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Effect of green light on the amount and activity of NDH-1–PSI supercomplex in *Synechocystis* sp. strain PCC 6803

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Abstract

Cyanobacterial NDH-1 interacts with PSI to form NDH-1–PSI supercomplex. CpcG2, a linker protein for the PSI-specific peripheral antenna CpcG2-phycobilisome, is essential for stabilization of the supercomplex. Green light (GL) increased the expression of CpcG2 but had little effect, if any, on the expression of NDH-1 and PSI, when compared to the abundance of these components under red light (RL). The increased expression of CpcG2 intensified the band of NDH-1–PSI supercomplex after blue-native gel electrophoresis of the thylakoid membrane, possibly by stabilizing the supercomplex. The activity of NDH-1-dependent cyclic electron transport around PSI increased when cells grown under RL were transferred to a low intensity GL but was suppressed when cells were grown under high intensities of GL. The functionality of PSI showed the same trend. We thus conclude that GL increases the expression of CpcG2, thereby increasing the abundance of the NDH-1–PSI supercomplex and its activity at low GL but not at higher GL.

Additional key words: chlorophyll fluorescence; cyanobacteria; cyclic electron transport around PSI; light-harvesting antenna; light quality; P700 analysis.

Introduction

Cyanobacterial NDH-1 is predominantly, if not totally, located in the thylakoid membrane (Ohkawa *et al.* 2001, 2002, Zhang *et al.* 2004, Xu *et al.* 2008, Battchikova *et al.* 2011), and participates in a variety of bioenergetic reactions, including respiration, cyclic electron transport around PSI (NDH-CET), and CO_2 uptake (Ogawa, 1991, Mi *et al.* 1992, Ohkawa *et al.* 2000). Recently, cyanobacterial NDH-1 was found to interact with PSI to form the NDH-1–PSI supercomplex *via* CpcG2-phycobilisome (PBS; Gao *et al.* 2016a), a PSI-specific peripheral antenna (Kondo *et al.* 2007). Furthermore, the supercomplex is involved in NDH-CET but not in respiration or CO_2 uptake (Gao *et al.* 2016a). The NDH-CET allows optimal functioning of photosynthesis by increasing the pH gradient and supplying extra ATP for CO_2 assimilation. This function would be particularly important under conditions of environmental stresses, such as high light (Battchikova *et al.* 2011, Dai *et al.* 2013, Zhang *et al.* 2014, Zhao *et al.* 2014a, Wang *et al.* 2016) and high temperature (Zhao *et al.* 2015, Gao *et al.* 2016b), in which the ATP demand is increased. However, whether the amount and activity of the NDH-1–PSI supercomplex change under environmental stresses remains elusive.

In the last few decades, the effect of GL on photosynthesis has been extensively studied in cyanobacteria. GL is predominantly absorbed by PBS, a main light-harvesting antenna in cyanobacteria and red algae. In the cyanobacterium *Synechocystis* sp. strain PCC 6803 (hereafter *Synechocystis* 6803), PBS is divided into two types, CpcG1–PBS and CpcG2–PBS (Kondo *et al.* 2005). The former is usually linked with PSII (Wang *et al.* 1977, Katoh and Gantt 1979) and is not involved in formation of NDH-1–PSI supercomplex (Gao *et al.* 2016a), while the latter is always associated with PSI *via* the C-terminal hydrophobic segment of CpcG2 linker protein (Kondo *et al.* 2007, 2009) and is necessary to form the supercomplex (Gao *et al.* 2016a). GL is absorbed by CpcG1–PBS, a conventional peripheral antenna in cyanobacteria,

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Abbreviations: BN-PAGE – blue-native-PAGE; CBB – *Coomassie Brilliant Blue*; Chl – chlorophyll; DCMU – 3-(3,4-dichlorophenyl)-1,1-dimethylurea; GL – green light; NDH-CET – NDH-1-dependent cyclic electron transport around PSI; PBS – phycobilisome; P_m – the maximal P700 change; RL – red light; *Synechocystis* 6803 – *Synechocystis* sp. strain PCC 6803.
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selectively drives PSII (Wang *et al.* 1977, Katoh and Gantt 1979), thereby triggering a transition to the state 2 and altering the activities of cyclic and respiratory electron transport in a short-time acclimation (Ma *et al.* 2007, Zhao *et al.* 2014b) and decreasing the PSII/PSI ratio (evaluated as the activity of both photosystems) in a long-term acclimation (Myers *et al.* 1980, Fujita *et al.*1985, Manodori and Melis 1986, Fujita and Murakami 1987, Melis *et al.* 1989).

