Artículo original

Solar UV radiation and temperature effects on fatty acids of *Microcystis aeruginosa*

Efectos de la radiación UV solar y temperatura en ácidos grasos de Microcystis aeruginosa

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Manuscrito recibido: 12 de octubre de 2022; aceptado para publicación: 16 de noviembre de 2022

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Abstract

One of the most common regulatory strategies to adapt to stress is by adjusting the degree of fatty acids (FAs) unsaturation. The ability to modify the type and quantity of cellular lipids allows cyanobacteria to avoid damage and be protected against the effects of extreme conditions. The combined effects of increased temperature and solar UVR on *Microcystis aeruginosa* cultures were analyzed in terms of FA content and lipid damage. The M. aeruginosa culture was incubated to natural sunlight in two outdoor water baths at 26 and 29°C during 4 days. Cells were exposed to both temperatures and three radiation treatments: full radiation (UVBR + UVAR + Photosynthetic Available Radiation, PAR), UVAR+PAR and only PAR (control). During the first two exposure days, UVAR modulates lipid damage as a function of temperature in consequence of an increase in reactive species and the FAs composition. After four exposure days the cells were adapted to both increased temperature and UVR. Thus, increased temperature and UVR changes could impact the ω6/ω3 PUFAs balance of cyanobacteria. This response can further be transferred from cyanobacteria to higher trophic levels and can influence the overall functioning of freshwater bodies.

Key words: ω6/ω3 ratio, cyanobacteria, climate change, oxidative stress

Resúmen

Una de las estrategias regulatorias más conocidas para adaptarse al estrés comprende ajustar el grado de insaturación de los ácidos grasos (AG). La capacidad de modificar el tipo y la cantidad de lípidos en la membrana permite a las cianobacterias evitar daños y estar protegidas contra los efectos de condiciones extremas. Los efectos combinados del aumento de la temperatura y la radiación UV solar en cultivos de Microcystis aeruginosa se analizaron en términos de contenido de AG y daño de lípidos. El cultivo de M. aeruginosa se incubó a la luz solar natural en dos baños termostáticos a 26 y 29°C durante 4 días. Las células se expusieron a ambas temperaturas y tres tratamientos de radiación: radiación completa (RUVB + RUVA + radiación fotosintéticamente activa, RFA), RUVA+RFA y solo RFA (control). Se encontró durante los dos primeros días de exposición, que la RUVA modula el daño lipídico en función de la temperatura como consecuencia de un aumento de las especies reactivas y de la composición de AGs. Después de cuatro días de exposición, las células se adaptaron tanto al aumento de temperatura como a la radiación UV. Por lo tanto, el aumento de la temperatura y los cambios de RUV podrían afectar el equilibrio de AGPI ω6/ω3 de las cianobacterias. Esta respuesta podría transferirse, inclusive a niveles tróficos superiores e influir en el funcionamiento general de los cuerpos de agua dulce.

Palabras clave: *índice ω6/ω3, cianobacteria, cambio climático, estrés oxidativo.*

DOI: http://doi.org/10.34073/286

INTRODUCCIÓN

One of the effects of global climate change is increased exposure to solar UV radiation (UVR, 280-400 nm) which affects aquatic phytoplankton. Stratospheric ozone decrease produced by emission of chlorinated fluorocarbons (CFCs) (Previdi and Polvani, 2014) resulted in increasing solar ultraviolet B radiation (UVBR, 280–315 nm) on the Earth's surface. Especially, this increase is substantial in polar regions and at mid-latitudes (McKenzie et al., 2011). Global change also includes modifications in other environmental variables such as precipitation and wind stress (Barbieri et al., 2006). Increased precipitation or wind speed will modify the amount of organic and inorganic (Häder et al., 2011), responsible for different degrees of UVR attenuation throughout the water column (Williamson *et al.*, 2014). Also, both events could increase the amount of nutrients that come from a terrestrial origin. The combination of elevated temperatures and high nutrient availability produces harmful algal blooms (HABs) (Paerl *et al.*, 2014), including those produced by *Microcystis* species. *Microcystis* can form blooms and often cause serious problems in water quality management due to toxin production. Its optimal temperature for growth and photosynthesis is 25 °C or above (Reynolds, 2006; Paerl and Huisman, 2008). Giannuzzi *et al.* (2016) predicted that increases in the temperature up to 29°C produced an increase in the biomass of *M. aeruginosa* with an increase of the most toxic microcystin (MC, variant MC-LR).

Due to climate change, global temperatures are expected to increase about additional 2–5°C (Gattuso *et al.*, 2015), causing shallower surface mixing depths which have the potential to increase the UVBR doses exposure and as such damaging aquatic organisms that live in the upper layers of water bodies (Kraemer *et al.*, 2015).

High temperature stimulates the metabolic rate of plankton (Thyssen et al., 2011) by raising oxygen consumption and a possible increase of the reactive species concentrations (Halliwell, 2006). Solar UVBR can exert its detrimental action either directly by attacking vital biomolecules or by the formation of reactive oxygen species (ROS) such as singlet oxygen (1O2) or hydrogen peroxide (Rastogi *et al.*, 2014). The increased production of ROS could be due to higher water temperatures (Hernando *et al*., 2018a) as well as increased

UVR (He and Häder, 2002; Hernando et al., 2018b). An increase of ROS could produce decrease in the activity of photosystem II (Saison *et al.*, 2010) and inhibition of cyanobacteria growth (Giannuzzi et al., 2016; Dziallas and Grossart, 2011; de la Rosa *et al.*, 2020). Furthermore, due to the high density of double bonds, ROS may damage the membrane lipids polyunsaturated fatty acids (PUFAs) (Bandyopadhyay *et al.*, 1999). Thus, lipid peroxides generated by reactive oxygen species (ROS) could damage PUFAs, resulting in the formation of Thiobarbituric Acid Reactive Substances (TBARS) (He *et al.,* 2002). The fatty acid (FA) composition of the membrane phospholipids regulates membrane fluidity (Canganella and Wiegel, 2011) increasing or decreasing the degree of FA unsaturation (homeoviscous adaptation, Hazel, 1995). Therefore, their ability to modify the type and quantity of their cellular lipids allows cyanobacteria to avoid damage and to be protected against the effects of extreme conditions (Sato *et al.*, 2000).

