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MORPHOLOGY, GROWTH AND PHOTOSYNTHETIC RESPONSES OF THE CYANOBACTERIUM *ARTHROSPIRA PLATENSIS* TO DIFFERENT WAVEBANDS IN SOLAR SPECTRUM

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Abstract: Light is known to regulate morphological development and photosynthetic performance of the economically important cyanobacterium, *Arthrospira platensis*. However, light quality under different wavelengths on its growth and physiology is yet to be understood. In this study, we grew *A. platensis* D-0083 trichomes in quartz tubes covered with different cutoff foils and one band-pass filter, so that the cells received different wavebands of irradiances, and measured its growth, morphology and photosynthetic performances. Spirals of *A. platensis* D-0083 were compressed and the biomass increased with exposures under all wavebands. Both the wavebands of UV-A + blue light (320—500 nm) and red light (600—700 nm) could initiate the spiral compression, growth and photosynthetic activities in *A. platensis* D-0083 efficiently. The efficiencies per unit energy of irradiance to induce helix pitch changes in wavebands 320—500, 395—700, 510—700 and 610—700 nm were 0.070, 0.015, 0.021 and 0.045 $\mu\text{m}/(\text{W}\cdot\text{m}^2)$ respectively. Waveband 320—500 nm had little suppression on effective quantum yield (F_v'/F_m'), electron transfer rate (ETR) and phycocyanin (PC) fluorescence emission of the filaments but led to spiral compression and growth efficiently. The waveband-dependent responses in spiral compression and specific growth rate appeared to be consistent with the photosynthetic capability under the different light regimes.

Key words: *Arthrospira platensis*; Growth; Morphology; Photosynthetically active radiation (PAR); Photosynthesis

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Light quality and intensity are critical environmental signals that allow cells to sense the time of day, the potential intracellular energy status, and to tune metabolic activities towards its optimal growth potential^[1]. Rates of photosynthesis, growth, morphogenesis^[2–7] and pigment composition^[8–11] are some of the light-dependent growth characteristics of cyanobacteria. Recently, blue light was suggested to promote the metabolism of nitrogen-derived compounds such as mycosporine-like amino acids (MAAs), phycoerythrin and proteins in *Porphyra leucosticta*^[12]. Blue light increases the chlorophyll and phycocyanin contents and biomass production in

Spirulina fussiformis^[13]. Light intensity is a major trigger in the heterocyst and akinete differentiation of many cyanobacterial species^[7, 14–17].

The genes responsible for these light-sensitive growth responses are well characterized and the signaling mechanisms are reasonably well established^[18]. In many cyanobacterial species, chromatic acclimation (CA) results in lesser phycoerythrin (PE) and more phycocyanin (PC) when grown under red than in green light^[19, 20]. The morphology of the *Fremyella diplosiphon* is also affected during the CA process when grown in red or green light^[19, 21].

Cyanobacteria contain phytochrome, blue-light,

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and UV-A receptors which can receive irradiance spanning visible spectrum and near-UV^[22-25]. *Arthrospira platensis* is an economically important cyanobacterium and commercially cultured around the world to supply biomass and provide a rich source of protein for the health food industry^[26, 27]. Environmental factors such as light and temperature determine the gross biomass productivity in *Arthrospira* cultures^[27]. Elevated photosynthetically active radiation (PAR) levels decrease the helix pitch of *A. platensis*^[6], while UV radiation adding to PAR leads to compressed spirals^[28]. Oxidative stress induced by light or UV stresses lead to broken trichomes in *A. platensis* and *A. variabilis* PCC 7937^[29, 30].

