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A newly developed SGB buffer greatly enhances energy transfer efficiency from phycobilisomes to photosystem II in cyanobacteria *in vitro*

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Abstract

The transfer of light energy from phycobilisomes (PBS) to photosystem II (PSII) reaction centers is vital for photosynthesis in cyanobacteria and red algae. To investigate the relationship between PBS and PSII and to optimize the energy transfer efficiency from PBS to PSII, isolation of the PBS-PSII supercomplex is necessary. SPC (sucrose/phosphate/citrate) is a conventional buffer for isolating PBS-PSII supercomplex in cyanobacteria. However, the energy transfer occurring in the supercomplex is poor. Here, we developed a new buffer named SGB by adding 1M glycinebetaine and additional sucrose to SPC buffer. Compared to SPC, the newly developed SGB buffer greatly enhanced the associated populations of PBS with thylakoid membranes and PSII and further improved the energy transfer efficiency from PBS to PSII reaction centers in cyanobacteria *in vitro*. Therefore, we conclude that SGB is an excellent buffer for isolating the PBS-PSII supercomplex and for enhancing the energy transfer efficiency from PBS to PSII reaction centers in cyanobacteria *in vitro*.

Additional key words: energy transfer efficiency; photosystem II; phycobilisome; SGB buffer; *Synechocystis* sp. PCC 6803; thylakoid membrane.

Introduction

The effective absorption of sunlight by antenna pigments is the critical first step in oxygenic photosynthesis. Phycobilisome (PBS) is the major accessory light-harvesting antennae molecule in cyanobacteria and red algae, while photosystem II (PSII) is the first photosynthetic membrane protein complex in the light-dependent reactions. Commonly, PBS attaches to the PSII surface in thylakoid membranes and transfers captured solar energy to the PSII reaction centers (Wang *et al*. 1977, Katoh and Gantt 1979). This is a main pathway that delivers sunlight to the reaction centers of PSII. Therefore, optimizing the energy transfer efficiency in the pathway, namely from PBS to PSII reaction centers, would improve the photosynthetic efficiency of cyanobacteria and red algae.

For isolation of cyanobacterial PBS and PSII complexes, highly concentrated buffers of phosphate (Gantt and Lipschultz 1972, Gray *et al.* 1973) and sugar (Ono and Murata 1978) has been commonly used. To further investigate the relationship between PBS and PSII and to optimize the energy transfer efficiency from PBS to PSII, the separation and purification of the PBS-PSII supercomplex is necessary. However, none of these buffers is suitable for isolating the PBS-PSII supramolecular complex. Under these circumstances, a sucrose/phosphate/citrate (SPC) buffer was developed to isolate and purify the PBS-PSII supercomplex. This was done by combining the main components of sugar and phosphate buffers and adding citrate as a new component, which facilitated the energy transfer from PBS to PSII reaction centers (Katoh and Gantt 1979). Although SPC buffer can efficiently separate the PBS-PSII supercomplex *in vitro*, the transfer of light energy from PBS to PSII reaction centers is poor, in particular after a detergent is added to the thylakoid membrane (Mullineaux 2008). Therefore, an improved buffer for isolating the PBS-PSII

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Abbreviations: APC – allophycocyanin; Chl – chlorophyll; GB – glycinebetaine; NQ – 1,4-naphthoquinone; PBS – phycobilisome; PC – phycocyanin; PSII – photosystem II; SGB – sucrose/phosphate/citrate/glycinebetaine; SPC – sucrose/phosphate/citrate; Suc – sucrose; *Synechocystis* 6803 – *Synechocystis* sp. strain PCC 6803.
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supramolecular complex with a high-energy transfer efficiency is required.

It has been repeatedly proposed that glycinebetaine (GB) and sucrose (Suc) can efficiently enhance the associating populations of PBS with the thylakoid membrane *in vitro* (Li *et al*. 2001, 2003, 2007, Joshua and Mullineaux 2004, Ma *et al*. 2007, 2010, Yang *et al.* 2007,) and protect the activity of PSII (Papageorgiou *et al*. 1991, Papageorgiou and Murata 1995, Allakhverdiev *et al*. 1996). It seems likely that GB and Suc can improve the energy transfer efficiency from PBS to PSII reaction centers. In this study, we developed an SGB buffer (Suc/phosphate/citrate/GB) by adding 1M GB and additional Suc to conventional SPC buffer. Furthermore, we isolated the PBS-thylakoid membrane and the PBS-PSII supercomplex by using SPC and SGB buffers. Finally, we compared the associating amounts of PBS with thylakoid membranes and with PSII reaction centers, as well as the energy transfer efficiency of PBS to PSII reaction centers using biochemical and spectral methods. Our results indicated that the newly developed SGB buffer greatly enhanced the energy transfer efficiency from PBS to PSII reaction centers in cyanobacteria *in vitro*.

