Biochimica et Biophysica Acta 809 (1985) 396–402
Elsevier

BBA 41852

Different degrees of phosphorylation and lateral mobility of two polypeptides belonging to the light-harvesting complex of Photosystem II

Ulla K. Larsson and Bertil Andersson

Department of Biochemistry, University of Lund, P.O. Box 124, S-221 00 Lund (Sweden)

(Received April 23rd, 1985)

Key words: Light-harvesting complex; Protein phosphorylation; Membrane lateral heterogeneity; Photosystem II; Thylakoid membrane; (Spinach chloroplast)

Several studies have shown that a subpopulation of the light-harvesting chlorophyll *a*/*b*-protein complex of Photosystem II (LHC-II) migrates from the appressed to the stroma-exposed thylakoids upon its phosphorylation. In this study we have analyzed the 27 and 25 kDa apopolypeptides of LHC-II, resolved by two-dimensional electrophoresis, with respect to their relative abundance and phosphorylation in thylakoids and subfractions derived from appressed or stroma-exposed thylakoid regions. The results show that the two polypeptides are heterogeneous with respect to both phosphate incorporation and degree of lateral migration. In intact thylakoids, the specific phosphorylation of the 25 kDa polypeptide exceeded that of the 27 kDa polypeptide by a factor of 3. Following phosphorylation, the 25 kDa polypeptide of the stroma lamellae showed as much as 4–5-times higher specific phosphorylation compared to the 27 kDa polypeptide. Moreover, there was a time-dependent increase in the amount of the 25 kDa polypeptide relative to the 27 kDa polypeptide in the stroma-exposed thylakoids. These results demonstrate a different polypeptide composition of the LHC-II tightly bound to Photosystem II and the free pool of LHC-II able to migrate laterally upon phosphorylation. The mobile pool of LHC-II is estimated to have two 27 kDa polypeptides for every 25 kDa polypeptide, while the ratio in the immobile pool is 4:1.

Introduction

The thylakoid membrane of higher plant chloroplasts exhibits a pronounced lateral asymmetry in the distribution of supramolecular complexes involved in light-harvesting, electron transport and ATP synthesis [1]. Whereas photosystem I and the ATP-synthase are concentrated in the non-appressed stroma membranes, most of Photosystem II and its light-harvesting chlorophyll *a*/*b* complex (LHC-II) are concentrated in the appressed grana membranes [1–5]. Despite this spatial segregation of Photosystem I and II, it has been shown that chloroplasts have a mechanism that can balance the excitation energy distribution between the photosystems (for a review, see Ref. 6).

Several studies [6–10] have suggested that this regulatory effect is due to protein phosphorylation causing changes in the organization of the thylakoid membrane that would allow an increased degree of interaction between LHC-II and Photosystem I. Protein phosphorylation causes a limited destacking of grana thylakoids as judged from electron microscopy [11,12], linear dichroism [13] and subfractionation [14] studies. Moreover, several studies have shown that phosphorylation induces a lateral migration of phosphorylated

Abbreviations: Hepes, 4-(2-hydroxylethyl)-1-piperazineethanesulphonic acid; LHC-II, light-harvesting chlorophyll *a*/*b*-protein complex of Photosystem II; Tricine, *N*-[2-hydroxy-1,1-bis(hydroxymethyl)ethyl]glycine.

LHC-II from the Photosystem II-rich appressed regions of grana to the Photosystem I-rich stroma-exposed thylakoid regions, since (i) the proportion of LHC-II in stroma lamellae vesicles isolated from phosphorylated thylakoids is increased compared to stroma lamellae vesicles isolated from control thylakoids [14–16], (ii) there is a 7–10-times higher specific phosphorylation of LHC-II in stroma lamellae vesicles compared to that in everted thylakoids derived from the appressed thylakoid regions [17,18], (iii) a pulse-chase experiment shows an increased proportion of [^{32}P]phosphate label in LHC-II of stroma lamellae with time following phosphorylation [15], (iv) freeze-fracture analysis reveals that 8 nm particles of the PF fracture face, inferred to be associated with LHC-II, migrate from grana to stroma regions of phosphorylated thylakoids [11].

