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Regular paper

Changes in composition of membrane proteins accompanying the regulation of PS I/PS II stoichiometry observed with *Synechocystis* PCC 6803

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Abstract

Changes in composition of membrane proteins in *Synechocystis* PCC 6803 induced by the shift of light regime for photosynthetic growth were studied in relation to the regulation of PS I/PS II stoichiometry. Special attention was paid to the changes in abundance of proteins of PS I and PS II complexes. Composition was examined using a LDS–PAGE and a quantitative enzyme immunoassay. Abundance of PsaA/B polypeptides and the PsaC polypeptide of the PS I complex, on a per cell basis, increased under the light regime exciting preferentially PS II and decreased under the light regime exciting mainly PS I. Similar changes were observed with polypeptides of 18.5, 10 and 8.5 kDa. The abundance of other proteins associated with membranes, including PsbA polypeptide of the PS II complex, was fairly constant irrespective of light regime. These results are consistent with our previous observations with other strains of cyanophytes (*Anabaena variabilis* M2 and *Synechocystis* PCC 6714) that PS I is the variable component in changes in PS I/PS II stoichiometry in response to changing light regimes for photosynthesis.

Abbreviations: CBB – Coomassie brilliant blue; Chl – chlorophyll; EIA – enzyme immunoassay; LDS – lithium dodecyl sulfate; PAGE – polyacrylamide gel electrophoresis; PS – photosystem; PVDF – polyvinylidene difluoride

Introduction

In oxygenic photosynthesis electron transport in the thylakoid system is driven by the cooperative action of the two photosystems, PS I and PS II. The incident light regime for photosynthetic growth does not necessarily provide for a balance between PS I and PS II actions. When an imbalance occurs, cells can adjust the stoichiometry between PS I and PS II in the thylakoid system, so as to balance their actions under such a light regime (Murakami and Fujita 1988, Melis et al. 1989, Chow et al. 1990, Murakami and Fujita 1991).

In cyanophytes, the ratio of PS I to PS II becomes higher under light regimes exciting preferentially PS II, and the ratio is lowered under the light regimes exciting mainly PS I

(Myers et al. 1978, 1980, Fujita et al. 1985, 1987a,b, Manodori and Melis 1986a,b). Our previous studies for *A. variabilis* M2 (Kawamura et al. 1979) and for *Synechocystis* PCC 6714 (Fujita et al. 1987a, Fujita and Murakami 1987) have indicated that the abundance of PS I is changed in response to light regime. The change was found to be due to the control of formation of PS I during cell growth (Fujita et al. 1988). These results have been obtained mainly by spectrophotometric and kinetic determination of components involved in the photochemical reactions of the two photosystems. The present study aims at confirming our previous observations by determining the levels of membrane-bound proteins in cells grown under different light regimes. The results indicate that the levels of PS I determined by the PsaA/B and the PsaC polypeptides are variable in response to light regime while PS II levels, as determined by the PsbA polypeptide, remain constant.

Material and methods

Synechocystis PCC 6803 was grown in modified Detmer's medium (Watanabe 1960), but at double-strength of K_2HPO_4. Glucose at 0.1% (w/v) was added to the medium. Cells were illuminated with a weak orange light exciting mainly PS II ($3\,W\,m^{-2}$, we call PS II light) or a weak red light exciting mainly PS I ($4\,W\,m^{-2}$, we call PS I light) as described previously (Fujita et al. 1985). Addition of glucose accelerated cell growth but did not affect the changes in PS I/PS II stoichiometry induced by light quality, similar to the case of *Synechocystis* PCC 6714 (Fujita et al. 1987b). Cells were grown for more than 8 days under respective light regimes. The exponential growth phase was maintained by dilution with the fresh medium. Growth constants under the two light regimes were almost identical, 1.0 and $0.92\,d^{-1}$ under PS I and PS II light, respectively. Under a light microscope, no difference was found in sizes and shapes of cells of the two types.

