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EFFECTS OF pH ON REACTIONS ON THE DONOR SIDE OF PHOTOSYSTEM II

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Summary

The effects of pH on the increase of fluorescence yield measured in the microsecond range, and on the microsecond delayed fluorescence have been studied in dark adapted chloroplasts as a function of flash number.

(1) At pH 7, the amplitude of the fast-phase of the microsecond fluorescence yield rise oscillated as a function of flash number with period 4 and with maxima on flashes 1 and 5, and minima on flashes 3 and 7. The damped oscillations were apparent over the range between 6 and 8, although the absolute amplitude of the fast phase was diminished at the lower end of the range. At pH 4, there was no fast phase in the rise and, at pH 9, an enhanced fast-phase occurred only for the first flash.

(2) The decay of microsecond delayed fluorescence was described by the sum of exponentials with half-times of 10—15 μs and 40—50 μs. Over the pH range 6— <8, the extrapolated initial amplitude and the proportion of the change due to the faster component showed oscillations which were opposite in phase to those observed for the prompt fluorescence yield rise; the slower component showed weaker oscillations of the same phase. At pH 4, there were no oscillations and the slow phase predominated. At pH 9, the delayed fluorescence intensity was diminished on the first flash, and high on subsequent flashes.

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Abbreviations: DCMU: 3-(3,4-dichlorophenyl)-1,1-dimethylurea; Mops: 3-(*N*-morpholino)propane sulphonic acid; Mes: 2-(*N*-morpholino)ethane sulphonic acid; Chl a_{II}: chlorophyl a_{II}; PS I, Photosystem I; PS II, Photosystem II; ADRY, acceleration of the deactivation reactions of the watersplitting enzyme system Y.

(3) The results are interpreted in terms of a model in which protons are released during all transitions of the S-states with the exception of $S_1 \rightarrow S_2$, and in which there are two sites of inhibition on the donor side of the photosystem at extreme pH values. At pH 4, electron donation to P^+ occurs with a half-time approx. 135 μs, either by a back reaction from Q^-, or from D; electron transport is interrupted between Z_1 and P. At pH 9, electron transport is inhibited between Z_1 and Z_2; rapid re-reduction of P^+ by Z_1 occurs after 1 flash, and on subsequent flashes electrons from D, an alternative donor reduce P^+. The location of the positive charge on states S_2 and S_3 is discussed.

Introduction

The reduction of $P\text{-}680^+$, the primary donor to Photosystem II, following charge separation, occurs through electron transfer reactions which convey electrons ultimately from water to the reaction centre. These reactions, as expressed in the rapid phases of delayed fluorescence decay and prompt fluorescence rise, are not greatly affected by pH over the range pH 5—8 [1—3], but are more sensitive outside the physiological range ($4 \geqslant pH \geqslant 9$) [4,5]. A diminution in the fast phase of the fluorescence yield rise [4] and slowing of the faster components of the decay of the delayed light intensity [3] are consistent with the displacement of the equilibrium concentrations of reactants in the secondary donor pools as the result of the change in concentration of protons in the inner thylakoid space, and with the effects of these on the relative forward and reverse rate constants.

We have extended these observations by measuring the rise in microsecond fluoresence yield and microsecond delayed fluorescence as a function of pH and flash number in dark-adapted chloroplasts. The measurements have been made for the range of pH over which the steady-state oxygen yield remains essentially constant [6], and also at extreme values of pH where oxygen evolution no longer occurs.

Until recently, the release of protons which accompanies water splitting was thought to occur synchronously with the release of oxygen [7]. If this were so, then the transition of the S-states involving oxygen evolution, $S_3 \rightarrow S_0$, would be expected to show a marked pH dependence.

