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Characterization of genes that encode subunits of cucumber PS I complex by N-terminal sequencing

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N-terminal amino acid sequencing was carried out to characterize the genes of the cucumber PS I complex (PSI-100) that contains eight polypeptides and catalyzes the light-dependent transfer of electrons from plastocyanin to ferredoxin. The genes of all subunits except the 17.5 kDa polypeptide in PSI-100 have been identified. These are *psaA/psaB* (65/63 kDa), *psaD* (20 kDa), *psaE* (19.5 kDa), *psaF* (18.5 kDa), *psaH* (7.6 kDa), and *psaC* (5.8 kDa). The 17.5 kDa polypeptide is a new protein and is designated tentatively as the gene product of *psaM*. N-terminal amino-acid sequencing indicated the presence of two polypeptides in the 7.6 kDa band. One of these is the gene product of *psaH* and is essential for the activity of the PS I complex, and the other one is as yet unrecognized and largely depleted in the the PSI-100 complex. Gene products of *psaG, psaI,* and *psaK*, which have been proposed as the components of PS I complex, are not involved in the PSI-100 complex, but are involved in the PS I complex (PSI-200), which contains 120 chlorophyll per reaction center chlorophyll (P700) and light-harvesting chlorophyll *a/b* protein complexes. Three polypeptides (26, 23 and 22.5 kDa) are not involved in the PSI-100 and are assigned as the apo-protein of light-harvesting chlorophyll *a/b* protein complexes.

Introduction

The recent characterization of cDNAs and N-terminal amino-acid sequences for the subunits of the Photosystem I (PS I) complex has provided substantial information on the structure of individual components as well as on the topology of the complex [1–5]. Hitherto, eleven genes (*psaA–psaK*) have been proposed to encode the subunits of PS I complex [1–3]. Of these genes, the *psaA* and *psaB* have been shown to encode two large polypeptides to which the electron carriers P700, A_0, A_1 and F_X are thought to be bound [6]. The *psaC* gene encodes the apo-protein of two remaining electron acceptors F_A and F_B [7–9]. The *psaD* and *psaF* have been proposed as the genes which encode the ferredoxin- and plastocyanin-docking proteins, respectively [10–14]. The funtion of the *psaE* gene product has been tested by using the deletion mutant of *psaE* from *Synechocystis* sp. PCC 6803, but no positive function was determined [15]. The roles of other genes (*psaG-psaK*) are completely unknown.

Although extensive studies have been carried out on the polypeptide composition of the PS I complex, there is still uncertainty concerning the number of polypeptides in the PS I complex. For example, when the subunit compositions of PS I complexes from spinach [3,5] and barley [16] are compared, the polypeptides corresponding to 14 and 4 kDa of the barley PS I complex are not reported in the spinach PS I complex, whereas the polypeptides corresponding to the gene products of *psaG, psaK* and *psaJ* of the spinach PS I complex have not been reported in the barley PS I complex. Moreover, controversial results have been reported concerning whether or not the *psaG* and *psaI* gene products are associated with the spinach PS I core complex [3,5,17,18]. Similarity of subunit compositions and photochemical properties of PS I complexes from cyanobacteria and higher plants has been reported [3,19–21]. But, it is not clear whether or not light-harvesting chlorophyll *a/b* protein complexes

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Abbreviations: Chl, chlorophyll; PS I, Photosystem I; P700, Photosystem I reaction-center chlorophyll; LHCP I, light-harvesting Chl *a/b* protein complex associated with PS I complex; DCIP, 2,6-dichloroindophenol; PAGE, polyacrylamide gel electrophoresis; SDS, sodium dodecyl sulfate.

(LHCP I) in higher plants are essential for the electron transport from plastocyanin to ferredoxin, because LHCP I is absent in cyanobacteria.

