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Effect of chloride ions on the S-state distribution and deactivation kinetics in preparations of the cyanobacterium *Anacystis nidulans*

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The roles of Ca^{2+} and Cl^- on the photosynthetic O_2 yield under flash illumination have been examined in EDTA-washed preparations of the cyanobacterium *Anacystis nidulans*. Especially the effect of Cl^- deficiency on the O_2 yield and on the S-state distribution was analyzed. As the results show, omission of both Ca^{2+} and Cl^- (Mn^{2+} present) almost totally inhibited O_2 evolution. When Ca^{2+} was replaced by Na^+, a substantial reduction of the O_2 yield was observed, but only a minor change in the S-state distribution occurred. However, when Cl^- was displaced by NO_3^-, which is equivalent to Cl^- deficiency of the water-splitting complex, a substantial reduction of the O_2 yield and in addition a significant change in the S-state distribution was observed. The comparison of deactivation kinetics in NO_3^- containing samples with those in control samples indicated that Cl^- deficiency allowed accumulation of oxidizing equivalents up to the S_3 state but modified the final step of O_2 evolution. Moreover, those centers which advanced to the S_3 state in the absence of Cl^- deactivated in a special way which involved a faster deactivation of S_2 and an increased formation of S_{-1}.

Introduction

The O_2-evolving complex of Photosystem II catalyzes the oxidation of two water molecules to one dioxygen molecule by four successive photoreactions. Thus, illumination of dark-adapted photosynthetically active material results in a damped oscillation with a periodicity of four [1,2]. However, when such flash patterns are analyzed according to the four-state Kok model, a substantial abnormality can be observed under the first flash in some preparations [3–5], although not in all [6]. It appears that chloroplast preparations in general show a better fit in the four-state Kok model than algae or algal preparations. This abnormality under the first flash was originally thought to be due to an especially high level of double hits occurring under the first flash [7]. However, Thibault [3] was recently able to demonstrate that this abnormality would disappear if a contribution of an additional S-state, which was called S_{-1}, was assumed to be present in the initial dark population of S-states. S_{-1} would be more reduced than S_0 according to definition. The designation of S_{-1} was chosen according to Velthuys and Kok [8]. In this model S_3 deactivates to S_0 and S_2, and S_2 deactivates to S_1 and S_{-1} in different proportions in the dark.

Previously we have shown that photosynthetic O_2 evolution in EDTA-washed preparations of the cyanobacterium *Anacystis nidulans* requires the cations Mn^{2+} and Ca^{2+} [9,10]. In addition to these cations, the anion Cl^- (or Br^-) was necessary for photosynthetic O_2 evolution [11]. All other tested anions were inhibitory when the O_2 evolution was measured in continuous light. In this

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paper we examine the influence of various cations and anions on the O_2 evolution under flash illumination in EDTA-washed preparations of *A. nidulans*. Especially, the effect of Cl^- deficiency on the O_2 yield and on the S-state distribution was analyzed.

Materials and Methods

A. nidulans (Synechococcus leopoliensis) B 1402-1 was obtained from the Sammlung von Algenkulturen, Universität Göttingen. The growth of the cells, the preparation of the lyophilized and lysozyme-treated cells of *A. nidulans* and the washing with EDTA are basically the same as described previously [10]. The *Anacystis* cells were harvested after 2 days by centrifugation for 15 min at $3000 \times g$. The cells were washed with 200 ml distilled water and resuspended in 15 ml 0.02 M Hepes buffer (pH 7)/5% sucrose/40 mM $MgCl_2$ (100 µl cells/ml). The sample was lyophylized for about 2 h and then resuspended in 0.02 M Hepes buffer (pH 7)/ 40 mM $MgCl_2$. To 15 ml of this suspension were added 90 mg lysozyme (6 mg lysozyme/ml suspension) and 15 µg DNAase and 150 µg RNAase. The sample was kept at 25°C for 90 min in the dark with shaking and was centrifuged for 10 min at $7700 \times g$. The subsequent steps were performed at 0–5°C. After centrifugation the sample was washed with the following solutions. Once with 30 ml 0.02 M Hepes buffer (pH 7)/40 mM $MgCl_2$; twice with 30 ml 0.02 M Hepes buffer (pH 7)/5% sucrose/10 mM EDTA and once with 30 ml 0.02 M Hepes buffer (pH 7)/5% sucrose. The sample was resuspended in 0.01 M Hepes buffer (pH 7)/5% sucrose to give a chlorophyll content of about 0.5 mg/ml. When the sample was washed with EDTA a 10 min incubation period was allowed before centrifugation. The O_2 evolution under short light flashes was measured as described in Ref. 10. O_2 evolution as the consequence of short saturating light flashes was measured with a three-electrode system described earlier [12]. Flashes of white light were produced by a Xenon lamp (Stroboscope 1539 A from General Radio), the flash duration was 8 µs. Usually 15 flashes spaced 300 ms apart were given. The S-state distribition was calculated from the O_2 amplitudes of the first four flashes in the respective flash pattern [3,4,13]. With these four amplitudes we have made a mathematical fit on the 'shape factors' by means of the recurrence law established by Lavorel [14]. The reaction mixture contained, in a total volume of 1 ml, 50 µmol Hepes-NaOH (pH 7.0) and the *Anacystis* preparation containing 50–60 µg chlorophyll. Cations and anions were added as indicated in the legends to the figures and tables. 0.5 ml of the mixture was used on the electrode.

