Biotechnology and Bioprocess Engineering 19: 250-256 (2014)
DOI 10.1007/s12257-013-0700-y

RESEARCH PAPER

Profiles of Photosynthetic Pigment Accumulation and Expression of Photosynthesis-related Genes in the Marine Cyanobacteria *Synechococcus* sp.: Effects of LED Wavelengths

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Received: 30 November 2013 / Revised: 18 February 2014 / Accepted: 1 March 2014

Abstract Light quality is a significant environmental factor that influences photosynthetic pigments in cyanobacteria. In the present study, we illuminated the marine cyanobacteria *Synechococcus* sp. with white (350 ~ 700 nm), red (630 nm), green (530 nm), and blue (450 nm) light emitting diodes (LEDs) and measured pigment levels (chlorophyll, carotenoid, and phycobiliprotein) and expression of photosynthesis-related genes (*pebA*, *psbB*, and *psaE*). The amount of photosynthetic pigments (total pigments, chlorophyll, and phycobiliproteins) was higher in the green and blue LED groups than in the white and red LED groups after 8 days of culture. The cells were prepared in a 1.5 mL solution for the analysis of the total pigments, chlorophyll, and carotenoid, and in a 2 mL for analysis of phycobiliproteins. The mRNA expression levels of *pebA* and *psbB* significantly increased after 8 days of cultivation under green and blue light, while the mRNA expression levels of *psaE* decreased. These results indicate that green and blue light increase the accumulation of photosynthetic pigments. In contrast red light induced mRNA expression of *psaE* and stimulated cell growth in *Synechococcus* sp.

Keywords: photosystem, photosynthetic pigment, light emitting diodes, blue-green light, *Synechococcus* sp.

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1. Introduction

Light conditions (quality and intensity) affect the growth and photosynthesis of photoautotrophs, including that of microalgae [1], and the effects light conditions on organisms have been extensively studied in aquatic systems since these conditions change at different water depths and under changing weather [1]. Recently, most studies have focused on investigating the effects of light intensity and light quality on microalgae physiology, such as growth, morphology, pigmentation, reproductive induction, and photosynthesis [1-4].

Microalgae are important primary producers and conduct up to 90% of all of the photosynthetic activity that occurs on earth [5,6]. Algae cultures are influenced by a variety of environmental factors, and these factors play a role in the production of photosynthetic pigments [7].

Cyanobacteria are an example of such primary producers [5,6], and most cyanobacteria are shade-adapted organisms, meaning that they use efficient mechanisms to counteract the harmful effects of solar radiation. Cyanobacteria acclimate their light harvesting to the available irradiance and spectral composition by modulating their antenna pigment composition [8,9], *Synechococcus* sp., in particular, are important nitrogen-fixing organisms found in virtually every ocean, ranging from the tropical coasts to the polar regions [10]. These organisms are abundant in coastal waters and contribute up to 20% of the total primary

photosynthetic production [5].Phycobilisomes are a major pigment-protein component of the cyanobacterial cell and can constitute up to 50% of the cell material [10].

Along with the intensity, the color temperature of the light also influences growth, phycobiliprotein production, and nitrogen availability in cyanobacteria [11]. Light quality also has a strong influence on the light harvesting system of cyanobacteria [8,12]. For example, Lönneporge *et al*. [13] have shown that a light shift from white light (high intensity) to red light (low intensity) increases phycocyanin and chlorophyll synthesis in the cyanobacterium *Anacystis nidulans*.

Photosystems are activated in the thylakoid membrane and in the chloroplasts of cyanobacteria [14], and recently, photosynthesis-related genes have been discovered in marine cyanobacteria [14,15]. Previous studies have elucidated the functions of some of these photosynthesis-related genes, such as *psbB*, which encodes a pigment-binding inner antenna of Photosystem II (citation); *pebA*, which encodes a 15,16-dihydrobiliverdin: ferredoxinoxido reductase involved in the bilin biosynthesis pathway; and *psaE*, which encodes Photosystem I protein expression which is regulated by light [16,17].