Cells in the late-exponential growth phase were suspended in 50 mM Tris–HCl (pH 7.6), 2 mM EDTA and protease inhibitors (0.01% (w/v) phenylmethylsulfonyl fluoride, 1 mM 6-amino-n-caproic acid and 1 mM benzamidine-HCl). Cell suspensions were passed three times through a chilled French pressure cell at $1100\,Kg/cm^2$. Cell wall fragments and unbroken cells were removed by centrifugation at $6000 \times g$ for 10 min. Membrane fractions were collected by centrifugation at $100\,000 \times g$ for 1 h, and washed twice with 6 mM Tris–maleate (pH 7) containing the protease inhibitors described above.

LDS–PAGE of membrane proteins was performed at room temperature following the method of Delepelaire and Chua (1979) after slight modifications. Concentrations of urea and LDS in stacking and resolving gels were 6 M and 0.1% (w/v), respectively, and the acrylamide concentration in the latter gel, 12.5%. Anode and cathode buffers contained 25 mM Tris, 192 mM glycine, 0.1% LDS and 1 mM EDTA. As the markers of molecular mass, LMW protein standards (BIO-RAD, Richmond, CA) were used. Membrane proteins were solubilized in 25 mM Tris–HCl (pH 6.8) containing 3% LDS, 5% (v/v) 2-mercaptoethanol and 20% (w/v) glycerol on ice for 30 min (membrane concentration, equivalent to 50–250 μg Chl *a* ml^{-1}). Protein assay by the bicinchoninic acid method of Brown et al. (1989) indicated that more than 90% of membrane proteins was extracted by this treatment. After running gels, proteins were stained with CBB R-250 or blotted onto PVDF membrane (Millipore, Bedford, MA) in the mixture of 25 mM Tris, 192 mM glycine, 0.1% LDS, 1 mM EDTA and 20% (v/v) methanol. More than 80% of proteins in the gels was transferred to the PVDF membrane. Blotted membrane proteins were probed with anti-spinach CP1, anti-spinach PsaC or anti-PsbA antibodies (Johanningmeier 1987), and detected using a horse radish peroxidase conjugated to antibodies against the rabbit IgG. Blocking and washing treatments were performed as described by Takabe et al. (1986). Antigen-antibody complexes were detected in 10 mM phosphate (pH 7), 0.012% (w/v) 4-chloro-1-naphtol, 0.01% (v/v) H_2O_2 and 20% methanol. Photometric determinations were made at 580 nm or 300 nm as described by Domingo and Marco (1989).

P_{700} and cytochrome b_{559} (Cytb_{559}) were determined spectrophotometrically as described

previously (Fujita and Murakami 1987, Murakami and Fujita 1991) using the difference absorption coefficients of Hiyama and Ke (1972) for P_{700} and Garewal and Wasserman (1974) for Cytb_{559}, respectively. Chl *a* was determined spectrophotometrically with acetone extracts using the absorption coefficient of Mackinney (1941). Cell numbers were counted on a hemacytometer under a light microscope.

Results

Abundance of PS I and PS II polypeptides in cells grown under PS I and PS II light

LDS–PAGE resolved the membrane proteins of *Synechocystis* PCC 6803 into more than 20 species (Fig. 1A). Similar highly resolved patterns by LDS–PAGE were also obtained for membranes prepared from *Synechocystis* PCC 6714 (data not shown). Patterns of enzyme immunoassay (EIA) for the polypeptides of PS I and PS II complexes are shown in Fig. 1B, C and D. Molecular masses of PsaA/B polypeptides and PsaC polypeptide of the PS I complex and PsbA polypeptide of the PS II complex were found to be 60–70 (Fig. 1B), 10–11 (Fig. 1C) and 25–27 kDa (Fig. 1D), respectively. The band at 100 kDa in Fig. 1B is due to an associated form of the PsaA/B polypeptides. This complex was dissociated into species of 60–70 kDa when it was run again on the LDS–PAGE after extraction from the first gel (data not shown). The molecular size of PsbA polypeptide in the pattern of LDS–PAGE (Fig. 1D) is smaller than 32 kDa, which has been commonly recognized as a standard size of PsbA polypeptide (Marder et al. 1986). However, the PsbA polypeptide prepared from spinach leaves by the method of Marder et al. (1986) behaved identically to the PsbA polypeptide from *Synechocystis* PCC 6803 under our conditions for LDS–PAGE. Thus, the band at 25–27 kDa is not due to a degraded form of PsbA polypeptide, but PsbA polypeptide migrates slightly faster under our LDS–PAGE conditions. As observed previously with *Synechocystis* PCC 6714 (Fujita and Murakami 1987), the abundance of P_{700} in cells of *Synechocystis* PCC 6803 grown under PS II light was two-fold greater than that under PS I light when compared on a per cell basis (Table 1). Quantitative EIA revealed that the abundance of the PsaA/B and the PsaC polypeptides of PS I was also greater in the former cells, while no difference was observed in the abundance of the PsbA polypeptide of PS II in the two cell types. Since PsbA polypeptide has been known to turn over rapidly (cf. Mattoo et al. 1989), the value obtained for PsbA polypeptide does not

