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RESEARCH PAPER

Effects of Climate Change on the Production of Polysaccharides and Phycobiliproteins by *Nostoc commune* Vaucher ex Bornet et Flahault

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Abstract

Nostoc commune synthesizes polysaccharides and phycobiliproteins under natural conditions, but little is known about how environmental changes could affect their production. In this study, colonies of *N. commune* were subjected to increases in ultraviolet radiation, ammonium concentration, electrical conductivity, and temperature, to assess the potential changes in the concentrations of polysaccharides and phycobiliproteins. The results indicate that UVB radiation significantly increased the synthesis of polysaccharides ($F=62.691$; $p<0.01$), while UVA radiation caused a significant increase in the production of total phycobiliproteins ($F=22.472$, $p<0.01$) phycocyanin ($F=8.546$, $p<0.01$), phycoerythrin ($F=12.876$, $p<0.01$), and allophycocyanin ($F=58.143$, $p<0.001$). Also, 50 µM NH_4Cl significantly increased the synthesis of polysaccharides ($F=45.706$; $p<0.01$) while increased near significant total phycobiliproteins ($F=5.043$, $p<0.1$), phycoerythrins ($F=4.57$, $p<0.1$), allophycocyanin ($F=4.892$, $p<0.1$), and phycocyanin ($F=4.921$, $p<0.1$). Furthermore, a conductivity value of 4 $mScm^{-1}$ enhanced near significant the production of polysaccharides ($F=4.816$; $p<0.1$) and phycocyanin ($F=9.728$, $p<0.1$). Nevertheless, a significant effect of total phycobiliproteins was observed ($F=23.686$, $p<0.01$), as well as allophycocyanin ($F=57.092$, $p<0.001$), and phycoerythrin ($F=13.928$, $p<0.01$). Finally, the optimal temperature for the synthesis of polysaccharides was 30 °C. Also, 30 ºC significantly increased the synthesis of total phycobiliproteins ($F=292.211$, $p<0.001$), as well as on phycocyanin ($F=126.433$, $p<0.001$) and allophycocyanin ($F=7.991$, $p<0.05$). These data indicate the ability of *N. commune* to modify its synthesis of polysaccharides and phycobiliproteins in response to extreme environmental conditions related to climate change, underscoring the interest in *N. commune* for future applied research on the biotechnological and pharmaceutical production of both types of compounds.

Article Highlights

- *Nostoc commune* **could adapt the content of polysaccharides and phycobiliproteins in response to extreme environmental conditions related to climate change as ultraviolet radiation, ammonium, conductivity and temperature.**
- **UV radiation significantly increased the synthesis of polysaccharides and phycobiliproteins in** *N. commune.*
- **50 µM NH_4Cl significantly enhanced the synthesis of polysaccharides and near significant the synthesis of phycobiliproteins in** *N. commune*
- **4 $mScm^{-1}$ significantly increased near significant the production of polysaccharides and phycocyanin. Nevertheless, a significant effect of total phycobiliproteins, allophycocyanin, and phycoerythrin was observed in** *N. commune***.**

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- **30 °C was the optimal temperature for the synthesis of polysaccharides and significantly enhanced the synthesis of phycobiliproteins in *N. commune* was 30 °C**

Keywords Climate change · Cyanobacteria · Environmental parameters · Pharmaceutical and biotechnological applications · Phycobiliproteins · Polysaccharides

Introduction

Cyanobacteria are photosynthetic prokaryotic organisms widely distributed in habitats ranging from aquatic to terrestrial environments, including extreme conditions such as hot springs, hypersaline water, deserts, and polar regions (Whitton and Potts 2000). As an adaptation strategy, to successfully compete in the different habitats of the planet, they produce a wide variety of bioactive compounds (Helm and Potts 2012) with a wide range of biological properties—including antiviral, antibacterial, antifungal, antitumor, and anti-inflammatory activities. Cyanobacteria have proven to be one of the richest sources of bioactive compounds, especially polysaccharides and proteins (Sivonen and Börner 2008).

Polysaccharides are complex molecules composed of six or more different monosaccharides out of a total of at least 12 sugars (De Philippis and Vincenzini 1998). Cyanobacteria produce polysaccharides that can be classified into three groups: (i) endogenous polysaccharides that serve as storage compounds or polyglucan granules; (ii) cell envelope polysaccharides or lipopolysaccharides (LPS); (iii) extracellular polysaccharides, which can be of two types: capsular polysaccharides (CPS) and exopolysaccharides (EPS) (Pereira et al. 2018).