Light-emitting diodes (LEDs) emit a single wavelength of light and are used as a light source [18,19]. LED lamps were first used in the 1960s [20] in commercial devices as on-off light indicators, and since then have also been used to cultivate terrestrial plants and to promote the growth of fish [18,21]. Previous studies have shown that blue-green light increases the concentration and synthesis of the photosynthetic pigments chlorophyll and phycoerythrin [22]. Currently, very few marine research studies have investigated the effects of light spectra on the synthesis of pigment proteins and mRNA expression levels of photosynthesis-related genes in algae.

In this study, we examined the effects of white, red, green, and blue light on the marine cyanobacteria *Synechococcus* sp. with respect to the cellular levels of photosynthetic pigments (chlorophyll, carotenoid, and phycobiliprotein) and the expression of three photosynthesis-related genes over 8 days in culture.

2. Materials and Methods

2.1. Organism and culture conditions

A stock of *Synechococcus* sp. (KMMCC-314) was obtained from the Korea Marine Microalgae Culture Center (KMMCC, Busan, Korea). The organism was grown in 500 mL of sterilized 33-psu Conway medium, which is a modified version of the Walne medium [23], at 25 ± 1°C for 8 days. The composition of the Conway medium used in this study was as follows: 1 L of natural sea water; $NaNO_3$, 100 mg; Na_2EDTA, 45 mg; H_3BO_3, 33.6 mg; NaH_2PO_4-$2H_2O$, 26.00 mg; $FeCl_3$-$6H_2O$, 1.28 mg; $MnCl_2$-$4H_2O$, 0.36 mg; trace metal solution, 1 mL; and vitamin solution, 50 mL. The composition of the trace metal solution used in the medium was as follows: $ZnCl_2$, 1.05 g; $CoCl_2$-$6H_2O$, 1 g; $(NH_4)_6Mo_7O_{24}$-$4H_2O$, 0.45 g; $CuSO_4$-$5H_2O$, 1 g; and H_2O, 50 mL. The composition of the vitamin solution used in the medium was as follows: vitamin B1, 400 mg; vitamin B12, 20 mg; and H_2O, 100 mL. Additionally, we maintained the nitrogen (N)/ carbon (C) rate at a value of 5.4 during cultivation. The cultured samples (50 mL) were harvested *via* centrifugation (4°C, 3,000 × *g*, 10 min) and stored at -80°C until RNA extraction.

2.2. Light sources

Four LEDs were chosen for the microalgae cultures—white (350 ~ 700 nm White; ST-4836C, S-tech LED Co., Kyunggi, Korea), red (peak at 630 nm; ST-4836 Red, S-tech LED Co., Kyunggi, Korea), green (peak at 530 nm; ST-4836 Green, S-tech LED Co., Kyunggi, Korea), and blue (peak at 450 nm; ST-4836 Blue, S-tech LED Co., Kyunggi, Korea) (Fig. 1). All of the LEDs were driven by a 12 V power supply (SMPS-100, S-tech LED Co., Kyunggi, Korea), and the light intensity was tuned *via* a custom-made potentiometer. A three-channel fiber optic spectrometer (Avantes Inc., Broomfield, CO, USA) with SpectraWin software (Avantes Inc.) was used to measure the wavelengths and intensities of the light sources, and the light intensity was measured *via* a light meter (LI-250A, LI-CORInc., USA) with a quantum sensor (LI-190, LI-COR Inc., USA). The light intensity was maintained at 55 μmol quanta/m/L^2/ sec (2,000 Lux) during cultivation.