Results

Influence of cations and anions on the O_2 yield under flash illumination

O_2 evolution as a consequence of short saturating light flashes was measured in EDTA-washed preparations of *A. nidulans* as described previously [10]. In Fig. 1 the dual requirement of $MnCl_2$ and $CaCl_2$ is shown for photosynthetic O_2 evolution in flash light experiments. Addition of $MnCl_2$ alone (Fig. 1, curve B) did not result in activation of O_2 evolution. (Addition of 0.1 mM $MnCl_2$ was saturating for Mn^{2+} but not for Cl^-.) The combination of 0.1 mM $MnCl_2$ and 50 mM $CaCl_2$ (Fig. 1, curve A) was optimal for O_2 evolution in these preparations as shown previously [10]. This condition will be referred to as control condition throughout the paper (Fig. 1, curve A or Fig. 3, curve A). In Fig. 2 we demonstrate the requirement of the O_2 evolution for the anion Cl^- and the cation Ca^{2+} (in addition to Mn^{2+}), since $Ca(NO_3)_2$ (Fig. 2, curve A) or NaCl (Fig. 2, curve B) caused only a small activation of the O_2 evolution in the presence of Mn^{2+} (about 10% of the O_2 yield of the control). The experiments of Fig. 1 and 2 were done with the same *Anacystis* preparation and can therefore be compared directly.

Because of the dual requirement of Ca^{2+} and Cl^- (besides Mn^{2+}) for O_2 evolution, it is difficult to exmaine the Cl^- effect independently from the cation effect, since addition of cation always implies addition of an anion. We have previously shown that addition of other anions, such as NO_3^-, causes reduction of the O_2 evolution, even in the presence of Cl^- [11]. Oxygen measurements in chloride-deficient, nitrate-containing samples by Sinclair [15] support our observation. Therefore, we have investigated the influence of Cl^- on the

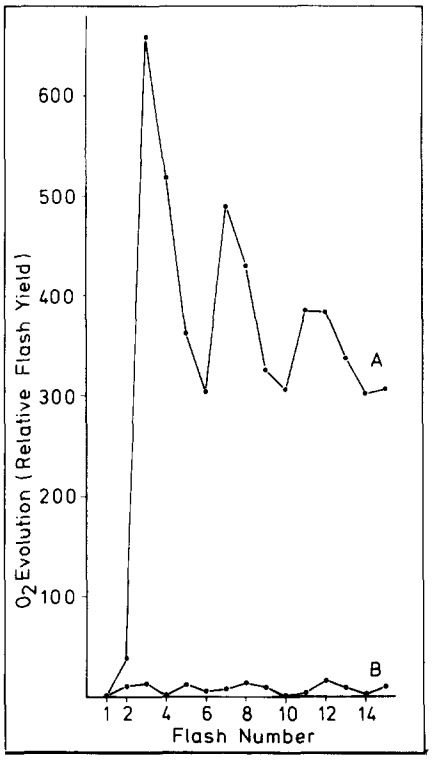

Fig. 1. Effect of $MnCl_2$ and $CaCl_2$ on O_2 yield. EDTA-washed preparation of *A. nidulans* was suspended in Hepes buffer (pH 7) as described under Materials and Methods. In addition were added: (A) 0.1 mM $MnCl_2$ and 50 mM $CaCl_2$; (B) 0.1 mM $MnCl_2$.