Among the functions attributed to polysaccharides are the protection of cyanobacteria—from desiccation, intake by herbivores, and the entry of toxic substances—and the promotion of the adhesion and immobilization of the organism (Decho et al. 2009). The polysaccharides act like an adhesive favoring interactions and cellular associations among microorganisms. In this manner, they create micro-environments within which the transfer of metabolites is very common, so providing a way for microorganisms to ensure their survival in nutrient-starved environments (Elsakhawy et al. 2017).

The most important characteristic of polysaccharides is their high and varied bioactivity (Garbacki et al. 2000). For this reason, they have countless applications, for example: in biotechnology, as emulsifiers, stabilizers, and thickeners (Parker et al. 1996; Mallick, 2002); in pharmacology, as antitumor, antiviral, antibacterial, and antifungal agents (Garbacki et al. 2000; Zhang et al. 2008); and in environmental protection, as the restoration of degraded soils since polysaccharides are able to concentrate charged organic molecules and inorganic ions and they also provide against high or low temperature and salinity (Micheletti et al. 2008; Abed et al. 2006).

Phycobiliproteins are holoproteins with linear tetrapyrrolic prosthetic groups (phycobilins) that are covalently linked to apoprotein-specific cysteine residues. They are classified into three main groups: bluish-green allophycocyanins (APC) (maximum absorption, A_{max} = 650–655 nm), blue phycocyanins (PC) (A_{max} = 610–620 nm), and phycoerythrins (PE), red in color with an A_{max} of 540–570 nm (Asencio and Hoffmann 2013). Phycobiliproteins are assembled in supramolecular complexes called phycobilisomas that are located on the external face of the thylakoid membrane, where phycobiliproteins are organized in order of their maximum absorption. This arrangement ensures the transfer of energy to the reaction centers, achieving close to 100% efficiency in light conduction (Raghav et al. 2015).

In addition to serving as accessory pigments for photosynthesis, phycobiliproteins are a reserve of nitrogen that is mobilized when this element is scarce in the environment.

Phycobiliproteins, due to their fluorescent properties, have applications in clinical and immunological analyses such as flow cytometry, fluorescence immunoassays, and fluorescence microscopy for biomedical diagnosis and research (Telford et al. 2001). They also have therapeutic value due to their antioxidant, anti-cancer, neuroprotective, anti-inflammatory, hepatoprotective, and hypocholesterolemic effects (Sonani et al. 2015). Their use as natural colorants in foods (fermented dairy products, ice creams, beverages, chewing gums, etc.) and cosmetics (eyeshadows, lipstick, nail polish, etc.) is notable (Raghav et al. 2016).

Different cultures, especially the Chinese, started using cyanobacteria 2000 years ago and used *Nostoc* to survive during times of famine. However, the biotechnological exploitation of microalgae did not really begin to develop until the middle of the last century (Spolaore et al. 2006).

The overexploitation of some *Nostoc* species in China shows the need for more research on their growth. This is not only to establish and optimize the production process but also to identify the conditions that favor the production of bioactive compounds, among which phycobiliproteins and polysaccharides stand out, since they are increasingly in demand for their numerous biotechnological and pharmaceutical applications (Mota et al. 2013; Sonani et al. 2015).

Currently, besides *Nostoc*, the most economically relevant genera of cyanobacteria are *Arthrospira*, and *Aphanizomenon*, which are collected and/or cultivated for purposes

mainly related to food and health due to their chemical composition.

In recent years it has been observed that primary producers are especially sensitive to climate change, mainly due to the alteration of the photosynthetic process and the stress conditions. In the case of cyanobacteria, these would especially affect phycobiliproteins, as they are photosynthetic pigments, and polysaccharides, for their protection against desiccation.

Studies have been conducted with some indeterminate *Nostoc* species to reveal the influence on polysaccharide production of UVB radiation (Wang et al. 2008) and nitrogen (Otero and Vincenzini 2003). Regarding the production of phycobiliproteins, the effect of UVC has been studied in *Nostoc muscorum* (Phukan et al. 2018) and the effect of UVB in an undetermined species of *Nostoc* (Kannaujiya and Sinha 2017). However, nothing is known about the effect of environmental factors linked to climate change—such as salinity, temperature, and ultraviolet radiation—on the synthesis of polysaccharides and phycobiliproteins in *Nostoc commune*.

