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CHARACTERISTICS OF THE PHOTOSYSTEM II REACTION CENTRE

I. ELECTRON ACCEPTORS

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The EPR characteristics of Photosystem II electron acceptors are described, in membrane and detergent-treated preparations from a mutant of *Chlamydomonas reinhardii* lacking Photosystem I and photosynthetic ATPase. The relationship between the quinone-iron and pheophytin acceptors is discussed and a heterogeneity of reaction centres is demonstrated such that only a minority of reaction centres were capable of secondary electron donation at temperatures below 100 K. Only these centres were therefore able to stabilise a reduced acceptor below 100 K. Parallel experiments using a barley mutant (viridis zb63) which also lacks Photosystem I, provide similar results indicating that the *C. reinhardii* system can provide a general model for the Photosystem II electron acceptor complex. The similarity of the system to that of the purple photosynthetic bacteria is discussed.

Introduction

The electron acceptors of PS I and the purple bacterial reaction centre have been well characterised by indirect and direct measurements, particularly by the use of EPR spectrometry which detects all the components of the electron acceptor complex. However, the electron acceptors of the PS II reaction centre have been more difficult to characterise. Fluorescence measurements have indicated the presence of two acceptors with redox potentials around 0 and −250 mV [1–4]. A variety of experiments suggest that at least one acceptor is a quinone in a special environment [5,6], whilst direct absorption measurements also support the identity of a quinone electron acceptor, Q [7–12] and of a pheophytin intermediary electron carrier [13] between the reaction centre chlorophyll, P-680 and Q. These results taken together with the similarities between PS II and the purple bacterial reaction centre [14–17], which has a quinone-iron acceptor, suggest the following electron-transfer sequence:

P-680 → Pheophytin intermediate → QFe

Analogy with the bacterial reaction centre suggested that EPR signals should be detected from both the pheophytin and the quinone-iron complex, and that an interaction between these acceptors and formation of reaction centre triplet should be observed under appropriate conditions. Recently Klimov and co-workers [18,19], using a Triton preparation of PS II from spinach, were able to detect a split radical signal similar to that observed in purple bacteria from the interaction of

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Abbreviations: PS, photosystem; Chl, chlorophyll; Hepes, *N*-2-hydroxyethylpiperazine-*N*-2′-ethanesulphonic acid.

reduced pheophytin and quinone-iron components. Rutherford and co-workers [20] with another detergent preparation detected and characterised the PS II reaction centre triplet and using a preparation from *Chlamydomonas reinhardii* we were able to detect the quinone-iron acceptor and demonstrate its photoreduction at cryogenic temperatures [21].

We have now used the *C. reinhardii* mutant and a barley mutant lacking PS I [22] to characterise the pheophytin intermediate, quinone-iron acceptor and reaction centre triplet in detergent preparations and untreated membrane fractions. We have investigated the conditions under which each can be observed in a single preparation and the interactions that occur between the components detected.

Materials and Methods

Barley (*Hordeum vulgare* c.v. Svalofs Bonus) viridis zb63 chloroplasts were prepared as described in Ref. 23 with centrifugation at 9000 × *g* for 10 min to pellet the broken chloroplasts. The chloroplasts were resuspended in a buffer containing 50 mM Hepes, pH 7.6, 5 mM $MgCl_2$ and 0.33 M sorbitol. Intact particles and the further purified DEAE particles were prepared from membranes of the *C. reinhardii* mutant F54-14 as described in Ref. 24 and these were stored at 77 K at about 1 mg Chl/ml until use. The study in Ref. 24 showed that intact particles prepared by digitonin and Triton detergents were devoid of PS I and the secondary acceptor of PS II. They showed a 4–7-fold increase in the specific activity of PS II and therefore a reduced antenna chlorophyll-to-reaction centre chlorophyll ratio. Further treatment by DEAE ion-exchange chromatography further decreased the size of the antenna chlorophyll.

The detergent particles referred to as intact particles and DEAE particles, were used where a high signal-to-noise ratio was required. Intact membranes were used to provide evidence of the applicability of the results to untreated preparations.

EPR spectrometry was conducted as described in Ref. 23 using a Jeol Fe1X X band spectrometer. Field and *g* value scales shown in figures are approximate. Continuous illumination of samples was performed using a Barr and Stroud LS II 150 W fibre optic light source whilst laser flash illumination (800 ns) was performed with a Chromatix tunable dye laser at 660 nm. Illumination at 200 K was performed either in the spectrometer cavity or in an ethanol/solid CO_2 bath. Illumination of the 200 K ethanol bath was performed with a 1000 W projector.