The production of protons can be followed directly using a pH-sensitive glass electrode [7,8] or indicator dyes [9,10]; the recent results of such measurements have indicated that protons are released on transitions other than $S_3 \rightarrow S_0$ [8—10]. Saphon and Crofts [9] and Fowler [8], using dark-adapted chloroplasts, showed a pattern of proton release for the majority of centers of 1, 0, 1, 2, for the transitions $S_0 \rightarrow S_1$, $S_1 \rightarrow S_2$, $S_2 \rightarrow S_3$ and $S_3 \rightarrow S_0$, respectively. Junge and colleagues [10], using a chloroplast suspension in which relaxation of the S-states was accelerated by ADRY reagents [11], showed a pattern of proton release of 0, 1, 1, 2 for the above transitions. We have recently demonstrated that the former pattern in which proton release accompanies all transitions of the states with the exception of $S_1 \rightarrow S_2$, can also be observed using another method [12]; we made measurements of millisecond-delayed fluorescence using dark-adapted chloroplasts which had been preilluminated by 0—8 flashes

prior to the addition of DCMU, so as to trap the oxygen evolving apparatus in a particular state. For transitions during which proton production occurred, the delayed light was stimulated when PS I was allowed to turn over and pump protons into the thylakoids. In this case, the equilibrium of the reaction yielding protons was displaced by the lowered internal pH, and the delayed fluorescence substrate P^+ was stabilized.

A model is presented which is compatible with data from our measurements and those of Renger et al. [13] who monitored Chl a_{II} re-reduction kinetics as a function of pH. A brief, preliminary report of these results has appeared elsewhere [14].

Methods

Preparations of chloroplasts

Chloroplasts were prepared from market or greenhouse spinach as previously described [15], in a medium containing 0.4 M sucrose, 10 mM NaCl and 50 mM potassium phosphate buffer pH 7.8. A range of buffers of appropriate pK was used to dilute the chloroplasts to a final concentration of chlorophyll ~5—10 μg/ml for measurement; 0.4 M sucrose, 10 mM $MgCl_2$, 50 mM KCl plus one of the following buffers at 50 mM, Tricine (pH 8, 9), Mops (pH 7), Mes (pH 5, 6), or glycylglycine (pH 4). All measurements were carried out on chloroplasts which had been dark-adapted for 10 min at room temperature. In some experiments, chloroplasts were preilluminated by 25 flashes before recording, in order to approach the steady-state conditions used by others [13]. Chlorophyll was assayed according to the method of Arnon [16].

Microsecond fluorescence yield

Measurements of the kinetics of the yield of prompt fluorescence were carried out essentially as described by Duysens et al. [1]. The change in fluorescence yield during each of a series of Xenon flashes (half-width ~20 μs) was obtained from the fluorescence intensity profile after division by the flash intensity. The flash duration and profile were a function of the flash tube and capacitors used. In most of the experiments reported here, the flash (20 μs half-width) was generated using an Osram X1E100 Xenon lamp, connected to a capacitor discharge system (1 kV, 7.5 μF). The flash intensity was adjusted with neutral density filters so that rapid transients due to triplet formation were minimal, but the integrated intensity was saturating. Under these conditions, the rate of fluorescence yield change was limited by flash intensity.

The anode current from the photomultiplier was fed through a 1 K resistor across the input of a Datalab DL905 transient-recorder (Datalab, Mitcham, Surrey, U.K.; minimal acquisition time 200 ns, 1024 data points per trace). The digitized data were read directly into a minicomputer (Digital Equipment Co., PDP11/10). Points corresponding to the first 50 μs of the trace were stored for each of 8 successive flashes (1/320 ms). Computation including signal averaging and display were carried out on line using appropriate Fortran and assembly language programs.

Delayed fluorescence in the microsecond range

The intensity and decay of the microsecond-delayed fluorescence following

a series of 20 ns laser flashes given to dark-adapted chloroplasts were measured using a gated photomultiplier switched on 7 μs after the flash. The laser beam (Laser Associates, Slough, U.K., Nd-doped YAG laser, pockel-cell Q-switched and frequency doubled to emit at 530 nm; 10 Hz fastest repetition) entered the cuvette at 90° to the photomultiplier which was covered by an interference filter (685 nm Balzer type B-40) and a red cut-off filter (Wratten Kodak 70). Apart from the gating electronics, the apparatus used for the measurements was essentially the same as that used in the fluorescence yield experiments.