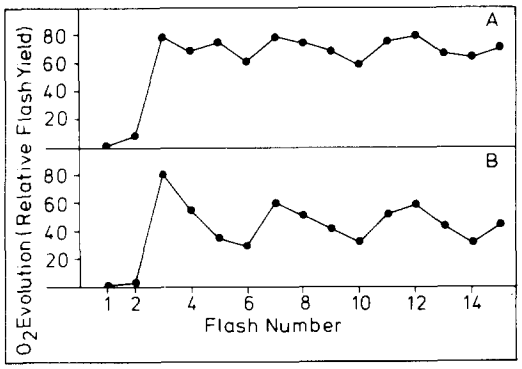

Fig. 2. Effect of $Ca(NO_3)_2$ or NaCl on O_2 yield. Conditions as in Fig. 1. (A) 0.1 mM $MnCl_2$ and 50 mM $Ca(NO_3)_2$ and (B) 0.1 mM $MnCl_2$ and 100 mM NaCl. The experiments of Fig. 1 and 2 were done with the same *Anacystis* preparation and can therefore be compared directly.

flash pattern in experiments where the O_2 evolution was initially measured under optimal conditions (presence of $MnCl_2$ and $CaCl_2$). In addition NaCl (as a control for the effect of Na^+) or $NaNO_3$ (for substitution of Cl^- with NO_3^-) was added. Na^+ was used as the counter-ion, because Ca^{2+} becomes inhibitory at higher concentrations [11]. As we have shown earlier, Na^+ can displace Ca^{2+} to only a minor extent, whereas NO_3^- ions effectively displace Cl^- ions [11]. Fig. 3 shows that addition of NaCl had only a minor effect on the flash pattern, as expected. However, when the flash patterns A and C of Fig. 3 were compared, a significant effect of NO_3^- on the O_2 evolution could be observed. NO_3^- decreased the O_2 yield and also caused a drastic change in the flash pattern. The quantitative evaluation of these flash patterns is discussed in the next sections.

Calculation of the S-state distribition

When the O_2 evolution pattern of the control (Fig. 1, curve A) was analyzed according to the four-state Kok model, no satisfactory results were obtained (Tables I and II). Such a comparison has been described in detail in earlier publications [13,16]. The results presented here indicated that

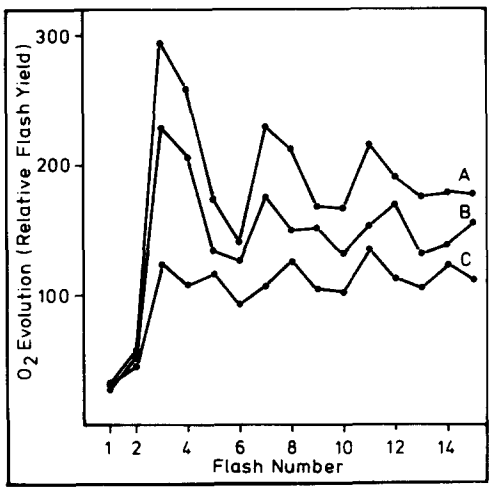

Fig. 3. Displacement of Cl^- by NO_3^-. Conditions as in Fig. 1. (A) The O_2 yield was measured under optimal conditions: 0.1 mM $MnCl_2$ and 50 mM $CaCl_2$; (B) 20 mM NaCl was added in addition to 0.1 mM $MnCl_2$ and 50 mM $CaCl_2$ as a control for the effect of Na^+; (C) 20 mM $NaNO_3$ was added in addition to 0.1 mM $MnCl_2$ and 50 mM $CaCl_2$ to investigate the effect of Cl^- displacement by NO_3^-.

