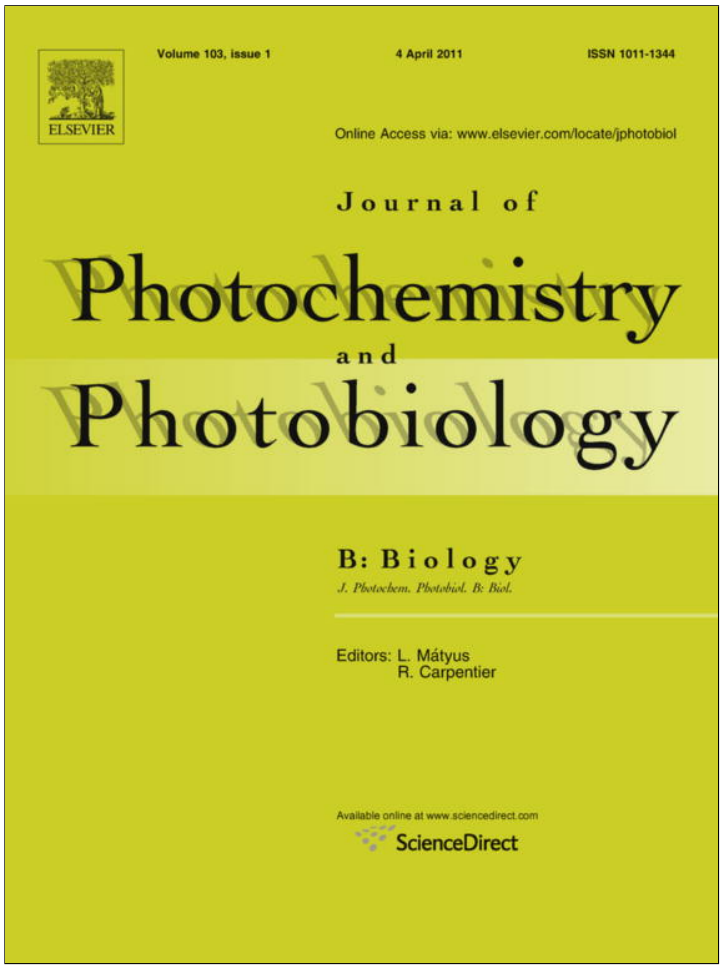

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Influence of temperature and UVR on photosynthesis and morphology of four species of cyanobacteria

M. Valeria Fiorda Giordanino [a,b], Sebastian M. Strauch [a], Virginia E. Villafañe [a,b], E. Walter Helbling [a,b,*]

[a] Estación de Fotobiología Playa Unión, Casilla de Correos No. 15 (9103) Rawson, Chubut, Argentina
[b] Consejo Nacional de Investigaciones Científicas y Técnicas, Argentina

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ABSTRACT

During the late austral spring of 2009 we carried out experiments (4 days of duration) with four cyanobacteria species, *Anabaena* sp., *Nostoc* sp., *Arthrospira platensis* and *Microcystis* sp., to assess the combined effects of temperature and solar radiation on photosynthesis performance and morphology. Two experimental temperatures (18 °C and 23 °C, simulating a 5 °C increase under a scenario of climate change) and three radiation treatments (by using different filters/materials) were implemented: (*i*) P (PAR, 400–700 nm), (*ii*) PA (PAR + UV-A, 320–700 nm) and, (*iii*) PAB (PAR + UV-A + UV-B, 280–700 nm). In general, samples under the P treatment had less decrease/higher recovery rates of effective photochemical quantum yield (*Y*) than those receiving UV-A or UV-A + UV-B. The effects of increased temperature were species-specific: At the end of the experiments, it was seen that increased temperature benefited photosynthetic performance of *Anabaena* sp. and *Nostoc* sp. but not of *Microcystis* sp. and *A. platensis*. Higher temperature was also associated to an increase in the chain area of *Anabaena* sp., and to bigger trichomes in *A. platensis*; however, no morphological effects were observed in *Microcystis* sp. In addition, in *Nostoc* sp. the increase in temperature counteracted the UVR impact on the reduction of the chain area. How these effects and mechanisms will affect the trophodynamics and production of aquatic ecosystems is still uncertain, but the specificity of the responses suggests that not all cyanobacteria would be equally benefited by temperature increases therefore affecting the balance and interaction among species in the water column.

1. Introduction

Climate change is known to affect directly and indirectly both the structure and function of aquatic ecosystems [1,2]. While climate change is a very complex process, forcing mechanisms mainly include changes in solar radiation and temperature [3]. Thus, great efforts have been put to assess the impact on diverse organisms of both solar ultraviolet radiation (UVR, 280–400 nm) – especially increased UV-B (280–315 nm) due to the depletion of the ozone layer – and global warming due to the input of greenhouse gases [4–6].

Cyanobacteria are the largest and most widely distributed group of prokaryotic organisms that have colonized a variety of aquatic and terrestrial ecosystems [7]. Some cyanobacteria species have symbiotic associations with several organisms [8], others form massive blooms, and some others produce toxins [7]. Moreover, cyanobacteria are the only known oxygenic phototrophs capable of fixing atmospheric nitrogen [9]. Therefore, there has been an obvious interest in evaluating the impact of climate change variables on these ecologically relevant organisms. UVR is currently considered an stressor for aquatic organisms even under its normal levels (see review of Helbling and Zagarese [10]) and for cyanobacteria in particular, it has been shown that it causes inhibition of photosynthesis [11,12], DNA damage [13], pigments photobleaching [14] and morphological changes [12], among other effects. However, cyanobacteria have developed a suite of mechanisms to avoid or minimize UVR stress which include vertical migration [15] or synthesis of protecting compounds such as carotenoids, mycosporine like aminoacids (MAAs) or scytonemines [13], or proteins [16] and some repairing enzymes [17]. In relation to increased temperature, it seems that it favors the dominance of cyanobacteria [7] as already observed in lakes of the Northern Hemisphere [18,19].