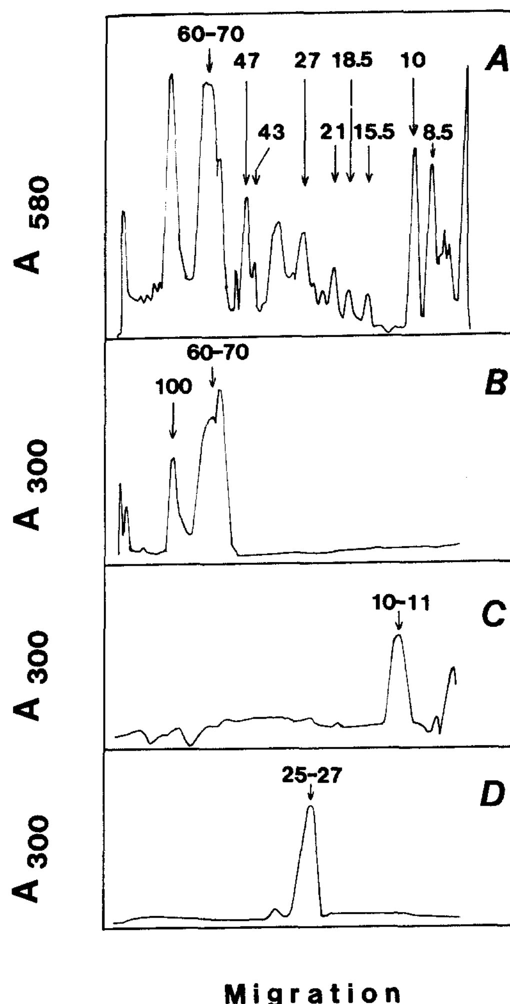

Fig. 1. LDS–PAGE patterns of membrane proteins obtained from *Synechocystis* PCC 6803 grown under PS II light. (A) Densitometric pattern of CBB-stained LDS-gel. (B) Densitometric pattern of membrane proteins blotted on PVDF and probed by EIA with anti-CP1 antibody; (C), with anti-PsaC antibody; (D) with anti-PsbA antibody. Numbers indicate molecular mass (kDa) of the respective polypeptides. For experimental details, see the text.

Table 1. Abundance, on a per cell basis, of P_{700}, PsaA/B polypeptides, PsaC polypeptide and PsbA polypeptide in cells of *Synechocystis* PCC 6803 grown under PS I and PS II light

Cell type	Relative abundance[a]				PS I/PS II[b]
	P_{700}	PsaA/B	PsaC	PsbA	
Grown under PS II light					
Exp. 1	100[c]	100	100	100	3.0
2	82	81	95	125	–
3	99	91	97	106	–
Grown under PS I light					
Exp. 4	53	55	53	120	1.5
5	48	44	50	111	–
6	55	46	57	114	–

[a]Abundance, on a per cell basis, relative to that of respective components in Exp. 1 is presented.
[b]The ratios were calculated from the abundance of P_{700} and Cytb_{559} (cf. Fujita and Murakami 1987).
[c]Equivalent to 4.53×10^{-19} mol/cell.

necessarily correspond to the amount stably present in PS II complex. However, the abundance of Cytb_{559} in cells grown under two light regimes was also constant (3.0 and 3.2×10^{-19} mol/cell in cells grown under PS I and PS II light, respectively). The constant ratio of PsbA polypeptide to Cytb_{559} indicates that the value obtained in our experiments is safe from such a possible error.