TABLE I

S-STATE DISTRIBUTION IN THE FIVE-STATE KOK MODEL

S-state distribution (%) in the five-state Kok model was calculated from flash sequences obtained after 20 min dark adaptation. The first four samples are identical to those of Figs. 1 and 2. Δ%: relative quadratic deviation. A negative percentage represents mathematically 'the equivalent situation' and is caused when the fitting system normalized the sum of S-states to 100%. The low negative values in this table represent a value close to zero within the error deviation of the fit.

Addition	S_{-1}	S_0	S_1	S_2	S_3	Misses α	Double hits γ	Δ%	Δ% belonging to the fit in the four-state Kok model
0.1 mM $MnCl_2$ 50 mM $CaCl_2$	29.2	28.9	49.5	−8.6	1.0	7.7	9.0	1.8	7.2
0.1 mM $MnCl_2$	30.1	5.3	58.4	8.3	−2.1	15.0	23.0	23.0	–
0.1 mM $MnCl_2$ 50 mM $Ca(NO_3)_2$	60.8	1.7	47.3	−13.3	3.5	5.5	15.4	5.2	14.3
0.1 mM $MnCl_2$ 100 mM NaCl	19.6	26.1	56.6	−2.5	0.1	8.0	3.9	3.5	9.7
Untreated intact cells of *A. nidulans*	31	27	42	−0.5	0.5	9	6	1.1	5.0

the flash pattern was more reduced than patterns which have been described for plant chloroplasts [6]. This was further supported by a deviation of the ratio Y_5/Y_6 from ratios given in the literature [17]. Therefore, calculation of the S-state distribution in the five-state Kok model according to Thibault and Thiery [4] was advised. The results of such calculations in the five-state Kok model are given in Tables I and II.

The S-state distribution of the control pattern showed that the initial dark state population contained more than 20% S_{-1}. Omission of $CaCl_2$ caused almost total inhibition of O_2 evolution, but the small remaining O_2 yield (probably due to

TABLE II

S-STATE DISTRIBUTION IN THE FIVE-STATE KOK MODEL

S-state distribution (%) in the five-state Kok model was calculated from flash sequences obtained after 20 min dark adaptation. The samples are identical to those of Fig. 3. Δ%: relative quadratic deviation.

Addition	S_{-1}	S_0	S_1	S_2	S_3	Misses α	Double hits γ	Δ%	Δ% belonging to the fit in the four state Kok model
0.1 mM $MnCl_2$ 50 mM $CaCl_2$	22.1	33.9	40.8	−1.1	4.3	6.2	9.4	2.1	7.6
0.1 mM $MnCl_2$ 50 mM $CaCl_2$ 20 mM NaCl	14.7	36.9	46.0	−2.5	4.9	11.6	10.5	4.3	9.4
0.1 mM $MnCl_2$ 50 mM $CaCl_2$ 20 mM $NaNO_3$	43.7	8.6	39.8	−1.3	9.2	0	17.3	7.3	15

small amounts of $CaCl_2$ which remained in the preparation after the washing procedure) gave a S-state distribution which corresponded essentially to the pattern obtained with the control, although a considerable relative quadratic deviation was observed as would be expected with such a low O_2 yield. Substitution of $CaCl_2$ by $Ca(NO_3)_2$ lowered the O_2 amplitude to about 10% of the control and also had a drastic effect on the S-state distribution. The contribution of the reduced state S_{-1} increased to about 60% and some metastable S_3 appeared, while the contribution of S_0 dropped to about 2%. When $CaCl_2$ was replaced by NaCl, the S-state distribution was very similar to the distribution obtained with the control, although the O_2 amplitude was also lowered to about 10% of the control. Only a shift to a slightly more oxidized sequence than the control was observed. The calculation in the five-state Kok model of these remaining O_2 amplitudes, which presented about 10% of the control in the samples with NaCl or $Ca(NO_3)_2$, was no problem, since the O_2 amplitudes could be accurately determined. Within this size of O_2 amplitudes we have repeatedly made the observation that NaCl gave a decreased and normal pattern, while $Ca(NO_3)_2$ gave a decreased and abnormal pattern as compared to the control pattern (Table I). This abnormal pattern was observed regardless whether the remaining amplitude corresponded to approx. 10% (Fig. 2A) or approx. 35% (Fig. 3C) of the control.