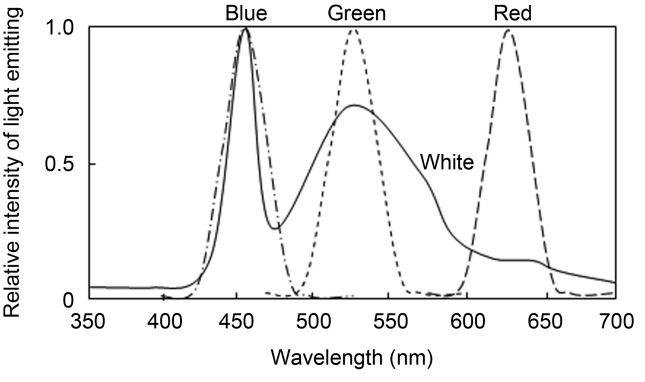

Fig. 1. Relative intensity and colors of the light from the white, blue, green, and red light-emitting diodes (LEDs) are shown. Reprinted from ref. (Shin *et al*. 2011), with permission from Comparative Biochemistry and Physiology, Part-A.

2.3. Determining photosynthetic pigment levels

The concentrations of chlorophyll *a*, chlorophyll *b*, and carotenoid were determined according to the equation proposed by Wellburn [24]. Briefly, pigment extractions were conducted in stoppered tubes, and cell samples (1.5 mL) were prepared *via* centrifugation at 3,000 × *g* for 15 min, three times with 1.5 mL of fresh water. Then, 90% cold methanol was added to attain the required extraction volume, and the homogenized mixture was centrifuged at 3,000 × *g* for 15 min. Concentration levels were determined using a Helios α spectrophotometer at wavelengths of 653 and 666 nm, for chlorophyll *a* and *b* (according to each extraction solvent) and at 470 nm for carotene. The formulas for Chlorophyll *a* and carotene are Chl *a* = 15.65 A_{666} − 7.34 A_{653} and Carotene = (1000 A_{470} − 2.86 Chl *a*) /221, respectively.

To collect the phycobiliproteins, *Synechococcus* sp. cells (2 mL) were centrifuged at 3,000 × *g* for 15 min and sonicated for 25 sec, streptomycin sulfate (1%) was added, and the homogenate was centrifuged [25]. Using the resulting supernatant, the phycobiliprotein concentration was determined in sonicated cell supernatant using a spectrophotometer at 620 nm (135 μg phycobiliproteins/ 1OD) [25].

2.4. Quantitative real-time PCR

The total RNA was extracted from the cells using a TRIzol kit (Gibco/BRL, Grand Island, NY, USA), and Reverse transcription (RT) was performed using the M-MLV reverse transcriptase (PRM1701, Promega, Madison, WI, USA) according to the manufacturer's instructions.

Quantitative real-time PCR (QPCR) was performed using cDNA and was conducted to determine the relative expression levels of *pebA*, *psbB*, and *psaE* using the total RNA extracted from the *Synechococcus* sp. cells (accession no. CT978603). Primers for the QPCR were designed using known *Synechococcus* sp. sequences as reference and are shown in Table 1. QPCR amplification was conducted using a BIO-RAD iCycler iQ Multicolor Real-Time PCR Detection System (Bio-Rad) and an iQ™ SYBR Green Supermix (Bio-Rad, Hercules, CA, USA) according to the manufacturer's instructions. The following settings were used for QPCR: 1 cycle of denaturation at 95°C for 5 min, 35 cycles of denaturation at 95°C for 20 sec, annealing at 55°C for 20 sec, and extension at 72°C for 20 sec. Each experimental group was run in triplicate to confirm consistency. As an internal control, the experiments were duplicated with *16s rRNA*. The efficiency of the reactions was determined by performing QPCR, and the efficiency was found to be 95.7% for *16s rRNA*. All the data were expressed as a change relative to the corresponding *16s rRNA*-calculated cycle threshold (ΔCt) level. The calibrated ΔCt value (ΔΔCt) for each sample and internal control (*16s rRNA*) was calculated as ΔΔCt = 2^ − (ΔCt_{sample} − $\Delta Ct_{internal\ control}$). To ensure that the primers amplified a specific product, we performed a melt curve; a single melting point was observed for the products of each primer pair.

