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Differential responses of *Nostoc sphaeroides* and *Arthrospira platensis* to solar ultraviolet radiation exposure

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Abstract

During October to December 2003 we carried out experiments to assess the impact of high solar radiation levels (as normally occurring in a tropical region of Southern China) on the cyanobacteria *Nostoc sphaeroides* and *Arthrospira (Spirulina) platensis*. Two types of experiments were done: a) Short-term (i.e., 20 min) oxygen production of samples exposed to two radiation treatments (i.e., PAR+UVR—280–700 nm, and PAR only—400–700 nm, PAB and P treatments, respectively), and b) Long-term (i.e., 12 days) evaluation of photosynthetic quantum yield (Y) of samples exposed to three radiation treatments (i.e., PAB; PA (PAR+UV-A, 320–700 nm) and P treatments, respectively). *N. sphaeroides* was resistant to UVR, with no significant differences ($P > 0.05$) in oxygen production within 20 min of exposure, but with a slight inhibition of Y within hours. A fast recovery of Y was observed after one day even in samples exposed to full solar radiation. *A. platensis*, on the other hand, was very sensitive to solar radiation (mainly to UV-B), as determined by oxygen production and Y measurements. *A. platensis* had a circadian rhythm of photosynthetic inhibition, and during the first six days of exposure to solar radiation, it varied between 80 and 100% at local noon, but cells recovered significantly during afternoon hours. There was a significant decrease in photosynthetic inhibition after the first week of exposure with values less than 50% at local noon in samples receiving full solar radiation. Samples exposed to PA and P treatments recovered much faster (within 2–3 days), and there were no significant differences in Y between the three radiation treatments when irradiance was low (late afternoon to early morning). Long-term acclimation seems to be important in *A. platensis* to cope with high UVR levels however, it is not attained through the synthesis of UV-absorbing compounds but it seems to be mostly related to adaptive morphological changes.

Abbreviations: Fm, Maximal fluorescence in dark-adapted cells (all reaction centers are closed); Fo, Initial chlorophyll fluorescence in dark-adapted cells (all reaction centers are open); Fv, Variable fluorescence (=Fm-Fo); Fo', Fm' and Fv': The same for light-adapted state; Ft, Current fluorescence of light-adapted cells; PAR, Photosynthetic Active radiation (400–700 nm); UV-A, Ultraviolet-A radiation (315–400 nm); UV-B, Ultraviolet-B radiation (280–315 nm); UVR, Ultraviolet radiation (280–400 nm); Y, Fv'/Fm': Quantum yield (Genty-parameter).

Introduction

Cyanobacteria are cosmopolitan organisms that have colonized a variety of aquatic and terrestrial environments—ocean, lakes, rivers and various terrestrial soils (Garcia-Pichel, 1998). Furthermore, they dominate microbial communities in extreme places of the Earth such as hot springs, Antarctic ice shelves

and deserts (Ehling-Schulz & Scherer, 1999), and they also form symbiotic associations with several organisms. Cyanobacteria play a very important role within ecosystems, such as in successional processes, global biomass production and nutrient cycling (Sinha & Häder, 1996).

As photosynthetic prokaryotes, cyanobacteria rely on solar radiation, mainly on the portion of the electromagnetic spectrum corresponding to visible wavelengths (Photosynthetic Active Radiation, PAR: 400–700 nm) as their main source of energy. However, they might be potentially threatened by solar ultraviolet radiation (UVR, 280–400 nm), especially by the very energetic waveband of UV-B (280–315 nm). In fact, numerous studies carried out with these organisms have shown that growth, survival, pigmentation, nitrogen fixation, carbon uptake and membrane permeability are severely affected by UVR (Ehling-Schulz & Scherer, 1999), (Sinha et al., 2001a). However, cyanobacteria have also developed a number of mechanisms to minimize the deleterious effects caused by UVR. They include the synthesis of protective substances such as mycosporine like amino acids (MAAs) or scytonemin (Banaszak, 2003), induction of "shock" proteins (Sass et al., 1997), carotenoids and scavenging enzymes, e.g. superoxide dismutase, SOD (Miyake et al., 1991), (Quesada & Vincent, 1997). Furthermore, cyanobacteria also possess the ability to migrate to avoid hazardous UVR wavelengths (Quesada & Vincent, 1997) as well as an active photorepair capacity—mainly through photoreactivation and excision repair mechanisms (Eker et al., 1990).