Results

Microsecond fluorescence yield

Fig. 1 shows the fluorescence yield changes during the 1st, 2nd, 3rd, and 5th

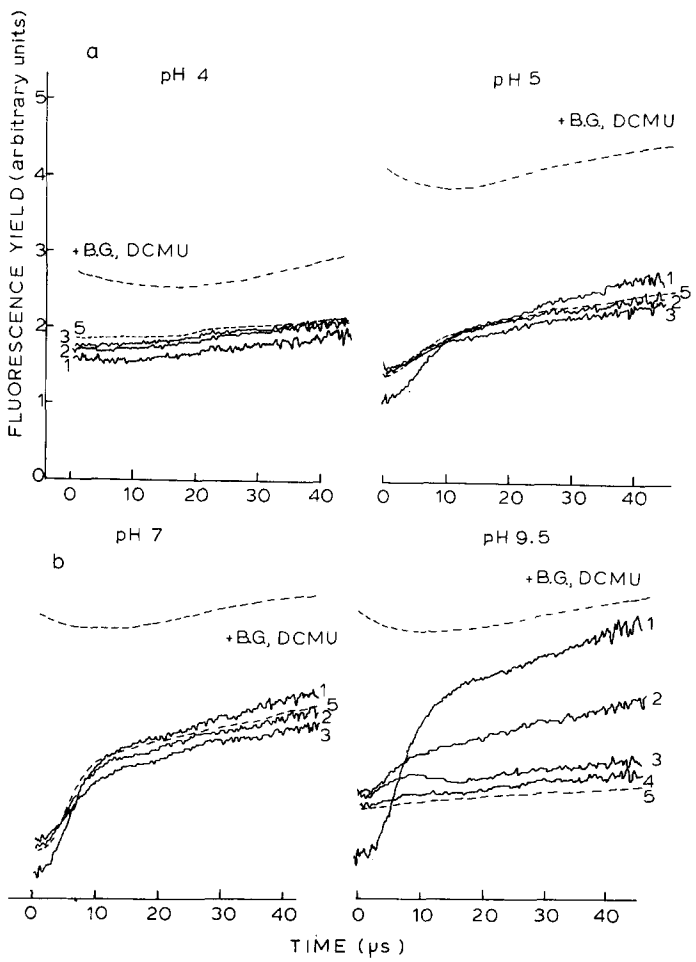


Fig. 1. Fluorescence yield change during 1st, 2nd, 3rd, and 5th flashes of a sequence given to dark-adapted chloroplasts preincubated in the dark for 10 min at pH 4, 5, 7, 9.5. Maximal yield obtained with blue background illumination (1 mW · cm^{-2}) plus 5 μM DCMU also shown (- - - - -). Each trace is an average of 4. Chloroplasts (2 μg/ml chlorophyll) were suspended in a medium containing 0.4 M sucrose, 10 mM NaCl, 10 mM $MgCl_2$ plus 50 mM Tricine (pH 9.5), Mops (pH 7) or Mes (pH 5, 4).

flashes of a sequence given to chloroplasts preincubated in the dark for 10 min at several values of pH. The maximal yield obtained with DCMU and background illumination is also shown. The yield increased biphasically on each flash, particularly at pH 7 and 8, and less markedly at pH 5; at pH 4, the fluorescence yield rise was completely inhibited as previously observed [4]. The maximal yield at pH 7 was greater than at 5.

Microsecond fluorescence yield as a function of flash number

The extent of the fluorescence yield increase during the first 20 μs for a series of flashes given to dark-adapted chloroplasts which had been preincubated at different values of external pH, is plotted as a function of flash number in Fig. 2. There was no uncoupler present; a preincubation time of 10 min is sufficient for equilibration of pH across the membrane. The effects of pH in the range pH 5—8 do not appear to be restricted to a single transition of the S-states, since damped oscillations with a period of 4 were apparent over the entire range. The amplitude of the oscillations observed in these experiments was less than that originally reported by Delosme [28], perhaps because the flash was long enough to give a significant proportion of double hits, and of insufficient intensity to saturate the maximal electron donation rate (see Discussion).