PSI-100, which contains eight polypeptides, has a high NADP photoreduction activity (our unpublished data). This fact indicates that several genes of *psaA-psaK* are not involved in the PS I complex. It was interesting to investigate which genes are involved in the PSI-100 and the PSI-200 ('native PS I complex'). In this paper, we show that the genes encoding subunits of cucumber PSI-100 are *psaA, psaB, psaC, psaD, psaE, psaF, psaH*, and a new one (*psa M*) that encodes the 17.5 kDa polypeptide. It is also shown that *psaG, psaI, psaK* and LHCP I (26, 23 and 22.5 kDa) are not involved in the PSI-100 complex, but are involved in the PSI-200. The polypeptide compositions of PS I complexes from several species are compared and discussed.

Materials and Methods

The preparation of PSI-200, PSI-100, PSI-100S and PSI-DEAE will be described elsewhere (Takabe, Iwasaki, Hibino and Ando, T., unpublished data). The polypeptide compositions of PS I complexes were determined by sodium dodecyl sulfate polyacrylamide gel electrophoresis (SDS-PAGE) as will also be described. Chlorophyll (Chl) protein complexes were analyzed by SDS-PAGE containing 12.5% (v/v) acrylamide at 4 °C essentially according to the procedure of Anderson et al. [23]. The relative amounts of polypeptides in PS I complexes were estimated by scanning the Coomassie brilliant blue stained bands with a densitometer (Shimadzu Dual-Wavelength TLC Scanner CS-910). Fluorescence emission spectra at 77 K were measured using a Jasco FP-500 spectrometer, as previously described [24].

N-terminal amino acid sequencing was carried out as follows. The protein complex was subjected to SDS-PAGE as described above. The polypeptides separated were transferred to a PVDF filter (Immobilon, Millipore) and stained with Coomassie brilliant blue R. Bands of interest were excised and sequenced on a gas-phase protein sequencer (Applied Biosystems, model 470A). Before applying the subunit 13 (2.0 kDa polypeptide) onto a protein sequencer, the protein was treated in 0.25 M HCl solution for 12 h at room temperature.

Results and Discussion

N-terminal amino-acid sequencing

Since several genes of PS I complexes have been characterized, it was anticipated that N-terminal amino-acid sequencing could be used to identify the genes of the cucumber PS I complex. The polypeptide composition of 'native' PS I complex (PSI-200) isolated from cucumber cotyledons is shown in Fig. 1. It consists of thirteen major subunits. We have determined the N-terminal amino-acid sequences of ten polypeptides (subunits 5, 6, 7, 8, 9a, 9b, 10, 11, 12 and 13) and their results are shown in Fig. 2. The alignments with the corresponding sequences of other organisms are summarized in Fig. 3.

The sequence of subunit 11 (5.8 kDa) is highly homologous to that of *psaC* gene product of higher plants which carries the non-heme iron-sulfur centers F_A and F_B [7–9,25]. Since cysteine is the one residue which cannot be determined by our present sequencing system, it is likely that the four determined residues at positions 10, 13, 16 and 20 in middle of the analyzed sequence are presumably Cys that might be assumed to coordinate the iron-sulfur centers.

We have already isolated the *psaD* gene from cucumber cotyledons and identified that the subunit 5 (20 kDa) is a *psaD* gene product [14]. The result from N-terminal amino-acid sequencing of subunit 5 confirmed the result from nucleotide sequencing [14].

The N-terminal region of subunit 6 (19.5 kDa) shows a limited homology with the *psaE* gene product among higher plants [25–27]. In the N-terminal region of subunit 6 of cucumber, the contents of Pro and Ala are rich (eleven amino acids in nineteen amino-acid residues determined). This property is found in the *psaE* gene products isolated from barley and spinach [26,27]. Since the *psaD* gene products of higher plants have also high Ala and Pro contents [14,25,26,28–30], discrimination between the *psaD* and *psaE* gene products by only the contents of Ala and Pro would be