Materials and methods

Culture conditions: *Synechocystis* 6803 (*Synechocystis* sp. strain PCC 6803) cells were cultured at 30°C in BG-11 medium (Allen 1968), buffered with Tris-HCl (5 mM, pH 8.0), bubbled with the air containing 2% CO_2 (v/v) and under the continuous illumination by fluorescent lamps [40 μmol(photons) m^{-2} s^{-1}].

Isolation of PBS-thylakoid membranes of *Synechocystis* 6803 cells was performed according to the previously reported methods (Brimble and Bruce 1989, Li *et al*. 2004) with slight modifications. Briefly, the cells cultured for 4 d (A_{730} = 1.0–1.2) were harvested by centrifugation (5,000 × *g* for 5 min at 4°C), washed twice with the SPC or SGB buffer, and then resuspended in the corresponding buffer.

Buffer component	SPC [M]	SGB [M]
Sucrose	0.5	0.8
Phosphate	0.5	0.5
Citrate	0.3	0.3
Glycinebetaine	0	1

Subsequently, the cells were disrupted by 10 pulses lasting 10 s with a *Bead-beater* (*Biospec*, Japan), followed by a 5-min incubation on ice. The homogenate was centrifuged at 2,000 × *g* for 10 min at 4°C to remove unbroken cells and debris. The supernatant was subjected to further centrifugation at 18,000 × *g* for 1 h at 4°C. The pellet contained the PBS-thylakoid membrane. Subsequently, the samples were immediately subjected to microscopic observations, to the determination of absorption spectra, and 77 K fluorescence emission spectra.

Microscopic observation: The PBS-thylakoid membranes from *Synechocystis* 6803 incubated in SPC and SGB buffers were observed according to the previously reported methods (Katoh and Gantt 1979) with slight modifications. The samples were fixed in 8% glutaraldehyde (pH 7.0) prior to staining with 1% ammonium molybdate. The observation of samples was performed on a *JEOL JEM-2100* transmission electron microscope (*JEOL*, Japan) with an operating voltage of 200 kV.

Analysis of photosynthetic pigments: Absorption spectra of PBS-thylakoid membrane from *Synechocystis* 6803 incubated in SPC and SGB buffers were recorded on a *U-3010 UV-Vis* spectrophotometer (*Hitachi*, Japan). The ratios of phycocyanin (PC) to chlorophyll (Chl) *a* and allophycocyanin (APC) to Chl *a* were evaluated as $(67.5 \times A_{620} - 17.3 \times A_{678})/(7.3 \times A_{678} - 0.3 \times A_{620})$ and $487.56 \times (A_{652} - 0.208 \times A_{615})/5.09 \times (7.3 \times A_{678} - 0.3 \times A_{620})$, respectively (Bennett and Bogorad 1973, Arnon *et al.* 1974).

Measurements of Chl fluorescence at 77 K: Before spectral measurement, the samples were resuspended in the SPC or SGB buffer to a concentration of 5 μg(Chl *a*) mL^{-1} and then frozen in a liquid nitrogen. The Chl concentrations were estimated from the absorbance at 665 nm in methanol extracts (Porra *et al*. 1989). Fluorescence emission spectra were obtained at 77 K using an *F-4500* spectrofluorimeter (*Hitachi*, Japan). The excitation wavelength was 580 nm and the excitation and emission slit widths were set in 5 and 2.5 nm, respectively. The fluorescence spectrum was obtained as a mean of 6 spectra obtained for each sample in different tubes.