Additionally, PUFA are important biomarkers and human health promoters, in particular essential fatty acids such as ω6 and ω3. Studies have shown that lower ratio of ω6/ω3is more desirable since it reduces the risk of many chronic diseases. Hence its interest in evaluating the environmental factors that favor its production in organisms, especially at the lower levels of the food web (Simopoulos 2002, 2011; Mozaffarian *et al.*, 2006).

The objective of this study was to determine the combined effects of solar UVR and increased temperature in reactive species production, lipid damage, FA composition and changes on ω6/ω3 ratio of M. aeruginosa exposed for 4 days.

MATERIAL Y MÉTODO

1. Experiment set up

The *M. aeruginosa* strain CAAT 2005-3 (Rosso *et al.*, 2014) was grown at 26 °C under artificial light at a photon flux density of 30 μE m^{-2} s^{-1} (monitored daily with an ILT 950 spectroradiometer, International Light Technologies, Inc., USA) under 14:10 h light:dark photocycle, until reaching the exponential growth phase.

After that *M. aeruginosa* cultures were exposed to natural sunlight at Buenos Aires (34°35′S; 58°22′W) during spring sunny days, in two outdoor water bath at 26°C (control temperature) and 29°C (high temperature) (±1°C), using running tap water at stable controlled temperatures during the entire incubation (4 days). At these two temperatures, cells were exposed to three radiation treatments:

(1) Full radiation (UVBR, UVAR and PAR) (TUVR treatment)

(2) UVAR and PAR—tubes covered with UV cut-off filter foil (Montagefolie No. 10155099, Folex, Germany: 50% transmission at 320 nm) (TUVA treatment)

(3) PAR -tubes covered with an Ultraphan film (UV Opak, Digefra, Munich, Germany- 50% transmission at 395 nm) (PAR treatment).

Three replicate samples were used for each of the treatments and controls at which M. aeruginosa was exposed to daily doses that are normally recorded in spring at temperate latitudes (Buenos Aires) i.e. between 8000 and 10800 kJ m^{-2} (Orce and Helbling, 1997).

2. FAs analysis

For FA determination, 10 mL culture aliquots were filtered through glass filter fibers (0.7 μm) and then extracted and methylated according to Abdulkadir and Tsuchiya (2008), modified by De Troch *et al.* (2012). FA separation and identification was achieved with a gas chromatograph (HP 6890 N) coupled to a mass spectrometer (HP 5973) according to Hernando *et al.* (2018a).

3. Reactive species determination

Cell generation of reactive species was determined by in vivo measuring of the oxidation of 2', 7'-dichlorodihydrofluorescein diacetate (DCFH-DA). DCFH-DA pre-filtered samples (8 mL) were treated as described by Bass *et al.* (1983), modified by Malanga et al. (2001). Then was monitored in a microplate reader (Beckman counter DTX 880, Multimode Detectors) with $\lambda_{excitation}$ = 498 nm and $\lambda_{emission}$ = 525 nm.

4. Lipid damage analysis

TBARS allow a rough estimate of the presence of aldehydes, yet most reactivity originates from malondialdehyde (MDA), a product of lipid peroxidation, which after the reaction with TBARS allows a colorimetric assay (Janknegt *et al.*, 2008).

In consequence, cellular TBARS were used as an indicator of lipid peroxidation. Filtered samples (6 mL) by fiber filters, were analyzed according to Malanga and Puntarulo (1995). The absorbance of the organic layer (upper layer) was spectrophotometrically measured at $\lambda = 535$ nm.

5. Statistical analyses

Repeated measures analyses of variance (RMANOVA, Statistica, version 9.0) were used to determine the significance of the differences in the measured parameters among treatments in pairs throughout the incubation time. In all cases, normality was verified using a one-sample Kolmogorov–Smirnov test ($p > 0.05$), whereas the sphericity assumption that concerns variance homogeneity was checked using the Mauchley's test. The experimental treatments were the fixed factors and exposure time (i.e. day of incubation) was the random factor. The interaction between factors (treatment vs time) was also analyzed. In all cases of significant interactions ($p < 0.05$), the differences between treatments at different days were analyzed using one-way ANOVA followed by Tukey test (Scheiner, 2001).

Changes in the relative amount of unsaturated FAs in relation to incubation time was further evaluated by RMANOVA analyses based on the concentration ratio of PUFAs/saturated FAs (PUFAs/SFAs, thereafter mentioned as "relative concentration FAs"). The FAs used for results, according to a >15% threshold contribution respect to the total FAs were PUFAs: linoleic acid (LA, 18:2ω6), γ-LinoleicAcid (18:3ω6), Alfa-linolenic acid (ALA, 18:3ω3) and Stearidonic acid (18:4ω3).The SFAs used for such index were 16:0 plus 18:0 considering that both of them showed the same increasing trends in their concentrations as a function of incubation time ($R = 0.96$).

