

Photoregulation of morphological structure and its physiological relevance in the cyanobacterium *Arthrospira (Spirulina) platensis*

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Abstract The spiral structure of the cyanobacterium *Arthrospira (Spirulina) platensis* (Nordst.) Gomont was previously found to be altered by solar ultraviolet radiation (UVR, 280–400 nm). However, how photosynthetic active radiation (PAR, 400–700 nm) and UVR interact in regulating this morphological change remains unknown. Here, we show that the spiral structure of *A. platensis* (D-0083) was compressed under PAR alone at 30°C, but that at 20°C, the spirals compressed only when exposed to PAR with added UVR, and that UVR alone (the PAR was filtered out) did not tighten the spiral structure, although its presence accelerated morphological regulation by PAR. Their helix pitch decreased linearly as the cells received increased PAR doses, and was reversible when they were transferred back to low PAR levels. SDS-PAGE analysis showed that a 52.0 kDa periplasmic protein was more abundant in tighter filaments, which may have been responsible for the spiral compression. This spiral change together with the increased abundance of the protein made the cells more resistant to high PAR as well as UVR, resulting in a higher photochemical yield.

Keywords *Arthrospira platensis* · Morphology · PAR · Photosynthesis · Protein · UVR

Abbreviations

F'_v/F'_m	Effective quantum yield, where F'_m is the maximal fluorescence yield in illuminated samples and F'_v is the variable fluorescence in illuminated samples
PAR	Photosynthetic active radiation
PSII	Photosystem II
UVR	Ultraviolet radiation, composed of UV-A and UV-B

Introduction

Arthrospira (Spirulina) platensis is an economically important cyanobacterium, which has been commercially produced for food and for useful ingredients worldwide. Regular helical coiling or spirals are the key characteristics of *Arthrospira* spp. and have been used as a taxonomic criterion and in the ranking of product quality (Belay 1997). Therefore, it is of general interest to know how spiral length, helix pitch and orientation of *A. platensis* are regulated under different conditions (Fox 1996; Mühling et al. 2003). The spiral of *A. platensis* can become linear during laboratory cultivation or commercial production (Wang and Zhao 2005; Hongsthong et al. 2007), and morphological transformation from linear to spiral or vice versa has been shown with genetic modification (Wang and Zhao 2005). Intensive ultraviolet radiation (UVR, 280–400 nm) combined with photosynthetic active radiation (PAR, 400–700 nm) results in spiral breakage of *A. platensis*, and the presence of UV-B (280–320 nm) plays a role in tightening the spirals (Wu et al. 2005a). However, a recent finding shows that UV-induced breakage is not observed at a higher temperature (30°C), and DNA damage is also much less compared with that at lower temperatures

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(Gao et al. 2008). Wu et al. (2005a) hypothesize that periplasmic proteins might be responsible for the tightened spirals of *A. platensis*. However, changes in periplasmic protein during spiral morphological alteration have not yet been documented.

PAR and UVR usually act in an antagonistic way, with the former driving photosynthesis and the latter inhibiting physiological processes (Häder et al. 2007; Ma and Gao 2009). UVR is known to decrease photosynthetic rates (Wu et al. 2005a), damage DNA (Gao et al. 2008) and decrease the growth rate (Gao and Ma 2008) of *A. platensis*. On the other hand, positive effects of UVR, especially UV-A (315–400 nm), have also been reported. UV-A acts as an additional source of energy for photosynthesis in tropical marine phytoplankton assemblages (Gao et al. 2007). Addition of UV-A brings about higher biomass production of *A. platensis* under natural levels of solar radiation (Wu et al. 2005b). Nevertheless, little is known concerning the interactive effects of PAR and UVR on morphological changes and the related physiological performance of *Arthrospira* spp.

This study aimed to investigate the effect of combined PAR and UVR on the spiral morphology and photosynthetic quantum yield of *A. platensis* at different temperatures, and the possible role of membrane-bound proteins in such morphological changes.

Materials and methods

Experimental organism

Arthrospira platensis (D-0083) was obtained from the Hainan DIC Microalgae Co. Ltd., Hainan, China. A single healthy spiral was chosen and all other trichomes were propagated from it in Zarrouk's medium (Zarrouk 1966) aerated with filtered (0.22 μm) air at 30°C and illuminated with cool-white light at 60 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (12 L:12 D). Cells which had been cultured with fresh Zarrouk medium for 3–4 days (exponential growth phase) were used in subsequent sub-cultures or experiments.