Results

EPR spectral characteristics of the C. reinhardii mutant, F54-14

Fig. 1 shows the EPR spectra of detergent particles from the *C. reinhardii* mutant, F54-14. A

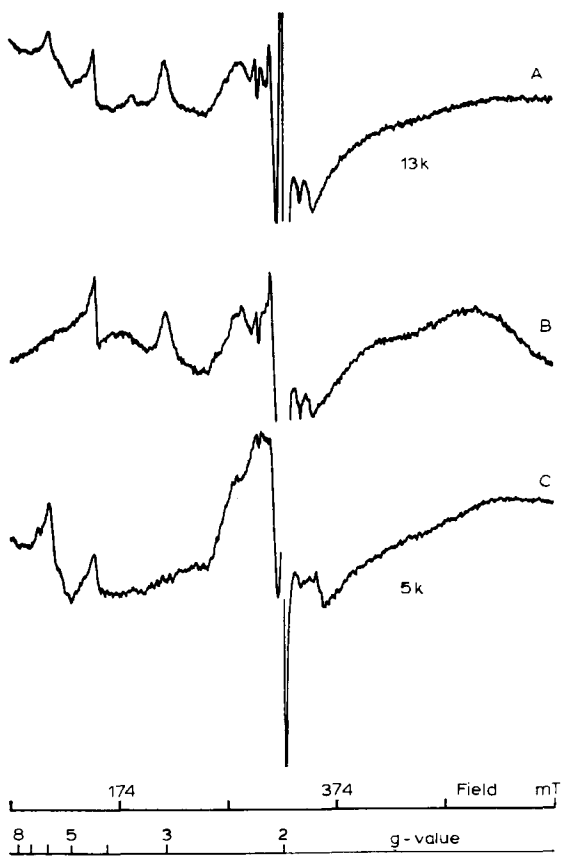

Fig. 1. Overall EPR spectral characteristics of *C. reinhardii* detergent particles. 500 mT EPR spectra of (A) mutant F54-14 intact particles; (B) F54-14 DEAE-treated particles. EPR conditions: microwave power 10 mW; temperature 15 K; modulation amplitude 1 mT; (C) F54-14 intact particles at 5 K, other EPR conditions as in A. Chlorophyll concentration 1 mg/ml.

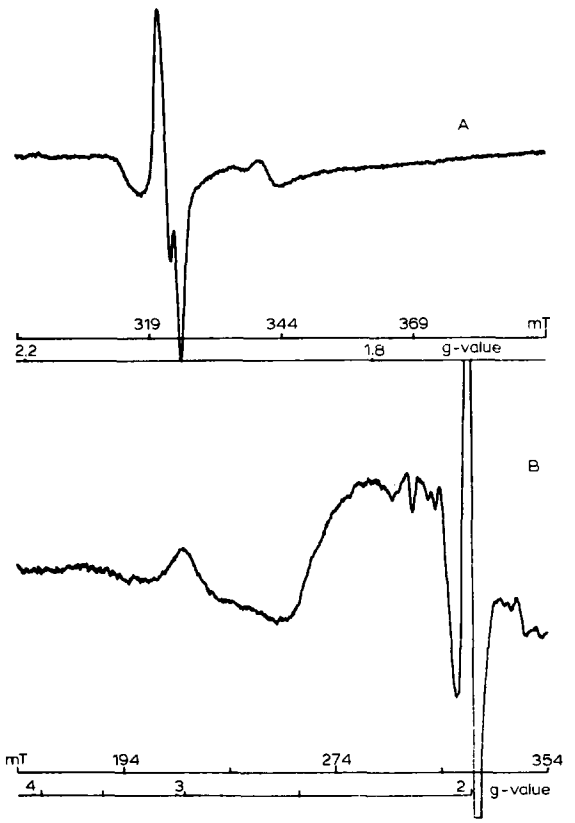

Fig. 2. EPR spectrum of *C. reinhardii* mutant F54-14 membranes reduced by 10 mM ascorbate and frozen in the dark. Spectrum illustrates high-potential iron protein (Hipip-type) and Rieske *g* 1.89 signals; (B) F54-14 intact particles frozen in the dark and illuminated at 14 K. Spectrum illustrates low-spin cytochrome *g* 3 and Rieske signals. EPR conditions: microwave power 10 mW; temperature 14 K; modulation amplitude 1 mT.