The main objectives of this study were: (i) to assess whether environmental factors (ultraviolet radiation, ammonium concentration, electrical conductivity, and temperature) affect the synthesis of polysaccharides and phycobiliproteins in *Nostoc commune*, in a climate change scenario and (ii) to provide data of interest for future research on the production of both types of compounds for biotechnological and pharmaceutical purposes.

Material and Methods

In this section, the species selected were collected and cultured in the basic medium modified depending on the experiment. In all the experiments, the average values of the environmental conditions in the Clot de Galvany Nature Reserve throughout the year were used as a control. After 12 days, extraction and quantification of polysaccharides as extraction and quantification of phycobiliproteins were carried out. Data obtained in this study were analyzed statistically. Next, successive steps are explained in detail:

Species Selected

Nostoc commune Vaucher ex Bornet et Flahault can grow in different habitats but develops fairly large colonies in semiarid environments that are exposed all year round to extreme conditions of light; these conditions might be altered in a hypothetical climate change scenario. This cyanobacteria usually form colonies of up to several centimeters in the largest dimension, with a brown to dark-brown coloration.

Material Collection

The study area was the Clot de Galvany Nature Reserve in Alicante, SE Spain (N 38.2385960, E-0.52094400) where the average values of the environmental conditions throughout the year were a temperature of 20 °C, a source of nitrogen of 0 µM NH_4Cl, a conductivity of 2.85 $mScm^{-1}$ and, for radiation exposures, a PAR of 60 Wm^{-2}. Young colonies of *N. commune* were collected on the same day as the experiment. All the material was washed by eliminating debris and mineral salts. Similar numbers of colonies (2.5 × 2.5 cm^2) were placed in Petri dishes and three replicates were used per treatment.

Culture Medium

The BG11 medium SAG Culture collection was used as the basic medium and was modified depending on the experiment.

Experimentation

Four different basic experiments were carried out inside an illuminated culture chamber (Telstar AH-100; Telstar, Terassa, Spain) for 12 days. Light was provided for 16 h daily. The light and temperature conditions were monitored with a quantum photo radiometer and a thermometer, connected to a Delta OHM DO 9721 datalogger (DeltaOhm, Caselle de Selvazzano, Italy), respectively. The positions of the replicate Petri dishes were changed daily, in a random way, to eliminate any location effects due to minor differences in the external conditions. In all the experiments, the abovementioned average values of the environmental conditions in the study area were used as a control. The experiments consisted of modifying a single parameter at a time (the ammonium concentration as a source of nitrogen, conductivity, temperature and radiation).

Ammonium Experiment

Three different ammonium concentrations were assayed: 0, 50, and 300 µM NH_4Cl (0 µM was set as the control value, as it corresponds to the natural values in the Clot de Galvany Nature Reserve).

Conductivity Experiment

As the final conductivity of the BG11 medium was 8.17 $mScm^{-1}$, sterilized water was added to give values of 4.11 $mScm^{-1}$ (used as a control) and 2.09 $mScm^{-1}$. The conductivity was measured with an Oakton Waterproof PCD

650 (Oakton Instruments, Vernon Hills, Illinois, USA) multiparametric sensor.

Temperature Experiment

Three different temperatures were assayed: 20 °C, 30 °C, and 40 °C. The 20 °C temperature was set as a control, as it corresponds to the mean summer values of the Clot de Galvany Nature Reserve.

Radiation Experiment

A PAR irradiance (P) of 60 W m^{-2} provided by F36W/54–765-TB was set for the radiation experiment, and ultraviolet radiation A (UVA), provided by FL-PHP-40 W/09 tubes (6.44 W m^{-2}, 16 h per day), was supplemented with 4 h of ultraviolet radiation B (UVB) provided by TL-40 W/12-RS tubes (1.51 W m^{-2}). Three treatments were implemented by cutting off radiation using UV filters: (i) the samples exposed to P + UVA + UVB (PAB; colonies covered with a Lee 216 filter); (ii) the samples exposed to P + UVA (PA; colonies covered with a Lee 130 filter); and (iii) the samples exposed to only P (colonies covered with a Lee 226 filter).

