particle preparations [17]. Satoh et al. reported that the ratio of signal II to reaction centers is similar in PS II particles to that in thylakoids [24]. Here we report the presence and quantitation of signal II in CP2b and E-1 preparations and discuss the localization of Z and D.

Materials and Methods

The thermophilic cyanobacterium *Synechococcus* sp. (a gift from S. Katoh, Department of Pure and Applied Sciences, Tokyo University, Tokyo, Japan) was grown at 53°C for 3 days with continuous bubbling of 5% CO_2 in air in the light [25,26]. Thylakoid membranes were prepared as in Ref. 4, except that 1 mM PMSF was added to the medium during the thylakoid membrane preparation after lysozyme treatment.

The PS II reaction center complex (E-1) was prepared as in Ref. 9 with slight modification. The PS II reaction center complex was extracted from the thylakoid membranes with 0.8% β-octylglucoside. The crude extract of PS II was diluted by a factor of 2 with 50 mM Tris-HCl (pH 7.5)/10 mM NaCl medium and collected by centrifugation, $250\,000 \times g$ for 2 h, and stored at −80°C. The crude extract was suspended in the Tris-HCl (pH 7.5)/NaCl medium containing 0.8% β-octylglucoside and then purified by digitonin-polyacrylamide gel electrophoresis (0.2% digitonin, 4.5% acrylamide), as described previously [4,9].

CP2b was prepared as in Ref. 9. Gels containing CP2b were stored at −80°C until use. Frozen gels were homogenized with a Teflon tissue homogenizer in 50 mM Mes/NaOH (pH 6.0). Gel debris was separated from the homogenate by $30\,000 \times g$, 30 min centrifugation, and the complex was recovered by $260\,000 \times g$, 2 h centrifugation. The precipitate was suspended in Mes buffer and used immediately for the measurement.

Steady state and kinetic EPR measurements were performed on a Varian E-109 EPR spectrometer using 100 kHz magnetic-field modulation. Instrument settings for each measurement are listed in the figure captions. Data were averaged on a laboratory-built signal averager and sent to a VAX 11-780 for data analysis and display. The kinetics were analyzed using a nonlinear least-squares fitting routine as previously described [18,19]. Double integration of steady-state spectra was done on the VAX using a laboratory-written program. Samples were suspended in 50 mM Mes (pH 6.0) containing 1 mM potassium ferricyanide and 1 mM potassium ferrocyanide, unless otherwise stated. The temperature was set at 0°C by a cooled N_2 gas flow and monitored by a thermo-

couple. Continuous white light of saturating intensity was provided by a microscope illuminating system. Light pulses for kinetic measurements (640 nm, 50 mJ/Flash, 0.3–0.5 μs FWHM) were provided by a dye laser (Phase-R DL-1400) using rhodamine 640 (Exciton) in methanol as laser dye. To estimate the concentration of radical species, signal II spectra were collected using nonsaturating microwave power (5 mW). Spectra were double integrated and compared with an optically calibrated solution of potassium nitrosodisulfonate (Aldrich) in a carbonate buffer according to Babcock et al. [17], except that the light-induced signal II spectra were taken at only one magnetic-field modulation amplitude to prevent light-induced damage to the samples. Chlorophyll concentrations were obtained by the method of Arnon [27].

Results

The EPR spectra of the Photosystem II reaction center complex, E-1, are shown in Fig. 1a. The E-1 complex has 47, 40, 31, 28 and 9 kDa protein subunits [9,10], and has been found to contain 1 Q_A, 1 photoreducible pheophytin and 1 cytochrome *b*-559 per 32–46 Chl [10]. The dark- and light-induced spectra show the characteristic line shape of signal II reported earlier for thylakoid membrane preparations [12,13,16,20] and PS II samples [17,24]. Only a small amplitude of signal II is present before initial illumination (D) following 1–2 h dark adaptation. During illumination (L) a large amplitude of signal II is induced, half of which decays in the subsequent 5 min dark period before completion of the collection of the next spectrum (D(L)). The pool of signal II observed in the dark after illumination has a decay half-time of 25–30 min under the measuring conditions, and could account for the small amplitude of signal II seen before the initial illumination.

