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Solar PAR and UV radiation affects the physiology and morphology of the cyanobacterium *Anabaena* sp. PCC 7120

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Abstract

Solar UV radiation (280–400 nm) may affect morphology of cyanobacteria, however, little has been evidenced on this aspect while their physiological responses were examined. We investigated the impacts of solar PAR and UVR on the growth, photosynthetic performance and morphology of the cyanobacterium *Anabaena* sp. PCC7120 while it was grown under three different solar radiation treatments: exposures to (a) constant low PAR (photosynthetic active radiation, 400–700 nm), (b) natural levels of solar radiation with and (c) without UV radiation (290–400 nm). When the cells were exposed to solar PAR or PAR + UVR, the photochemical efficiency was reduced by about 40% and 90%, respectively, on day one and recovered faster under the treatment without UVR over the following days. Solar UVR inhibited the growth up to 40%, reduced trichome length by up to 49% and depressed the differentiation of heterocysts. Negligible concentrations of UV-absorbing compounds were found even in the presence of UVR. During the first 2 d of exposure to natural levels of PAR, carotenoid concentrations increased but no prolonged increase was evident. Heterocyst formation was enhanced under elevated PAR levels that stimulated quantum yield and growth after an initial inhibition. Higher concentrations of carotenoids and a twofold increase in the carotenoid to chlorophyll *a* ratio provided protection from the high levels of solar PAR. Under radiation treatments with UVR the relatively greater decrease in chlorophyll *a* concentrations compared with the increase in carotenoids was responsible for the higher carotenoid: chlorophyll *a* ratio. Heterocyst formation was disrupted in the presence of solar UVR. However, the longer term impact of heterocyst disruption to the survival of *Anabaena* sp. requires further study.

Keywords: *Anabaena*; Cyanobacteria; Growth; Heterocyst differentiation; Photosynthesis; UV radiation

1. Introduction

Depletion of the stratospheric ozone layer results in increased levels of incident solar UV-B radiation (280–315 nm) at the Earth's surface [1,2]. It is well established that UV radiation can affect many biological processes [3,4], principally because it is readily absorbed by important biomolecules such as nucleic acids, proteins and lipids that are essential for genetic, biochemical and physiological functions within cells [5–8]. As a consequence, there are widespread concerns about the potentially damaging effects on aquatic ecosystems and, in particular, on primary producers [9]. Cyanobacteria, an ancient and morphologically diverse group of photosynthetic prokaryotes [10,11], are the largest and most widely distributed group of photoautotrophs on the Earth, occurring in aquatic and terrestrial environments and contributing significantly to global CO_2 and N_2 fixation [12,13]. The negative effects of UVR on cyanobacteria are well documented; for example, UV-B radiation has been shown to impair various physiological and biochemical processes including growth [14],

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photosynthesis [15–17], pigmentation [18], nitrogen metabolism [19], CO_2 uptake and ribulose 1,5-bisphosphate carboxylase/oxygenase (RuBisCO) activity [14]. It can also affect the motility and photo-orientation of cells and alter the morphology, through breakage and changes to the spiral structure, of filamentous cyanobacteria [20,21]. However, despite this cyanobacteria can be found living under high levels of solar radiation, implying that they must possess efficient mechanisms to counteract the harmful effects of UVR. Previous studies indicate that cyanobacteria have a wide range of tolerances to UVR and that there are several mechanisms to deal with the damaging effects of UVR, including synthesis of UV-absorbing pigments and extracellular polysaccharides [22,23], efficient DNA repair mechanisms [24,25] and avoidance of brightly lit habitats [26].

Anabaena sp. PCC 7120 is a filamentous cyanobacterium that is capable of both oxygenic photosynthesis and atmospheric nitrogen fixation, accomplished by vegetative cells and heterocysts, respectively. Heterocysts can not fix CO_2, as they lack RuBisCO, and are reliant on vegetative cells for a supply of fixed C to support N_2 fixation. The N_2 is assimilated via the glutamine synthetase–glutamate synthase (GS–GOGAT) pathway, to form glutamine and glutamate which is then exported to the vegetative cells [27–29]. Thus, any alteration in the balance between heterocysts and vegetation cells could have a detrimental impact on survival.

Here, we report on an investigation into the effects of solar radiation on growth, photosynthetic activity, trichome morphology and heterocyst differentiation, and the protective measures used to counteract such impacts in the cyanobacterium *Anabaena* sp. PCC 7120.

