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Light-induced excitation energy redistribution in *Spirulina platensis* cells: "spillover" or "mobile PBSs"?

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Abstract

State transitions induced by light and redox were investigated by observing the 77 K fluorescence spectra for the intact cells of *Spirulina platensis*. To clarify if phycobilisomes (PBSs) take part in the state transition, the contributions of PBSs to light-induced state transition were studied in untreated cells and the cells treated by betaine which fixed PBSs firmly on the thylakoid membranes. It was observed that the betaine-treated cells did not show any light-induced state transition. This result definitely confirmed that the light-induced excitation energy regulation between the two photosystems is mainly dependent on a spatial movement of PBSs on the thylakoid membranes, which makes PBS cores partially decoupled from photosystem II (PSII) while PBS rods more strongly coupled with photosystem I (PSI) during the transition from state 1 to state 2. On the other hand, an energy exchange between the two photosystems was observed in both untreated and betaine-treated cells during redox-induced state transition. These observations suggested that two different mechanisms were involved in the light-induced state transition and the redox-induced one. The former involves only a physical movement of PBSs, while the latter involves not only the movement of PBS but also energy spillover from PSII to PSI. A model for light-induced state transition was proposed based on the current results as well as well known knowledge.

Keywords: C-PC; APC; PSI; PSII; State transition; Energy transfer

1. Introduction

In photosynthetic organisms, excitation energy distribution between photosystem II (PSII) and photosystem I (PSI) is regulated via a process commonly known as light state transition, a regulatory mechanism to compensate the less excited photosystem for the excitation energy from the preferentially excited photosystem [1–3]. For LHC Chl *a*/*b*-containing organisms, the regulation mechanism has been well understood [4,5], however, the mechanism for cyanobacteria and red algae remains controversial up to now [6–8], though some models were proposed. Among those, the "spillover" model was proposed based on an assumption of a closer approximation of the two photosystems, which regulates the rate of excitation energy transfer from PSII to PSI [9–13]. The "mobile phycobilisome (PBS)" model was proposed by suggesting a physical movement of PBSs, quite analogous to that of Chl *a*/*b*-containing organisms [14–16]. Besides, there are also some other models proposed to explain the experimental observations [8,17] but similar to the two basic models mentioned above. In fact, investigation on the state transition is not only for learning the energy regulation mechanism but also for probing the structural matches and functional associations of the three functional groups, PBS, PSII and PSI.

In previous studies [18–20], a parallel model was proposed to explain the non-synchronous features of the allophycocyanin (APC) fluorescence from the C-phycocyanin (C-PC) based on the observations of temperature-induced decoupling of PBS from PSII in the PBS–thylakoid membrane complexes as well as in the intact

Abbreviations: Chl, chlorophyll; PSI, photosystem I; PSII, photosystem II; C-PC, C-phycocyanin; APC, allophycocyanin; PBS, phycobilisome; DCMU, 3-(3,4-dichlorophenyl)-1,1-dimethylurea

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cells of *Spirulina platensis*. In the current work, the excitation energy redistribution between the two photosystems during the state transition induced by light and redox was studied.

It was reported previously that betaine could fix PBSs firmly on the thylakoid membranes [18]. In the current work, it was definitely proved that PBSs in betaine-treated cells could hardly be washed off by a detergent and it was also found that betaine could lock the cells either at state 1 or state 2, therefore, it was used to clarify if PBSs were mobile during the state transition. Just as expected, betaine-treated cells did not show any light-induced state transition, confirming that the mobility of PBSs should be responsible for the light-induced state transition. On the other hand, the state transition induced by redox did occur in the betaine-treated cells. Based on the experimental observations, it was deduced that the mechanisms of state transition would depend on the inducing technologies.

2. Materials and methods

2.1. Culture and growth conditions

S. platensis, a cyanobacterium, was cultured in a 5-l bottle at 28 °C, bubbled with air and irradiated with 40-W fluorescence lamps continuously. Ten-day-old cultures were used for the experiments.

2.2. Preparation of PBS–thylakoid membrane complexes

The PBS–thylakoid membrane complexes were isolated from untreated and betaine-treated cells according to the previously reported method [21]. The isolated complexes were washed by Triton X-100 (1%) and then centrifuged at 50,000 × *g* for 15 min. The supernatant was discarded and the pellet was resuspended in the 1.0 M sucrose solution containing 20 mM tricine (pH 8.0).