The amplitude of the fast component of the yield was inhibited as the pH was lowered from 8 to 5, but its relative amplitude as a function of flash number did not vary markedly. The variation of yield as a function of flash number at pH 7 is well known [28]. At pH 4, no fast phase in the yield was observed for any flash. For values of pH >8.5, the fast phase on the first flash was enhanced, but the changes on all subsequent flashes were diminished.

Microsecond delayed fluorescence

Microsecond-delayed fluorescence excited by a series of 8 saturating laser

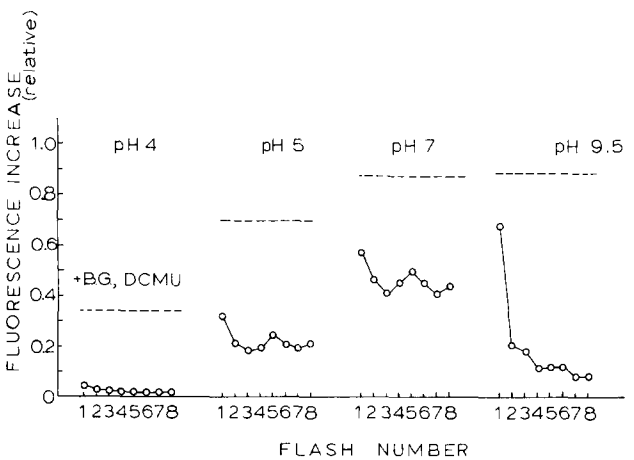


Fig. 2. Dependence of the extent of the fluorescence yield increase during the first 20 μs of the flash at pH 4, 5, 7, 9.5 on flash number. Data points taken were from Fig. 1. Dashed lines show $F_m - F_0$ for first flash, where F_0 = initial yield and F_m = maximal yield obtained with blue background light plus 5 μM DCMU. Vertical scale: $[1 - (F_m - F_{20\mu s})/(F_m - F_0)]$.

flashes given to dark-adapted chloroplasts is shown in Fig. 3. The initial amplitude (measured at 7 μs from the traces, or by extrapolation of the fitted curves to the time of the flash; see below) oscillated with a periodicity of 4 as a function of flash number, with minima after 1 or 5 flashes, maxima after 3 or 7 flashes.

The decays were described by the sum of two exponentials (Fig. 4); two subsets of data points were chosen for regions in the curve where the two decays predominated; a computer program performed a least squares fit on the longest lived component, which was then subtracted from the experimental decay curve. The amplitudes of the components and their half-times were calculated as described under Methods (see also Lavorel [18]). If the decays were deconvoluted into three components, then the fit to the original data was not as good. Typical analyses are shown in Fig. 4 for flashes 1 and 3 at pH 7. During the time course of our measurements (7—200 μs) we did not see a significant contribution from a longer lived component (~200 μs) of the decay, as observed by Zankel [19], and as seen in the *P*-680 kinetics by Renger et al. [13]. However, when the decay curves measured under steady state conditions were deconvoluted, longer lived components were apparent as previously reported [3].

Fig. 5 shows the results of the analysis of the decays of delayed fluorescence for chloroplasts dark adapted at different values of external pH. The extrapolated initial amplitude of the delayed fluorescence and the amplitude of the fast and slow components which contribute to the decay, are plotted as a function of flash number (Fig. 5a). The amplitude of the delayed fluorescence for the first flash given to chloroplasts at pH 9 is not shown because it was too small to allow analysis. Fig. 5b shows the half-times for the fast and slow portions of the decays plotted as a function of flash number. Damped oscillations are apparent over the range between pH 6 and <8 for the initial amplitude, and over a narrower pH range between pH 6 and 7, they can also be seen for the fast component of the delayed fluorescence decay. As observed