2. Materials and methods

2.1. Organisms and growth conditions

Anabaena sp. PCC 7120 was obtained from the Freshwater Algae Culture Collection of the Institute of Hydrobiology, the Chinese Academy of Sciences. Stock cultures were maintained in BG-11 medium at 15 °C under fluorescent white light (PAR, 400–700 nm) of 25 μmol m^{-2} s^{-1} measured by a PAR sensor (SKP-200, Skye Instruments Ltd, Wales, UK) on a 12:12-h light:dark cycle. Exponentially growing cells were transferred to 20 °C and −70 μmol m^{-2} s^{-1} PAR on a 12:12-h light:dark cycle and cultured for 1 d prior to experimentation. At the start of the experiment (t_0), the cultures were re-suspended in fresh BG-11 medium at an initial concentration of 1.1×10^6 cells ml^{-1}, and dispensed into six UV transparent PLEXIGLAS vessels (20 × 12 × 2 cm) that allow transmittance of full solar radiation (Fig. 1). All cultures were aerated (ca. 0.36 L min^{-1}) with sterile air by filtration through 0.45-μm grid membranes (Nalge Sybron Corp., Rochester, NY). Cells were grown semi-continuously and every 24 h they were sub-cultured with fresh medium to re-establish the initial density.

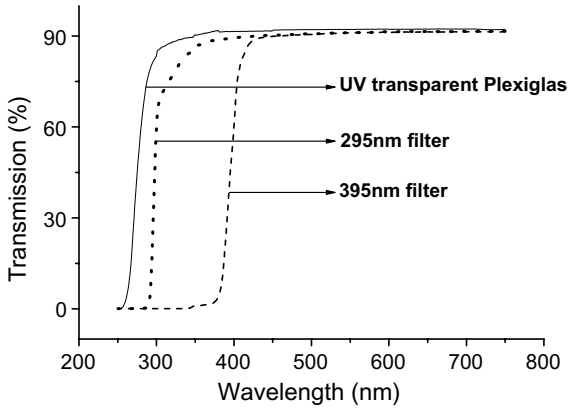

Fig. 1. The transmission spectra of different materials (Ultraphan 295 and Ultraphan 395) and the UV transparent PLEXIGLAS used in the study.

2.2. Experimentation

2.2.1. Solar radiation measurement

Incident solar irradiances of PAR (400–700 nm), UV-A (315–400 nm) and UV-B radiation (280–315 nm) were continuously monitored using an ELDONET filter radiometer (Real Time Computer, Möhrendorf, Germany). The reliability of this instrument has been internationally recognized [9], and certificated with the correspondence error less than 0.5% in comparison with the most accurate instrument (Certificate no. 2006/BB14/1). The device was installed on a roof of Shantou University (116.6°E, 23.3°N) where the experiments were carried out.

2.2.2. Radiation treatments

From April 7th to 12th 2005, daily solar dose ranged 8.85–1.97 MJ m^{-2} for PAR, 1.38–0.32 MJ m^{-2} for UV-A and 0.04−0.008 MJ m^{-2} for UV-B, respectively. *Anabaena* cultures were exposed to one of the three radiation treatments (duplicate cultures per treatment): Indoor PAR (IP), fluorescent white light of 70 μmol m^{-2} s^{-1}, transmitting 400–700 nm, at 20 °C in a controlled environment cabinet (control treatment) ; outdoor PAR (OP), vessels covered with Ultraphan film 395 (UV Opak, Digefra, Germany) to remove UVR, transmitting 395–700 nm, and outdoor PAR plus UV-A + B (PAB), vessels, covered with Ultraphan film 295, transmitting 295–700 nm; the temperature of the outdoor cultures was maintained at 20–22 °C by placing them in a flow-through water bath. Measurements were taken daily (cell counts, photosynthesis, concentrations of pigments and UV-absorbing compounds) or every 2nd day (morphology) at 17:00, about 2 h before sunset.

2.3. Measurements and determinations

2.3.1. Growth

Cell numbers were counted using a haemocytometer and viewed with a compound microscope (Olympus BX50F4, Japan). The specific growth rate (SGR, μ) was calculated for each day using the equation:

$$\mu = \ln(C_n/C_{n-1})/(T_n - C_{n-1}),$$

where C_n and C_{n-1} represent the number of cells in 1 ml of culture medium on days T_n and T_{n-1}, respectively. Inhibition of growth in the different radiation treatments was calculated as

$$\text{Inh}\ (\%) = (G_P – G_X)/G_P * 100,$$

where G_P and G_X indicates the specific growth rate under the treatments without or with UVR, respectively.

