PsaK2 Subunit in Photosystem I Is Involved in State Transition under High Light Condition in the Cyanobacterium Synechocystis sp. PCC 6803*

Received for publication, January 11, 2005, and in revised form, March 18, 2005
Published, JBC Papers in Press, April 11, 2005, DOI 10.1074/jbc.M500369200

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To avoid the photodamage, cyanobacteria regulate the distribution of light energy absorbed by phycobilisome antenna either to photosystem II or to photosystem I (PSI) upon high light acclimation by the process so-called state transition. We found that an alternative PSI subunit, PsaK2 (sll0629 gene product), is involved in this process in the cyanobacterium Synechocystis sp. PCC 6803. An examination of the subunit composition of the purified PSI reaction center complexes revealed that PsaK2 subunit was absent in the PSI complexes under low light condition, but was incorporated into the complexes during acclimation to high light. The growth of the psaK2 mutant on solid medium was inhibited under high light condition. We determined the photosynthetic characteristics of the wild type strain and the two mutants, the psaK1 (srr0390) mutant and the psaK2 mutant, using pulse amplitude modulation fluorometer. Non-photochemical quenching, which reflects the energy transfer from phycobilisome to PSI in cyanobacteria, was higher in high light grown cells than in low light grown cells, both in the wild type and the psaK1 mutant. However, this change of non-photochemical quenching during acclimation to high light was not observed in the psaK2 mutant. Thus, PsaK2 subunit is involved in the energy transfer from phycobilisome to PSI under high light condition. The role of PsaK2 in state transition under high light condition was also confirmed by chlorophyll fluorescence emission spectra determined at 77 K. The results suggest that PsaK2-dependent state transition is essential for the growth of this cyanobacterium under high light condition.

The effective absorption of light energy is the first step in photosynthesis. All oxygenic photosynthetic organisms share common core antenna pigments of ~40 chlorophyll a in PSII1 and ~100 chlorophyll a in PSI (1). Cyanobacteria have an additional light-harvesting system, phycobilisome, which is primarily associated with PSII (2, 3). Thus, cyanobacteria use two kinds of antenna pigments with totally different absorption wavelengths.

Because neither light quality nor light quantity is constant in natural environments, cyanobacteria have to distribute the light energy absorbed by antenna pigments to two photosystems in order to optimize the photosynthetic performance in response to changing light environments. When cells are exposed to illumination favoring either PSII or PSI, the distribution of light energy between two photosystems would be adjusted (4). When cells have been pre-illuminated with light mainly absorbed by phycobiliproteins (PSII light), the energy transfer to PSI increases, whereas the energy transfer to PSII decreases (state 2). Pre-illumination of cells with light mainly absorbed by chlorophyll a (PSI light) causes a reverse effect leading to the increase of energy transfer to PSI and the decrease of energy transfer to PSI (state 1) (5). Distribution of light energy to two photosystems is regulated in response to the light regime not only in cyanobacteria but also in green algae and higher plants. This regulation of energy distribution between PSII and PSI has been generally called “state transition.” Since its discovery in 1969 (6, 7), many research groups have been involved in the research of state transition in cyanobacteria, green algae, and higher plants.

State transition is induced not only by the change in light quality but also by the change in light quantity. When exposed to excess light, cyanobacteria are able to change the distribution of light energy between two photosystems. Under normal light condition, the light energy absorbed by phycobilisome is preferentially transferred to PSII. On the contrary, under high light condition, the energy can be transferred not only to PSII but also to PSI (8). In this case, the physiological significance may not be in the effective photosynthesis but in the avoidance from the photodamage.