Temperature treatments

The cells were filtered (GF/F filter, \varnothing 25 mm), washed off the GF/F filter and diluted with fresh Zarrouk's medium to an initial $\text{OD}_{560 \text{ nm}}$ of 0.30 (Riccardi et al. 1981), before being transferred to quartz tubes (\varnothing 4 cm, 16 cm long) and irradiated with PAR (P treatment) or full spectrum solar radiation (PAR + UV-A + UV-B: PAB treatment). To investigate whether the effects of different radiation treatments on spiral structure were temperature dependent, the cultures were grown at 20 and 30°C. The cells were first incubated for 4 days at 20°C (24–27 March 2007) and

subsequently divided into two groups. One group was further incubated at 20°C and the other group was incubated at 30°C. Temperature was controlled with a thermostatic controller (Eyela, CAP-3000, Tokyorikakikai Co. Ltd., Tokyo, Japan), which circulated water to a water bath.

Radiation treatments and measurement

Cells in their quartz tubes were irradiated with either solar PAR alone (P) or PAR + UVR (PAB). For the P treatment, the tubes were wrapped with 395 cut-off foil (UV Opak, DigeFra, Munich, Germany); for the PAB treatment, they were covered with 295 nm cut-off filter (Ultraplan, DigeFra, Munich, Germany). Since full solar radiation causes breakage of the spiral structure (Wu et al. 2005a), which may affect measurement of the helix pitch of *A. platensis*, neutral density filters (black plastic nets with uniform meshes) which reduce proportionally UV and PAR irradiances were used to reduce the solar radiation to 30% of its full level. Details related to the transmission of the cut-off foils (about 90%) are published elsewhere (Zheng and Gao 2009). These foils reflected 4% of PAR underwater (Gao et al. 2007), and therefore, the cells received 4% less PAR under the P treatment than under the PAB treatment.

To examine the morphological changes which occurred under different radiation treatments, the cells were grown in quartz tubes (\varnothing 2 cm, 12 cm long) and then placed in a container made of opaque plastic, with a cover over the top and a window on one side, so that different cut-off filters could be inserted or removed in each position. The combination of different cut-off filters allowed the cells to face different treatments: (1) darkness (control), where the container was covered and the window was sealed with lightproof plastic; (2) UVR alone, using a UG11 filter (Schott, Germany) that screened off 100% PAR and transmitted 53.7% of UV-A and 63.8% of UV-B as the container cover; (3) UVR + 4% PAR, where the window was covered with 395 nm cut-off foil and the top was covered with UG11; (4) UVR + 2% PAR, similar to treatment 3 but neutral filters were added to the side window to screen out 50% PAR; (5) 25% PAR, where the container was covered with 395 nm cut-off foil combined with neutral filters, and the window was covered with opaque plastic. The container was placed in a thermostatic shaking water bath for temperature control at 30°C as mentioned above. Morphological examination of *A. platensis* spirals was carried out every day 2 h after sunset during the period 19–25 July 2006.

In order to examine the effect of PAR doses on morphological changes of *A. platensis*, the quartz tubes covered with 395 cut-off foil were incubated at 30°C under a solar simulator (Sol 1200W, Dr. Hönle, Martinsried, Germany). The levels of the PAR dose were achieved in

two ways: (1) incubating for 10 h at different PAR levels (0, 200, 400, 600, 800 and 1,000 $\mu\text{mol m}^{-2} \text{s}^{-1}$) then maintained in darkness for 14 h; and (2) incubating at 800 $\mu\text{mol m}^{-2} \text{s}^{-1}$ of PAR for different durations (0, 2, 4, 6, 8, 10 and 12 h). After exposure, the morphology of the spirals was examined at the time when the cells under all treatments had grown for 24 h (the same length of time). Obvious morphological changes in the spirals could be observed in 24 h even after they had been maintained in darkness following the irradiations. In order to see if the tightened spirals achieved under high PAR would become loose again under dim light, the cultures were re-grown at 60 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for 4 weeks and morphological examination carried out every day.

Solar irradiances were measured using a broadband ELDONET filter radiometer (Real Time Computer, Möhrendorf, Germany) that has three channels for PAR, UV-A and UV-B (Häder et al. 1999). This instrument has an error less than 0.5% and was calibrated annually.

Determination of biomass density and specific growth rate

Biomass density of the cultures was measured by filtering 30 mL of the culture through a pre-dried Whatman GF/F filter (\varnothing 25 mm), drying in an oven at 80°C for 24 h, and cooling it off in a desiccator, before weighing it on an electronic balance and subtracting the known weight of the dried filter. While the sample was being filtered, it was washed with 20 mL distilled water in order to remove residual salts. The specific growth rate (μ , day^{-1}) was calculated as $\mu = (\ln x_2 - \ln x_1)/(t_2 - t_1)$, where x_1 and x_2 were the biomass densities at time t_1 and t_2 , respectively.