Although PAR is known to control the morphology and photosynthesis^[6], we have yet to ascertain the influence of the PAR region (i.e. 400 to 700 nm) in the growth patterns, morphological and photosynthetic changes in *A. platensis*. PAR penetration depth decreased with wavelength in water body due to water absorption generally increases with wavelength^[31]. The filaments of *Arthrospira* spp. in natural water body have to face the fluctuations of light quality and intensity when they stayed at different depth in natural water body. Algal acclimation to fluctuating irradiance can lead to differently photosynthetic rate, growth rates and cellular pigments content compared to the cells acclimated to constant irradiance^[32]. Therefore we predict that morphology, growth and photosynthesis of *A. platensis* are waveband-specific responding to solar PAR. Under this scenario, we investigated the morphology, growth and photosynthesis of *A. platensis* D-0083 filaments grown in quartz tubes that were selectively exposed to various regions of the PAR using three cut-off and one bandpass light filters.

1 Materials and Methods

1.1 Experimental organism

Arthrospira platensis (D-0083) was obtained from the Hainan Dainippon Ink and Chemicals (DIC) microalgae CO. LTD. Hainan, China. A single healthy spiral was chosen and all the trichomes were propagated from it in a Zarrouk medium^[33] containing (g/L): NaHCO₃—16.8, NaNO₃—2.5, K₂HPO₄—0.5, K₂SO₄—1.0, NaCl—1.0, MgSO₄·7H₂O—0.2, CaCl₂—0.04, FeSO₄·7H₂O—0.01, EDTA—0.08 and micronutrients. The cultures were aerated with filtered (0.22 μm) air at 30°C and 60 μmol/m²·s of cool-white light (12 L : 12 D). Cells in the exponential growth phase were sampled at the beginning of dark period and used in subsequent experiments.

1.2 Radiation treatments and measurement

The *A. platensis* cells were filtered, washed and removed from the GF/C filter (25 mm Ø, Whatman) and diluted with fresh Zarrouk medium to 0.16 optical densities at 560 nm (*A*_{560 nm}). The cells were then transferred to quartz tubes (2 cm Ø, length 12 cm) and horizontally placed in opaque plastic containers with removable and replaceable lids. The lids were fitted with light filters for different wavebands (i.e. Ultraphan395 (395—700 nm), JB510 (510—700 nm), HB610 (610—700 nm) and QB24 (320—500 nm) that can be inserted and pulled out of the containers upon demand to supply the *A. platensis* cells with the appropriate radiation wavelengths (Fig. 1). The loosened trichomes grown in laboratory, aerated with filtered (0.22 μm) air at 30°C and 60 μmol/(m²·s) of cool-white light (12 L : 12 D), were set as the control group, since the same irradiance level of full solar spectrum would result in tightened spirals due to the UV-stimulating effects^[6].

The incident solar irradiance falling on the quartz tube was measured by using a broadband EL-

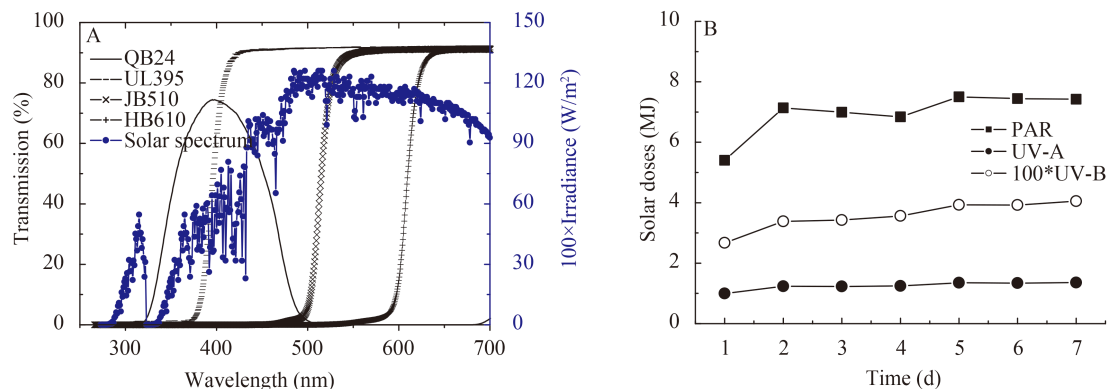


Fig. 1 Irradiance spectrum of local solar radiation and the transmission characteristics of the Ultraphan 395 (395—700 nm), JB510 (510—700 nm), HB610 (610—700 nm) cut-off films and band-passing filter QB24 (320—500 nm) (A), and the corresponding doses (MJ) of PAR, UV-A and UV-B during the period of 6 to 12 May, 2007 (B)