2.5. Determination of growth rate

Culture samples (10 mL) were filtered through pre-weighed nitrocellulose filters (pore size, 0.4 mm). After removal of the medium, the filters were washed with demineralized water, dried in a microwave oven for 4 h at 85°C and weighed. Duplicate determinations gave results that varied by 1%. The dry weight of the diluted samples was then measured and used to construct a standard curve. The average relative growth rate (R) was calculated using the following formula: $R = (\ln Q_2 - \ln Q_1) / (t_2 - t_1)$, where Q_1 is the dry weight of the algae cells at the first point in time of the sampling (t_1) and Q_2 is the dry weight at the second point in time of the sampling (t_2). The data were collected at 48 h intervals, with three replications per sample.

2.6. Statistical analysis

All data were analyzed using the SPSS statistical package (version 10.0; SPSS Inc., USA). One-way ANOVA followed by Tukey's *post hoc* test was used to compare the differences in the data ($P < 0.05$). Values are expressed as

Table 1. Primers used for QPCR amplification

Gene	Primer	DNA sequence
pebA	Forward	5'-TCA GCA GGA CAA GGA TTA CC-3'
	Reverse	5'-GCA AAA CAG CAG CCA AGG-3'
psbB	Forward	5'-GAT GAA GGC GGC AAA GAA-3'
	Reverse	5'-TG AGC GTC TCT ACA AGG C -3'
psaE	Forward	5'-AGC GGC GAC TGG TCC TAC G-3'
	Reverse	5'-CGT CTC CAT CAA ACC TCC CAC AG-3'
16s rRNA	Forward	5'- AAC TGT AAG ACT AGA GTG TGG TA -3'
	Reverse	5'- ACT GGT GTT CTT CCC GAT A -3'

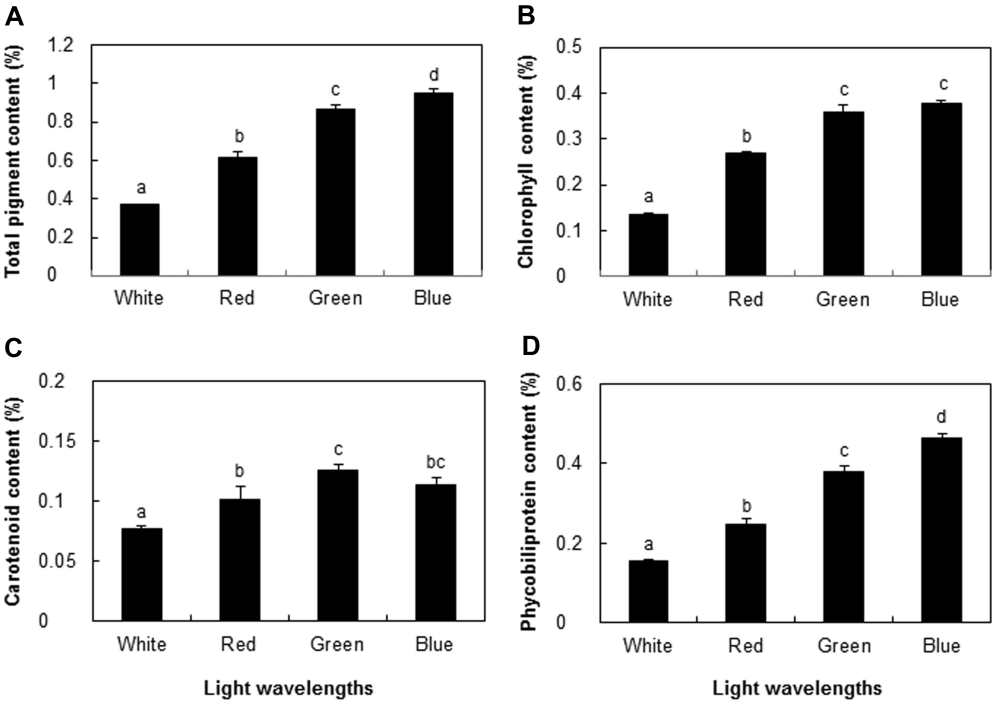

Fig. 2. Total amount of total pigment (A) and individual photosynthetic pigment (B, chlorophyll; C, carotenoid; D, phycobiliprotein) in *Synechococcus* sp. on day 8 of culture under white, red, green, and blue LEDs. The values with different characters are significantly different at the LED wavelengths used ($P < 0.05$). All values are of the mean ± SE ($n = 5$).

the mean ± SE of the three independent measurements.