number of signals were observed at 15 K (Fig. 1A) which included those near *g* 6.0 due to high-spin cytochrome *b*-563 [25], *g* 3.5 from cytochrome *f* [25,26], *g* 3.0 attributed to low-spin cytochromes including cytochrome *b*-559 [26–28], *g* 2.0 due to Mn^{2+} and EPR Signal II [29] and finally at *g* 1.89 due to the Rieske iron-sulphur protein [30]. At 5 K in the same preparation (Fig. 1C), low-spin cytochromes were not observed, whilst high-spin iron signals near *g* 6 were enhanced. In addition, the semiquinone-iron type signal of the primary acceptor appeared near *g* 1.8 [21]. A subsequent treatment of detergent particles with DEAE resulted in the removal of signals at *g* 6, *g* 3.5 and *g* 1.89 under all EPR conditions (Fig. 1B). The loss of these components following the DEAE ion-exchange chromatography, probably as a cytochrome b_6-*f* complex, parallels the loss of several peptide bands [24].

A more detailed spectrum of the region around *g* 2.0 is shown in Fig. 2. Fig. 2A shows a signal of unknown origin at *g* 2.03 observed in membranes of the mutant, but which was removed by detergent treatment. The signal which has EPR characteristics of a high-potential iron-sulphur protein does not originate from the Rieske iron-sulphur centre which gives the signal at *g* 1.89.

Fig. 2B shows the Rieske centre at *g* 1.89, low-spin cytochrome near *g* 3.0 and a hydrated manganese signal around the *g* 2.0 organic radical region. The size of the maganese radical was greatly reduced by DEAE treatment. The low-spin cytochrome signal was maintained during all purification steps and was assigned in part to cytochrome *b*-559. No photo-oxidation of this signal was observed at cryogenic temperatures in F54-14 preparations unlike that demonstrated in other PS II preparations from spinach or *Phormidium laminosum* [28]. The effects of this on PS II electron donation are discussed in the accompanying paper [29].

Fig. 2B also confirms the absence of any signals from PS I components in preparations from the mutant F54-14 as indicated by earlier studies [21]. A similar result was obtained with the chloroplasts of barley mutant zb63, the characterisation of which was published previously [22, 31]. Therefore, with these preparations, the light-induced electron transport observed was solely from PS II.

PS II electron acceptors

We have recently shown that an EPR signal similar to that of the quinone-iron electron acceptors of the purple photosynthetic bacteria can be observed in detergent preparations of the F54-14 mutant [21]. This signal was most easily observed if samples were prepared by freezing under illumination in the absence of any added electron donor. Fig. 3 shows that in samples prepared in this way, the semiquinone-iron can be detected in intact membranes (Fig. 3A), intact detergent particles (Fig. 3B), and DEAE-treated detergent particles (Fig. 3C).

As indicated in Ref. 21, dark-adapted samples of F54-14 preparations were found to have either a

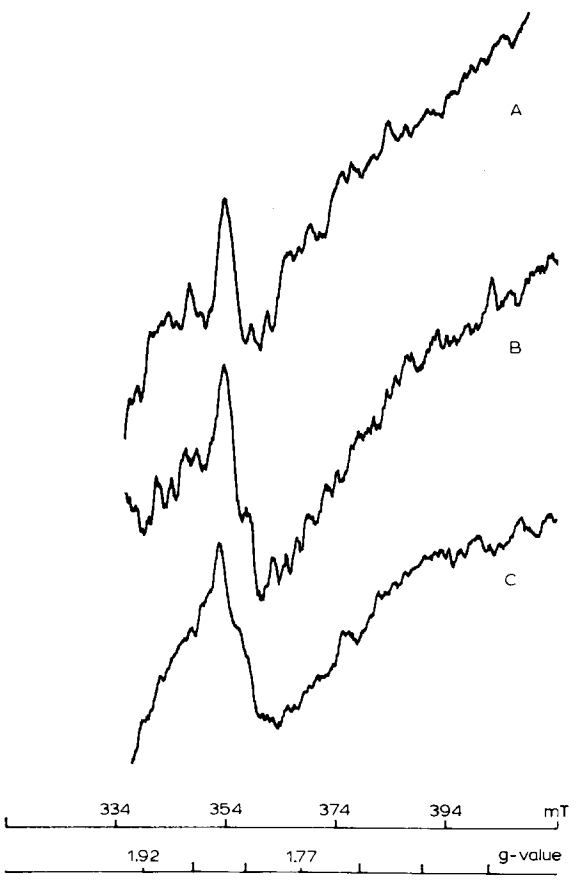

Fig. 3. EPR spectra of the semiquinone-iron acceptor, Q. Samples of *C. reinhardii* F45-14, frozen under illumination; (A) freshly prepared membranes; (B) detergent-treated intact particles; (C) DEAE particles. EPR conditions: microwave power 25 mW; temperature 5 K; modulation amplitude 1 mT.

