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High pH effect on S-state turnover in chloroplasts studied by thermoluminescence. Short-time alkaline incubation reversibly inhibits S_3-to-S_4 transition

I. Vass *, H. Koike and Y. Inoue

Solar Energy Research Group, The Institute of Physical and Chemical Research (RIKEN), Hirosawa, Wako-shi, Saitama 351-01 (Japan)

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The influence of high pH on the functioning of the oxygen-evolving system was studied with isolated thylakoids by measuring flash oxygen yield in parallel with thermoluminescence B band which originates in the recombination between the positive charges on S_2 and S_3, the oxidized states of the water-oxidizing enzyme, and the negative charges on Q_B^-, the semireduced form of the secondary quinone acceptor of Photosystem II. It was found that a mild alkaline incubation of thylakoids (3 min at pH = 8.8–9.1 in darkness) largely inhibits O_2 evolution, while much less the B-band amplitude. The flash-induced period-four oscillation of the B band was abolished at high pH, showing normal oscillatory response only after the 1st and 2nd flashes, but no more oscillation after the 3rd flash. These observations indicated an inhibition of S_3-to-S_4 transition by high pH and were correlated primarily with the liberation of the 33 kDa peripheral protein followed by release of functional Mn. The above phenomena were largely reversed when the pH was returned to neutral. A possible mechanism of high pH inhibition of oxygen-evolving system is discussed.

Introduction

Alkaline conditions cause inactivation of the O_2-evolving apparatus in chloroplast membranes [1–3]. The inactivation observed with chloroplasts is accompanied by release of thylakoid bound Mn [4,5] and that observed with O_2-evolving PS II particles is accompanied by release of both Mn and three peripheral proteins (33, 24 and 18 kDa) [6,7]. While the inactivation by extremely high pH is irreversible, relatively mild treatments cause a reversible inactivation [8]. The inactivation effect is usually enhanced with illumination [1–3], probably because the S_2 state is most sensitive [4,5]. In spite of such wealth of available data, the mechanism of inactivation is not fully understood yet.

Thermoluminescence is a useful tool in studying the electron transport in photosynthetic O_2 evolution [9–11]. The oscillatory behavior of the B band observed under repetitive short flashes enables us to follow the S-state turnover even when O_2 evolution is inhibited [12]. Thus, application of thermoluminescence measurements is expected to provide unique information about the inhibitory effect of high pH on O_2 evolution.

This communication describes the results obtained by parallel measurements of flash oxygen yield and thermoluminescence with thylakoids exposed to mild alkaline conditions. The results

* On leave from Department of Theoretical Physics, József Attila University, Szeged, Hungary.

Abbreviations: Chl, chlorophyll; DCMU, 3-(3,4-dichlorophenyl)-1,1′-dimethylurea; Hepes, 4-(2-hydroxyethyl)-1-piperazineethanesulfonic acid; Mes, 4-morpholineethanesulfonic acid; PS II, Photosystem II; Q_B, secondary acceptor of Photosystem II.

demonstrate that the treatment affects the O_2-evolving system preferentially at high oxidized state concomitant with a partial release of the 33 kDa protein and that these events are largely reversible.

Materials and Methods

Thylakoids were isolated daily from market spinach using standard isolation techniques [13], resuspended at a high concentration (3–5 mg Chl/ml) in 50 mM Hepes (pH = 7.5)/5 mM $MgCl_2$/10 mM NaCl/0.4 M sorbitol and stored on ice in darkness until use. For thermoluminescence and flash-oxygen-yield measurements, thylakoids were diluted to the final concentrations of 300 and 1000 μg Chl/ml, respectively, using 50 mM of either Mes (pH = 6.0 – 7.0)/Hepes (pH = 7.0–7.8)/glycylglycine (pH = 7.8–9.5)/glycine (pH = 9.5–10.0) buffers with the same additions as indicated above. Above pH = 7.8, 10^{-6} M gramicidin D was included in the medium to equilibrate the inside and outside pH of thylakoids. In reversibility check experiments, the pH of the suspension was reversed to neutral (pH = 7.8) by addition of HCl in calibrated amounts after high pH incubation. For EPR measurements, thylakoids were suspended in the above medium with 50 mM glycylglycine (pH = 7.8) at 2 mg Chl/ml, and the pH was raised by NaOH or reversed by HCl added in a predetermined amount.