Fig. 1b shows the EPR spectra of CP2b, which has no 40 kDa chlorophyll-binding subunit (see Introduction). The EPR spectrum obtained before illumination is composed of mainly a small structureless free radical signal centered at $g = 2.0025 \pm 0.0003$ with an 8 gauss linewidth. This free radical is similar to P-680$^+$ [28,29], and could be due to oxidized bulk chlorophyll. The structureless free radical signal similar to that seen in CP2b samples in the dark was also observed in

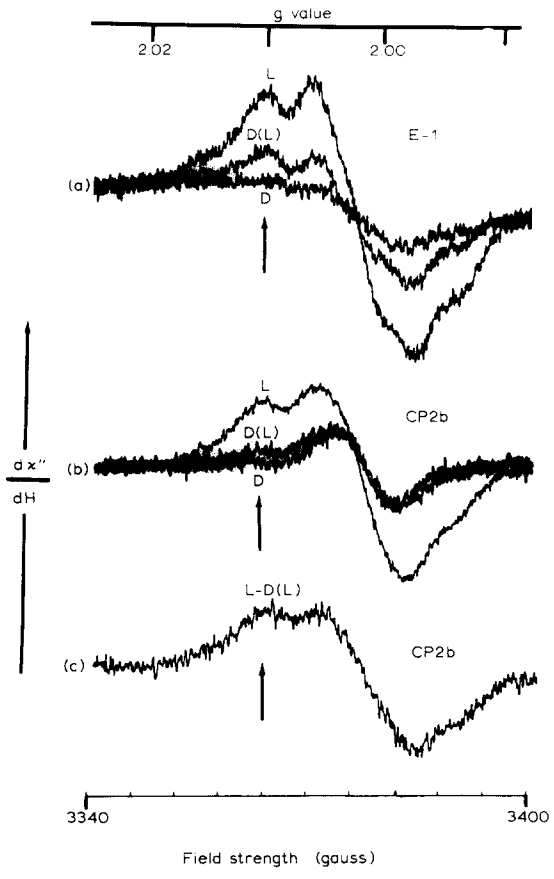

Fig. 1. Dark- and light-induced EPR spectra at 0°C in E-1 (a) and CP2b (b and c) Photosystem II particles. Spectrum D was recorded in the dark, L during continuous saturating illumination and D(L) within 5 min following the end of continuous illumination. Microwave power, 5 mW; modulation frequency, 100 kHz; modulation amplitude, 2 G in (a), 4 G in (b). Signals were averaged for one and five passes in (a) and (b), respectively. Scan time of 8 min in (a) and 4 min in (b) with time-constants of 0.25 s in (a) and 0.128 s in (b). Arrows indicate field position where kinetics in Figs. 2 and 3 were obtained. The difference between L and D(L) in (b) is displayed in (c).

aged E-1 samples in the dark. Illumination clearly causes the appearance of signal II. There is no significant increase of the structureless free radical signal induced by continuous illumination; the light-minus-dark difference spectrum (Fig. 1c) displays the same lineshape as is seen in E-1 samples (Fig. 1a). It can also be seen that there is very little of the slowly decaying portion of signal II present in CP2b after illumination (Fig. 1b, curve D(L)).

Spin concentrations of E-1 and CP2b were measured by double integration of the EPR spec-

TABLE I

SPIN CONCENTRATION IN PS II REACTION-CENTER COMPLEXES

Spectra were taken of the spin standard (potassium nitrosodisulfonate) and signal II in the dark after illumination, D(L), at a variety of modulation amplitudes according to the protocol of Babcock et al. [17]. The spectra under illumination, L, were taken either at 2 G (E-1(1)) or 4 G (E-1(2) and CP2b) magnetic-field modulation amplitude. All spectra were taken at 5 mW microwave power on a Varian E-109 EPR spectrometer as described in Materials and Methods. Samples ranging from 0.5 to 0.7 mg Chl/ml were suspended in 50 mM Mes buffer (pH 5.5) containing 1 mM ferricyanide and 1 mM ferrocyanide. The temperature was set at 0°C. Estimated uncertainty of Chl/spin is ±20%. The third column indicates spin concentration obtained from the difference spectra, L-D(L).

Sample	Chl/spin (mol/mol)		
	L	D(L)	L-D(L)
E-1 (1)	17	38 [a]	31 [b]
E-1 (2)	20	57 [a]	31 [b]
CP2b	42	316	49 [b]

[a] Signal II_{s+u}.
[b] Signal II_f.