The content of membrane proteins on a per cell basis, estimated from the patterns of CBB-strained LDS–PAGE gel, was 1.34 times greater in cells grown under PS II light than under PS I light. The difference suggests a possibility that development of thylakoids is not the same in the two cell types. However, the former cells contained PS I at two-fold greater amount than the latter cells. The difference only for the amount of PsaA/B polypeptides in the two cell types was as great as 50% of the difference for the total membrane proteins, indicating that most of difference in the contents of membrane proteins in the two cell types is attributed to the higher concentration of PS I in cells grown under PS II light. Difference in development of thylakoids is probably insignificant in the two cell types, and so the values in Table 1 can be recognized to correspond to the concentrations of PS I and PS II complexes in thylakoids. Therefore, the results obtained with *Synechocystis* PCC 6803 are consistent with our previous view that the change to a higher or lower PS I/PS II ratio in cyanophytes is due to changes in the abundance of the PS I complex (Fujita et al. 1987a, Fujita and Murakami 1987).

Stoichiometry between levels of P_{700} and PS I polypeptides during changes in PS I level induced by the shift of light regime

Table 1 also shows that the stoichiometry among three components of PS I complex, P_{700}, the PsaA/B polypeptides and the PsaC polypeptide, are constant in the two cell types. Further, this stoichiometry remained constant in the time courses of changes in PS I level induced by shifting light regime. These results are summarized in Fig. 2A for the stoichiometry between P_{700} and PsaA/B polypeptides and in Fig. 2B for that between PsaA/B and PsaC polypeptides. Regression lines in both cases cross the Y axis at, or nearly at, zero (Fig. 2A, B), indicating that changes in the levels of the three components of PS I complex are identical to each other. Stable assembly of PsaC polypeptide in PS I complex has been reported to require the *psa*D gene product (Zhao et al. 1990), which forms a part of the ferredoxin-binding site of the PS I complex. The level of the *psa*D gene product is probably changed similarly to that for PsaA/B and PsaC polypeptides. These results strongly suggest that changes in P_{700} levels observed upon the shift of light regime correspond to changes in the levels of complete PS I complexes.

We could not find any bands by EIA, which cross-reacted with anti-CP1 antibody but showed

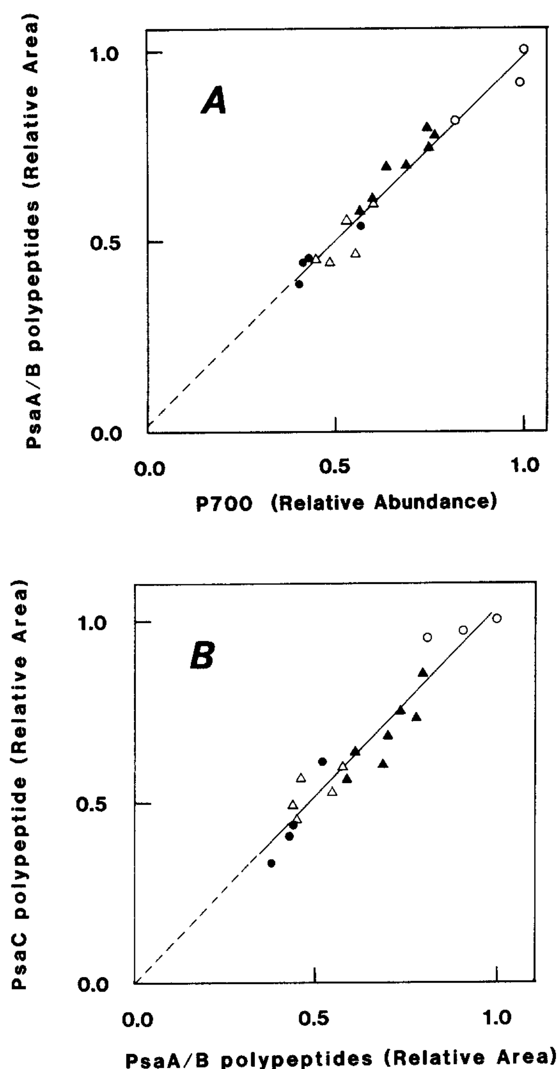

Fig. 2. Correlation between abundance of PsaA/B polypeptides and that of P_{700} (A) and between abundance of PsaA/B polypeptides and that of PsaC polypeptide (B). Data obtained from the experiments for the shift from PS II to PS I light (●) and from PS I to PS II light (▲) and from the cells grown under PS I light (△) and PS II light (○) are combined and plotted. Values of respective components relative to the maxima are plotted ($r^2 = 0.95$ for regressed line in (A) and 0.90, in (B)). For experimental details, see the text.