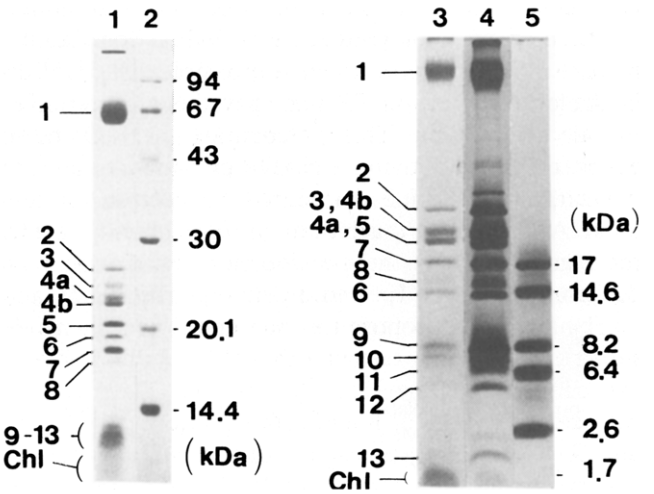

Fig. 1. The polypeptide compositions of PSI-200. SDS-PAGE was carried out as described in Materials and Methods. Lanes 1 and 2, according to Laemmli; lanes 3, 4 and 5, according to Schagger et al. Lanes 2 and 5 were molecular weight markers. Lanes 1, 2, and 3 were stained with Coomassie brilliant blue and lanes 4 and 5 were stained with silver. The Chl concentration of PSI-200 was 15 μg.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	(Reference)
Sub5	E	A	E	T	S	V	E	A	P	A	G	F	S	P	P	E	L	D	P	S	T	P	S											(14)
Sub6	X	D	E	A	A	P	P	P	A	A	T	A	P	X	A	A	X	T	E															(This study)
Sub7	D	I	S	G	L	T	P	X	K	E	S	K	Q	F	X	K	R	E	K	Q	Q	X	K	X	L	E								(This study)
Sub8	I	Q	A	D	X	P	T	F	Q	V	I	Q	D	D	N																			(This study)
Sub9a	X	V	X	E	D	Y	L	E	K	S	K	A	N	L	E	L	N	D	K	K	X	X	X	T										(This study)
Sub9b	X	Y	X	D	K	S	V	Y	F	D	L	E	D	K	G	N	T	X	G	Q	X	X	X	Y										(This study)
Sub10	E	L	N	P	S	L	V	I	S	L	S	X	G	L																				(This study)
Sub11	S	X	S	V	K	I	Y	D	T	X	I	G	X	T	Q	X	V	R	A	X	P	T	D	V										(This study)
Sub12	W	D	Y	I	G	S	P	T	N	V	I	M	V	I	S	T	S	L	M	L	F	A	G	R	F	G	L	A	P	S	A	N	R	(This study)
Sub13	M	X	X	L																														(This study)

Fig. 2. N-terminal amino-acid sequences of cucumber PS I complex. Amino-acid residues are designated by the standard one-letter abbreviations. Positions with unassigned residues are indicated by X. Only firm assignments are shown.

difficult. In the case of cucumber PS I complex, the subunit 5 was identified as the *psaD* gene product [14]. Therefore, the subunit 6 is presumably a *psaE* gene product.

The sequence of subunit 7 (18.5 kDa) is highly homologous to the *psaF* gene products isolated from higher plants [13,25,31,32] and *Chlamydomonas* [33] and identified as the *psaF* gene product. It has been shown (unpublished data) that plastocyanin cross-links to the subunit 7 of the PS I complex. These results are compatible with the view that the *psaF* gene product is the plastocyanin-docking protein [12,13].

The N-terminal amino-acid sequencing of subunits 8 (17.5 kDa) was also performed. The result of computer research of a homologous sequence with the subunit 8 indicated that there is no corresponding gene product in the polypeptides of PS I complexes so far reported for any organisms. This polypeptide is new and is essential for the activity of NADP photoreduction (our unpublished data). We designated this polypeptide tentatively as the gene product of *psaM*, because recently the gene of 14 kDa polypeptide from barley has been designated as *psaL* (personal communication).

The result of N-terminal amino acid sequence of subunit 9 (7.6 kDa) revealed that this subunit contains two different polypeptides, 9a and 9b. The result of computer research of homologous sequences with subunit 9a indicated the absence of any homologous sequence in any polypeptide of PS I complexes so far reported. On the other hand, the sequence of subunit 9b is highly homologous to those of the *psaH* gene products isolated from higher plants [25,34] and *Chlamydomonas* [35].

