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Calcium content of oxygen-evolving Photosystem II preparations from higher plants. Effects of NaCl treatment

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The abundance of bound Ca^{2+} in four Photosystem II oxygen-evolving preparations from spinach and rice were determined after removal of contaminating Ca^{2+} with chelex 100 (Kashino, Y., Satoh, K. and Katoh, S. (1986) FEBS Lett. 205, 150–154). (1) Spinach membrane preparations which evolved oxygen at rates of 350–500 μmol per mg chlorophyll (Chl) per h contained, on average, 1.8 Ca^{2+} per 200 Chl, whereas a mean value of 2.1 Ca^{2+} per 200 Chl was obtained with more active spinach preparations, showing oxygen-evolving rates of 500–800 μmol per mg Chl per h. The most active membrane preparations, which evolved oxygen at rates of 750–1050 μmol per mg Chl per h, were isolated from rice seedlings. The rice preparations also contained 2.1 Ca^{2+} per 200 Chl. Thus, different activities of the three preparations cannot be related to difference in their Ca^{2+} abundance and the maximum number of Ca^{2+} needed to promote high rates of oxygen evolution is 2 Ca^{2+} per 200 Chl in higher plants. (2) Highly purified spinach oxygen-evolving complexes (Ikeuchi, M., Yuasa, M. and Inoue, Y. (1985) FEBS Lett. 185, 316–323) contained 1 Ca^{2+} per 50 Chl. (3) Treatment of the spinach membrane preparations with high concentrations of NaCl, either in the dark or light, caused no significant loss of the bound Ca^{2+}, although the treatment strongly inhibited oxygen evolution and the inhibition was considerably reversed by addition of 5 mM $CaCl_2$. Exposure of the NaCl-washed membranes to EGTA failed to reduce the amount of bound Ca^{2+}. Thus, inactivation of oxygen evolution by the salt wash is not related to release of Ca^{2+}. (4) The abundance of Ca^{2+} in spinach membrane preparations was not, or only slightly, affected by treatments with 1 mM NH_2OH, 1 M $MgCl_2$ or 0.8 M Tris, which solubilized either Mn or the three extrinsic proteins associated with the membranes, or both. It is concluded that the three proteins are not involved in the Ca^{2+} binding. The number of Ca^{2+} functioning in Photosystem II electron transport of higher plants is discussed.

Introduction

There are several lines of evidence suggesting that Ca^{2+} is an essential cofactor of photosynthetic oxygen evolution in higher plants and cyanobacteria [1–9]. In particular, effects of exogenously added Ca^{2+} on oxygen evolution has been extensively studied with PS II membrane preparations associated with three extrinsic proteins of 17, 23 and 33 kDa molecular mass classes. Removal of the 17 and 23 kDa proteins from the membranes by washing with high concentrations of NaCl is accompanied by a partial inactivation of oxygen evolution and the inhibition is largely reversed by addition of Ca^{2+} [10–14]. Illumination of samples during the NaCl wash causes a stronger

Abbreviations: Chl, chlorophyll; EGTA, ethylene glycol bis-(β-aminoethyl ether)-*N*,*N*′-tetraacetic acid; Mes, 4-morpholineethanesulphonic acid; PS II, Photosystem II.

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inhibition than the dark treatment and the restoration of the activity requires Ca^{2+} [14,15]. The Ca^{2+} demand for oxygen evolution was also found in highly purified oxygen-evolving complexes, which lack the 17 and 23 kDa proteins [16,17]. It is suggested that NaCl treatment inhibits oxygen evolution by extracting Ca^{2+} essential for PS II electron transport, and added Ca^{2+} restores the activity by rebinding to its original functional site [13,14]. Based on the Ca^{2+}-dependent reactivation of oxygen evolution and related reactions in NaCl-washed membrane preparations, several functional sites of the metal cation have been proposed [11,15,18–21].