In the old days, phycobilisome was assumed to act as a light-harvesting antenna solely for PSII. However, energy transfer studies on the wild type (9) and a PSII-deficient mutant (10) of Synechocystis sp. PCC 6803 indicated that phycobilisome could interact with and efficiently transfer energy to PSI, depending on the growth condition of the cells. Phycobilisome was found to be able to move rapidly on thylakoid membranes (11, 12). The study using inhibitor of electron transport suggested that state transition was controlled by the redox complex II; LHCl, light-harvesting complex I; RpaC or rpaC, regulator of phycobilisome association; DCMU, dichlorophenylidimethylurea; MOPS, 3-[N-morpholino]propanesulfonic acid; TES, N-tris(hydroxymethyl)methyl-2-aminoethanesulfonic acid.

* This work was supported in part by Grant-in-aid for Scientific Research (B) (14340250) from the Japan Society for the Promotion of Science and Grant-in-aid for Scientific Research on Priority Area “Genome Biology” (15013214) from the Ministry of Education, Science, Sports and Culture. The costs of publication of this article were defrayed in part by the payment of page charges. This article must therefore be hereby marked “advertisement” in accordance with 18 U.S.C. Section 1734 solely to indicate this fact.

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‡ The abbreviations used are: PSI, photosystem I; PSII, photosystem II; PSI, phycobilisome I; qN, non-photochemical quenching; qP, photochemical quenching; Fo, the maximum level of fluorescence; Fm, the minimal level of fluorescence; Pn, the stable level of fluorescence; LHCII, light-harvesting complex II; LHCl, light-harvesting complex I; RpaC or rpaC, regulator of phycobilisome association; DCMU, dichlorophenylidimethylurea; MOPS, 3-[N-morpholino]propanesulfonic acid; TES, N-tris(hydroxymethyl)methyl-2-aminoethanesulfonic acid.
state of the plastoquinone pool via cytochrome b6/f complex (13). Oxidation of plastoquinone induces state 1, whereas reduction induces state 2. As for proteinaceous factors, it was reported that ApdC and ApdF, phycobilisome core components, were involved in state transition (14). RpaC (regulator of phycobilisome association) was also shown to function in state transition (15). The rpaC gene was isolated by screening for mutants displaying no changes in fluorescence yield in response to changes in light quality. The deduced amino acid sequence of the rpaC gene has no recognizable sequence motifs. The rpaC mutant can perform state transition upon excitation of chlorophyll but not upon excitation of phycobilisome. At very low photon flux densities of yellow or white light, the growth of the rpaC mutant was slower than that of the wild type. However, actual function of this protein is unknown. Moreover, we have no information on the PSI-side component working for the cyanobacterial state transition.

Upon acclimation of cells of Synechocystis sp. PCC 6803 to high light, the expression of all of the PSI genes was simultaneously suppressed with only one exception of the psaK2 gene (16). The expression of psaK2 was eminently induced after the shift of cells to high light, implying that PsaK2 might be involved in high light acclimation. PsaK is a subunit of PSI complexes and localized on the outside edge of cyanobacterial PSI trimer (17). The genomic DNA of Synechocystis sp. PCC 6803 contains two unlinked psaK genes, psaK1 and psaK2. Cyanobacterial psaK seems to be the common ancestor of higher plants psaK/psaG (18). Cyanobacterial genomes contain one to three psaK genes, whereas only one psaK gene has been found in green algae and higher plants so far. Deduced amino acid sequences of the psaK1 and the psaK2 genes in Synechocystis sp. PCC 6803 are notably different in length (86 amino acids for the PsaK1 protein and 128 amino acids for the PsaK2 protein) because of long N-terminal extension in PsaK2. The two gene products show 42% homology with each other. In the past studies, both the psaK1 and the psaK2 mutants were characterized but clear phenotype was not observed under normal growth condition (19, 20). In this study, we investigated the physiological role of PsaK2 in Synechocystis sp. PCC 6803 under high light condition. The results indicate that PsaK2 is involved in the energy transfer from phycobilisome to PSI under high light condition and that PsaK2-dependent state transition is essential for the growth of this cyanobacterium under high light condition.