DONET filter radiometer (Real Time Computer, Möhrendorf, Germany) equipped with three channels dedicated for PAR (400—700 nm), UV-A (315—400 nm) and UV-B (280—315 nm) wavebands. The quartz containers were manually shaken for 4—5 times everyday to mix the culture and alleviate the accumulations of cells at the bottom of the tube^[5]. Furthermore and to minimize damage to cells caused by the O₂ or reactive oxygen species (ROS) accumulation in the tubes triggered by photosynthetic activities during the daytime^[29], the cultures were aerated with ambient air for 1 min every night. Five replicates were done for each treatment.

1.3 Temperature control

During the growth experiments, the containers holding the quartz tubes were placed in a water bath to maintain a (30±1)°C temperature using a circulating refrigerator (Eyela, CAP-3000, Tokyorikakikai Co. Ltd. Tokyo, Japan).

1.4 Morphological examination

Morphological changes in *A. platensis* spirals were examined with a microscope (Zeiss Axioplan 2, Carl Zeiss, Germany) after one week of growth (13—19 April 2007) under different filters. Digital images were recorded with a Zeiss AxioCam and were analyzed with an image analysis system (Axio Vision 3.0). Because the spirals of *A. platensis* D-0083 are highly compressed, the helix pitch (the distance between two neighboring spirals) was calculated as the number of spirals per a given length. We randomly estimated the helix pitch from at least 50 individual filaments.

1.5 Determination of biomass and specific growth rate

After the morphological examination of *A. platensis*, cells in each tube were filtered to pre-dried Whatman GF/C glass fiber filter (25 mm Ø, Whatman) and washed with 20 mL acidified distilled water (pH 4) to remove residual salts. The cells were then dried in an oven at 80°C for 24h for the determination of biomass. Specific growth rate (μ , /d) of *A. platensis* was calculated as $\mu = (\ln x_2 - \ln x_1) / (t_2 - t_1)$, where x_1 and x_2 were the biomass at time t_1 and t_2 , respectively.

1.6 Determination of photosynthetic activity

To examine the effects of solar irradiance in different waveband on the photosynthetic capacity, the effective photochemical quantum yield (F_v'/F_m') and relative electron transport (*ETR*) of cells grown under different filters for a week were determined with a portable pulse amplitude modulated fluorometer (Water-PAM, Walz, Effeltrich, Germany). The actinic light set at 100 $\mu\text{mol photons}/(\text{m}^2 \cdot \text{s})$ and saturating

pulse was 5000 $\mu\text{mol photons}/(\text{m}^2 \cdot \text{s})$ (0.8s). The *ETR* was calculated as follows^[34]: $ETR [\mu\text{mol e}/(\text{m}^2 \cdot \text{s})] = F_v'/F_m' \times 0.5 \times \text{PFD} \times A$, where F_v'/F_m' represents the effective PSII quantum yield, PFD is the photosynthetically active photon flux density, and A is the fraction of incident photons absorbed by *A. platensis* filaments^[35]. The rapid light curves for *ETR* were measured under eight different PAR levels (every measurement lasted for 10s). The parameters of the *ETR* curves were analyzed according to Webb, *et al.*^[36]: $ETR = ETR_{\text{max}} \times [1 - e^{-(2\alpha \times E/ETR_{\text{max}})}]$, where α is the efficiency of electron transport and E is the irradiance. Five replicates were measured for each treatment.

1.7 Measurement of chlorophyll fluorescence emission spectra

Arthorspira species contains chlorophyll *a* (Chl.*a*), phycocyanobilin and allophycocyanin as light harvesting pigments^[37, 38]. In order to investigate whether phycobilisome (PBS) was changed, we examined the changes in room-temperature chlorophyll fluorescence of the cells grown under different filters for a week. The chlorophyll fluorescence emission spectra were measured with the spectrofluorimeter (RF-5310PC, Shimadzu). The excitation wavelength was set at 580 nm for PBS^[29, 39].

