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Some properties of Photosystem II preparations from the cyanobacterium *Synechococcus* sp. – presence of an L-amino acid oxidase in Photosystem II complexes from *Synechococcus* sp.

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A highly active O_2-evolving Photosystem II complex has been purified from the cyanobacterium *Synechococcus* sp., and this complex has been compared with the Photosystem II complex previously isolated from this cyanobacterium (Ohno, T., Satoh, K. and Katoh, S. (1986) Biochim. Biophys. Acta 852, 1–8). Further treatment of the O_2-evolving complex with the detergent sodium taurodesoxycholate resulted in a complex which consisted mainly of the 47 and 40 kDa peptides and which had lost the O_2-evolving activity, but which could still reduce 2,6-dichlorophenolindophenol with 1,5-diphenylcarbazide. Previously, we have shown that a flavoprotein of 49 kDa which has an L-amino acid oxidase activity under certain conditions, is a component of highly active Photosystem II preparations from the cyanobacterium *Anacystis nidulans* (Pistorius, E.K. and Gau, A.E. (1986) FEBS Lett. 206, 243–248). Based on immunological studies with the antiserum raised against the L-amino acid oxidase protein from *A. nidulans*, we show that a protein which cross-reacts with this antiserum is present in the highly purified Photosystem II preparations from *Synechococcus* sp. Moreover, an L-amino acid oxidase activity could also be detected in Photosystem II preparations from *Synechococcus* sp. The enzyme preferentially oxidizes basic L-amino acids as L-arginine, L-ornithine, 2,3-diamino propionic acid and L-citrulline. In contrast to the enzyme from *A. nidulans* L-lysine is not oxidized. The here shown presence of an L-amino acid oxidase protein in Photosystem II preparations from *Synechococcus* sp. is an additional support of our hypothesis that a flavoprotein is a functional component of the water-oxidizing enzyme complex.

Introduction

Several types of O_2-evolving PS II reaction center complexes have recently been isolated from cyanobacteria, algae and higher plants. Such complexes have a multisubunit structure and contain the catalytic components necessary for the light-driven oxidation of water to molecular O_2 and the reduction of plastoquinone [1–5]. Thus, such complexes contain those peptides which carry out the primary photochemical charge separation, and also the peptide(s) which catalyzes the water oxidation. However, the question which polypeptide(s) actually is (are) the water-oxidizing enzyme and carries (carry) the organic prosthetic group 'Z' of unknown identity and the inorganic cofactors (Mn, Ca^{2+} and Cl^-) has remained uncertain [6,7]. Our experiments with the cyanobacterium *Anacystis*

Abbreviations: Hepes, 4-(2-hydroxyethyl)-1-piperazineethanesulfonic acid; PS, Photosystem; Chl, chlorophyll; DCMU, 3-(3,4-dichlorophenyl)-1,1-dimethylurea; DP 15, 2,4,6,2′,4′,6′-hexanitrodiphenylamine; DCIP, 2,6-dichlorophenolindophenol; DPC, 1,5-diphenylcarbazide; Mes, 4-morpholineethanesulphonic acid.

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nidulans have indicated that a flavoprotein of 49 kDa is a functional component of the water-oxidizing complex [8,9]. This flavoprotein has an L-amino acid oxidase activity in the absence of ions (such as Mn^{2+}, Ca^{2+} and Cl^-), which on the other hand are required for photosynthetic O_2 evolution [10,11]. Based on these results we have recently suggested that this flavoprotein is modified in the light and in the presence of Ca^{2+} and Cl^- in such a way that it can now interact with Mn^{2+} (possibly mediated by the extrinsic Mn^{2+} stabilizing peptide [12,13]) and catalyze the water-oxidizing reaction of PS II.

To obtain further information about the identity of the catalytic peptide(s) of the water-oxidizing reaction, we have investigated whether PS II complexes from the cyanobacterium *Synechococcus* sp. would also have a protein which is similar to the 'L-amino acid oxidase protein' of *A. nidulans*. We have chosen *Synechococcus* sp. because the PS II complex from this cyanobacterium has been very well characterized by Katoh's group [14–17] and because the PS II complex from this cyanobacterium seems to be very stable and can therefore be purified by various chromatographic procedures.