Thermoluminescence measurements were done as described in Ref. 10 with a heating rate of 0.7°C/s. Samples were preilluminated with continuous white light (0.7 mW/cm^2) for 1 min and relaxed in darkness for 5 min at room temperature to ensure a reproducible distribution of Q_B^-/Q_B and S_0/S_1 in the initial dark-adapted condition. In high pH experiments the preillumination and dark-adaptation took place at neutral pH (7.5–7.8) to avoid alkaline photoinactivation. Thermoluminescence was excited by a series of xenon flashes (4 μs, 2 J) at an interval of 1 s at 2°C. DCMU-treated samples were excited by a single flash given at −5°C.

Flash oxygen yield was measured at 23°C with a Joliot-type O_2-electrode [14]. The illuminating xenon flash (4 μs, 2 J) train was provided by a Sugawara MS-230 stroboscope with a repetition frequency of 1 Hz. Samples were preilluminated and then dark-adapted as indicated above. After adjusting the pH to a required value in the dark, the thylakoids were applied to the electrode surface under very dim green light, then incubated in complete darkness for 3 min before the flashes were fired. No artificial acceptor was used.

Protein composition was analyzed by SDS-polyacrylamide gel electrophoresis in a buffer system of Ref. 15 containing 6 M urea as in Ref. 16. The gels were stained in 0.1% Coomassie brilliant blue R-250. The densitograms of the stained gels were obtained with a Shimadzu dual-wavelength chromatoscanner (CS-900) equipped with a microcomputer system (Shimadzu, Chromatopac C-R3A) for peak area calculation.

The abundance of Mn was determined by a Shimadzu atomic absorption spectrometer (AA-640-13) equipped with a graphite furnace atomizer (GFA-3) as in Ref. 16. The EPR spectrum of Mn was measured at room temperature with a JEOL EPR spectrometer (JES-FE1XG) as described in Ref. 16 at 9.45 GHz with a microwave power 30 mW, modulation amplitude 20 G and time constant 1 s.

Results

The glow curves of isolated thylakoids when excited by short flashes exhibit a characteristic band, so-called B band, with a peak position at around 30°C [17]. The B band originates in the radiative recombination of positive and negative charges of the oxidized S_2 and S_3 states of the water-oxidizing enzyme and Q_B^-, the semireduced form of the secondary quinone acceptor of PS II, respectively [10,11]. Thus the amplitude of the B band is proportional to the number of centers having $S_2Q_B^-$ and $S_3Q_B^-$ charge pairs after flashes, while its peak position reflects the energetic depth of the traps of the above charge pairs which in turn provide a measure of the redox span between the separated charges [18].

High pH conditions affected both the amplitude and peak position of the B band (Fig. 1). On raising the pH from 7.5 to 8.8 the amplitude of the B band after one or two flashes decreased and simultaneously the peak position was shifted from 33°C to 38–39°C (bottom and middle curves). Further pH raise caused gradual disappearance of

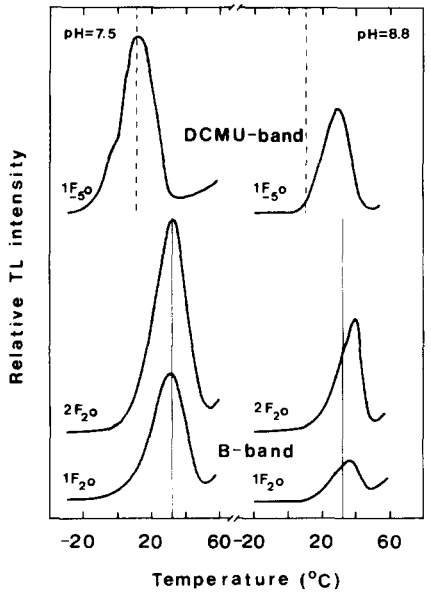

Fig. 1. Thermoluminescence glow curves of thylakoids excited by one or two flashes at +2 or −5°C as indicated by F on each curve. Glow curves measured at pH = 7.5, left side; at pH = 8.8, right side; in the presence 10 μM DCMU, upper curves; no further addition, bottom and middle curves.

