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Changes in cyclic and respiratory electron transport by the movement of phycobilisomes in the cyanobacterium *Synechocystis* sp. strain PCC 6803

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Abstract

Phycobilisomes (PBS) are the major accessory light-harvesting complexes in cyanobacteria and their mobility affects the light energy distribution between the two photosystems. We investigated the effect of PBS mobility on state transitions, photosynthetic and respiratory electron transport, and various fluorescence parameters in *Synechocystis* sp. strain PCC 6803, using glycinebetaine to immobilize and couple PBS to photosystem II (PSII) or photosystem I (PSI) by applying under far-red or green light, respectively. The immobilization of PBS at PSII inhibited the increase in cyclic electron flow, photochemical and non-photochemical quenching, and decrease in respiration that occurred during the movement of PBS from PSII to PSI. In contrast, the immobilization of PBS at PSI inhibited the increase in respiration and photochemical quenching and decrease in cyclic electron flow and non-photochemical quenching that occurred when PBS moved from PSI to PSII. Linear electron transport did not change during PBS movement but increased or decreased significantly during longer illumination with far-red or green light, respectively. This implies that PBS movement is completed in a short time but it takes longer for the overall photosynthetic reactions to be tuned to a new state.

Keywords: Chlorophyll fluorescence parameters; Phycobilisome mobility; State transitions; *Synechocystis* sp. strain PCC 6803; The electron transport

1. Introduction

Phycobilisomes (PBS) are the main accessory light-harvesting complexes in cyanobacteria. They are supramolecular assemblies of colored phycobiliproteins and colorless linker proteins attached to the stromal surfaces of the thylakoid membrane (for review, see [1,2]). Energy transfer studies using mutants have demonstrated that PBS couple directly to photosystem II (PSII) and photosystem I (PSI) in response to changes in spectral quality and intensity of light [3–6]. A recent study showed that PBS mobility is required for state transitions in cyanobacteria [7]. In the green alga *Chlamydomonas reinhardtii*, the transition to state 2 involves a switch from linear electron flow to cyclic electron flow, which is thought to play an important role in generating the ATP required to adapt to various environmental stresses [8–11]. However, little is known about the effect of state transitions on photosynthetic and respiratory electron transport in cyanobacteria, which share the same electron carriers between the two photosystems. One of the purposes of this study is to investigate the effect of PBS movement on state transitions and consequently on photosynthetic and respiratory electron transport.

Another purpose of this study is to examine the effect of PBS movement on parameters derived from saturation pulse-induced chlorophyll fluorescence analysis. Two photochemical quenching parameters, qP and qL, have been proposed to estimate the fraction of PSII reaction centres in open states. qP is based on a pure "puddle" antenna model, where each PSII reaction centre possesses its own independent antenna system. In this model, the fluorescence parameter $(1-qP)$ is used to estimate the redox state of Q_A. In contrast, qL is based on a "lake" model, where reaction centres are connected by shared antennae, such as PBS [12]. Since PBS couple with the PSII (PSI) reaction centre after FR (GL) treatment, we used qL to estimate more accurately the

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photochemical quenching of PSII fluorescence and the redox state of Q_A (= 1 − qL). In chlorophyll *a/b*-containing plants, NPQ is commonly interpreted to reflect thermal dissipation, which protects the photosynthetic apparatus from photodamage under excess light [13,14]. In cyanobacteria, the qN value has been proposed to reflect the state transitions for the equilibration of excitation energy from PBS to the two photosystems [15]. Since any changes in the rate constant of PSII photochemistry will modify qN but not NPQ, NPQ is more appropriate than qN to measure non-photochemical quenching [12]. Thus, in cyanobacteria, the relationship between the NPQ level and the reversible movement of PBS is worthy of further investigation.

The movement of PBS is inhibited by glycinebetaine (GB) in *Spirulina platensis* regardless of changes in spectral quality and intensity of light [16], which has been confirmed in this study using *Synechocystis* sp. strain PCC 6803 (hereafter *Synechocystis* 6803). We applied GB to cells to immobilize and couple PBS to PSII or PSI under the light preferentially excites PSI or PSII, respectively. Comparison of photosynthetic and respiratory electron transport and various quenching parameters of PSII fluorescence in untreated and GB-treated cells enabled us to study the physiological role of PBS movement and its effect on fluorescence parameters in cyanobacteria.

2. Materials and methods

2.1. Culture conditions

Synechocystis 6803 cells were cultured at 30 °C in BG-11 medium [17] buffered with Tris–HCl (5 mM, pH 8.0) and bubbled with 2% (v/v) CO_2 in air, under continuous illumination by fluorescent lamps (40 μE m^{-2} s^{-1}).