The sequence of subunit 10 (6.8 kDa) is highly homologous to those of the *psaG* gene products isolated from higher plants [25,31], *Chlamydomonas* [35] and cyanobacteria [21,36].

The sequence of subunit 12 (4.5 kDa) is highly homologous to that of the 5 kDa polypeptide of spinach PS I complex [17,18] and the P37 subunit of *Chlamydomonas* [35]. Its gene has recently been designated as *psaK* [21].

The N-terminal amino acid of the subunit 13 (2.0 kDa) was blocked. After blotting to a PVDF filter, the subunit 13 was treated in 0.25 M HCl solution for 12 h at room temperature and then subjected to amino-acid sequencing. Only two amino-acid residues (first Met and fourth Leu) in eleven Edman degradation steps were firmly assigned. Recently, the N-terminal amino-acid sequence of the 1.5 kDa polypeptide of the PS I complex from barley has been reported [16]. The sequence was homologous to the deduced sequence of tobacco ORF36 in chloroplast DNA [42] and the polypeptide was designated as the *psaI* gene product [16]. The N-terminal amino acid of the barley *psaI* gene product was also blocked. Although only two amino acids of cucumber subunit 13 were assigned, these two amino acids matched those of the *psaI* gene product of tobacco and barley [16,42] (data not shown). Thus, we would assign the subunit 13 as the *psaI* gene product.

Characterization of other subunits of the PS I complex

In the above, all subunits except five (1, 2, 3, 4a, and 4b) of PSI-200 were assigned by N-terminal sequencing. The remaining five subunits were characterized by using physicochemical techniques. When the PSI-200 complexes were analyzed by SDS-PAGE at 4 °C using