different molecular mass, except for the band at 100 kDa, which is the associated form of PsaA/B polypeptides (Fig. 1B). This was true even when PS I formation was accelerated by the shift of light regime. Accumulation of precursor(s) of the PsaA/B polypeptides may not occur at levels detectable by EIA. The band(s) cross-reacting with anti-PsaC antibody was always found in the region for peptides of very small molecular mass (Fig. 1C). Occurrence of this band was independent of light regime. Our LDS–PAGE system cannot resolve such small peptides, and so the nature of the band(s) is not clear at present.

Besides the results for PsaA/B and PsaC polypeptides described above, changes in the abundance induced by the shift of light regime were observed for three other membrane proteins detected by CBB-staining. As shown in Figs. 3A and 4A, the direction of the change was the same as that for known PS I polypeptides; a decrease occurs under PS I light, and an increase occurs under PS II light. The 10 kDa band appears to correspond to the PsaC polypeptide in its molecular mass. However, the PsaC polypeptide is poorly stained by CBB (Koike et al. 1989), and so the 10 kDa band detected by CBB-staining may contain polypeptide(s) other than the PsaC polypeptide, such as the PsaE polypeptide (Chitnis et al. 1989). Changes in the levels of the 18.5 kDa polypeptide were much marked than those in PS I polypeptides (Fig. 3A, 4A); the difference caused by the shift of light regime was more than double that for known PS I polypeptides. The polypeptide may not be a component of PS I complex, though the apparent molecular mass is similar to that of the *psa*D or *psa*F gene product (Alhadeff et al. 1988, Reilly et al. 1988, Wynn and Malkin 1988, Koike et al. 1989, Franzén et al. 1989, Chitnis et al. 1991). However, if the band corresponds to one of, or both of, these PS I polypeptides, the pattern suggests that such the polypeptide(s) is overproduced when PS I formation is stimulated under PS II light.

In contrast, the abundance of the 47, 43, 27, 21 and 15.5 kDa polypeptides remained fairly constant (Figs. 3B and 4B), similar to the abundance of the PsbA polypeptide (Table 1) upon the shift of light regime in either direction. Some of these must be components of PS II complex. Further characterization of these polypeptides is now in progress. As far as has been examined, the abundance of all peptides detected by our LDS–PAGE shows only changes of PS I- or PS II-type upon the shift of light regime. Other types of changes, such as a decrease under PS II light or an increase under PS I light, could not be observed.

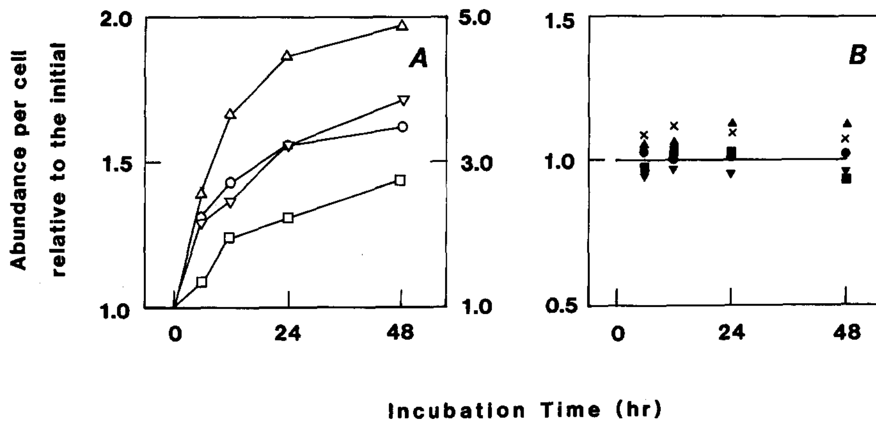

Fig. 3. Changes in abundance of membrane proteins in *Synechocystis* PCC 6803 induced by the shift of PS I to PS II light. Abundance, on a per cell basis, of each polypeptide relative to that at the time zero is plotted against the time after the shift of light. Light was shifted at time zero. In (A) abundance of 18.5 (○), 10 (□) and 8.5 kDa (△) polypeptides are plotted, and in (B), that of 47 (●), 43 (■), 27 (▲), 21 (▼) and 15.5 (×) kDa polypeptides. Abundance was determined by the peak area of each polypeptide in the densitograms stained with CBB. As a reference, changes in P_{700} levels (▽) are presented. The scale for abundance of 18.5 kDa polypeptide in (A) is twice larger. For experimental details, see the text.