2.3.2. Chlorophyll a fluorescence

The ratio of variable to maximal chlorophyll *a* fluorescence (F_v/F_m) of dark-adapted (for 10 min) filaments (5 ml cultures with $1.1–2.4 \times 10^6$ cells ml^{-1}) was determined with a portable pulse amplitude modulated fluorometer ((PAM – WATER-ED, Walz, Germany). F_v/F_m represents the photochemical efficiency of PSII or the maximal quantum yield of the photosynthetic apparatus.

2.3.3. Pigments

Cultures were filtered onto Whatman GF/F glass fibre filters (25 mm) and photosynthetic pigments and UV-absorbing compounds extracted in 10 ml of absolute methanol (>12 h), centrifuged (5000*g* for 5 min) and supernatants scanned between 250 and 750 nm using a scanning spectrophotometer (DU530, Beckham Counter, USA). Chlorophyll *a* (chl *a*) concentrations were calculated according to Porra [30], the concentrations of carotenoids were determined using the equation of Parsons and Strickland [31].

2.3.4. Morphology and heterocyst frequency

Morphological examination was performed every two days at sunset with an inverted compound microscope (Olympus IX51, Japan). Digital images were recorded with a digital camera (Cannon Power Shot S50, Japan) and analyzed with a Vision Analysis System (Canon Vision 6.0). Measurements of cell diameter and cell number per trichome were used to estimate the lengths of 60–100 filaments viewed from at least 20 fields. Heterocyst frequency was defined as the number of heterocysts per 100 vegetative cells.

2.3.5. Statistical analysis

Data were analyzed using the statistical package SPSS 10.0 for Windows. To account for the dependency of the time variable, the General Linear Model Repeat Measures analysis was performed on the data. To compare individual means the *post hoc* Tukey HSD test was used with the significance level set at 0.05. For the physiological and biochemical parameters, two parallel cultures were run and two samples taken from each culture; for the morphological measurements, 60–100 filaments from each culture were observed.

3. Results

3.1. Incident solar radiation

The daily dose of solar radiation over the course of the experiment is presented in Fig. 2a. Four consecutive days of high solar radiation with mean daily doses for PAR, UV-A and UV-B of 8.85 MJ m^{-2}, 1.38 MJ m^{-2} and