EXPERIMENTAL PROCEDURES

Growth of Cultures and Strains—Wild type and mutant strains of Synechocystis sp. PCC 6803 were grown in BG-11 medium (21) supplied with 10 mM MES. Liquid cultures were grown at 30 °C in 50-mI glass tubes and bubbled with air under continuous illumination provided by fluorescent lamps. Photon flux density at 20 and 200 mol M⁻² s⁻¹ was regarded as low light and high light, respectively. The psaK1 mutant was constructed by the replacement of nucleotide sequence corresponding to positions 6–70 of amino acid of PsaK1 with the kanamycin-resistant cassette using two SacI sites in the psaK1 gene (19). The psaK2 mutant was constructed by insertion of the kanamycin-resistant cassette into AgeI site in the psaK2 gene. The rpaC gene was disrupted by insertion of the spectinomycin-resistant cassette into Styl site in the rpaC gene. Mutants were usually maintained with kanamycin and/or spectinomycin at the final concentration of 20 μg ml⁻¹.

Analysis of Chlorophyll Fluorescence—Chlorophyll fluorescence was measured with a pulse-amplitude modulation chlorophyll fluorometer (PAM 101/102F, Heinz Waltz, Effeltrich, Germany) with a high sensitivity emitter-detector unit (ED-101US, Heinz Waltz, Effeltrich, Germany) as described by Sonoi et al. (22). Cells were dark-adapted for 5 min, and then the measuring light was turned on to obtain the minimal fluorescence level (Fm). The stable level of fluorescence (Fm') was determined during the exposure of cells to actinic light with defined photon flux density (KL 1500, Schott, Wiesbaden, Germany). The fluorescence level with fully reduced Qa (F0') was obtained by applying multiple turnover flashes (XMT 103, Heinz Waltz, Effeltrich, Germany) under actinic light. The far-red light from a photodiode (FR 102, Heinz Waltz, Effeltrich, Germany) was applied just after turning off the actinic light. 

RESULTS

Although the psaK2 gene expression specifically increased during acclimation to high light (16), the amounts of Psak1 and Psak2 proteins in PSI complex of high light-acclimated cells were unknown. We purified PSI complex from the wild type cells grown under low (20 μmol M⁻² s⁻¹) and high light (200 μmol M⁻² s⁻¹) conditions and also from the psaK1 and the psaK2 mutant cells grown under high light condition. Proteins in the purified PSI complexes were resolved by SDS-PAGE and visualized by silver staining (Fig. 1). PSI complex isolated from low light-acclimated wild type cells contained a considerable amount of PsaK1 with only a trace amount of PsaK2. High light treatment increased the amount of PsaK2 in PSI complexes. In PSI complexes from high light-acclimated psaK1 or psaK2 mutant, PsaK1 or PsaK2 subunit was missing, respectively, whereas the amount of the
The Role of PsaK2 Subunit in State Transition

Fig. 1. Subunit composition of PSI complexes isolated from the wild type and the mutant cells of Synechocystis sp. PCC 6803 grown under low and high light conditions. Subunits of PSI complexes equivalent to 1 μg of chlorophyll were separated by SDS-PAGE and visualized by silver staining. The fraction enclosed by the dotted box in panel A was enlarged in panel B with higher contrast. WT, wild type.

other subunits of PSI was not affected, in good agreement with a previous report (20). We identified the protein band that increased under high light condition as PsaK2 subunit by using matrix-assisted laser desorption ionization time-of-flight mass spectrometry (data not shown).

To examine whether the failure to accumulate PsaK2 subunit in PSI affects the growth under high light condition, we examined the growth property of the wild type as well as the psaK1 and the psaK2 mutants. 10 μl of the liquid culture was spotted on an agar plate and grown under low or high light condition for 3 days. Minor differences in growth between the wild type and the two mutants were observed under low light condition (Fig. 2A). Under high light condition, the growth of the psaK2 mutant was considerably lower compared with that of the wild type and the psaK1 mutant (Fig. 2B). These results demonstrate that the accumulation of PsaK2 in PSI is essential for the growth of this cyanobacterium under high light condition.