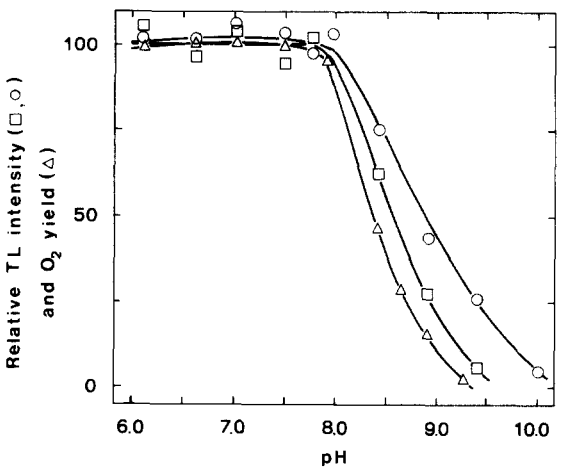

Fig. 2. Comparative pH dependence of the B-band amplitude and flash oxygen yield. The B band was excited at 2°C by one (□) or two flashes (○). Flash oxygen yield was measured with a Joliot-type electrode and the steady-state signal amplitude was plotted (△). The three curves were normalized for the values found between pH = 6.0–7.5

the B band (see later), but no further peak position shift was observed (data not shown). High pH also affected the thermoluminescence band in the presence of DCMU. The DCMU band is known to originate in the recombination of $S_2Q_A^-$ charge pair, where Q_A^- stands for the reduced primary quinone acceptor of PS II [10,11]. The DCMU band showed a surprisingly large shift in peak temperature from 11°C (pH = 7.5) to 30°C (pH = 8.8) (upper curves), while the B band showed a relatively small shift of about 6°C (middle and bottom curves). Since the positive charge carrier after one flash for both the B and DCMU bands are the same S-state (S_2), the different extent of peak position shift will be ascribed to a different effect of high pH on the redox potential of Q_A^- and Q_B^-.

Raising the pH above 8.0 results in gradual inactivation of O_2 evolution [19,20]. As the positive charges for the B band originate in the O_2 evolving apparatus [17], we may be able to follow the inactivation process by means of thermoluminescence. Fig. 2 compares the pH dependence of the B-band amplitude with that of oxygen yield. The steady state flash oxygen yield was nearly constant in the pH range of 6.0–8.0 in accordance with previous data [19,20], but declined steeply at higher pH and diminished totally at around pH = 9.2. The pH dependence of the B band amplitude showed roughly a similar course, but the extent of decrease, especially after two flashes, was distinctly less than that of flash oxygen yield. Obviously, high pH affects different S-state transitions in different ways, allowing the formation of S_2 and S_3 states for the B band, while inhibiting the S_3-to-S_4 transition indispensable for O_2 evolution.

The above assumption was checked by measuring the oscillation of the B-band amplitude at high pH. In those thylakoids which are preilluminated and dark adapted for 5–10 min, the oscillation of the B-band amplitude is known to reflect the changes in the concentration of S_2 and S_3 states during turnovers of the water-oxidizing enzyme starting from the initial distribution of 25% S_0/75% S_1 on the donor side and 50% Q_B/50% Q_B^- on the acceptor side of PS II [10,11]. In accordance with these previous results, the oscillatory pattern of the B band at pH = 7.8 exhibited maxima after the second and sixth flashes and minima after the fourth and eighth flashes (curve a in Fig. 3). Raising the pH to 9.1 resulted in a dramatic change in the oscillatory behavior of the B band.

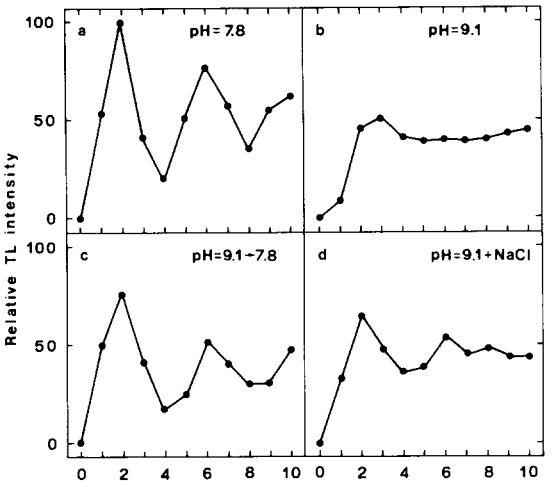

Fig. 3. Reversible inhibition of the oscillation of the B band by high pH. Thermoluminescence was excited by a variable number of flashes at +2°C: (a), measured at pH = 7.8; (b), measured after dark adaptation at pH = 7.8 followed by 3 min dark incubation at pH 9.1; (c), the same as (b) except that the pH of the suspension was returned to 7.8 just before the measurement; (d), the same as (b) except that 100 mM NaCl was present during incubation and measurement.