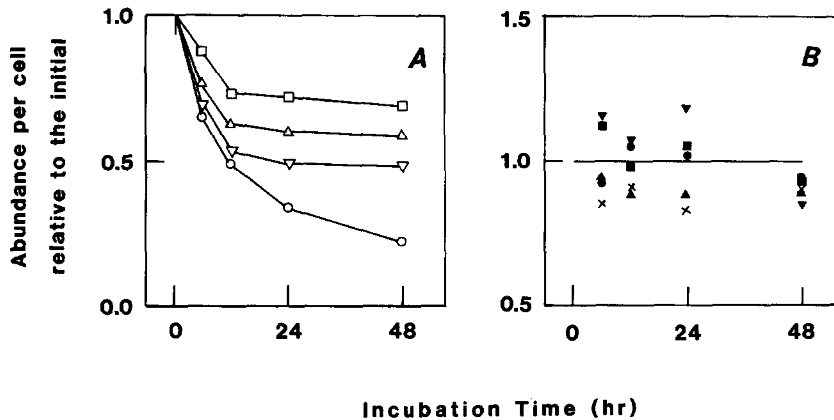

Fig. 4. Changes in abundance of membrane proteins in *Synechocystis* PCC 6803 induced by the shift of PS II to PS I light. For explanation of the figure, see Fig. 3.

Discussion

Results of the present study for *Synechocystis* PCC 6803 are consistent with those of our previous studies for *A. variabilis* M2 (Kawamura et al. 1979) and for *Synechocystis* PCC 6714 (Fujita and Murakami 1987) in that PS I is the variable component in changes in PS I/PS II stoichiometry in response to the light regime for photosynthesis. However, Cunningham et al. (1990) have reported that in the red alga *Porphyridium cruentum*, the abundance of both photosystems is changed by a shift of light regime. They found that the level of PS I increases under PS II light similarly to our observation with cyanophytes, but the PS II level decreases at the same time; PS I light induced a decrease in PS I and an increase in PS II level. We have also found a similar variation of PS II level in the red alga *Porphyra yezoensis* (Abe et al. in preparation). The different patterns in the systems of different phyla suggest the occurrence of different types of regulation for PS I/PS II stoichiometry in the two phyla. However, we have also found a variation of PS II level in the marine cyanophyte *Synechococcus* sp. NIBB 1071, which contains

phycobilisomes (PBS) associated with multiple PS II centers (Murakami et al. in preparation). PBS in both *Porphyridium cruentum* (Ley 1984, Ohki et al. 1987) and *Porphyra yezoensis* (Abe et al. in preparation) are associated with multiple PS II centers, while the PBS in *A. variabilis* M2 (Ohki et al. 1987) and *Synechocystis* PCC 6714 (Fujita and Murakami 1987) is an antenna for only one PS II center. This stoichiometric relationship between PBS and PS II centers may correlate to the difference in the patterns of changes in PS I/PS II stoichiometry. However, the reason is not clear at present.

In etiolated barley seedlings, the formation of PsaA/B polypeptides on the membrane-bound polysomes and their assembly are strictly regulated by Chl *a* supply (Klein et al. 1988, Eichacker et al. 1990). Results of the present study indicate that (1) PsaA/B polypeptides are always present at constant stoichiometry with P_{700}, and (2) accumulation of precursors or degraded products is insignificant even when the rate of the synthesis of PS I is accelerated or suppressed upon the shift of light regime. These features suggest that PS I formation in our case is controlled under a similar mechanism to that for the greening of etiolated seedlings. Our previous finding that suppression of Chl *a* synthesis causes a decrease in PS I level even under PS II light (Fujita et al. 1990) supports this idea.