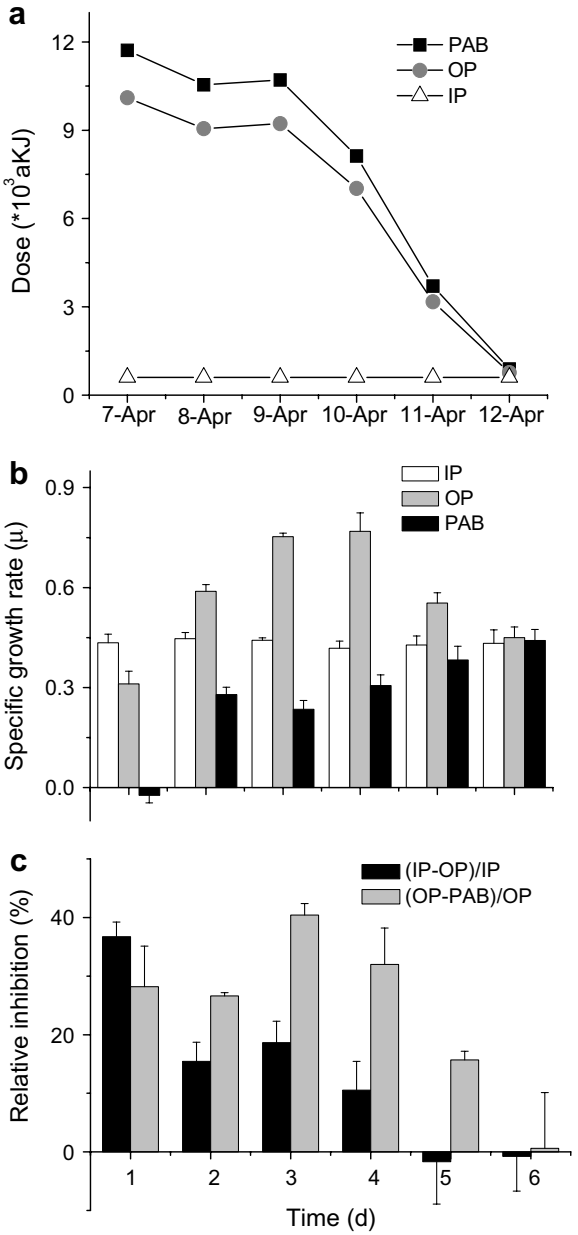

Fig. 2. (a) Daily solar doses from Apr. 7, 2005 to Apr. 12, 2005. (b) The specific growth rate (SGR) of *Anabaena* sp. PCC7120 in semi-continuous culture during a 6 d exposure period to indoor PAR supplied by fluorescent white light (IP), solar PAR radiation (OP) and solar PAR plus UV-A and B radiation (PAB) with an inoculated cell concentration of 1.1×10^6 cells ml^{-1}. (c) Daily relative inhibition of the growth rate, either caused by the exposure to solar PAR in contrast IP [(IP – OP)/IP] or by the exposure to PAB in contrast to OP[(OP – PAB)/OP]. Data in b and c represent means ± 95% confidence interval ($n = 4$).

0.04 MJ m^{-2}, respectively, were followed by two days of overcast conditions with low levels of solar radiation (mean doses of 1.97, 0.32 and 0.008 MJ m^{-2} for PAR, UV-A and UV-B, respectively).

3.2. Growth

Changes in specific growth rate (SGR) under different light treatments and with time were observed (Fig. 2b), as indicated by a significant interaction ($P < 0.001$) between these two variables. The SGRs of indoor PAR (IP) cultures (mean = 0.45 d^{-1}) did not differ significantly ($P > 0.05$) with time. After 1 d the SGRs of the cultures grown outdoors under solar PAR (OP) and PAR + UV-A + B radiation (PAB) were significantly lower ($P < 0.05$) than indoor cultures, with the greatest inhibition under PAB ($\mu_{max} = -0.01$ d^{-1}; indicating a loss of biomass due to the cell death caused by UV-B). From days 2 to 4, the SGRs of OP cultures significantly increased ($P < 0.05$) to a maximum of ca. 0.77 d^{-1} and were significantly higher ($P < 0.05$) than both the IP and PAB cultures. For PAB cultures there was a significant increase ($P < 0.05$) in the SGR from the rate measured on day 1 to about 0.3 d^{-1} on day 4, but the values were significantly lower ($P < 0.05$) than those measured for IP and OP cultures over the same period. By day 5 the SGR of PAB cultures had increased to the value of IP ($P > 0.05$) and the SGR of OP had significantly decreased (ca. 0.5 d^{-1}), but was still higher ($P < 0.05$) than the two other treatments. On day 6 there was no significant difference between any of the three treatments (mean SGR of 0.45 d^{-1}). Over the first four days, the relative inhibition caused by exposure to PAB compared with OP ranged 28–40%, and compared with IP varied by 11–37% (Fig. 2c), whereas by day 6 the relative inhibition of both was zero, reflecting the low dose of natural solar radiation measured on that day.

3.3. Chlorophyll a fluorescence

The maximum quantum yield (F_v/F_m) of IP cultures on day 1 was 0. 3 (cells acclimated to low light usually show low yield) and did not vary significantly ($P > 0.05$) with time (Fig. 3). On day 1, values of F_v/F_m for OP and PAB were significantly lower (40% and 90%, respectively) than the control. Thereafter, a steady recovery for both treatments was observed with time. Within 2 days, F_v/F_m values for OP cultures had recovered to the initial value of controls and, subsequently exceeded it, whereas PAB cultures recovered more slowly and did not reach the initial value until day 5. By day 6 F_v/F_m values of the OP and PAB cultures were the same and significantly higher ($P < 0.05$) than IP cultures.

3.4. Pigments

The spectral characteristics of *Anabaena* sp. PCC 7120 grown under the three radiation treatments over 6 d are shown in Fig. 4. A very small absorption peak of UV-absorbing compounds (absorbance between 300 and 360 nm) was discernable but no significant increase with time was observed for any of the treatments. In contrast, significant ($P < 0.001$) changes in the concentrations of carotenoids and chlorophyll *a* were obtained between treatments and with time (Fig. 5a,b). In the IP treatment, concentrations of both pigments did not change significantly over the course of the experiment ($P > 0.05$). Under OP, the carotenoid concentration after 2 d was significantly higher ($P < 0.05$) than that of IP, remained stable until day 4 and then declined to that ($P > 0.05$) of the IP control by day 6. The carotenoid concentrations of PAB cultures after 2 d was also significantly ($P < 0.05$) higher than IP and was similar to that of the OP treatment ($P > 0.05$), decreasing thereafter to the same concentration as the IP control by day 6. The initial chlorophyll *a* concentrations were 5.8 μg mg^{-1} DW. After 2 d there was a significant ($P < 0.05$) difference in concentrations between the IP treatment and those of OP and PAB. Minimum concentrations of 4.05 and 2.85 μg mg dry wt^{-1} in OP and PAB cultures, respectively were obtained on day 4 (OP > PAB; $P < 0.05$); the concentrations of OP cultures increased to those of the IP controls by day 6, and the presence of UVR in the PAB cultures reduced the chlorophyll contents over the period.