2.2. Immobilization of PBS

Cells cultured for 4 days (A_{730}=0.6–0.8), which showed the highest photosynthetic activity [18], were harvested by centrifugation (5000×*g* for 5 min at 25 °C) and suspended in fresh BG-11 medium buffered with Tris–HCl (5 mM, pH 8.0) at a chlorophyll *a* concentration of 20 μg mL^{-1}. After exposure to far-red light (FR, 5.2 μE m^{-2} s^{-1}; Ditric Optics 705 nm long pass filter) or green light (GL, 15 μE m^{-2} s^{-1}; Ditric Optics 520 nm long pass and 546 nm short pass filter) for 20 min, the cells were treated with GB (0.8 M) under the same FR or GL illumination for 20 min to immobilize and couple PBS to the stromal surface of the PSII or PSI core complex in the thylakoid membrane.

2.3. FRAP measurements

The fluorescence recovery after photobleaching (FRAP) experiments were carried out using a scanning confocal microscope with a 633 nm helium-neon laser. Fluorescence passed through Schott RG665 red glass with excitation at 633 nm light arose predominantly from PBS cores, as described elsewhere [19]. Cells from untreated and GB-treated *Synechocystis* 6803 were individually dispersed and immobilized in a 1.5% low melting point agarose gel in BG-11 medium, then covered with a glass coverslip and placed on a temperature-controlled stage under the microscope objective lens. To avoid the effect of temperature on PBS movement, cells were added to the agarose gel below 35 °C. After images of cells were recorded at a low laser power, a selected rectangular area of a cell was photobleached at a high laser power, and then recovery of fluorescence was monitored by scanning the whole cell at low laser power in 1- or 3-s intervals to record the fluorescence recovery curves or a series of images. The recovery curves were normalized to correct for variations of background fluorescence and loss of fluorescence during bleaching [20]. The scanning laser intensity did not significantly photobleach the sample over the time course of the experiment.

2.4. Measurements of chlorophyll fluorescence and redox changes of P700

Changes in chlorophyll fluorescence yield were measured using a pulse-amplitude-modulated (PAM) chlorophyll fluorometer (Walz, Effeltrich, Germany) and an emitter-detector-cuvette assembly (ED-101US) with a unit 101ED as described elsewhere [21–23]. The untreated and GB-treated cells were dark-adapted for 35 s and then a modulated non-actinic measuring beam (1.6 kHz) was turned on to obtain the minimal fluorescence value, Fo. Multiple turnover flashes (XMT 103, Walz, Effeltrich, Germany) were applied under FR or GL illumination to obtain the fluorescence level of Fm'. The stable level of fluorescence (Fs) was determined during exposure of cells to FR or GL. At every indicated period (0.5, 1, 2, 5, 10, 20 or 30 min), FR or GL was turned off to determine the Fo′ value. The maximum fluorescence (Fm) was obtained by adding 3-(3,4-dichlorophenyl)-1,1-dimethylurea (DCMU; 10 μM) to the sample under actinic light. Q_A and NPQ were calculated as $1-[(Fm'-Fs)/(Fm'-Fo')\times(Fo'/Fs)]$ and $[(Fm/Fm')-1]$, respectively.

Redox changes in P700 were monitored by measuring the absorbance at 810–830 nm, using a PAM chlorophyll fluorometer (Walz, Effeltrich, Germany) and an emitter–detector–cuvette assembly (ED-101US) with a unit ED-P700DW-E. Cells were pre-illuminated by FR or GL for the indicated periods followed by 35 s of dark incubation before FR illumination to measure the initial rate of $P700^+$ dark reduction, as described elsewhere [24–26].

2.5. Measurements of chlorophyll fluorescence at 77 K

The untreated and GB-treated cells were pre-illuminated either with FR or GL for 5 min and then rapidly frozen in liquid nitrogen. Fluorescence emission spectra were obtained at 77 K using an F4500 spectrofluorimeter (Hitachi,