Materials and Methods

Synechococcus sp. was grown at 50 °C for 3 days in a medium according to Castenholz [18] with 0.5 g $NaHCO_3$ per 1 l medium in addition, in 1 l flasks, in the light (neon tubes: Osram warm-white and Osram fluora) and in a stream of 5% CO_2 in air. Thylakoids were obtained according to Refs. 14 and 15 with slight modifications. The lysozyme treatment was only performed for 1 h at 45 °C, the following French press treatment was done at 138 MPa and the DNAase treatment was reduced in time to the following centrifugation period (20 min). PS II membranes were prepared as in Ref. 15, but the resulting band pattern of the sucrose cushion centrifugation was slightly different from the published one. We obtained on top of the 1 M sucrose usually one homogenous green fraction which we used for further purification, an additional green band at the boundary between 0.5 M and 1 M sucrose and a pellet. Further purification of the complex was achieved as in Ref. 15 by using a Sepharose 6B and a DEAE cellulose (Whatman DE 23) column. The ion-exchange column was run in a stepwise manner with 0.1 M NaCl in the medium which eluated an orange band, and with 0.8 M sodium phosphate in the medium which gave the purified PS II complex. This purified O_2-evolving PS II complex was further treated in the following way: a sample was incubated with 2% sodium taurodesoxycholate for 1 h in ice and in the dark and then loaded onto a Sephacryl S-200 column (1 × 110 cm) which was equilibrated with a medium containing 50 mM sodium phosphate buffer (pH 7.5), 150 mM NaCl, 1% sodium taurodesoxycholate, 40 mM ϵ-amino caproic acid, 1 mM 4-amino benzamidine and 75 $\mu g \cdot ml^{-1}$ phenylmethylsulfonylfluoride. Elution was performed with the same medium and yielded two distinct visible bands: a green one in the exclusion volume with the main protein and a yellow-orange one later. All columns were run at 4 °C.

Polypeptide compositions were examined by SDS polyacrylamide gel electrophoresis according to Laemmli [19] with 4 M urea and 0.1% SDS in the gel and a 10–20% polyacrylamide gradient. Gels were run at 4 °C with a constant current of 4.5 $mA \cdot cm^{-2}$. The gels were stained and scanned as in Ref. 8. When it was used, silver staining was performed as in Ref. 20. Samples were prepared as in Ref. 15. Mn was determined as in Ref. 8 and cytochrome *b*-559 as in Ref. 21. O_2 evolution was monitored with a Clark-type oxygen electrode (Yellow Springs Instruments) at 40 °C under illumination with red light (filtered through a layer of 2 cm 2% $CuSO_4$). The basal reaction mixture contained: 1 M sucrose, 10 mM NaCl, 5 mM $MgCl_2$, 50 mM Mes-NaOH (pH 5.5), 3 mM potassium ferricyanide, 0.5 mM phenyl-*p*-benzoquinone. DCIP reduction was measured at 40 °C with a Perkin Elmer spectrophotometer λ 3 at 590 nm. The basal reaction mixture contained 0.1 M sucrose, 50 mM Mes-NaOH (pH 5.5) 10 mM NaCl, 5 mM $MgCl_2$, 1.7 mM DCIP and 58 μM DPC. Illumination was the same as for O_2 evolution.