We then determined the photosynthetic characteristics of the wild type and the psaK1 and the psaK2 mutants grown under low and high light conditions for 24 h using pulse-amplitude modulation chlorophyll fluorometer. The level of maximum fluorescence was lower under actinic light (Fm') than under actinic light in the presence of DCMU (Fm) (Fig. 3). DCMU locks the cells in state 1, and the difference between Fm' and Fm reflected the decrease in fluorescence intensity (non-photochemical quenching) due to state transition. The relative level of Fm' in the psaK2 mutant was lower in high light-acclimated cells of wild type and the psaK1 mutant than in low light-acclimated cells (Fig. 3, compare A and B with D and E). However, in the case of the psaK2 mutant, the Fm' level was not much different between low light-acclimated cells and high light-acclimated cells (Fig. 3, C and F). The result suggests that the high light acclimation induces state transition, and the process is impaired in the psaK2 mutant.

The quantified values of the fluorescence measurements were shown in Table I. In low light-acclimated cells, we observed no significant differences between the wild type and the mutants in relation to non-photochemical quenching (qN) as well as photochemical quenching (qP) (Table I). However, in high light-acclimated cells, qN in the wild type and the psaK1 mutant was notably higher than that in the psaK2 mutant, although there was no significant difference in qP among three strains. Thus, the increase of non-photochemical quenching upon high light acclimation, which reflects state transition in cyanobacteria, was specifically suppressed in the psaK2 mutant.

Since the analysis of non-photochemical quenching suggested the role of PsaK2 in state transition, we examined the energy transfer from phycobilisome to two photosystems by monitoring 77-K emission spectra of chlorophyll fluorescence from cells either in state 1 or in state 2. When cells were excited with blue light (400–600 nm) absorbed by phycobilin and chlorophyll a, the fluorescence emission spectra for cells adapted to either state 1 or state 2 had emission peaks at 663, 685, 695, and 725 nm. The peak at 663 nm arises from phycobilisome. The peak at 685 nm arises from PSII and possibly from the terminal emitters of phycobilisome. The 695-nm peak arises from PSI, and the 725-nm peak arises from PSI. In the wild type and the psaK1 mutant grown under high light condition, relative intensity of PSI fluorescence was much greater in state 2 than in state 1 (Fig. 4, A and B, and Table II). This increase of PSI fluorescence in state 2 reflects the enhanced energy transfer from phycobilisome to PSI. In the psaK2 mutant, the relative intensity of PSI fluorescence in state 2 was very close to that in state 1 (Fig. 4C and Table II). These results indicate that the high light-acclimated cells of the psaK2 mutant are not able to perform state transition, supporting the conclusion drawn from the analysis of non-photochemical quenching (Table I). The relative intensity of PSI fluorescence was greater in the low light-acclimated cells than in the high light-acclimated cells (compare Figs. 4 and 5) because of the regulation of photosystem stoichiometry in acclimation to the changes in photon flux density (29). In low light-acclimated cells of the wild type, the psaK1, and the psaK2 mutants, the relative intensity of PSI fluorescence was greater in state 2 than in state 1, indicating that the psaK2 mutant as well as the wild type can perform state transition under low light condition (Fig. 5 and Table II). PsaK2-dependent state transition is apparently specific to high light condition.
The Role of PsaK2 Subunit in State Transition

We also examined state transition of the psaK2ΔpsaC double mutant by chlorophyll fluorescence emission spectra at 77 K. In high light-acclimated cells, the psaK2ΔpsaC double mutant displayed the same phenotype as the psaK2 mutant (data not shown). In low light-acclimated cells, the double mutant can partially perform state transition (data not shown).