Effect of Cl^- deficiency on the deactivation of the S-states

The above results showed that omission of $CaCl_2$ or replacement of Ca^{2+} by Na^+ and replacement of Cl^- by NO_3^- drastically reduced the O_2 yield. However, only the latter condition (replacement of Cl^- by NO_3^-) had any significant effect on the S-state distribution. In order to obtain further information on the effect of Cl^- on the S-states, we have followed the deactivation of the S-states in the dark under those three conditions which are shown in Fig. 3 and Table II. The results given in Figs. 4–6 are based on the simple assumption that under steady-state conditions the S-state distribution is $S_0 = S_1 = S_2 = S_3 = 25\%$ and no S_{-1} is present.

The deactivation of the control (Fig. 4) could basically be considered normal except that the deactivation of all states was much slower than normally observed [18]. This slow deactivation of the higher S-states was not a consequence of the particle preparation, but was also observed with whole *Anacystis* cells (unpublished results). Other cyanobacteria as, for example, *Oscillatoria chalybea* [13] or thylakoids obtained from the early stages of greening oat etioplasts [19] have also been reported to have slow decay times. The deactivation pattern of the control also showed that S_{-1}

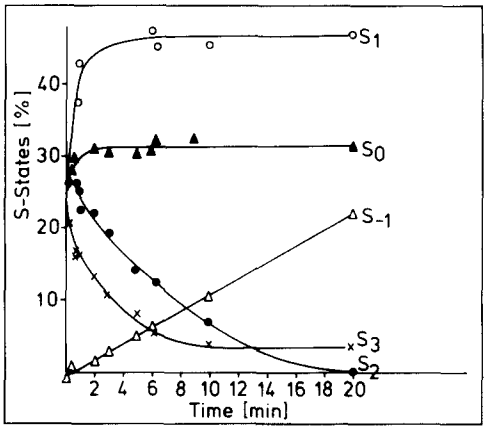

Fig. 4. Deactivation kinetics in presence of $MnCl_2$ and $CaCl_2$. Deactivation of the S-states was analyzed in the presence of 0.1 mM $MnCl_2$ and 50 mM $CaCl_2$. The sample is the same as in Table II, line 1, and Fig. 3, curve A.

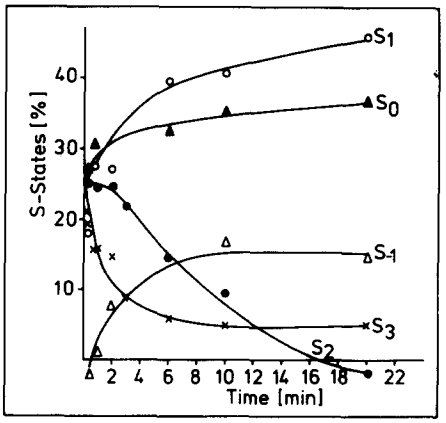

Fig. 5. Deactivation kinetics in presence of $MnCl_2$, $CaCl_2$ and NaCl. Deactivation of the S-states was analyzed in the presence of 0.1 mM $MnCl_2$, 50 mM $CaCl_2$ and 20 mM NaCl. The sample is the same as in Table II, line 2 and Fig. 3, curve B.

was continuously formed in the dark as is characteristic for this state [3]. Fig. 5 gives the deactivation pattern for the effect of adding NaCl (in addition to $MnCl_2$ and $CaCl_2$). The deactivation essentially corresponded to that of the control with the minor difference that the system accumulated less S_{-1} (about 15% S_{-1}) than the control (about 20% S_{-1}).