Extraction and Quantification of Polysaccharides

To determine the amount of polysaccharides present in each sample, the phenol–sulfuric acid colorimetric method for the determination of carbohydrates was adapted (Dubois et al. 1956). In this method, phenol reacts with the carbohydrate in the presence of heat, giving rise to hydroxymethylfurfural. Preliminary tests, to find the appropriate concentration of phenol, showed that 75% phenol was ideal due to the high amount of polysaccharides in this species of cyanobacteria. Once the frozen sample had been thawed, it was placed in a 20-ml glass tube, where it was crushed with the help of a Potter–Elvehjem (Sigma). Then, 1 ml of 75% phenol was added and the mixture was stirred in a Heidolph Reax vortex mixer, in 10-s bursts, before being allowed to stand for another 10 s to complete the 5-min extraction. Subsequently, 5 ml of concentrated sulfuric acid were added, and 60 min later the radiation absorbed at 750 nm was measured in a UV/Visible spectrophotometer (Zuzi 4201/50 model) in order not to obtain erroneous results due to the turbidity of the sample. The appropriate dilutions were made until any turbidity that caused erroneous results were eliminated and, finally, the radiation absorbed at 490 nm was measured as the colorimetric intensity. Pellet was dried in an oven at 60 ºC overnight. The standard curve was set up a posteriori, adjusting it to the absorbance signal range of the polysaccharide test samples. Glucose was used for the standard curve, with the X-axis corresponding to the known concentrations of glucose and the Y-axis to the absorbance at 490 nm obtained for those concentrations. Polysaccharides values were expressed as mgg^{-1} dw (dry weight).

Extraction and Quantification of Phycobiliproteins

Once the samples had been thawed, they were transferred to a test tube covered with aluminum foil. Here, in 2.5 ml of phosphate buffer at pH 6.5, the material was ground with the aid of a Potter–Elvehjem (Sigma), to extract the phycobiliproteins. This whole process was carried out on the ice, maintaining a temperature around 4 ºC. The water-soluble extract was centrifuged for 15 min at 4 ºC and 10,000 g, in an Eppendorf 5415 R centrifuge. Pellet was dried in an oven at 60 ºC overnight. Subsequently, the absorbances of the supernatant at 652 nm, 615 nm, and 562 nm were measured with a UV/Visible spectrophotometer (Zuzi 4201/50 model). From these values, the concentrations of phycobiliproteins in the samples were calculated using the Bennett and Bogorad (1973) formulas. Phycobiliproteins values were expressed as mgg^{-1} dw (dry weight).

Statistical Analysis

The analysis of the data obtained in this study was carried out with the statistical program SPSS Statistics v22.0. To determine if the differences among the cultures subjected to different conditions (according to the radiation, temperature, conductivity, and ammonium concentration) were significant or not, an analysis of variance (one-way ANOVA) was carried out with a post hoc Tukey HSD test. The level of statistical significance was established with evidence of significant ($p < 0.05$) or near significant ($0.05 \leq \mathbf{p} < 0.1$).

Results

Effects of Radiation

A significant influence of radiation on polysaccharide synthesis was observed ($F = 62.69$, $p < 0.01$). The production of polysaccharides was highest with UVB light (PAB), followed by PAR (P) and UVA (PA) (Fig. 1).

A significant effect of radiation was recorded for the synthesis of total phycobiliproteins ($F = 22.472$, $p < 0.01$) and for the synthesis of phycocyanin ($F = 8.546$, $p < 0.01$), phycoerythrin ($F = 12.876$, $p < 0.01$), and allophycocyanin ($F = 58.143$, $p < 0.001$). The production of total phycobiliproteins was highest with UVA (PA) light, followed by UVB (PAB) and PAR (P). The same pattern was followed by phycocyanin, whereas the synthesis of phycoerythrin and allophycocyanin was greatest with UVA (PA) radiation, followed by PAR (P) and UVB (PAB) (Fig. 1).

Effects of the Ammonium Concentration

The production of polysaccharides was highest with 50 µM NH_4Cl, significantly so ($F = 45.706$, $p < 0.01$). The absence of ammonium and the presence of 300 µM NH_4Cl produced values that were very similar, did not differ statistically from each other and were lower than that at 50 µM NH_4Cl (Fig. 2).