Separation of PBS-PSII supercomplexes by sucrose density gradient centrifugation: The PBS-PSII supercomplexes were separated by sucrose density gradient centrifugation according to the previously reported methods (Clement-Metral and Gantt 1983) with slight modifications. The isolated PBS-thylakoid membranes were washed twice with buffer containing 50 mM Bis-Tris (pH 7.0), and 1 mM phenylmethylsulfonyl fluoride (PMSF) (*Sigma-Aldrich*, St. Louis, MO, USA), and then resuspended in 50 mM Bis-Tris (pH 7.0), 10 mM $MgCl_2$, 0.1 units RNase-Free DNase RQ1 (*Promega*, Madison, WI, USA) at a Chl *a* concentration of 10 mg mL^{-1}, and 1 mM PMSF. The samples were incubated on ice for 10 min, and an equal volume of 2% Triton X-100 was added. Solubilization was performed on ice for 10 min. After centrifugation at 10,000 × *g* for 30 min at 4°C, the cleared supernatant (1 mL) was loaded on the top of a 12 mL linear sucrose density gradient (0–1.33 M)

prepared with a buffer containing 0.5 M phosphate, 0.3 M citrate, 0.02% Triton X-100, and 50 mM Bis-Tris (pH 7.0). PBS-PSII supercomplexes were separated by ultracentrifuge (*Himac CP100WX*, *Hitachi*, Japan) for 17 h at 150,000 × *g* at 4°C in a *P40ST* rotor, and equal amounts of bands I and II fractions were used for further analyses of immunoblot and 77 K fluorescence spectra.

Western blot analysis: SDS-PAGE electrophoresis was carried out on 12% polyacrylamide gels according to the method of Laemmli (1970). Western blot analysis was performed with an *ECL assay* kit (*Amersham Pharmacia Biosciences*, NJ, USA) according to the manufacturer's protocol. Antibodies against the rod (C-phycocyanin α) and core (allophycocyanin α) subunits of the *Synechocystis* 6803 PBS were raised in our laboratory, and antibody against the PSII reaction centers (D1) was purchased from *Agrisera Co.* (Vännäs, Sweden).

Results

The associating populations of phycobilisomes with thylakoid membrane: It has been previously reported that GB and Suc can enhance the associating amounts of PBS with the thylakoid membrane (Li *et al*. 2001, 2003, 2007; Joshua and Mullineaux 2004, Ma *et al*. 2007, 2010; Yang *et al.* 2007). To increase the associating populations of PBS with the thylakoid membrane, we improved the SPC buffer by adding 1 M GB and extra Suc to the conventional buffer, and named the newly developed buffer SGB. As expected, the associating populations of PBS with the thylakoid membrane in SGB buffer were more abundant than those in SPC buffer, as judged by electron micrographs (Fig. 1*A*,*B*) and pigment analysis (Fig. 1*C*). Furthermore, the pigment ratios obtained in PBS-thylakoid membrane prepared by SGB buffer were almost identical to those from intact cells of *Synechocystis* 6803 (data not shown). Therefore, we concluded that the newly developed SGB buffer increased the associating populations of PBS with the thylakoid membrane.

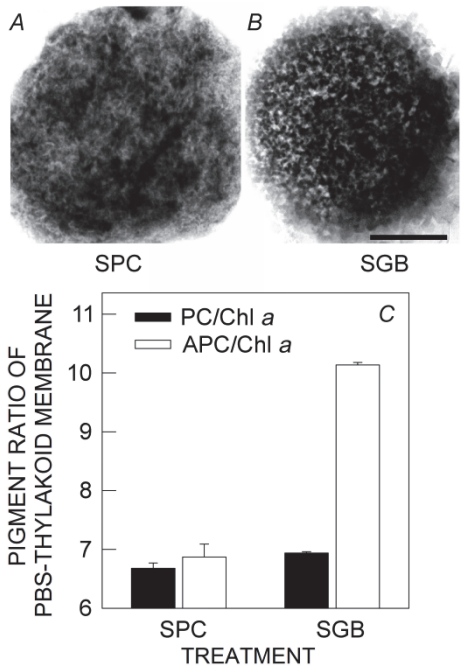

Fig. 1. Electron micrographs and pigment analysis of PBS-thylakoid membranes from *Synechocystis* 6803 incubated in different buffers. The incubation of PBS-thylakoid membranes in (*A*) SPC and (*B*) SGB buffers. The samples were fixed in glutaraldehyde prior to staining with 1% ammonium molybdate. (*C*): The ratios of PC to Chl *a* and APC to Chl *a* in PBS-thylakoid membranes prepared by SPC and SGB buffers, respectively. Bar – 0.5 μm.