1.8 Statistical analysis

A one-way ANOVA was used to analyze the differences among treatments. When significant differences occurred, Tukey's HSD test was used to identify differences among treatment means. A confidence level of 95% was used in all statistical analyses.

2 Results

The spectrum of local solar radiation and the transmission of light intensities through the different filters used in the radiation experiments were shown in Fig. 1A. Transmitted light to solar radiation ratios through Ultraphan 395 (395—700 nm), JB510 (510—700 nm), HB610 (610—700 nm) and QB24 (320—500 nm) were 284: 187: 88: 47 (Fig. 1A). The sky was clear and provided with similar doses of solar radiation throughout the duration of the experiments (6—12 May 2007) (Fig. 1B).

Compared to the loosened filaments grown in lab, the spirals of *A. platensis* D-0083 compressed after one week exposure to solar irradiance in different wavebands (Fig. 2A). The length of trichomes in various treatments was affected by the wavelength of irradiance (Tab. 1). The length of filaments before exposure (Control) and those cultured under QB24 ranged from 0 to 400 μm , but most (70%) of the filaments under QB24 were shorter than 200 μm . No fila-

ments longer than 300 μm were observed when cells of *A. platensis* D-0083 were cultured outdoors under Ultraphan395, JB510 and HB610 cut-off films. Furthermore, the distribution of filaments with length shorter than 100 mm followed the order Ultraphan395 (62%) > JB510 (46%) > HB610 (43%) > QB24 (21%) > Control (11%) indicating that more intense irradiance doses led to shorter filaments. The helix pitch of the spirals decreased significantly ($P < 0.01$) in cells grown under various cut-off films and band-pass filter compared with the Control. There were significant differences ($P < 0.05$) in helix pitch between means except in the comparison of JB510 with HB610 treatments (Tab. 1, Fig. 2A).

When the variation in helix pitch of *A. platensis* D-0083 was normalized to the energy that transmitted through the filters, the efficiency of waveband 320—500 nm (i.e. UV-A + blue light or QB24) to compress the spirals was much higher ($P < 0.01$) than other wavebands (Fig. 2B). The lowest effective irradiance to compress a spiral was the waveband covering full visible irradiance (395—700 nm, Ultraphan395). The efficiencies per unit energy of irradiance to induce helix pitch changes in wavebands

320—500, 395—700, 510—700 and 610—700 nm were 0.070, 0.015, 0.021 and 0.045 $\mu\text{m}/(\text{W}\cdot\text{m}^2)$, respectively (Fig. 2B).

Specific growth rate (μ , /d) of the cells after one week exposure to different wavebands was highest under Ultraphan395 and JB510, followed by HB610 and QB24 (Fig. 3A). It was 0.198 (± 0.021), 0.048 (± 0.007), 0.098 (± 0.007), 0.099 (± 0.003) and 0.090 (± 0.005) /d when grown indoors (Control) and covered with QB24, Ultraphan395, JB510 and HB610 filters during the exposure period (Fig. 3A). The efficiency of luminous energy to influence the growth rate of *A. platensis* D-0083 was similar to the variation in helix pitch (Fig. 3B). Waveband-specific light efficiency to induce specific growth rate variations for 320—500, 395—700, 510—700 and 610—700 nm were 0.0010 (± 0.0002), 0.0003 (± 0.0000), 0.0005 (± 0.0000) and 0.0010 (± 0.0000) /d/($\text{W}\cdot\text{m}^2$), respectively.