2.3. Oxygen electrode measurements

Rates of oxygen evolution and dark respiration in the cells were measured at 25 °C by a Clark-type oxygen electrode (Hansatech oxygraph). The untreated and betaine-treated cells (15 μg/ml Chl *a*) in growth medium were illuminated with white light of 250 μE m^{-2} s^{-1} (saturating intensity). The data were averaged over those from three separate measurements.

2.4. Absorbance cross-section measurements

PSII absorbance cross-sections were determined by flash saturation curves of Chl *a* fluorescence yield at room temperature [22]. The wavelength of the actinic laser pulse (250-ns half-width, 620 nm) was generated by a Phase-R DL-32 flash lamp pumped dye laser. Flash saturation curves were fit with a single-hit Poisson distribution [23]. And the PSII absorbance cross-sections were determined for excitation of PBSs at 625 nm and Chls at 678 nm. The data were averaged over those from three separate measurements.

2.5. Spectra measurements

Absorption spectra were recorded on a UV-1601 ultra-vis spectrophotometer (Hitachi, Japan). Fluorescence emission spectra were obtained at 77 K on an F4500 spectrofluorimeter (Hitachi, Japan). Before spectral measurement, the cells were harvested by centrifugation and resuspended in the growth medium to a concentration of 5 μg Chl *a* ml^{-1}. The chlorophyll concentrations were estimated from the absorbance at 665 nm in methanol extracts [24]. The cells were exposed to light of the specified intensity and spectral quality for 5 min before rapidly frozen by plunging into liquid nitrogen. To correct the fluorescence yields of frozen samples for random scattering and heterogeneity, the spectrum was averaged on the measurements of the same sample in six different tubes, for which the errors were determined to be within 3%. In our present work, the excitation and emission slit widths were set in 5 nm and all the samples were from the same capture of the cells.

2.6. State transition

As described in Ref. [25], for the intact cells, the light state 1 was induced by pre-illumination with blue light (Ditric optics 460-nm short-pass filter) for 5 min at 350 μE m^{-2} s^{-1} and state 2 with orange light (Ditric optics 580-nm long-pass and 600-nm short-pass filter) for 5 min at 20 μE m^{-2} s^{-1} at room temperature; while the redox-induced state 1 was achieved by the treatment with DCMU before pre-illumination with strong blue light

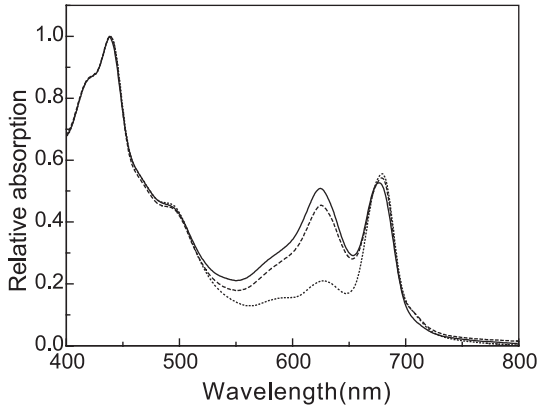

Fig. 1. The absorption spectra of the PBS–thylakoid membrane complexes isolated from untreated cells (solid line) and further washed by Triton X-100 (1%) (dotted line) and those isolated from betaine-treated cells and washed by Triton X-100 (1%) (dashed line). The spectra were normalized to 440 nm.

Table 1
Rates of oxygen evolution under a saturating light source and oxygen uptake in the dark for untreated and betaine-treated cells in growth medium

	Oxygen evolution [μmol of O_2 (mg of Chl)$^{-1}$ h^{-1}]	Oxygen uptake [μmol of O_2 (mg of Chl)$^{-1}$ h^{-1}]
Cells in growth medium	187 ± 20	24 ± 3
Betaine-treated cells in growth medium	192 ± 25	22 ± 2

and the state 2 by the dark adaptation (adapted in darkness more than 15 min).