The aim of this study was to evaluate the responses to solar UVR of two cyanobacteria of commercial interest–*Nostoc sphaeroides* and *Arthrospira platensis*. *N. sphaeroides*, also known as Ge-Xian-Mi, is a species that develops from hormogonia and forms dark green / pearl-shaped colonies up to 2.5 cm in diameter (Gao & Ai, 2004); this organism is usually found in rice fields in China and it has been used as food delicacy for long time (Qiu et al., 2002). *A. platensis* (commercially known as *Spirulina platensis*), is a filamentous cyanobacterium that has been isolated from a wide range of habitats (Vonshak & Tomaselli, 2000) and it is commercially cultivated outdoor as a source of proteins and pharmaceuticals (Vonshak, 1990). The basic approach used in our study was to evaluate the impact of UVR on the photosynthetic quantum yield during long -term incubations (i.e., several days), with additional measurements/determinations of oxygen evolution and morphology structure. The implications of our work are twofold: On the one hand, we gain new insights on the autoecology of these cyanobacteria species, especially concerning some photobiological aspects and, on the other hand, we present results that can be of application for cultivation in outdoor conditions.

Materials and methods

Culture of specimens/study site

Monospecific cultures of the cyanobacteria *Nostoc sphaeroides* Kützing and *Arthrospira* (*Spirulina*) *platensis* (Nordst.) Gomont (strain 439) were obtained from the Freshwater Algae Culture Collection of the Institute of Hydrobiology, the Chinese Academy of Sciences. Cells of *N. sphaeroides* and *A. platensis* were maintained in BG11 (Stanier et al., 1971) and Zarrouk (Zarrouk, 1966) media, respectively, in a temperature-controlled incubator (LRG-250-G, Zhujiang, Guangdong, China) at 23°C, receiving 90 μmol m^{-2} s^{-1} of PAR irradiance, with a photoperiod 12 L:12 D. Experiments to evaluate the effects of solar UVR on *N. sphaeroides* and *A. platensis* were carried out during fall (October–December 2003) at the Institute of Marine Biology, Shantou University, Shantou (23.3 °N, 116.6 °E), China.

Experimentation

When cells reached the exponential growth phase they were diluted (1:4) and transferred to 4 l quartz tubes and exposed to solar radiation (with continuous bubbling of ambient air) under three radiation treatments (duplicate samples for each treatment): (1) cultures that received full radiation (UVR and PAR)—uncovered quartz tubes (PAB treatment); (2) cultures that received UV-A and PAR—tubes covered with UV cut-off filter foil (Montagefolie N° 10155099, Folex—50% transmission at 320 nm) (PA treatment); and (3) cultures that received only PAR—containers covered with Ultraphan film (UV Opak, Digefra, Munich, Germany—50% transmission at 395 nm) (P treatment). The spectra of the materials used in our experiments are published elsewhere (Figueroa et al., 1997). The tubes containing the cultures were placed in a water bath with running water for temperature control (22°C ± 2) for twelve days to assess the responses of species and their potential acclimation to UVR. In addition to continuous measurements of photosynthetic quantum yield we also determined, at the beginning of this

long-term experiment, oxygen evolution and other parameters such as chlorophyll-*a* (chl *a*), UV-absorbing compounds and number of cells/morphological structure as described below.

Analyses and measurements

(a) Photosynthetic quantum yield: A portable pulse amplitude modulated fluorometer (Hansatech Instruments model PEA, Norfolk, England) was used to determine *in vivo* chlorophyll fluorescence (Schreiber et al., 1986); this instrument determines fluorescence signals from chl *a* in the photosystem II (PSII). The overall photosynthetic quantum yield (Y) was calculated using the equations of Genty et al. (1989) and Weis and Berry (1987), as:

$$Y = (Fm' - Ft)/Fm' = Fv'/Fm'$$

where Fm' is the maximal fluorescence induced by a saturating white light pulse, and Ft the current steady state fluorescence induced by weak red light in light-adapted cells. The optimal quantum yield was measured in dark-adapted cells, where Fm is the maximal fluorescence induced by a saturating pulse and Fo the ground fluorescence induced by a weak red background light. Ten measurements were done in each sample at three times during the day (i.e., 8 a.m., local noon, and 5 p.m.).