small proportion or none of the semiquinone-iron radical, showing that Q was oxidised in most centres. Further work showed that at each stage of purification a low-temperature photoreduction of the semiquinone-iron signal was observed in these types of samples. The maximum semiquinone-iron signal induced in dark-adapted samples by a period of saturating illumination at 5 K was smaller than that obtained by room-temperature illumination. About one third of the total signal size was photoreduced, but a subsequent period of illumination at 200 K induced the full semiquinone-iron signal. This heterogeneity between centres at low temperatures may be taken as existing in the native membrane, the effect being present in freshly prepared oxygen-evolving membranes and not being dramatically altered by subsequent treatments.

DEAE particles were, however, found to have a less efficient donor system as suggested by the original research on this mutant [32]. The result of this was that illumination at 200 K did not generate the full content of *g* 1.82 signal, although more than two thirds of the signal size compared to room-temperature illumination was achieved. The electron donors appear to be identical EPR components at both 5 and 200 K [29].

The characteristic requirements of high power and low temperature for the observation of a semiquinone-iron EPR signal were shown by the *g* 1.82 radical in all preparations. Fig. 4 shows the

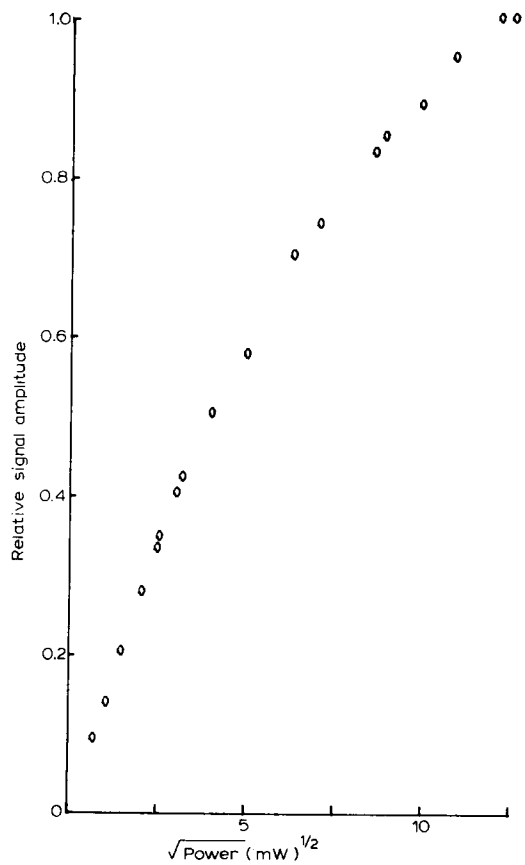

Fig. 4. Microwave power saturation profile of the EPR signal from the semiquinone-iron acceptor, Q, in intact particles of *C. reinhardii* mutant F54-14. Measurements of the *g* 1.82 peak were taken at 4.5 K and modulation amplitude 1 mT. The EPR signal was generated by freezing the samples under illumination.

microwave power saturation characteristics of the signal at 5 K, saturation being observed near 10 mW and maximum signal size beyond 150 mW. No significant differences in power saturation occurred between preparations. The temperature dependence study of the semiquinone-iron radical showed that it was only observed below about 12 K, and increased rapidly in size down to liquid helium temperatures. As indicated by Fig. 3, the line shape of the semiquinone-iron signal broadened during purification of the F54-14 membranes. The signal obtained from fresh membranes was sharp and a second inflexion occurred near *g* 1.7. In detergent-treated preparations, the *g* 1.82 peak was broadened with the appearance of a shoulder on the peak, together with loss or broadening of the *g* 1.7 inflexion indicating a change of the interaction between semiquinone and iron, perhaps due to loss of the secondary quinone B [33]. No significant differences in line shape were observed between signals generated by 5, 200 K or room temperature illumination within each preparation.

The decay of the *g* 1.82 signal showing the reoxidation of the semiquinone-iron at room temperature was followed by freezing untreated samples of F54-14 particles at various times after a period of illumination designed to fully reduce the acceptor. These results were consistent with fluorescence data [24] in showing that the signal decayed slowly (over several minutes in this case) following illumination.