RESULTS

1. FAs

The absolute concentration of all FAs ($\mu g\ L^{-1}$) referred to original culture is shown in **Table 1** (see Appendix). Initially, at exposure day 1 (D1), the relative concentration of 18:3ω6 in relation to SFAs was significantly lower ($p<0.01$) for UVAR and PAR treatments at 29°C compared to 26°C. No significant differences were found for irradiation which included UVB. The same trend was found for 18:2ω6 relative concentration in relation to SFAs but without significant differences ($p>0.05$) (**Fig. 1**). Moreover, ω3 FA18:3ω3 and 18:4ω3 relative concentrations decreased even further than

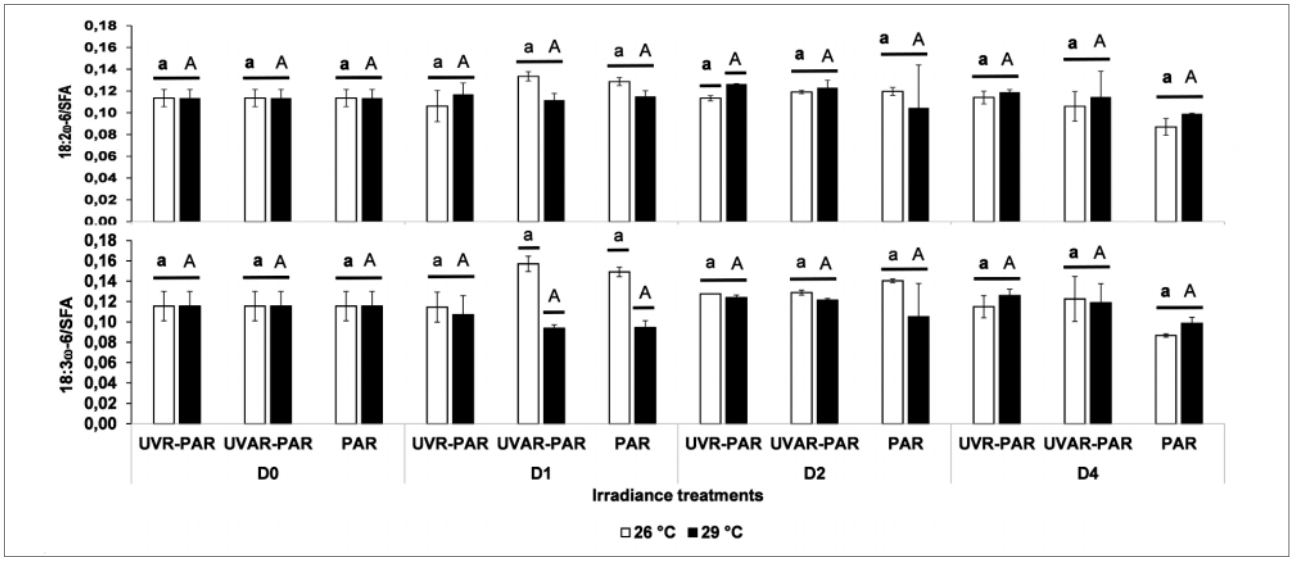

Figure 1. Relation between the relative abundance of ω6 PUFA (18:2ω6/SFA and 18:3ω6/SFA) as a function of exposure days when exposed cultures at 26°C (white bars) and 29°C (black bars) for each irradiance treatment. *Each bar represents the mean ± SD. Different letters correspond to significant differences (Tukey test) between experimental days (normal for 26°C and capital letters for 29°C). Horizontal line at same level is showing no significant differences between temperature treatments for the same day. Each bar represents the mean +/- SD.*

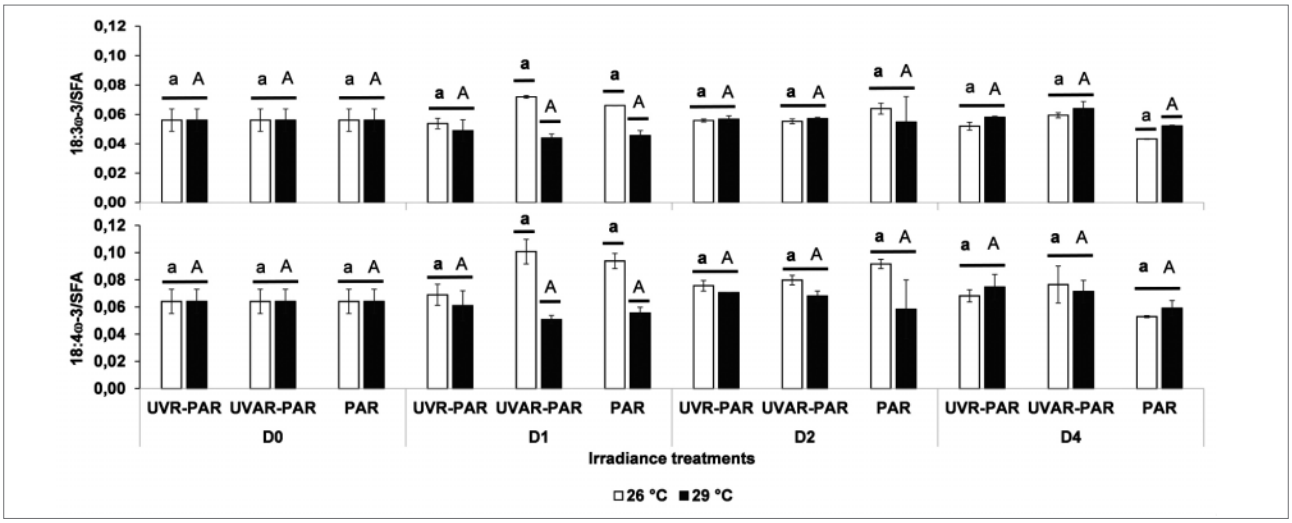

Figure 2. Relation between the relative abundance of ω3 PUFA (18:3ω3/SFA and 18:4ω3/SFA) as a function of exposure days when exposed cultures at 26°C (white bars) and 29°C (black bars) for each irradiance treatment. *Each bar represents the mean ± SD. Different letters correspond to significant differences (Tukey test) between experimental days (normal for 26°C and capital letters for 29°C). Horizontal line at same level is showing no significant differences between temperature treatments for the same day.*

the ω6 FA at both UVAR and PAR exposure ($p<0.01$) when were exposed at 29ºC (**Fig. 2**). No significant differences were found as a consequence of irradiation which included UVB or only UVA during the four days of exposure for ω6 or ω3 FAs ($p> 0.05$) (**Figs. 1, 2**). Neither were found significant differences due to 29ºC or irradiation which included UVB/UVA exposure ($p> 0.05$) at days 2 and 4 (**Figs. 1, 2**).