3. Results and discussion

3.1. The evidence for PBSs fixed on thylakoid membranes by betaine

To provide a direct evidence for PBSs fixed on thylakoid membranes by betaine, the PBS–thylakoid membrane complexes isolated from untreated and beatine-treated cells were washed by the use of detergent Triton X-100 (1%) and then the absorption spectra were measured (Fig. 1). For the unwashed PBS–thylakoid membrane complexes (solid line), the absorption peaks for PBSs and carotenoids appear at 625 and 490 nm, respectively, whereas those for Chls appear at 418, 436 and 678 nm. On the other hand, washed by the detergent, the peak of PBSs is absent for the PBS–thylakoid membrane complexes (dotted line) from the untreated cells while it basically remains for the complexes from the beatine-treated cells (dashed line), confirming the expected function of betaine.

3.2. Does betaine have an effect on the photosynthetic and respiratory electron flow?

Table 1 shows the rates of oxygen evolution and respiration for the untreated and betaine-treated cells. From the data in Table 1, there is no indication that the photosynthetic or respiratory electron transport is affected in the betaine-treated cells, confirming that betaine exerts no effect on the electron transport in the thylakoid membrane.

Table 2
Absorbance cross-sections of PSII (σ_{II}) in *S. platensis* under different light state

Prior condition	Excitation	σ_{II} (Å^2)	$\Delta\sigma_{II}$ (%)
Blue light	PBS	411 ± 24	− 32
Orange light		279 ± 10	
Blue light	Chl *a*	120 ± 7	− 7
Orange light		112 ± 4	
DCMU + blue light	PBS	427 ± 25	− 40
Dark adaptation		256 ± 11	
DCMU + blue light	Chl *a*	156 ± 8	− 19
Dark adaptation		126 ± 5	

$\Delta\sigma_{II}$ is defined as: $\Delta\sigma_{II}=(\sigma_{II(2)}-\sigma_{II(1)})/\sigma_{II(1)}$. The $\sigma_{II(1)}$ and $\sigma_{II(2)}$ represent the PSII absorbance cross-section at state 1 and state 2, respectively.

3.3. Absorbance cross-sections of PSII

To determine whether the pre-illumination induced a change in the antenna sizes or phycobilin antenna associa-