(b) Oxygen evolution: At the beginning of the long-term experiment, and when cultures reached the exponential growth phase, sub-samples were transferred (during the light period) to an oxymeter (Real Time Computer Inc., model Oxym 5). The instrument has five 20 mL quartz tubes inside of an acrylic UV transparent chamber with circulating water as temperature control. Five oxygen microelectrodes (Yellow Spring Instruments Co., model 5331) were attached to the quartz tubes. To test the effects of solar UVR on oxygen production, the samples were incubated under two radiation treatments: PAB treatment (as above)-triplicate samples and, P treatment (as above) - duplicate samples. The oxymeter containing the samples was then exposed to natural radiation during 20 min (around local noon), and data from the five oxygen sensors, together with temperature and PAR irradiance, were acquired every two seconds and recorded in a laptop computer.

(c) Chlorophyll-a (chl *a*) and UV-absorbing compounds: Chl *a* and UV-absorbing compounds were measured by filtering a variable volume of sample (5–10 ml) onto a Whatman GF/F glass fiber filter (25 mm), followed by extraction with absolute methanol (Holm-Hansen & Riemann, 1978) for 2 h and subsequent determination of the optical density (O.D.) in a scanning (250–700 nm) spectrophotometer (Shimadzu UV 2501-PC). Chl *a* concentration was calculated from the O.D. using the equation of Wellburn (1994) whereas the concentration of UV-absorbing compounds was estimated from the peak height at 334 nm (Dunlap et al., 1995).

(d) Enumeration of cells/morphological changes: Enumeration of cells was done under a compound microscope (Zeiss Axioplan 2, Carl Zeiss Germany) using a 1 mL Sedwick-Rafter chamber and following the methodology described in Villafañe and Reid (1995). Digital images, to record morphological changes at the end of the experiments, were obtained using a CCD Hi-Res camera (DSP® Color Camera) attached to the microscope and the data were analyzed using image analysis software (WinTrack®, Real Time Computer Inc., Germany).

(e) Measurements of solar radiation: Incident solar radiation was continuously measured using a filter radiometer (ELDONET, Real Time Computers, Inc., Germany) which was installed on the roof of the Institute of Marine Biology (Shantou University). The instrument records irradiance in the UV-B (280–315 nm), UV-A (315–400 nm) and PAR (400–700 nm) wavebands with a frequency of one datum per minute.

(f) Statistics: Data were reported as the mean and standard deviation for the different measurements. For the calculations of photosynthetic quantum yield, a total of 20 measurements per sample were used. For oxygen evolution, we averaged 20 seconds intervals ($n = 10$) and we used these values in the calculations. The experiments were repeated twice. The Kruskal-Wallis non-parametric test (Zar, 1984) was used to establish differences between radiation treatments (confidence level = 0.05) during determination of oxygen production and photosynthetic quantum yield.

Results

Atmospheric conditions

Incident solar radiation during the period October 18 to December 14, 2003 is shown in Figure 1. There was a day-to-day variability in daily doses due to cloud cover, with maximum values of 8,000 KJ m^{-2}, 1,200 KJ m^{-2} and 27 KJ m^{-2} for PAR, UV-A and UV-B, respectively (Figures 1A–C). Despite this variability,