In general, most studies dealing with the effects on cyanobacteria of these variables associated to climate change have considered one variable at a time. Indeed, and for these organisms, very little is known about the interactive effects of UVR and temperature that may act synergic or antagonistically [20]. In this sense, Roos and Vincent [21], working with Antarctic cyanobacteria, found that UVR-induced inhibition of growth increased linearly with

* Corresponding author at: Estación de Fotobiología Playa Unión, Casilla de Correos No. 15 (9103) Rawson, Chubut, Argentina. Tel.: +54 2965 498019.
E-mail address: whelbling@efpu.org.ar (E.W. Helbling).

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decreasing temperature, whereas there was no apparent effect of temperature on the magnitude of UVR-induced photoinhibition; Gao et al. [22] found that increased temperature benefited *Arthorspira platensis* cells that were damaged by exposure to UVR. Therefore, and with the aim of gaining knowledge on the combined effects of temperature and UVR on photosynthesis and morphology, here we carried out a comparative study with four species of cyanobacteria. The experimental approach was to incubate monospecific cultures under solar radiation in a Patagonian site (43.3°S; 65°W) during the late Austral spring using two temperature treatments: 18 °C (control) and 23 °C, thus simulating a 5 °C increase as expected by the year 2100 [23].

2. Materials and methods

2.1. Culture conditions and study site

The cyanobacteria species used in this study were obtained from the Estación de Fotobiología Playa Unión (EFPU) Algal Culture Collection. *Microcystis* sp. Kützing ex Lemmermann, *Anabaena* sp. (Bory de Saint-Vincent ex Bornet & Flahault), and *Nostoc* sp. (Vaucher ex Bornet et Flahault) were grown in BG-11 medium [24] whereas *Arthrospira* (*Spirulina*) *platensis* (Nordstet) Gomont was grown in Zarrouk medium [25]. The cultures were diluted and placed in 6-l bottles filled up to 40% of their volume and pre-acclimated for at least 3 days before experimentation at either 18 or 23 °C in culture chambers (Minicella and Sanyo MLR 350, respectively). Both chambers had illumination provided by daylight fluorescent tubes (300 μmol photons m^{-2} s^{-1} of PAR (Photosynthetic Active Radiation, 400–700 nm)) with a 12L:12D cycle. After the pre-acclimation period, the cultures were used in experiments as described below. The experiments were carried out during the late Austral spring (from 30 November to 3 December, and from 14 December to 17 December, 2009) at the Estación de Fotobiología Playa Unión, located in the Patagonian coast of Argentina (43.3°S; 65°W).

2.2. Experimental set up and sampling protocol

Duplicate samples of the pre-acclimated cultures were put in UVR-transparent vessels (500–1000 ml) under three radiation treatments: (*i*) P [PAR (400–700 nm), tubes covered with Ultraphan UV Opak 395 filter], (*ii*) PA [PAR + UV-A (320–700 nm), tubes covered with Montagefolie 320 filter] and, (*iii*) PAB [PAR + UV-A + UV-B (280–700 nm), uncovered tubes]. Two different temperatures were implemented for each radiation treatment by putting the tubes in a thermostatic bath (Frío 21, Argentina) with two independent circuits for temperature control set at 18 °C and 23 °C, respectively. Samples were incubated under solar radiation for 4 days and measurements of fluorescence of chlorophyll-a – Chl-*a* (see below) were done with a frequency of once every hour. Just before sunset, samples were additionally collected for determination of Chl-*a* and cell concentrations, dry weight and morphometry. In the case of *Anabaena* sp., *Nostoc* sp. and *Microcystis* sp., the morphometrical measurements were done at the beginning and at the end of the experimental period, whereas for *A. platensis* it was done on daily basis (see below).

2.4. Analysis and measurements

The following analysis and measurements were performed during these experiments:

2.4.1. Fluorescence parameters

In vivo photosynthetic parameters were measured every hour with a pulse amplitude modulated (PAM) fluorometer (Walz, Water PAM, Effeltrich, Germany). Briefly, aliquots of 3 ml of sample were placed in a cuvette, and measured six times immediately after sampling, without dark adaptation. The effective photochemical quantum yield (Y) was calculated using the equations of Genty et al. [26] and Weis and Berry [27] as:

$$Y = \Delta F/F'_m = (F'_m - F_t)/F'_m \quad (1)$$

where F'_m is the maximum fluorescence induced by a saturating light pulse (ca. 5300 μmol photons m^{-2} s^{-1} in 0.8 s) and F_t the current steady state fluorescence induced by an actinic light in light-adapted cells.

2.4.2. Pigment concentrations and UVR-absorbing compounds

An aliquot of 20 ml of sample was filtered onto GF-C filters (Munktell, Sweden) and photosynthetic pigments and UVR-absorbing compounds were extracted in 5 ml of methanol. The tubes containing the methanolic extract were then sonicated at 20 °C for 20 min. After another 40 min of extraction, the samples were centrifuged and absorption spectra were obtained by doing scans between 250 and 750 nm with a spectrophotometer (Hewlett Packard, model HP 8453E). Chl-*a* concentration was calculated with the equations of Porra [28]; the same sample was used to calculate Chl-*a* concentration from the fluorescence of the extract [29] before and after acidification (1 N HCl) using a fluorometer (Turner Designs, model TD 700). UVR-absorbing compounds were estimated by the peak height at 330 nm as described in Dunlap et al. [30].

2.4.3. Cell counts and morphology

Samples of 5 ml were taken daily and fixed with buffered formalin (final concentration 0.4% of formaldehyde). Cells were counted under an inverted microscope (Leica DM IL) and using a Sedgwick-Rafter cell. Changes in morphology were analyzed from pictures taken with a video camera (Watec, High Resolution) attached to the inverted microscope and using a specific software for image analysis and processing (Image *J* – 1.43 r15, http://www.softpedia.com/get/Multimedia/Graphic/Graphic-Editors/ImageJ.shtml). Different parameters were determined for each species: The area of the chain was considered for *Anabaena* sp. and *Nostoc* sp., whereas the area of the colony was measured in *Microcystis* sp. For *A. platensis*, changes in the area of the trichome were determined.

2.4.4. Dry weight

An aliquot of 20 ml of sample was collected for dry weight analyses. Cells were filtered onto pre-weighted GF/C glass fiber filters (Munktell, Sweden) and dried in an oven (65 °C) overnight. The filters were then placed in a desiccator for 3–4 h until constant weight. Dry weight was calculated as the difference between the final and initial weight of each filter.