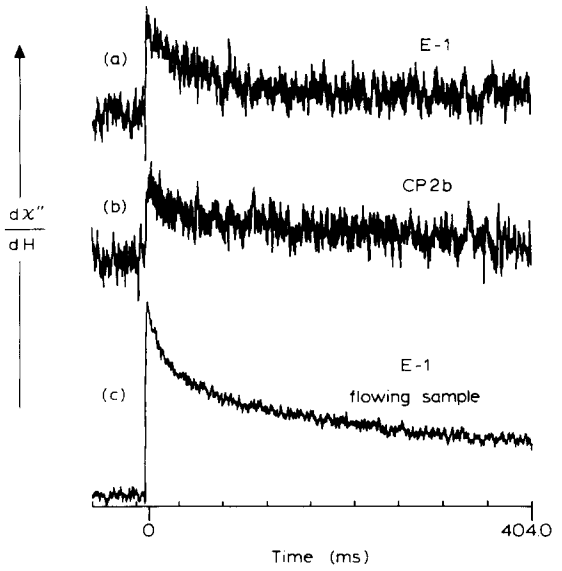

Fig. 2. Flash-illumination-induced EPR signal II in E-1(a and c) and CP2b(b) Photosystem II particles. Signals were recorded at the field position indicated by arrow in Fig. 1. Microwave power, 20 mW; modulation frequency, 100 kHz; time-constant = out (250 μs rise half-time); modulation amplitude, 4 G (a and b) or 5 G (c). Signals were averaged for 200 flashes (a and b) or 2000 flashes (c) at a repetition rate of 0.2 Hz. Temperature, 0°C (a and b) or 15°C (c). Sample was flowed as in Ref. 19 for (c).

tra and comparing the amplitude to an optically calibrated spin standard as in Ref. 17. These analyses yielded the spin concentrations shown in Table I. The total amount of signal II present in the E-1 sample under illumination is 1 equivalent per 17–20 Chl. Approx. half this signal decays before the dark measurement 5 min later. However, in CP2b the total quantity of free radicals visible in the light was 1 equivalent per 42 Chl. As can be seen in Fig. 1b, almost all of the signal II decayed before the dark measurement after illumination.

The decay kinetics of signal II in E-1 are shown in Fig. 2 and summarized in Table II. The signal was monitored at the position indicated by the arrows in Fig. 1 ($g = 2.010$), where there is no contribution from any other free-radical signals. As can be seen in Fig. 2b, the amplitude of each of the two decay components in the biphasic decay of signal II_f in CP2b is the same as in E-1 within the signal-to-noise of this measurement; however, the decay times decreased from 20 ms in E-1 to 7 ms in CP2b for the fast component and from 300 ms in E-1 to 200 ms in CP2b for the slow component. This indicates that not only the functional connection between P-680 and Z which oxidizes Z, but also the components in the membrane which effect signal II reduction, are preserved in CP2b, although the geometry may be altered by the removal of the 40 kDa polypeptide.

Fig. 2c and Fig. 3 show the decay kinetics of E-1 measured on a sample flowing through the cavity and back into an ice-cooled reservoir to allow extensive signal averaging while avoiding sample degradation. The kinetics of signal II in E-1 (Fig. 2c, Fig. 3 and Table II) shows biphasic decay behavior. One component has a decay half-time of about 300 ms. The other decay component has a decay half-time of about 20 ms. The addition of ferricyanide to a sample which had no redox reagent increased the amplitude of signal II. The decay times of the two components remained similar; the amplitude increase was mainly due to the increase of the slow component. One possible explanation is that having ferricyanide present to allow Q_A to be reoxidized between flashes is necessary for the subsequent photo-oxidation of P-680 to be stabilized, allowing more complete oxidation of Z. Another possibility will be dis-