2. Oxidative stress parameters

Reactive species increased significantly as consequence of

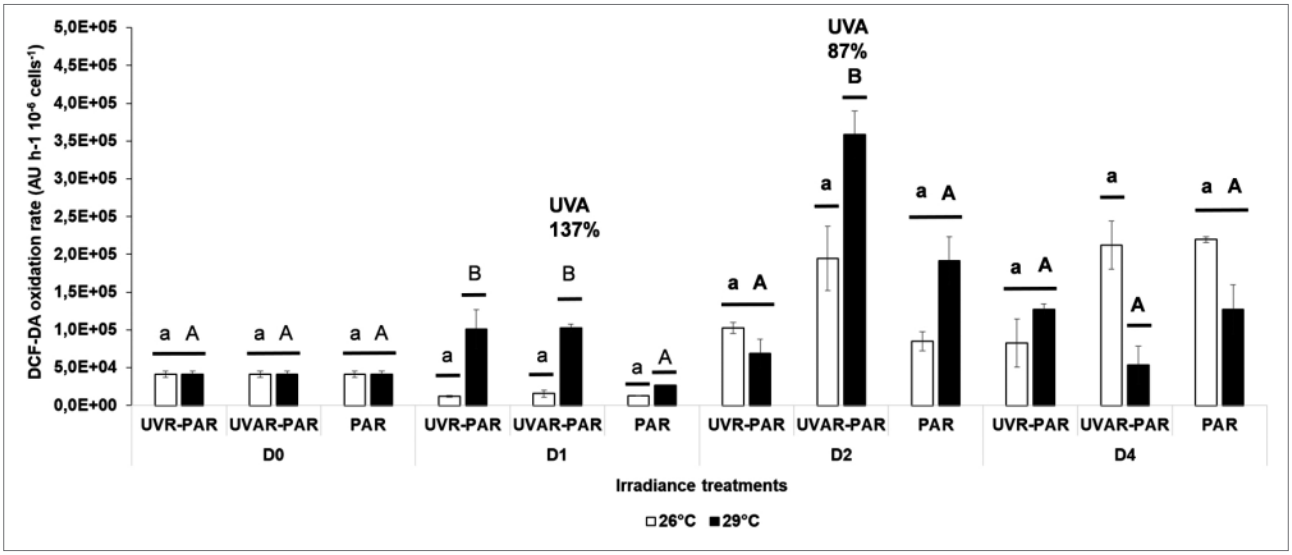

Figure 3. Celular DCF-DA oxidation rate in M. aeruginosa cultures exposed to 26°C (white bars) and 29°C (gray bars) as a function of experimental time. *Each bar represents the mean ± SD. Different letters correspond to significant differences (Tukey test) between experimental days (normal for 26°C and capital letters for 29°C). Horizontal line at same level is showing no significant differences between temperature treatments for the same day.*

high temperature in cultures exposed to all radiation treatments at D1 ($p<0.05$), in those exposed to UVAR at D2 ($p<0.01$) and a significant decrease in those exposed to 29ºC compared with 26ºC in cells irradiated with UVAR at D4. Moreover, UVAR produced a significant increase of reactive species of 137 and 87% ($p<0.01$) at D1 and D2 respectively. No further differences was determined by TUVR at D4 ($p>0.05$) (**Fig. 3**).

Lipid damage (estimated by TBARS) was significantly lower in cells exposed to 29ºC and irradiation which included UVB at D1 ($p<0.01$) compared with those exposed to 26ºC. At D2 the lipid damage was significantly higher in cells exposed to 29ºC and UVAR compared with 26ºC ($p<0.01$). Moreover, the exposure to UVAR produced a significant decrease respect to PAR in cells exposed to 26ºC of 20 and 24% at D1 and D2 respectively ($P<0.01$). No TUVR effects were determined on lipid damage at D4 ($p>0.05$) (**Fig. 4**).

studies have already shown that exposure to solar light, including UVR, considerably modifies the FA composition and therefore the nutritional value of cyanobacteria (Leu *et al.*, 2006; Hernando et al., 2022). In line with the results of our experiment, during the four exposure days, no effects were observed in ω6 or ω3 FAs when cells were exposure to irradiation which included UVB. These findings are contrasting with those described by Wang and Chai (1994), and Guihéneuf et al. (2010) showing that UVBR induced a reduction in the ω3 FA levels (EPA and DHA) in eight species of microalgae. In addition, Gupta et al. (2008) found that Spirulina platensis exposed to UVBR showed an increase in SFAs and PUFAs when compared with PAR control.

The high reactive species concentration produced as response to high temperature exposure, in coincidence with de la Rosa *et al.* (2020), did not produce an increase in lipid damage when cells were exposed to UVAR at D1 and D2. However, the decreased lipid damage observed in cells exposed