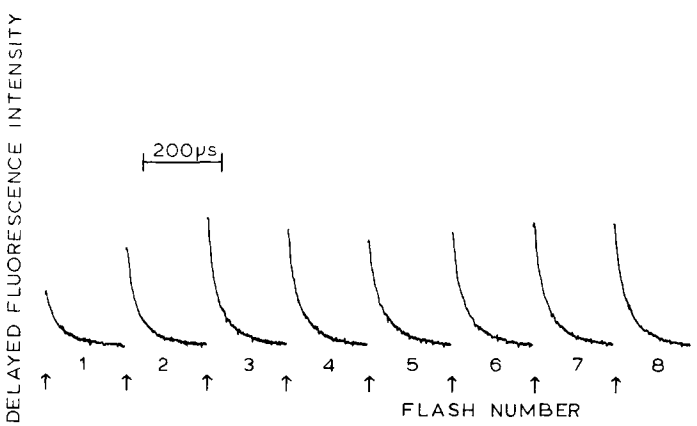


Fig. 3. Microsecond delayed fluorescence excited by 8 saturating laser flashes given to dark-adapted chloroplasts at pH 7.0. Chloroplasts (6.6 μg/ml chlorophyll) were preincubated in the dark with 1 μM nigericin plus 1 μM valinomycin for 10 min in a medium containing 0.4 M sucrose, 50 mM KCl, 10 mM $MgCl_2$, 50 mM Mops buffer, pH 7.0. Each trace is an average of 8.

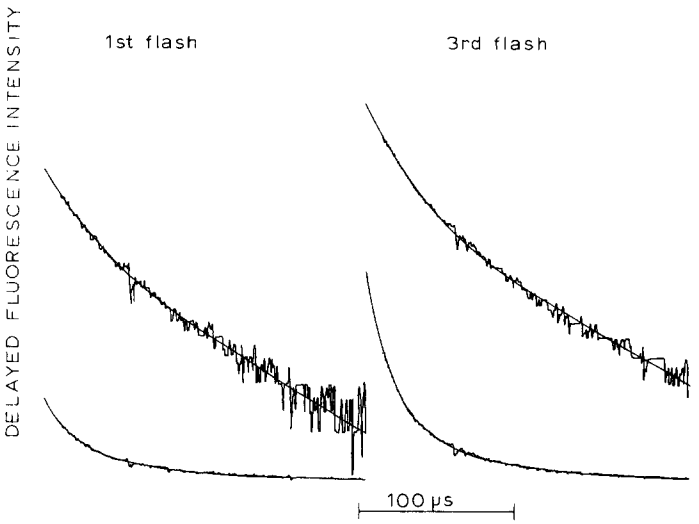


Fig. 4. Decay of the delayed fluorescence at pH 7.0 for 1st and 3rd flash showing analysis of curve into 2 exponentials (for procedure, see text). The original and fitted curves are shown, plus a log plot and fitted log plot of the original trace (upper traces). Data are from traces shown in Fig. 3.