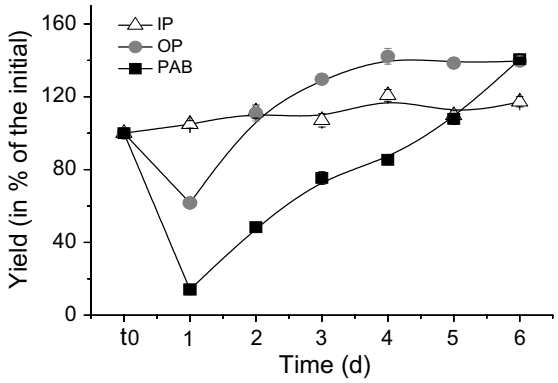

Fig. 3. Photochemical efficiency (yield in % of the initial, 0.3) for dark-adapted cells of *Anabaena* sp. PCC7120 before and during a 6 d exposure period to solar PAR radiation (OP) and solar PAR plus UV-A and B radiation (PAB). Data represent means ±95% confidence interval ($n = 4$).

The carotenoid:chlorophyll *a* ratios of cultures grown under OP and PAB were significantly higher ($P < 0.05$) than that of the IP treatment on days 2 and 4, with the PAB treatment having a significantly ($P < 0.05$) higher value than that of OP on day 4 (Fig. 5c). On day 2 the higher values were due to a greater relative change in carotenoid content compared with that of chlorophyll *a*, whereas on day 4 it was due to a greater relative change in chlorophyll *a*. By day 6, the car:chla ratio for both OP and PAB had declined and was a result of the relatively greater change in chlorophyll *a* concentration.

3.5. Morphological changes

There was no effect on cell size but changes in filament length were observed (Fig. 6a). At the start of the experi-