There was an effect near significant of the ammonium concentration on the synthesis of total phycobiliproteins ($F = 5.043$, $p < 0.1$), phycoerythrins ($F = 4.57$, $p < 0.1$), allophycocyanin ($F = 4.892$, $p < 0.1$) and phycocyanin ($F = 4.921$, $p < 0.1$). The production of total phycobiliproteins, allophycocyanin, and phycoerythrin was highest at 50 µM NH_4Cl, followed by 0 µM NH_4Cl and 300 µM NH_4Cl, while phycocyanin was most abundant at 50 µM NH_4Cl, followed by 300 µM NH_4Cl and 0 µM NH_4Cl (Fig. 2).

Effects of the Conductivity

The production of polysaccharides was highest, near significant so ($F = 4.816$, $p < 0.1$), at the conductivities of 4.11 $mScm^{-1}$ and 8.17 $mScm^{-1}$, and was lowest at 2.09 $mScm^{-1}$ (Fig. 3).

A significant effect of conductivity on the synthesis of total phycobiliproteins was observed ($F = 23.686$, $p < 0.01$), as well as on allophycocyanin ($F = 57.092$, $p < 0.001$), and phycoerythrin ($F = 13.928$, $p < 0.01$) while in phycocyanin ($F = 9.728$, $p < 0.1$) was near significant effect. The concentrations of total phycobiliproteins, phycocyanins, and phycoerythrins were highest at a conductivity of 4.11 $mScm^{-1}$, followed by the high conductivity (8.17 $mScm^{-1}$) and the low conductivity (2.09 $mScm^{-1}$), respectively. In the case of allophycocyanin, the highest production was also recorded with the moderate conductivity (4.11 $mScm^{-1}$), but in this case followed by the low and then the high conductivity (Fig. 3).

Effects of the Temperature

The production of polysaccharides was highest, but not significantly so, at 30 °C, followed by 20 °C and then 40 °C (Fig. 4).

A significant effect of the temperature was observed for the synthesis of total phycobiliproteins ($F = 292.211$, $p < 0.001$), as well as on phycocyanin ($F = 126.433$, $p < 0.001$) and allophycocyanin ($F = 7.991$, $p < 0.05$). The highest concentration of phycobiliproteins, both total and of the different types, was obtained in those cultures that had been subjected to a temperature of 30 ºC, followed by those that had been at 40 ºC and finally those that had been at 20 ºC (Fig. 4).

Discussion

Exposure to ultraviolet radiation caused an increase in the synthesis of polysaccharides in *Nostoc commune*, especially with UVB radiation, coinciding with the findings of Ehling-Schulz et al. (1997) and Wang et al. (2008) for several *Nostoc* species. Also, ultraviolet radiation produced increases in the concentrations of the three types of phycobiliproteins studied here in *N. commune*, especially with UVA radiation; contrastingly, Kannaujiyi et al. (2016) achieved a similar effect in *Nostoc* sp. but with UVB radiation. Phycoerythrin and allophycocyanin were more susceptible than phycocyanin to the damage caused by UVB radiation in *N. commune*. This coincides with previous findings for *Lyngbya* sp. (Prasad et al. 2015) but contrasts with those of Richa et al (2013), who detected that phycocyanin was more susceptible to UVB than phycoerythrin in an undetermined species of *Nostoc*.

Coinciding with Moreno et al. (1998), who indicated that the presence of a combined source of nitrogen at high concentrations decreased the production of polysaccharides in *Anabaena* sp., here, in *N. commune*, 300 µM NH_4Cl decreased the synthesis of polysaccharides. Apparently, this is due to the fact that nitrogen fixation requires large amounts of energy, meaning that less energy is available for the production of carbohydrates. According to Moreno et al. (1998), chlorophyll shows a progressive increase as the external ammonium concentration increases, so the cell could be carrying out metabolism for the fixation of added nitrogen. The production of polysaccharides in *N. commune* was maximal at 50 µM NH_4Cl, suggesting that there was a balance between carbon and nitrogen that promoted the incorporation of carbon into the polysaccharides of this cyanobacteria (Otero and Vincenzini 2003).

It is quite possible that the production of mucilage by cyanobacteria is the result of unbalanced growth caused by nutrient deficits (Lange 1976). In particular, a shortage or deficiency of nitrogen and sulfur results in stagnation of protein synthesis, while the full photosynthetic capacity is maintained. Under such conditions, cyanobacteria can accumulate large amounts of glycogen in polyglucan granules (Allen and Smith 1969; Lehmann and Wöber 1976). The cell's ability to store glycogen is limited and any additional polysaccharides can be excreted as mucilage.