If the *g* 1.82 signal is due to the primary acceptor Q, then it should be observed in other PS II preparations. Fig. 5 shows that a similar signal can be observed in chloroplasts from the barley mutant viridis zb63. The signal was small, but was observed both in samples frozen under illumination (Fig. 5A), and as a signal induced by illumination at 4.5 K (Fig. 5B), showing that the *g* 1.82 signal is likely to be a general property of the PS II electron acceptor. Fig. 5C and D shows for comparison the equivalent signals in a sample of F54-14 intact particles. These spectra confirm that both the line shape and *g* value were similar in both species.

Fig. 5 also shows part of a series of small signals (arrowed) which were observed in viridis zb63 chloroplasts and which showed apparent *g* value shifts during illumination at cryogenic temperatures. This caused difficulties when recording the difference spectrum of the *g* 1.82 semiquinone-iron signal, the peaks of which are indicated by Q in Fig. 5. The small signals were either artifacts or perhaps related to be multiline manganese spectrum reported to originate from the oxygen evolving complex [34].

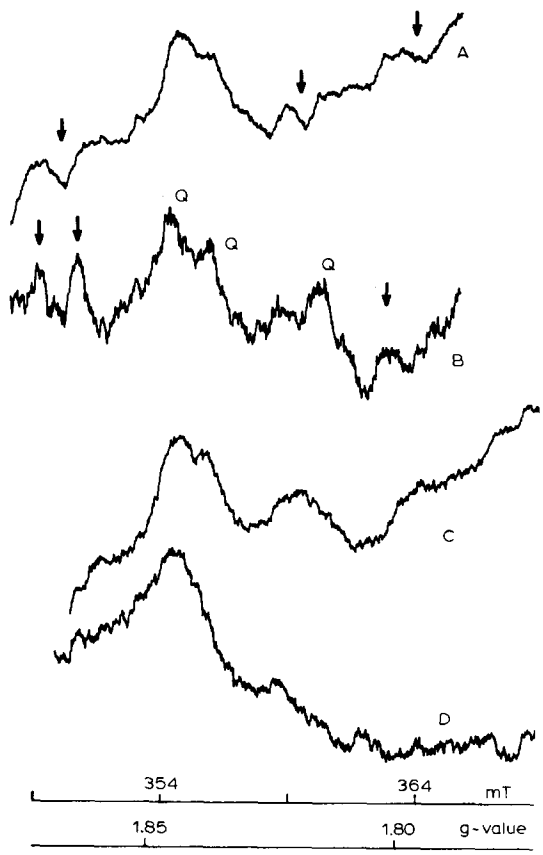

Fig. 5. EPR spectra of the semiquinone-iron, Q^-, in barley zb63 chloroplasts and *C. reinhardii* F54-14 intact particles. (A) zb63 chloroplasts frozen under illumination. Chlorophyll concentration 4 mg/ml; (B) Q^- photoinduced in zb63 chloroplasts by illumination at 4.5 K, chlorophyll concentration 4 mg/ml; arrows indicate signals mentioned in text; (C) F54-14 intact particles after illumination at 4.5 K; chlorophyll concentration 0.5 mg/ml; (D) Q^- photoinduced in F54-14 intact particles at 4.5 K, chlorophyll concentration 0.5 mg/ml. EPR conditions: microwave power 25 mW; temperature 4.5 K; modulation amplitude 1 mT.

The quinone-iron can be reduced chemically to the semiquinone-iron by brief (1–2 min) exposure to sodium dithionite prior to freezing [21]. Prolonged reduction results in a lower signal size

possibly due to double reduction to the quinol, or loss of iron. We have made preliminary redox titrations which indicate a midpoint potential near 0 mV for the reduction to the semiquinone-iron, but the instability of the preparation under titration conditions has prevented a more precise determination of the potential.

As the preparation contains a low-temperature electron donor, illumination of samples in which Q is reduced prior to freezing would be expected to result in reduction of the pheophytin intermediary electron carrier, together with some formation of a reaction centre triplet attributed to decay of the radical pair $P\text{-}680^{+}I^{-}$ [20].