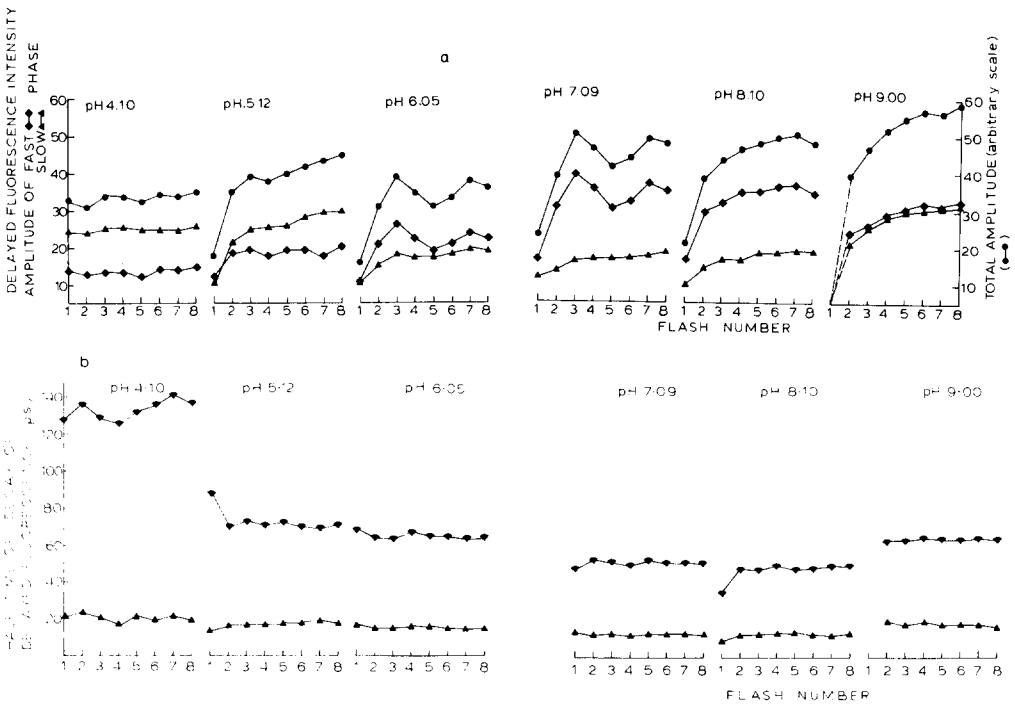


Fig. 5. (a) The total delayed fluorescence (●———●) and amplitudes of the fast (◆———◆) and slow (▲———▲) components revealed in the kinetic analysis plotted as a function of flash number at different values of pH. The corresponding half-times of the two reactions are also shown (b) (▲———▲ fast, ◆———◆ slow). The measurements were carried out as described in Fig. 4 and in the text. Chloroplasts (6.6 μg/ml chlorophyll) were suspended in a medium containing 0.4 M sucrose, 50 mM KCl, 10 mM $MgCl_2$, plus 50 mM Tricine (pH 8, 7.5), Mops (pH 7), Mes (pH 6.5 → 5.5), or glycylglycine (pH 5 → 4).

previously [1], the oscillations of the rapid (10—15 μs) phase of the delayed fluorescence decay and those of the initial amplitude (Fig. 5a) were opposite to those of the fast phase (~3 μs) of the prompt fluorescence yield rise (Figs. 1 and 2). The slower component of the decay (~40—60 μs), showed a weaker oscillation with 4-fold periodicity between pH 5 and 8 similar to that observed for the initial amplitude and fast component. There was no apparent oscillation in either phase at pH values 4 or 9.

The relative proportion of the decay due to the fast component was greatest at pH 7, 8 and 9; the slower component predominated at pH 4 and 5. At pH 6, the proportions of the components were more nearly equal. The half-time of the fast phase was relatively independent of pH between pH 5 and 9, having a value between 10—15 μs (Fig. 5b); at pH 4, the half-time was ~20 μs. The half-time of the slow phase was also relatively independent of pH over the range 5—9, although it increased slightly at lower pH values (pH 7, 40 μs; pH 5, 70 μs). The most marked change occurred at pH 4, when the half-time was increased to ~135 μs [3]; the increase in half-time of the slow phase which occurred as the pH was lowered, was slightly more marked for the first flash of the series than for subsequent flashes; otherwise the half-times were relatively independent of flash number (Fig. 5b).

Discussion

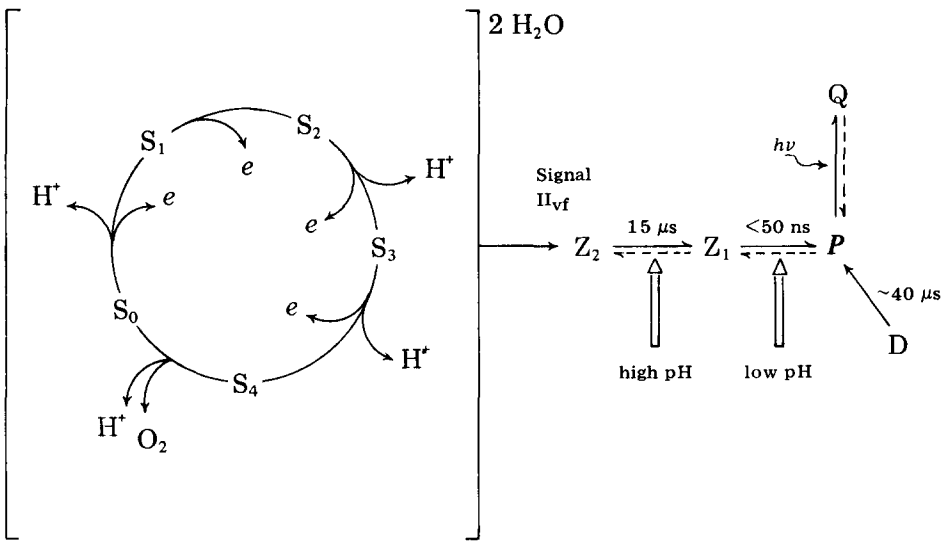
The release of protons during water splitting