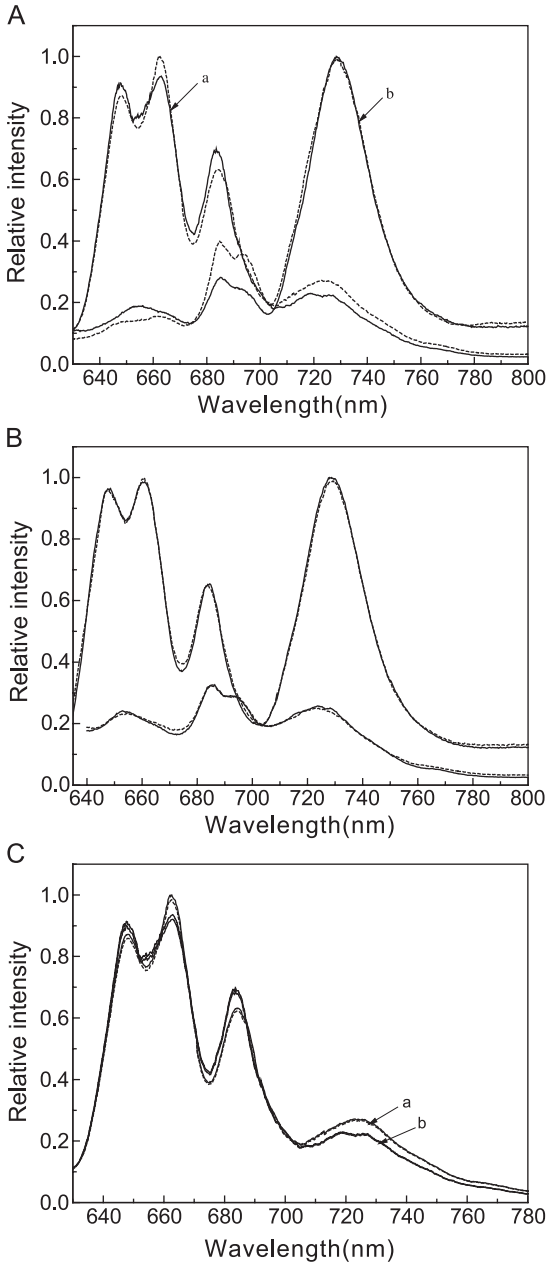

Fig. 2. 77 K Fluorescence emission spectra of *S. platensis* cells excited at 580 nm (a) and 436 nm (b). Solid line: pre-illuminated by blue light, dashed line: pre-illuminated by orange light. The untreated and betaine-treated cells are shown in panels A and B, respectively. (C) a: cells pre-illuminated by blue light before addition of betaine (solid line), and subsequently adapted to the orange light (dashed line); b: cells pre-illuminated by orange light before addition of betaine (short dotted line) and subsequently adapted to the blue light (short dashed dotted line).

Table 3
The fluctuation percentages (ΔF) of individual fluorescence component for untreated and betaine-treated cells excited at 580 nm under different inducing condition

Prior condition (λ_{ex} = 580 nm)	Light-induced				Redox-induced			
	ΔF_{685}	ΔF_{725}	ΔF_{647}	ΔF_{660}	ΔF_{685}	ΔF_{725}	ΔF_{647}	ΔF_{660}
Untreated cells	− 8.68%	+20.5%	− 4.7%	+7.0%	− 18.4%	+17.8%	− 5.87%	+6.30%
Betaine-treated cells	− 0.42%	+0.56%	− 0.63%	+0.38%	− 8.9%	+21.77%	− 0.76%	+0.39%

Prior condition	Blue light	Orange light	DCMU + blue light	Dark adaption
Relative error (untreated cells)	1.86%	1.56%	2.13%	1.73%
Relative error (betaine-treated cells)	1.42%	1.21%	1.33%	2.25%

ΔF is defined as: $\Delta F_i = (F_{i(2)} - F_{i(1)})/F_{i(1)}$. $F_{i(1)}$ and $F_{i(2)}$ represent fluorescence intensities of the i component at state 1 and state 2, respectively.

tion of PSII, the PSII absorbance cross-sections at state 1 and state 2 were measured at room temperature with selective excitation of PBS at 625 nm and Chl *a* at 678 nm in *S. platensis* cells. Table 2 shows a summary of the PSII absorbance cross-sections (σ_{II}) at state 1 and state 2. Compared to those in light-induced state 1, it can be seen from Table 2 that σ_{II} decreases at state 2 with selective excitation of PBS but remains invariable with excitation of Chl *a*, suggesting a change in the association of phycobilin antenna with PSII instead of the antenna size of PSII. On the other hand, for redox-induced transition, σ_{II} decreases with either selective excitation of PBS or Chl *a*, suggesting a change in antenna size of PSII [27] or some kind of excitation energy exchange between PSII and PSI. These results suggest that the light-induced and redox-induced state transitions may undergo different mechanisms.

3.4. Light-induced state transition-mobile PBS mechanism?

Fig. 2A shows the 77 K fluorescence emission spectra for cells with C-PC excited selectively at 580 nm (a) and Chl *a* at 436 nm (b) after pre-illuminated by blue light (solid line) or orange light (dashed line). The four partially resolved peaks could be reasonably ascribed to C-PC (647 nm), APC (665 nm), PSII (685 nm) and PSI (725 nm), respectively. From Fig. 2A (a), it can be seen that both the PSII and C-PC components decrease while the APC and PSI increase synchronously on transition to state 2 induced by orange light, very similar to the temperature-dependent behavior [19]. In Fig. 2A (b), the PSII component increases and the PBSs decreases synchronously while the PSI is invariable on transition to state 2. The quantitative change in fluorescence intensity (ΔF) for individual component was listed in Table 3 (excited at 580 nm) and Table 4 (excited at 436 nm). It can be seen that the ΔF values for C-PC and PSII are negative but those for APC and PSI are positive during the light-induced transition. It can be imagined that the fluctuation of C-PC fluorescence should have been synchronous with that of the APC if a PBS were connected with only one photosystem (PSII or PSI) at a certain light state. However, from Fig. 2A (a) and Table 3, it can be clearly seen that the fluorescence fluctuation for C-PC is not synchronous with that for APC, confirming the parallel model, i.e., a PBS should couple with PSII via the terminal emitters and with PSI via PBS rods (C-PC), which was also observed before [19,20,26]. The decrease in PSII fluorescence matched with the increase in the APC implies an energetic decoupling at state 2, while the increase in PSI fluorescence matched with the decrease in the C-PC implies a more efficient coupling. The fluorescence fluctuation with excitation at 436 nm (Fig. 2A (b) and Table 4) also suggests an energetic decoupling of PBS from PSII, the same as that derived from that with excitation at 580 nm, but involves an opposite energy transfer pathway, i.e., the former reflects energy transfer from PSII to PBSs while the latter from PBSs to PSII. Some facts should be noticed based on Fig. 2A (b) and Table 4 as well as Table 3. (1) With 436-nm excitation, PSI fluorescence was invariable during the state transition, suggesting that PSI did not take part in the energy exchange with PSII or PBSs and, therefore, should not be responsible for the