Adding $NaNO_3$ in addition to $CaCl_2$ and $MnCl_2$ (Fig. 6) shows that the deactivation of S_2 became much faster than in the control and was now faster than S_3. Under control conditions S_3 deactivated more quickly than S_2, which is in agreement with the coherent Kok model [2]. Therefore it appeared that adding NO_3^- (which is equivalent to Cl^- deficiency) had an effect on S_3 by blocking the deactivation of S_3 to S_0. The kinetics of the remaining decay route to S_2 apparently were also changed and as a consequence S_3 deactivated much slower than S_2 over the entire time. The results also show that S_{-1} accumulated to about 45% of all the S-states in 2 min, while very little S_0 was formed, which permits the conclusion that the deactivation of S_3 to S_0 was blocked. Thus, the increased accumulation of S_{-1} under Cl^- deficiency seemed to be a consequence of the blocked deactivation of S_3 to S_0. Since S_3 could only deactivate to S_2, more S_2 was formed and this S_2 in turn deactivated to S_1 and S_{-1} (as is normal), but the ratio of these two states was drastically changed in favor of S_{-1}. The conclusion that S_{-1} originated from S_2 and not from S_0 (as could have superficially been concluded from the S-state distribution pattern given in Table II, line 3) was supported by the observation that $(S_1 + S_{-1} + S_2)/2$ remained constant over a reasonable long time period. This result showed that S_2 deactivated to give S_1 or S_{-1} [3]. Since the course of S_1 was practically normal, the deactivation of S_2 led essentially to S_{-1}. In summary, our results indicate that Cl^- deficiency created a block at S_3 which could now only deactivate to S_2, and in turn S_2 preferentially deactivated to S_{-1} under these conditions.

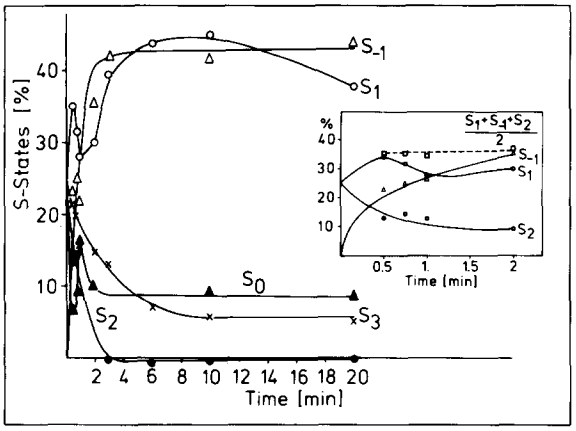

Fig. 6. Deactivation kinetics in presence of $MnCl_2$, $CaCl_2$ and $NaNO_3$. Deactivation of the S-states was analyzed in the presence of 0.1 mM $MnCl_2$, 50 mM $CaCl_2$ and 20 mM $NaNO_3$. The sample is the same as in Table II, line 3, and Fig. 3, curve C.

Discussion

The results in this and previous [9–11] papers clearly demonstrate that photosynthetic O_2 evolution in EDTA-washed preparations of *A. nidulans* requires the addition of Mn^{2+}, Ca^{2+} and Cl^-. Since cyanobacteria [20–22] do not seem to contain the extrinsic peptides of about 16 and 24 kDa which are present in plant Photosystem II preparations, and which are involved in high-affinity binding of Ca^{2+} and Cl^- to the water-splitting enzyme [23], the requirement of relatively high concentrations of Ca^{2+} and Cl^- for O_2 evolution can be shown in *Anacystis* preparations without any further treatment. Therefore, these preparations are very suited for such studies. We were mainly interested to see what influence Ca^{2+} or Cl^- deficiency would have on the S-state distribution. As the results show, omission of both Ca^{2+} and Cl^- (Mn^{2+} added) practically totally inhibited O_2 evolution. In this case practically no O_2 evolution is measurable (Fig. 1B) and the remaining O_2-evolution exhibits a pattern with an increased miss parameter (Table I). This seems to indicate that the water-splitting enzyme is totally inactive in the absence of Ca^{2+} and Cl^-. Replacement of $CaCl_2$ by NaCl reduced the O_2 amplitude to about 10% of the control, but had no significant effect on the S-state distribution, which means that the properties of the centers had been modified. This indicated that, although Na^+ was much less efficient than Ca^{2+}, all the centers were active and basically showed the same properties as the

control. Moreover, the pattern observed had an unchanged miss parameter, an observation which, together with the unchanged S-state distribution, seemed to exclude that the remaining O_2 amplitude was due to a few but normally functioning centers (compare Table I, samples 1 and 4). However, displacing of Cl^- with NO_3^- which is equivalent to Cl^- deficiency of the water-splitting enzyme, showed – in addition to a substantial reduction of the O_2 amplitude – a significant change in the S-state distribution pattern in which the miss parameter again was not increased in comparison to the control (Tables I and II). This shows that the redox properties of the reaction centers have been modified by chloride deficiency, as described very recently by Homann et al. [24]. From deactivation kinetics of this modified system it could be concluded that Cl^- deficiency allowed accumulation of oxidizing equivalents up to S_3 but blocked the final step of O_2 evolution. Moreover, the centers which advanced to the S_3 state in the absence of Cl^-, seemed to deactivate in a special way to give more S_{-1} than S_1. In addition to blocking the conversion of S_3 to S_0, Cl^- deficiency also caused a significant acceleration of the decay rate of S_2.