Morphological examination

Morphological changes in *A. platensis* (D-0083) spirals were examined (200 \times) with a Zeiss Axioplan 2 microscope (Carl Zeiss, Germany). Digital images were recorded with a Zeiss Axicam HRC color camera (Carl Zeiss Jena, Pentacon, Germany) and were analyzed with a vision analysis system (Axio Vision 3.0). Since the spirals of *A. platensis* (D-0083) are highly compressed, the helix pitch (distance between two neighboring spirals) was calculated as the ratio of the length to the number of spirals per individual filament. This was estimated randomly from at least 50 individual filaments.

Protein synthesis inhibition, soluble protein extraction and SDS-PAGE

In order to determine how the morphological transformation was associated with protein synthesis, chloramphenicol was

used at a final concentration of 40 μM (Mühling et al. 2003) prior to exposure.

For the extraction of soluble proteins, Tris-HCl (0.15 M NaCl, 0.125 M Tris-HCl, pH 6.8) was added to cell pellets (4 mL g^{-1} wet biomass) before they were frozen at -20°C . After thawing, the mixtures were sonicated with an ultrasonic homogenizer (CPX 600, Cole Parmer) until all cells ruptured. The proteins in the supernatant were precipitated with four volumes of 100% cold acetone at -20°C for 1 h and centrifuged at 12,000 $\times g$ at 4°C. The precipitated proteins in each sample were re-dissolved in Tris-HCl (Wang and Zhao 2005) and the concentrations were determined according to Bradford (1976).

In order to see how the periplasmic proteins changed during the spiral transformation, the cells were treated with trypsin at a final concentration of 10 g L^{-1} at 25°C for 5 min to wash off the periplasmic proteins (Nimer et al. 1998). For protein analysis by SDS-PAGE according to Laemmli (1970), 10 μg of extracted protein was added to the loading buffer (64 mM Tris-HCl, 10% glycerol, 2% SDS, 5% β -mercaptoethanol, pH 6.8).

The concentrations of the separating and stacking gels were 10 and 5%, respectively. Molecular mass was calibrated with low molecular weight standard proteins ranging from 14.4 to 97.0 kDa (Amersham Pharmacia Biotech Ltd., Hong Kong, China). The gel was photographed using a VersaDoc Imaging System 3000 (Bio-Rad Laboratories, Hercules, CA, USA) after being stained with Coomassie blue R-250. The bands in the pattern were analyzed using the software Quantity One (Bio-Rad Laboratories).

Measurement of photochemical yields

In order to see if the compressed spirals played a role of photoprotection by self-shading, photochemical yields were compared between the compressed and loosened spirals when they reached an identical criterion for physiological status. The tightened spirals achieved under high PAR (30% natural solar radiation) were subsequently grown at 60 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for 1 week, when their pigment content and effective quantum yield (F'_v/F'_m) were identical with the loose ones grown at 60 $\mu\text{mol m}^{-2} \text{s}^{-1}$ throughout (Table 1). Then these two types (loose and tight) of spirals were simultaneously irradiated with PAR + UV-A (320–400 nm) + UV-B (295–320 nm) from a solar simulator (Sol 1200W, Dr. Hönle, Martinsried, Germany). The intensities of PAR, UV-A and UV-B were 326.2 (1,500 $\mu\text{mol m}^{-2} \text{s}^{-1}$), 75.90 and 2.44 W m^{-2} , respectively. The biologically weighted UV-B irradiance (normalized at 300 nm) was 0.24 W m^{-2} (Setlow 1974), estimated on the basis of the irradiance reaching the cells in the quartz tubes covered with 295 nm cut-off filter. The F'_v/F'_m values were measured with a pulse amplitude

modulated fluorometer (WATER-ED, Walz, Effeltrich, Germany). The actinic light was set as $80 \mu\text{mol m}^{-2} \text{s}^{-1}$ under a modulated measuring light of $0.3 \mu\text{mol m}^{-2} \text{s}^{-1}$, and the saturating pulse was about $5,600 \mu\text{mol m}^{-2} \text{s}^{-1}$ and lasted for 0.8 s.

Statistical analysis

Data were analyzed using one-way ANOVA followed by a multiple comparison using the Tukey test. A confidence level of 95% was used in all analyses.