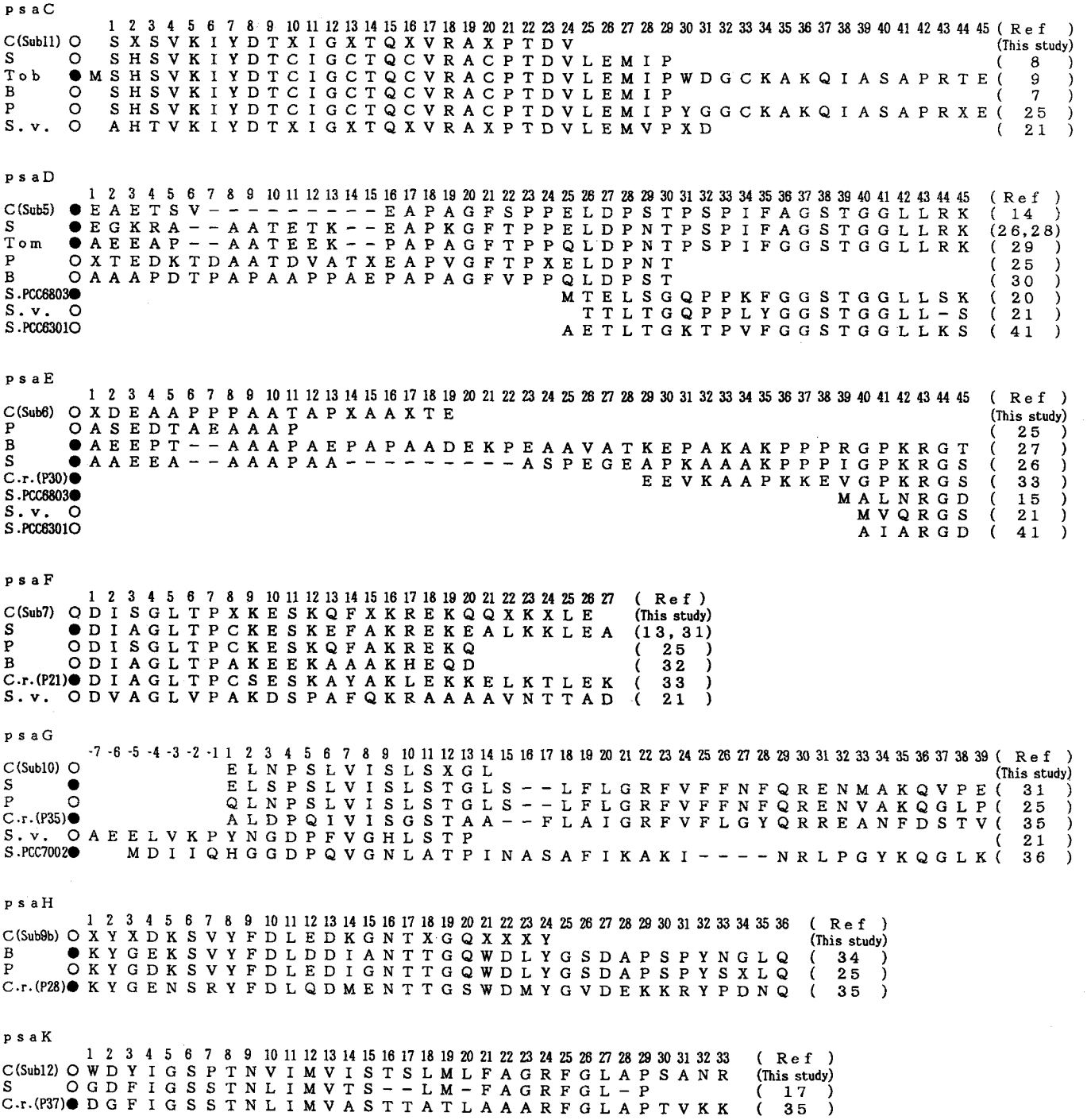

Fig. 3. Amino-acid sequences of N-terminal region of cucumber PS I subunits and their alignments with corresponding sequences of some organisms from higher plants, *Chlamydomonas*, and cyanobacteria. Amino-acid residues are designated by the standard one-letter abbreviations. Positions with unassigned residues are indicated by X and a hyphen denoted a deletion. C, S, P, B, Tom, Tob, C.r., S.PCC6301, S.PCC6803, S.PCC7002, and S.v. stand for cucumber, spinach, barley, tomato, tobacco, *Chlamydomonas reinhardtii, Synechocystis* PCC6301, *Synechocystis* PCC6803, *Synechocystis* PCC7002, and *Synechocystis vulcanus*, respectively. Open circles (○) indicate the sequence determined by amino acid sequencing and closed circles (●) indicates the sequence deduced from the nucleotide sequence.

the method of Anderson et al. [23], three different green bands (C1, C2 and C3) were resolved (Fig. 4A). SDS-PAGE of these Chl protein complexes under the denatured conditions indicated that the C1 fraction consisted mainly of subunit 1 (65/63 kDa) as shown in Fig. 4B. The C2 band consisted of two different subunits, 4a (23 kDa) and 4b (22.5 kDa), while the C3 band consisted of the subunit 2 (26 kDa). It was shown that the C1 band has the photochemical activity of P700 (data not shown) and subunit 1 was assigned as

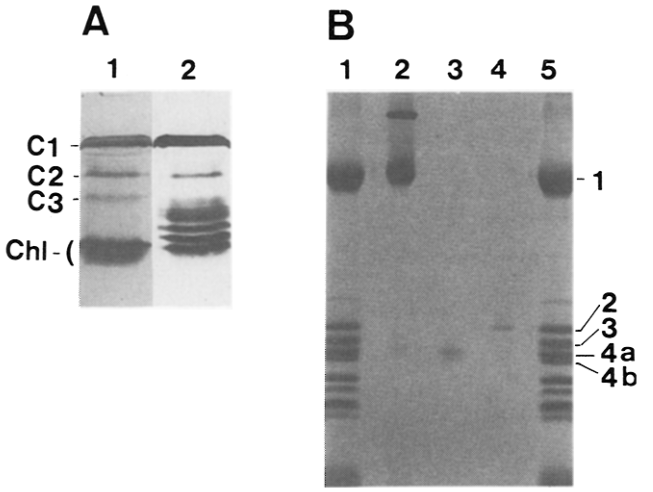

Fig. 4. (A) SDS-PAGE of PSI-200 under mild conditions at low temperature (4 ° C). The electrophoresis was carrid out as described in Materials and Methods. The Chl concentration of PSI-200 was 40 μg. Lane 1, unstained; lane 2, stained with Coomassie brilliant blue. (B) SDS-PAGE of C1, C2 and C3 bands under denatured conditions at room temperature. The green bands C1, C2 and C3 were excised and subjected to SDS-PAGE after dissociation. Lanes 1 and 5, PSI-200; lanes 2, 3 and 4, C1, C2 and C3, respectively. The Chl concentration of PSI-200 was 12 μg.

