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sll1961 is a novel regulator of phycobilisome degradation during nitrogen starvation in the cyanobacterium *Synechocystis* sp. PCC 6803

Hanayo Sato, Tamaki Fujimori, Kintake Sonoike*

Department of Integrated Biosciences, Graduate School of Frontier Sciences, The University of Tokyo, Box 101, Kashiwanoha 5-1-5, Kashiwashi, Chiba 277-8562, Japan

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Abstract **The *sll1961* gene was reported to encode a regulatory factor of photosystem stoichiometry in the cyanobacterium *Synechocystis* sp. PCC 6803. We here show that the *sll1961* gene is also essential for the phycobilisome degradation during nitrogen starvation. The defect in phycobilisome degradation was observed in the *sll1961* mutant despite the increased expression of *nblA*, a gene involved in phycobilisome degradation during nitrogen starvation. Photosystem stoichiometry is not affected by nitrogen starvation in the *sll1961* mutant nor in the wild-type. The results indicate the presence of a novel pathway for phycobilisome degradation control independent of *nblA* expression.**

Keywords: Cyanobacteria; Nutrient limitation; Photosystem stoichiometry; Phycobilisome degradation

1. Introduction

Photosynthetic organisms have developed various mechanisms that enable them to acclimate to ever-changing environmental conditions such as light or nutrient availability. These processes involve the coordination of different reactions in photosynthesis, or that of photosynthesis with other metabolic pathways [1,2]. For example, nitrogen assimilation requires reducing power produced by photosynthetic electron transfer, so that coordination between these two metabolic pathways is indispensable [3]. Modulation of photosystem stoichiometry, i.e. the ratio of two photosystems (PSI and PSII), is one of the regulatory mechanisms of photosynthesis and is important for the optimization of photosynthesis in response to changes in light intensity [4,5], light quality [6–8] and certain environmental stress conditions [9,10]. Under high light conditions, modulation of photosystem stoichiometry is essential to down-regulate photosynthetic electron transfer [11]. In our previous study, the *sll1961* was identified as a gene involved in the modulation of photosystem stoichiometry in *Synechocystis* sp. PCC 6803 [12]. The phenotype of *sll1961* disruptant is similar to that of *pmgA* mutant, *pmgA* being another gene that is involved in the regulation of photosystem stoichiometry under high light condition [5,11,13]. Both mutants lost the ability to suppress the level of PSI under high light condition [11,12]. Although several other genes were reported to be involved in the regulation of photosystem stoichiometry [14], the relationship among these components remains unknown.

An ortholog of the *pmgA* gene in *Synechococcus elongatus* PCC 7942 is necessary for the degradation of phycobilisome (PBS) upon nitrogen starvation, and was named *nblC* [15]. During nitrogen starvation, the degradation of PBS plays a critical role to meet cellular nitrogen demand [16]. The degradation of PBS results in a color change of the culture from blue-green to yellow, a process called bleaching [17,18]. During nitrogen starvation, NblC regulates transcriptional induction of *nblA*, whose product was reported to interact with some phycobiliprotein subunits [19,20] and to be involved in PBS degradation in *S. elongatus* PCC 7942 [15]. NblA orthologs are found in many cyanobacteria and red algae [21–23]. In *Synechocystis* sp. PCC 6803, there are two *nblA* genes, namely *nblA1* (*ssl0452*) and *nblA2* (*ssl0453*). Both genes are required for PBS degradation during nitrogen starvation [21].

The fact that the *Synechococcus* sp. PCC 7942 ortholog of *pmgA*, previously reported to be involved in the regulation of photosystem stoichiometry under high light conditions, is involved in the response to nitrogen starvation may suggest existence of a crosstalk between the two acclimatory responses. In the present study, we compare the effects of nitrogen starvation on *pmgA* and *sll1961* mutants: while the *pmgA* mutant is able to degrade its PBS, the *sll1961* mutant has a non-bleaching phenotype, demonstrating that the gene product of sll1961 participates in the degradation of PBS.