Results

When *A. platensis* (D-0083) spirals were grown under solar radiation at 20°C, their helix pitch increased (the spirals loosened) under PAR alone; however, it decreased (the spirals tightened) in the presence of UVR (Fig. 1a). When the cultures were transferred to 30°C (optimal temperature for growth), the spirals became compressed quickly under either PAR alone (P treatment) or PAR + UVR (PAB treatment). Under PAR, the helix pitch of spirals at 30°C was much smaller ($P < 0.01$) than that at 20°C. For the cells receiving both PAR and UVR, the helix pitch decreased obviously from day 5 at 20°C. However, compression of the spirals occurred much faster at 30°C than at 20°C. Along with these morphological changes, the growth rate fluctuated with solar radiation and was faster at 30°C except for the last 2 days, when there were low solar doses because of the cloud cover (Fig. 1b). The treatment with 30% full solar radiation (Fig. 1c) did not result in significant breaking of the spirals (data not shown).

To further investigate the roles played by UVR and/or PAR during the morphological change, cells were cultured at 30°C in darkness, with UVR alone, with UVR + 2% or 4% PAR and with PAR alone (25%) for 1 week, outdoors (Table 2). The mean incident solar irradiances at noon were 427.92, 74.05 and 2.49 W m^{-2} for PAR, UV-A and UV-B, respectively. Neither darkness nor the UVR alone treatments resulted in compressed spirals, while the

addition of PAR led to significant ($P < 0.01$) reduction of the helix pitch, even at the 2% level (Table 2). When the spirals were grown at different levels of PAR dose, either as a function of time or irradiance, their helix pitch decreased with increased PAR doses (Fig. 2).

After *A. platensis* (D-0083) cells had been irradiated at $1,000 \mu\text{mol m}^{-2} \text{s}^{-1}$ PAR for 10 h and the tightened spirals re-grown at $60 \mu\text{mol m}^{-2} \text{s}^{-1}$, they remained compressed under the low PAR even after 200 h. Thereafter, the helix pitch increased gradually and the spirals were loosened by 480 h (Fig. 3).

To examine whether the compression of spirals was related to increased or newly synthesized proteins in the cells, chloramphenicol, an inhibitor of protein synthesis, was added to the cultures before exposure to intensive PAR ($1,000 \mu\text{mol m}^{-2} \text{s}^{-1}$ for 10 h). The spirals under the chloramphenicol treatment were more loose ($P < 0.01$) compared with those without the inhibitor in the cultures (Table 3). In addition, increased PAR doses led to severe breakage of the spirals in the presence of chloramphenicol (data not shown). When the soluble proteins in the compressed and loosened spirals were compared, a 52.0 kDa protein was more abundant in the compressed spirals compared with the spirals which had been loosened from the compressed ones (Fig. 4). At 20°C, the presence of UVR did not increase the amount of this protein (lane 3) compared with that under solar PAR alone (lane 2). However, at 30°C, the 52.0 kDa protein became more abundant under either PAR (lane 4) or PAR + UVR (lane 5). The presence of UVR in the PAR + UVR treatment also increased the abundance of this protein in contrast to the PAR alone treatment. When the periplasmic proteins were washed off with trypsin, the 52.0 kDa protein band almost disappeared (lane 6) from the spirals, but was found in the wash-off (Fig. 5), reflecting that it was a periplasmic protein.

When the compressed spirals were re-grown under low PAR for 7 days, their structure still remained tight, but their chlorophyll *a*, carotenoid and F'_v/F'_m values were reversed to equal the levels of the loose ones (Table 1). When they were exposed to irradiances including 326.1 W m^{-2} PAR ($1,500 \mu\text{mol m}^{-2} \text{s}^{-1}$), 75.9 W m^{-2} UV-A and

Table 1 Identical levels of chlorophyll *a* (Chl *a*), carotenoid (Car) and photochemical yield (F'_v/F'_m) of the compressed and loosened spirals of *A. platensis* (D-0083)

Spiral	Chl <i>a</i>	Car	Helix pitch (μm)	F'_v/F'_m
Loose	16.53 ± 0.21	3.32 ± 0.09	13.60 ± 0.47	0.48 ± 0.02
Compressed	16.64 ± 0.32 (10.10 ± 0.28)	3.39 ± 0.05 (2.87 ± 0.19)	$11.00 \pm 0.52^{**}$ (11.92 ± 0.56)	0.47 ± 0.04 (0.25 ± 0.07)

The loose spirals were grown at a PAR intensity of $60 \mu\text{mol m}^{-2} \text{s}^{-1}$, while the compressed ones were achieved under 30% solar PAR for 3 days and then re-grown at $60 \mu\text{mol m}^{-2} \text{s}^{-1}$ for 1 week. The means and standard errors were based on at least 50 randomly measured trichomes. The data in parentheses show the parameters measured at the end of the high PAR treatment and before re-culture under low irradiance

The loose and compressed spirals only with significant (** $P < 0.01$) difference in the helix pitch are included