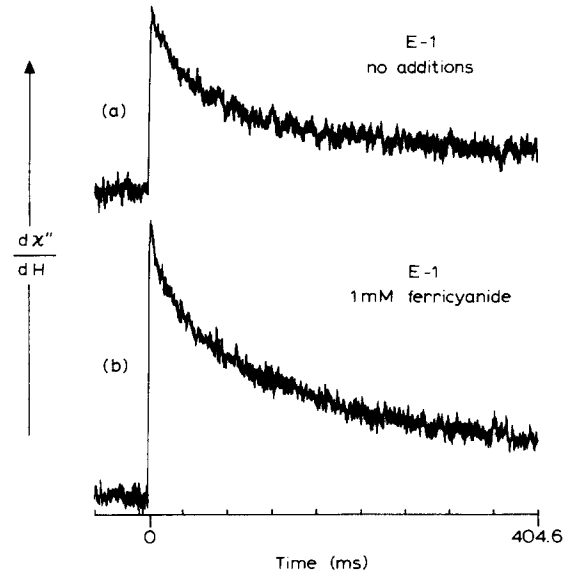

Fig. 3. The effect of ferricyanide on EPR signal II kinetics of E-1 Photosystem II particles. Samples were suspended in Mes-NaOH buffer (pH 5.5) and signals were measured in the absence (a) or in the presence (b) of 1 mM potassium ferricyanide at 15°C. Measuring conditions were as in Fig. 2c, including sample flow. No ferrocyanide was present during these measurements.

cussed later. Further addition of the lipophilic electron acceptor 2,5-dichloro*para*benzoquinone had no additional effect (Table II). This is suggestive that the rate of electron transfer from Q_A to exogenous acceptors has only a small effect on the rate of signal II reduction. Further addition of 1 mM ferrocyanide caused no significant changes in kinetics. Accordingly, 1 mM ferricyanide and 1 mM ferrocyanide were added to CP2b and E-1 in the previous measurements (Figs. 1 and 2). Only a small effect was observed upon the addition of DCMU (100 μM) to an E-1 sample containing 1 mM ferricyanide and 1 mM ferrocyanide (Table II). DCMU at this concentration has been shown to inhibit electron transport rates in E-1 [4], indicating that the electron transport beyond Q_A has only a small effect on signal II kinetics under this condition.

Discussion

Both a rapidly decaying EPR signal (signal II_f) and a slowly decaying component (signal II_{u+s}) are clearly present in E-1, as they are in several types of PS II particles [17,24]. Signal II_f arises from Z^+, the oxidized form of the direct electron donor to P-680$^+$ [16,18]. Signal II_s reflects a one time donor (D) on a side path of the electron transfer chain on the donor side of PS II [16,23]. The concentration of the EPR-detectable Z^+ is about 1 equivalent /30 Chl and that of D^+ is about 1/40 Chl in E-1. The antenna size in E-1 has been estimated to be 32–46 Chl per reaction center, based on the measurement of several redox components in E-1 [10]. Accordingly, the amounts of Z^+ and D^+ estimated here correspond to about one of each species per reaction center. This corresponds well with the amount of D^+ measured in thylakoid membranes and some PS II prepara-

TABLE II

THE EFFECT OF SEVERAL REAGENTS ON THE DECAY COMPONENTS OF SIGNAL II IN E-1 PHOTOSYSTEM II REACTION-CENTER COMPLEXES

Experimental conditions are the same as in Figs. 2c and 3. Each set of measurements was carried out sequentially after addition of the components listed. Signal II decay kinetics was analyzed as the sum of two exponential decay components.

Addition	Amplitude			Halftime (ms)	
	total	fast	slow	fast	slow
Experiment 1					
No Additions	65	36	29	28	330
+1 mM ferricyanide	99	39	60	22	220
+250 μM DCBQ	100	40	60	22	240
+1 mM ferrocyanide	97	42	55	22	230
Experiment 2					
1 mM ferricyanide/ferrocyanide	100	43	57	17	340
+100 μM DCMU	87	46	40	20	300

tions per reaction center and of Z^+ measured in Tris-treated thylakoid membranes [17], although lower amounts of Z^+ were reported for some PS II preparations. These facts support a model where Z plays an essential role as a direct electron donor to P-680 [18,19]. The presence of equimolar D^+ indicates the possible importance of this species in electron transfer on the donor side.

However, in CP2b almost all of the signal II observed is rapidly reduced after illumination (about 1 equivalent/50 Chl), with only a small amount of mainly a structureless free radical seen in the dark (Table I, fig. 1b). The amount of Z^+ observed (1/50 Chl) is the same as the amount of functional Q_A in CP2b [10]. The amount of D^+ is very small (less than 1/400 Chl), but some of this slowly decaying species is present in CP2b in addition to the structureless free radical seen before illumination (see the difference between D(L) and D at $g = 2.010$, Fig. 1b).

Omata et al reported two plastoquinone molecules per reaction center in spinach PS II preparations [30]. This seems to be the case also in E-1 preparations [31]. There is one primary acceptor Q_A present per reaction center in both E-1 [10] and spinach PS II preparations [32]. The remaining one plastoquinone per reaction center is not enough to explain two signal II spins (D^+ and Z^+) per reaction center. Thus, (i) either Z or D is a quinone other than a plastoquinone and other than a vitamin K_1, (ii) either Z or D is not extractable by organic solvents, or (iii) either Z or D is not a quinone at all.