3. Results

3.1. Photosynthetic pigment content

We investigated the amounts of different photosynthetic pigments in *Synechococcus* sp. that were cultured for 8 days under light sources of different spectral properties. After 8 days of culture, the photosynthetic pigment content (total pigment, chlorophyll, phycobiliprotein) was found to be higher in the green and blue LED groups than in the white and red LED groups (Fig. 2).

3.2. Transcript levels of selected photosynthesis-related genes during cultivation

Using QPCR, we examined the mRNA expression levels of *pebA, psbB* and *psaE* genes in *Synechococcus* sp. Over 8 days of culture under different light sources (Fig. 3). In all of the experimental groups, the transcript levels significantly increased during the period of cultivation relative to that at day 8 of cultivation. Additionally, the mRNA expression levels of the *pebA* and *psbB* genes were significantly higher in the blue and green LED groups compared to those in the other groups (Figs. 3A and 3B). The *psaE* mRNA expression level, however, was significantly higher in the red and green LED groups than in the other groups (Fig. 3C).

3.3. Growth rate of *Synechococcus* sp.

We measured the growth rate of *Synechococcus* sp. during the 8 days of experimental exposure to light (Fig. 4) and found that the dry weight increased over this 8-day period in all experimental groups. Additionally, the growth rates (r) for the groups with red and green LED treatment (0.332 ± 0.004 and 0.334 ± 0.003, respectively) were significantly higher than those for the groups with white and blue LED treatments (0.278 ± 0.005 and 0.303 ± 0.003, respectively).

4. Discussion

In this study, we examined photosynthetic pigment concentrations (chlorophyll, carotenoid, and phycobiliprotein) and mRNA expression levels of three photosynthesis-related genes (*pebA*, *psbB*, and *psaE*) in *Synechococcus* sp. cultured under lights generated by different LEDs (white, red, green, and blue) during an 8 day culture period.

We observed that the increase in the amount of photosynthetic pigments in *Synechococcus* sp. was significantly greater in the groups with green (2.3-fold) and blue (2.5-fold) LED treatments compared those in the groups with white