The LHC-II is heterogeneous with respect to polypeptide composition [19–23], and usually two major polypeptides are resolved by SDS-polyacrylamide gel electrophoresis. These two main polypeptides are synthesized from distinct mRNAs [24], but as judged by amino acid analyses, immunological comparisons and proteolytic digestions, they are very similar [24–30]. In this study we have compared the two polypeptide subunits of LHC-II with respect to kinase-dependent incorporation of phosphate and their relative abundance in the grana and stroma lamellae regions before and after phosphorylation. The results demonstrate pronounced differences in both phosphorylation and lateral migration of these two LHC-II subunits.

Materials and Methods

Phosphorylation of thylakoids

Stacked thylakoids were isolated [31] from spinach leaves (*Spinacia oleracea* L.) in 50 mM sodium phosphate buffer (pH 7.4), 5 mM $MgCl_2$, 300 mM sucrose and washed twice in 50 mM sodium phosphate buffer (pH 7.4), 5 mM $MgCl_2$, 50 mM sucrose. Then they were further washed in 50 mM Hepes-KOH (pH 8.0), 10 mM $MgCl_2$, 100 mM sucrose and resuspended in the same medium to a concentration of 200 μg chlorophyll/ml. Before phosphorylation, NaF was added to a final concentration of 10 mM in order to inhibit phosphatase activity. Thylakoids were phosphorylated by illumination for 10 min (500 $\mu E \cdot m^{-2} \cdot s^{-1}$) in the presence of 0.2 mM [γ-^{32}P]ATP (300000 cpm/nmol ATP). Control thylakoids were kept in the dark without addition of ATP. (Other controls were thylakoids illuminated in the absence of ATP and thylakoids kept in the dark with added [γ-^{32}P]ATP.) The thylakoids were sedimented at 5000 $\times g$ for 10 min and washed in 10 mM sodium phosphate buffer (pH 7.4), 5 mM EDTA, 10 mM NaF, and finally suspended in 50 mM sodium phosphate buffer (pH 7.4), 140 mM NaCl, 10 mM NaF.

Phosphorylation of thylakoids for pulse-chase experiments was performed mainly according to Ref. 15 at a chlorophyll concentration of 400 μg/ml in a medium containing 15 mM Tricine (pH 7.8), 10 mM NaCl, 5 mM $MgCl_2$, 10 mM NaF, 100 mM sorbitol. Phosphorylation was carried out by illumination (500 $\mu E \cdot m^{-2} \cdot s^{-1}$) for 2 min in the presence of 0.4 mM [γ-^{32}P]ATP (300000 cpm/nmol ATP). Typical [^{32}P]phosphate label of the thylakoids in the two types of phosphorylation experiments was 5 nmol/mg chl.

Subfractionation of thylakoids

Control and phosphorylated thylakoids were fragmented in a Yeda press at a nitrogen pressure of 10 MPa [31]. The time between illumination and disintegration was approx. 2 h. The Yeda press homogenate was centrifuged at 40000 $\times g$ for 30 min. The supernatant, containing stroma lamellae vesicles from the non-appressed region was sedimented by centrifugation at 100000 $\times g$ for 60 min, yielding the Y-100 fraction. The 40000 $\times g$ sediment was resuspended in a low salt medium of 10 mM sodium phosphate buffer (pH 7.4), 5 mM NaCl, 100 mM sucrose and passed again through the Yeda press. The thylakoid material thus obtained was separated by partitioning in an aqueous dextran/poly(ethylene glycol) two-phase system [32] including five partition steps as in Ref. 33. The B5 fraction, highly enriched in inside-out vesicles originating from the appressed thylakoid region, was collected by centrifugation at 100000 $\times g$ for 45 min.

For the pulse-chase experiment, phosphorylated thylakoids were disrupted with digitonin (final concentration, 0.4%) at 2, 12 or 32 min after start

of phosphorylation. The detergent treatment was terminated after 2 min by a 10-fold dilution of the samples with the incubation buffer at 0°C. The homogenates were centrifuged at 40000 × *g* for 30 min. The supernatant, containing the stroma lamellae fraction (D-100) was collected by centrifugation at 100000 × *g* for 60 min.

Clorophyll *a/b* ratios were determined according to Arnon [34].