2.4.5. Radiation and temperature measurements

Solar radiation was continuously monitored using a broadband filter radiometer (ELDONET, Real Time Computer, Möhrendorf, Germany) permanently installed on the roof of the EFPU; the instrument measures UV-B (280–315 nm), UV-A (315–400 nm) and PAR (400–700 nm) every second, averages data over 1-min interval and stores them in a computer [31]. This radiometer is calibrated every year using a solar calibration procedure. Water temperature in the thermostatic baths was controlled with sensors attached to each temperature channel and adjusted automatically throughout the experimental period.

2.4.6. Statistics and calculations

Only one experiment with each cyanobacteria species was done, due to the time dependence of incident radiation over the study area that precluded comparisons under similar radiation conditions. For each experiment, radiation treatments were done in duplicate therefore, all data is reported as the mean and half mean range. One-way repeated measurements ANOVA test was used to determine differences among irradiances, temperatures and species while a two-ways ANOVA test was used to determine interactions between irradiance and temperature, using a 95% confidence limit [32].

The following calculations were done with the data obtained:

(i) The decrease of Y at noon due to PAR, UV-A and UV-B radiation were calculated by comparing the initial effective photochemical quantum yield value during early morning (before sunrise) and the effective photochemical quantum yield value at noon and expressed as percentages of inhibition as:

$$\text{Decrease of } Y \text{ due to PAR}(Inh_{PAR}) = 100 * (Y_{Pt0} - Y_{Ptnoon})/Y_{Pt0} \quad (2)$$

$$\text{Decrease of } Y \text{ due to UV-A}(Inh_{\text{UV-A}}) = 100 * (Y_{\text{UV-At0}} - Y_{\text{UV-At noon}})/Y_{\text{UV-At0}} - Inh_{\text{PAR}} \quad (3)$$

$$\text{Decrease of } Y \text{ due to UV-B}(Inh_{\text{UV-B}}) = 100 * (Y_{\text{UV-Bt0}} - Y_{\text{UV-Bt noon}})/Y_{\text{UV-Bt0}} - Inh_{\text{UV-A}} \quad (4)$$

where Y represents the effective photochemical quantum yield at the beginning of the experiment (t_0) and at noon (t_{noon}) under each radiation treatment for each day.

(ii) The recovery of yield during the afternoon was calculated as:

$$\text{Light Recovery} = (\%Y_{t_{\text{light}}} - \%Y_{\text{t0}}) \quad (5)$$

where Y represents the effective photochemical quantum yield under a particular radiation treatment (P, PA or PAB) at the end of the light period (t_{light}) and at the time zero point (t_0).

(iii) The recovery of yield during the night period was calculated as:

$$\text{Dark Recovery} = (\%Y_{t_{\text{night}}} - \%Y_{t0}) \quad (6)$$

where Y represents the effective photochemical quantum yield under a particular radiation treatment (P, PA or PAB) at the beginning of the following day of exposure (t_{night}) i.e., after recovering during the night, and at the time zero point (t_0).

3. Results

The radiation conditions during the experimental period were characterized by important cloud covering as shown in Fig. 1. Maximum irradiances were ~550, 68 and 1.6 W m^{-2} for PAR, UV-A and UV-B, respectively. The mean irradiances during the experiments carried out with *Anabaena* sp. and *Nostoc* sp. (November 30 to December 3) were 247, 33.7 and 0.77 W m^{-2} for PAR, UV-A and UV-B, respectively. During the experiments carried out with *A. platensis* and *Microcystis* sp. (December 14 to December 17) the mean irradiances were slightly higher: 274.4, 37.4 and 0.84 W m^{-2} for PAR, UV-A and UV-B, respectively.

The variations of the effective photochemical quantum yield (Y) at the two experimental temperatures are shown in Fig. 2. In all species, a general pattern of decrease in Y values from the morning towards noon, and of recovery during the afternoon was observed

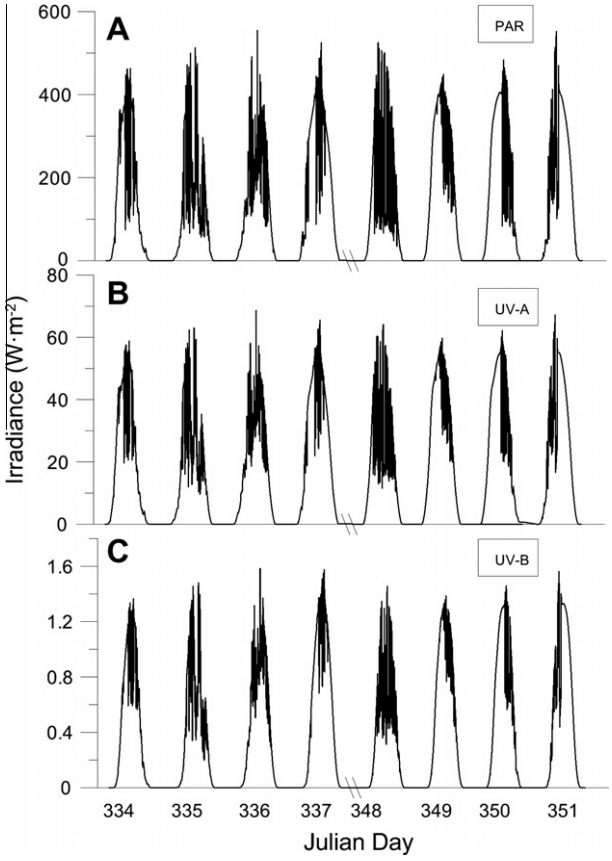

Fig. 1. Irradiance conditions (in W m^{-2}) during the study period: (A) PAR (400–700 nm), (B) UV-A (315–400 nm) and, (C) UV-B (280–315 nm). The experiments carried out with *Anabaena* sp. and *Nostoc* sp. were done during the period 30 November to 3 December, 2009 (Julian days 334–337) whereas those with *Arthrospira platensis* and *Microcystis* sp. were done during 14–17 December, 2009 (Julian days 348–351). Note the axis break between Julian days 337 and 348.