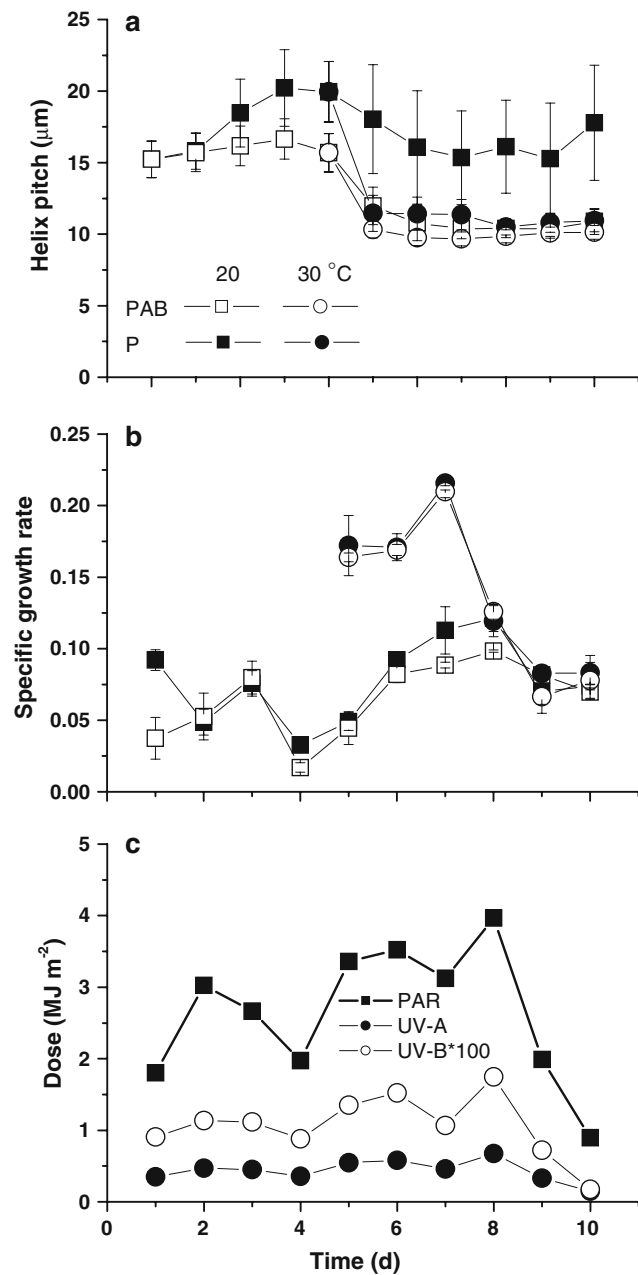


Fig. 1 Changes in helix pitch (a) and specific growth rate (b) of *A. platensis* (D-0083) when grown under solar radiation (c) with (PAB) or without UVR (P) at 20 or 30°C during the period of 24 March to 2 April 2007. The means and standard errors were based on at least 50 randomly measured trichomes

2.44 W m^{-2} UV-B, their F'_v/F'_m value decreased to a different extent in 4 h (Fig. 6). F'_v/F'_m values decreased in both spiral types with prolonged exposure time, but at a faster pace in the loose spirals. The difference in F'_v/F'_m between the tightened and loose spirals became significant ($P < 0.05$) at 4 h and even greater later (Fig. 6), indicating that the compression of the spirals into a tighter helix pitch led to less photoinhibition.

Table 2 The helix pitch of *A. platensis* (D-0083) cultured at 30 (± 0.5)°C under different treatments for the period 19–25 July 2006

Treatments	Helix pitch (μm)
Darkness	14.14 \pm 0.87
UVR	14.92 \pm 1.18
UVR + 2% PAR	12.58 \pm 1.06
UVR + 4% PAR	11.09 \pm 0.58
25% PAR	10.17 \pm 0.47

The means and standard errors were based on at least 50 randomly measured trichomes

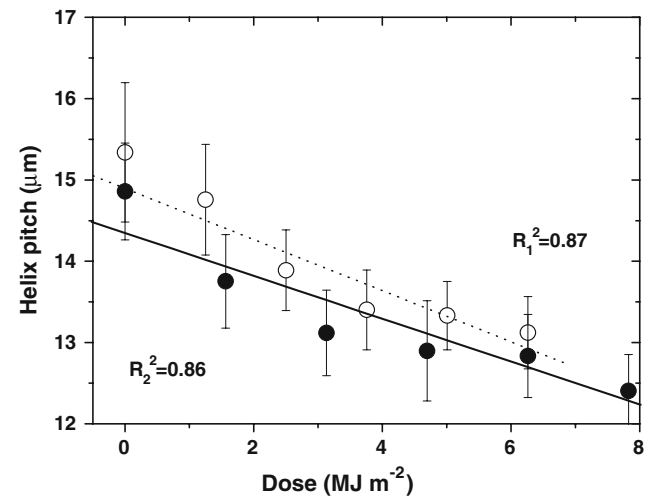


Fig. 2 Helix pitch of *A. platensis* (D-0083) as a function of PAR doses at 30°C. The trichomes were exposed to PAR levels of 0–1,000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for 10 h then kept in the dark for 14 h (open symbol) or exposed to fixed PAR (800 $\mu\text{mol m}^{-2} \text{s}^{-1}$) for 0–12 h and then transferred to darkness for 24 h (solid symbol). The means and standard errors were based on at least 50 randomly measured trichomes