Two-dimensional gel electrophoresis

For the first-dimension electrophoresis, chlorophyll-protein complexes from the thylakoid membrane were resolved by a mild SDS-polyacrylamide gel electrophoresis mainly according to Ref. 35, with modifications as in Ref. 2. Solubilization of the material was performed at 4°C with an SDS/chlorophyll ratio of 6.5. Gradient gels of 8–12% acrylamide were used. Electrophoresis was run at 4°C for 3–4 h at a constant current density of 0.05 mA/mm^2. The green bands resolved corresponding to the monomeric (LHCP3) and trimeric (LHCP1) forms of LHC-II were excised from the gel. No dimeric form of LHC-II (LHCP2) was obtained. For the second-dimension electrophoresis, the gel pieces were incubated in the solubilizing buffer of Laemmli [36] and reelectrophoresed under more denaturing conditions in the buffer system of Laemmli, using 12–22.5% gradient gels. The second-dimension gels were stained with Coomassie brilliant blue and scanned using a laser densitometer. The polypeptides were quantified from their peak areas. In experiments using [γ-^{32}P]ATP, the second-dimension gels were sliced, solubilized in H_2O_2/perchloric acid and counted for radioactivity in Aquasol.

Results and Discussion

Different specific phosphorylation of the 27 and 25 kDa apopolypeptides of LHC II

Fig. 1 shows a gel scan of the 27 and 25 kDa apopolypeptides of LHC-II (previously designated 25 and 23 kDa respectively [17,18]) in intact phosphorylated thylakoids resolved by two-dimensional gel electrophoresis. The relative amount of the 27 kDa polypeptide, determined from the peak area, is approx. 4-times higher than that of the 25 kDa polypeptide (Table I). For this quantification

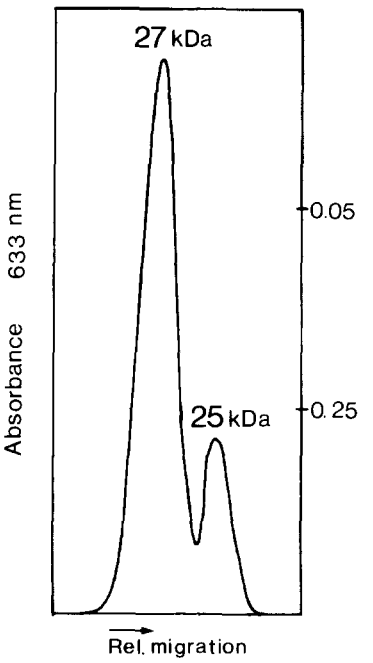

Fig. 1. Gel scan of the 27 and 25 kDa apopolypeptides of LHC-II after two-dimensional gel electrophoresis. The second dimension gel was stained with Coomassie brilliant blue, destained and scanned using a laser densitometer.

TABLE I

EFFECTS OF PHOSPHORYLATION ON THE PROPORTION BETWEEN THE 27 kDa AND 25 kDa APOPOLYPEPTIDES OF LHC-II IN INTACT THYLAKOIDS, APPRESSED GRANA AND STROMA LAMELLAE VESICLES

Appressed grana (B5) and stroma lamellae (Y-100) vesicles were isolated from non-phosphorylated and phosphorylated thylakoids. The amounts of the two apopolypeptides of LHC-II were quantified from gels after two-dimensional gel electrophoresis. The second-dimension gel was stained with Coomassie brilliant blue, destained and scanned using a laser densitometer. The relative amounts of the 27 kDa and 25 kDa apopolypeptides were quantified from their peak areas. Data represent the mean values from five independent experiments with standard deviation of 0.02–0.08.

Treatment	Ratio between the 27 kDa and 25 kDa polypeptides		
	intact thylakoids	appressed membranes (B5)	stroma-exposed membranes (Y-100)
Nonphosphorylated	4.0	4.0	4.2
Phosphorylated	3.9	4.0	3.2

it assumed that the 27 kDa and 25 kDa polypeptides had the same binding constant for the gel stain (Coomassie brilliant blue), an assumption that appears valid in the light of the similar size and pronounced homology between these two polypeptides [24–30]. When the [^{32}P]phosphate label (cpm) of these two polypeptides was analyzed it was found that the total phosphate incorporation of the 25 kDa polypeptide was only slightly lower than for the 27 kDa polypeptide (Table II). Therefore, the specific phosphorylation (cpm/relative amount of protein) of the 25 kDa polypeptide is nearly 3-times as high as for the 27 kDa polypeptide.