The decay kinetics of signal II have been studied in Tris-washed chloroplasts and Tris-washed PS II preparations. Babcock and co-workers [16,17,20, 23,33–36] have studied the effects of midpoint potential, donor concentration, salt concentration, pH and DCMU on signal II_f decay kinetics in Tris-washed chloroplasts. With no additions or with 10 mM ferricyanide added to Tris-washed chloroplasts a slow decay of 0.4 to 1.2 s has been observed [16,35,36]. This decay was attributed to a species on the donor side of PS II with a midpoint potential of 480 mV [16]. A donor capable of reducing $P\text{-}680^+$ (possibly through Z) at 77 K has been reported by Malkin and Bearden [28] and is presumably a chlorophyll molecule [37].

The addition of ferricyanide increases the slow component amplitude from 29 to 60 while increasing the total amplitude from 65 to 99, presumably by oxidizing Q_A^- in competition with the back-reaction. Addition of 100 μM DCMU to an E-1 sample containing 1 mM ferricyanide scarcely changes the amount of the fast component; from 43 to 46. Thus we conclude that the fast decay is probably due to back-reaction of Z^+ with Q_A^- and that the slow decay component is due to donation from some intrinsic donor, as in the model of Babcock and co-workers [16,35]. The decay times are faster than those observed in thylakoid membranes for both reactions; however, the combination of samples derived from a different organism and manipulations for the purpose of achieving biochemical purity may affect the geometry of the reactants, their midpoint potentials, or both. Even isolating PS II from PS I by making BBY * particles changes the apparent back reaction time at pH 6.0 to 50 ms [38] from 100–300 ms [35]. Dekker et al. [38] studied Tris-washed PS II particles and concluded that signal II was being rereduced by both Q_A^- and ferrocyanide with half-times of 120 ms and 80 ms, respectively, to give an overall decay time for signal II_f of 50 ms. In E-1, the back-reaction time is decreased to about 20 ms, with the slower forward donation decreased to about 300 ms at pH 5.5. However, this model does not explain the change in the decay time of the slow component upon addition of ferricyanide to the E-1 preparation. Possibly, the differences arise from the presence of multiple donors, such as ferrocyanide and an endogenous donor.

In CP2b, signal II_f is clearly observed. The line-shape of the light-minus-dark signal is the same as that observed in E-1. The decay kinetics is similar, though slightly faster than in E-1 (see Results). These results clearly indicate that both the environment to produce the characteristic line shape of signal II_f and the components in E-1 which rereduce Z^+ are well preserved in CP2b, although an alteration of the geometry and thereby the kinetics may occur when the 40 kDa protein is removed. This is different from the results of Takahashi and Katoh, [31] where no signal II is reported to be seen in CP2b. This apparent discrepancy may owe to the difference of the measuring temperature (20°C in Ref. 31) for this labile protein complex.

* Particles called after Berthold, Babcock and Yocum [39].

In conclusion, we can state that the 40 kDa protein is not necessary for the function of Z^+ as a donor to P-680; the 47, 32, 28 and 9 kDa proteins are sufficient to support these reactions. Z, which exists in a 1 : 1 ratio with P-680, must be integral to the reaction-center complex. These conclusions are supported by the retention of the amplitude, line-shape, and kinetics of signal II_f seen in both E-1 and CP2b. Although the amount is small, D seems also to be present in CP2b. Because the amount of D is very low in CP2b and the amount of D is less than that of Z in E-1, D may be more susceptible to the detergent or purifiation process used than is Z. From the kinetics observed in E-1 under various conditions, electron transfer must be similar to that of Tris-washed chloroplasts [16,34,35], where a slow donor, probably intrinsic to the protein complex, competes with the back reaction between Q_A^- and Z^+. This probably holds also in CP2b, based on the similarity in the kinetics of signal II_f.

Acknowledgements

We would like to thank Elizabeth Rychlik for aid in sample preparation. This work was supported by the Director, Office of Energy Research, Office of Basic Energy Sciences, Division of Biological Energy Conversion and the Department of Energy, under contract DE-A03-76SF00098, and a grant from the National Science Foundation (DMB 84-16676). One of us (A.Y.) wishes to acknowledge support from the McKnight Foundation.

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