2. Materials and methods

A wild-type strain, the *sll1961* mutant (*0205-79*) [12] and *pmgA* (*sll1968*) mutant disrupted by spectinomycin cassette [24] of *Synechocystis* sp. PCC 6803 were grown with bubbling of air (i.e. about 0.04% CO_2) as described previously [12], except for the growth light condition (50 μmol m^{-2} s^{-1}). To confirm the non-bleaching phenotype, deletion mutant of *sll1961* with spectinomycin cassette [12] was also used. For nitrogen starvation experiments, exponentially grown cells were harvested by centrifugation and washed with BG11 medium lacking nitrate ($BG11_0$). The washed cells were resuspended in $BG11_0$ and used for experiments.

Disruptant of *nblA* was generated by the replacement of a part of *nblA* genes (53rd nucleotide of *nblA1* to 97th nucleotide of *nblA2*) with a spectinomycin-resistant cassette using SphI and HpaI sites. The *nblA* disruptant was grown in the presence of 20 μg/ml spectinomycin.

Absorption spectra of whole cells were measured using a spectrophotometer (Model 356, Hitachi, Tokyo, Japan) [15]. Chlorophyll (Chl) and phycocyanin (PC) contents were calculated using the equa-

*Corresponding author. Fax: +81 4 7136 3651.
E-mail address: sonoike@k.u-tokyo.ac.jp (K. Sonoike).

Abbreviations: PS, photosystem; PBS, phycobilisome; PC, phycocyanin; Chl, chlorophyll

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tions of Arnon et al. [25]. The number of cells was determined by measuring OD_{730} (1.1×10^8 cells/ml at 1 OD_{730} [14]) with a spectrophotometer (GeneSpecIII, Hitachi, Tokyo, Japan).

Fluorescence emission spectra at 77 K were measured as described in [12] with a band-pass filter (CS 4-96, Corning, NY, USA) and a dichroic filter (DF Blue, Optical Coatings Japan, Tokyo, Japan) for Chl excitation. Before fluorescence measurements, cells were dark adapted (>10 min) at room temperature to lock the cells to state II and frozen in the dark with liquid nitrogen.

For Northern blot analysis, total RNA was isolated from the cells as described in [32]. RNA was subjected to electrophoresis on 0.9% agarose gels (10 μg of total RNA was loaded per lane) and blotted onto nylon membranes (Pall Corporation Biodyne PLUS). DIG labeling and detection were performed according to the system application manual (Roche, Mannheim, Germany). To make a DIG-labeled DNA probe, *nblA1–2* was amplified by PCR and then labeled with DIG (Roche, Mannheim, Germany). The following primers were used for the probe by PCR: *nblA* forward: 5′-TTGGAGGGGCAACAGCT ATGAA-3′, *nblA* reverse: 5′-GGGGAGGAGTGAATTTTTCATC-3′. Dig labeled transcripts were detected by chemiluminescence using an LAS1000 image analyzer (Fuji Photo Film, Tokyo, Japan).

For RT-PCR, total RNA was isolated by the RNeasy Midi kit (Qiagen, Hilden, Germany) and treated with DNaseI to eliminate genomic DNA. RT-PCR was performed by TaKaRa RNA PCR kit (TaKaRa, Tokyo, Japan) using 0.5 μg of total RNA. The following primers were used for amplification of *sll1961* or *rnpB*: *sll1961* forward: 5′-ATGCT ACAGTTCCAAATTCA-3′, *sll1961* reverse: 5′-TTAAGCCGTGGC CACTTTTG-3′, *rnpB* forward: 5′-CGCCCAGTGCGCGCGAGCG TGAGGA-3′, *rnpB* reverse: 5′-CCTCCGACCTTGCTTCCAACCG GGG-3′. DNA was amplified using PTC-200 Peltier thermal cycler (MJ Research, USA).