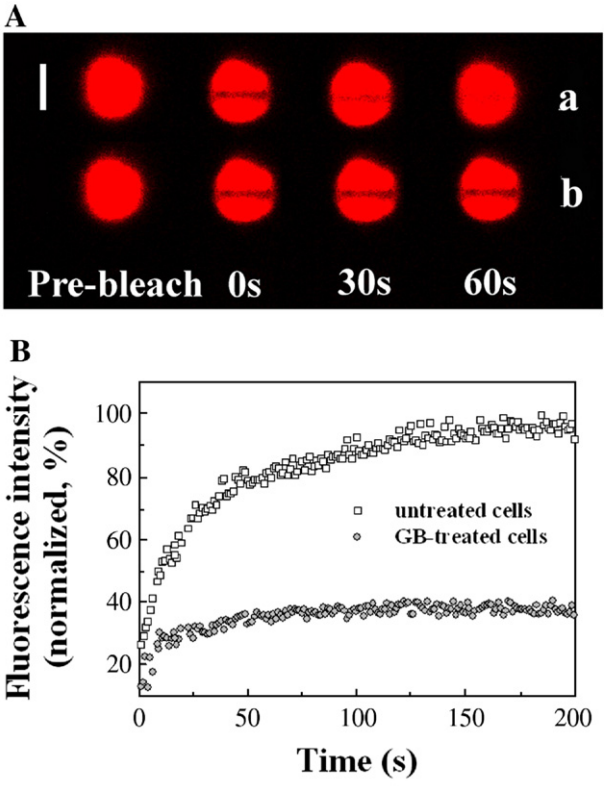

Fig. 1. Qualitative FRAP measurements (A) showing the diffusion of PBS in untreated (a) and GB-treated (b) cells, as observed by the FRAP image sequential scanning method at 28 °C. The bar indicates 3 μm. To directly compare the recovery curves (B), the fluorescence intensity of untreated (square) and GB-treated (circle) cells was normalized. See Materials and methods for experimental details.

Japan). The excitation wavelength was 580 nm. The fluorescence spectrum was obtained by averaging 6 spectra obtained for each sample in different tubes.

2.6. Photosynthetic oxygen evolution and respiration

Photosynthetic oxygen evolution and respiratory oxygen uptake were measured at 30 °C with a Clark-type oxygen electrode (Hansatech, UK) as described elsewhere [27]. The untreated and GB-treated cells were pre-illuminated with FR or GL for the indicated periods, and then white growth light (WL) or GL was turned on for the measurement of photosynthetic O_2 evolution, or the samples were incubated in the dark for the measurement of dark respiration after turning off the FR or GL. The photon flux density of WL and GL used for photosynthetic O_2 evolution was 40 and 15 μE m^{-2} s^{-1}, respectively. Under WL conditions, PBS were associated with PSII (see Ref. [15]).

3. Results

3.1. GB inhibits PBS movement

To test the effect of GB on the movement of PBS in *Synechocystis* 6803, we used FRAP to observe the diffusion of PBS on the thylakoid membrane. PBS fluorescence in the bleached area was completely recovered in the absence of GB but not in the presence of GB within the time scale of 60 s (Fig. 1), confirming previous results obtained in *S. platensis* showing that GB inhibits the diffusion of PBS [16]. In this study, we used GB to immobilize and couple PBS to PSII or PSI in *Synechocystis* 6803 cells.

3.2. State transitions dependent on PBS movement

Fig. 2A–D shows the changes in chlorophyll fluorescence yield at room temperature in untreated and GB-treated *Synechocystis* 6803 cells upon switching from FR (5.2 μE m^{-2} s^{-1}, >705 nm) to GL (15 μE m^{-2} s^{-1}, ~540 nm; Fig. 2A and B) or from GL to FR (Fig. 2C and D). The transition from state 1(2) to state 2(1) was clearly observed in untreated cells by switching from FR (GL) to GL (FR) and was completed within 1–2 min (Fig. 2A and C), confirming that state transitions are dependent on PBS movement [7]. The transitions were strongly inhibited when PBS was immobilized by GB (Fig. 2B and D). This was confirmed by measuring the 77 K chlorophyll fluorescence spectra, showing that the state transitions occurred in untreated cells (Fig. 3A) but were strongly inhibited by GB treatment (Fig. 3B and C). These results clearly showed that the state transitions depend predominantly on PBS movement and that the contribution of "spillover" is insignificant.

3.3. Reactions affected by PBS movement

3.3.1. Photosynthetic and respiratory electron transport

Oxygen evolution of FR-exposed cells was measured under white light (WL; 40 μE m^{-2} s^{-1}), which does not affect the movement of PBS from PSII to PSI, whereas O_2 evolution of GL-exposed cells was measured under GL to avoid PBS