The oscillatory pattern was normal up to the second flash, but was almost completely abolished thereafter, showing a nearly constant amplitude independent of flash numbers. Based on the interpretation of the B-band oscillation [10,11] as reflecting the S-state turnover [21], this result shows that high pH inhibits S_3-to-S_4 transition. If the same inhibition occurs uniformly in all centers, the steady state amplitude of the B band at pH = 9.1 (after the second and higher flash numbers) should exhibit a level equal to or a little higher than the maximum amplitude after the second flash at pH = 7.8 due to the contribution by centers in S_0 in the initial dark-adapted condition. However, the steady-state amplitude at pH = 9.1 was found to be less than half of the maximum amplitude (at pH = 7.8). This implies that about 50%–60% of the centers were not able to emit the B band at pH = 9.1. The steady-state amplitude was further decreased by raising the pH above 9.1, by increasing the incubation time, or by illumination during incubation (data not shown).

Curves a and b in Fig. 3 also show that high pH affected the B-band amplitude after the 1st flash much more strongly than after two or more flashes (see also Figs. 1 and 2). One may attribute this phenomenon to the greater sensitivity of the S_2 state to high pH. However, this interpretation is unlikely, since the DCMU band was affected by high pH much less than the B band after one flash (see upper and bottom curves in Fig. 1). Since these two bands arise from $S_2Q_A^-$ and $S_2Q_B^-$ recombinations, respectively, i.e., from the charge pairs with identical oxidants (S_2) but different reductants (Q_A^-, Q_B^-), this difference will not arise from an effect on S_2 state, but from a change in charge stabilization properties at the level of Q_B.

These changes caused by mild alkaline treatment were found to be reversible, when the pH of the sample solutions was brought back to 7.8 after 3 min dark incubation at pH = 9.1. As shown by curve c in Fig. 3, the B band amplitude decreased by high pH was restored to a considerable extent, and the original period-four oscillation was regained. The pH jump back to 7.8 also reversed the peak position shift of the B and DCMU bands (not shown).

A reversal or prevention of the high pH effect was also possible by simply adding 100 mM NaCl in the sample solution. High pH conditions in the presence of NaCl caused the peak position shift of both the B and DCMU bands in a similar way as in the absence of NaCl (data not shown). However, a part of the high pH effects was prevented by NaCl as shown for the B-band oscillation (curve d, Fig. 3), in which the B-band amplitude underwent appreciable period-four oscillation with a peak position shifted to high temperature (39°C). These results suggest that the peak shift of thermoluminescence bands is not directly related to the high pH-induced damage on the capability of the centers to undergo normal S-state turnover. It is in turn of note that high pH reversibly changes the redox span of $S_2Q_B^-$, $S_3Q_B^-$ as well as that of $S_2Q_A^-$.

Fig. 4 shows the flash oxygen yield of the samples used for the above thermoluminescence measurements. On lowering the pH to 7.8 after 3 min dark incubation at pH = 9.1, the almost complete inhibition of flash oxygen yield (trace b) was largely reversed (trace c). Similarly to the thermoluminescence data, the presence of 100 mM NaCl partially prevented the inhibition of flash oxygen yield (trace d). We confirmed that the sensitivity of Joliot-electrode was not affected by NaCl. It is

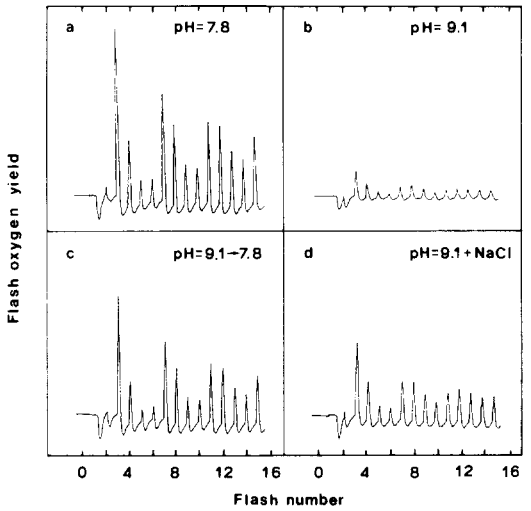

Fig. 4. Reversible inhibition of O_2 evolution by high pH in thylakoids. Flash-oxygen yield was measured at 23°C with a Joliot-type electrode under the same experimental conditions as indicated in Fig. 3: (a), at pH = 7.8; (b), at pH = 9.1; (c), at pH = 7.8 after 3 min dark incubation at pH = 9.1; (d), at pH = 9.1 in the presence of 100 mM NaCl.