The L-amino acid oxidase activity was measured by determining the NH_4^+ formed in the oxidative deamination reaction with L-arginine as substrate. The reaction was carried out in War-

burg flasks with one side arm. The reaction mixture contained in a total volume of 3 ml: 27 mM L-arginine, 20 mM EDTA and the sample (1 or 2 ml of the supernatant or PS II complexes in 50 mM Hepes-NaOH, pH 7.5, 1 M sucrose, 10 mM NaCl and 5 mM $MgCl_2$). The Warburg flasks were placed in a thermostat of 47°C and gassed with O_2 for 10 min. The reaction was started by tipping L-arginine from the side arm into the main compartment. After 6 h of incubation the reaction was stopped by adding 0.6 mmol H_2SO_4. The sample was then centrifuged for 20 min at 48000 $\times g$. In aliquots of the supernatant (after neutralization with NaOH) NH_4^+ was determined enzymatically by measuring the decrease of the absorbance of NADPH in the presence of excess α-ketoglutarate and glutamate dehydrogenase, as previously described [22]. The L-amino acid oxidase seemed to be stable over the 6 h incubation period (and even longer), since the NH_4^+ produced was proportional to the incubation time during that period (not shown).

The antibody raised against the purified L-amino acid oxidase protein from *A. nidulans* was the same as in Ref. 11. *Synechococcus* sp. was a kind gift from Prof. Sakae Katoh, University of Tokyo, and DP 15 from Prof. Walter Oettmeier, Ruhr-Universität Bochum.

Results and Discussion

Purification and characterization of the PS II complex

The PS II complex from *Synechococcus* sp. was solubilized from the thylakoid membranes with the detergent octyl-β-D-glucopyranoside and then purified by sucrose density gradient centrifugation and chromatography on a Sepharose 6B column and a DEAE cellulose column, basically as described by Satoh et al. [15]. The values for O_2 evolution, Mn and cytochrome *b*-559 content are given in Table I. The corresponding peptide patterns of the PS II complex at the different stages of purification are shown in Fig. 1A–C. The purified O_2-evolving PS II complex (Fig. 1C) consisted of four main peptides (47, 40, 37 and 32 kDa), while only small amounts of the 34 and 10 kDa peptides (hardly visible on the gel) were present. In addition to these peptides small impurities of a 18 and 20 kDa peptide were also present. The corresponding PS II complex isolated by Ohno et al. [16] contained the peptides of 47, 40, 35, 31, 28, 9 and 8 kDa. If we compare the two PS II complexes, then the main difference (besides small differences in the molecular weight of the peptides) seems to be that we found much less of the 8–10 kDa peptide and also of the 34 kDa peptide.

TABLE I

PHOTOSYNTHETIC ACTIVITIES, Mn AND CYTOCHROME *b*-559 CONTENT OF THE PS II COMPLEX FROM *SYNECHOCOCCUS* sp. AT THE DIFFERENT PURIFICATION STEPS

Details of the purification and assays are given under Materials and Methods. n.d. = not determined, + reaction could be inhibited by 3 μM DP 15 to 70%.

Purification step of the PS II complex	Photosynthetic activities (μmol per mg Chl per h)		Inhibition of O_2 evolution by 20 μM DCMU (% inhibition)	Mn content (g atom per mol Chl)	Cytochrome *b*-559 content (mol per mol Chl)
	O_2 evolution	DCIP reduction by DPC			
After sucrose cushion centrifugation	1983	1000	60–66	1:14	1:57
After Sepharose 6B column	1760	n.d.	12–78	n.d.	1:53
After DEAE cellulose column	1182	n.d.	0–32	1:19	1:154
After sodium taurodesoxycholate treatment	0	73–415	n.d. +	n.d.	n.d.

The O_2-evolving activity (1000–1400 μmol O_2 evolved per mg Chl per h) and the Mn content (4 Mn per 76 Chl) were fairly similar to the values obtained by Ohno et al. [16], while the cytochrome *b*-559 content was significantly lower (1 cytochrome *b*-559 per 154 Chl) (Table I). This was in agreement with the low amount of the 10 kDa peptide in our preparation. O_2 evolution in the crude complex could be inhibited by DCMU, while the O_2 evolution in the purified complex was not or only partly inhibited (Table I). This indicated that electron flow to the secondary quinone acceptor (Q_B) was not anymore possible in the purified complex – either due to removal of the DCMU-binding peptide or due to disjunction of the peptide from the complex.