Effective quantum yields (F_v'/F_m') and electron transfer rate [ETR , $\mu\text{mol e}/(\text{m}^2\cdot\text{s})$] of *A. platensis* D-0083 on the last noontime of exposure period (12 May, 2007) was highest under QB24 and lowest in Ultraphan395 (Figs. 4A, B). Furthermore, quantum yields and ETR increased with PAR wavebands to-

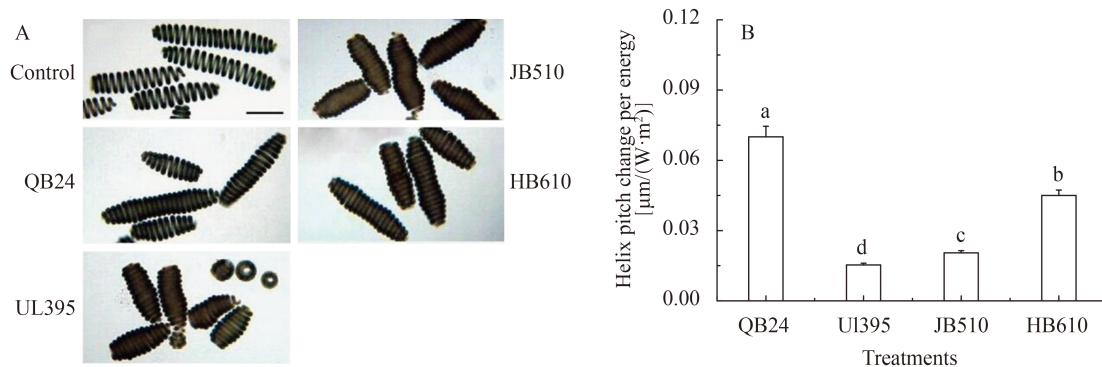


Fig. 2 Morphological changes (A) helix pitch change per energy [$\mu\text{m}/(\text{W}\cdot\text{m}^2)$] (B) of *Arthrospira platensis* D-0083 filaments under solar exposures of different wavebands during the exposures (Fig. 1)

Scale bars in Fig. 2A indicate 100 μm (200 magnification). Means superscripted with different letters are significantly different ($P < 0.05$). Wavebands associated with each treatment are shown in Fig. 1A. The means and standard errors were based on 40 trichomes

Tab. 1 Distribution of trichome lengths and helix pitch of *A. platensis* D-0083 after one week of exposure under solar irradiance of the different wavebands

Treatments	Distribution of trichome lengths (%)				Helix pitch (μm)
	0—100 mm	100—200 mm	200—300 mm	300—400 mm	
Control	11	33	38	18	15.13 \pm 1.52 ^a
QB24	21	50	25	4	11.81 \pm 0.77 ^b
UL395	62	30	8	0	10.78 \pm 0.52 ^c
JB510	46	41	13	0	11.29 \pm 0.51 ^d
HB610	43	47	10	0	11.15 \pm 0.57 ^d

Note: More than 100 trichomes in each treatment were randomly measured for the length determination. Means and standard errors of helix pitch were calculated from at least 40 randomly measured trichomes. Means superscripted with different letters are significantly different ($P < 0.05$)

wards longer wavelength (UL395<JB510<HB610). The F_v'/F_m' of filaments cultured indoors (Control) and those under filter QB24, Ultraphan395, JB510 and HB610 were $0.50 (\pm 0.03)$, $0.51 (\pm 0.03)$, $0.18 (\pm 0.03)$, $0.24 (\pm 0.04)$ and $0.31 (\pm 0.04)$, respectively (Fig. 4A). And the corresponding maximal electron transfer rate (ETR_{max}) were $208.73 (\pm 2.13)$, $255.72 (\pm 7.98)$, $103.45 (\pm 1.66)$, $135.53 (\pm 7.09)$, $153.59 (\pm 7.50) \mu\text{mol e}/(\text{m}^2 \cdot \text{s})$, respectively (Fig. 4B). Compared with the Control, the photosynthetic capability (F_v'/F_m' and ETR) was not ($P>0.05$) inhibited by the irradiance between 320-500 nm but was significantly ($P<0.01$) depressed by other wavebands.