3. Results and discussion

3.1. *sll1961* is involved in PBS degradation under nitrogen starvation

Wild-type (WT) cells grown in complete BG11 medium showed typical blue-green color (Fig. 1A-1), while those grown in medium lacking nitrogen source ($BG11_0$) showed bleaching after 48 h (Fig. 1A-4). Although the *sll1961* disruptant was indistinguishable from the WT when grown in BG11 (Fig. 1A-2), the mutant grown in $BG11_0$ remained blue-green (Fig. 1A-5), suggesting that the reduction in the amount of PBS was impaired in the *sll1961* mutant. In contrast, the *pmgA* mutant became chlorotic in $BG11_0$ (Fig. 1A-6). These changes in color could be confirmed by the change in the absorption spectra of the cell cultures. The absorption around 620 nm due to PC in PBS decreased during nitrogen starvation of the WT and the *pmgA* mutant cells but not of the *sll1961* mutant cells (Fig. 1B). The levels of both Chl and PC decreased in all strains after the shift to $BG11_0$ (Fig. 1C and D), but the decrease in the PC content of the *sll1961* mutant was less prominent, leading to the constant PC/Chl ratio upon nitrogen starvation (Fig. 1E, squares). Non-bleaching phenotype was also observed in the deletion mutant of *sll1961* with spectinomycin cassette (data not shown). The results indicate that the *sll1961* mutant has a defect in the reduction of PBS content upon nitrogen starvation, in addition to the defect in the regulation of photosystem stoichiometry under high light conditions that was previously reported [12]. The lack of decrease of PBS upon nitrogen starvation in the *sll1961* mutant is not due to the enhanced synthesis of phycobiliproteins, since the suppression, rather than the enhancement, of the expression of the *cpc* genes encoding PBS components was observed during nitrogen starvation (Fig. 2). The *pmgA* mutant showed normal pigment reduction upon nitrogen starvation, unlike the *nblC* mutant in *S. elongatus* PCC 7942. In *Synechocystis* 6803, mutations in the orthologs of *nblS* (*dspA*) and *nblR*, which regulate PBS degradation in *S. elongatus* PCC 7942, result in normal PBS degradation and normal expression of *nblA* under nitrogen starvation [26,27]. Apparently, the mechanism of bleaching is different between *S. elongatus* PCC 7942 and *Synechocystis* sp. PCC 6803.