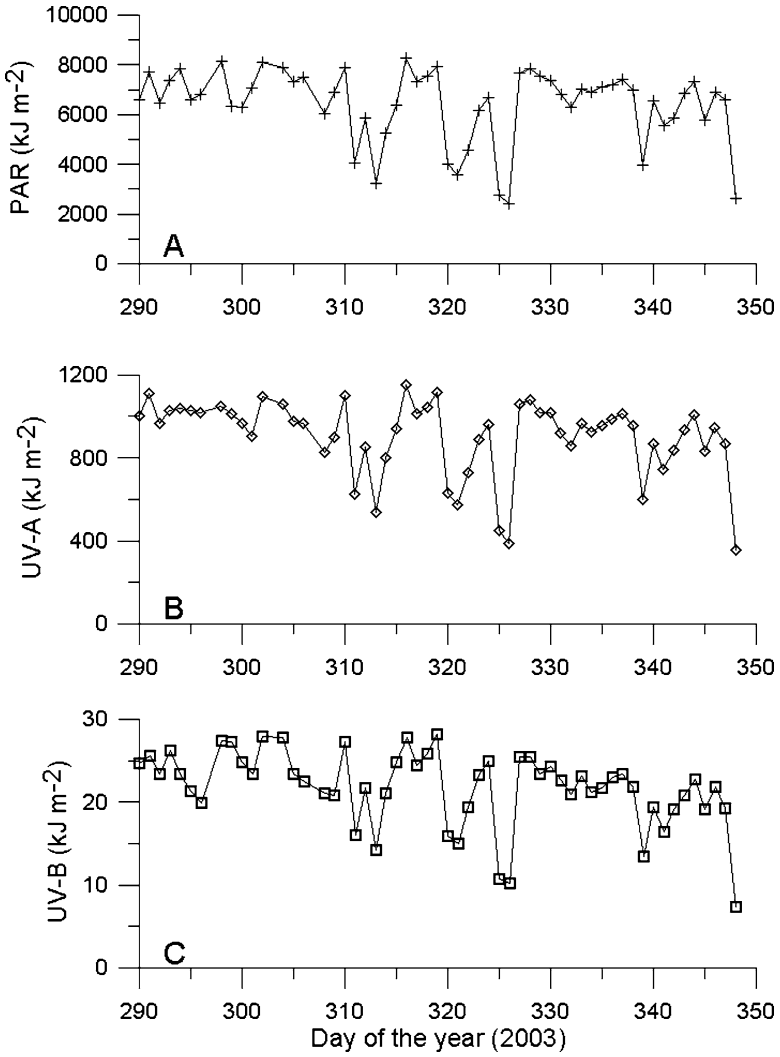

Figure 1. Radiation conditions for the period October 16 to December 14, 2003 over the study area in Shantou, China. Daily doses of: **A**) PAR, 400–700 nm (in kJ m^{-2}); **B**) UV-A, 315–400 nm (in kJ m^{-2}) and **C**) UV-B, 280–315 nm (in kJ m^{-2}).

there was a trend of decreasing values towards winter, with the lowest registered in November—December (i.e., 2,000, 400 and 7–10 KJ m^{-2} for PAR, UV-A and UV-B, respectively, Figures 1A–C). During the study period, mean ozone column concentration above Shantou was 245 Dobson Units (data from http://jwocky.gsfc.nasa.gov).

Short-term experiments

Oxygen concentration in *N. sphaeroides* at the beginning of the long-term experiment (i.e., when cells were transferred from the culture chamber to outdoor conditions) had a significant increase from a mean value of 8.9 to 10.3 mg l^{-1} (Figure 2). The mean irradiance levels received by the samples during the 20 min exposure were 323, 53.1 and 1.3 W m^{-2} for PAR, UV-A and UV-B, respectively. No significant differences ($P > 0.05$) were detected in dissolved oxygen values between radiation treatments during the 20 min exposure to solar radiation. The net mean oxygen production during the experiment was 0.066 and 0.074 mg O_2 l^{-1} min^{-1}, for PAB and P treatments, respectively.

Oxygen evolution in *A. platensis*, when exposed to solar radiation, was significantly different ($P < 0.05$) between radiation treatments (Figure 3). The mean irradiances received during the incubation period were 328, 63.9, and 1.5 W m^{-2} for PAR, UV-A and UV-B, respectively. Variability in oxygen evolution throughout the experiment was most probably related to changes

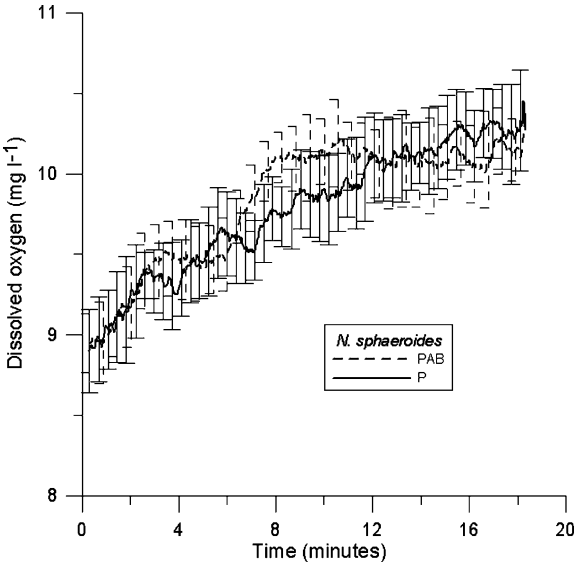

Figure 2. Mean dissolved O_2 concentration (in mg O_2 l^{-1}) for *Nostoc sphaeroides* as a function of time (in min) during a short-term exposure to solar radiation. The solid lines indicate samples exposed to PAR only (P treatment), whereas the broken lines indicate samples exposed to full radiation (PAB treatment). The thin lines represent one standard deviation.