This O_2-evolving complex was further treated with the detergent sodium taurodesoxycholate and

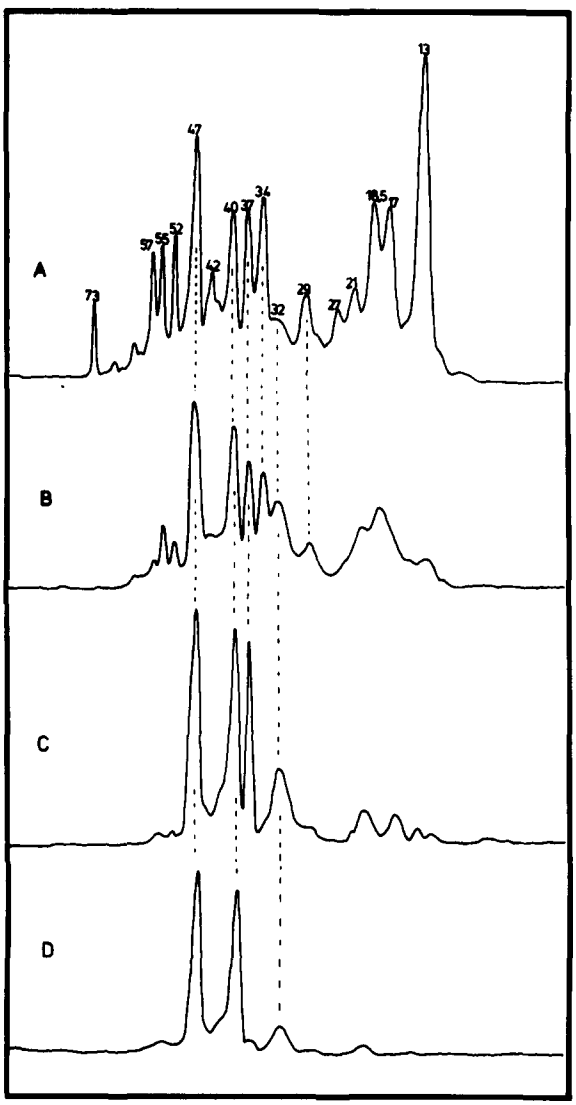

Fig. 1. Densitometer scans of polypeptide pattern of the PS II complex at the different steps of purification. The polypeptides were resolved by SDS-urea polyacrylamide gel electrophoresis as described under Materials and Methods. The scans show the PS II complex: (A) after sucrose cushion centrifugation; (B) after Sepharose 6B column; (C) after DEAE cellulose column; and (D) after sodium taurodesoxycholate treatment. Numbers indicate the apparent molecular weight in thousands.

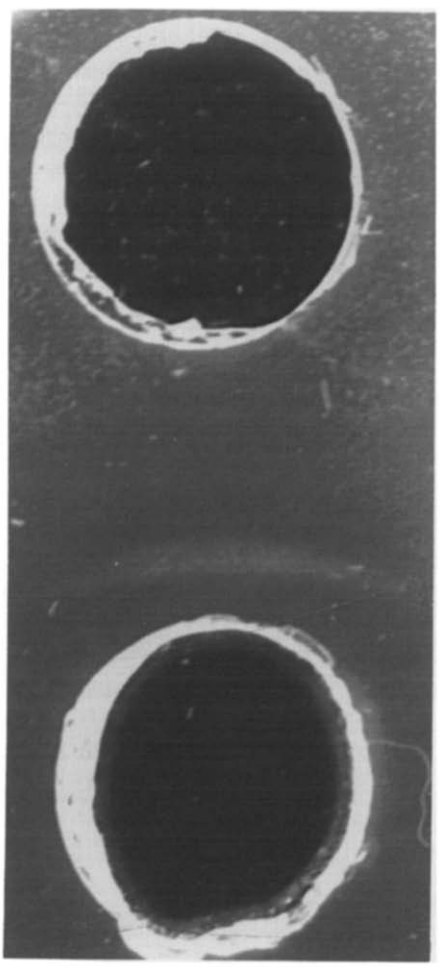

Fig. 2. Ouchterlony double-diffusion test. The upper well contained the purified PS II complex from *Synechococcus* sp. after sodium taurodesoxycholate treatment (peptide pattern as in Fig. 1D) and the lower well contained the antibody raised against the purified L-amino acid oxidase protein from *A. nidulans*.