It is emphasized, however, that evidence for the involvement of Ca^{2+} in oxygen evolution is still indirect. Release of Ca^{2+} by NaCl wash has not yet been confirmed by measuring the Ca^{2+} contents of the PS II membrane preparations before and after the treatment. Even the number of calcium atoms associated with PS II preparations from higher plants is a matter of controversy [11,22–24]. In view of accumulating data on the Ca^{2+} effect, it is crucially important to determine the number of Ca^{2+} needed for PS II electron transport and whether or not NaCl treatment solubilizes Ca^{2+} essential for oxygen evolution.

Recently, a simple procedure to determine Ca^{2+} bound to an oxygen-evolving preparation from the cyanobacterium *Synechococcus* sp. has been introduced [25]. The method involves treatment of sample suspensions with a chelating resin, chelex 100, to remove Ca^{2+} contaminating in the medium as well as the metal cations loosely and unspecifically associated with the preparations. Cyanobacterial PS II preparations highly competent in oxygen evolution contain one Ca^{2+} per Q_A [24–26], indicating that only one Ca^{2+} is needed for oxygen evolution in the cyanobacterium.

In the present work, the abundance of tightly bound Ca^{2+} in PS II membrane preparations from higher plants were measured with the chelex method. Three membrane preparations, which are widely different in the oxygen-evolving capacities, were used to examine whether there is any correlation between the activity and Ca^{2+} content of the preparations. The amount of Ca^{2+} bound to a highly purified oxygen-evolving complex from spinach was also measured. Then, effects of the NaCl wash and several other treatments of the PS II membranes on their Ca^{2+} contents were studied.

Materials and Methods

Spinach *(Spinacia oleracea* L.) was purchased from a local market. Rice (*Oryza sativa* L. var. Nipponbare) was grown for 5–7 weeks in a green house as described in Ref. 27.

Oxygen-evolving PS II membranes of spinach were prepared according to the method described by Kuwabara and Murata [28], except that 1 mM $MgCl_2$ was added to the isolation mediums (KM preparation *). The addition of $MgCl_2$ was effective in minimizing unspecific binding of Ca^{2+} [24]. The method described by Berthold et al. [29] was also used for preparation of PS II membranes from spinach and rice (BBY preparation *). Spinach thylakoid membranes were treated once with Triton X-100 at a detergent-to-chlorophyll weight ratio of 25 : 1 for 25 min in the dark. Rice membranes were treated for 10 min at a Triton X-100-to-chlorophyll ratio of 12 : 1. PS II membranes were collected by centrifugation, suspended in 0.4 M sucrose, 40 mM Mes/NaOH (pH 6.5), 10 mM NaCl and 5 mM $MgCl_2$ and stored in liquid nitrogen. Before use, the membranes were washed twice with, and finally suspended in, the suspending medium. Highly purified oxygen-evolving complexes were isolated from KM preparations by the procedure described by Ikeuchi et al. [16]. The complexes were suspended in the above medium, from which $MgCl_2$ was omitted, and stored at 77 K.

For NaCl wash, suspension of PS II membranes (2 mg Chl/ml) were diluted with an equal volume of concentrated NaCl to make the final NaCl concentration to 1–2 M and kept for 30 min at 0 °C either in the dark or light (1500 lx). Then, the membranes were collected by centrifugation at $35\,000 \times g$ for 10 min and washed once with the suspending medium. For treatments with $MgCl_2$ and NH_2OH, membrane suspensions were diluted with an equal volume of 2 M $MgCl_2$ or 2 mM NH_2OH. The medium used for Tris treatment

* KM is called after Kuwabara and Murata [28]; BBY is called after Berthold, Babcock and Yocum [29].

contained 0.8 M Tris/HCl (pH 8.5). The three treatments were carried out for 30 min at 0°C under room light.