The difference in [^{32}P]phosphate incorporation between the two polypeptides was seen also in thylakoid subfractions derived from appressed or non-appressed thylakoids (Table II). In stroma lamellae vesicles (Y-100), which have the highest specific phosphorylation of LHC-II in agreement with previous studies [17,18] even the total phosphate incorporation is highest for the 25 kDa polypeptide. Thus, in the stroma lamellae, the specific phosphorylation of the 25 kDa polypeptide exceeds that of the 27 kDa polypeptide by as much as 4.5-times . Also in the appressed thylakoid vesicles (B5) the specific phosphorylation is highest for the 25 kDa polypeptide.

It was essential that these quantification could be done without disturbance of comigrating polypeptides. This was accomplished by a two-dimensional electrophoresis which in the first dimension resolves LHC-II into two green bands; a monomeric (LHCP3) and a trimeric form (LHCP1). In the second dimension, LHC-II dissociates and since undenatured chlorophyll-protein complexes migrate differently to the fully denatured polypeptides during electrophoresis [37,38], the polypeptides comigrating with LHCP1 and LHCP3 in the first dimension will have a mobility quite distinct from the LHC-II apopolypeptides. This purification effect is of course most pronounced for the trimeric form of LHC-II. In our quantifications we have therefore mainly relied on LHCP1, but in all cases similar results were obtained with LHCP3.

Some previous studies [15,17,18,29,39] have indicated a rather even distribution of radioactive label between the two apopolypeptides of LHC-II when resolved by one-dimensional SDS-polyacrylamide gel electrophoresis. However, these studies did not allow for a determination of the specific phosphorylation of the two polypeptides to unequivocally demonstrate their different degree of phosphorylation.

The molecular mechanism responsible for the higher degree of phosphorylation of the 25 kDa polypeptides compared to the 27 kDa polypeptides is not obvious considering the similarity between the two polypeptides. Possibly, the conformation of the 25 kDa polypeptide makes it a better substrate for the kinase or it may structurally be more intimately associated with the kinase. Alternatively, the 27 kDa polypeptide would be

TABLE II

TOTAL AND SPECIFIC INCORPORATION OF [^{32}P]PHOSPHATE INTO THE 25 kDa AND 27 kDa APOPOLYPEPTIDES OF LHC-II IN INTACT THYLAKOIDS, APPRESSED GRANA AND STROMA LAMELLAE VESICLES

Thylakoids were phosphorylated and fractionated into appressed grana (B5) and stroma lamellae (Y-100) vesicles. The relative amounts of the 25 kDa and 27 kDa apopolypeptides were quantified from their peak areas after two-dimensional gel electrophoresis as described in the legend to Table I. The total incorporation of [^{32}P]phosphate, expressed in cpm, of the two apopolypeptides was analyzed after cutting out the individual apopolypeptide bands from the second-dimension gel. The specific phosphorylation (cpm/relative amount of protein) was calculated by normalizing the total phosphate label to the corresponding amount of protein. The values are presented as mean values from five independent experiments. Standard deviations are given in parentheses.

Apopolypeptides of LHC-II	Intact thylakoids		Appressed membranes (B5)		Stroma-exposed membranes (Y-100)	
	tot. incorp.	spec. incorp.	tot. incorp.	spec. incorp.	tot. incorp.	spec. incorp.
25 kDa	1250	4580	1310	3170	2740	9560
27 kDa	1740	1650	2550	1490	1960	2150
25/27	0.72(0.001)	2.8(0.05)	0.51(0.001)	2.1(0.03)	1.4(0.02)	4.5(0.08)

more susceptible to dephosphorylation, but this is less likely, since the phosphorylation and subfractionation were carried out in the presence of phosphatase inhibitor (NaF). The higher degree of phosphorylation of the 25 kDa subunits could be due to a greater number of phosphorylation sites. Alternatively, the proportion of all 25 kDa polypeptides that become phosphorylated is higher than the proportion of phosphorylated 27 kDa polypeptides.