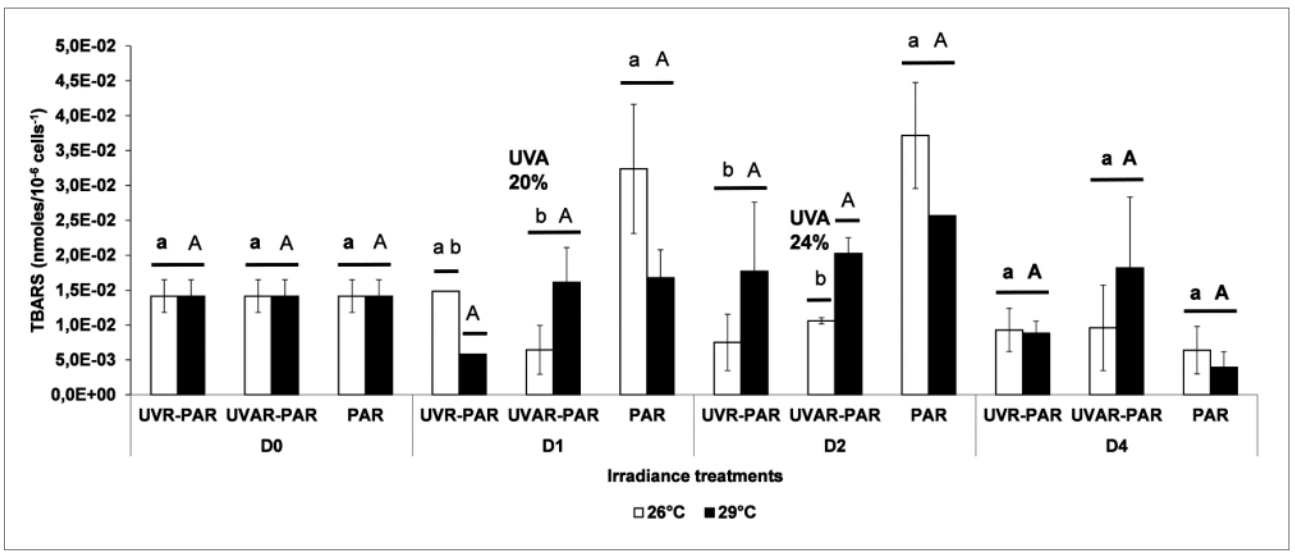

Figure 4. Lipid peroxidation (TBARS cell content) in cultures exposed to 26°C (white bars) and 29°C (gray bars) as a function of experimental time. *Each bar represents the mean ± SD. Different letters correspond to significant differences (Tukey test) between experimental days (normal for 26°C and capital letters for 29°C). Horizontal line at same level is showing no significant differences between temperature treatments for the same day.*

DISCUSSION

Growth temperature has been established as a factor that modifies concentration and composition of PUFAs (Renaud *et al.*, 2002; de la Rosa *et al.*, 2020). In addition, several

to UVAR at 26ºC for D1 and D2, could be due to an increased relative abundance of LA and γ-Linoleic Acid as well as of Stearidonic acid which have a lower sensitivity to UVAR (Huang and Cheung, 2011) or were better protected by me-

tabolites such as carotenoids (Kirilovsky, 2007). Furthermore, recent research has shown other protection mechanisms against the generation of reactive species such as the scavenger in situ activity of most abundant MCs produced for our strain (Malanga *et al.*, 2019). The main potential damage of both UVAR and UVBR on phytoplankton cells is related to direct and indirect effects via the production of ROS (He and Häder, 2002). In several studies was demonstrated an increase of reactive species after exposure *M. aeruginosa* to high UVR doses or temperature (Hernando et al. 2018a, b; Malanga *et al.*, 2019). In addition, Hernando et al. (2018b) showed that different responses were activated in M. aeruginosa depending on the exposure to UVAR or UVBR as well as the dose level.

PUFAs in cyanobacteria membranes are highly susceptible to radical attack by high density of double bonds (Bandyopadhyay *et al.*, 1999). However, de la Rosa *et al.* (2020) determined no changes in the relative abundance of UFAs/SFAs when M. aeruginosa was exposed to increasing temperature (29ºC), even though reported a higher sensitivity of ω3 than ω6 FAs.

Cyanobacteria have developed a great number of strategies to avoid or mitigate the ROS damage in PUFAs. Catalase (CAT) is one enzyme that exclusively dismutate H2O2, the most stable ROS (Chelikani *et al.*, 2004). Giannuzzi *et al.* (2016) demonstrated that antioxidant activity could be the cause of differential sensitivity of M. aeruginosa exposed to 29°C. Thus, an increased CAT activity was determined by exposure to UVAR but there were no effects of UVBR exposure of the same M. aeruginosa strain (Hernando *et al.*, 2018b). For the present experiment CAT content was significantly lower at D1 and D2 in cells exposed to UVAR compared with PAR (data not shown). Other studies showed the ability of scavenging free radicals generated by UVAR due to a higher level of total carotenoids and hence the decrease of UVAR inhibitory growth effect on two species of green microalgae Platymonas (*P. subcordiformis* and *P. cruentum*) (Huang and Cheung, 2011). Also, the significant decreased reactive species concentration at D2 and the significant decreased lipid damage at D1 both in cells exposed to irradiation which included UVB could be due to the production of protective compounds like MAA´s or Scytonemine (Diaz, 2020). In addition, the enzymatic activity of desaturases and gene expression related to PUFA synthesis might be activated by UVR (Kis *et al.*, 1998). It has been shown that the expression of genes for Δ12 andΔ6 desaturases were significantly upregulated by 10-fold under exposure to sunlight (Kis *et al.*, 1998). In relation to PAR exposure, Steinoff (2011) showed a decrease of 18:2ω6 over time due to high PAR irradiance in the algae Alaria esculenta. Additionally, PAR exposure reduced 18:2ω6, 18:3ω3 and18:3ω6 (Saha *et al.*, 2013). In contrast, in our experiment, high solar PAR doses (exposure D2 and D4, 9700 kJ m-2 in average) did not produce significant differences between temperature treatments at any TUVR. On the contrary, an increased ω6 production at 29ºC was observed after the exposure to low PAR doses (day 1, 7800 kJ m-2 in average) (de la Rosa *et al.*, 2020). According to de la Rosa *et al.*, (2020) results, we expected an increase in the ω6/ω3 ratio after several days of exposure to 29ºC. However, such results were not evident in four days of incubation, at least under PAR irradiance in coincidence with what was previously observed. This could be due to the need for a longer period of exposure considering that just after four days a significant decrease in reactive species was observed when the cells are exposed to UVAR and there was no lipid damage in any treatment. This could show that the cells have adapted to the changes in the experimental variables by activation of antioxidant protection or production of protective compounds and thus, with a few more days of exposure, the ω6 FAs could have increased significantly as has already been observed.