Table 4
The fluctuation percentages (ΔF) of individual fluorescence component for untreated and betaine-treated cells excited at 436 nm under different inducing condition

Prior condition (λ_{ex} = 436 nm)	Light-induced				Redox-induced			
	ΔF_{685}	ΔF_{695}	ΔF_{725}	ΔF_{660}	ΔF_{685}	ΔF_{695}	ΔF_{725}	ΔF_{660}
Untreated cells	+41.23%	+39.27%	− 0.72%	− 24.35%	− 18.03%	− 19.0%	+8.6%	− 7.47%
Betaine-treated cells	+0.48%	+0.7%	− 0.86%	− 0.62%	− 14.0%	− 17.4%	+13.75%	− 0.87%

Prior condition	Blue light	Orange light	DCMU + blue light	Dark adaption
Relative error untreated cells	2.24%	1.69%	2.15%	1.76%
Relative error betaine-treated cells	1.92%	1.54%	2.38%	1.47%

ΔF is defined the same as in Table 3.

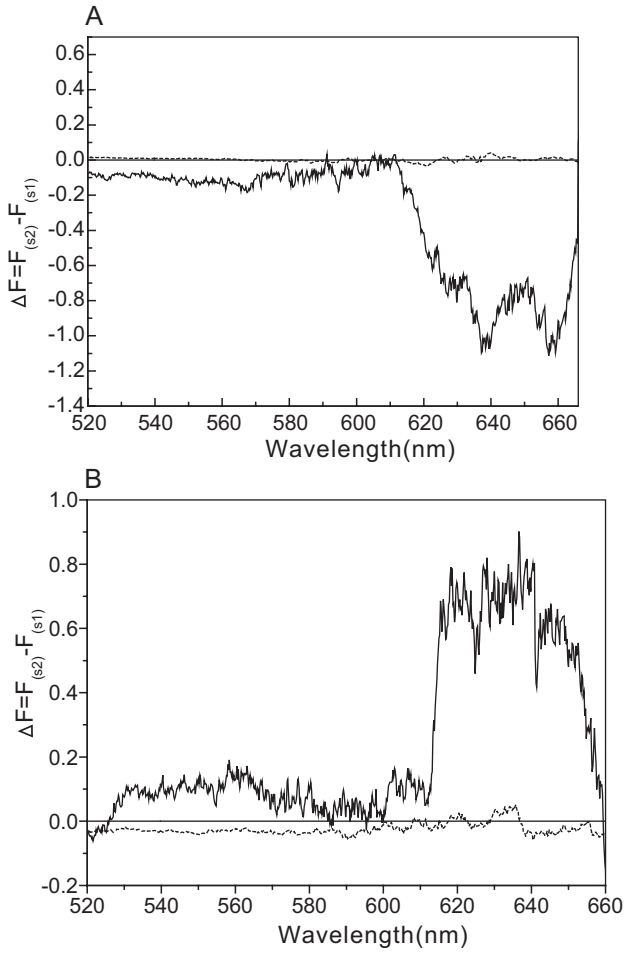

Fig. 3. 77 K difference excitation spectra with fluorescence monitored at 695 nm (panel A) and 730 nm (panel B) during the state transition induced by light. Solid line: untreated cells; dashed line: betaine-treated cells.