When the cells grown under different filters were excited at 580 nm, the emitted phycoerythrin (PC) fluorescence intensity of the cells cultured indoors (Control) and under QB24, Ultraphan395, JB510 and HB610 filters were 144.5, 122.4, 149.8, 171.9 and 180.1, respectively (Fig. 5). Furthermore, compared with the PC emission fluorescence of indoor cultures (with peak at 646 nm), the emission peaks of cells cultured under QB24, Ultraphan395, JB510 and

HB610 filters for a week shifted to longer wavelength by 1, 7, 6 and 3 nm, respectively.

3 Discussion

Spirals of *A. platensis* D-0083 were compressed and the biomass increased with exposures under different light wavebands. Both the wavebands of UV-A + blue light (320—500 nm) and red light (600—700 nm) could initiate the spiral compression, growth and photosynthetic activities in *A. platensis* D-0083 efficiently. Our observations are in agreement with the literatures with respect to the influence of various wavebands to the growth and morphological regulation of cyanobacteria. For example, cells of *F. diplosiphon* are long, brick-shaped and red under green light, and smaller, spherical and blue-green under red light due to synthesis of phycoerythrin or phycocyanin, respectively^[19]. Furthermore, filaments of *F. diplosiphon* are shorter when grown in red light compared to green light^[19, 21]. Pure UV radiation seems not capable of spiral modification in *A. platensis*^[6]. However, the waveband spanning UV-A (320—400 nm) to blue light (400—500 nm) could tighten the spirals

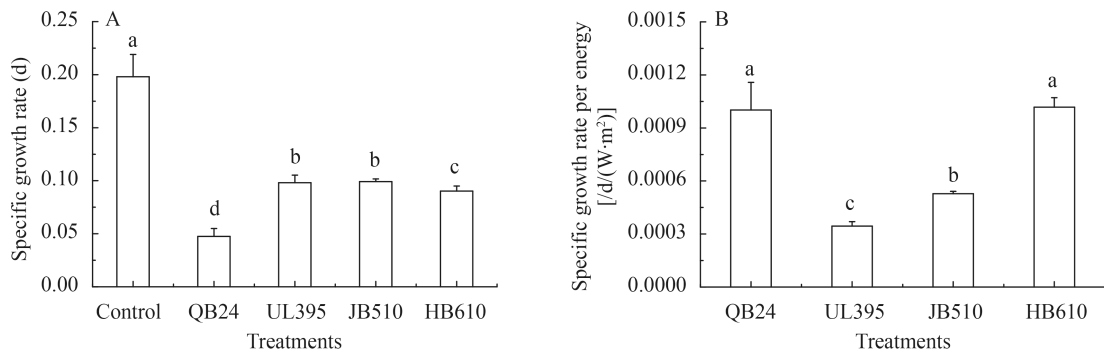


Fig. 3 Specific growth rate (1/d) (A) and Specific growth rate per energy [1/d/(W·m²)] (B) of *Arthrospira platensis* D-0083 exposed to different wavebands of solar radiation from 6 to 12 May, 2007

Means superscripted with different letters are significantly different ($P<0.05$). Wavebands associated with each treatment are shown in Fig. 1A. The means and standard errors were based on five replicates

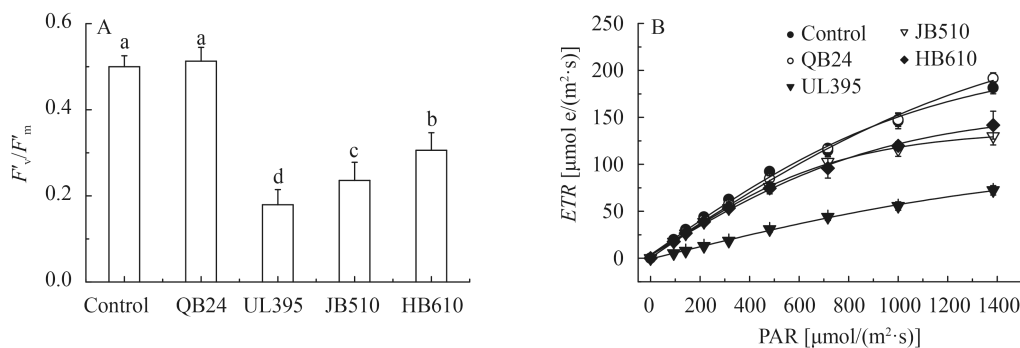


Fig. 4 Effective quantum yield (A) and relative electron transfer rate (B) at noontime of *Arthrospira platensis* D-0083 exposed to different wavebands of solar radiation from 6 to 12 May, 2007