Fig. 6A shows the result of illuminating a sample of F54-14 DEAE particles which had been reduced by dithionite at pH 5.9 before freezing. The illumination at 5 K did not affect the semiquinone-iron signal, seen at *g* 1.82, which had been chemically reduced by the dithionite. However, at *g* 2 the doublet signal caused by an interaction between the semiquinone-iron and the photoreduced pheophytin acceptor in the same centre was observed. The electron donation at 5 K was inefficient and only in a fraction of the centres was the pheophytin intermediate reduced, even after prolonged illumination. Fig. 6B shows the spectrum of the light-induced doublet at 5 K by subtraction of the spectrum of the dark-adapted sample from the spectrum in Fig. 6A. The full shape of the doublet was not observed (Fig. 7), which may be due to the contribution of the spectrum of the electron donor at 5 K or may be a further result of the heterogeneity of centres discussed elsewhere in this and the accompanying paper [29].

Illumination at 200 K for 6 min of a similar sample to that shown in Fig. 6 resulted in extensive reduction of the pheophytin, as electron donation could now compete successfully with the back reaction in all centres. This is demonstrated by Fig. 7, where in the dithionite-reduced dark-adapted sample (Fig. 7A) no doublet was present, but the semiquinone-iron signal near *g* 1.82 was fully developed. Fig. 7B shows the same sample after the period of illumination at 200 K and Fig. 7C the light-induced spectrum by subtraction of (A) from (B). The doublet had the characteristics previously described by Klimov and co-workers [18], requiring observation at high microwave

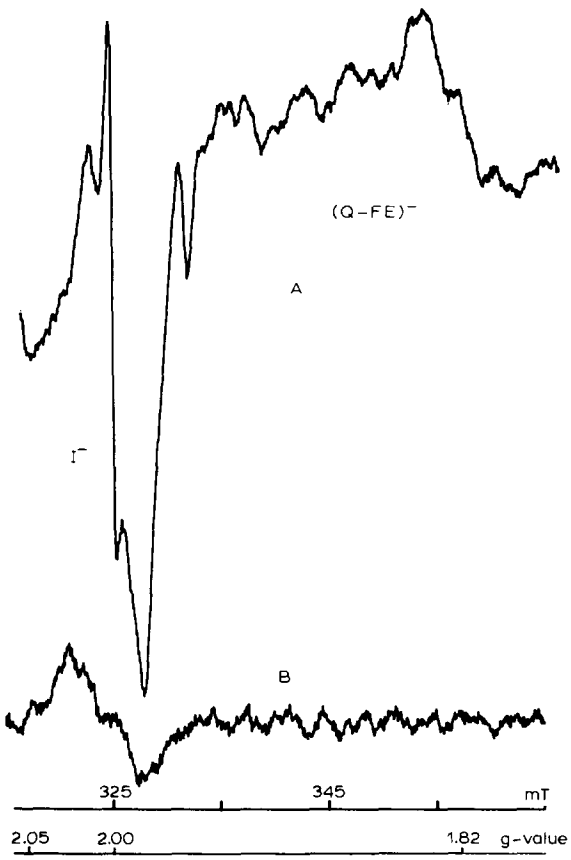

Fig. 6. EPR spectra of the doublet signal resulting from the interaction of reduced pheophytin and semiquinone-iron acceptors. (A) F54-14 DEAE particles reduced by dithionite for 5 min, frozen in the dark, and then illuminated for 10 min at 5 K. Spectrum shows chemically reduced semiquinone-iron at *g* 1.82 and the EPR doublet near *g* 2; (B) light-induced spectrum of EPR doublet by subtraction of the spectrum from a dark-adapted sample from that in A. This shows the lack of fully developed splitting. EPR conditions: microwave power 50 mW; modulation aplitude 1.0 mT; temperature 5 K.

powers and temperatures below 10 K, as well as the presence of the semiquinone-iron acceptor. At higher temperatures and lower powers, the doublet was replaced by the singlet pheophytin spectrum [18, 22]. As indicated by the lack of change in Fig. 7, the presence of the doublet signal did not have any significant effect on the line shape, line width or microwave saturation properties of the semiquinone-iron signal. As only partial irreversible reduction of the pheophytin occurs at 4.5 K, when the dithionite sample was continuously illuminated, a spin-polarised reaction centre triplet