PSII fluorescence increase or the PBS fluorescence decrease. (2) The absorbance cross-section of PSII was invariable during light-induced state transition with excitation of Chl *a* and, therefore, should not be responsible for the PSII fluorescence increase too. (3) PSII fluorescence increase and PBS fluorescence decrease occurred synchronously during the light-induced transition, which suggests an energy exchange between PSII and PBSs. Therefore, the fluorescence fluctuation of PSII and PBSs with excitation at both 580 and 436 nm can be well explained by light-induced decoupling of PBSs from PSII at the state 2.

The 77 K fluorescence emission spectra for betaine-treated cells are shown in Fig. 2B with selective excitation at 580 nm (a) and 436 nm (b). The fluorescence emission spectra for the cells pre-illuminated by orange light (dashed line) are nearly the same as those pre-illuminated by blue light (solid line), suggesting that the light-induced state transition would not occur as long as PBSs were fixed on thylakoid membrane by betaine. Further, it can be clearly seen that betaine can lock the cells in either state 1 (Fig. 2C (a)) or state 2 (Fig. 2C (b)) depending on betaine added after pre-illuminated by orange light or blue light, suggesting a PBS fixed at a certain site of thylakoid membrane. Based on these results, it can be directly deduced that the light-induced state transition originates from the mobility of PBSs.

Fig. 3 shows the difference excitation spectra at state 1 and state 2 induced by light with fluorescence monitored at 695 nm (PSII, Fig. 3A) and 730 nm (PSI, Fig. 3B) for untreated (solid line) and betaine-treated (dashed line) cells. For the untreated cells, APC and C-PC contribute less to the PSII fluorescence (Fig. 3A, solid line) but more to the PSI (Fig. 3B, solid line) at state 2 than at state 1. On the other hand, for the betaine-treated cells, the contributions of APC and C-PC to both PSII (Fig. 3A, dashed line) and PSI fluorescence (Fig. 3B, dashed line) are invariable either induced by orange light or by blue light, i.e., the light-induced state transition did not occur, similar to that obtained from the fluorescence emission spectra (Fig. 2B).

3.5. Redox-induced state transition—dual mechanism?

Fig. 4A shows the 77 K fluorescence emission spectra at state 1 (solid line) induced by DCMU-poisoned before strong blue light illumination and state 2 (dashed line)

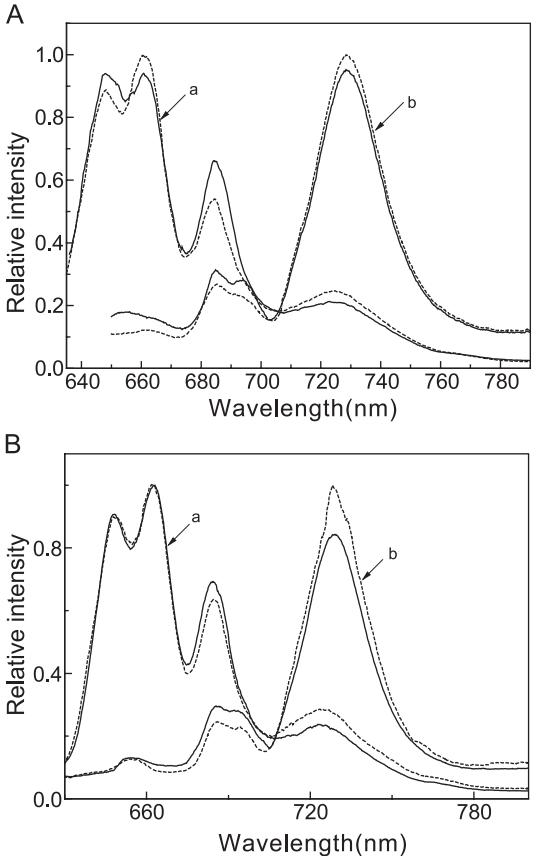

Fig. 4. 77 K fluorescence emission spectra of untreated cells (panel A) and betaine-treated cells (panel B) excited at 580 nm (a) and 436 nm (b). Solid line: DCMU-treated before preillumination with strong blue light; dashed line: dark-adapted.