Different lateral mobility of the phosphorylated 27 and 25 kDa polypeptides of LHC-II

The higher specific phosphorylation of the 25 kDa polypeptide would indicate that this polypeptide population carries more negative charges than the 27 kDa polypeptide population and according to Barber [6] it would therefore show a higher probability of being excluded from the appressed thylakoid regions. This would be consistent with the particularly high specific phosphorylation observed for the 25 kDa polypeptide in the stroma lamellae vesicles (Table II). To examine whether the different [^{32}P]phosphate incorporation into the two LHC-II subunits indeed was accompanied by a corresponding difference in lateral migration behavior, the amounts of the 27 kDa and the 25 kDa polypeptides were determined after two-dimensional gel electrophoresis of the two thylakoid subfractions isolated from control or phosphorylated thylakoids (Table I). The ratio between the 27 kDa and the 25 kDa polypeptides of 4 : 1 in unfractionated control thylakoids was found also in the Y-100 and B5 fractions, demonstrating that before phosphorylation the LHC-II has the same subunit composition in both the appressed and stroma-exposed thylakoid regions. After phosphorylation the ratio in the intact thylakoids remained close to 4 : 1, showing that phosphorylation itself did not change the amount of the two LHC-II apopolypeptides. In contrast, in stroma lamellae vesicles, isolated 2 h after phosphorylation of the thylakoids, the ratio between the amount of the 27 kDa and the 25 kDa polypeptides was 3.2, compared to a ratio of 4.2 in stroma lamellae vesicles isolated from control thylakoids (Table I). This lower ratio indicates a significant increase in the relative amount of the 25 kDa polypeptide in stroma lamellae following phosphorylation.

The increased proportion of the 25 kDa polypeptide in the LHC-II of phosphorylated stroma lamellae was further demonstrated by a development of the pulse-chase experiment of Kyle et al. [15]. Thylakoids were illuminated for 2 min in the presence of [γ-^{32}P]ATP. Digitonin was added at different times after phosphorylation, and stroma lamellae particles (D-100) were isolated by differential centrifugation. As shown in Table III, the total phosphate incorporation into LHC-II in intact thylakoids was almost constant over the 30 min chase period, demonstrating that there was no incorporating of phosphate into the apopolypeptides in the dark. In contrast, the total incorporation of phosphate into LHC-II of stroma lamellae increased with time even after the light was turned off. This was accompanied by a continual increase in the proportion of LHC-II in the stroma lamellae (not shown) in accordance with previous studies [14,15]. This clearly confirms that most of the phosphorylated LHC-II found in the stroma lamellae originates from the grana regions. When the amounts of the 27 kDa and the 25 kDa polypeptides in the D-100 fractions isolated at different times after phosphorylation were quantified (Table III), it was demonstrated that a time-dependent increase in the 25 kDa polypeptide relative to the 27 kDa polypeptide accompanied the migration of [^{32}P]phosphate-labelled LHC-II to the stroma-exposed thylakoid regions.

Both the Yeda press and digitonin fractionations of phosphorylated thylakoids (Table I and III) clearly show that the mobile pool of phosphorylated LHC-II have a high content of the 25 kDa polypeptide compared to the bulk of LHC-II. The polypeptide composition of the laterally migrating LHC-II population was estimated. This was done by using the observed ratios between the 27 kDa and the 25 kDa polypeptides of stroma lamellae vesicles before and after phosphorylation (Table III) and the previous finding [14] that the amount of LHC-II chlorophyll in the stroma lamellae increases from 13 to 21% following phosphorylation. Assuming that the polypeptides carry the same amount of chlorophyll, these values give a ratio close to 2 between the 27 kDa and the 25 kDa polypeptides in the migrating population of LHC-II compared to 4 for total LHC-II.