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References

Alhadeff M, Lundell DJ and Glazer AN (1988) Structural studies on cyanobacterial Photosystem I. Purification and characterization of two low molecular weight polypeptides. Arch Microbiol 150: 482–488

Brown RE, Jarvis KL and Hyland KJ (1989) Protein measurement using bicinchoninic acid: Elimination of interfering substances. Anal Biochem 180: 136–139

Chitnis PR, Reilly PA, Miedel MC and Nelson N (1989) Structure and targeted mutagenesis of the gene encoding 8-kDa subunit of Photosystem I from the cyanobacterium *Synechocystis* sp. PCC 6803. J Biol Chem 264: 18374–18380

Chitnis PR, Purvis D and Nelson N (1991) Molecular cloning and targeted mutagenesis of the gene *psa*F encoding subunit III of Photosystem I from the cyanobactierum *Synechocystis* sp. PCC 6803. J Biol Chem 266: 20146–20151

Chow WS, Melis A and Anderson JM (1990) Adjustments of photosystems stoichiometry in chloroplasts improve the quantum efficiency of photosynthesis. Proc Natl Acad Sci USA 87: 7502–7506

Cunningham FX Jr, Dennenberg RJ, Jursinic PA and Gantt E (1990) Growth under red light enhances Photosystem II relative to Photosystem I and phycobilisomes in the red alga *Porphyridium cruentum*. Plant Physiol 93: 888–895

Delepelaire P and Chua N-H (1979) Lithium dodecyl sulfate/polyacrylamide gel electrophoresis of thylakoid membranes at 4 °C: Characterizations of two additional chlorophyll *a*-protein complexes. Proc Natl Acad Sci USA 76: 111–115

Domingo A and Marco R (1989) Visualization under ultraviolet light enhances 100-fold the sensitivity of peroxidase-stained blots. Anal Biochem 182: 176–181

Eichacker LA, Soll J, Lauterbach P, Rudiger W, Klein RR and Mullet JE (1990) In vitro synthesis of chlorophyll *A* in the dark triggers accumulation of chlorophyll *A* apoproteins in barley etioplasts. J Biol Chem 265: 13566–13571

Franzén L-G, Frank G, Zuber H and Rochaix J-D (1989) Isolation and characterization of cDNA clones encoding the 17.9 and 8.1 kDa subunits of Photosystem I from *Chlamydomonas reinhardtii*. Plant Mol Biol 12: 463–474

Fujita Y and Murakami A (1987) Regulation of electron transport composition in cyanobacterial photosynthetic system: Stoichiometry among Photosystem I and II complexes and their light-harvesting antennae and cytochrome $b_6 f$ complex. Plant Cell Physiol 28: 1547–1553

Fujita Y, Ohki K and Murakami A (1985) Chromatic regulation of photosystem composition in the photosynthetic system of red and blue-green algae. Plant Cell Physiol 26: 1541–1548

Fujita Y, Ohki K and Murakami A (1987a) Chromatic regulation of photosystem composition in the cyanobacterial photosynthetic system: Kinetic relationship between change of photosystem composition and cell proliferation. Plant Cell Physiol 28: 227–234

Fujita Y, Murakami A and Ohki K (1987b) Regulation of photosystem composition in the cyanobacterial photosynthetic system: the regulation occurs in response to the redox state of the electron pool located between the two photosystems. Plant Cell Physiol 28: 283–292

Fujita Y, Murakami A, Ohki K and Hagiwara N (1988) Regulation of photosystem composition in cyanobacterial photosynthetic system: Evidence indicating that Photosystem I formation is controlled in response to the electron transport state. Plant Cell Physiol 29: 557–564

Fujita Y, Murakami A and Ohki K (1990) Regulation of the stoichiometry of thylakoid components in the photosyn-

thetic system of cyanophytes: Model experiments showing that control of the synthesis or supply of Chl *a* can change the stoichiometric relationship between the two photosystems. Plant Cell Physiol 31: 145–153

Garewal HS and Wasserman AR (1974) Triton X-100-4M urea as an extraction medium for membrane proteins. I. Purification of chloroplast cytochrome b_{559}. Biochemistry 13: 4063–4071

Hiyama T and Ke B (1972) Difference spectra and excitation coefficient of P_{700}. Biochim Biophys Acta 267: 160–171

Johanningmeier U (1987) Expression of the *psb*A gene in *E. coli*. Z Naturforsch 42c: 755–757