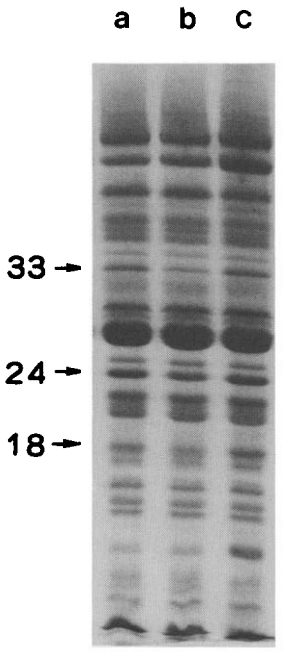

Fig. 5. Effect of high pH incubation on the protein composition of thylakoids. After incubation (a), at pH = 7.8; (b), at pH = 9.1; (c), at pH = 7.8 after 3 min dark incubation at pH = 9.1, thylakoids were briefly sonicated, spun down, and then equal amounts (on Chl basis) of the pellet were run on SDS-polyacrylamide gel electrophoresis.

noteworthy that when flash oxygen yield was measured over 20–25 flashes at pH > 8.8–9.0 a gradual decrease of the steady-state signal was seen (data not shown). This would probably reflect the light-accelerated inactivation at high pH [1,4].

The irreversible inactivation of O_2 evolution by high pH is considered to be caused by the release of functional Mn in thylakoids [4,5]. In O_2-evolving PS II particles, the loss of O_2 evolution caused by alkaline wash is also accompanied by release of Mn and the three peripheral proteins [6,7]. We attempted to check whether our partially reversible inhibition of O_2 evolution and the B-band oscillation will involve any release of peripheral proteins and/or membrane bound Mn.

Thylakoids were incubated at pH = 7.8 or 9.1 for 3 min in the dark, briefly sonicated to break up the membranes to allow any proteins released in the lumens to move into the bulk of the medium. The sonicated samples were pelleted, resuspended in a medium of pH = 7.8 and the protein composition was analyzed by SDS-polyacrylamide gel electrophoresis. As Fig. 5 shows, after incubation at high pH the contents of 33-kDa protein (and to a less extent the 24- and 18-kDa proteins) was decreased (trace b) compared with that after incubation at pH = 7.8 (trace a). When the pH had been reversed to 7.8 before sonication, the protein release was partially suppressed (trace c). Sonication at pH = 7.8 (control condition) removed about 20% of the 33-kDa protein (not shown), but this may not much affect the above qualitative conclusion that our mild alkaline treatment enhances the liberation of peripheral proteins.

The effect of high pH on Mn content was also investigated. Thylakoids were treated in three different ways as described above, and then the Mn abundance was measured for the pellet and supernatant. The Mn content of the pellet from high pH-treated samples was markedly less than that from the samples kept at, or returned to pH 7.8 (Table I), indicating that our mild alkaline treatment results in partial release of membrane-bound Mn. The Mn abundance of the supernatant was in a complementary relation to that of the pellet, and sum of the amounts in the pellet and supernatant was about 6.7 Mn/400 Chl at each pH. This value verifies the validity of our Mn determination.

The release of membrane bound Mn at high pH

TABLE I

REVERSIBILITY OF THE HIGH pH EFFECT ON VARIOUS CHARACTERISTICS CORRELATED WITH THE O_2-EVOLVING ACTIVITY

All the data shown are the averages of 6–8 independent measurements with the indicated standard deviation.

	Flash-oxygen yiled [a]	B-band amplitude [a]	Abundance of membrane-bound 33 kDa protein [b]	Mn-abundance [c] (atoms per 400 Chl)	EPR Mn signal amplitude [d]
pH 7.8	100±7	100±11	83±19	72 ±5 (4.8±0.3)	100±20
pH 9.1	11±5	40± 5	35± 9	51 ±8 (3.3±0.5)	173±22
pH 9.1 → 7.8	62±6	81± 8	80±15	64 ±6 (4.3±0.4)	118±25

[a] O_2 evolution and B-band amplitude were determined as in Figs. 1–4.

[b] The amounts were estimated from peak areas on the densitograms in Fig. 5, and normalized for 47 plus 43 kDa proteins as inner standard. About 17% of the protein was lost by the treatment under the control conditions (pH = 7.8).

[c] Samples were the same as those used for SDS-polyacrylamide gel electrophoresis analysis. The total Mn abundance in the original thylakoids was 6.7 Mn/400 Chl, about 30% of which were lost by the treatment under the control condition (pH = 7.8).