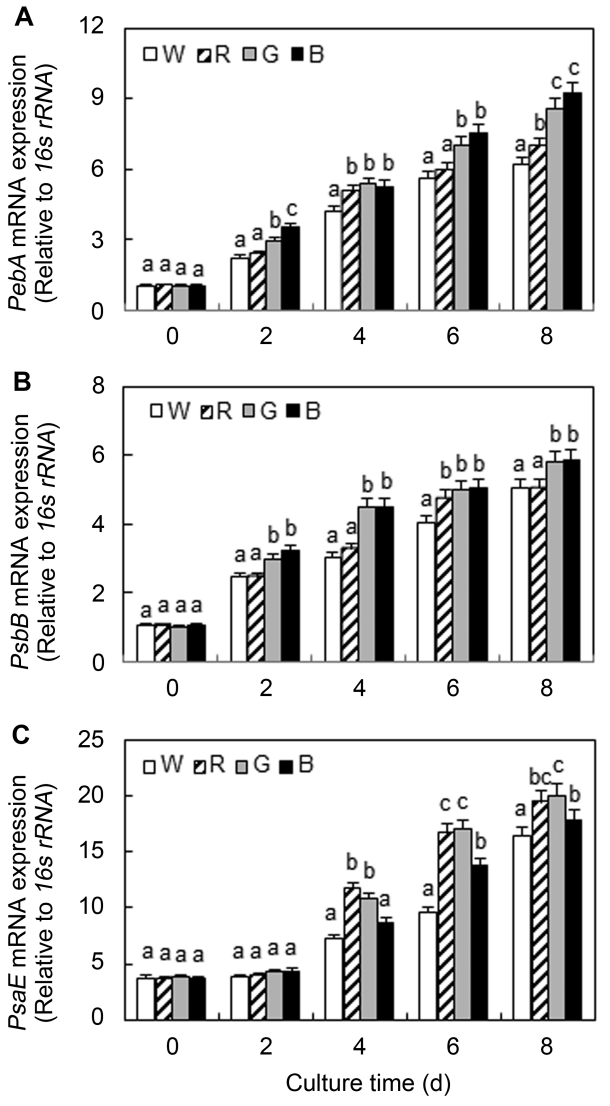

Fig. 3. The mRNA expression levels of photosynthesis-related genes (A, *pebA*; B, *psbB*; C, *psaE*) in *Synechococcus* sp. measured by QPCR over 8 days of culture under white (W), red (R), green (G), and blue (B) LEDs. Values with different characters are significantly different at the respective LED wavelengths on the same culture day ($P < 0.05$). All values are of the mean ± SE ($n = 5$).

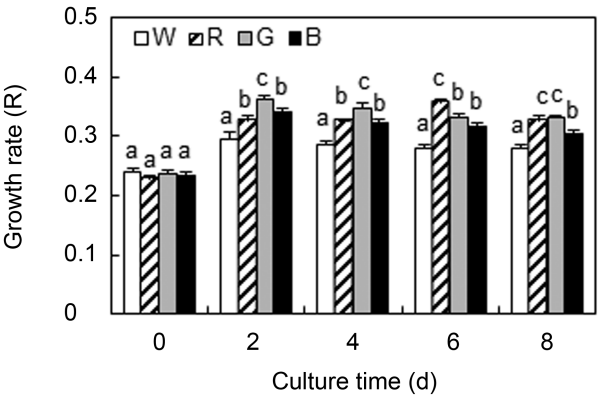

Fig. 4. Change in levels of growth rate in *Synechococcus* sp. under treatment with white, red, green, and blue LEDs. The lowercase letters indicate significant differences between different LED spectra within the same culture days ($P < 0.05$). All values are of the mean ± SE ($n = 5$). Temperature, 25 ± 1°C; 33 salinity; pH 8.0; N/C 5.4.

and red LED treatments (Fig. 2A).

We also observed that the total pigment contents, including chlorophyll, carotenoids, and phycobiliproteins, in *Synechococcus* sp. on day 8 were significantly higher groups under LEDs of shorter wavelength, green and blue, than in those under other LED spectra (Figs. 2B, 2C, and 2D). The result of this study are similar to the findings in a previous study by Figueroa *et al.* [26], where short-wavelength blue light increased the amount of pigment in the rhodophyceae *Porphyra umbilicalis*.

Phycobiliproteins are photosynthetic accessory pigment-protein complexes specifically found in cyanobacteria (formerly known as blue-green algae) and red algae and more than 90% of the the absorbed solar energy is emitted as fluorescence [27,28]. In this study, the amount of phycobiliprotein increased under green and blue LED conditions (Fig. 3D), and this finding is consistent with the results from a previous study where the level of phycobiliproteins in *Anabaena ambigua* also increased under a blue LED condition [7]. Phycobilisomes consist of phycoerythrin- and/or phycocyanin containing rods attached to an allophycocyanin binding core that is mostly associated with Photosystem II. Therefore, blue light that is mostly absorbed by Photosystem I stimulates the synthesis and accumulation of Photosystem II proteins and of their antenna complexes, phycobilisomes, to reach equilibrium among various parts of the photosynthesis electron flow [26].