the P700-apoprotein. Next, low-temperature fluorescence emission spectra of three green bands were examined and their results are shown in Fig. 5. The C1

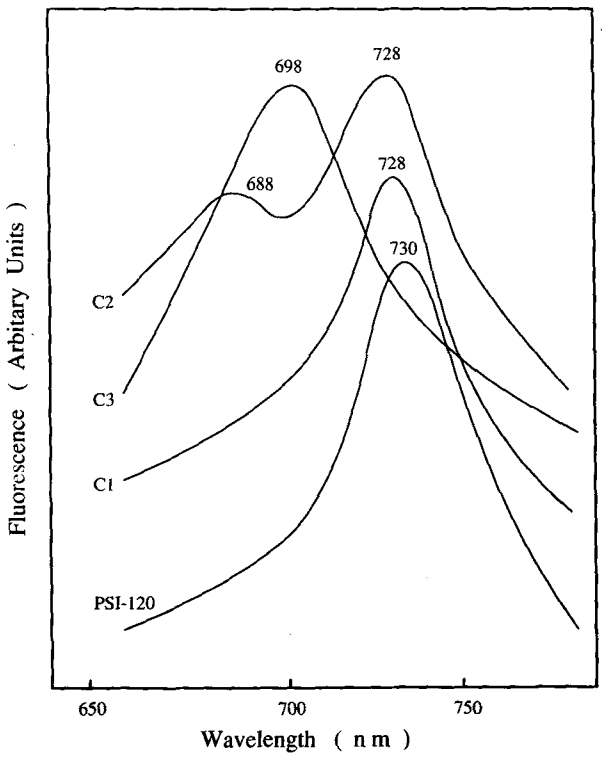

Fig. 5. Fluorescence emission spectra of PSI-200, C1, C2 and C3 at 77 K. Spectra were obtained using 435 nm excitation with a slit width of 5 nm and an emission slit width of 10 nm.

and C3 bands had emission maxima at 728 and 698 nm, respectively. The C2 band had two emission maxima of major one at 728 nm and minor one at 688 nm. These results indicate that PSI-200 contains two different LHCP I complexes (C2 and C3) and that the subunits 2 (26 kDa), 4a (23 kDa), and 4b (22 kDa) are the apoproteins of LHCP I. When the PSI-200 was treated with Triton X-100, the subunit 3 (24 kDa) was dissociated from the PSI-200 in concomitant with the loss of subunits 2, 4a and 4b. But this polypeptide could not be detected in sufficient amount in the C2 and C3 bands. Therefore, at the present time, we could not determine whether or not this polypeptide is the apoprotein of LHCP I.

Characterization of subunits of PSI-200, PSI-100, PSI-100S and PSI-DEAE

Four PS I complexes (PSI-200, PSI-100, PSI-100S and PSI-DEAE) isolated from cucumber cotyledons exhibited different activities (unpublished data). To compare the polypeptide compositions of the four PS I complexes by a more quantitative method, the relative amounts of subunits in the PSI-200, PSI-100, PSI-100S and PSI-DEAE were estimated from the relative intensities of bands stained with Coomassie brilliant blue R. The PSI-200 was used as the control and the results are shown in Table I. It should be mentioned that the relative amounts of polypeptides in the complexes change finely, depending on the extent of various treatments. Moreover, due to the poor resolution of bands on SDS gels and the different sensitivity of staining