The means and standard errors were based on five replicates. Means superscripted with different letters are significantly different ($P<0.05$) from each other. Please see Fig. 1A for the wavebands associated with each treatment

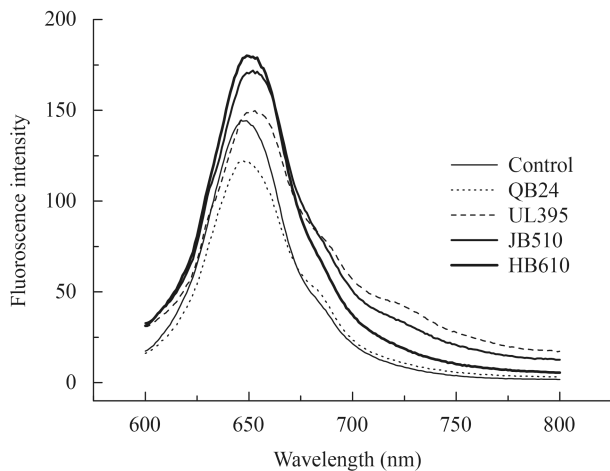


Fig. 5 Changes in fluorescence emission of phycocyanin (PC) in *A. platensis* D-0083 cells grown under the exposures (Fig. 1). The excitation wavelength 580 nm and the means were based on triplicate incubations

of *A. platensis* D-0083 efficiently (Figs. 2A, B). It indicates that blue light was more effective in triggering spiral compression in *A. platensis*, although any irradiance with wavelength between 400 and 700 nm might also induce the change. The similarity in spiral helix pitch in JB510 and HB610 treatments and the 2X irradiance level under JB510 suggests that the waveband 610—700 nm was a more effective trigger to the spiral compression than 510—610 nm.

The specific growth rates of *A. platensis* D-0083 were similar when exposed to Ultraphan395 and JB510, although the irradiance dose that the cells actually received was 1.5X in Ultraphan 395 compared to JB510. This observation may mean that the maximal growth rate of the cells was not reached under filter JB510, HB610 and QB24 but was inhibited under Ultraphan395. The lower specific growth rates observed in this study than those under Ultraphan395 and aerated with ambient air^[40] could be ascribed to the build up of ROS produced from the photosynthetic process^[29, 30]. The cell depositions in the bottom of quartz tubes could be attributed to the carbohydrate accumulation during the photosynthesis^[5] and the cell deposits may have blocked the irradiance to reach the entire photosynthetic cells of *A. platensis* D-0083. Furthermore, the similar patterns in helix pitch and specific growth rate (Figs. 2, 3) of *A. platensis* D-0083 suggests the same irradiance waveband may be responsible for morphological changes and growth rate in *Arthrospira* species.

Cyanobacterial phytochrome (Cph)^[41, 42] is similar to plant phytochromes (red/farred photoreceptors) that influence plant development including accessory roles to sense the presence of UV-B and blue li-