CONCLUSIONS

Global warming enhances water temperatures and thus stratification, reducing the thickness of the upper mix layer with the consequent increase exposure to UVR. The differential sensitivity of ω FAs composition in *M. aeruginosa* demonstrated here could be due, among other factors, to an increased reactive species production and/or specific activation or production of scavenger molecules. Based on the short incubation time that we applied, we determined a high sensitivity of ω3 FAs when exposing *M. aeruginosa* to high temperature. Our results emphasize a differentiated sensitivity between ω6 and ω3 FAs. Thus, climate change could impact the balance of ω3/ω6 PUFAs for higher trophic levels through the food chain. The transfer of the response

of the cyanobacteria to high temperature and UVAR doses to higher trophic levels will influence the overall functioning of freshwater bodies and still, in the human diet. Links between global warming and human health merits further investigation, about the factors that modify availability of omega-3.

ACKNOWLEDGMENT

The research leading to these results received funding from the European Union's Horizon 2020 research and innovation program under grant agreement No 730984, ASSEMBLEPLUS 2019359 project. The FA analyses were carried out with infrastructure partly funded by EMBRC Belgium - FWO agreement 20151029-03. This study was supported by grants from the University of Buenos Aires (UBACyT, 20020170 100199BA), the National Council for Science and Technology (CONICET, PIP 0635), and the University of Morón (PI3/18-00-CC-001).

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APPENDIX

Table 1. Average (± S.D.) absolute FAs concentration (µg L-1) of* M. aeruginosa *culture exposed to 26°C and 29°C for each experimental day under radiation treatments. *The sum of all SFAs, PUFAs, ω6, ω3 and the ω6/ω3 ratio is shown. Numbers in bold indicate statistically significant differences between temperature treatments for each exposure day according to Tuckey test ($p < 0.05$). Numbers marked with a * indicate statistically significant differences of TUVR and TUVA in comparison with PAR values for each exposure day according to Tuckey test ($p < 0.05$).*

	UVR+PAR		UVR+PAR		PAR		UVR+PAR		UVR+PAR		PAR		UVR+PAR		UVR+PAR		PAR	
	29°C	26°C	29°C	26°C	29°C	26°C	29°C	26°C	29°C	26°C	29°C	26°C	29°C	26°C	29°C	26°C	29°C	26°C	29°C	26°C
10:0	0,03 ± 0,002	0,03 ± 0,002	0,03 ± 0,00	0,03 ± 0,001	0,03 ± 0,001	0,02 ± 0,001	0,03 ± 0,00	0,02 ± 0,004	0,04 ± 0,01	0,02 ± 0,003	0,04 ± 0,003	0,03 ± 0,001	0,03 ± 0,002	0,02 ± 0,002	0,04 ± 0,005	0,05 ± 0,01	0,03 ± 0,01	0,04 ± 0,02	0,06 ± 0,001	0,06 ± 0,01
12:0	0,07 ± 0,01	0,07 ± 0,01	0,10 ± 0,03	0,07 ± 0,01	0,08 ± 0,004	0,06 ± 0.01	0,06 ± 0,004	0,04 ± 0,004	0,06 ± 0,01	0,04 ± 0,01	0,06 ± 0,01	0,07 ± 0,01	0,07 ± 0,01	0,10 ± 0,03	0,05 ± 0,01	0,04 ± 0,01	0,04 ± 0,01	0,05 ± 0,02	0,07 ± 0,01	0,10 ± 0,02
14:0	0,32 ± 0,04	0,32 ± 0,04	0,50 ± 0,07	0,38 ± 0,01	0,47 ± 0,02	0,43 ± 0,05	0,40 ± 0,005	0,31 ± 0,07	0,32 ± 0,01	0,26 ± 0,05	0,28 ± 0,05	0,43 ± 0,06	0,35 ± 0,002	0,39 ± 0,04	0,31 ± 0,03	0,25 ± 0,04	0,24 ± 0,05	0,29 ± 0,12	0,44 ± 0,005	0,52 ± 0,01
Iso-15:0	0,15 ± 0,02	0,15 ± 0,02	0,59 ± 0,01	0,58 ± 0,06	0,72 ± 0,04	0,60 ± 0,02	0,67 ± 0,01	0,38 ± 0,001	0,51 ± 0,15	0,33 ± 0,09	0,46 ± 0,06	0,67 ± 0,02	0,57 ± 0,04	0,78 ± 0,05	0,49 ± 0,01	0,40 ± 0,10	0,45 ± 0,08	0,63 ± 0,25	0,90 ± 0,04	1,14 ± 0,07
Anteiso-15:0	0,12 ± 0,02	0,12 ± 0,02	0,18 ± 0,00	0,12 ± 0,01	0,17 ± 0,004	0,13 ± 0,003	0,14 ± 0,01	0,10 ± 0,02	0,10 ± 0,02	0,09 ± 0,01	0,13 ± 0,02	0,23 ± 0,003	0,12 ± 0,005	0,18 ± 0,005	0,15 ± 0,06	0,10 ± 0,03	0,14 ± 0,01	0,25 ± 0,05	0,21 ± 0,07	0,20 ± 0,04
15:0	0,13 ± 0,02	0,13 ± 0,02	0,13 ± 0,01	0,10 ± 0,002	0,13 ± 0,01	0,10 ± 0,01	0,11 ± 0,00	0,10 ± 0,02	0,08 ± 0,00	0,07 ± 0,01	0,08 ± 0,01	0,08 ± 0,01	0,08 ± 0,002	0,07 ± 0,02	0,08 ± 0,02	0,08 ± 0,03	0,08 ± 0,01	0,13 ± 0,04	0,08 ± 0,01	0,09 ± 0,02
Iso-16:0	0,03 ± 0,005	0,03 ± 0,005	0,005 ± 0,00	0,002 ± 0,00	0,01 ± 0,005	0,01 ± 0,004	0,003 ± 0,00	0,01 ± 0,01	0,005 ± 0,00	0,02 ± 0,001	0,002 ± 0,00	0,01 ± 0,005	0,004 ± 0,00	0,01 ± 0,002	0,01 ± 0,004	0,01 ± 0,004	0,02 ± 0,02	0,10 ± 0,09	0,09 ± 0,02	0,10 ± 0,03
16:0	24,14 ± 3,38	24,14 ± 3,38	23,29 ± 0,01	22,83 ± 1,68	22,52 ± 0,60	26,12 ± 2,30	19,23 ± 0,94	19,36 ± 3,59	14,79 ± 0,04	14,10 ± 2,99	12,04 ± 1,80	20,67 ± 0,72	16,78 ± 0,07	18,44 ± 0,63	14,80 ± 5,31	15,44 ± 4,73	16,95 ± 0,17	18,07 ± 0,24	19,39 ± 0,33	25,68 ± 5,80