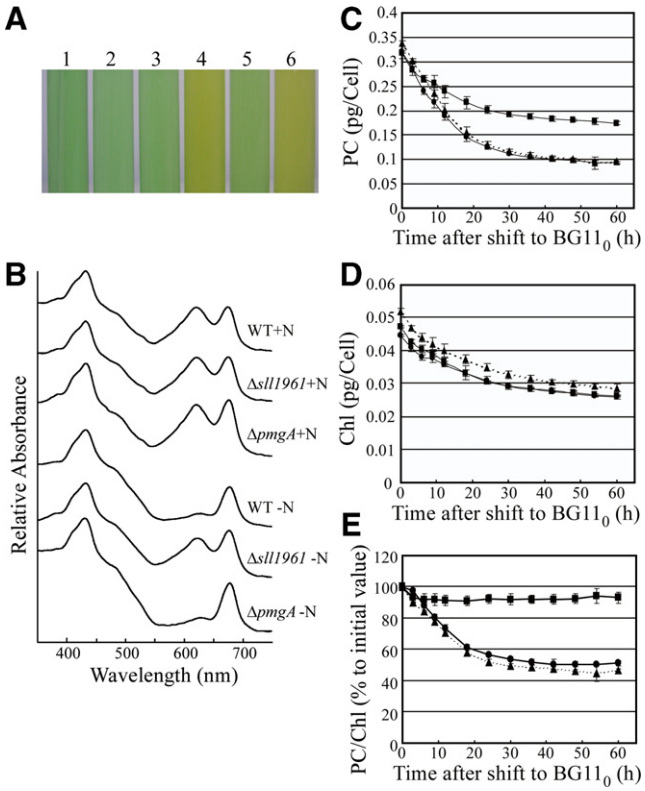

Fig. 1. Pigment profiles during nitrogen starvation. (A) Color of liquid culture of WT (1 and 4), the *sll1961* mutant (2 and 5) and *pmgA* mutant (3 and 6) grown in complete medium (1–3) or in nitrogen-deficient medium ($BG11_0$) for 48 h (4–6). (B) Absorbance spectra of whole cells of WT, the *sll1961* mutant (Δ*sll1961*) and the *pmgA* mutant (Δ*pmgA*) with (+N) and without (−N) nitrogen in BG11 medium. (C) The levels of phycocyanin (PC) on a per-cell basis and (D) the levels of chlorophyll (Chl) on a per-cell basis in WT (circles), *sll1961* mutant (squares) and *pmgA* mutant (triangles) during nitrogen starvation. (E) PC/Chl ratio. The 100% values correspond to the values before the shift to $BG11_0$. This initial PC/Chl ratio of WT, the *sll1961* and *pmgA* mutant was 7.17, 6.75 and 6.51, respectively.

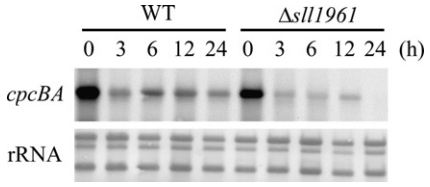

Fig. 2. Expression of *cpc* genes encoding phycocyanin during nitrogen starvation. Northern blot analysis of *cpcBA* expression was performed in WT and the *sll1961* mutant at 0, 3, 6, 12, 24 h following the shift to $BG11_0$. A DNA probe specific for *cpcA* was used for hybridization (upper panel). rRNA was used as a loading control (lower panel).

3.2. Effect of sll1961 disruption on the expression of nblA under nitrogen starvation

In all the *nbl* (non-bleaching) mutants reported so far, the level of *nblA* expression is lower than that in WT under nitrogen starvation [15,28–31], suggesting that *nblA* is a primary factor in PBS degradation. In WT cells, the transcript levels of *nblA* (*nblA1* plus *nblA2*) increased after the shift to $BG11_0$ medium (Fig. 3). The increase of the transcript level of *nblA* during 12 h of incubation in $BG11_0$ medium was more prominent in the *sll1961* mutant than in the WT. Thus, the inactivation of *sll1961* leads to enhancement, rather than suppression, of the transcription of *nblA* under nitrogen starvation. In contrast, inactivation of *pmgA* partially lowered the transcript level of *nblA*. The result suggests that *pmgA* may function in the positive regulation of *nblA* during nitrogen starvation, as previously reported for *nblC* in *S. elongatus* PCC 7942 [15]. In spite of less expression of *nblA*, normal bleaching was observed in the *pmgA* mutant, implying that mRNA level of *nblA* was sufficient for PBS degradation during nitrogen starvation in the *pmgA* mutant. In *S. elongatus* PCC 7942, disruptants of *nblR*, *nblS* and *nblC* all showed defects leading to a decreased *nblA* expression under nitrogen starvation [15,28–31]. Thus, it was assumed that the phenotype of the disruptants of *nbl* genes was ascribed to the decreased level of *nblA* in the mutants. The *pmgA* mutant, however, exhibits typical bleaching phenotype with lowered expression of *nblA*. This raises the possibility that there is some mechanism of PBS degradation independent of the mRNA accumulation of *nblA*.

3.3. mRNA level of sll1961 was lower in the nblA mutant under nitrogen starvation

The transcript level of *sll1961* was low in WT cells grown in BG11 medium but increased after the shift to $BG11_0$ medium (Fig. 4). In contrast, the transcript level of *sll1961* in an *nblA1–nblA2* deletion mutant did not show significant increase even after the shift to $BG11_0$ medium (Fig. 4). The *nblA* mutant showed non-bleaching phenotype when grown in $BG11_0$ medium for 48 h (data not shown) as previously reported [26]. The result implies a decreased stability of *sll1961* mRNA in the *nblA* mutant during nitrogen starvation, although one could not rule out the possibility that NblA acts upstream of *sll1961* and up-regulates *sll1961* to produce or activate other factor(s) such as protease during nitrogen starvation. Furthermore, the non-bleaching phenotype of the *nblA* mutant might be linked to the reduced level of the *sll1961* transcript.