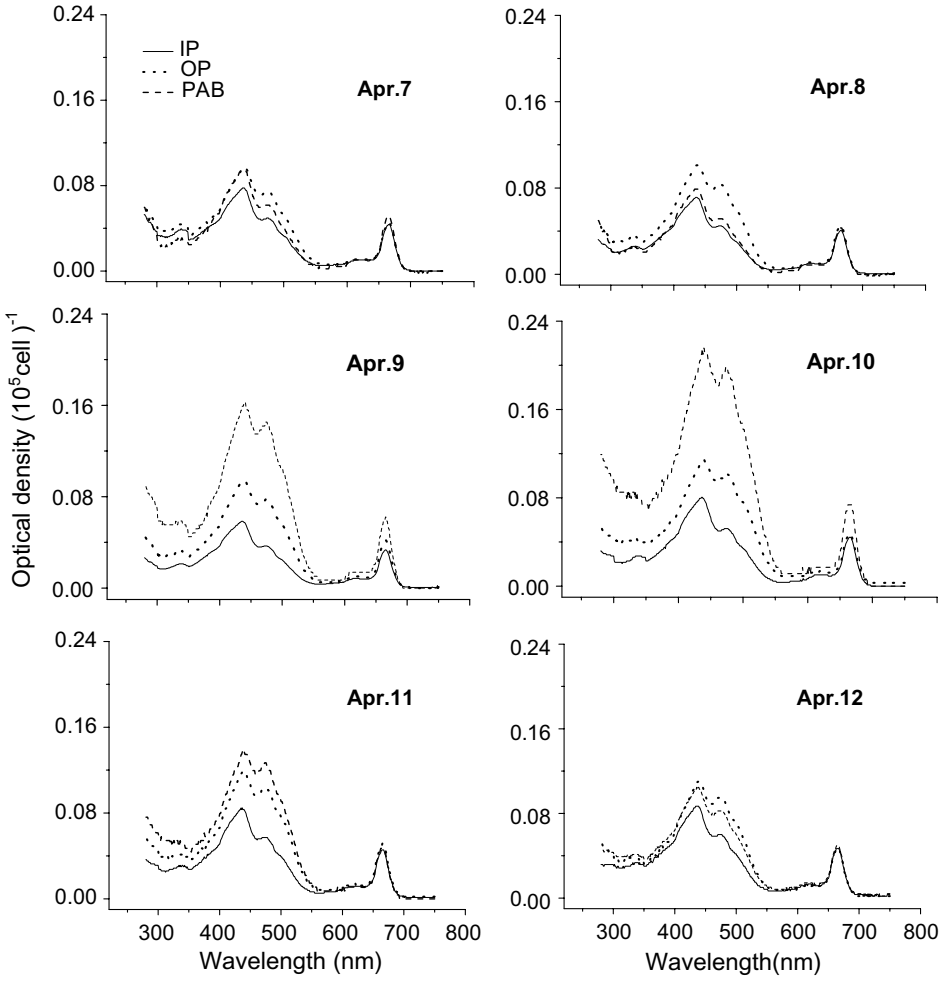

Fig. 4. Absorption spectra of the methanol-extracts of *Anabaena* sp. PCC7120 cells after exposure to indoor PAR supplied by fluorescent white light (IP), solar PAR radiation (OP) and solar PAR plus UV-A and B radiation (PAB). Note the negligible peaks (300–360 nm) for the UV-absorbing compounds.

ment, trichome lengths ranged from ca. 100 to 250 μm, with a mean of approximately 180 μm. Over the course of the experiment, the lengths of trichomes varied significantly with treatment and time of exposure ($P < 0.001$). By day 2, trichome length had decreased significantly ($P < 0.001$) in all treatments. A reduction in the length of filament was also evident for indoor cultures (IP) transferred from 25 to 70 μmol m^{-2} s^{-1} PAR. The lengths of trichomes in the cultures grown under OP and PAB were ca. 30% and 50% smaller ($P < 0.05$), respectively than IP grown cultures and, by day 4, the lengths of trichomes under PAB were significantly shorter (mean = 60 μm; $P < 0.05$) than those grown under OP and IP, which were of the same length (mean = 90 μm). On day 6 there was no significant difference ($P > 0.05$) between the three treatments (mean = 70 μm).

At the start of the experiment, the heterocyst frequency was about 1.0%, reflecting that cells were grown in a medium containing sufficient quantities of nitrogen. Heterocyst formation was induced in IP (irradiance of 70 μmol m^{-2} s^{-1}) and OP cultures but not PAB (Fig. 6b). Under the high solar PAR received by OP cultures on days 2 and 4, the heterocyst frequency (ca. 5%) was significantly higher ($P < 0.05$) than IP cultures (ca. 3%) and double contiguous heterocysts were formed (Fig. 6c). Under PAB the heterocyst frequency was about 0.9% and did not vary significantly ($P > 0.05$) with time.

4. Discussion

In view of the growth and photochemical yield, acclimation of the cells was faster under solar PAR than that under PAR + UVR, indicating chronic photoinhibition of cells in the presence of UVR characterized by degradation and restoration of PSII proteins [24,32,33]. However, by day 5 the maximum quantum yield of the cells exposed to UVR had recovered to their initial values, reflecting a change in the balance between damage and repair processes of the photosynthetic machinery [34,35].

The highest SGRs were obtained for cultures grown under high solar PAR alone, indicating that these levels of PAR did not negatively affect the growth; SGRs only declined, to values equivalent to those of the controls (IP), when solar PAR decreased during the final two days