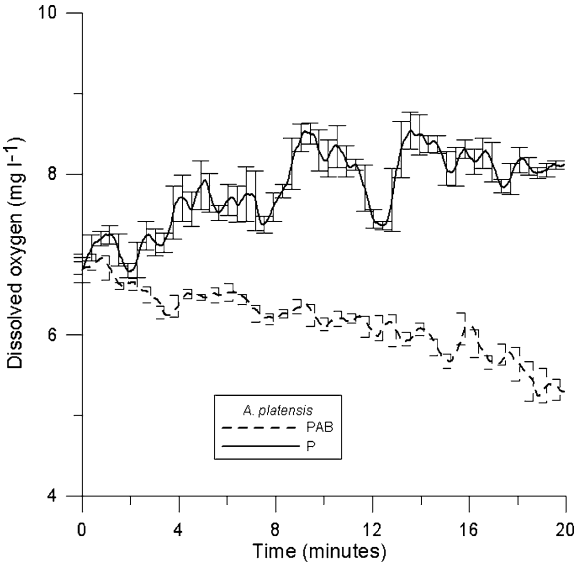

Figure 3. Mean dissolved O_2 concentration (in mg O_2 L^{-1}) for *Arthrospira platensis* as a function of time (in min) during a short-term exposure to solar radiation. The solid lines indicate samples exposed to PAR only (P treatment), whereas the broken lines indicate samples exposed to full radiation (PAB treatment). The thin lines represent one standard deviation.

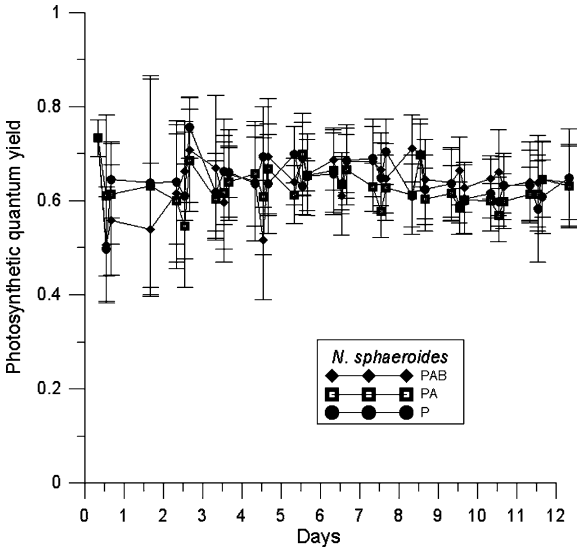

Figure 4. Photosynthetic quantum yield in *Nostoc sphaeroides* exposed to solar radiation during 12 days with incubations starting October 27. The samples were exposed to three radiation treatments—PAB, PA, and P. The lines indicate one standard deviation.

in irradiance conditions due to differences in cloud cover. However, there was a clear trend of oxygen consumption (i.e., from an initial value of 7 mg L^{-1} to 5.8 mg L^{-1} at the end of 20 min exposure) in cells exposed to full solar radiation. Cells receiving only PAR however, had a significant oxygen production from 7 mg L^{-1} to 8.2 mg L^{-1}. The net oxygen production was 0.062 mg O_2 L^{-1} min^{-1} in the P treatment; whereas the net oxygen consumption in the PAB treatment was 0.064 mg O_2 L^{-1} min^{-1}.

Long-term experiments

Photosynthetic quantum yield (Y) in *N. sphaeroides* cells during the 12-days incubation period under solar radiation (Figure 4) did not show significant differences ($P > 0.05$) between radiation treatments at any time. Daily variability was evident (especially during the first week of experimentation), with relatively low Y values at midday and higher ones during the morning and afternoon hours; nevertheless these differences were not significant ($P > 0.05$). Moreover, the responses of *N. sphaeroides* seemed to be associated to high PAR levels rather than to UVR stress (Figure 4).