Oscillations of periodicity 4, both for the rise of the prompt fluorescence yield and the delayed fluorescence in the microsecond time scale, were seen over the complete physiological pH range. This is in contrast to the strong controlling effect of pH expected if protons were released solely on the transition $S_3 \rightarrow S_0$ [7]. If this reaction involved the release of 4 H^+/e, it would be expected to show a very strong dependence on pH so that even at moderately low values of internal pH the reaction would be inhibited, and the cycle of the S states blocked. The lack of effect of pH may therefore be taken as supporting evidence for the suggestion that protons are also released on earlier transitions of the S states [8—10,12]. Over this range of pH, the major effect of pH is to vary the proportions of delayed fluorescence decay contributed by the 10—15 μs and ~50 μs phases, with a shift to the slower phase at lower pH (Fig. 5). At pH 5, there is some indication that the transition $S_1 \rightarrow S_2$ (transition effected by the first flash) is less affected by the lower pH than the others. However, because of the lower intensity of the delayed fluorescence following the first flash, the scatter of data is greater, and in other experiments this effect at pH 5 is less marked. Nevertheless, the effect is that anticipated from our model, which is itself strongly supported by our other data (see Introduction) [9,12].

Effects of pH on electron donors to the reaction centre of Photosystem II

The effects of pH and the involvement of protons in reactions on the donor side of the Photosystem will be discussed in terms of the model shown in Scheme I.

It seems probable that the initial concentration of P^+Q^- produced by a saturating flash of short duration would be the same regardless of the state of



Scheme I. Scheme for reactions on the donor side of Photosystem II.

the oxygen evolving apparatus, so that the intensity of delayed fluorescence measured sufficiently soon after the flash would be independent of flash number. The differences we observe at ~7 μs must therefore reflect a loss of P^+Q^- which has occurred since the flash, which differs according to the S-state. We may attribute this either to a loss of P^+ due to rapid reduction by Z_1, or with loss of an electron from Q^- on reduction of a secondary acceptor, or possibly with the existence of an alternative primary acceptor [15,20—24]. Rapid re-reduction by Z_1 implies that the component Z_1 is present in a reduced form. The oscillations in extrapolated initial amplitude suggest that in centres adapted to the dark, Z_1 is substantially reduced, but that in centres preilluminated by one or more flashes, a proportion of Z_1 is already oxidized. This suggests that the redox potential of Z_1 may be lower than that of Z_2 or components of the water oxidizing complex, in which case, in the normal operating condition, a proportion of the reaction centre complexes would contain Z_1^+, and the electron transfer rate to P^+ formed during a flash in these complexes would be determined by the electron transfer rate to Z_1^+ from Z_2. This linear model accounts well for the variation in extrapolated initial intensity with flash number. To test the hypothesis, it will be necessary to resolve the component of the delayed fluorescence which we cannot at present detect in our measurement. If this 'lost' component reflects electron transfer from Z_1, then the 10—15 μs component of the delayed fluorescence would be attributable to electron flow from Z_2, the component associated with signal IIvf [25].