Discussion

Light and temperature usually interact in regulating physiological behavior of cyanobacteria and eukaryotic photoautotrophs. Changes in the spiral structure of *A. platensis* have been related to changes in nutrient or CO_2 availability (Hongsthong et al. 2007), white light intensity (Van Eykelenburg 1979), osmotic pressure (Van Eykelenburg et al. 1980) and temperature (Mühling et al. 2003). Recently, solar UVR was found to break the spiral structure of *A. platensis* when cultured under natural solar radiation during winter when the temperature ranged from 18 to 20°C (Wu et al. 2005a). It has been shown that such UVR-induced spiral breakage is temperature dependent and accompanied by DNA damage (Gao et al. 2008). The damage caused by UVR decreases with increased temperature ranging from 15 to 30°C (Gao et al. 2008). In the present study, we demonstrated that it was PAR which

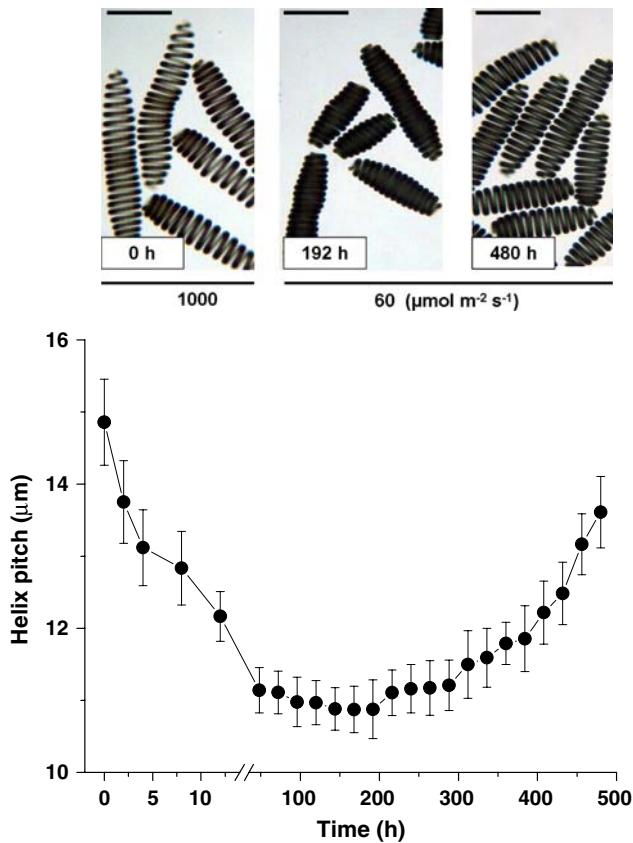


Fig. 3 Change in helix pitch of *A. platensis* (D-0083) over time while grown at 30°C under high PAR (1,000 $\mu\text{mol m}^{-2} \text{s}^{-1}$) and then moved to low PAR (60 $\mu\text{mol m}^{-2} \text{s}^{-1}$). The images above the figure were taken at 0, 192 and 480 h. The means and standard errors were based on at least 50 randomly measured trichomes. Scale bars 100 μm ($\times 200$)

Fig. 4 SDS-PAGE of *A. platensis* (D-0083). **a** Loose spirals cultured under a PAR intensity of 60 $\mu\text{mol m}^{-2} \text{s}^{-1}$ throughout; **b** compressed spirals induced after 10 h exposure to 1,000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PAR; **c** loosened spirals produced from the tightened ones re-grown at 60 $\mu\text{mol m}^{-2} \text{s}^{-1}$