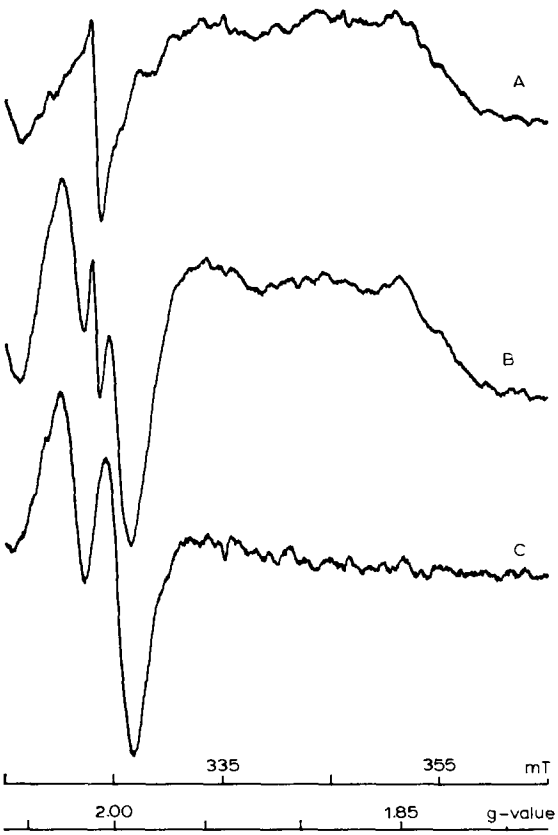

Fig. 7. EPR spectra of the doublet signal induced by 200 K illumination. (A) F54-14 DEAE particles reduced by dithionite at pH 5.9 in the dark before freezing; (B) sample after illumination for 6 min at 200 K; (C) difference spectrum (B−A) showing doublet and lack of change near g 1.82. EPR conditions: microwave power 50 mW; modulation amplitude 0.8 mT; temperature 4.5 K.

was also observed. This triplet (Fig. 8A) is similar to that reported by Rutherford and co-workers [20] from a spinach PS II preparation, having a width of 618 G and a zero-field splitting constant, $D = 0.0289\ cm^{-1}$. Prolonged illumination at 4.5 K resulted in a decrease in the size of the triplet signal as the pheophytin acceptor was partially reduced and the triplet was completely removed in samples illuminated at 200 K for a few minutes, where the pheophytin became fully reduced.

We have also been able to observe this signal in F54-14 preparations or chloroplasts of viridis zb63 frozen under illumination without reduction (Fig. 8B). In such samples, the semiquinone-iron signal was present and no pheophytin interaction doublet was detected, although a large Signal II radical at g 2.0 [29] interfered with detection of the doublet and allowed the possibility of reduced pheophytin being present in a minority of centres.

If samples of *C. reinhardii* F54-14 DEAE particles were frozen under illumination in the presence of dithionite, the semiquinone-iron signal was

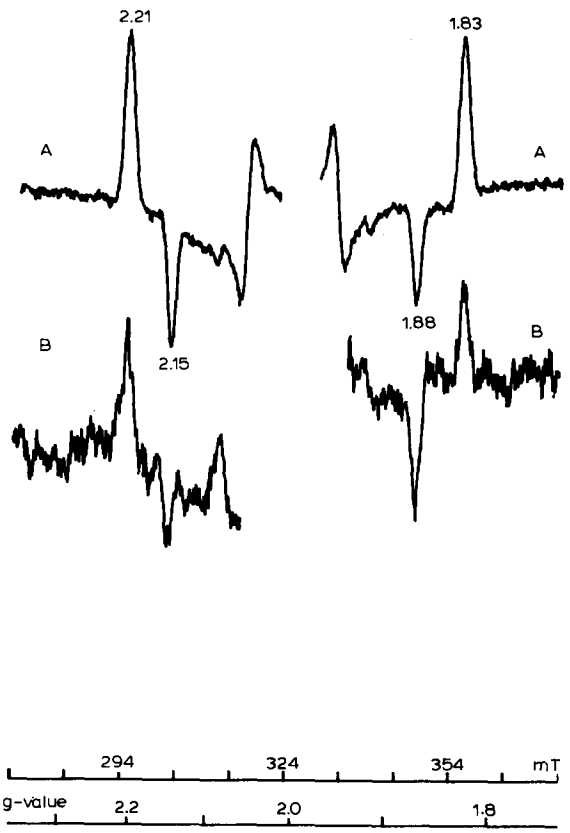

Fig. 8. EPR spectra of the PS II reaction centre triplet. (A) F54-14 DEAE particles reduced by dithionite for 10 min and frozen in the dark. Triplet observed on continuous illumination at 4.5 K.

$$DP\text{-}680^{+}I^{-}Q^{-}Fe \quad (T^{*})$$

(B) Barley viridis zb63 chloroplasts frozen under illumination and illuminated at 4.5 K. An average of eight spectra were taken.

$$D^{+}P\text{-}680^{+}I^{-}Q^{-}Fe \quad (T^{*})$$

EPR conditions: microwave power 25 μW; modulation amplitude 1.25 mT.

lost, probably by double reduction and the large 13 G singlet of reduced pheophytin was observed near g 2.0 [18, 22]. No doublet or reaction centre triplet were observed, indicating that the reaction centres are closed, with pheophytin reduced and quinone-iron doubly reduced.