Figs. 2 and 5 show the complementary oscillations of the rapid (10—15 μs) component of the decay of the delayed fluorescence and the fast phase of the fluorescence yield rise. Under the conditions of our experiments, the fast rise of fluorescence yield was flash-intensity limited and presumably reflected the reduction of P^+ by pathways with half-times faster than ~10 μs. Since this would include at least a fraction of the electron flow from Z_2 we cannot make a direct comparison between these oscillations and those of the 'lost' phase of

the delayed fluorescence decay. Nevertheless, the oscillations are in phase with those observed at shorter times by Delosme [28] and probably the major contribution to the kinetics is the rapid electron transfer from Z_1 to $P\text{-}680^+$.

The time constants we have measured probably correspond to the two faster components in the re-reduction kinetics of Chl a_{II} reported recently by Renger et al. [27], (half-times of 2—5 μs and 35 μs). However, since Renger's measurements were made in steady-state conditions, a direct comparison may not be appropriate. In our measurements, we did not observe a significant portion of decay corresponding to the 200 μs phase seen by Renger [13]. The 200 μs component which was also observed by Zankel [19], probably reflects a reaction closer to the water splitting enzyme. Renger [27] also concluded that a more rapid phase of reduction was 'lost' in his direct measurements.

It should be noted that the transitions showing a maximal initial intensity of delayed fluorescence and a minimal rapid fluorescence yield change are those in which the initial state (S_2 or S_3) would be expected from our model for proton release to carry one positive charge [9]. Delosme [28] has previously pointed out that the pattern of oscillations follows closely the concentration of S_2 plus S_3 before the flash. Our interpretation therefore would be that the positive charge in these states rests on Z_1^+, and that the oscillations reflect the equilibria between the components Z_1 and Z_2 and the intermediates of the oxygen evolving reactions. If this is the case, the damping at lower pH, and diminishing amplitude of the fast phase must reflect the increased redox potential of the intermediates. Duysens (paper read at the 6th Int. Cong. Biophys., Kyoto, Japan) and Joliot (personal communication) have considered similar models to explain the oscillations in fluorescence yield.

The complementary relationship between delayed fluorescence and prompt fluorescence yield rise was particularly evident at the higher pH values studied. At pH 9, the delayed fluorescence after the first flash given to dark-adapted chloroplasts was very low (Fig. 5), while the rapid phase of the fluorescence yield rise was maximal (Fig. 2). Subsequent flashes gave a low fluorescence yield, and marginally-stimulated delayed light. It seems likely from these results that at high pH, the electron transfer chain is disconnected between Z_2 and Z_1; thus high pH has the same effect as Tris-washing [26].

At pH 4, the chain appears to be disconnected between Z_1 and $P\text{-}680^+$ so that electron flow occurs largely by reversal of the photochemical charge separation [4].

The component in the decay of the delayed fluorescence with a half-time ~50 μs (pH 7), showed a much weaker oscillation than that of the faster decay (Fig. 5). This slower decay predominated under conditions in which electron transfer from Z_1 or Z_2 was inhibited, and its half-time was similar to that of electron transfer to $P\text{-}680^+$ from a donor D whose effects are seen in chloroplasts treated with high concentrations (~10 mM) of hydroxylamine [17]. We have previously suggested that it probably reflects electron flow from this or a similar component, which donates electrons to $P\text{-}680^+$ in parallel with Z_1 [14,15]. At physiological pH the amplitude of this component was always much less than that of the 10 μs component, which makes it seem unlikely that the two phases represented donors of equal importance implied by models with two parallel pathways for donation to P^+ of electrons from water.

Conclusions

The model of Scheme I summarizes our discussion. Electrons donated by the S-states to the donor side of PS II are accompanied by a release of protons except for the transition $S_1 \rightarrow S_2$. An intermediate, Z_2, passes electrons from the S-states to Z_1 in a reaction which is inhibited by high pH or by Tris-washing. Electron transport between Z_1 and the reaction centre is interrupted by low pH, and in these conditions the re-reduction of P^+ occurs mainly from another donor, D, which is apparently insensitive to extremes of ambient pH, or by a back reaction. The midpoint potentials of the intermediates Z_1 and Z_2 are probably pH-independent, and it seems probable that in states S_2 and S_3, a proportion of Z_1 is in the oxidised state and carries a positive charge.

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