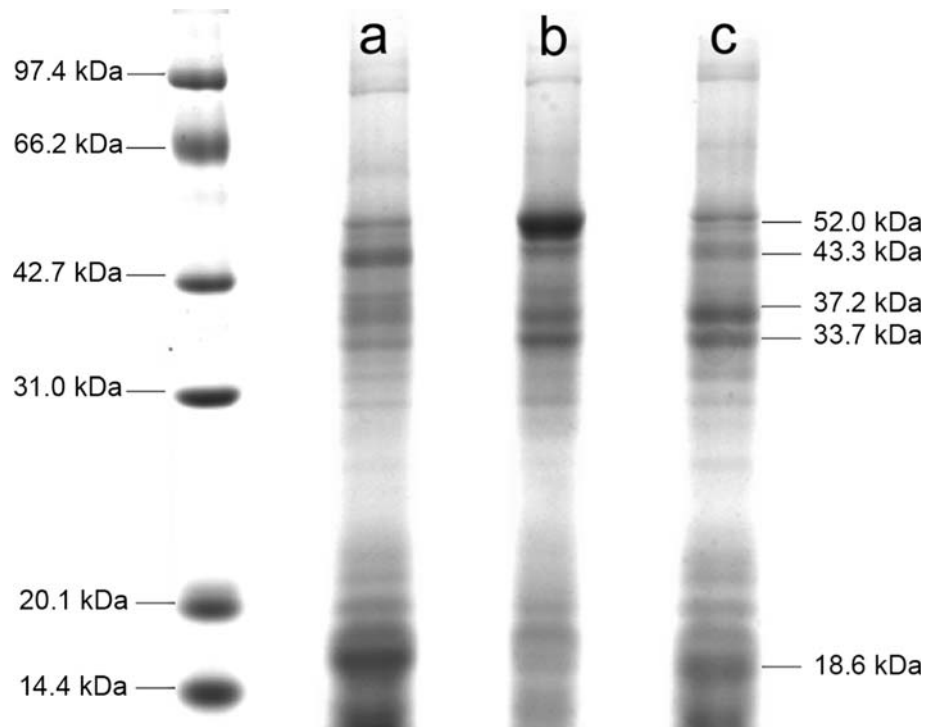


Table 3 Change in helix pitch and length of *A. platensis* (D-0083) trichomes grown under a PAR intensity of 1,000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for 10 h then kept in darkness for 14 h (obvious morphological changes happen in 24 h) with (+) or without (–) chloramphenicol (cpl, 40 μM) in the cultures

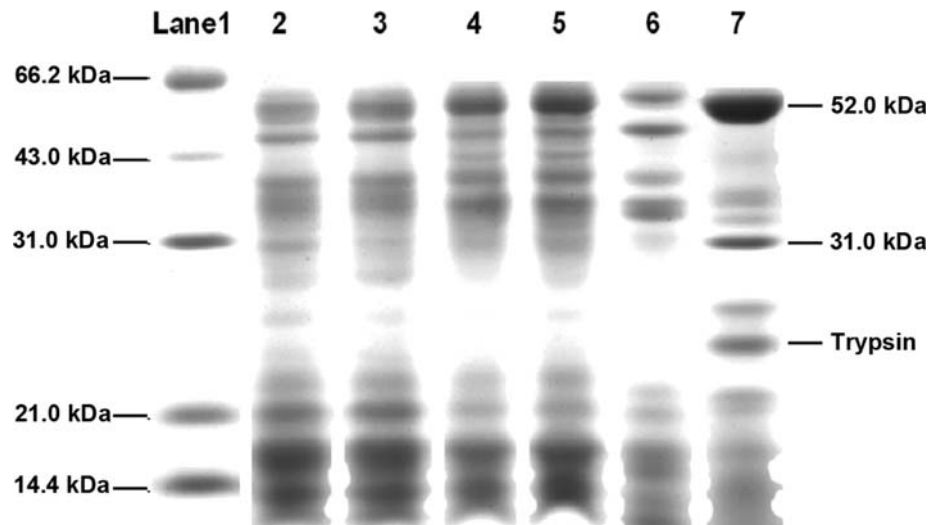
	T_0	+cpl	–cpl
Helix pitch (μm)	13.48 ± 0.87	14.04 ± 1.03	$11.92 \pm 0.56^{**}$
Length (μm)	187.35 ± 36.92	187.07 ± 39.15	186.90 ± 42.19

T_0 denotes cultures before exposed to intensive PAR; the means and standard errors were based on at least 50 randomly measured trichomes
 ** Significant at $P < 0.01$

caused the spirals of *A. platensis* to tighten, and the presence of UVR accelerated this compressing process (Fig. 1a; Table 2).