Variability of photosynthetic quantum yield in *A. platensis* throughout the 12-day experiment is shown in Figure 5. In the three radiation treatments, there was an initial sharp decrease in Y values, from 0.55 to almost

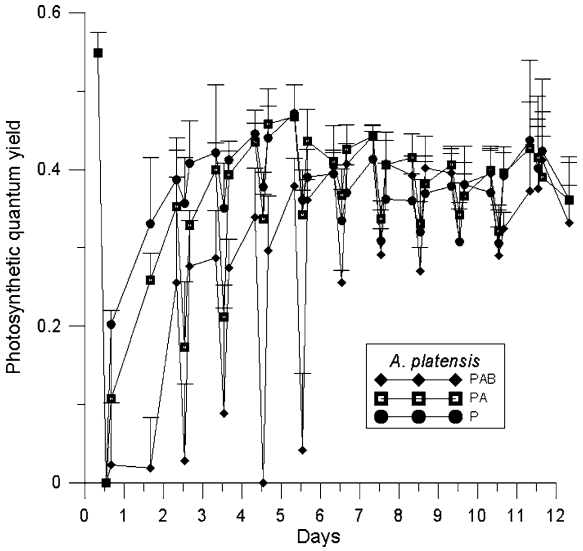

Figure 5. Photosynthetic quantum yield in *Arthrospira platensis* exposed to solar radiation during 12 days with incubations starting October 15. The samples were exposed to three radiation treatments—PAB, PA, and P. The lines indicate one standard deviation.

zero at local noon after the samples being transferred to outdoor conditions. After this initial shock, *A. platensis* cells partially recovered, although the recovering dynamics was different in the three radiation treatments, with cells exposed to full solar radiation displaying higher daily variability as compared to those under the PA and P treatments. In the PAB treatment, Y remained very low (almost 0) during the first two days of experimentation. The culture however, slowly recovered by morning of the third day having a Y value of ∼0.25, but still a significant noon depression was observed ($Y < 0.1$). After five days of exposure to solar radiation, cells attained Y values of ∼0.4–0.44 at morning / afternoon, whereas noon values were still inhibited (Y varying between 0.25 and 0.3). These noon values however, were significantly higher than those measured at noon in the previous 6 days. Cells in the PA treatment had a comparatively faster recovery dynamics, with Y values rapidly increasing after the initial shock at day 1 (i.e., when *A. platensis* cells were exposed to ambient solar radiation). Noon Y values were 0.16–0.2 at days 2 and 3, respectively but, after that, they remained around a mean of 0.35. Maximum Y (i.e., 0.45) was attained at days 4 and 5 but, overall, Y values were 0.4 throughout the experiment. Finally, *A. platensis* cells exposed only to visible radiation had a much faster recovery dynamics as compared to those receiving UVR wavelengths. The cells reached maximum values (i.e., 0.45–0.47) at days 4 and 5 but then, Y oscillated around a mean of 0.35; midday values were always in the order of 0.3–0.35 after two days of experimentation. Although recovery was observed at different stages of the experimentation, Y at the end of the experiment (day 12) was significantly lower ($P < 0.05$) than that registered at t_0, but 20–30% of inhibition was still observed. It should be noticed that the impact of solar radiation during the first week of experimentation was also evident in growth rates, with μ values of 0.3 and 0.33 for samples exposed in the PAB and PA treatments, respectively, whereas samples exposed to PAR only had a μ of 0.51.

Spectral characteristics of N. sphaeroides *and* A. platensis

The spectral characteristics of *N. sphaeroides* and *A. platensis* at the beginning and at the end of the long-term experiment are shown in Figure 6. There was a slight increase (but not significant) in the concentration of UV-absorbing compounds ($\lambda_{max} = 337$ nm)