The energy transfer efficiency from PBS to PSII in PBS-thylakoid membranes: We compared the 77 K fluorescence emission spectra excited at 580 nm in PBS-thylakoid membranes, which were isolated using SPC and SGB buffer systems, respectively. It has been previously demonstrated in *Synechocystis* 6803 that the 655 and 664 nm emission peaks originate from PBS, the 685 and 695 nm emissions originate from PSII, and that the 725 nm band is the most effectively produced by PSI (Fork *et al*. 1987, Krause and Weis 1991, Salehian and Bruce 1992, Govindjee 1995, Ma *et al*. 2008). However, the 685 nm peak also comes from the allophycocyanin B of PBS, although the 695 nm emission exclusively originates from PSII (Karapetyan 2008). As shown in Fig. 2*A*,*B*, a low PBS peak and a high PSII peak occurred in PBS-thylakoid membranes prepared by SGB buffer when compared with those prepared by SPC. This suggested that more energy was transferred from PBS to PSII reaction centers in the SGB-isolated supramolecular complexes. Furthermore, the fluorescence emission spectra obtained in PBS-thylakoid membranes prepared by the SGB buffer were similar to those from intact cells (Fig. 2*C*,*D*). Based on these results, we concluded that the newly developed buffer SGB greatly enhanced the efficiency of energy transfer from PBS to PSII reaction centers in PBS-thylakoid membranes in cyanobacteria *in vitro*.

The energy transfer efficiency from PBS to PSII in PBS-PSII supercomplex: We monitored the 77 K fluorescence spectra to further investigate, whether the newly developed buffer SGB could still maintain a high efficiency of energy transfer from PBS to PSII after the PBS-thylakoid membrane was solubilized with 1% Triton X-100. To distinguish the origin of the 685 nm peak, we measured first the 77 K fluorescence spectra with and without 1,4-naphthoquinone (NQ), a quencher of Chl fluorescence (Amesz and Fork 1967) but not of PBS

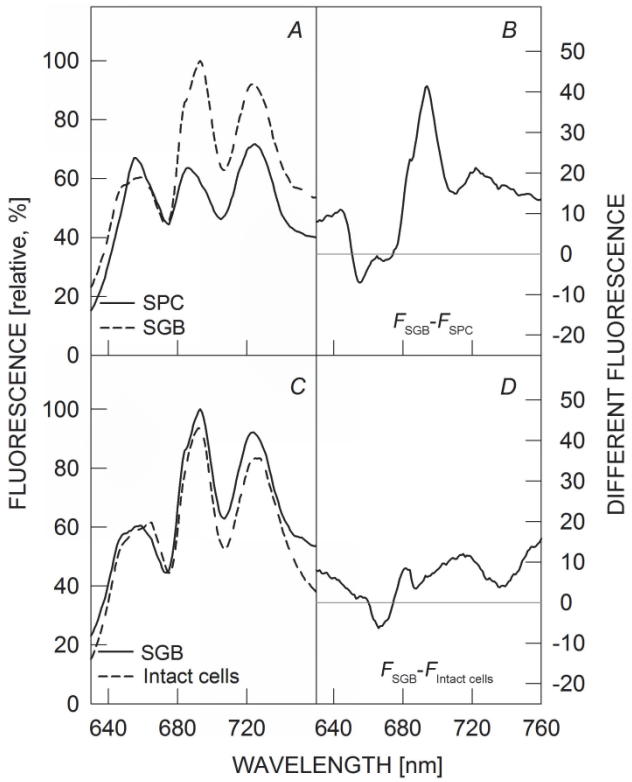

Fig. 2. The 77 K fluorescence emission (*A*,*C*) and difference (*B*,*D*) spectra in PBS-thylakoid membranes and intact cells of *Synechocystis* 6803. Each spectrum is a mean of 6 spectra of the same sample in different tubes by exciting phycobilins at 580 nm and normalizing at 670 nm.