In *Synechocystis* 6803, GL also induces the change in gene expression through the action of GL receptor, CcaS, and *cpcG2* is one of the target genes that are regulated by GL (Hirose *et al.* 2008). Specifically, illumination of *Synechocystis* 6803 cells with GL induces expression of *cpcG2*, leading to accumulation of CpcG2–PBS in the thylakoid membrane (Hirose *et al.* 2008). This suggested that GL may stabilize the NDH-1–PSI supercomplex by increasing the CpcG2–PBS (Gao *et al.* 2016a). We demonstrate in this study that GL induces accumulation of NDH-1–PSI supercomplex, possibly by stabilizing the supercomplex as a result of increased CpcG2. The activity of the supercomplex increased in cells grown under low intensity GL but decreased in cells grown under high intensities of GL. The functional role of NDH-1–PSI supercomplex in light stress is discussed based on the present results.

Materials and methods

Culture conditions: A glucose-tolerant strain of wild-type (WT) *Synechocystis* 6803 and WT-CpcG2-Yellow fluorescence protein (YFP)-His6 (WT-CpcG2-YH; Gao *et al.* 2016a) were cultured at 30°C in BG-11 medium (Allen 1968) buffered with Tris-HCl (5 mM; pH 8.0) by bubbling with 2% (v/v) CO_2 in air. The WT-CpcG2-YH strain was constructed by adding the YFP-His6 tag on the C terminus of CpcG2 in the WT background as described previously (Gao *et al.* 2016a). Cells were irradiated with 20 μmol (photon) m^{-2} s^{-1} of green light (GL; peak at 520 nm, half bandwidth 50 nm) or 15 μmol(photon) m^{-2} s^{-1} of red light (RL; peak at 660 nm, half bandwidth 20 nm), which was supplied by color fluorescent lamps (*FL20S-G* or *FL20SL-R*; *Panasonic*). The mutant strain was grown in the presence of 20 μg(spectinomycin) mL^{-1}.

Isolation of crude thylakoid membranes: Cells in cultured medium (800 mL) were harvested at the logarithmic phase of growth and washed twice by suspending in 50 mL of fresh BG-11 medium; the thylakoid membranes were isolated according to Gombos *et al.* (1994) with some modifications as follows. The cells suspended in 5 mL of disruption buffer (10 mM HEPES-NaOH, 5 mM sodium phosphate, pH 7.5, 10 mM $MgCl_2$, 10 mM NaCl, and 25% [v/v] glycerol) were mixed with 18 g of 0.5-mm-diameter zirconia/silica beads (*Biospec*, USA) and broken by vortexing 20 times at the highest speed for 30 s at 4°C with 5 min of cooling on ice between the runs. The crude extract was centrifuged at 5,000 × *g* for 5 min to remove the glass beads and unbroken cells. By further centrifugation at 20,000 × *g* for 30 min, we obtained crude thylakoid membranes as precipitates.

Electrophoresis and immunoblotting: Blue-native (BN)-PAGE of *Synechocystis* 6803 membranes was performed as described previously (Kügler *et al.* 1997) with slight modifications (Battchikova *et al.* 2011, Dai *et al.* 2013, Zhang *et al.* 2014, Zhao *et al.* 2014a, 2015, Wang *et al.* 2016, Gao *et al.* 2016a,b). Isolated membranes were prepared for BN-PAGE as follows. Membranes were washed with 330 mM sorbitol, 50 mM Bis-Tris, pH 7.0, and 0.5 mM phenylmethylsulfonyl fluoride (PMSF; *Sigma*) and resuspended in 20% (w/v) glycerol, 25 mM Bis-Tris, pH 7.0, 10 mM $MgCl_2$, 0.1 units of RNase-free DNase RQ1 (*Promega*) at a chlorophyll (Chl) *a* concentration of 0.25 mg mL^{-1}, and 0.5 mM PMSF. The samples were incubated on ice for 10 min, and an equal volume of 3% *n*-dodecyl-β-D-maltoside was added. Solubilization was performed for 40 min on ice. Insoluble components were removed by centrifugation at 18,000 × *g* for 15 min. The collected supernatant was mixed with one-tenth volume of sample buffer, 5% (w/v) *Serva Blue G*, 100 mM Bis-Tris, pH 7.0, 30% (w/v) sucrose, 500 mM ε-amino-*n*-caproic acid, and 10 mM EDTA. Solubilized membranes were then applied to a 0.75-mm thick, 5–12.5% (w/v) acrylamide gradient gel (*Hoefer Mighty Small* mini-vertical unit). Samples were loaded on an equal Chl *a* basis per lane. Electrophoresis was performed at 4°C by increasing the voltage gradually from 50 up to 200 V during the 5.5-h run. After electrophoresis, the proteins were visualized by *Coomassie Brilliant Blue* staining.