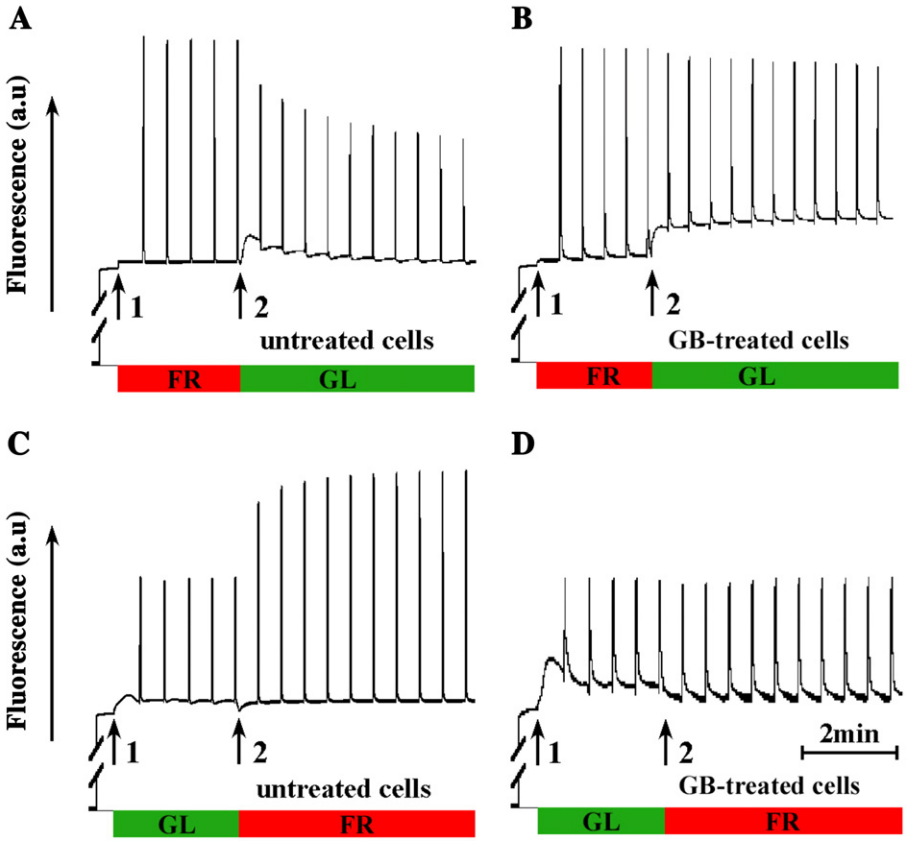

Fig. 2. Pulse-amplitude-modulated (PAM) fluorescence kinetic traces of untreated cells (A, C) and GB-treated cells in which PBS was immobilized and coupled to PSII (B) and PSI (D) under FR and GL, respectively. Samples in A and B were illuminated with FR as indicated by arrow 1, and then FR was switched to GL (arrow 2). Samples in C and D were first illuminated with GL (arrow 1), which was switched to FR as indicated by arrow 2. a.u., arbitrary units.

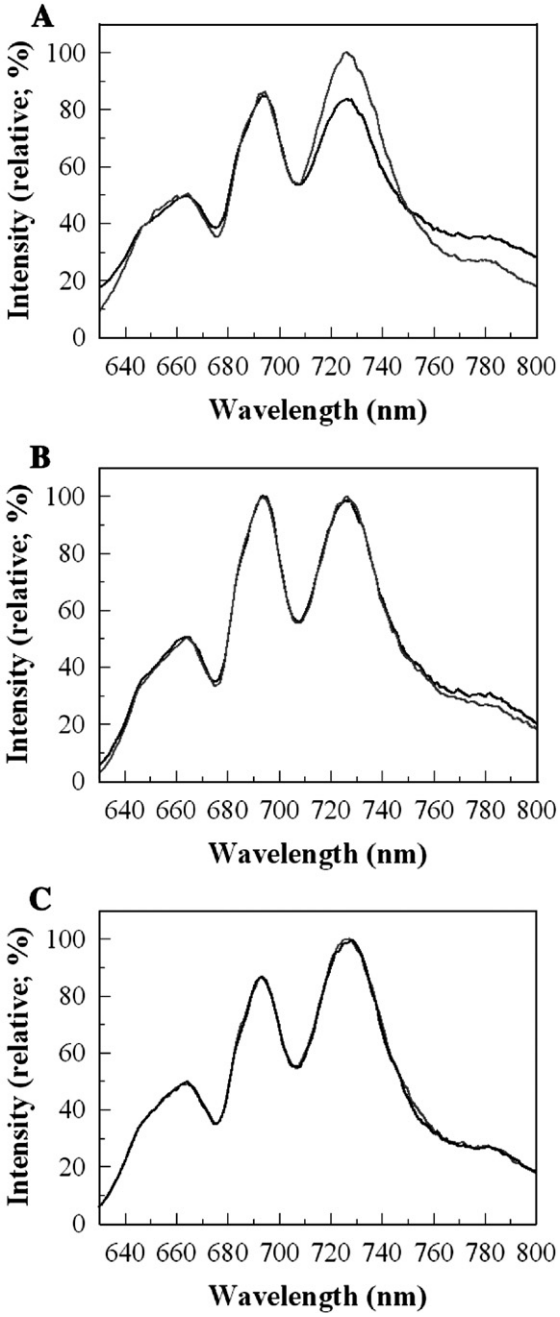

Fig. 3. Fluorescence emission spectra at 77 K of untreated cells (A) and GB-treated cells in which PBS was immobilized and coupled to PSII (B) and PSI (C) under FR and GL, respectively. Cells were pre-illuminated with either FR (black line) or GL (grey line) for 5 min and then rapidly frozen in liquid nitrogen. Each spectrum was obtained by averaging 6 spectra of the same sample in different tubes by exciting phycobilins at 580 nm and normalizing at the PSII fluorescence peak.