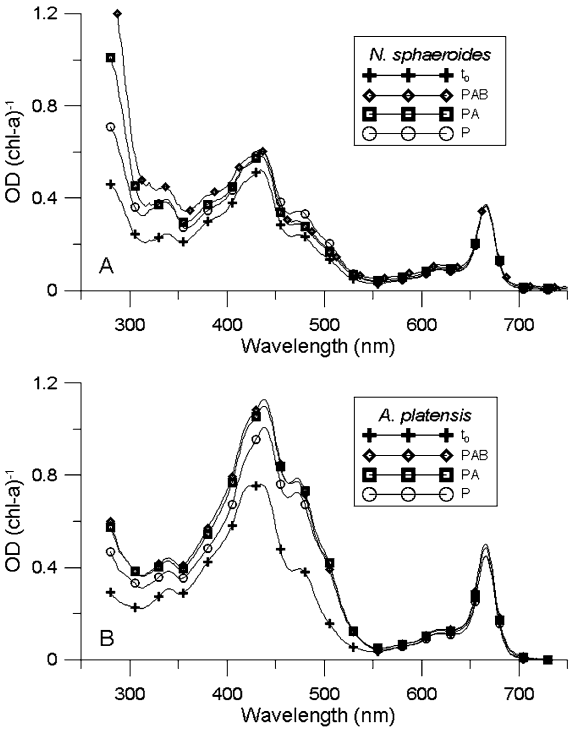

Figure 6. Spectral absorption characteristics (O.D. chl^{-1}) of *Nostoc sphaeroides* (**A**) and of *Arthrospira platensis* (**B**) as a function of wavelength at the beginning and at the end of the long-term incubation period.

in *N. sphaeroides* (Figure 6A) after 12 days of exposure to solar radiation; however, no differences between radiation treatments were observed. In *A. platensis* (Figure 6B), the concentration of UV-absorbing compounds also increased slightly (but not significantly) from t_0 towards the end of the experiment. On the other hand, the concentration of carotenoids increased in all radiation treatments from the t_0 value towards the end of the experiment.

Discussion

Cyanobacteria display different degrees of sensitivity towards solar radiation, as seen in studies conducted with specimens collected from a variety of environments (Quesada & Vincent, 1997; Sinha et al., 2001a). One of the most common effects caused by both PAR and UVR is the reduction of photosynthetic rates, i.e., photoinhibition (Osmond, 1994). Photoinhibition occurs in most autotrophic organisms—higher terrestrial plants (Caldwell et al., 1995), macroalgae (Hanelt, 1996), phytoplankton (Marwood et al., 2000); (Sobrino et al., 2004), and cyanobacteria (Sinha et al., 2003). Chronic photoinhibition is due to the degradation of D1 protein of the photosystem II, whereas dynamic photoinhibition is commonly thought as a protective mechanism by which organisms thermally dissipate excess energy and thus prevent photodamage (Hanelt, 1996). In general, the degree of photoinhibition depends on several variables, including the differential sensitivity of species, as well as the radiation levels impinging the cells. For comparative purposes with the work carried out with related *Nostoc* species (Sinha et al., 2003), it should be mentioned that in our tropical study site in southern China, both PAR and UVR levels were higher (2 to 5 times, respectively) than those registered in a temperate marine location in Patagonia (Villafañe et al., 2004) at comparable times of the year. Thus, our study site offered a unique opportunity to evaluate the sensitivity of *Nostoc sphaeroides* and *Arthrospira platensis*, as these organisms were exposed to extreme radiation levels, as also seen in other studies conducted in the area (Villafañe et al., 2005).

Our data clearly stress the differential sensitivity of *N. sphaeroides* and *A. platensis* when exposed to similar experimental radiation conditions, as seen in both oxygen evolution (Figures 2 and 3) and photosynthetic quantum yield (Figures 4 and 5). In general, the responses of *N. sphaeroides* suggest that this species is highly resistant to UVR, and moreover, the small (although not significant) daily pattern of low Y values at noon hints for a dynamic rather than chronic photoinhibition of the photosystem II. This pattern has also been observed in field experiments conducted with macroalgae from different parts of the World (Franklin & Forster, 1997). On the other hand, our results on the acclimation to UVR of *N. sphaeroides* are different from those obtained with a related species, i.e., *N. commune*, that reported a high sensitivity of this species due to a complex combination of induction and repression of a large number of proteins (Ehling-Schulz & Scherer, 1999).