It could be argued that the increase in the 25

TABLE III

TIME-DEPENDENT INCORPORATION OF [^{32}P]PHOSPHATE INTO TOTAL LHC-II AND EFFECTS OF PHOSPHORYLATION ON THE RATIO BETWEEN THE 27 kDa AND 25 kDa APOPOLYPEPTIDES OF INTACT THYLAKOIDS AND STROMA LAMELLAE

Thylakoids were illuminated for 2 min in the presence of [γ-^{32}P]ATP. Digitonin was added after a chase period of 0, 10 or 30 min. The stroma lamellae fraction (D-100) was collected by differential centrifugation. Total incorporation of [^{32}P]phosphate and the relative amounts of the 27 kDa and 25 kDa apopolypeptides were determined as described in legends of Table I and II. For comparison, the ratio before phosphorylation (control) between the two apopolypeptides in isolated stroma lamellae is included.

Chase period (min)	Tot. incorp. of [^{32}P]phosphate in LHC-II (cpm)		27/25 polypeptide ratio in stroma lamellae
	intact thylakoids	stroma lamellae	
Control			4.3
0	2610	2180	3.6
10	2650	4220	3.1
30	2680	5870	3.0

kDa polypeptide relative to the 27 kDa polypeptide in the stroma lamellae vesicles upon phosphorylation could simply indicate proteolytic degradation of the 27 kDa polypeptide, which then could lose a 2 kDa segment [22,30,40]. However, this explanation cannot be applicable, since the 2 kDa segment lost upon proteolysis also carries the phosphorylation sites [40,41]. Thus, proteolytic degradation of the 27 kDa polypeptide would result in a 25 kDa polypeptide with a low specific phosphorylation. In contrast, as shown in Table II, the 25 kDa polypeptide of the stroma lamellae vesicles showed the highest specific phosphorylation of all samples tested.

In this and previous studies [14,17,18], we report that although phosphorylated LHC-II is found primarily in the stroma lamellae, significant amounts remain in the grana regions even 2 h after phosphorylation. This has also been found by Kyle and coworkers [11,15] who suggest that there are two pools of LHC-II, one tightly bound to the Photosystem II core and one structurally free to migrate from grana to stroma lamellae regions upon phosphorylation. Our present findings suggest that the mobile and immobile LHC-II subpopulations have different polypeptide compositions.

The size of the LHC-II units that migrate laterally upon phosphorylation is 8 nm as revealed by freeze-fracture electron microscopy [11]. This size excludes the possibility that the apopolypeptides migrate as individual units; instead, they have to be organized in clusters possible containing six units [42,43]. It remains to be determined whether each mobile unit contains four 27 kDa and two 25 kDa polypeptides or each cluster contains only one type of polypeptide. The physiological significance of the different polypeptide composition of the two LHC-II pools is at present not obvious. Possibly, the composition of the mobile LHC-II, containing a high proportion of the 25 kDa polypeptide, makes it particularly suited for functional interaction with Photosystem I located in the stroma lamellae.

Acknowledgements

We thank Dr. Bengt Jergil for supplying [γ-^{32}P]ATP. U.K.L. acknowledges the receipt of a fellowship from the Lennander Foundation. This study was supported by the Swedish Natural Science Research Council.

References

1 Anderson, J.M. and Andersson, B. (1982) Trends Biochem. Sci. 7, 288–292
2 Andersson, B. and Anderson, J.M. (1980) Biochim. Biophys. Acta 593, 427–440
3 Berzborn, R.J., Müller, D., Roos, P. and Andersson, B. (1981) in Photosynthesis (Akoyunoglu, G., ed.) Vol. 2, pp. 107–119, Balaban International Science Service, Philadalphia PA.
4 Andersson, B. and Haehnel, W. (1982) FEBS Lett. 146, 13–17
5 Anderson, J.M. and Melis, A. (1983) Proc. Natl. Acad. Sci. USA 80, 745–749
6 Barber, J. (1982) Annu. Rev. Plant Physiol. 33, 261–295
7 Allen, J.F., Bennett, J., Steinback, K.E. and Arntzen, C.J. (1981) Nature 291, 25–29
8 Haworth, P., Kyle, D.J., Horton, P. and Arntzen, C.J. (1982) Photochem. Photobiol. 36, 743–748
9 Bennett, J. (1983) Biochem. J. 212, 1–13
10 Horton, P. (1983) FEBS Lett. 152, 47–52
11 Kyle, D.J., Staehelin, L.A. and Arntzen, C.J. (1983) Arch. Biochem. Biophys. 222, 527–541