movement during the measurements. Switching from FR (GL) to GL (FR) caused a rapid decrease (increase) in photosynthetic O_2 evolution in both untreated and GB-treated cells due to changes in spectral quality and intensity of light (Fig. 4A and C). There were no significant changes in the activity of O_2 evolution in both untreated and GB-treated cells during 2 min of GL or FR illumination (Fig. 4A and C). However, this does not mean that the activity of PSII reaction did not change, since the activity of O_2 evolution depends on the activities of PSII, PSI, and CO_2 fixation. The activity of O_2 evolution decreased (increased) in untreated cells after longer illumination with GL (FR) (Fig. 4A and C). The increase in the activity under FR was observed even in GB-treated cells but was much slower than in untreated cells (Fig. 4C). The results suggested that the activity of O_2 evolution was not limited by the activity of the PSII reaction, which might have changed during the state transitions completed within 2 min, but it took longer for overall photosynthetic reactions to be tuned to a new state.

Switching from FR to GL markedly increased (about 30%) PSI-dependent cyclic electron flow (the initial rate of $P700^+$ dark reduction) in untreated cells but only slightly in GB-treated cells (Fig. 5A). In contrast, switching from GL to FR decreased the activity of PSI-dependent cyclic electron transport in untreated cells (Fig. 5B). The activity remained at a high level when the PBS were immobilized and coupled with PSI by GB even after treatment with GL (Fig. 5B). The results indicated that the movement of PBS between the two photosystems changed the activity of cyclic electron flow.

The movement of PBS also changed the activity of respiration. When FR was switched to GL, the respiration rate decreased rapidly and significantly in untreated cells but there was no significant change in GB-treated cells (Fig. 4B). In contrast, switching from GL to FR increased the respiration rate in untreated cells but only slightly increased the rate in GB-treated cells (Fig. 4D). Thus, the activity of respiration is high when PBS associates with PSII but low when PBS associates with PSI.

3.3.2. Redox state of Q_A

Fig. 6 shows the effect of FR and GL on the redox state of Q_A (= 1 − qL; see [12]). When cells were exposure to FR, Q_A was highly oxidized. Switching from FR to GL resulted in rapid reduction of Q_A to a high level in GB-treated cells but Q_A was transiently reduced and then oxidized to a stationary redox level in untreated cells (Fig. 6A). In contrast, when cells exposed to GL were transferred to FR, Q_A was rapidly oxidized in both untreated and GB-treated cells (Fig. 6B). The oxidation level of Q_A was higher in untreated cells than in GB-treated cells. Thus, the movement of PBS poises the redox state of the intersystem electron carriers at a highly oxidized state.

3.3.3. Non-photochemical quenching

When FR-exposed cells were transferred to GL, the non-photochemical quenching (NPQ) rapidly increased to a high level in untreated cells but only slightly increased in GB-treated cells (Fig. 7A). In contrast, when GL-exposed cells were transferred to FR, NPQ rapidly decreased from a high level to a low level in untreated cells but stayed at a high level in GB-treated cells (Fig. 7B). These results indicated that NPQ is low in cells in state 1 (PBS associated with PSII) but is high in cells in state 2 (PBS associated with PSI). Since it is difficult to observe the movement of PBS *in vivo*, it is convenient to use this fluorescence parameter, which can be easily measured, to