Ca^{2+} was determined with a Shimadzu atomic absorption spectrophotometer (AA640-01) equipped with a graphite furnace atomizer (GFA-2). Calibration curves were constructed daily with a standard Ca^{2+} solution (Wako Pure Chemical Industries) prior to measurements. Contaminating Ca^{2+} was removed as described in Ref. 25. In short, PS II preparations (150–200 μg Chl/ml) were suspended in 0.2 M sucrose, 20 mM Mes/NaOH (pH 6.5), 5 mM NaCl and 2.5 mM $MgCl_2$ and, to 0.8 ml of the suspension, 0.4 g of Chelex 100 was added. The suspension was gently shaken for 1 min and kept still for 2 min to allow the resins to sediment, then Ca^{2+} concentration of the supernatant was measured. The cycle of 1 min shaking and 2 min standing was repeated until a constant Ca^{2+} concentration was attained. The procedures do not affect the oxygen-evolving activity [24,25]. It is to be mentioned here that Triton X-100 is strongly adsorbed by the resin granules so that, when an excess of the sample was used, the suspensions became cloudy due to aggregation of the membranes. This strongly interferes with determination of the metal cations. Unless otherwise stated, Ca^{2+} contents presented are means with standard deviations, which were obtained from at least four separate preparations.

Oxygen evolution was measured at 27°C with a clark-type oxygen electrode. Reaction medium contained 0.4 M sucrose, 40 mM Mes/NaOH (pH 6.5), 10 mM NaCl and 5 mM $MgCl_2$. Electron acceptors used were 1 mM ferricyanide and 0.4 mM 2,6-dichloro-*p*-benzoquinone for spinach KM preparations and 2 mM 2,5-dimethyl-*p*-benzoquinone for BBY preparations. Oxygen evolution of purified oxygen-evolving complexes was determined in the same medium, to which 5 mM $CaCl_2$, 0.1% digitonin and 1 mM ferricyanide were supplemented.

Q_A was determined spectrophotometrically at 325 nm as described previously [30].

Chlorophyll concentration was determined according to the method of Arnon [31].

Results

Numbers of Ca^{2+} bound to Photosystem II membrane preparations

In the present work, Ca^{2+} contents of three different PS II membrane preparations were measured. PS II membranes prepared from spinach by the method of Kuwabara and Murata [28] usually had slightly less than 2 Ca^{2+} per 200 Chl, yielding a mean value of 1.8 per 200 Chl (Table I). Spinach PS II membranes prepared by the procedure of Berthold et al. [29] were slightly more abundant in Ca^{2+} than KM preparations. BBY preparations also showed higher rates of oxygen evolution than KM preparations. It appears therefore that higher rates of oxygen evolution in BBY preparations are related to their higher Ca^{2+} contents. However, close examination of the activity and Ca^{2+} content of individual samples revealed that oxygen-evolving activity varies mainly depending upon preparation procedures rather than their Ca^{2+} contents. Thus, BBY preparations having 2.0 Ca^{2+} per 200 Chl were significantly more active than KM preparations with the same Ca^{2+} abundance. PS II membranes isolated from leaves of rice seedlings were the most active preparations examined in the present work, showing oxygen-evolving rates of 750–1050 μmol per mg Chl per h. The rice preparation also contained 2.1 Ca^{2+} per 200 Chl. We have determined that Q_A, the first stable electron acceptor of PS II, is present per 190–230 chlorophyll in the PS II membrane preparations used here (see also Ref. 29). Thus, the number of Ca^{2+} needed for oxygen evolution is maximally two per PS II reaction center in higher plants.

TABLE I

Ca^{2+} CONTENTS AND RATES OF OXYGEN EVOLUTION IN THREE PS II MEMBRANE PREPARATIONS AND AN OXYGEN-EVOLVING COMPLEX

Materials	Preparations	Ca^{2+} per 200 Chl	μmol O_2 per mg Chl per h
Spinach	KM	1.8±0.5	350– 500
Spinach	BBY	2.1±0.1	500– 800
Rice	BBY	2.1±0.4	750–1050
Spinach	IYI [a]	4.4±0.8	700– 800

[a] IYI is called after Ikeuchi, Yuasa and Inoue [16].