We found an increase in the synthesis of phycobiliproteins in *N. commune* at a high concentration of a combined nitrogen source (50 µM NH_4Cl), coinciding with the results of Loreto et al. (2004) for *Anabaena* sp. For *N. commune* the results suggest that the availability of nitrogen affected the abundance of the distinct types of phycobiliproteins without altering the total content of phycobiliproteins. This implies the maintenance of balanced pigment abundances as

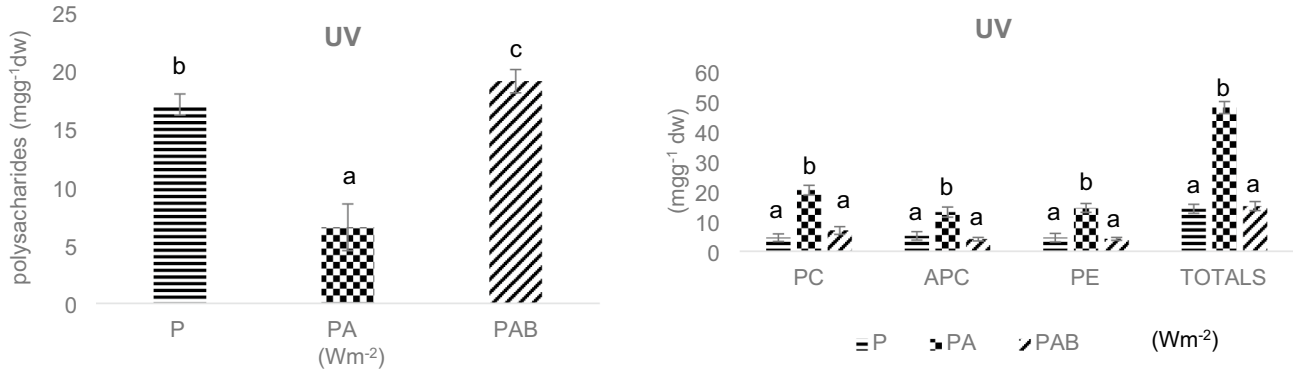

Fig. 1 Polysaccharides concentration and phycobiliproteins (totals), phycocyanins (PC), phycoerythrins (PE) and allophycocyanins (APC) concentrations expressed in mg g^{-1}dw ± SD in the different radiation conditions assayed expressed in Wm^{-2}: PAR (P), UVA (PA) and UVB (PAB). Different lowercase letters indicated significant differences in means comparisons according to Tukey´s test

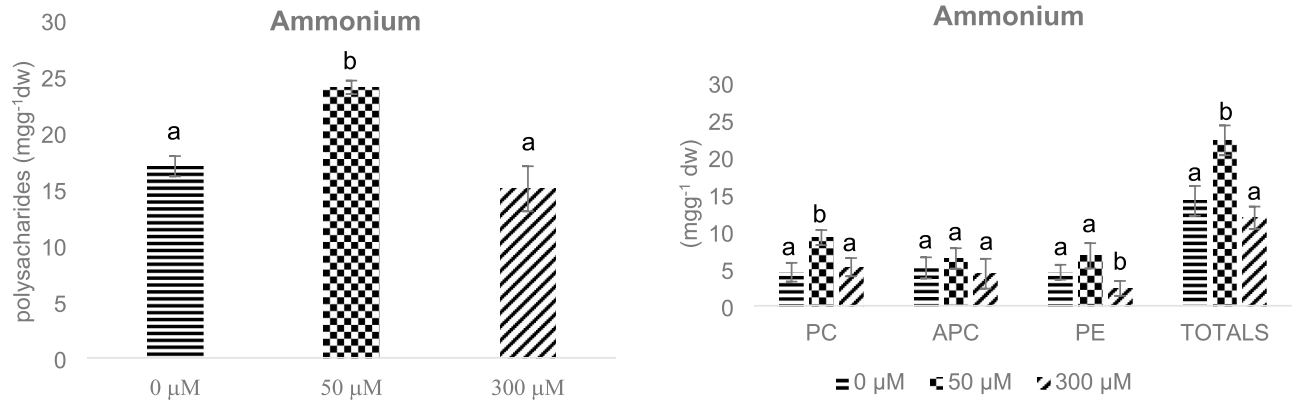

Fig. 2 Polysaccharides concentration and phycobiliproteins (totals), phycocyanins (PC), phycoerythrins (PE) and allophycocyanins (APC) concentrations expressed in mg g^{-1}dw ± SD in the different ammonium concentration assayed: 0, 50, and 300 µM NH_4Cl. Different lowercase letters indicated significant differences or near significant differences in means comparisons according to Tukey´s test