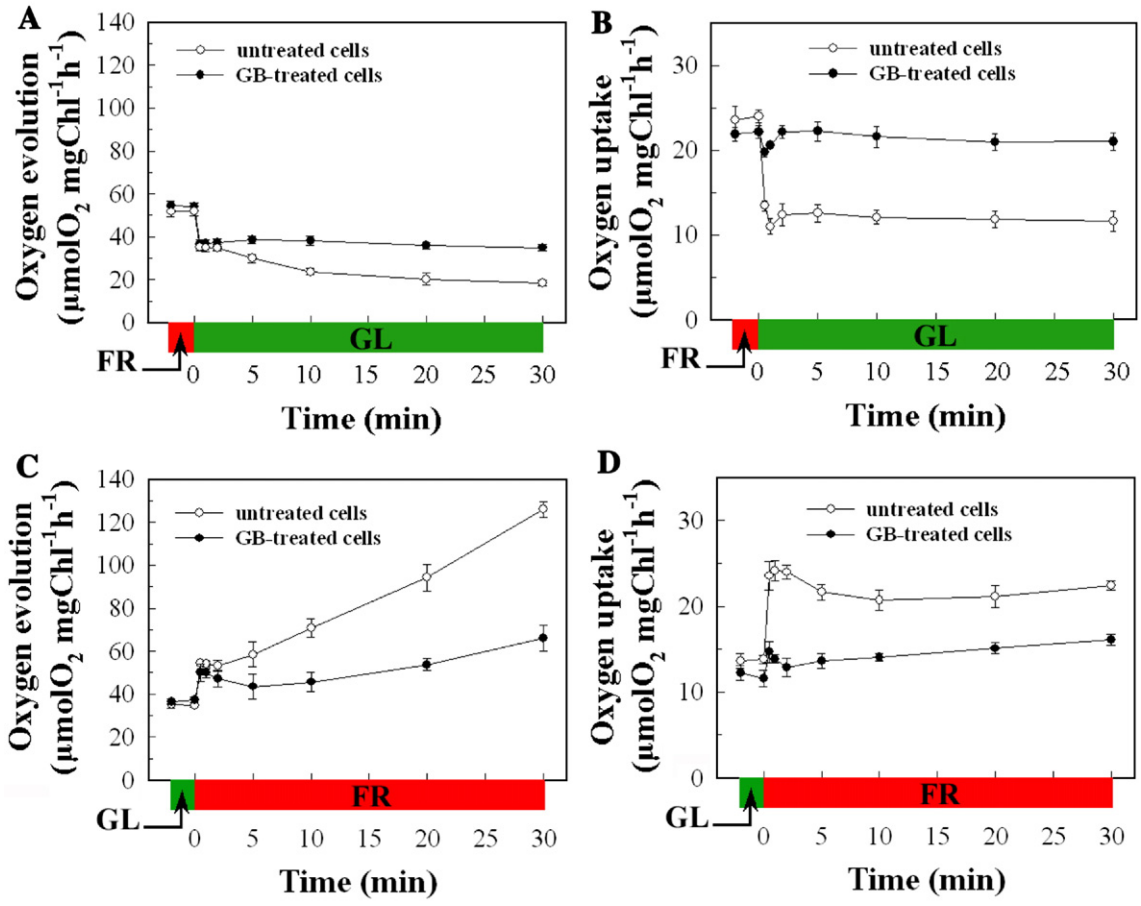

Fig. 4. Effects of switching GL (FR) to FR (GL) on photosynthetic O_2 evolution and respiration in untreated (open circles) and GB-treated (closed circles) cells. Cells where PBS are associated with PSII (A and B) or PSI (C and D) were illuminated with GL and FR, respectively, for various periods and then incubated in the dark for 35 s. Oxygen evolution was measured under GL (A) or WL (C). Respiration was measured in the dark after switching off the light (B and D). Experiments were repeated at least six times and standard errors were calculated.

monitor the movement of PBS between the two photosystems in cyanobacteria.

4. Discussion

4.1. Inhibition of PBS movement by GB

The inhibition of PBS movement by GB may occur by the following mechanisms. First, the strong polarity of GB molecules weakens electrostatic interactions between the link polypeptides and the C-phycocyanin (C-PC) hexamers or allophycocyanin (APC) trimers, thus weaken the coupling of the rods to cores [28]. Second, high concentrations of GB replace the water molecules at the interface between the hydrophobic thylakoid membrane and the water-soluble PBS, thus making the hydrophobic interaction of the loop domain of L_{CM}, a colored *l*inker polypeptide at the *c*ore-to-thylakoid *m*embrane junction, to the lipid membrane much stronger to fix PBS firmly [28]. Since GB had much less effect on the structure of APC trimers [5,29], the second mechanism is more plausible. Phosphate, sucrose, and potassium chloride solutions had similar effects on PBS movement as GB, and this effect appears to depend on the osmotic strength of the buffers [7,30]. Cells treated with phosphate buffer showed a significant inhibition of photosynthetic O_2 evolution [30], while O_2 evolution was much less affected by GB in *S. platensis* [16] and *Synechocystis* 6803 (Fig. 4A and C). Thus, it appears that different mechanisms are involved in the inhibition of PBS movement by GB and by other solutions.

GB has been used to maintain membrane fluidity, which is affected by temperature change and by high pressure [31,32]. These results indicate that GB does not inhibit membrane fluidity.

4.2. Light-induced state transitions depend predominantly on PBS movement

Several models have been proposed regarding the mechanism of state transitions in cyanobacteria. The major models are the “mobile PBS” model, which involves physical movement of PBS to explain the energy transfer from PBS to PSI [33–35], and the “spillover” model to interpret energy exchange from PSII to PSI, assuming a closer approximation of the two photosystems [36–38]. Others are similar to the two basic models [39–41]. A previous study showed that “mobile PBS”