for all radiation and temperature treatments. With the exception of *Microcystis* sp., higher Y values were determined at higher temperatures, with Y being even higher at the end than at the beginning of the experiments, as clearly seen, for example, in *Nostoc* sp. (Fig. 2D). Significant effects of the different wavebands were in general observed, with Y values being higher in samples under the P than under the PA and PAB treatments. The only exception was *A. platensis* samples at the end of the experiment carried out at 18 °C (Fig. 2E) that had the highest Y values in the PAB treatment. There were also some specific features when comparing the responses towards solar radiation and temperature of the four species tested: *Anabaena* sp. showed a strong decrease of Y throughout the experiment carried out at 18 °C (Fig. 2A) but with almost complete recovery towards every night under the P treatment, and although this was also observed in the experiment done at 23 °C (Fig. 2 B) Y values were higher at the end of the experiment. *Nostoc* sp. had low Y values during the first 2 days of experimentation at 18 °C and then its recovery was higher (Fig. 2C); in samples exposed at 23 °C much higher recovery was attained since the first day (Fig. 2D) especially in the P treatment. Similarly, *A. platensis* (Fig. 2E and F) had strong decrease of Y and partial recovery at the beginning of the experiment at 18 °C, but complete recovery at 23 °C at the same time. Finally, *Microcystis* sp. displayed the least variations in both temperature and radiation treatments, having strong decrease of Y during the first 3 days at 18 °C (Fig. 2G) but less at 23 °C (Fig. 2H); rather low recovery was observed during the afternoon and night.

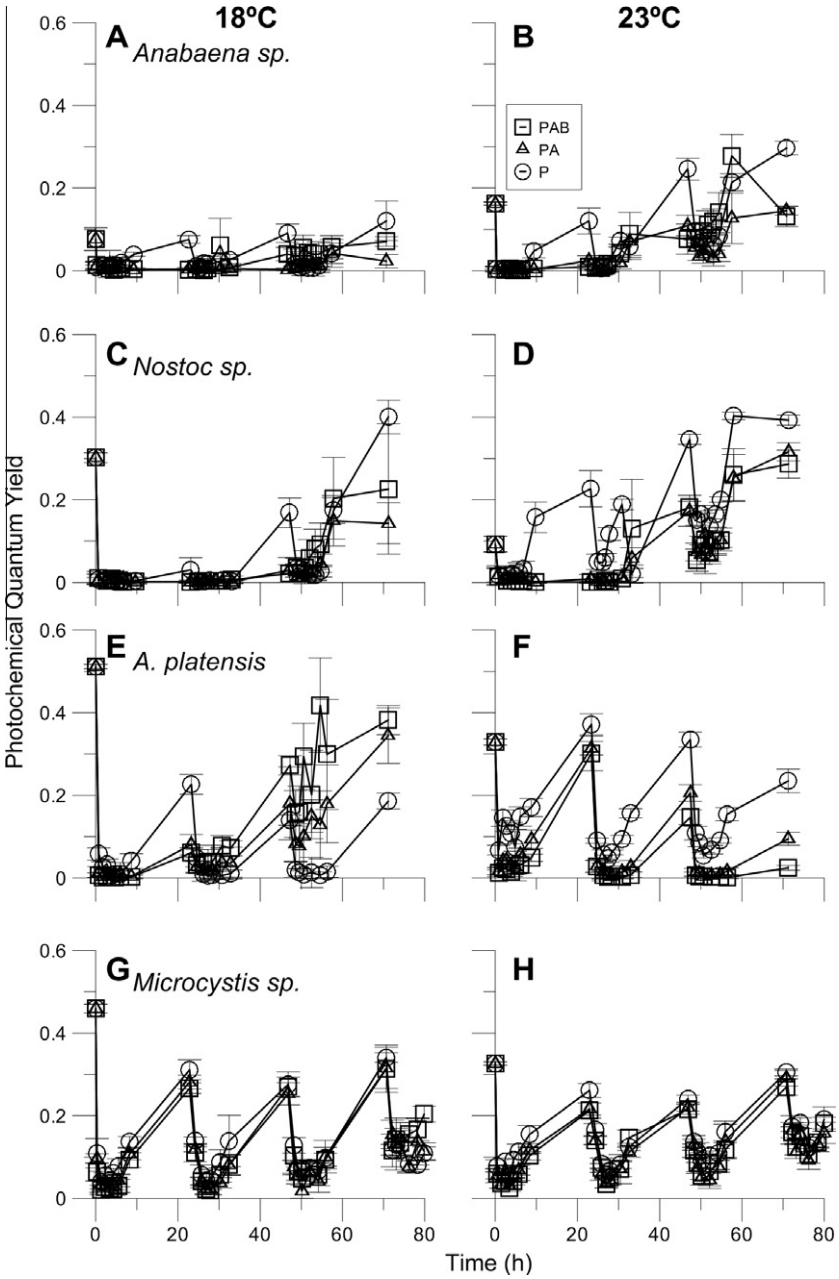

Fig. 2. Variations in the effective photochemical quantum yield (*Y*) during the experiments carried out with *Anabaena* sp. (A and B), *Nostoc* sp. (C and D), *Arthrospira platensis* (E and F) and *Microcystis* sp. (G and H). Left panels are experiments carried out at 18 °C whereas in the right are those done at 23 °C. The symbols indicate mean values of the different radiation treatments (squares: PAB, triangles: PA, circles: P), while the vertical lines on top are the standard deviation.

Detailed information about the dynamics of decrease and recovery of *Y* is presented in Figs. 3 and 4. In relation to the decrease of *Y* caused by different portions of the spectra (Fig. 3) it was seen that most of it was due to PAR, with both UV-A and UV-B contributing with similar (and very low) share in most cases. A decrease in *Y* induced by PAR was observed as the experiments progressed in samples incubated at 23 °C, especially in *Anabaena* sp. and *Nostoc* sp. (Fig. 3B and D). This decrease was followed by an increase in the UV-A contribution in all species incubated at 23 °C (Fig. 3B, D, F and H). It is worth to note that in *Nostoc* sp. at 23 °C (Fig. 3D) the P treatment had negative values i.e., promoted photosynthesis. In relation to recovery (Fig. 4), the general trend was of higher values towards the end of the experiments than at the beginning, as clearly seen in *Anabaena* sp. (Fig. 4A and B) and *Nostoc* sp. (Fig. 4C and D), but the opposite occurred in *A. platensis* incubated at 23 °C (Fig. 4F); however, this trend was less evident during the afternoon. Not all species had complete recovery throughout the experiment (i.e., values < 0) and this was especially evident in the experiments carried out with *Microcystis* sp. (Fig. 4G and H). It is important to note the clear effect of temperature on the night recovery of *Nostoc* sp., where samples exposed at 23 °C reached significantly higher values than those exposed at 18 °C (Fig. 4C and D); in contrast, *Microcystis* sp. had a similar behavior at the two experimental temperatures. Finally, and in relation to radiation treatments, a clear effect was observed in the night recovery of *Anabaena* sp. (Fig. 4A and B) whereas no effects were determined in *Nostoc* sp. (Fig. 4C and D) and *Microcystis* sp. (Fig. 4G and H).