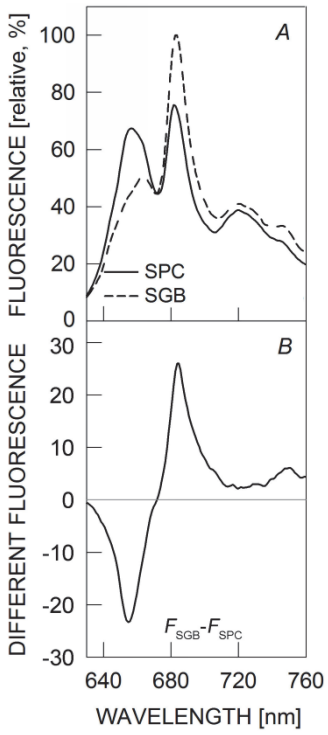

Fig. 3. The 77 K fluorescence emission (*A*) and difference (*B*) spectra after the addition of a detergent to the PBS-thylakoid membranes. Each spectrum is a mean of 6 spectra of the same sample in different tubes by exciting phycobilins at 580 nm and normalizing at 670 nm.

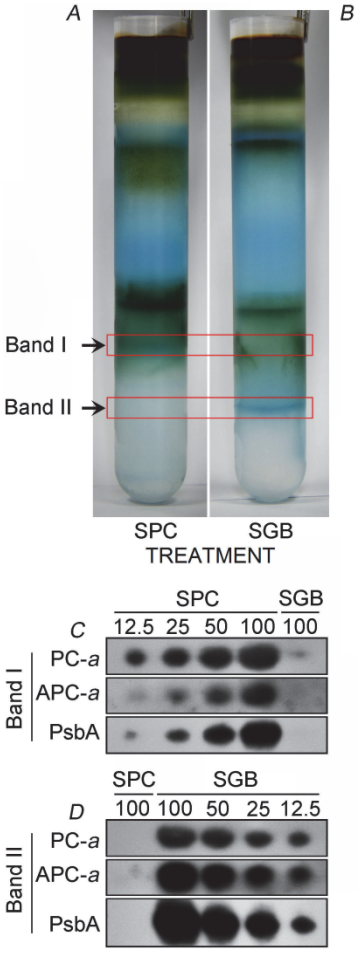

Fig. 4. Isolation and identification of bands I and II prepared by SPC and SGB buffers, respectively. *A*,*B*: The isolation of bands I and II by using sucrose density gradients. *C*,*D*: The identification of bands I and II by using immunoblotting against antibodies of PBS and PSII.

fluorescence (Mohanty *et al.* 1985). The usage of NQ resulted in a significant fluorescence quenching of the 685 nm peak (data not shown). In this case, therefore, the 685 nm emission mainly originated from PSII. As shown in Fig. 3, a low PBS peak (655 nm) and a high PSII peak (685 nm) occurred in PBS-PSII supramolecular complexes prepared by SGB buffer, when compared with those by SPC buffer. These findings suggested that more sunlight energy was transferred from PBS to PSII reaction centers in the SGB-isolated supramolecular complexes.

We also isolated the PBS-PSII supercomplexes using sucrose density gradient centrifugation, which facilitates the separation of protein supercomplexes under milder conditions. After centrifugation, we obtained PBS-PSII supercomplexes from bands I and II (Fig. 4*A*,*B*). Their components were also confirmed by immunoblotting, using the protein antibodies of PBS and PSII complexes, respectively (Fig. 4*C*,*D*). Moreover, the size of PBS-PSII supercomplex prepared by SGB buffer was much larger (bands I and II in Fig. 4*A*,*B*), when compared with those prepared by SPC buffer. Based on these results, we concluded that the newly developed buffer SGB increased the associating populations of PBS with PSII reaction centers.

Finally, we analyzed the energy transfer efficiency of PBS-PSII supercomplexes prepared by SGB and SPC buffer systems using the 77 K fluorescence emission spectra. Here, the 685 nm emission peak also mainly originated from PSII, as confirmed by NQ (data not shown). A low PBS peak (655 nm) and a high PSII peak (685 nm) also occurred in PBS-PSII supercomplexes prepared by SGB buffer in comparison with those prepared by SPC buffer (Fig. 5). Again, this indicated that more energy was transferred from PBS to PSII reaction centers in the supercomplexes isolated by SGB buffer.