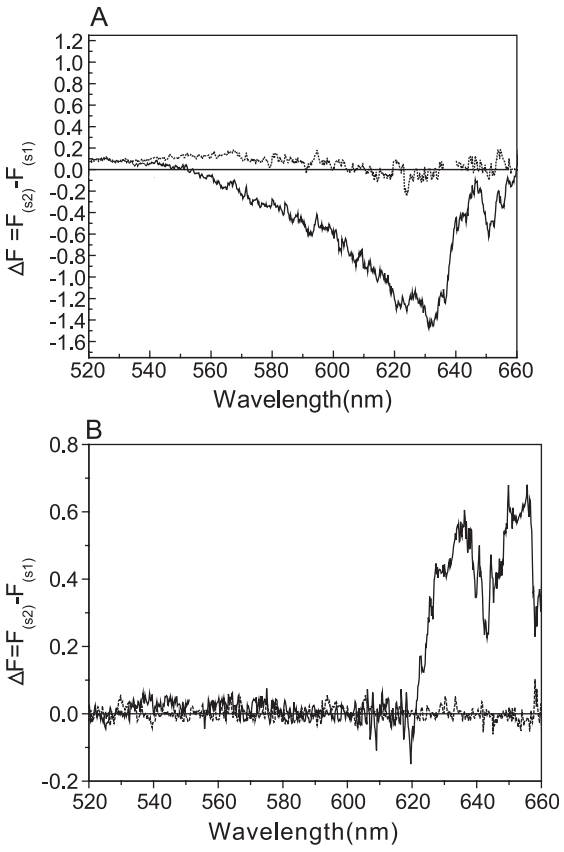

Fig. 5. 77 K difference excitation spectra with fluorescence monitored at 695 nm (panel A) and 730 nm (panel B) during the state transition induced by redox. Solid line: untreated cells; dashed line: betaine-treated cells.

induced by dark adaptation for the untreated cells excited at 580 nm (a) and 436 nm (b). From Fig. 4A (a) and Table 3, it can be seen that the fluorescence fluctuation for the individual component during the state transition is similar to those induced by light, though ΔF is larger. However, redox-induced state transition did occur for betaine-treated cells regardless of selective excitation at 580 or 436 nm, suggesting that the state transition induced by redox is obviously different from that induced by light. With regard to redox-induced state transition for betaine-treated cells excited at 580 and 436 nm, the fluorescence intensities of C-PC and APC remain almost constant during the state transition, shown in Fig. 4B (a, b), while those of the PSII and PSI are changed. These results suggest that redox-induced state transition involves some kind of energy exchange mechanism between PSII and PSI, besides the changes in the associations of phycobilin antenna with PSII and PSI [27]. Examining quantitatively (Table 3), it can be seen that the absolute values of ΔF for PSII in the untreated cells are larger than that in betaine-treated cells, which may be an indication of the contribution of PBS mobility to the state transition induced by redox. These results further confirm that betaine exerts an effect on the connection of PBSs with thylakoid membranes but not on the energy exchange between photosystems, suggesting a dual mechanism for redox-induced state transition, i.e., not only some kind of energy exchange between the two photosystems (spillover or variable antennal sizes) but also the mobility of PBSs.

Fig. 5A and B shows the difference excitation spectra of untreated and betaine-treated cells at state 1 and state 2 induced by redox with PSII and PSI fluorescence monitored, respectively. For the untreated cells, very similar to Fig. 3A and B, APC and C-PC contribute less to the PSII fluorescence (Fig. 5A, solid line) but more to the fluorescence of PSI (Fig. 5B, solid line) at state 2 than those at state 1, while the contributions of APC and C-PC to both PSII (Fig. 5A, dashed line) and PSI fluorescence (Fig. 5B, dashed line) are invariable for the betaine-treated cells, confirming that PBSs are not responsible for the energy exchange between PSII and PSI, which is consistent with that obtained from Fig. 4B.