Morphological changes observed during the experiments are presented in Fig. 5 and 6. There were significant inter-specific differences as well as responses related to temperature and/or solar

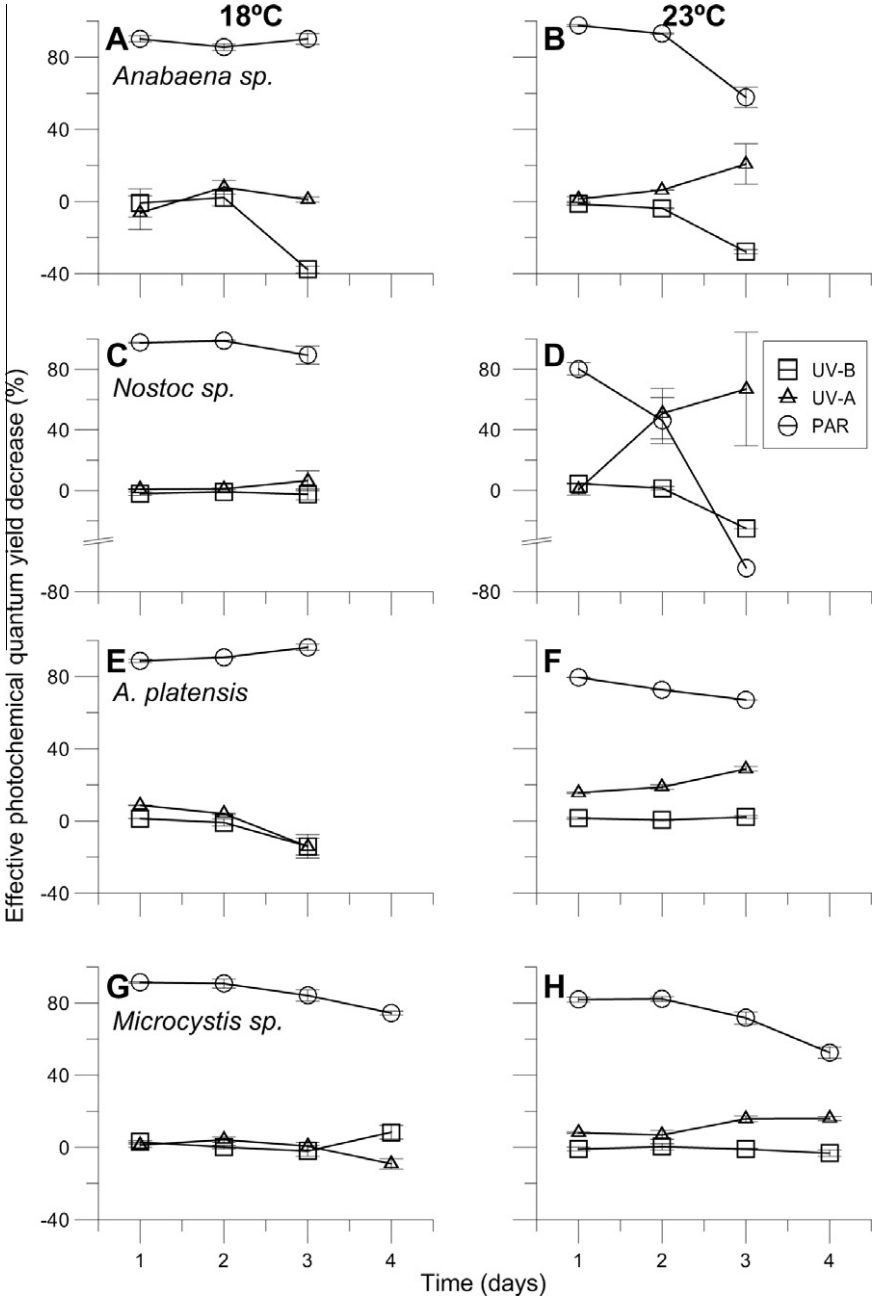

Fig. 3. Percentage decrease (%) of the effective photochemical quantum yield (*Y*) due to UV-B (squares), UV-A (triangles) and PAR (circles) throughout the experiments carried out with *Anabaena* sp. (A and B), *Nostoc* sp. (C and D), *Arthrospira platensis* (E and F) and *Microcystis* sp. (G and H). Left panels are experiments carried out at 18 °C whereas in the right are those done at 23 °C. The symbols indicate the mean value of inhibition under the different radiation treatments and the vertical lines indicate the half mean range.

radiation conditions: At 18 °C the initial area of the chain of *Anabaena* sp. (Fig. 5A and 6) was significantly higher than at the end, that presented similar values for the three radiation treatments. At 23 °C, however, the area of the cells at the end of the experiment was significantly smaller in the PAB treatment than in the other radiation treatments (Fig. 5B and 6). In *Nostoc* sp., significant differences in the chain area were found between the beginning and the end of the experiment done at 18 °C, with samples under the P treatment having higher values than those under PA or PAB (Fig. 5C and 6) while no differences were determined at 23 °C both in time and within radiation treatments (Fig. 5D and 6). In *A. platensis* a strong reduction in the trichome area was observed with time (Fig. 5E, F and 6) being this greater at 18 than at 23 °C. In general, and for this species, samples under the P treatment had larger area than those under PA or PAB. Finally, no significant differences were found for *Microcystis* sp. in the colony size (Fig. 5G, H and 6) at the two experimental temperatures and radiation treatments.