Ca^{2+} content of a purified oxygen-evolving complex

Highly purified PS II complexes competent in oxygen evolution have been isolated from spinach [16,32], wheat [17] and *Synechococcus* [26,33]. *Synechococcus* preparations contain 0.7–0.9 Ca^{2+} per PS II and there is a good correlation between oxygen-evolution rates and Ca^{2+} contents, indicating that one Ca^{2+} associated with the complex is essential for oxygen evolution [26]. It is interesting therefore to determine the number of Ca^{2+} bound to purified oxygen-evolving complexes from higher plants. Highly purified complex prepared from spinach with β-octylglucoside [16] contained 4.4 Ca^{2+} per 200 Chl. The complexes, which lack light-harvesting chlorophyll-proteins, are enriched in the PS II reaction center [16]. We determined that there is one Q_A per 53 chlorophyll in our complex preparations. Thus, the Ca^{2+} content of the complexes is 1.2 Ca^{2+} per PS II. This shows that one of the two bound Ca^{2+} in the membrane preparations was removed during the purification procedures of the complexes.

Effects of NaCl-wash

Having established the amount of Ca^{2+} associated with PS II membrane preparations, we proceeded to examine effects of NaCl treatment on the Ca^{2+} contents of two spinach preparations (Table II). The abundance of Ca^{2+} in KM preparations was little affected by washing with 1 M NaCl in the dark. Treatment of BBY preparations with 2 M NaCl in the dark resulted in only a slight decrease in the amount of bound Ca^{2+}. In contrast, the salt treatment caused nearly half inactivation of oxygen evolution, which was significantly reversed on addition of 5 mM $CaCl_2$

TABLE II

EFFECTS OF NaCl WASH ON Ca^{2+} CONTENTS OF KM AND BBY PREPARATIONS OF SPINACH

NaCl concentrations used were 1 M for KM preparations and 2 M for BBY preparations.

Preparations	Ca^{2+} per 200 Chl		
	untreated	NaCl-washed	
		dark	light
KM	1.8±0.5	1.8±0.5	2.0±0.3
BBY	2.1±0.1	1.9±0.4	1.9±0.3

TABLE III

EFFECTS OF NaCl-WASH ON RATES OF OXYGEN EVOLUTION IN KM AND BBY PREPARATIONS OF SPINACH

NaCl concentrations used were 1 M for KM preparations and 2 M for BBY preparations. Where indicated, 5 mM $CaCl_2$ was added. Figures presented are rates of oxygen evolution (μmol per mg Chl per h).

Preparations	Untreated		NaCl-washed			
			dark		light	
	$-Ca^{2+}$	$+Ca^{2+}$	$-Ca^{2+}$	$+Ca^{2+}$	$-Ca^{2+}$	$+Ca^{2+}$
KM	438	444	218	329	149	288
BBY	769	765	355	492	299	398

with both preparations (Table III) [11,12]. Preliminary experiments showed that dark NaCl treatment caused no loss of Ca^{2+} from rice preparations (data not shown). Thus, regardless of membrane preparations and NaCl concentrations used, the inactivation of oxygen evolution by dark NaCl treatment is not related to release of the bound Ca^{2+}.

NaCl treatment under illumination caused a stronger inhibition of oxygen evolution than did the dark treatment (Table III). The activity was partly restored by addition of $CaCl_2$. However, effects of the light treatment on the Ca^{2+} content were not much different from those of the dark treatment. In this case again, therefore, loss of the activity is not related to release of the bound Ca^{2+}.

Stability of the Ca^{2+}-binding in the NaCl-washed spinach PS II membranes was examined by exposing them to 2 mM EGTA for 30 min at 0 °C in the dark. The Ca^{2+} content of the membranes was determined after removal of EGTA by washing with the suspending medium. Unexpectedly, the EGTA treatment often resulted in a significant increase in the amount of Ca^{2+} associated with the membranes (data not shown). This suggests unspecific binding of contaminating Ca^{2+} in the medium. Presumably, EGTA removed Mg^{2+} which had been associated with the membranes and consequently increased the number of binding site for Ca^{2+}. The effect of EGTA was therefore examined as follows: NaCl-washed membranes were treated with EGTA as above, then overlayed

TABLE IV

EFFECTS OF EGTA-TREATMENT ON Ca^{2+} CONTENTS OF NaCl-WASHED MEMBRANE PREPARATIONS

Spinach BBY preparations were treated with 1.5 M NaCl and then incubated with 2 mM EGTA in a medium containing 40 mM Mes (pH 6.5), 0.4 M sucrose and 10 mM NaCl for 30 min at 0 °C. Other procedures were described in the text. The data were obtained from three separate preparations.