16:1 + iso-17:0	0,38 ± 0,06	0,38 ± 0,06	0,34 ± 0,01	0,32 ± 0,05	0,32 ± 0,02	0,36 ± 0,02	0,27 ± 0,00	0,28 ± 0,06	0,24 ± 0,004	0,24 ± 0,02	0,18 ± 0,04	0,36 ± 0,07	0,18 ± 0,01	0,21 ± 0,003	0,20 ± 0,08	0,24 ± 0,03	0,23 ± 0,01	0,29 ± 0,01	0,28 ± 0,01	0,33 ± 0,08
Cis 9-16:1	1,09 ± 0,19	1,09 ± 0,19	0,78 ± 0,01	0,74 ± 0,20	0,78 ± 0,02	1,08 ± 0,07	0,64 ± 0,04	0,80 ± 0,16	0,43 ± 0,01	0,50 ± 0,12	0,41 ± 0,08	0,82 ± 0,01	0,36 ± 0,13	0,75 ± 0,02	0,56 ± 0,25	0,58 ± 0,21	0,54 ± 0,01	0,73 ± 0,08	0,58 ± 0,08	0,75 ± 0,18
Anteiso 17:0 + 16:1	0,12 ± 0,02	0,12 ± 0,02	0,15 ± 0,01	0,11 ± 0,01	0,14 ± 0,002	0,12 ± 0,004	0,10 ± 0,01	0,09 ± 0,01	0,11 ± 0,01	0,10 ± 0,02	0,12 ± 0,03	0,17 ± 0,02	0,11 ± 0,02	0,13 ± 0,01	0,12 ± 0,03	0,08 ± 0,01	0,12 ± 0,01	0,21 ± 0,05	0,20 ± 0,002	0,31 ± 0,09
17:0	0,18 ± 0,03	0,18 ± 0,03	0,23 ± 0,005	0,20 ± 0,01	0,21 ± 0,01	0,17 ± 0,02	0,16 ± 0,004	0,13 ± 0,02	0,13 ± 0,004	0,11 ± 0,02	0,11 ± 0,02	0,17 ± 0,02	0,16 ± 0,01	0,15 ± 0,02	0,12 ± 0,04	0,13 ± 0,04	0,13 ± 0,002	0,15 ± 0,01	0,15 ± 0,005	0,22 ± 0,07
17:1	0,22 ± 0,03	0,22 ± 0,03	0,17 ± 0,02	0,15 ± 0,04	0,17 ± 0,001	0,24 ± 0,01	0,15 ± 0,01	0,17 ± 0,04	0,10 ± 0,003	0,10 ± 0,02	0,08 ± 0,01	0,14 ± 0,02	0,08 ± 0,04	0,13 ± 0,005	0,11 ± 0,05	0,12 ± 0,04	0,10 ± 0,02	0,13 ± 0,02	0,09 ± 0,00	0,12 ± 0,03
18:0	1,01 ± 0,14	1,01 ± 0,14	1,45 ± 0,19	0,94 ± 0,001	1,26 ± 0,04	1,05 ± 0,11	1,01 ± 0,02	0,78 ± 0,16	0,91 ± 0,09	0,70 ± 0,15	0,68 ± 0,14	1,10 ± 0,14	0,99 ± 0,005	0,89 ± 0,07	0,71 ± 0,24	0,82 ± 0,28	0,94 ± 0,01	0,92 ± 0,12	1,14 ± 0,01	1,54 ± 0,43
Cis 9-18:1	2,89 ± 0,42	2,89 ± 0,42	3,16 ± 0,41	1,87 ± 0,56	2,75 ± 0,004	2,46 ± 0,16	2,25 ± 0,02	1,81 ± 0,30	1,39 ± 0,002	1,32 ± 0,32	1,18 ± 0,20	2,29 ± 0,58	1,20 ± 0,53	1,60 ± 0,09	1,33 ± 0,42	1,63 ± 0,65	1,38 ± 0,34	1,34 ± 0,23	1,29 ± 0,005	1,69 ± 0,54
Cis 11-18:1	0,52 ± 0,10	0,52 ± 0,10	0,81 ± 0,02	0,38 ± 0,10	0,71 ± 0,01	0,47 ± 0,05	0,55 ± 0,001	0,42 ± 0,07	0,69 ± 0,01	0,48 ± 0,09	0,64 ± 0,15	0,84 ± 0,08	0,44 ± 0,21	0,63 ± 0,03	0,61 ± 0,16	0,47 ± 0,08	0,75 ± 0,12	1,02 ± 0,26	1,09 ± 0,00	1,69 ± 0,44
18:2ω-6	2,85 ± 0,46	2,85 ± 0,46	2,89 ± 0,24	2,55 ± 0,52	2,65 ± 0,08	3,64 ± 0,44	2,33 ± 0,22	2,60 ± 0,56	1,98 ± 0,01	1,68 ± 0,39	1,58 ± 0,32	2,59 ± 0,07	1,86 ± 0,71	2,31 ± 0,01	1,83 ± 0,62	1,88 ± 0,67	2,05 ± 0,44	2,01 ± 0,22	2,03 ± 0,02	2,43 ± 0,91
18:3ω-6	2,88 ± 0,54	2,88 ± 0,54	2,65 ± 0,44	2,75 ± 0,54	2,22 ± 0,02	4,28 ± 0,58	1,92 ± 0,23	3,02 ± 0,65	1,95 ± 0,05	1,89 ± 0,40	1,55 ± 0,26	2,80 ± 0,06	1,87 ± 0,59	2,72 ± 0,14	1,99 ± 0,79	1,81 ± 0,40	2,13 ± 0,36	2,32 ± 0,38	2,03 ± 0,15	2,37 ± 0,74
18:3ω-3	1,40 ± 0,26	1,40 ± 0,26	1,21 ± 0,18	1,28 ± 0,17	1,04 ± 0,04	1,96 ± 0,20	0,93 ± 0,11	1,33 ± 0,25	0,89 ± 0,04	0,83 ± 0,19	0,73 ± 0,12	1,20 ± 0,01	0,97 ± 0,31	1,24 ± 0,12	0,90 ± 0,31	0,83 ± 0,22	1,14 ± 0,09	1,13 ± 0,01	1,07 ± 0,01	1,18 ± 0,34