In this study, we found that the amount of carotenoids in *Synechococcus* sp. increased in the red LED group to a level similar to those observed in the green and blue LED groups, with the white LED group containing a lower amount of carotenoid (Fig. 2C). Carotenoids are widely distributed in nature and are synthesized by all photosynthetic organisms (cyanobacteria, algae, and plants) as well as non-photosynthetic microorganisms, such as fungi and some bacteria. Carotenoids comprise a wide group of lipophilic pigments that provide a series of colors, including yellow, orange, and red [29], and they accumulate in the cytoplasmic membrane of cyanobacteria and rhodophyceae when they are stimulated by light. Carotenoids are thought to be the first line of defense protecting the cytoplasmic membrane against photo-oxidative agents, such as H_2O_2, and lipid peroxidation [30,31]. The results of the present study are

consistent with the results obtained by Chen in a previous study [32], where the amount of β-carotene increased in cyanobacterium under red LED illumination as a result of the photosynthetic and antioxidative activity. Therefore, the results of the present study suggest that red light increases the content of carotenoid to prevent photo-oxidation of chlorophyll and to influence the antioxidant response.

In this study, we also analyzed the expression levels of photosynthesis-related genes, such as those encoding proteins involved in phycobilinprotein biosynthesis (*pebA*) and the Photosystem II and Photosystem I components (*psbB* and *psaE* genes, respectively), in *Synechococcus* sp. cultured under different LED light sources. Over the culture period, their expression levels appeared to increase under all illumination conditions (Fig. 3). The mRNA expression levels of *pebA* and *psbB* genes, however, were significantly higher (5.7 and 8.4-fold, respectively) under the blue and green LED lights than under the other lights after 8 days (Figs. 3A and 3B). We conclude from this result that the shorter wavelength green and blue LED lights increase the stimulation of cytoplasm in the thylakoid membrane during photosynthesis. This result is also consistent with the findings from previous studies performed by Glover *et al*. [33] and Stomp *et al*. [4] where a green light source increased the photosynthetic rate and growth rate of phycoerythrin-rich *Synechococcus* sp. Another previous study had reported that the mechanism for photosynthesis involves various components, including photosynthetic pigments and photosystems, the electron transport system (photosynthesis related genes), and CO_2 reduction pathways [34]. So, we have determined that green-wavelength light increases photosynthesis and growth by increasing the amount of photosynthetic pigment in microalgae in the oceans.

We also found that the mRNA expression level of *psaE*, a Photosystem I gene, and the growth rate of the cyanobateria increased under red and green lights (Fig. 3C). This result agrees with the widely-held thought that absorption of red light by phycobilisomes preferentially delivers energy to the photosynthetic reaction center of Photosystem II, and therefore more Photosystem I complexes are needed to balance the electron flow. Since Photosystem I complexes are the most abundant complexes in thylakoids, higher accumulation of Photosystem I is also related to higher cell growth. Previous studies by Hauschild *et al.* [35] and Korbee *et al.* [12] have shown that red light conditions result in high photosynthesis efficiency in *Synechococcus* sp. and *Phorophyra umbilicalis*.

However, expression of *psaE*, Photosystem I gene, under blue light was lower than under green and red light, and this differed from the expression of *pebA* and *psbB* genes under blue light. Blue light stimulates the synthesis of pigments associated to Photosystem II, whereas red light stimulates synthesis of the reaction center of Photosystem I by phycobilisomes [36]. Also, Figuero *et al.* [26], similar to present study, reported that two different growth and metabolic patterns were found depending on the quantity of light. In red light, higher photosynthetic efficiency and growth were promoted while in blue light, accumulation of phycobilinproteins and pigmentation was produced without acceleration of growth due to a lower carbon assimilation related to nitrogen.

Indeed, we observed that over 8 days of culture, the growth rate of *Synechococcus* sp. showed a larger increase under the red and green LED treatments than under the white and blue LED treatments (Fig. 4). In previous studies with the diatom *Thalassiosira gravid* [37] and Rhodophyceae *Porphyra umbilicalis* [26], red wavelengths also induced a high growth rate and increased the carbon accumulation size of the cells. So, in conclusion, the results of this study confirmed that in *Synechococcus* sp., shorter wavelengths induce the expression of Photosystem II and phycobilisome while longer wavelengths stimulate growth *via* induction of Photosystem I synthesis.

Acknowledgement

This research was supported by the MSIP under the ITRC support program supervised by NIPA (2013-H0301-13-2009).

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