12 Telfer, A., Hodges, M., Millner, P.A. and Barber, J. (1984) Biochim. Biophys. Acta 766, 554–562
13 Biggins, J. (1982) Biochem. Biophys. Acta 679, 479–482
14 Larsson, U.K., Jergil, B. and Andersson, B. (1983) Eur. J. Biochem. 136, 25–29
15 Kyle, D.J., Kuang, T.-Y., Watson, J.L. and Arntzen, C.J. (1984) Biochim. Biophys. Acta 765, 89–96
16 Owens, G.C. and Ohad, I. (1983) Biochim. Biophys. Acta 722, 234–241
17 Andersson, B., Åkerlund, H.-E., Jergil, B. and Larsson, C. (1982) FEBS Lett. 149, 181–185
18 Larsson, U.K., Jergil, B., Larsson, C., Åkerlund, H.-E. and Andersson, B. (1984) in Advances in Photosynthesis Research (Sybesma, C., ed.), Vol. III, pp. 187–190, Martinus Nijhoff/Dr. W. Junk Publishers, Dordrecht
19 Burke, J.J., Ditto, C.L. and Arntzen C.J. (1978) Arch. Biochem. Biophys. 187, 252–263
20 Ryrie, I.J., Anderson, J.M. and Goodchild, D.J. (1980) Eur. J. Biochem. 107, 345–354
21 Delapelaire, P. and Chua, N.-H. (1981) J. Biol. Chem. 256, 9300–9307
22 Andersson, B., Anderson, J.M. and Ryrie, I.J. (1982) Eur. J. Biochem. 123, 465–472
23 Süss, K.-H. (1983) Photobiochem. Photobiophys. 5, 317–324
24 Schmidt, G.W., Bartlett, S.G., Grossman, A.R., Cashmore, A.R. and Chua, N.-H. (1981) J. Cell Biol. 91, 468–478
25 Apel, K. (1977) Bichim. Biophys. Acta 462, 390–402
26 Chua, N.-H. and Blomberg, F. (1979) J. Biol. Chem. 254, 215–223
27 Hoober, J.K., Millington, R.H. and D'Angelo, L.P. (1980) Arch. Biochem. Biophys. 202, 221–234
28 Cuming, A.C. and Bennett, J. (1981) Eur. J. Biochem. 118, 71–80
29 Bennett, J., Markwell, J.P., Skrdla, M.P. and Thornber, J.P. (1981) FEBS Lett. 131, 325–330
30 Thaler, T., Kühlbrandt, W. and Mühlethaler, K. (1984) in Advances in Photosynthesis Research (Sybesma, C., ed.), Vol. II, pp. 121–124, Martinus Nijhoff/Dr. W. Junk Publishers, Dordrecht
31 Andersson, B., Åkerlund, H.-E. and Albertsson, P.Å. (1976) Biochim. Biophys. Acta 423, 122–132
32 Andersson, B. and Åkerlund, H.-E. (1978) Biochim. Biophys. Acta 503, 462–472
33 Andersson, B. (1984) in Advances in Photosynthesis Research (Sybesma, C., ed.), Vol. III, pp. 223–226, Martinus Nijhoff/Dr. W. Junk Publishers, Dordrecht
34 Arnon, D.J. (1949) Plant Physiol. 24, 1–15
35 Anderson, J.M., Waldron, J.C. and Thorne, S.W. (1978) FEBS Lett. 92, 227–233
36 Laemmli, U.K. (1970) Nature 227, 680–685
37 Ferguson, K.A. (1964) Metabolism 13, 985–1002
38 Bar-Nun, S., Schantz, R. and Ohad, I. (1977) Biochim. Biophys. Acta 459, 451–467
39 Bennett, J., Steinback, K.E. and Arntzen, C.J. (1980) Proc. Natl. Acad. Sci. USA 77, 5253–5257
40 Mullet, J. E. (1983) J. Biol. Chem. 258, 9941–9948
41 Bennett, J. (1980) Eur. J. Biochem. 104, 85–89
42 McDonnel, A. and Staehelin, L.A. (1980) J. Cell Biol. 84, 40–56
43 Kühlbrandt, W., Thaler, T. and Wehrli, E. (1983) J. Cell Biol. 96, 1414–1424