a cyanobacterial response to the nitrogen source, coinciding with the findings of Simeunović et al. (2013) for terrestrial cyanobacteria in dry environments. Similarly, in *N. commune*, we observed that the concentration of phycoerythrin was lower than that of phycocyanin, as was found also for *Calothrix* sp. when it used ammonium as a combined source of nitrogen (Liotenberg et al. 1996).

For *N. commune*, the production of polysaccharides was similar at conductivity values of 4.11 $mScm^{-1}$ and 8.17 $mScm^{-1}$. However, a decrease to 2.09 $mScm^{-1}$ diminished the accumulation of polysaccharides, probably due to the fact that this species grows in an environment of high salinity (data not shown) and is used to tolerating high salt concentrations. Polysaccharides can represent up to 65% of the dry weight in *Nostoc* sp. under saline conditions (Shi 2016). This high amount of carbohydrates is believed to regulate water loss and absorption and to serve as a matrix that protects the entire cyanobacteria (Inoue-Sakamoto et al. 2017). The cell morphology may also have an influence since *Nostoc* species with spherical cells showed greater tolerance of water stress and salinity than *Nostoc* species with cells having a distinct morphology; the former were able to restore degraded soil better than the latter (Obana et al. 2007).

The conductivity plays an important role in the production of phycobiliproteins in cyanobacteria since, here, high values (4.11 $mScm^{-1}$) increased their production in *N. commune*, coinciding with *Oscillatoria* sp (Fatma 2009) and *Spirulina* (Sharma et al 2014). Of all the phycobiliproteins analyzed, phycocyanin was the one whose synthesis in *N. commune* was increased most by high values of conductivity, coinciding with *Spirulina* (Sharma et al 2014).

The production of polysaccharides in *N. commune* was maximal at 30 °C. However, an increase to 40 °C caused a decrease in polysaccharides production, indicating that

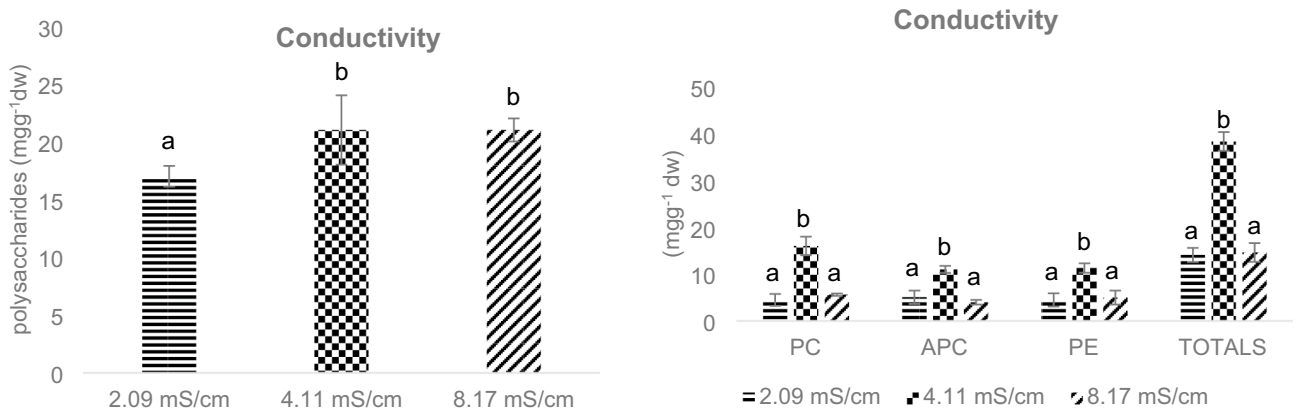

Fig. 3 Polysaccharides concentration and phycobiliproteins (totals), phycocyanins (PC), phycoerythrins (PE) and allophycocyanins (APC) concentrations expressed in mg g^{-1}dw ± SD in the different electrical conductivity conditions assayed: 2.09, 4.11 and 8.17 $mScm^{-1}$. Different lowercase letters indicated significant differences or near significant differences in means comparisons according to Tukey´s test