Using BLAST search program, we searched two types of PsaK proteins (PsaK1-type and PsaK2-type) in databases to examine whether this mechanism of PsaK2-dependent state transition is conserved in other cyanobacteria. Synechococcus elongatus PCC 7942 and Trichodesmium erythraeum IMS 101 have two types of PsaK proteins as well as Synechocystis sp. PCC 6803 (Fig. 6). The black boxes in the figure show the amino acid residues conserved only in PsaK1-type or in PsaK2-type protein. These amino acid residues might be responsible for the specific function of each type of protein. When unrooted dendrogram is constructed by the neighbor joining method through the ClustalW program, it is evident that PsaK1-type proteins and PsaK2-type proteins form distinct clades (Fig. 7). In the case of Nostoc punctiforme and Thermosynechococcus elongatus BP-1, there is only one psaK gene in each genome, the PsaK1...
Cells were either illuminated with blue light in the presence of 10 μM PsaK1-type and PsaK2-type proteins. The spectra were normalized to the intensity of the fluorescence peak at 695 nm (PSII peak).

**FIG. 5.** Chlorophyll fluorescence emission spectra of low light-acclimated cells determined at 77 K. The spectra of the wild type (A), the psaK1 mutant (B), and the psaK2 mutant (C) acclimated to low light were measured under state 1 (solid line) and state 2 (thin line). Cells were either illuminated with blue light in the presence of 10 μM DCMU (state 1) or incubated in the dark for more than 10 min (state 2).

**FIG. 6.** PsaK proteins in cyanobacteria. The amino acid sequences of PsaK1 (GI:163293111) and PsaK2 (GI:16332131) in Synechocystis sp. PCC 6803 were compared with PsaK1 (GI:46129567) and PsaK2 (GI:53763010) in Synechococcus elongatus PCC 7942 and PsaK2 (GI:48892689) in T. erythraeum IMS 101. Judging from the similarity to PsaK1-type one. One of psaK genes in Anabaena PCC 7120 is the PsaK1 type, but the other two genes are rather divergent and form the forth clade of cyanobacterial PsaK. PsaK and PsaG of chloroplasts seem to be equally distant from cyanobacterial PsaK as suggested previously (18).

**DISCUSSION**

Upon state transition of cyanobacteria, energy flow from phycobilisome is redirected to PSI. In cyanobacteria, several components of phycobilisome, such as ApcD and ApcE, were reported to be involved in state transition (14, 15). However, the factors on PSI side have not been reported. Here, we reported for the first time that PsaK2, a subunit of PSI, is a factor that regulates the energy transfer from phycobilisome to PSI under high light condition.

Cyanobacterial PsaK subunit of PSI has weak homology with both PsaK and PsaG of higher plant PSI (18). The crystal structure of higher plant PSI revealed that PsaK and PsaG are located on the outer edge of PSI complex and may serve for the association of light-harvesting complex I (LHCl) with core complex (30). Because the place for PsaG is open in the crystal structure of cyanobacterial PSI (17), it is tempting to assume that PsaK2 expressed in Synechocystis sp. PCC 6803 occupies the place for PsaG in higher plants under high light condition. Although energy transfer studies imply that phycobilisome can interact with PSI and transfer energy efficiently to PSI, in structure terms we know little about the direct association of phycobilisome with thylakoid membrane or with reaction centers. PsaK2 might become a clue to the elucidation of the interaction of phycobilisome with PSI in Synechocystis sp. PCC 6803.

In higher plants and green algae, state transition is induced by the dissociation of LHCl from PSI complex. The redox state of the plastocyanine pool controls the activation of the thylakoid kinase responsible for phosphorylation of LHClII proteins (4). The binding of LHClII to PSI requires PSI-H, PSI-I, PSI-L, or PSI-O (31–33). A chemical cross-linking study (33) suggested that the docking sites for LHClII in PSI might be PSI-H, PSI-I, and PSI-L. Although the absence of PSI-G or PSI-K also indirectly retards state transition to some extent (33–35), the main function of these two subunits seems to be related to the binding of LHClI judging from the crystal structure of PSI (30). Apparently, The PsaK/G proteins serving for state transition in cyanobacteria are recruited for the binding of LHClI in higher plants and PsaH protein is newly evolved for LHClI-type state transition of higher plants (31).