SDS-PAGE of *Synechocystis* 6803 crude thylakoid membranes was carried out on 12% (w/v) polyacrylamide gel with 6 M urea as described earlier (Laemmli 1970).

For immunoblotting, the proteins were electro-transferred to a polyvinylidene difluoride membrane (*Immobilon-P*; *Millipore*) and detected by protein-specific antibodies using an *ECL* assay kit (*Amersham*) according to the manufacturer's protocol. Antibodies against NdhI and NdhK were raised previously in our laboratory (Ma and Mi 2005). Antibody against His was purchased from *Shanghai Immune Biotech*., and antibodies against GFP, PsaB, and PsaD were purchased from *Agrisera*.

Chl fluorescence and P700 analysis: The transient rise in Chl fluorescence after actinic light (AL) had been turned off was monitored as described previously (Ma and Mi 2005).

The functionality of PSI was estimated by the P_m parameter. The Chl *a* concentration of *Synechocystis* 6803 cells was adjusted to 20 μg mL^{-1}. Prior to the P_m measurements, DCMU (10 μM final concentration) was

added. The P_m parameter was measured with a *Dual-PAM-100* (*Walz*, Germany) with an *ED-101US/MD* emitter-detector unit by monitoring absorbance changes at 830 nm and using 875 nm as a reference and its value was determined using a saturation pulse [100 ms; 10,000 μmol(photon) m^{-2} s^{-1}] under a far-red (FR) light background [720 nm; about 0.3 μmol(photon) m^{-2} s^{-1}] as described previously (Klughammer and Schreiber 2008).

Results

Effect of RL and GL on the amount of CpcG2: The content of CpcG2 was dependent on the color of light used for growth of cells. As shown in Fig. 1, the amount of CpcG2, as deduced from the abundance of its tags, in cells grown under GL was much higher than that in cells grown under RL. In contrast, light quality had little effect, if any, on the amounts of NDH-1 and PSI (Fig. 1), two key components of NDH-1–PSI supercomplex (Gao *et al.* 2016a). Thus, light quality used for growth of cells significantly affects the amount of CpcG2 but has little influence on the NDH-1 and PSI contents.

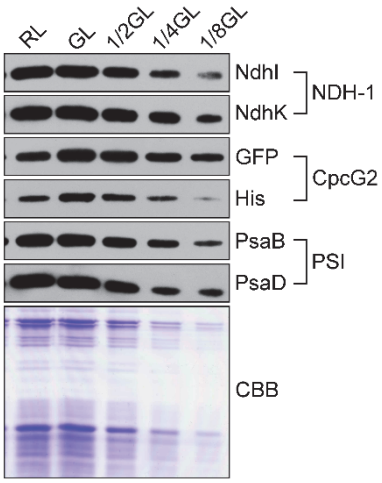

Fig. 1. Immunodetection of components of NDH-1–PSI supercomplex in cells grown under red light (RL) and green light (GL). *Coomassie Brilliant Blue* (CBB) staining profiles of total proteins prepared from cells grown under RL and GL (including indicated serial dilutions) and their immunoblotting using the antibodies against NdhI, NdhK (NDH-1), PsaB, and PsaD (PSI) subunits or GFP and His tags (CpcG2). Total proteins corresponding to 1 μg of chlorophyll *a* (100%) was loaded onto each lane.