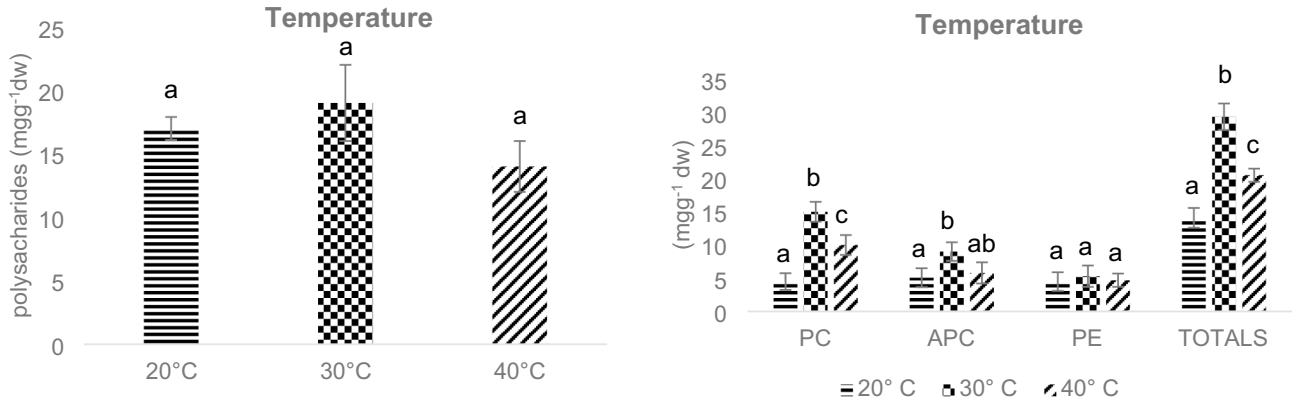

Fig. 4 Polysaccharides concentration and phycobiliproteins (totals), phycocyanins (PC), phycoerythrins (PE) and allophycocyanins (APC) concentrations expressed in mg g^{-1} dw ± SD in the different temperature conditions assayed: 20, 30 and 40 ºC. Different lowercase letters indicated significant differences in means comparisons according to Tukey´s test

temperatures above the optimum act as a stressor, as was found also with *Cyanothece* sp. (Trabelsi et al. 2009).

Regarding phycobiliproteins, the optimal temperature for their production by *N. commune* in this work was 30 ºC, in accordance with Tasneem (2009), who considered this the ideal temperature for the production of photosynthetic pigments in cyanobacteria. In *N. commune*, phycoerythrin seems to be less thermally stable than phycocyanin, since at 40 ºC it was less abundant in disagreement with Galetovic et al. (2020).

The semi-arid regions are characterized by water scarcity, high solar radiation, and low infiltration of water into the soil (Barberá et al. 2009). In these environments, the restoration of plant communities can be quite slow, with the exception of microalgae, which can reestablish communities almost completely in a few weeks after major floods (Asencio 2013). This suggests that the algae that live in such environments are well adapted to strong radiation, high temperatures, and high conductivity (Asencio 2014). Climate change models predict a reduction in precipitation but an increase in floods, as well as an exponential increase in maximum and minimum temperatures, salinity, and radiation (Brunet et al. 2009). All these factors will increase the production of protective compounds in microalgae; thus, these organisms will be of increasing economic interest due to the importance of these compounds in the biotechnological and pharmaceutical industries.

Conclusions

The experimental results obtained here show the great ability of *Nostoc commune* to modify its accumulation of polysaccharides and phycobiliproteins in response to extreme environmental conditions related to climate change as ultraviolet radiation, ammonium, conductivity and temperature. UVB radiation, 50 μM NH_4Cl and 4 $mScm^{-1}$ significantly increased the synthesis of polysaccharides while UVA radiation, 50 μM NH_4Cl, 4 $mScm^{-1}$, and 30 ºC significantly increased the synthesis of phycobiliproteins. These results will be of great application in future research on the production of both these types of biomacromolecules for biotechnological and pharmaceutical purposes.

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Author Contribution ADA and MTP conceived and designed the sampling and the experiments; PLL and LG performed the experiments; MAM and MMJ analysed the data; ADA and PLL wrote the paper. All the authors contributed to the general discussion, revision, and manuscript editing.

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Code Availability Not applicable.

Declarations

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Ethics Approval Not applicable.

Consent to Participate Not applicable.

Consent for Publication Not applicable.

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