4. Discussion

The results of our study presented here contribute to the understanding of the interactive effects of temperature and solar UVR upon different cyanobacteria species when exposed to solar radiation levels as normally occur in the Patagonia area, and simulating an increase of temperature due to climate change as predicted by

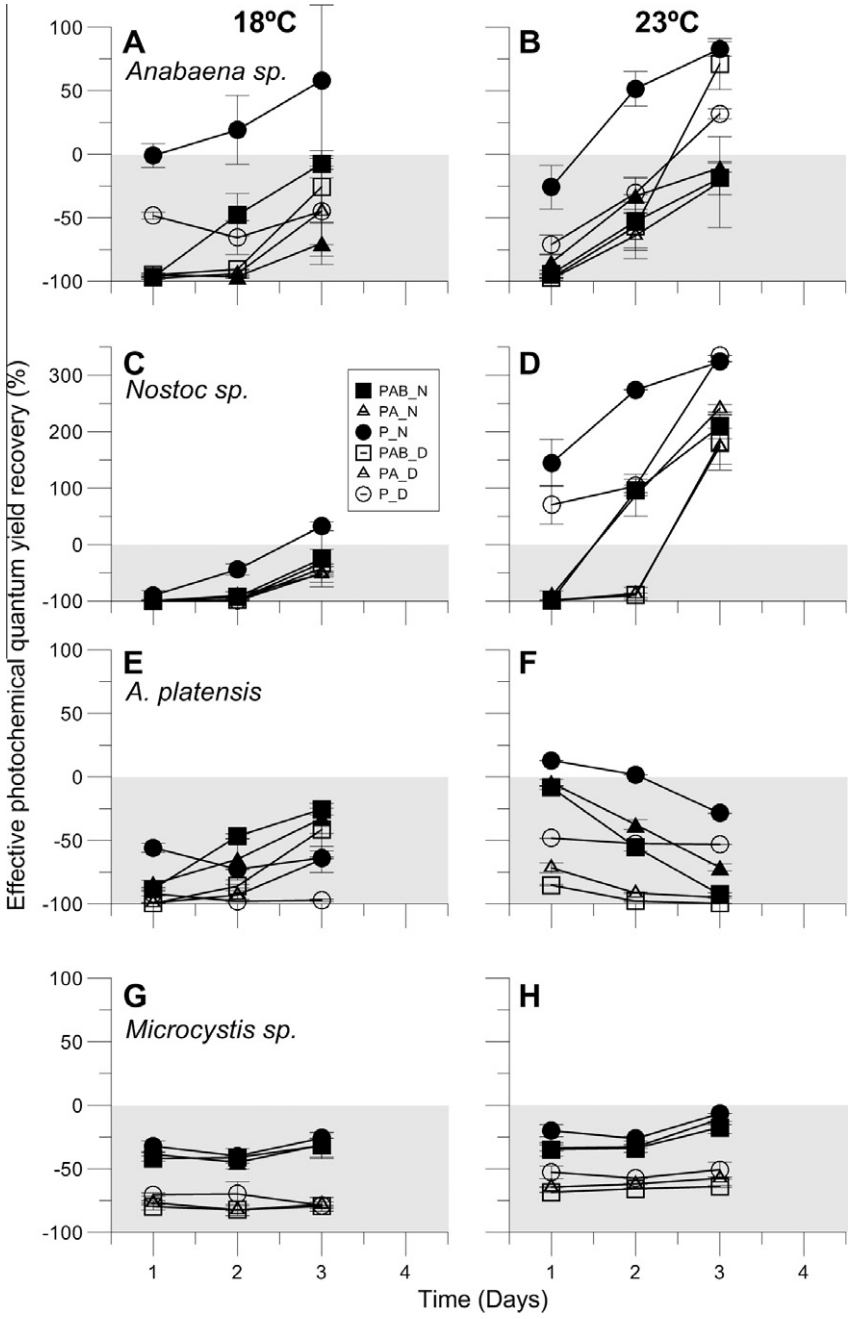

Fig. 4. Percentage recovery (%) of the effective photochemical quantum yield (*Y*) due to UV-B (squares), UV-A (triangles) and PAR (circles) throughout the experiments carried out with *Anabaena* sp. (A and B), *Nostoc* sp. (C and D), *Arthrospira platensis* (E and F) and *Microcystis* sp. (G and H). Left panels are experiments carried out at 18 °C whereas in the right are those done at 23 °C. The symbols indicate the mean value of recovery under the different radiation treatments and the vertical lines indicate the half mean range. Black symbols represent recovery during the night, whereas open symbols are those during the afternoon (under solar radiation). The grey area (i.e., negative recovery) indicates that *Y* values were lower than that at the beginning of experimentation.

the year 2100 [23]. The major finding of our study is that an increase in temperature have different outcomes: It benefited two of the four studied species (*Anabaena* sp. and *Nostoc* sp.) whereas in the other two (*A. platensis* and *Microcystis* sp.) no apparent effect was determined. The beneficial effects of temperature in *Anabaena* sp. and *Nostoc* sp. was translated in a better photosynthetic performance (Fig. 2) mostly accomplished by significantly higher recovery (both during the afternoon and night, Fig. 4) towards the end of the experiment. *A. platensis* and *Microcystis* sp., on the other hand, showed a better day-to-day performance (Fig. 2) while no temperature effect on photosynthesis recovery was evident (Fig. 4). The results of our study further highlight for the species-specific responses of cyanobacteria towards exposure to UVR and increased temperature. In the following paragraphs we will discuss the possible causes of the differential responses of species used in our study.