Treatments	Ca^{2+} per 200 Chl
–	1.9±0.3
EGTA-treated	2.0±0.1

on a cushion containing 1 M sucrose, which had been treated with chelex 100 and then supplemented with 1 mM $MgCl_2$. Centrifugation of the suspension at 70000 × *g* for 10 min pelleted the membranes at the bottom of tubes, while leaving EGTA in a layer above the cushion. The Ca^{2+} abundance of the membranes thus treated was similar to that of the NaCl-washed membranes determined prior to the EGTA treatment (Table IV). Thus, the two Ca^{2+} are still tightly associated to the membranes even after removal of the 17 and 23 kDa proteins.

Effects of treatments with $MgCl_2$, Tris and NH_2OH

Experiments were extended to treatments of the membranes with $MgCl_2$, Tris and NH_2OH. Washing of the PS II membranes with 1 M $CaCl_2$ or $MgCl_2$ was shown to solubilize all the three extrinsic proteins without any significant loss of the bound Mn [34]. Table V shows that the treatment with 1 M $MgCl_2$ caused only a slight decrease in the amount of bound Ca^{2+}. SDS-polyacrylamide gel electrophoresis of the treated membranes and the extracts confirmed that the treatment nearly completely removed the three extrinsic proteins from the membranes (data not shown). It is concluded therefore, that all the three extrinsic proteins are not involved in the Ca^{2+} binding. The conclusion is supported by an observation that Tris treatment, which also solubilizes the three proteins [35,36], had no significant effect on the Ca^{2+} abundance. In contrast to $MgCl_2$ treatment, Tris treatment extracted most of the bound Mn. NH_2OH treatment also extracted Mn [37] but no Ca^{2+}. Thus, there is a considerable difference in the mode of binding between the two metal cations.

Discussion

The first purpose of the present work was to determine the amounts of Ca^{2+} associated with oxygen-evolving PS II membranes from higher plants. We have shown previously that there are two Ca^{2+} per PS II in spinach KM preparations [24]. Cammarata and Cheniae [23] reported that spinach and wheat PS II preparations contain about two and three Ca^{2+} per PS II, respectively. Because the spinach preparations used in the two groups showed lower rates of oxygen evolution than the wheat preparations, diminished Ca^{2+} abundance of spinach PS II membranes may be related to the low activity of the preparations. In order to examine this possibility, we have compared Ca^{2+} contents of three PS II membrane preparations with different oxygen-evolving capacities in the present work. In particular, the rice PS II preparations are the most active membrane preparations so far reported and evolve oxygen at rates twice as high as those of the spinach KM

TABLE V

EFFECTS OF $MgCl_2$, Tris AND NH_2OH TREATMENTS ON CONTENTS OF Ca, Mn AND THE THREE EXTRINSIC PROTEINS IN SPINACH KM PREPARATIONS

Treatments	Ca per 200 Chl	Mn per 200 Chl	Proteins (kDa)		
			17	23	33
–	1.8±0.4	3.8	+++	+++	+++
1 M $MgCl_2$	1.6±0.3	3.6	–	–	–
0.8 M Tris	1.7±0.5	0.46	–	–	–
1 mM NH_2OH	1.8±0.7	0.70	++	++	++

preparations. Irrespective of the difference in the oxygen-evolving activity, the three PS II preparations showed similar Ca^{2+}-contents of about 2 Ca^{2+} per 200 Chl. Thus, there is no correlation between the activity and Ca^{2+} content among three preparations. Since the ratio of Q_A to chlorophyll were determined to be 190–230 in our membrane preparations, we conclude that the maximum number of calcium atoms needed for oxygen evolution is two per PS II reaction center in higher plants.