[d] Sample thylakoids were treated in the same way as those for thermoluminescence and O_2 evolution measurements. Signal amplitudes were corrected for sensitivity change due to different amount of HCl added to control the pH values.

was further confirmed by measuring the EPR signal of hydrated Mn. Again, the amount of free, EPR detectable, Mn was significantly increased after mild alkaline treatment, and the increase was reversed to a large extent by lowering the pH back to 7.8. These, and the other results, are summarized in Table I.

Discussion

The results in this paper show that mild alkaline incubation of thylakoids reversibly inhibits the functioning of the water-oxidizing system, in terms of flash oxygen yield and thermoluminescence B-band oscillation involving an interruption of S-state transition at S_3 to S_4.

The optimal O_2 evolution requires the presence of functionally active Mn [22,23], Cl^- [24,25] and the 33 kDa (as well as the 24 and 18 kDa) peripheral protein(s) [26,27]. Thermoluminescence enables us to monitor many of these factors, since the emission of the B band depends on the presence of functional Mn in the water-oxidizing enzyme [9,28] and the period-four oscillation of its amplitude requires an undistrubed S-state turnover [28].

From the distinct difference found between the extent of inhibition of O_2 evolution and the B-band amplitude, we can conclude that the primary event of high pH inactivation is not the release of Mn but the release of 33 kDa peripheral protein (or perhaps the depletion of Cl^-). The release of the protein will result in the inhibition of S-state turnover at the S_3-to-S_4 transition causing the complete loss of O_2 evolution and interruption of the B-band oscillation after the 2nd flash. The loss of 33 kDa protein would also cause the release of functional Mn as a secondary event, which would in turn result in a gradual (but reversible) decrease in B-band amplitude leading eventually to a complete and irreversible loss of thermoluminescence capability and disruption of electron flow between the water-oxidizing enzyme and PS II reaction center [29] during prolonged incubation at high pH. This view is supported by the results of Maison-Peteri et al. [5] that $MgCl_2$, which promotes the release of the peripheral proteins [16], accelerated the inactivation of O_2-evolving system by dark alkaline treatment.

It has also been reported that Mn-preserving extraction of the three peripheral proteins results in the loss of O_2 evolution followed by slow ($t_{1/2}$ = 2–4 h) release of about half of the Mn during incubation in a low salt medium [12,30]. The faster Mn release observed in this study suggests that alkaline conditions not only directly induce the

release of peripheral proteins, but also indirectly accelerate the release of Mn. A possible explanation for this effect is the well-known ability of high pH to facilitate Cl^- depletion [24,25] which, in turn would accelerate Mn release [31]. This reasoning is supported by the findings that the presence of 100 mM NaCl prevented the high pH effects on the B-band amplitude and its oscillation (Fig. 3), and O_2 evolution (Fig. 4). The effect of Cl^- depletion on the S-state turnover is not fully clarified yet, but a very recent result by Homann, P.H., Gleiter, H., Ono, T. and Inoue, Y. (unpublished results) confirms the earlier suggestion by Sinclair [32] that the Cl^- requiring step is the S_3-to-S_4 transition rather than the S_2-to-S_3 transition [33,34]. The results by Homann et al. agree well with our results. Regarding the role of 33 kDa peripheral protein in photosynthetic O_2 evolution, the present results are a confirmation with intact thylakoid system of the finding by Ono and Inoue [12] with purified PS II particles that the release of 33 kDa protein causes interruption of S-state turnover at the S_3-to-S_4 transition.

Besides these effects on the donor side of PS II, high pH seems to have another action site on the acceptor side. The different response of thermoluminescence bands to high pH found between $S_2Q_A^-$ (DCMU band) and $S_2Q_B^-$ (B band) recombinations in terms of both amplitude suppression (80% for the B band, while 50% for the DCMU band) and peak position shift (6°C for the B band, while 19°C for the DCMU band) (see Fig. 1) may indicate the high pH influence on the redox and charge stabilization properties of the primary (Q_A) and/or secondary (Q_B) quinone acceptors of PS II. Further experiments are obviously needed to clarify this point.

The reversible inhibition found for our mild alkaline conditions can be considered as the first step of the well-known irreversible inactivation of O_2-evolving system by high pH [1–5]. The irreversibility of this process is probably caused by the inability of the released Mn to bind back to the functional site either because the Mn becomes diluted due to diffusion out of the thylakoid lumen, or because high pH damages the Mn binding site.

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