Effect of GL on the amount and activity of NDH-1–PSI: CpcG2–PBS is considered to be located between NDH-1 and PSI in the NDH-1–PSI supercomplex, which is suggested to be closely linked with the amount of CpcG2–PBS (Gao *et al.* 2016a). Thus, it appears plausible that the rise in CpcG2–PBS content induced by GL illumination may increase the amount of NDH-1–PSI supercomplex. To test this possibility, we performed BN-PAGE on solubilized thylakoid membrane from cells grown under RL and GL, respectively, to separate the NDH-1–PSI supercomplex. Fig. 2, showing the profiles of BN-PAGE before and after CBB staining, indicated that the band of NDH-1–PSI supercomplex (pink arrows) is denser in GL-grown cells than in RL-grown cells. The results support the view that the formation of NDH-1–PSI supercomplex is limited by the amount of CpcG2–PBS and that the enhanced expression of CpcG2–PBS under GL led to the increased formation of NDH-1–PSI supercomplex.

To investigate whether the increased amount of NDH-1–PSI supercomplex affects the activity of NDH-CET, we monitored the postillumination rise in Chl fluorescence, which has been used to evaluate the NDH-CET activity in cyanobacteria (Mi *et al.* 1995, Ma and Mi 2005) and higher plants (Burrows *et al.* 1998, Shikanai *et al.* 1998). Unexpectedly, the activity, assessed as the amplitude of the fluorescence rise, was lower in GL-grown cells than that in RL-grown cells (Fig. 3).

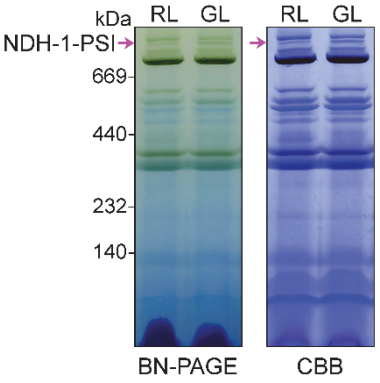

Fig. 2. Accumulation of NDH-1–PSI supercomplex in cells grown under RL and GL. Thylakoid membranes of cells grown in RL or GL were subjected to BN-PAGE. The profiles of gel before (left) and after stained by *Coomassie Brilliant Blue* (CBB; right) are shown with pink arrows representing the position of NDH-1–PSI supercomplex.

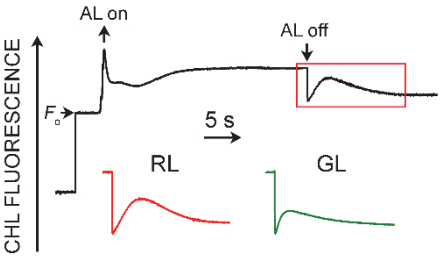

Fig. 3. Activity of NDH-CET of cells grown under RL and GL. The top curve shows a typical trace of chlorophyll fluorescence in WT *Synechocystis* 6803. The chlorophyll *a* concentration was adjusted to 10 μg mL^{-1} before measurement. Cells grown under RL or GL were exposed to actinic light [AL; 620 nm, 45 μmol(photon) m^{-2} s^{-1}] for 30 s. AL was turned off, and the subsequent change in the chlorophyll fluorescence level was monitored as an indicator of NDH-CET activity.

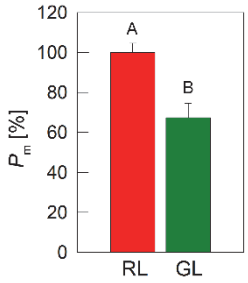

Fig. 4. Functional fraction of PSI in cells grown under RL and GL. Cells were collected during their logarithmic growth phase. The chlorophyll *a* concentration was adjusted to 20 μg mL^{-1}. Prior to the P_m measurement, DCMU (10 μM final concentration) was added to the cell suspension. The functionality of PSI reaction centers was determined by P_m parameter, expressed in percentage of the value obtained with RL-grown cells (100%). Values are means ± SD (n = 5). Different *capital letters* represent significant differences (p<0.05) between cells grown under conditions of RL and GL.

Effect of GL on the functionality of PSI: To understand why the increase of NDH-1–PSI supercomplex reduced the activity of NDH-CET, we measured the functional fraction of PSI in cells grown under RL and GL. The fraction of functional PSI was significantly reduced in GL-grown cells when compared to that in RL-grown cells (Fig. 4). It appears plausible that excess intensities of GL absorbed by the peripheral antenna PBS, including CpcG2-PBS, damaged the function of PSI. This view was supported by the following results. When cells grown in RL were transferred to various intensities of GL, the fractions of functional PSI increased under low GL intensity [2 μmol(photon) m^{-2} s^{-1}] but decreased under higher intensities (Fig. 5). Thus, the activity of NDH-CET under GL is associated with functional PSI but not always with the amount of the supercomplex.