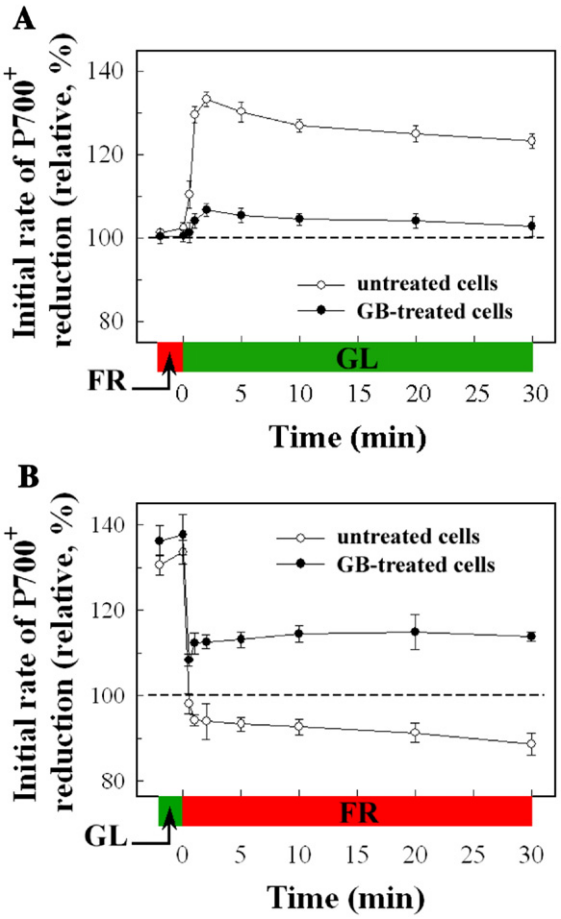

Fig. 5. Effects of switching GL (FR) to FR (GL) on the initial rate of $P700^+$ reduction in untreated (open circles) and GB-treated (closed circles) cells. Cells were illuminated with GL (A) or FR (B) and incubated in the dark, as described in the legend for Fig. 4, and then FR was applied to measure redox changes in P700. The value obtained for GB-treated cells under FR was taken as 100 (broken line). Standard errors were calculated from at least six independent experiments.

and "spillover" exist simultaneously during light-induced state transitions in cyanobacteria [41]. In contrast, a recent study has indicated that light-induced state transitions depend completely on "mobile PBS" regardless of the excitation wavelength, and "spillover" is only a special case when dark condition is involved [42].

It has been reported that PBS movement and membrane fluidity are essential for state transitions in cyanobacteria, and that the effect of membrane fluidity on state transitions is not associated with PBS-related NPQ mechanisms [7,43]. In contrast, the effect of PBS movement on light-induced state transitions is closely associated with NPQ levels ([44]; (Figs. 1, 2 and 7) in this paper). The strong inhibitory effect of GB on changes in electron transport activities and NPQ levels during light-induced state transitions indicates that these transitions are mainly dependent on PBS movement and the contribution of "spillover" is very small (Figs. 4, 5 and 7). This is supported by the absence of light-induced state transitions in GB-treated cells (Fig. 3B and C).

4.3. Electron transport affected by PBS movement

The activity of respiration was high when cells were in state 1 (PBS associated with PSII) and low in cells in state 2 (PBS associated with PSI) (Fig. 4B and D). In contrast, the activity of PSI-dependent cyclic electron transport was high when PBS was coupled to PSI and was low in the reverse movement (Fig. 5). Since respiratory electron flow and cyclic electron transport share the same plastoquinone (PQ) pool and cytochrome b_6f (Cytb_6f) in the thylakoid membrane in cyanobacteria, there was a competitive relationship between the electron flow to O_2 and that to PSI (cyclic electron transport) even in the dark after switching off FR or GL (Figs. 4B, D and 5). The changes in cyclic electron transport are ascribed to a result of redistribution of light energy absorbed by PBS between PSII and PSI and to the competition with respiration for electrons.

PBS movement dependent on state transitions occurred rapidly and was completed within 1–2 min (Figs. 1 and 2). No significant change was observed in photosynthetic O_2 evolution during this period (Fig. 4A and C), although the activity decreased (increased) slowly in untreated cells but not much in