TABLE I

Subunit composition of PSI-200, PSI-100, PSI-100S and PSI-DEAE

Subunit	Gene	Molecular mass (kDa)	Relative amount [a] (%)			
			PSI-200	PSI-100	PSI-100S	PSI-DEAE
1	*psaA / B*	65/63	100	100	100	100
2		26	100	20	5	60
3		24	100	20	5	60
4 [a]		23	100	20	5	60
4 [b]		22.5	100	20	5	60
5	*psaD*	20.3	100	100	100	100
6	*psaE*	19.5	100	100	100	100
7	*psaF*	18.5	100	100	75	30
8		17.5	100	100	100	100
9 [a]		7.6	100	40	n.d. [b]	20
9 [b]	*psaH*	7.6	100	100	n.d. [b]	100
10	*psaG*	6.8	100	20	5	50
11	*psaC*	5.8	100	100	100	100
12	*psaK*	4.5	100	30	5	50
13	*psaI*	2.0	100	30	30	20

[a] The relative amount of each subunit is expressed as the percent of PSI-200.

[b] n.d., not determined.

polypeptides by Coomassie brilliant blue, these values must be considered as tentative. Table I shows that the PSI-200 contains at least sixteen different polypeptides. As described above, it was found that the band at 7.6 kDa contains two polypeptides (9a and 9b). The polypeptides at 65/63, 20.3, 19.5 and 5.8 kDa in the PSI-100, PSI-100S and PSI-DEAE were completely retained, indicating that these polypeptides are common components of four PS I complexes. In comparison with PSI-200, the 18.5 kDa polypeptides was retained in PSI-100, but decreased about 25 and 70% in PSI-100S and PSI-DEAE, respectively. Other polypeptides, 26, 24, 23, 22.5, 6.8, 4.5 and 2.0 kDa are largely depleted in PSI-100, PSI-100S and PSI-DEAE. Interestingly, one of two polypeptides (subunit 9a) at 7.6 kDa was depleted about 60 and 80% in PSI-100 and PSI-DEAE, respectively, while other one (subunit 9b) remained constant in these complexes. One of the most remarkable differences among the three complexes (PSI-100, PSI-100S and PSI-DEAE) is the content of subunit 7 (18.5 kDa). The PSI-DEAE contains a low amount of this subunit, although relatively high amounts of other polypeptides (26, 24, 23, 22.5, 6.8, 4.5 and 2.0 kDa) are retained in this complex. From these results, we conclude that the eight polypeptides, subunit 1 (65/63 kDa), subunit 5 (20.3 kDa), subunit 6 (19.5 kDa), subunit 7 (18.5 kDa), subunit 8 (17.5 kDa), subunit 9b (7.6 kDa), and subunit 11 (5.8 kDa) are components of the active PS I complex (PSI-100).

The above-described results indicate that the genes which encode eight polypeptides of cucumber PSI-100 are *psaA/psaB* (subunit 1), *psaC* (subunit 11), *psaD* (subunit 5), *psaE* (subunit 6), *psaF* (subunit 7), *psaH* (subunit 9a) and *psaM* (subunit 8). Of these genes, the roles of five genes are now clear. The *psaA* and *psaB* genes encoding the P700-apoproteins [1,2,6]. *psaC* encodes the apo-protein of $F_{A/B}$ [7–9]. *psaD* and *psaF* encode the ferredoxin- and plastocyanin-binding proteins, respectively (Refs. 10–14 and our unpublished data). The role of *psaE* has been tested [15], but no positive function is known for this subunit. The role of *psaH* and *psaM* is completely unknown.

Comparison of subunit compositions of PS I complexes from different species

The polypeptide compositions of cucumber PS I complexes were compared with those from other species (Table II). Most of the PS I complexes have been classified as the 'native' and core complexes and their activities have been reported in only few cases (Refs 4, 12, 37 and our unpublished data). Therefore, it was difficult to compare the polypeptide compositions of PS I complexes from diffrent species. But the recent characterization of cDNAs and N-terminal amino-acid sequences for the subunits of PS I complexes will make it possible to compare the polypeptide compositions of PS I complexes. On the pea 'native' PS I complex, at least eleven polypeptides have been reported [38], of which three polypeptides were assigned as the LHCP I while the remaining eight polypeptides were assigned as the PS I core complex. Only partial assignment of genes for the pea PS I core complex was possible when the N-terminal amino-acid sequences had been reported by Dunn et al. [25]. We have compared the