Kawamura M, Mimuro M and Fujita Y (1979) Quantitative relationship between two reaction centers in the photosynthetic system of blue-green algae. Plant Cell Physiol 20: 697–705

Klein RR, Gamble PE and Mullet JE (1988) Light-dependent accumulation of radiolabeled plastid-encoded chlorophyll *a*-apoproteins requires chlorophyll *a* I. Analysis of chlorophyll-deficient mutants and phytochrome involvement. Plant Physiol 88: 1246–1256

Koike H, Ikeuchi M, Hiyama T and Inoue Y (1989) Identification of Photosystem I components from the cyanobacterium, *Synechococcus vulcanus* by N-terminal sequencing. FEBS Lett 253: 257–263

Ley AC (1984) Effective absorption cross-sections in *Porphyridium cruentum*. Implications for energy transfer between phycobilisomes and Photosystem II reaction centers. Plant physiol 74: 451–454

Mackinney G (1941) Absorption of light by chlorophyll solutions. J Biol Chem 140: 315–322

Manodori A and Melis A (1986a) Light-quality regulates photosystem stoichiometry in cyanobacteria. In: Akoyunoglou G and Senger H (eds) Regulation of Chloroplast Differentiation, pp 653–662. Alan R. Liss Inc., New York

Manodori A and Melis A (1986b) Cyanobacterial acclimation to Photosystem I or Photosystem II light. Plant Physiol 82: 185–189

Marder JB, Mattoo AK and Edelman M (1986) Identification and characterization of the *psb*A gene product: The 32-kDa chloroplast membrane protein. Methods in Enzymol 118: 384–396

Mattoo AK, Marder JB and Edelman M (1989) Dynamics of the Photosystem II reaction center. Cell 56: 241–246

Melis A, Mullineaux and Allen JF (1989) Acclimation of the photosynthetic apparatus to Photosystem I or Photosystem II light: Evidence from quantum yield measurements and fluorescence spectroscopy of cyanobacterial cells. Z Naturforsh 44c: 109–118

Murakami A and Fujita Y (1988) Steady state of photosynthesis in cyanobacterial photosynthetic systems before and after regulation of electron transport composition: Overall rate of photosynthesis and PS I/PS II composition. Plant Cell Physiol 29: 305–311

Murakami A and Fujita Y (1991) Steady state of photosynthetic electron transport in cells of the cyanophyte *Synechocystis* PCC 6714 having different stoichiometry between PS I and PS II: Analysis of flash-induced oxidation-reduction of cytochrome *f* and P_{700} under steady state of photosynthesis. Plant Cell Physiol 32: 213–222

Myers J, Graham J-R and Wang RT (1978) On spectral control of pigmentation in *Anacystis nidulans* (Cyanophyceae). J. Phycol 14: 513–518

Myers J, Graham J-R and Wang RT (1980) Light harvesting in *Anacystis nidulans* studied in pigment mutants. Plant Physiol 66: 1144–1149

Ohki K, Okabe Y, Murakami A and Fujita Y (1987) A comparative study of quantitative relationships between phycobiliproteins and Photosystem II in cyanobacteria and red algae. Plant Cell Physiol 28: 1219–1226

Reilly P, Hulmes JD, Pan Y-CE and Nelson N (1988) Molecular cloning and sequencing of the *psa*D gene encoding subunit II of Photosystem I from the cyanobacterium, *Synechocystis* sp. PCC 6803. J Biol Chem 263: 17658–17662

Takabe T, Takabe T and Akazawa T (1986) Biosynthesis of P_{700}-chlorophyll *a* protein complex, plastocyanin, and cytochrome b_6/f complex. Plant Physiol 81: 60–66

Watanabe A (1960) List of algal strains in collection at the Institute of Applied Microbiology, University of Tokyo. J Gen Appl Microbiol 6: 283–292

Wynn RM and Malkin R (1988) Interaction of plastocyanin with Photosystem I: A chemical cross-linking study of the polypeptide that binds plastocyanin. Biochemistry 27: 5863–5869

Zhao J, Warren PV, Li N, Bryant DA and Golbeck JH (1990) Reconstitution of electron transport in Photosystem I with PsaC and PsaD proteins expressed in *Escherichia coli*. FEBS Lett 276: 175–180