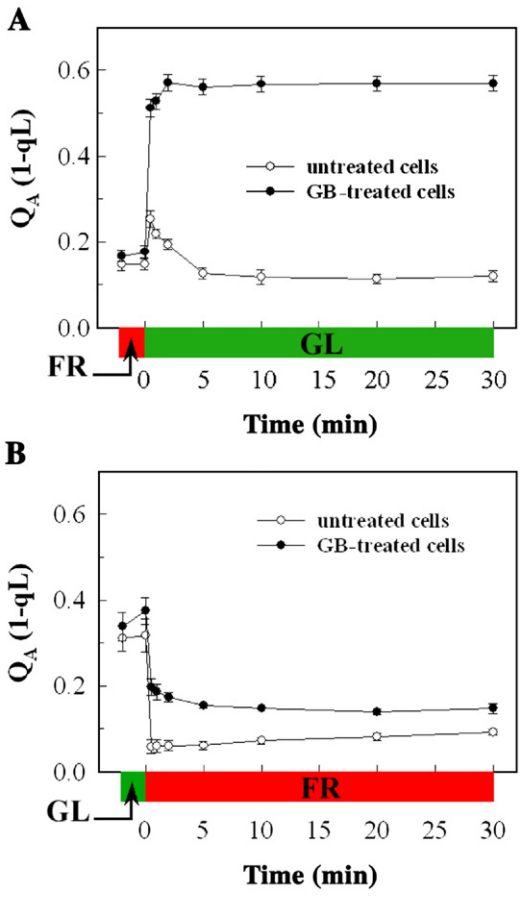

Fig. 6. Effects of switching GL (FR) to FR (GL) on the redox state of Q_A in untreated (open circles) and GB-treated (closed circles) cells. Cells were illuminated with GL (A) or FR (B) and incubated in the dark, as described in the legend for Fig. 4. The chlorophyll fluorescence parameters were measured as described in Materials and methods. Q_A was calculated as 1-qL. The vertical bars indicate standard errors calculated from at least five independent experiments.

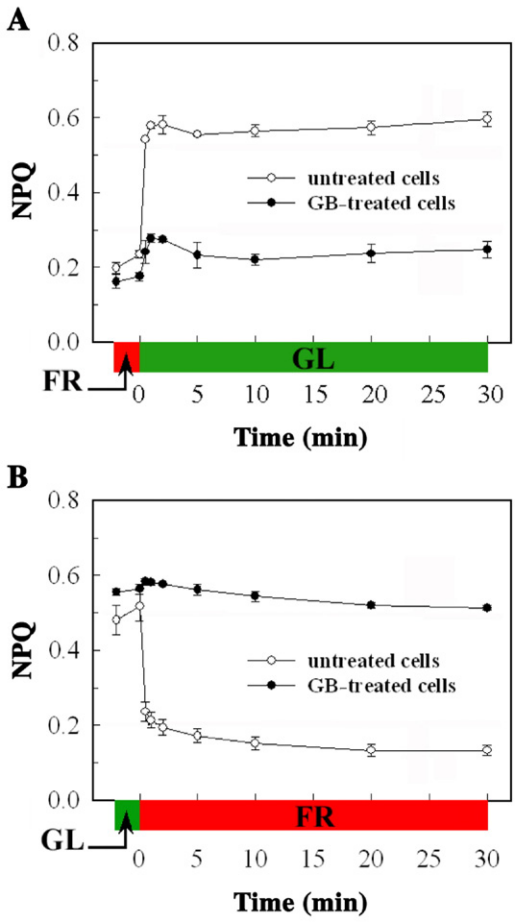

Fig. 7. Effects of switching GL (FR) to FR (GL) on the NPQ levels in untreated (open circles) and GB-treated (closed circles) cells. Cells were illuminated with GL (A) or FR (B) and incubated in the dark, as described in the legend for Fig. 4. The chlorophyll fluorescence parameters were measured as described in Materials and methods. NPQ was calculated as [(Fm/Fm′) − 1]. The vertical bars indicate standard errors calculated from at least five independent experiments.

GB-treated cells during prolonged GL (FR) illumination (Fig. 4A and C). The results suggested that it took longer for overall photosynthetic reactions to be tuned to a new state relative to short transitions. A similar tendency of oxygen evolution was also observed under lower photon flux densities (data not shown). Under these conditions, the activity of PSI may be not a rate-limiting step in linear electron transport, which is most likely limited by the activity of CO_2 fixation.

4.4. Fluorescence parameters affected by PBS movement

It has been reported that the redox balance of the interphotosystem electron carriers, such as PQ pool and Cytb_6f, regulates state transitions in cyanobacteria [45–49]. This was supported by the result that the reduction in the PQ pool by dark respiration caused a transition to state 2 [45–47,50]. The present result indicated that Q_A was reduced when FR was switched to GL. However, Q_A was oxidized again during prolonged illumination with GL (Fig. 6A). When GL was switched to FR, Q_A was oxidized and then reduced during prolonged illumination with FR to a level similar to the steady-state redox level of Q_A under GL (Fig. 6A and B). As a consequence, the redox state of Q_A, after transitory changes induced by light quality, comes again to the original steady-state level. Li et al. [16] showed that GB does not inhibit state transitions induced by redox changes of the PQ pool. This indicates that state transitions dependent on "spillover" and membrane fluidity are induced by redox changes of the PQ pool. Light-induced state transitions induced by PBS movement caused redox poise of the PQ pool but it is not clear whether they are induced by the redox changes of the PQ pool.

In cyanobacteria, a PBS-related NPQ mechanism has been suggested to be involved in a decrease in PBS fluorescence emission and a decrease in the transfer of excitation energy from PBS to PSII [43,51,52]. The time course of such a mechanism may be similar to that of state transitions because of the strong correlation between the NPQ level and the state transitions. Thus, the NPQ level can be used as a good measure of PBS movement.

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