ghts^[43, 44]. Phycobilisome (PBS), the pigment-protein complexes responsible for light harvesting in cyanobacteria, extend the absorption of light into red and green regions of the visible spectrum to increase energy capture for photosynthesis^[20, 45]. The PBS molds to light quality through CA depending on the genetic characteristics of an organism, which in turn is associated with its evolutionary environment^[46, 47]. The increased intensities and red shifted (to longer wavelengths) peaks of PC emission fluorescence (Fig. 5) under Ultraphan395, JB510 and HB610 revealed the damage and structural modification of PBS induced by the wavebands transmitted the filters^[29, 39]. Furthermore, the more changes in PC emission fluorescence peaks of cells under filters Ultraphan395 and JB510 compared with those under QB24 and HB610 indicated more structural modification of the PBS occurred in the former. Another phytochrome-like photoreceptor and regulator of CA in cyanobacteria is RcaE that regulates light-dependent changes in phycobiliprotein content^[45, 48] and the cellular and filament morphology of *F. diplosiphon*^[21]. However, the exact molecular mechanism behind this morphological regulation is unknown. In this study, the light quality and intensity could not be clearly separated due to the continuity and inhomogeneity of solar spectrum as well as the flaw in transmissions of the filters (Fig. 1A). Nevertheless, this study substantiated that light quality has significant effects on morphology and physiological activities of the filamentous cyanobacterium in that its spiral compression, growth and photosynthetic activities were waveband-specifically regulated.

Furthermore, *Spirulina fussiformis* when exposed to blue light increased the production of C-phycocyanin by photo-physiological mechanisms^[13] where the C-phycocyanin has high in vitro antioxidant activity^[49]. The effectiveness of blue and red light to trigger the growth and morphological change maybe related to the dominant absorbance of PC and chlorophyll *a* (Chl. *a*) in the blue and red light regions^[50] or the regulatory role of Cph, PBS and RcaE to promote cell development. As prokaryotic organism, the control of Cph, PBS and RcaE on morphology of cells or trichomes of *A. platensis* still needs to be understood. However, the natural physiological flexibility will undoubtedly facilitate the survival and adaptation of an organism under rapidly changing environmental conditions including changes in spectral component of solar radiation in natural water body.

4 Conclusion

In conclusion, the growth characteristics of *A.*

platensis D-0083 when exposed to solar irradiance revealed the wavelength-dependent influence in physiological and morphological regulations. Both the waveband of UV-A + blue light (320—500 nm) and the waveband of red light (600—700 nm) could initiate the growth, spiral compression and photosynthetic activities in *A. platensis* D-0083 efficiently. We speculated that the efficiency of visible light to induce changes in morphology and growth of *Arthrospira* spp. was related to the capabilities of wavelengths to regulate the photosynthetic activities.

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钝顶螺旋藻形态、生长及光合作用对不同波段太阳辐射的响应

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摘要: 为探讨中不同波段的光合有效辐射对钝顶螺旋藻(*Arthrospira platensis*)形态、生长及光合作用的影响, 实验将钝顶螺旋藻D-0083藻液转入带塞的石英管中, 石英管水平置于阳光下并在其上覆盖不同的截止型和带通型滤光片, 以使藻丝接受不同波段的太阳辐射; 并检测其生长、形态与光合活动的变化。结果发现: 所有波段(320—500、395—700、510—700和610—700 nm)光合有效辐射下的藻丝均螺旋变紧且生物量增加。其中以包含少量紫外辐射A(Ultraviolet-A)的蓝光波段(320—500 nm)和红光波段(600—700 nm)对藻丝形态变化、生长及光合速率的诱发效率较高。在320—500、395—700、510—700和610—700 nm波段上的单位能量光照引起钝顶螺旋藻螺距变化的效率分别为0.070、0.015、0.021、0.045 $\mu\text{m}/(\text{W}\cdot\text{m}^2)$ 。波段320—500 nm虽然会轻微抑制钝顶螺旋藻D-0083的有效光化学效率(F_v'/F_m')、电子传递速率(ETR)和藻蓝蛋白的荧光发射, 但是却能够有效诱导其藻丝变紧促进生长。此外, 钝顶螺旋藻D-0083的藻丝变紧程度、比生长速率变化与不同波段太阳辐射下藻丝体的光合性能相一致。该研究表明任何波段的光合有效辐射都能使螺旋藻藻丝螺旋变紧并引发生长和光合作用, 其中以蓝光和红光的效率最高。

关键词: 钝顶节螺旋藻; 生长; 形态; 光合有效辐射(PAR); 光合作用