20:3ω6	0,23 ± 0,04	0,23 ± 0,04	0,30 ± 0,05	0,25 ± 0,04	0,25 ± 0,01	0,33 ± 0,04	0,21 ± 0,02	0,24 ± 0,06	0,21 ± 0,001	0,18 ± 0,04	0,17 ± 0,02	0,25 ± 0,01	0,21 ± 0,09	0,26 ± 0,04	0,18 ± 0,06	0,19 ± 0,05	0,22 ± 0,07	0,22 ± 0,02	0,18 ± 0,01	0,19 ± 0,06
22:0	0,09 ± 0,01	0,09 ± 0,01	0,11 ± 0,03	0,03 ± 0,004	0,07 ± 0,002	0,03 ± 0,002	0,04 ± 0,01	0,02 ± 0,01	0,03 ± 0,002	0,03 ± 0,01	0,06 ± 0,03	0,14 ± 0,05	0,03 ± 0,002	0,06 ± 0,01	0,06 ± 0,03	0,03 ± 0,01	0,06 ± 0,03	0,09 ± 0,04	0,09 ± 0,03	0,14 ± 0,05
20:4ω-3	0,45 ± 0,08	0,45 ± 0,08	0,50 ± 0,07	0,41 ± 0,10	0,41 ± 0,03	0,65 ± 0,08	0,36 ± 0,03	0,47 ± 0,09	0,36 ± 0,02	0,33 ± 0,07	0,31 ± 0,05	0,44 ± 0,03	0,37 ± 0,09	0,45 ± 0,08	0,23 ± 0,02	0,18 ± 0,04	0,18 ± 0,04	0,21 ± 0,07	0,31 ± 0,03	0,39 ± 0,01
SFA	25,15 ± 3,52	25,15 ± 3,52	24,74 ± 0,20*	23,71 ± 1,68	23,78 ± 0,64	27,17 ± 2,41	20,25 ± 0,96	20,14 ± 3,75	15,7 ± 0,05	14,81 ± 3,14	12,72 ± 1,94	21,77 ± 0,85	17, 7 ± 0,07	19,33 ± 0,69	15,51 ± 5,55	16,26 ± 5,01	17,89 ± 0,18	18,99 ± 0,36	20,53 ± 0,32	27,23 ± 8,03
PUFA	8,75 ± 1,58	8,75 ± 1,58	8,25 ± 1,11	8,23 ± 1,54	7,12 ± 0,17	12,64 ± 1,71	6,31 ± 0,70	8,86 ± 1,93	5,93 ± 0,10	5,53 ± 1,27	4,72 ± 0,88	8,33 ± 0,13	5,74 ± 1,99	8,04 ± 0,39	5,92 ± 2,28	5,62 ± 1,55	6,60 ± 1,06	6,89 ± 0,84	6,34 ± 0,32	7,41 ± 2,39
ω6	5,97 ± 1,01	5,97 ± 1,01	5,84 ± 0,72	5,54 ± 1,10	5,12 ± 0,10	8,25 ± 1,06	4,46 ± 0,46	5,87 ± 1,27	4,14 ± 0,06	3,75 ± 0,83	3,29 ± 0,61	5,64 ± 0,14	3,94 ± 1,39	5,28 ± 0,19	4,00 ± 1,47	3,89 ± 1,12	4,39 ± 0,87	4,54 ± 0,61	4,24 ± 0,18	4,99 ± 1,71
ω3	3,46 ± 0,68	3,46 ± 0,68	3,21 ± 0,51	3,35 ± 0,58	2,66 ± 0,11	5,37 ± 0,77	2,41 ± 0,28	3,71 ± 0,81	2,36 ± 0.06	2,29 ± 0,55	1,91 ± 0,35	3,38 ± 0,03	2,38 ± 0,79	3,47 ± 0,32	2,33 ± 0,88	2,09 ± 0,52	2,61 ± 0,22	2,78 ± 0,17	2,59 ± 0,11	3,01 ± 0,73
ω6/ω3	1,72 ± 0,05	1,72 ± 0,05	1,82 ± 0,06	1,65 ± 0,04	1,93 ± 0,04	1,54 ± 0,02	1,85 ± 0,02	1,58 ± 0,004	1,75 ± 0,02	1,64 ± 0,04	1,72 ± 0,001	1,67 ± 0,06	1,65 ± 0,04	1,52 ± 0,09	1,71 ± 0,02	1,85 ± 0,07	1,69 ± 0,19	1,63 ± 0,12	1,64 ± 0,12	1,66 ± 0,17
Total FA	40,46 ± 5,78	40,46 ± 5,78	40,60 ± 0,43	37,33 ± 4,27	37,90 ± 0,60	46,42 ± 4,54	32,34 ± 1,70	33,94 ± 6,51	26,05 ± 0,06	24,2 ± 5,25	21,43 ± 3,55	36,8 ± 1,82	27,50 ± 3,10	32, 86 ± 1,3	25,86 ± 9,06	26,29 ± 7,87	29,02 ± 1,33	31,57 ± 0,10	32,72 ± 0,92	42,29 ± 12,1