TABLE II

Comparison of subunit compositions of PS I complexes from cucumber, spinach, barley, pea and Synechocystis

Gene	Function	Subunit	Cucumber		Spinach PS I		Barley PS I [c] (kDa)	Pea PS I core [d] (kDa)	*S. vulcanus* PS I [e] (kDa)
			PSI-200 (kDa)	PSI-100 (kDa)	native [a] (kDa)	core [b] subunit			
psaA/B	P700 binding	1	65/63	65/63	(CPI apo)	sub I	82/82	62/60	(CPI apo)
psaC	$Fe_{A/B}$ binding	11	5.8	5.8	9	sub VII	9	8	9.5
psaD	Fd docking	5	20.3	20.3	20	sub II	18	21	18
psaE		6	19.5	19.5	12	sub IV	16	13	9
psaF	PC docking	7	18.5	18.5	15	sub III	15	17	14
psaH		9b	7.6	7.6	10	sub VI	9.5	11	
psaM		8	17.5	17.5					
psaG		10	6.8		9	sub V		9	12
psaK		12	4.5		7				6.5
psaI		13	2.0		3.9		1.5		
psaL							14		
psaJ					4.1				4.1
	LHCP I	2	26		20				
	LHCP I	4a	23		18				
	LHCP I	4b	22.5						
		3	24		20.5		4		4.8
		9a	7.6		14				
					9				

[a] Ref. 3; [b] Ref. 5, 26, 31, 40; [c] Ref. 16, 39; [d] Ref. 25; [e] Ref. 21.

sequence data reported by Dunn et al. [25] with those of other species. As shown in Table II, eight subunits of pea PS I complex could be assigned as the genes products of *psaA/B* (62/60 kDa), *psaC* (8 kDa), *psaD* (21 kDa), *psaE* (13 kDa), *psaF* (17 kDa), *psaG* (9 kDa) and *psaH* (11 kDa). In the case of barly PS I complex, ten polypeptides have consistently been reported [16,39]. From N-terminal amino-acid sequencing and cDNA sequencing, the eight subunits were identified as the gene products of *psaA/B* (82/82 kDa), *psaC* (9 kDa), *psaD* (18 kDa), *psaE* (16 kDa), *psaF* (15 kDa), *psaH* (9.5 kDa) and *psaI* (1.5 kDa), although the 14 kDa polypeptide has been recently designated as the *psaL* gene product (personal communication). The structure of the 4 kDa polypeptide has not been reported. The eight polypeptides have been reported for the spinach PS I core complex [5,40]. Interestingly, it was found that the genes for the spinach PS I core complex [5,40] are the same as those of pea complex [25]. The polypeptide composition of the cucumber PS I complex (PSI-100) is similar to that of the spinach complex [5,40]. The only difference is the presence of the *psaG* gene product in the spinach PS I complex in place of the *psaM* gene product in the cucumber PS I complex. Concerning the *psaG* gene product, controversial results have been reported as to whether or not it is a component of the PS I core complex [3,5]. Ikeuchi et al. [3] have reported that the gene product of *psaG* was tightly associated with the 'native' spinach PS I complex, but easily depleted from the PS I core complex, which is compatible with our unpublished results from the cucumber PS I complex. Further studies are needed to clarify this point. The *psaM* gene is new and it could not be compared with those of other species.

After the pioneering work of Mullet et al. [38], it has been considered that the higher plant PS I complex consisted of the PS I core complex and LHCP I complexes. The present data indicated that LHCP I complexes and the gene products of *psaG, psaI, psaJ* and *psaK* are not involved in PSI-100 and are not necessary for the activity of NADP photoreduction, which is compatible with the facts that the PS I complex from cyanobacteria has no LHCP I complex but shows almost the same photochemical activity with the higher plant PS I complex [1–3]. Threfore, it might be important to compare the polypeptide compositions of cyanobacteria PS I complex and higher plant PS I 'core' complex, but not 'native complex'. These facts raise a question concerning the function of LHCP I and gene products of *psaG, psaI, psaJ* and *psaK* in photosynthesis.

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