Discussion

The results of this paper clearly define the components of the electron acceptor complex of PS II in the *C. reinhardii* F54-14 mutant and show that similar results can be obtained with a barley mutant, viridis zb63. This indicates that the results are likely to be generally applicable. The use of mutants lacking PS I has proved essential in order to detect the small EPR signals of the PS II reaction centre and the results confirm the very close analogy between the PS II and purple bacterial reaction centre complexes. In these reaction centres, electrons are transferred from the chlorophyll electron donor through a pheophytin intermediate to a quinone acceptor. Our results show that the quinone acceptor has an EPR spectrum very similar to that of the purple bacterial acceptor, indicating that the semiquinone interacts with an iron atom. The temperature dependence and power saturation characteristics of the signal support this interpretation. The signal is rather easily lost during purification or experimental treatment, perhaps due to loss of the iron interaction, which does appear to change during purification. The pheophytin intermediate may be reduced either at room temperature or by low-temperature illumination of reduced samples. In the latter case, the EPR spectra of the intermediate at very low temperatures show the formation of a doublet with a 6 mT splitting only when the acceptor is in the semiquinone-iron state. This indicates that a magnetic interaction occurs between the semiquinone-iron and reduced pheophytin similar to that seen in those purple bacterial species where an electron donation to the reaction centre can also occur at cryogenic temperatures. The interaction between semiquinone-iron and reduced pheophytin appears weak as in *Chromatium*, where the interaction also has no significant effect on the semiquinone-iron signal near g 1.82. The line width of the PS II doublet is also similar to that in *Chromatium* [17]. The fact that illumination at 200 K results in a characteristic doublet spectrum (Fig. 7), whilst illumination at 5 K (Fig. 6) only partially resolves the doublet, cannot be explained by invoking the interference of an electron donor radical. In the accompanying paper [29], evidence is presented showing that donation at either temperature gives identical electron donor spectra in the g 2 region. The doublet line shape differences therefore appear to be another feature of PS II reaction centre heterogeneity.

The formation of a spin-polarised reaction centre triplet indicates a similar mechanism of electron transfer to that in purple bacteria, which is confirmed by the loss of triplet formation when the pheophytin intermediate is reduced. The zero-field splitting parameter, D, of this signal is significantly different from that of purple bacteria, and has the same value in both the *C. reinhardii* and barley preparations as shown above, as well as being similar to that reported for spinach [20]. The value is also similar to that seen in PS I [35] and is evidence, although not conclusive, that P-680$^+$ is a monomeric and not a dimeric chlorophyll molecule. The study of the triplet was affected by the availability of an electron donor at cryogenic temperatures, which resulted in partial reduction of acceptor by illumination. This meant that some triplet was always observed, but as expected an increase in size occurred as the quinone-iron acceptor was fully reduced [36]. The detection of the triplet in samples frozen under illumination agrees with the results presented here and in Ref. 29, that this treatment induces the oxidation of the secondary electron donor and reduction of quinone-iron acceptor, leaving P-680$^+$ and reduced pheophytin to recombine via the triplet during subsequent illumination. However, the extent of triplet production was not as large as in chemically reduced samples, and although the redox potential of the samples was different and may explain this, it may also suggest the presence of other components in the reaction centre. However, interpretation is difficult, especially with electron donation where the high redox potentials of the oxidised components may allow non-specific oxidations to occur when normal pathways are blocked.

In all preparations from *C. reinhardii* F54-14, the PS II reaction centres appear to be heteroge-

neous. Illumination at temperatures below 100 K results in only partial reduction of either semiquinone-iron or pheophytin depending on the initial state of reduction in the reaction centre, with complete reduction occurring only at temperatures well above 150 K. This effect appears to be due to kinetic differences between centres, such that the electron donation to P-680$^+$ below 100 K can only compete with the back reaction from reduced acceptors in some centres. The donor at higher temperatures has characteristics similar to that described by Mathis and co-workers [37, 38], termed D1, and is discussed in the accompanying paper [29].

There is no obvious reason other than a conformational variation why two groups of reaction centres should behave differently, and we cannot exclude the possibility that each P-680 has two acceptors and two donors, one functioning only above 200 K.

Acknowledgements

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