Passive defense mechanisms (such as the accumulation of UV-screening compounds) are known to play important roles in protecting cyanobacteria from photodamage (Garcia-Pichel and Castenholz 1991; Rozema 2002). However, in *A. platensis*, the amount of UV-absorbing compounds is very low, and will not effectively protect the cells from harmful levels of UVR (Rajagopal 2000; Gupta et al. 2008; Gao and Ma 2008). Wu et al. (2005a) suggest that the self-shading provided by the compressed spirals provides photoprotection against harmful radiation. Our study provided evidence that compressed spiral structure induced by PAR might protect the PSII machinery of *A. platensis* from harmful levels of UVR, probably by enhancing self-shading by the cells (Fig. 6). Although the formation of gas vacuoles is suggested also as a possible

Fig. 5 SDS-PAGE of *A. platensis* (D-0083) for the samples obtained from different treatments. Lane 1 markers, lanes 2 and 3 under P (PAR) and PAB (PAR + UV-A + UV-B) treatments for 3 days (24–26 March 2007) at 20°C, lanes 4 and 5 under P and PAB treatments for 3 days at 30°C, lane 6 the same as lane 4 but without periplasmic proteins (previously washed off with trypsin), lane 7 the washed-off proteins



protective measure (Rajagopal et al. 2005), buoyancy provided by the gas vacuoles in *A. platensis* is reduced with enhanced photosynthesis stimulated by PAR (Ma and Gao 2009), suggesting that the synthesis of gas vacuoles was less than the accumulation of photosynthate and may not be an effective protective measure.

Induction of specific proteins is a common response to environmental stresses in organisms (Nicholson et al. 1987; Parsell and Lindquist 1993; Völker et al. 1994; Graumann et al. 1996; Nitta et al. 2005). In the present study, two lines of evidence indicated that spiral tightening was associated with protein expression: (1) inhibition of protein biosynthesis by the addition of 40 µM chloramphenicol interfered with the formation of tighter spirals and (2) the periplasmic 52.0 kDa protein was more highly expressed in the tightened spirals (Fig. 6). This 52.0 kDa protein was found previously during the morphological transformation from linear to spiral filaments of *A. platensis* (Wang and Zhao 2005). Here, we showed that the abundance of the protein can be enhanced by high levels of PAR and even further increased with addition of UVR. The protein, as a structural (constituent) component, might control morphological alteration in response to changes in solar radiation. It is well documented that many proteins are anchored to the gram-positive cell wall (Schneewind et al. 1992, 1993; Navarre and Schneewind 1999; Schroda et al. 2001), and that the cell wall layer in prokaryotic gram-positive bacteria and cyanobacteria, which is formed by peptidoglycans, determines their shape (Sugai et al. 1990; Tavares and Sellstedt 2000). When the cell wall is renewed during cell division cycles, insertion of newly synthesized protein molecules may affect the cell wall structure and even the shape of the bacteria (Glauner et al. 1988; Mühling et al. 2003). In *A. platensis*, different cross-linking between the 52.0 kDa protein and the cell wall envelope might have led to an alteration of the spiral

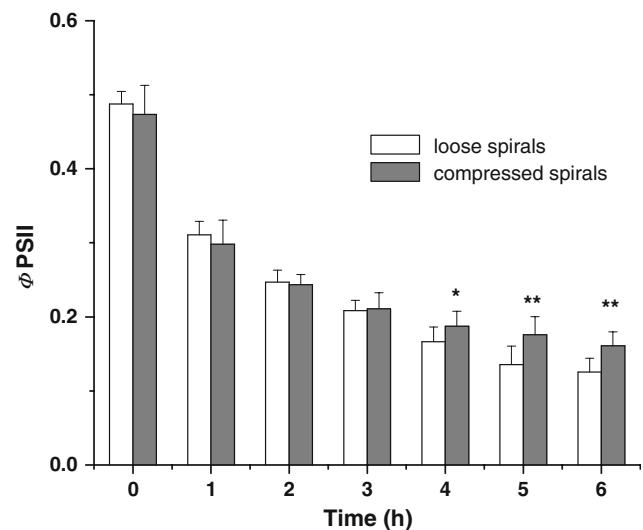


Fig. 6 Photochemical quantum yield of the loosened and tightened spirals. The intensity of PAR, UV-A and UV-B was 326.2 (1,500 µmol m⁻² s⁻¹), 75.90 and 2.44 W m⁻², respectively. Symbols * and ** indicate significant difference at *P* < 0.05 and *P* < 0.01, respectively

structures. So that when the 52.0 kDa protein or its subunits were “switched on”, the spiral structures were tightened. This PAR-sensitive protein might be related to photosynthetic Ci acquisition processes, facilitating faster supplies of Ci in addition to causing the morphological changes under high levels of PAR. In *Arthrospira* spp., reversible variations in the degree of coiling are of an extrinsic nature and related to environmental changes, although sometimes mutation occurs, leading to different strains (Wang and Zhao 2005). The loosening process of *A. platensis* spirals enabled the cells to receive more light for photosynthesis, while the tightening process facilitated the cells shading themselves when solar radiation became excessive.

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