In principle, a better photosynthetic performance would mean a better utilization of solar radiation for biomass production. It has been already shown [5] that some diatom species benefited from increasing temperature and that the balance between inhibition/recovery of photosynthetic performance shifted, as the cells recovered or dissipated more energy. In our study, a rather similar outcome was observed i.e., as an increased recovery (Fig. 2). Within the limits of tolerance and photosynthetic performance of species,

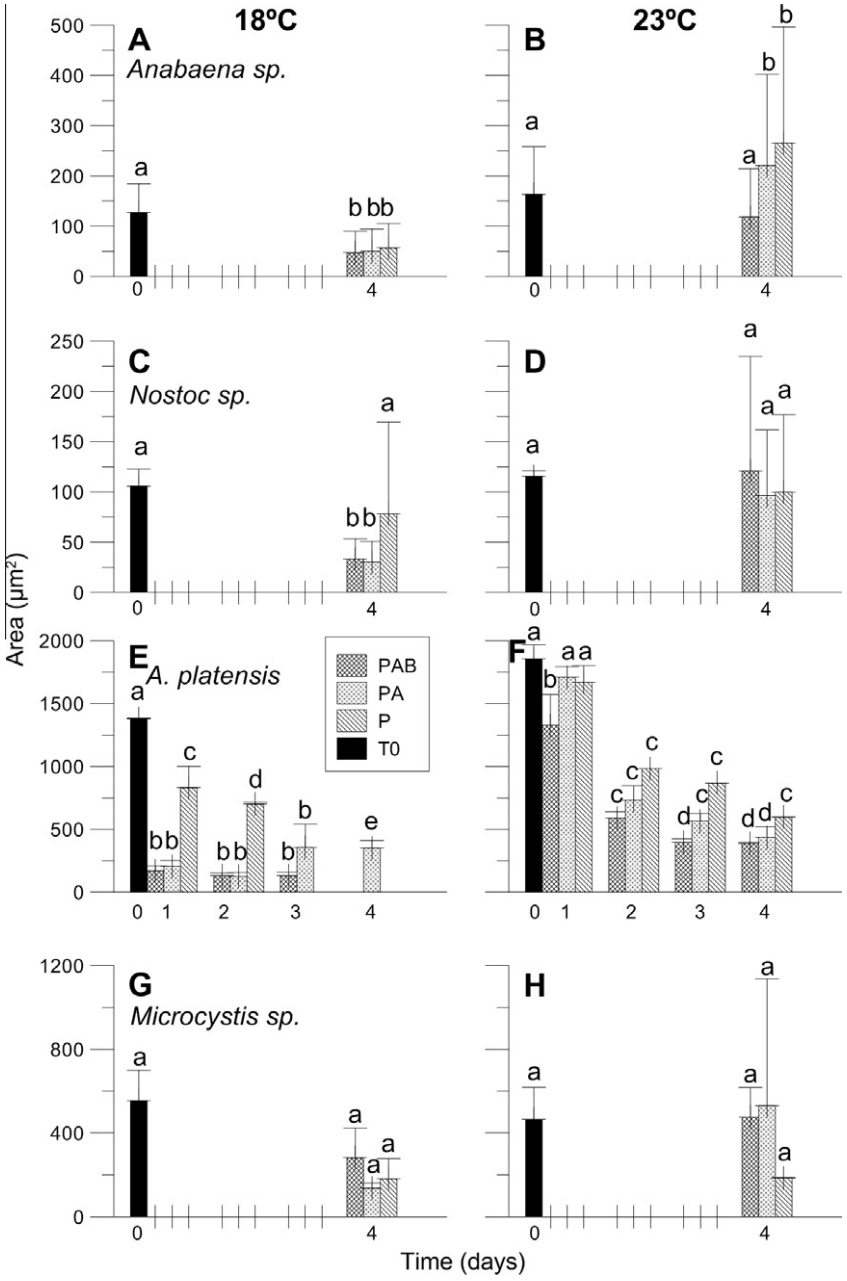

Fig. 5. Variations in the area (in µm^2) of: (A and B) *Anabaena* sp. chains, (C and D) *Nostoc* sp. chains, (E and F) *Arthrospira platensis* trichome and, (G and H) *Microcystis* sp. colonies. Left panels are experiments carried out at 18 °C whereas in the right are those done at 23 °C. Black columns indicate the area at the beginning of the experiment whereas the different shadings are the different radiation treatments: crossed: PAB; grey: PA; hatched: P. The lines on top of the bars indicate the standard deviation.

increased temperature would suppose increasing metabolic rates that would help cells to repair any potential damage caused by UVR. One of these targets of UVR within the photosystem II is the D1 protein [33] and it has been shown that increasing temperatures would result in a fast turn-over and repair of this protein, a fact that would be translated into a better photosynthetic response [34]. In our study, however, we did not measure the D1 protein, and a better photosynthetic performance at higher temperature was not observed in all species (Figs. 2–4). Therefore, this mechanism (i.e., fast D1 turn-over and repair) might have only partially accounted for the observed photosynthetic responses in some of the species used in our study. In addition, a better activity or higher RUBISCO quantities might have occurred at higher temperature in some of the species, but due to the limited amount of water samples (i.e., volume of the containers/space in the incubator) these measurements were not done.

The different responses and sensitivity to UVR of cyanobacteria were already determined in other studies [35,36]. It has been proposed that these are due to their different recent evolutionary history [35]; however, other studies [12] found that instead, the previous light history at which the cells were acclimated had a more important influence in the observed responses. In our case, and since all cultures were pre-acclimated and exposed to similar radiation conditions, the observed responses seem to be more related to other variables, such as temperature and/or changes in morphology occurring throughout the experiments. In addition, the differences in responses found among the four cyanobacteria species tested could be partially explained by the extent and/or efficiency of the different protecting mechanisms used by each species. For example, the synthesis of UV-absorbing compounds, such as mycosporine like aminoacids, was previously described for *Microcystis* sp. [37] and *Nostoc* sp. [13,38] but in our study, how-