Although SDS-PAGE analysis clearly showed the increase of PsaK2 subunit in PSI under high light condition, whether PsaK1 decreased under high light condition or not is unclear from the silver-stained gel presented in Fig. 1. At present, we could not deny the possibility that PsaK2 protein was incorporated to PSI complexes in place of PsaK1 protein. In Synechococcus sp. PCC 7942, high light induces the interchange between two forms (D1:1 and D1:2) of D1 protein, a reaction center subunit of PSI. D1:1 is predominant under low light condition, and D1:2 increases during acclimation to high light (36). The mutant defective in the gene encoding D1:2 is sensitive to photoinhibition because of the failure to exchange D1:1 for D1:2 (37). A similar interchange of two PsaK subunits might be induced upon high light acclimation also in PSI.

In any event, the incorporation of PsaK2 subunit into PSI complex is essential for the proper regulation of state transition under high light condition. The growth of the psaK2 mutant was severely suppressed under high light condition compared with the wild type and the psaK1 mutant (Fig. 2B). The result clearly indicates that state transition has the physiological importance under high light condition. It was reported that the mutant incapable of state transition under relatively low light condition could grow even under the light of specific quality
such as yellow light, albeit at the reduced rate (15). The situation may be totally different for the high light condition, and the proper state transition mediated by PsaK2 is essential for the growth under high light condition. It must be noted that previously identified regulatory factors are all involved in the light quality-induced state transition. To our knowledge, PsaK2 is the only factor that regulates state transition under high light condition.

Interestingly, no differences in state transition between the wild type and the psaK2 mutant were observed under low light condition (Fig. 5). This implies that at least two kinds of mechanisms for state transition might exist, such as light quality and light quantity or low light- and high light-dependent state transition. Under low light or biased light (PSII or PSI light) condition, RpaC-dependent state transition might enable the effective distribution of energy between PSII and PSI in order to perform photosynthesis as maximally as possible. Under high light condition, PsaK2-dependent state transition might allow cells to be protected against the photodamage. It seems that PsaK2-dependent state transition is the only mechanism of state transition under high light condition. On the other hand, the psaK2rpaC double mutant retained small but significant state transition under low light condition (data not shown). Thus, there must be the third mechanism of state transition under low light condition independent of psaK2 or rpaC. Although the rpaC mutant could not perform state transition upon phycobilisome excitation, the wild type and the mutant did show some kind of regulation of energy transfer from PSII to PSI under chlorophyll excitation (15). Small but significant state transition observed in the psaK2rpaC double mutant under low light condition may be ascribed to this chlorophyll-dependent state transition, because we used the actinic light absorbed by both phycobilin and chlorophyll a.

The mechanism of state transition revealed in this study is not specific to Synechocystis sp. PCC 6803, because at least two other cyanobacterial species also have both the psaK1-type and the psaK2-type genes in their genome (Fig. 6). Interestingly, Nostoc punctiforme has only the PsaK1-type gene and T. elongatus BP-1 has only the PsaK2-type gene in their genomes as far as we searched in Cyanobase. Marine cyanobacteria such as Prochlorococcus marinus or Synechococcus WH 8102 have unique psaK that is more or less similar to PsaK1 type (Fig. 7). The regulatory mechanism of state transition in these species must be examined in near future.

Acknowledgments—We thank to Dr. H. Nakamoto (Saitama University) for the gift of plasmid designed for the destruction of psaK1 gene. We are grateful to Dr. Mitsuhiro Abe for technical advice in mass spectrometry.

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J. Biol. Chem. 2005, 280:22191-22197.
doi: 10.1074/jbc.M500369200 originally published online April 11, 2005

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