Our suggestion that the block occurred at the S_3 state under Cl^- deficiency is in good agreement with experiments by Sinclair [15], who used a modulated O_2 electrode and who used anions, such as NO_3^- or CH_3COO^- to displace Cl^-. Sinclair also suggested that the S_3 to S_0 transition is a Cl^--requiring step. Ono and Inoue [25] showed that in manganese-containing spinach Photosystem II preparations which were depleted of three peripheral peptides (33, 24 and 16 kDa) by $CaCl_2$ washing, the S_3 to S_0 transition was blocked, while the preparations could still undergo the transitions from S_0 to S_3. Moreover, Dekker et al. [26] examined Photosystem II preparations from spinach after NaCl washing, which removed the 23 and 17 kDa peptides, and concluded that in such modified Photosystem II preparations the S_3 to S_0 transition was slowed down. However, Theg et al. [27] and Itoh et al. [28] found that only two oxidizing equivalents can be accumulated in Cl^--deficient pea thylakoids, indicating that S_2 is the critical state. Since the latter two groups used the anion SO_4^{2-} to replace Cl^-, a secondary effect of SO_4^{2-} (besides removing Cl^-) should be considered. SO_4^{2-} could possibly block bound Ca^{2+}. Sinclair [15] also noticed that SO_4^{2-} behaved differently as compared to NO_3^-. He suggested that SO_4^{2-} would just shut off the electron transport chain. This would be equivalent to omission of Ca^{2+} and Cl^- in our experiments.

The influence of Cl^- on O_2 evolution was observed as early as 1944 by Warburg and Lüttgens [29] and our present knowledge about the function of Cl^- has recently been reviewed by Critchley [30]. Although several groups have demonstrated in a number of ways that Cl^- is intimately involved in O_2 evolution, the role of Cl^- has remained uncertain. One of the suggestions for a possible role of Cl^- is that Cl^- could be a binding ligand for Mn^{2+} [29,31,32]. In our experiments Cl^- deficiency resulted in an inhibition of the conversion of S_3 to S_0, and as a consequence of a special deactivation of S_2, more of S_{-1} was formed as compared to control conditions. This is to our knowledge the first time that defined experimental conditions have been shown to lead to an increased formation of S_{-1} [16]. The question then of course arises as to what the state S_{-1} actually represents. According to definition, it is a more reduced state than S_0 [3,8]. However, it actually means that now the dark-adapted water-splitting enzyme requires preillumination by one flash before it can start the normal four successive photoreactions which lead to O_2 evolution. Since Mn^{2+} incorporation is a light-dependent step [33], it might be interesting to speculate that an increased amount of S_{-1} indicates that Mn^{2+} is not properly bound to the reaction center. The S-state distribution of the EDTA-washed *Anacystis* preparation shows the presence of more than 20% S_{-1}. Since we have removed part of the Mn^{2+} by EDTA washing [9,10], light is most likely required to incorporate the added Mn^{2+} into the reaction center. Then it might also be justified to speculate that removal or destabilization of the possible bridging ligand for Mn^{2+} [30–32] would further increase the state S_{-1}. This observation is actually made in our experiments when we displace Cl^- by addition of NO_3^-. This then would imply that the presence of S_{-1} in the dark population of S-states always indicates that the cofactors Mn^{2+} and Cl^- are not properly bound to the water-splitting center.

Experiments by various groups [15,25,26] as well as the experiments presented here show that Cl^- deficiency most likely only affects the S_3 state. As a consequence this would imply that this state plays a crucial role in the overall process of the water-splitting reaction. This is in agreement with recent experiments which seem to indicate that water oxidation takes place via a rapid concerted reaction during the S_3 to S_0 transition [34,35].

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