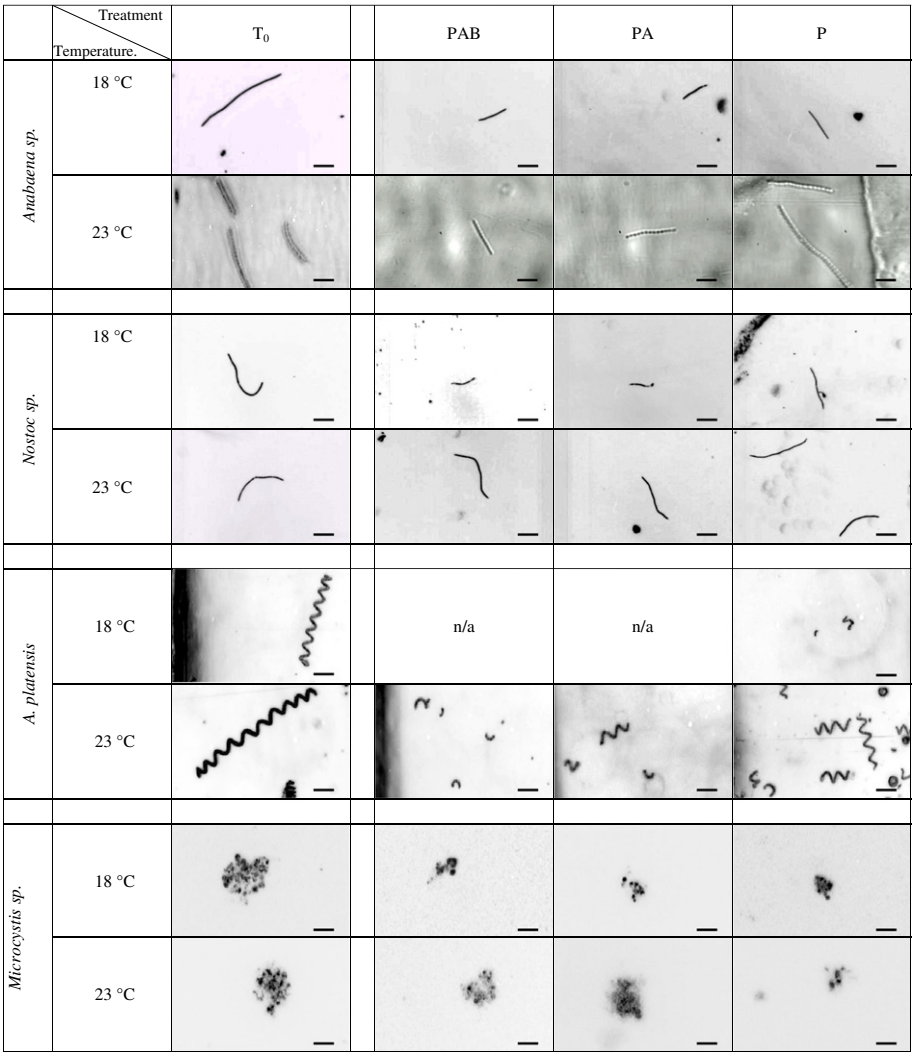

Fig. 6. Photographs showing morphological changes of *Anabaena* sp., *Nostoc* sp., *Arthrospira platensis* and *Microcystis* sp. cells exposed to different radiation and temperature treatments. Scale bar size is 20 μm.

ever, we did not find any significant amounts of UV-absorbing compounds in the methanolic extracts (i.e., spectrophotometric measurements) in these species. On the other hand, we did find important amounts of UV-absorbing compounds only in the P treatment of *Anabaena* sp. (data not shown); these compounds, however, were not induced by UVR as determined in previous studies [13]. Finally, in the case of *A. platensis* we found negligible amounts of UV-absorbing compounds, in agreement with previous studies done with these species [12,22].

In our study, the morphological changes observed in each cyanobacteria were diverse and in some cases they could not be associated to a single factor (i.e., temperature or UVR). Previous studies, nevertheless, already addressed the influence of various factors (e.g., temperature, growth media composition, salinity) on the morphology of *Anabaena* and *Nostoc* strains [39,40]. In the particular case of *Anabaena*, it was found that solar UVR inhibited the development of heterocysts responsible for the fixation of atmospheric nitrogen [41,42] and when incubated at 20 °C it reduced the trichome length up to 49% [42]. We found in our work that, when exposed to solar UVR at 18 °C, *Nostoc* sp. and *Anabaena* sp. had a significant reduction in the chain area at 18 °C, while at 23 °C an increase in the area was determined in *Anabaena* sp. but not in *Nostoc* sp. (Figs. 5 and 6). These results show that the increased temperature partially counteracts the effects that UVR has on the morphology of these species. The decrease in the trichome area observed for all treatments and temperatures in *A. platensis* is in agreement with previous findings [12,22]. The trichome area was significantly reduced under UVR exposure (Figs. 5 and 6) but it was also observed in samples exposed only to PAR. The observed morphological changes seem to partially counteract the UVR-induced decrease of *Y*, especially at 23 °C. This could be related to the self-shading mechanism proposed by Gao et. al. [22] that seems to be highly effective in dense cultures. However, and since we worked with diluted cultures, cells must have been overexposed to UVR, and the morphological changes might have not been enough to completely counteract the negative effects caused by relatively high levels of solar radiation as receiving in the study area (Fig. 1). Finally, and to the best of our knowledge, this is the first time that the combined effects of UVR and temperature on the morphology of *Microcystis* sp. are reported. No changes in the area of the colony were observed in all experimental conditions, in agreement with others studies [43] that showed that low temperature and darkness had no effect on the morphology of this species. These are also in agreement with the photosynthetic responses of *Microcystis* sp. observed by us (Fig. 2) where almost no differences could be observed between radiation treatments and temperatures. Nevertheless, other factors might influence morphology, as shown for *Microcystis aeruginosa* [44] where graz-

ing pressure induced the formation of colonies and thus increasing size. Morphological changes, either reduction or enhancement of the cell/colony area, should modify the surface-to-volume ratio and thus the irradiance received by the cell/colony, would also change. How these changes affect the photosynthetic performance depends on many variables that include pre-acclimation of cells, amount of incident irradiance, temperature, among others. In our case, as discussed above, this relationship between morphology and photosynthesis was evident for *A. platensis*. Nevertheless, other studies should be conducted in order to further elucidate how changes in morphology would condition the acclimation of the cells and so their photosynthetic performance.

Increased greenhouse (e.g., water vapor, carbon dioxide, nitrous oxide, etc.) and anthropogenic gases have caused a climate change process which is associated with increased global temperatures [23,45,46] and reduced ozone, thus increasing the radiation levels that are reaching the Earth's surface [47]. These factors have conditioned life in aquatic systems, affecting some organisms, i.e., either by causing species extinction [48], changes in population dynamics [49] and favoring others, among which are cyanobacteria that seem to benefit and proliferate under higher temperatures [46]. Here we show that the responses to climate change variables are species-specific: Increased temperature prevents *Anabaena* sp., *Nostoc* sp. and *A. platensis* from reducing the area of their trichome/chains while it also benefits the photosynthetic recovery of *Anabaena* sp. and *Nostoc* sp. after exposure to UVR. How these mechanisms will impact on the aquatic food web and production is still uncertain, but surely merits further research.

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