then subjected to gel filtration on a Sephacryl S-200 column. This procedure resulted in a complex which mainly consisted of the two Chl *a*-carrying peptides of 47 and 40 kDa (Fig. 1D). The 37 kDa peptide was almost totally removed by this procedure (this peptide could also be removed by $CaCl_2$ washing – not shown, see also Ref. 15), while varying amounts of the 32 kDa and 20 kDa peptides remained in the complex. This complex could not any longer evolve O_2, but was still able to reduce DCIP with DPC as donor (Table I). This treatment also removed large amounts of carotene from the complex.

Immunological detection of the 'L-amino acid oxidase protein' in PS II complexes from Synechococcus sp.

Bullerjahn et al. [23] have recently shown that an antibody raised against the polypeptide 5 (equivalent to CP 47) of *Chlamydomonas* cross-reacted with the 48 kDa peptide of the cyanobacterium *Aphanocapsa* 6714. These results indicated that this peptide must be well conserved during evolution. Therefore, it should be expected that the antibody which we raised against the purified flavoprotein with L-amino acid oxidase activity from *A. nidulans* [11], should also show a cross-reaction with the corresponding peptide in PS II of the closely related *Synechococcus* sp. In Fig. 2 we show that this is the case. The PS II complex of *Synechococcus* sp. which mainly consisted of the 47 and 40 kDa peptides (Fig. 1D) gave a cross-reaction with the antibody raised against the L-amino acid oxidase protein from *A. nidulans* in an Ouchterlony double diffusion test. A cross-reaction was also obtained with the O_2-evolving complexes (not shown). Since the antibody raised against the native L-amino acid oxidase protein did not react well with the SDS-urea denatured PS II complex in immuno-blotting experiments, we cannot at the present time distinguish which of the peptides present in the PS II complex of Fig. 1D cross-reacted with the antiserum. However, in analogy to *A. nidulans,* it should be the 47 kDa peptide. Work to isolate the 47 kDa peptide from *Synechococcus* sp. is in progress.

Detection of the L-amino acid oxidase activity in Synechococcus sp.

Since the antiserum experiments indicated that an immunologically similar protein as the L-amino acid oxidase protein from *A. nidulans* is also present in the highly purified PS II preparations from *Synechococcus* sp., we investigated whether we could also detect an L-amino acid oxidase activity with high specificity for basic L-amino acids in this cyanobacterium. The results in Table

TABLE II

L-AMINO ACID OXIDASE ACTIVITY AND PHOTOSYNTHETIC O_2 EVOLUTION AT VARIOUS PURIFICATION STEPS

Details of the purification and of the activity assays are given under Materials and Methods.

Purification step	Chlorophyll total (mg)	L-amino acid oxidase activity (NH_4^+ production)		Photosynthetic O_2 evolution	
		(μmol NH_4^+ per mg Chl per h)	(μmol NH_4^+ per h per total volume)	(μmol O_2 per mg Chl per h)	(μmol O_2 per h per total volume)
French press extract	28	2.25	63	370	10360
Supernatant	–	–	66	–	–
Thylakoid membranes	28	0.04	1.1	230	6440
PS II complex after sucrose cushion centrifugation	1.93	0.46	0.89	1700	3281
PS II complex after Sepharose 6B column	0.21	0.44	0.09	1600	336

TABLE III

INFLUENCE OF VARIOUS BUFFER SOLUTIONS ON THE SOLUBILITY OF THE L-AMINO ACID OXIDASE PROTEIN FROM *SYNECHOCOCCUS* sp.