Discussion

Over the last few decades, a significant achievement has been made in identifying the influence of GL on photosynthesis in cyanobacteria. GL triggers a transition to the state 2, alters the activities of cyclic and respiratory electron transport (Ma *et al.* 2007, Zhao *et al.* 2014b), reduces the PSII/PSI ratio (Myers *et al.* 1980, Fujita *et al.*1985, Manodori and Melis 1986, Fujita and Murakami 1987, Melis *et al.* 1989) and induces the change in gene expression *via* action of GL receptor, CcaS (Hirose *et al.* 2008). The results of this study further indicated that GL increased the amounts of CpcG2 protein but had little, if any, effect on NDH-1 or PSI (Fig. 1) and consequently, stabilized the NDH-1–PSI supercomplex (Fig. 2). This implies that stabilization of the supercomplex *via* increasing the CpcG2 contents may be one of important strategies on acclimation of cyanobacterial cells to stress conditions of GL. The important strategy appears to be specific to cyanobacteria and not to higher plants, since higher plants lack the homolog of CpcG2 (Kondo *et al.* 2005).

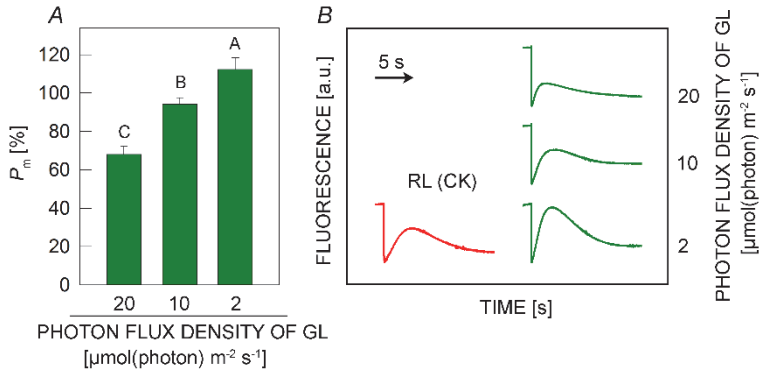

Fig. 5. Functional fraction of PSI and NDH-CET activity in cells grown under different intensities of GL. Cells were collected during their logarithmic growth phase and functional fraction of PSI (*A*) and NDH-CET activity (*B*) were determined. *A*, prior to the P_m measurement, DCMU (10 μM final concentration) was added to the cell suspension. The functionality of PSI reaction centers was determined by P_m parameter, expressed as in the legend for Fig. 4. Values are means ± SD (n = 5). Different *capital letters* represent significant differences (p<0.05) in cells grown under different intensities of GL. *B*, the NDH-CET activity was measured as described in the legend for Fig. 3.

In cyanobacteria, the NDH-1–PSI supercomplex is involved in NDH-CET but not in respiration or CO_2 acquisition (Gao *et al.* 2016a). The results of this study further indicated that the amount of the supercomplex was not always linked to its activity of NDH-CET (Fig. 3); the activity decreased under high intensities of GL although the amount of the supercomplex increased (Fig. 5). GL can be effectively absorbed by the CpcG1–PBS and CpcG2–PBS peripheral antennae and consequently, excess energy transferred from PBS to PSI under relatively high

intensities of GL may suppress the functionality of PSI and the activity of NDH-1–PSI supercomplex (Figs. 3–5).

In nature, cyanobacteria are distributed in the deep-water area (Moisander *et al.* 2010), where low intensity GL may be the major light source because GL is largely unused by photosynthetic organism on the surface area (Terashima *et al.* 2009). The results of this study showed that low intensity of GL slightly increases the functionality of PSI when compared to its functionality in RL-grown cells (Fig. 5). Therefore, GL captured by cyanobacteria in the deep-water area *via* the peripheral antenna PBS may increase the amount of NDH-1–PSI supercomplex and its activity NDH-CET. ATP production linked to NDH-CET may be important for cyanobacterial cells to distribute and acclimate in the deep-water areas.

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