3.6. A proposed model for the state transition induced by light

Current results definitely confirm that light-induced state transition of the intact cells of the cyanobacterium depends on a physical movement of PBSs on the thylakoid membranes. A model was proposed for the movement of a PBS on the thylakoid membrane during the light-induced state transition and illustrated in Fig. 6. It is commonly known that a part of a PSI complex is protruded out of the thylakoid membranes [28], therefore, the movement of a PBS may be limited to a certain range determined by a distance between the two neighboring PSI. In addition, the invariable PSI fluorescence (Fig. 2A (b)) implies that there is no energy exchange between PSI and PBSs with excitation at 436 nm. It is imaginable that the energy transfer from PSI to the terminal emitters of PBSs should have been observed if a PBS had moved so far and directly coupled with PSI via the

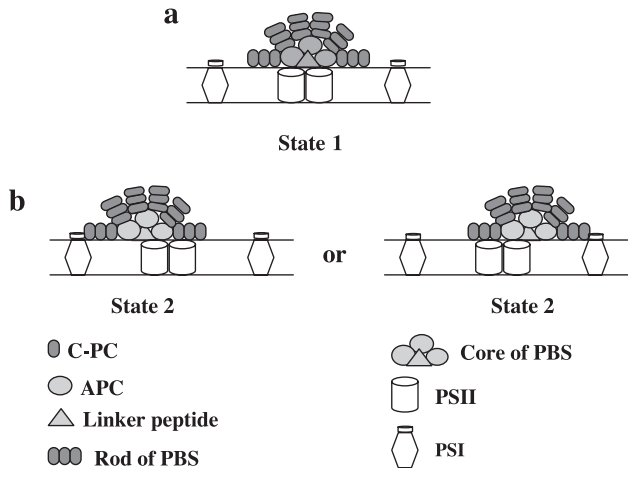

Fig. 6. Model for light-induced state transitions in cells from *S. platensis*. (a) State 1; (b) state 2.

terminal emitters. On transition to state 2, a PBS moves away from PSII to PSI that makes the PBS cores become less coupled with PSII and the PBS rods more efficiently coupled with PSI. On the other hand, the current results also suggest that both the movement of PBSs and the energy exchange between PSII and PSI are responsible for the state transition induced by redox. It was observed that PBSs were mobile while the photosystems were not [29,30]. And the energy spillover was also supported by a lot of observations [9–14]. A necessary condition for the energy spillover is that PSII and PSI get closer each other first, for which the driving force is still an interesting question. Some studies proved that a protein phosphorylation event was unlikely to match the rapid time range of the state transition in cyanobacteria [12]. Besides, it was ever suggested that a difference in charge distribution between PSI and PSII, generated by localized proton gradient, might be the driving force [10]; however, how such a local electrostatic force can drive the two distantly separated huge pigment–protein complexes remains unknown. It was reported that the state transition could also take place in a PBS-free mutant of cyanobacterium [11,13], but it does not necessarily mean that PBSs do not take part in the state transition. On the other hand, betaine-treated cells of the cyanobactrium did not show any light-induced state transition, but this also does not necessarily mean that the movement of PBSs is the only mechanism. Further, the force to drive PBS movement remains unknown. Much more researches are necessary to clarify the detailed mechanism for the state transition induced by light and by redox.

4. Conclusions

In the current work, it was confirmed that betaine could fix PBSs quite firmly on the thylakoid membranes and also could lock the cells either at state 1 or state 2, but did not have an effect on the photosynthetic and respiratory electron flow. It was observed that the betaine-treated cells of a cyanobacterium, *S. platensis*, did not show any light-induced state transition, confirming that PBS movement regulates the energy redistribution processes between the two photosystems, resulting in the PBS core less coupled with PSII but the PBS rods more efficiently coupled with PSI in the state 2. There are some differences between the state transitions induced by light and redox. First, differences in the fluorescence intensities for redox-induced cells are all larger than those for light-induced cells; second, for redox-induced state transition in the betaine-treated cells, the energy exchange from PSII to PSI was observed but the contribution from PBSs was absent, suggesting that both the energy spillover from PSII to PSI and the movement of PBSs are involved in this state transition. Betaine can inhibit the contribution from PBS but not that from the spillover from PSII to PSI, which suggests that state transition mechanism, mobile PBSs model or spillover model is dependent on the inducing technologies. Based on the observations and common knowledge, a model for light-induced state transitions was proposed.

Acknowledgements

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