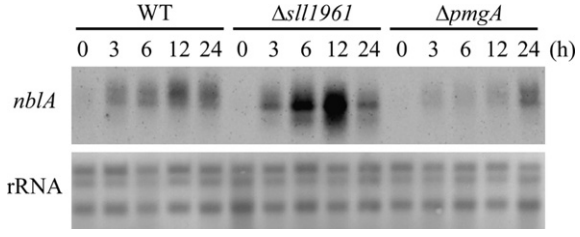

Fig. 3. Expression of *nblA* during nitrogen starvation. Cells of WT, the *sll1961* mutant and the *pmgA* mutant were shifted to $BG11_0$ medium, and sampled at 0, 3, 6, 12 and 24 h following the shift. Northern blot analysis was performed with DNA probe specific for *nblA* (upper panel). rRNA was shown as a loading control (lower panel).

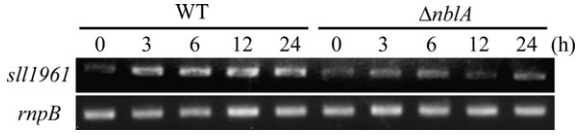

Fig. 4. Expression of *sll1961* during nitrogen starvation. Cells of WT and the *nblA* mutant were shifted to $BG11_0$ medium, and sampled at 0, 3, 6, 12 and 24 h following the shift. RT-PCR was performed using primers for *sll1961* (upper panel) or for *rnpB* whose expression is relatively constant (lower panel).

Table 1
Photosystem stoichiometry of WT and the *sll1961* mutant before or after the shift to $BG11_0$ medium for 48 h

Strain	F725/ F695	
	BG11	$BG11_0$
WT	6.84 ± 0.40	7.15 ± 0.85
Δ*sll1961*	6.70 ± 0.44	6.91 ± 0.86

The ratio of the peak height of PSI band (F725) and PSII band (F695) of the chlorophyll fluorescence spectra determined at 77 K was calculated for three different cultures and shown as means ± S.D.

3.4. Nitrogen starvation does not cause a change in photosystem stoichiometry

We then tested whether the change in photosystem stoichiometry is brought about by nitrogen starvation and is regulated by *sll1961*. When chlorophyll fluorescence emission spectra is determined at 77 K, cyanobacterial cells show PSI fluorescence band at around 725 nm (F725) and PSII fluorescence band at around 695 nm and 685 nm (F695, F685). As a result, we can use F725/F695 as an index of photosystem stoichiometry. We determined fluorescence spectra with Chl excitation to avoid secondary effect of the change in PBS content on the fluorescence spectra through energy transfer from PBS to photosystems. Neither WT nor the *sll1961* mutant showed any difference in photosystem stoichiometry after 48 h of nitrogen starvation (Table 1). The result demonstrates that photosystem stoichiometry is not different between WT and the *sll1961* mutant irrespective of nitrogen availability.

Photosystem stoichiometry is modulated under various environmental conditions including different photon flux densities, different light quality and different salinity. The modulation was induced by the change in the redox level of electron transport [32], although little is known about the actual sensing mechanism. Since excess CO_2 fixation under high light condition can induce a high carbon/nitrogen (C/N) ratio in cellular metabolisms, the change in C/N balance might be sensed as a high light signal [33]. However, we showed that photosystem stoichiometry was not affected by nitrogen starvation, indicating that the signal for high light and the signal for nitrogen starvation are completely different. We propose that Sll1961 is a bi-functional protein that regulates both photosystem stoichiometry under high light condition and PBS degradation under nitrogen starvation. The gene product of *sll1961* may act as a regulatory factor for PBS degradation independently of *nblA* induction under nitrogen starvation.

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