10 ml of the supernatant obtained after centrifugation of the French press extract (in a medium of 50 mM Hepes-NaOH (pH 7.5), 1 M sucrose, 10 mM NaCl and 5 mM $MgCl_2$ – see Table II) was dialyzed for 8 h against the buffer solutions as indicated in the table. After dialysis the solution was centrifuged for 20 min at 48000 × *g*. In the resulting supernatant and the pellet which was resuspended in 50 mM Hepes-NaOH (pH 7.5), containing 1 M sucrose, 10 mM NaCl and 0.7% octyl-β-D-glucopyranoside, the L-amino acid oxidase activity was determined. The activity before dialysis was 2.45 μmol NH_4^+ produced per h per 10 ml solution.

Dialysis buffers	L-Amino acid oxidase activity after dialysis (NH_4^+ production) (μmol NH_4^+ per h per total volume)		
	supernatant	pellet	total
25 mM Hepes-NaOH (pH 7.5)	0.26	1.94	2.20
25 mM Hepes-NaOH (pH 7.5) + 0.5 M sucrose	2.05	0.64	2.69
25 mM sodium phosphate buffer (pH 7.5)	2.67	0.10	2.77

II show that French press extracts from *Synechococcus* sp. could catalyze a deamination of L-arginine, and this activity was also associated with the thylakoid membranes and various PS II preparations. Unfortunately, it is difficult to assay the L-amino acid oxidase activity in a quantitative way when the enzyme is still bound to the thylakoid membrane, as discussed previously [8]. The activity depends on the degree to which the polar substrate L-arginine can reach the enzyme in the thylakoid membrane or in the detergent solubilized PS II complex and also on the degree to which the L-amino acid oxidase activity is suppressed by ions (Ref. 10; see also below). However, we could clearly detect the L-amino acid oxidase activity in the thylakoid membranes and in the PS II complex after gradient centrifugation and after the Sepharose 6B column. Because of the low yield of the highly purified PS II complex after the next two columns, it was difficult to measure the L-amino acid oxidase activity in those preparations accurately. However, as discussed above, the L-amino acid oxidase protein could clearly be detected by the antiserum in those highly purified PS II complexes (Fig. 2).

TABLE IV

SUBSTRATE SPECIFICITY OF THE L-AMINO ACID OXIDASE FROM *SYNECHOCOCCUS* sp.

Substrate	Relative activity (%)
L-Arginine	100
L-Ornithine	21
2,3-Diamino propionic acid	19
L-Citrulline	16
D-Arginine	3

The distribution of the 'detectable' L-amino acid oxidase activity (Table II) was very similar to the activity obtained in *A. nidulans* [8,9]. On the other hand, the absolute activity on Chl basis was much lower in *Synechococcus* sp. (approximately by a factor of 80) than in *A. nidulans*. For French press extracts the values were approx. 2 and 150 μmol NH_4^+ formed per mg Chl per h and for the PS II complex after the Sepharose 6B column the values were 0.4 and 30 μmol NH_4^+ formed per mg Chl per h for *Synechococcus* sp. and *A. nidulans* [8,9], respectively. Because of the low activity in the *Synechococcus* sp. preparations we have determined the NH_4^+ formed from L-arginine after a 6 h incubation period in Warburg flasks instead of measuring the O_2 uptake in an O_2 electrode as done for *A. nidulans*. It seems that *Synechococcus* sp. has a very stable PS II complex with one tightly bound Ca^{2+} [17]. This could possibly be the reason that the detectable activity was much lower in the *Synechococcus* sp. preparations than in the *Anacystis* preparations. On the other hand, it could also be possible that the turn-over number of the enzyme from *Synechococcus* sp. is lower than for the *Anacystis* enzyme which has an unusually high turn-over number for an amino acid oxidase [8]. This question can only be answered when we have purified the enzyme.