The second aim of the present work was to investigate effects of NaCl treatment on the Ca^{2+} content of the membrane preparations. Removal of the 17 and 23 kDa proteins by NaCl treatment, either in the dark or light, did not liberate any significant amount of the bound Ca^{2+}. Exposure of the salt-washed membranes to EGTA failed to decrease the Ca^{2+} content. Thus, the two Ca^{2+} are still tightly associated with their functional sites in the membranes depleted of the 17 and 23 kDa proteins. The results do not support the postulation that removal of the 23 kDa protein by NaCl wash leads to a liberation of Ca^{2+} essential for PS II electron transport and hence to an inhibition of oxygen evolution and added Ca^{2+} restores the activity by binding to the functional sites. Our data cannot exclude, however, a possibility that Ca^{2+}-binding sites are not exposed to the outer aqueous phase so that, although the salt wash results in a release of Ca^{2+} from the functional site, no apparent loss of Ca^{2+} occurs as the released Ca^{2+} is trapped somewhere inside the membranes. It is to be stressed that, in either event, reactivation of oxygen evolution by added Ca^{2+} cannot be attributed to rebinding of the metal cation to its original functional site. Thus, the results presented here cast a strong doubt on the view that the Ca^{2+} effect observed in NaCl-treated PS II membranes is directly related to the in situ function of Ca^{2+}.

The entire process of oxygen evolution takes place in a discrete protein complex in the thylakoid membrane, which is in essence the PS II reaction center complex with attached three extrinsic proteins. Association of the extrinsic proteins is needed for the complex to maintain its conformation optimal for oxygen evolution. Removal of the 17 and 23 kDa by NaCl wash results in an altered conformation which is unfavorable for oxygen evolution and rebinding of the 23 kDa protein restores the original conformation of the complexes. The effects of exogenous Ca^{2+} is related to the functional conformation of the complexes. The maximal restoration of oxygen evolution in NaCl-washed membranes requires a nonphysiologically high concentration of Ca^{2+} [11,12]. This suggests that the functional conformation of the complex is restored by binding of the metal cations to low-affinity sites exposed to the outer phase even in the absence of the 23 kDa protein. Illumination during NaCl wash causes a stronger inhibition of oxygen evolution than the treatment in the dark and Ca^{2+} has a protecting effect against the photoinhibition [14,38]. The light effect may also be related to the conformational changes of the complexes. The conformation of the complexes appears to have some bearing on the Cl^- binding because removal of the 23 and 17 kDa proteins strongly affects the Cl^- dependency of oxygen evolution [39,40].

Determination of Ca^{2+} in the highly purified oxygen-evolving complexes isolated with β-octylglucoside revealed important features of binding and function of Ca^{2+}. The complexes contain only one Ca^{2+} per PS II reaction center. This indicates that one of the two Ca^{2+} present in PS II membranes is tightly bound to a subunit of the PS II reaction center complex, whereas binding of another Ca^{2+} is either more susceptible to the detergent or related to extraneous proteins such as light-harvesting Chl *a/b* proteins. Importantly, the removal of one of the two bound Ca^{2+} failed to eliminate PS II electron transport completely. Although the purified complexes require Ca^{2+} to show a substantial rate of oxygen evolution, the Ca^{2+} concentration dependency of the complexes similar to that of the NaCl-washed PS II membranes [17] strongly suggests that the Ca^{2+} demand created by the detergent treatment is related to loss of the 23 kDa proteins rather than loss of Ca^{2+}. Thus, the Ca^{2+} removed by the β-octylglucoside treatment appears not to be essential for PS II electron transport.

Rate of oxygen evolution per chlorophyll in the complexes are comparable to those in the PS II membranes but, when compared on the basis of PS II reaction center, the complexes are consider-

ably less active than the PS II membranes. A possibility remains that the less tightly bound Ca^{2+} has some secondary role in the PS II electron transport and oxygen evolution is not completely, but partially suppressed by its removal. However, the low activity of the complexes may as well be attributed to a deleterious effect of the detergent on the electron transport, in particular, on the reducing side of the reaction center [17]. Highly active oxygen-evolving PS II preparations isolated from the thermophilic cyanobacterium *Synechococcus* contain only one Ca^{2+} per PS II reaction center [25,26]. Because the machinery of photosynthetic oxygen evolution has been well conserved during a long-term evolution from cyanobacteria to higher plants, it would not be surprising if the number of endogenous Ca^{2+} functioning in PS II electron transport is the same between cyanobacteria and higher plants.

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