A. platensis, comparatively, was very sensitive and within minutes it was inhibited, showing a decrease in oxygen concentration (Figure 3) that was most probably related to a direct impact of UVR on photosystem II and thus to a decrease in the electron transport rate. This species however, had partial acclimation after about a week of exposure to solar radiation, resulting in a decrease in the observed inhibition (Figure 5). *A. platensis* also showed a daily pattern, with significantly low Y values at local noon, but relatively high during early morning and late afternoon (Figure 5). This circadian rhythm was also observed in previous studies (Lu & Vonshak, 1999); in those experiments however, the authors exposed the samples only to PAR, and they determined a complete recovery at the end of the day. In our case however, and although our results do suggest dynamic inhibition, the recovery was not complete as the cells did not attain the original (i.e. t_0) Y value, and 20–30% inhibition was still determined at the end of the experiments. This clearly hints to some chronic photodamage to the photosynthetic apparatus; in fact, chronic photodamage in membranes and in the DNA molecule was also demonstrated for other cyanobacteria species (Ehling-Schulz & Scherer, 1999). In particular, studies have shown that prolonged exposure of *A. platensis* cells to moderate levels of UV-B affects the chlorophyll a-protein complex and alters the fluorescence emission spectral profile of the pigment-protein complexes of the thylakoid membranes (Rajagopal et al., 2000). Moreover, phycobilisomes effectively act as targets for UV-B-induced damage of photosynthetic apparatus in this cyanobacterium (Rajagopal et al., 1998).

The differential responses to solar radiation between the two species studied can be related to a number of variables. Part of the differences in the inhibition of photosynthetic quantum yield might be associated to different nutrient conditions, resulting from the use of different culture media combined to the variable uptake capacity of each species, as seen in studies carried

with Rhodophyta species (Korbee Peinado et al., 2004). Furthermore, differential damage/repair ratios might also account for part of the observed variability in responses, as this is related to the size and morphology of each species. *N. sphaeroides* colonies form rounded structures up to 2.5 cm in diameter (Gao & Ai, 2004) whereas *A. platensis* (i.e., this strain) forms a helicoideal colony with a up to 12 helices. Wu et al. (Wu et al., 2005) working with two different strains of *A. platensis* found that exposure to solar radiation resulted in a compression of the helix, with a decrease in the trichome length from 1.2 mm to ca. 0.3 and 0.8 mm in samples exposed to UV-A+PAR and PAR only, respectively. This minimum trichome length under UV-A was observed after 4–5 days of exposure to solar radiation. These authors also showed that self-shading, due to this compression, resulted indeed in an effective protection against high levels of solar radiation, at least during short-term experiments (<1 day). We lack of detailed information on morphological changes (i.e. every day) on our experiments but nevertheless, large amount of data was acquired in parallel experiments conducted by our group and they were reported elsewhere (Wu et al., 2005). However, image analyses observations (data not shown) collected at t_0 and at the end of the experiments further support the findings of Wu et al. (Wu et al., 2005), with morphological changes in *A. platensis* being UVR-dependent.

On the other hand, no significant changes were observed in the morphology of *N. sphaeroides* throughout the experiment and when exposed to different radiation treatments (data not shown). For this species, it can be also be speculated that given its spherical structure there would be a differential sensitivity/damage between the outer and inner cells so that self-shading would result in an overall good performance of the colony at expenses of the outer cells as seen in studies conducted by Garcia-Pichel (Garcia-Pichel, 1994). We did not notice, however, a visual deterioration or bleaching of the outer part of the colony, but detailed microscopic separation and further analysis of different parts of the colony should be done in the future to address this point.

Another potential mechanism found in cyanobacteria to acclimate to solar radiation is through the synthesis of UVR absorbing compounds such as MAAs or scytonemin that have been reported to be widely distributed within this group (Banaszak, 2003). In our experiments we did not find a significant increase of these compounds in any of the species studied after exposure to solar radiation (Figure 6). Moreover, our data also agree with previous studies (Wu et al., 2005) that did not find a significant increase of UV-absorbing compounds in two strains of *A. platensis*. However, they contrast with other results (Sinha et al., 2001b) that found a high induction of mycosporine like amino acids (MAAs) in *Nostoc commune* after three days of exposure to solar radiation, even under comparatively lower irradiances. However, we lack of high performance liquid chromatography (HPLC) data to identify the small peaks of UV-absorbing compounds observed in Figure 6 with maximum absorption between 310 and 360 nm.

Our data clearly point out at the differential response between the two cyanobacteria studied - a highly resistant one (*N. sphaeroides*) and one sensitive (*A. platensis*). However, *A. platensis* was able to acclimate and to partially cope with solar UVR during the long-term exposure. Morphological changes seem to play a role in the acclimation of this cyanobacterium and might explain, at least in part, the variability observed in the photoinhibition due to UVR. Further studies should evaluate to what extent morphological changes of the helix in *A. platensis* or the spherical structure of *N. sphaeroides* would protect the DNA molecule, and/or might influence the rate of damage/repair.

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