Discussion

It has been extensively reported that SPC buffer can reinforce the association between PBS and PSII in cyanobacteria and red algae *in vitro* (Clement-Metral and Gantt 1983, Pakrasi and Sherman 1984, Clement-Metral *et al*. 1985). However, the association is considered to be relatively loose, especially in the presence of a detergent, thereby resulting in a poor energy transfer from PBS to PSII reaction centers (Mullineaux 2008). In this study, we added 1M GB and extra Suc to the conventional SPC buffer to develop the novel buffer SGB. SGB buffer enhanced the associating populations of PBS with thylakoid membranes (Fig. 1*A*,*B*) and PSII (Fig. 4), thereby greatly improving the energy transfer efficiency from PBS to PSII reaction centers in the unicellular cyanobacterium *Synechocystis* 6803 *in vitro* (Figs. 2,3,5). Despite significant improvement by SGB buffer, however, the energy transfer within PSII reaction centers was considerably poor (data not shown), which might be an important reason, why the 695 nm PSII peak was absent in detergent-solubilized PBS-thylakoid membrane (Fig. 3*A*) and PBS-PSII supercomplex (Fig. 5*A*).

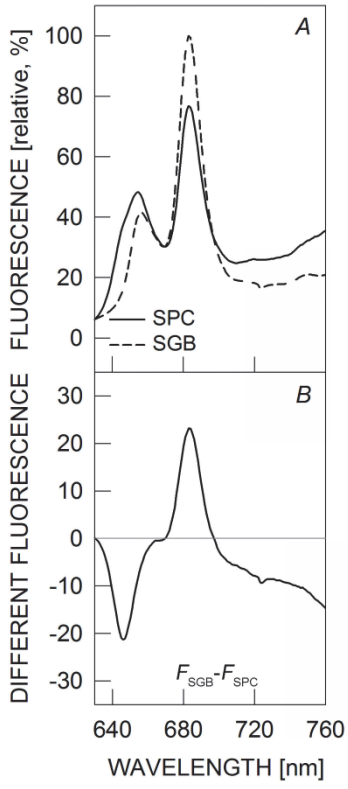

Fig. 5. The 77 K fluorescence emission (*A*) and difference (*B*) spectra in bands I and II prepared by SPC and SGB buffers, respectively. Each spectrum is a mean of 6 spectra of the same sample in different tubes by exciting phycobilins at 580 nm and normalizing at 670 nm.

Furthermore, SGB induced a tight association between PBS and PSII in a variety of more rigorous conditions than induced by SPC. These conditions included an increase in the intensity of broken cells and enhanced detergent concentration (data not shown). The SGB buffer, therefore, possessed a strong ability to maintain the association of PBS with PSII reaction centers, although they were not connected by a covalent bond.

It has been previously shown that high concentrations of GB and Suc, which were supplemented in SGB buffer, can inhibit the mobility of PBS on the surface of PSII in cyanobacteria (Joshua and Mullineaux 2004, Ma *et al*. 2007, Yang *et al.* 2007). The optimal concentration of GB and Suc required for the complete inhibition of PBS mobility on PSII is about 1 M (Li *et al*. 2001, Ma *et al*. 2007) and 0.8 M (Joshua and Mullineaux 2004), respectively. It seems likely that SGB buffer, which was developed by the addition of 1M GB and extra Suc (0.8 M) to conventional SPC buffer, had the ability to strengthen the association between PBS and PSII and improve the energy transfer from PBS to PSII. This might be an important reason, why the newly developed buffer SGB greatly enhanced the efficiency of energy transfer from PBS to PSII in cyanobacteria *in vitro*.

Furthermore, the associated populations and the energy transfer efficiency of the PBS-PSII supercomplex, prepared by other two newly developed buffers through adding either GB or more Suc to the SPC buffer, were much weaker than those prepared by the SGB buffer (data not shown). It has been previously reported that GB induces a partial dissociation of PBS (Li *et al*. 2007). It appears that the addition of more Suc to the SGB buffer could alleviate this dissociation effect. Therefore, the collaboration of GB and extra Suc in SGB buffer played an important role in enhancing the associating populations of PBS with PSII and in improving the energy transfer efficiency from PBS to PSII reaction centers in *Synechocystis* 6803 *in vitro*.

In conclusion, our results demonstrated that the newly developed buffer SGB greatly enhanced the associating populations of PBS with PSII and improved the energy transfer efficiency from PBS to PSII reaction centers. The improved effects were most likely the result of a collaboration between GB and additional Suc. The novel SGB buffer should be useful in investigating the energy transfer mechanisms and spatial structure of the PBS-PSII supercomplex in cyanobacteria *in vitro*.

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