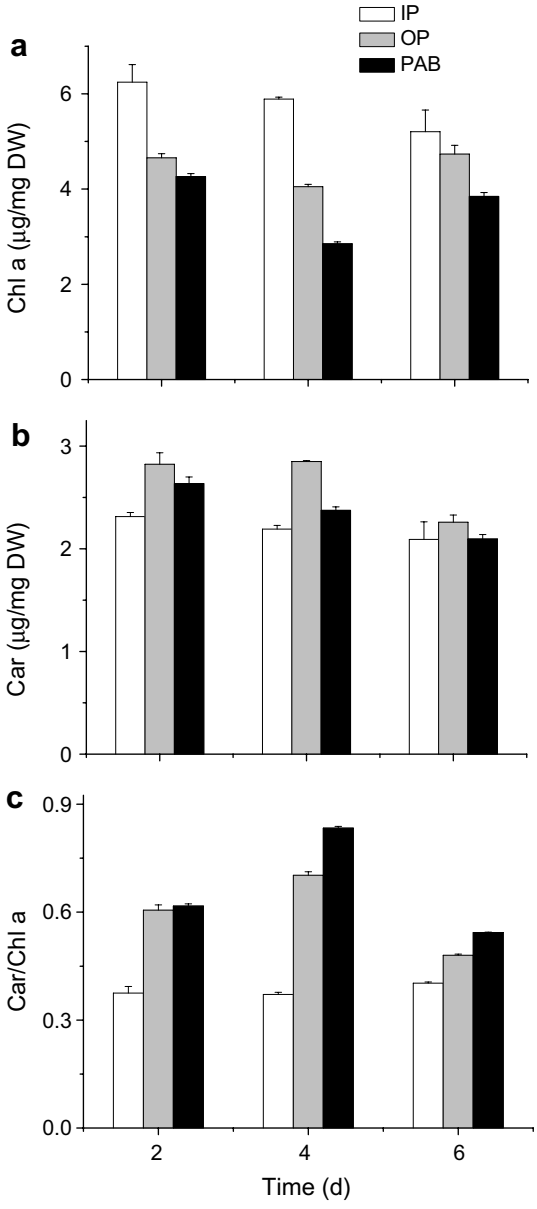

Fig. 5. The concentration of carotenoids (Car), chlorophyll *a* (Chl *a*) and the ratio of Car to Chl *a* in *Anabaena* sp. PCC7120 cells during a 6 d exposure period to indoor PAR supplied by fluorescent white light (IP), solar PAR radiation (OP) and solar PAR plus UV-A and B radiation (PAB). Data represent means ±95% confidence interval ($n = 4$). The initial concentrations of carotenoids and chlorophyll *a* were 2.2 and 5.8 μg mg^{-1} DW, respectively.

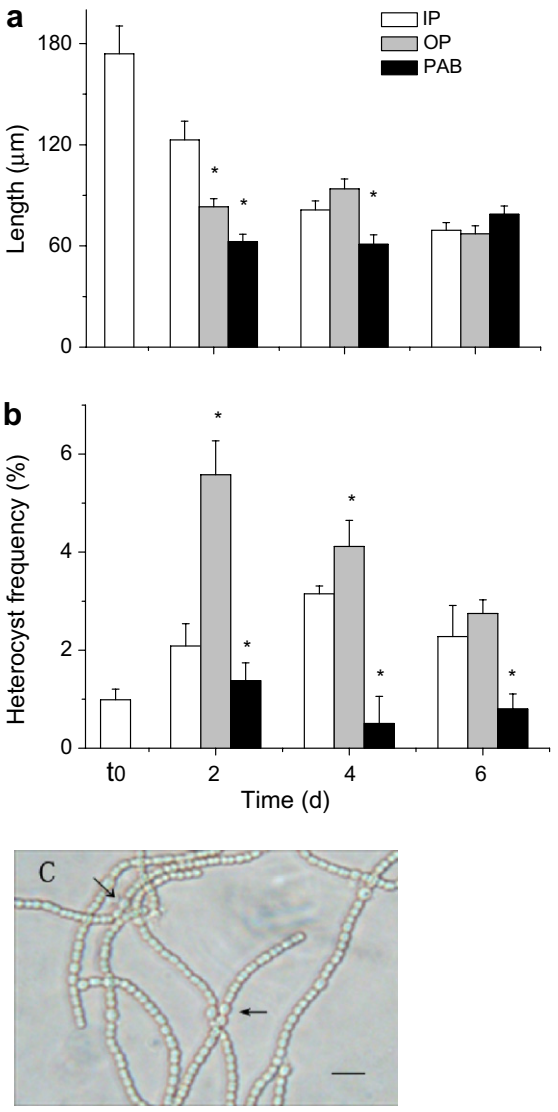

Fig. 6. The effect of solar radiation on trichome length (a) and heterocyst frequency (b) of *Anabaena* sp. PCC7120 during exposure to indoor PAR supplied by fluorescent white light (IP), solar PAR radiation (OP) and solar PAR plus UV-A and B radiation (PAB) over a 6 day exposure period. T_o represents the values at the start of the experiment. Photograph of contiguous heterocysts under OP. (C, Scal bar = 10 μm). Data in a and b represent means ±95% confidence interval ($n = 60$).

of the experiment as a consequence of increasing cloud cover. The negative SGRs after one day of exposure to PAR and UVR indicated a loss in cellular biomass due to lethal effect of UV-B and correlates with the very low levels of photosynthetic activity measured in these cultures. Despite the subsequent increase in SGRs of PAB cultures, the rates achieved did not match those of the controls (IP) untill day 5 when the solar radiation declined due to heavy overcast. While the lower growth rates under PAB are most likely due to reduced photosynthetic activity, it is also possible that a reduction in nitrogenase activity is responsible [14,19,36]. In our study very few heterocysts were observed in PAB cultures, as compared to those grown under solar PAR, suggesting that heterocyst formation and/or activation of the nitrogenase enzyme were hindered by the natural levels of solar UVR encountered during the experimental period.