As in *A. nidulans* [8] most of the 'detectable' L-amino acid oxidase activity was in the supernatant fraction obtained after centrifugation of

the French press extract. The L-amino acid oxidase protein in the supernatant could also be detected with the antiserum (not shown). However, in *Synechococcus* sp. the L-amino acid oxidase protein in the supernatant is not really a soluble protein (as would be expected for a membrane protein). Dialysis of the supernatant solution (containing 50 mM Hepes-NaOH (pH 7.5), 1 M sucrose, 10 mM NaCl and 5 mM $MgCl_2$) against 25 mM Hepes-NaOH (pH 7.5), resulted in precipitation of the L-amino acid oxidase protein. The precipitated protein could be solubilized again in 50 mM Hepes-NaOH (pH 7.5) containing 1 M sucrose, 10 mM NaCl and 0.7% octyl-β-D-glucopyranoside (Table III). The protein was also soluble in a hypertonic solution (Hepes buffer containing sucrose) and also in phosphate buffer. Obviously, multivalent ions also help to keep the protein in solution. This is not surprising, since we know from the work with the L-amino acid oxidase from *A. nidulans* that this protein is greatly influenced by cations and anions [10].

The best substrate for the enzyme from *Synechococcus* sp. is L-arginine, followed by L-ornithine, 2,3-diamino propionic acid and L-citrulline (Table IV). All other tested amino acids were only oxidized with a rate which was less than 10% of that for L-arginine. D-Arginine was not a substrate. In contrast to the enzyme from *A. nidulans* [24], L-lysine was not a substrate. For the enzyme from *A. nidulans* we have previously shown that ions have an inhibitory effect on L-arginine oxidation [10,22]. This was more difficult to show for the enzyme from *Synechococcus* sp., since the solubility of the enzyme was greatly influenced by ions (Table III). However, preliminary experiments also indicate that the activity can be suppressed by ions. Addition of EDTA to the supernatant solution (containing 10 mM NaCl and 5 mM $MgCl_2$) always increased the NH_4^+ production (approx. 40% stimulation). This aspect has to be examined in more detail when we have learned how to handle the enzyme when it is removed from the membrane.

Concluding remarks

The parallels of H_2O oxidation to O_2 and H_2S oxidation to S were the basis of Van Niel's unifying idea on photosynthesis in plants and photosynthetic bacteria [25,26]. Recently, this idea has again attracted some interest, since regional amino acid homology between the reaction center proteins L and M from purple photosynthetic bacteria and the D_1 and D_2 proteins of PS II has been shown to occur [27,28]. Therefore, it has been suggested that in PS II the photochemical charge separation is located on the D_1 and D_2 peptides [27–29]. However, this is still controverse, since there is also evidence which suggests that P-680 is located on the Chl binding protein of 51–47 kDa [30–34]. Moreover, Vermaas et al. [35] have recently concluded from mutant experiments that the 51–47 kDa peptide might play an essential role in the activity of the PS II reaction center.

For several photosynthetic bacteria – when grown autotrophically – the source of the inorganic reducing equivalents could be the oxidation of sulfide to sulfur, and it has been proposed that this reaction is catalyzed by a water-soluble FAD containing diheme cytochrome *c* enzyme [26]. On the other hand, the peptide(s) catalyzing the water oxidation of PS II is part of the hydrophobic PS II complex. It is well established that the water-oxidizing enzyme complex requires three inorganic cofactors (Mn^{2+}, Ca^{2+} and Cl^-) and an organic prosthetic group 'Z' of unknown identity, but it remained unclear to which peptide(s) these cofactors are bound [6,7]. Our experiments with the cyanobacterium *A. nidulans* have indicated that a flavoprotein of 49 kDa which has an L-amino acid oxidase activity in the absence of ions, is modified in the light and in the presence of Ca^{2+} and Cl^- in such a way that it can now interact with Mn^{2+} and catalyze the water oxidation [8,9]. The here shown presence of a similar L-amino acid oxidase protein in PS II preparations from the cyanobacterium *Synechococcus* sp. gives additional support to our hypothesis that the water-oxidizing enzyme has been derived from a substrate dehydrogenase type enzyme which has an L-amino acid oxidase activity in the absence of ions (Mn^{2+}, Ca^{2+} and Cl^-) which on the other hand are required for photosynthetic O_2 evolution. This would then imply that a flavin seems to be functional on the donor side of the reaction center of PS II as well as on the donor side of the reaction center from photosynthetic bacteria.

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