Cyanobacteria have several defense mechanisms against high UVR exposure. One of the most common is the synthesis of UV-absorbing compounds, mainly mycosporine-like amino acids (MAAs) and scytonemin, which protect cells by screening out deleterious UVR. Sinha et al. [37] found that an *Anabeana* sp. isolated from a rice-field exposed to UVR (but not high PAR) produced one MAA that was identified as shinorine, whereas in another

Anabaena sp., also isolated from rice paddy fields, no such synthesis of MAAs was observed [38]. In the present study, negligible concentrations of UV-absorbing compounds were found in *Anabaena* sp. PCC7120 under all treatments and no synthesis was apparent in PAB cultures. Alternative measures to minimize the impact of UVR can be active. Carotenoid pigments have different physiological roles within cells. Some act as light-harvesting pigments transporting excitation energy to Chl *a* while others are protective agents quenching highly reactive singlet oxygen and dissipating excess excitation energy as heat under high irradiance [15,39]. Although specific carotenoids were not determined, our results indicate their protective function in *Anabaena* sp. PCC7120 grown under high solar PAR and PAR + UV-A + B. Under high PAR alone, the ratio of carotenoid to chlorophyll *a* concentrations increased due to an accumulation of carotenoids, and this provided sufficient protection to allow the rapid recovery of cellular functions. By contrast, in the PAB cultures, while there was an increase in carotenoid concentration by day 2 that provided some protection to the cells, by day 4 the observed increase in the ratio reflected the relatively greater loss in chlorophyll *a* rather than changes in carotenoid concentration. Therefore, under PAB it appeared that the cellular concentrations of carotenoids were inadequate to prevent the breakdown of chlorophyll *a* by the levels of UVR encountered in this study. UVR and high levels of PAR had similar but independent effects on increasing the carotenoid/chla ratio [40,41], which could be related to dynamic photosystem synthesis and deactivation [42]. On day 6, reduced solar radiation appears to have up-regulated chlorophyll a, thus resulting in a lower ratio of carotenoid to Chl *a*.

While physiological responses to UV radiation are well studied, little has been documented on morphological modifications caused by UVR [21]. Significantly shorter trichomes were found in cultures exposed to high solar radiation (OP and PAB), with those under PAR + UVR being the shortest. Both UVR and PAR at high levels can result in breakage of cyanobacterial filaments, with UV-B resulting in most of the breakage and spiral alteration [21]. By day 6 trichomes under PAB had increased in length to be the same as those in the other two treatments, probably due to the reduced levels of solar irradiances. The increased frequency of heterocysts under the high level of solar PAR may be a response to higher growth rates and the requirement for additional nitrogen to support growth under such conditions. Although the heterocyst frequency under IP condition also increased, the SGRs did not rise accordingly. Such a discrepancy from that of the outdoor conditions could be due to the difference in energy distribution between the indoor artificial and solar PAR waveband. Presence of UVR significantly reduced the frequency of heterocyst, reflecting an inhibitory effect on the differentiation of vegetative cells into heterocysts [19,41,43]. Ca^{2+} ions are intimately involved in heterocyst induction and differentiation [44], and UVR may have affected the calcium signaling, which then affected the expression of the key genes responsible for heterocyst differentiation [10]. The formation of contiguous heterocysts under solar PAR could be attributed to the inhibited expression of the Ca^{2+}-compounded protein (CcbP). Over-expression of CcbP hinders the differentiation while inhibited expression of it enhanced the formation of contiguous heterocysts [44].

5. Abbreviations

IP	indoor PAR
OP	outdoor PAR
PAB	PAR+UV−A+UV−B
PAR (P)	photosynthetically active radiation (400–700 nm)
$\Delta F/F_m$	maximum photochemical quantum yield
UV-A	ultraviolet A (315–400 nm)
UV-B	ultraviolet B (280–315 nm)
UVR	ultraviolet radiation (280–400 nm)

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