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Photosynthetic UV stress tolerance of the Antarctic snow alga *Chlorella* sp. modified by enhanced temperature?

C. Rivas^{1,2*}, N. Navarro^{1,3}, P. Huovinen^{1,4} and I. Gómez^{1,4}

Abstract

Background: Photosynthetic characteristics and the effect of UV radiation and elevated temperature measured were studied in *Chlorella sp.* isolated from a snow microalgal community at King George Island, Maritime Antarctica through the chlorophyll florescence (rapid light curves and maximum quantum yield, respectively). The environmental context was monitored through measurements of spectral depth profiles of solar radiation (down to 40 cm) in the snowpack as well as a through continuous recording of temperature and PAR using dataloggers located at different depths (0–30 cm) within the snow column.

Results: The photochemistry of *Chlorella sp.* was affected by UV radiation in a 12-h laboratory exposure under all studied temperatures (5, 10, 15, 20 °C): the algae exposed to PAR + UV-A radiation were inhibited by 5.8 % whilst PAR + UV-A + UV-B radiation decreased F_v/F_m by 15.8 %. In both treatments the 12-h recovery after UV exposure was almost complete (80–100 %). Electron transport based P-l curve parameters maximal electron transport rate (ETR_{max}), photosynthetic efficiency (α) and the saturating irradiance (E_k) no varied in response to different temperatures.

Conclusions: Results revealed that *Chlorella sp.* not only shows high photosynthetic efficiency at ambient conditions, but also exhibits tolerance to solar radiation under higher temperatures and possessing a capacity for recovery after inhibition of photosynthesis by UV radiation.

Keywords: Antarctica, Snow algae, Chlorella sp, Photosynthesis, UV radiation, Temperature

Background

The Antarctic cryosphere represents a hostile habitat for life, characterized by extreme temperature conditions varying abruptly between freezing and melting points, high levels of solar radiation, especially harmful wavelengths of ultraviolet (UV) radiation, nutrient limitation, changes in pH and osmotic stress [1, 2]. The physico-chemical properties of melting snow allow psychrophilic algae to grow in liquid interstices, where the temperature is just above the freezing point [3–5]. In polar snowfields, the biomass of snow algae can become very important and due to their capacity to fix and store carbon they play a key role as primary producers in the biogeochemical cycles in Arctic and

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Antarctic regions [6]. In coastal areas of West Antarctic Peninsula and adjacent islands, an eco-region denominated Maritime Antarctica, processes occurring in glacier and snow ecosystems are closely interrelated with those of the marine realm. Melting of massive snow/ice accumulations and consequent run-off have strong impact on the physical and biological processes of near-shore pelagic and benthic communities [7, 8].

Due to that snow algae inhabit ecosystems highly sensitive and responsive to shifts in environmental conditions (e.g. temperature, light and precipitation), they can be regarded as excellent model organisms to examine the impact of climate change. Warming in several regions has been related with lower precipitation as snow, earlier runoff and hence, a shortened period of snow permanence [9, 10]. Under these scenarios, snow algae and their associated microbial community have to adapt to new regimes of melting and freezing [11], underlining not well-understood physiological adaptations.



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Unlike alpine and other continental snowfields, coastal snow packs located in Maritime Antarctica are tentatively eutrophic environments, mostly due to the presence of seabird and mammal colonies [12]. Thus, for this habitat, light and temperature remain as the major stressors for snow algae. However, the question how these factors, alone or in combination, impact snow communities in Antarctic coastal snowfields has been poorly addressed. Data from alpine snow algae indicate that light, especially due to scattering, can be elevated and thus, algae have to cope with irradiation stress, caused by Photosynthetically Active Radiation (PAR) and Ultraviolet (UV) in conditions of low temperatures. Especially during the sensitive motile green phase in their life cycle, microalgae are sensitive excess PAR and UV [13], which affect different molecules and processes (e.g. DNA, photosynthetic apparatus, lipid membranes, etc.; reviewed by [14]) and also cell motility [15]. However, some snow algae downregulate their photochemical processes via a series of dissipative mechanisms such as the violaxanthin cycle, synthesis and accumulation of astaxanthin, turnover of D1 proteins, antenna quenching, cold induced transcripts and cold-adapted proteins, etc. which operate at temperatures close to 0 °C [12, 16, 17]. The question whether these mechanisms operate efficiently at higher temperatures remains open.

Chlorella is a unicellular green alga, which has a single chloroplast, rigid cell wall and lacks flagella [18]. The genus is globally distributed including the Antarctic [19, 20]. In general this microalga inhabits soils and other ice-free environments, however, can also be found in snow packs during the summer melting season [21]. Teoh et al. [22] analysed the growth rates, biochemical composition and profile of fatty acids of six Antarctic strains, of which algae of the class Trebouxiophyceae, including Chlorella, presented the greatest growth rates at enhanced temperature of 20 °C. Significant alterations in the morphology and activity of the chloroplasts in response to enhanced UV-B radiation have been reported for this genus [23]. Due to that gradients in solar radiation along the snowpack can impose not only considerable stress as a consequence of detrimental and photoinhibitory levels of UV radiation and PAR, but also can result in light limitation for photosynthesis at lower snow depths, one could argue that an acclimation process or physiological flexibility are important to ensure primary production. Up to now, most of the studies on snow algal photobiology have been conducted in ubiquitous flagellate green algal genera such as Chlamydomonas, or Chloromo*nas*, which show an ability to actively migrate along the snow pack column and thus "regulate" their light environment [3, 24-26]. In a recent study was demonstrated that Antarctic strains of Chlorella are more sensitive to UV radiation under elevated temperature than their counterparts from temperate or tropical regions [27]. Thus, in the present study the question whether photosynthetic characteristics of non-motile *Chlorella sp.* isolated from snow fields in Maritime Antarctica (King George Island) match the light and temperature conditions prevailing at different snow depths was examined. Moreover, the ability of *Chlorella* to endure environmental stress was assessed in a series of controlled exposures to UV radiation and elevated temperature. The prediction that elevated temperatures will enhance the detrimental effects of UV radiation was tested.

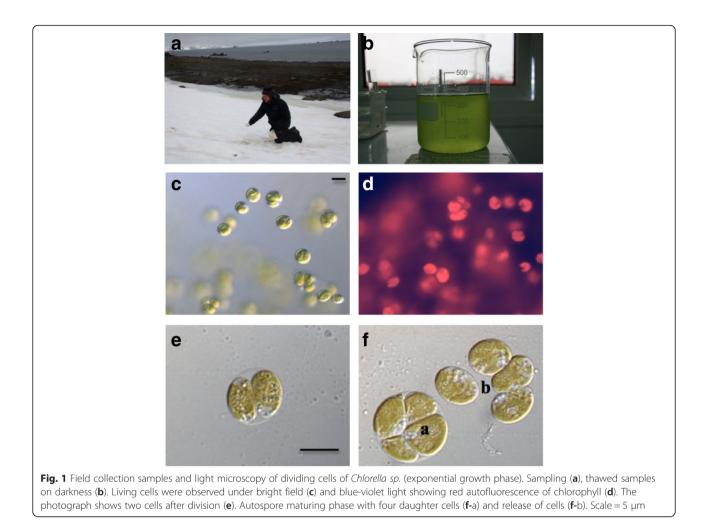
Methods

Collection and isolation of snow microalgae

During February 2015, snow samples with evident presence of snow algae (green coloration) were collected at depths below 10 cm (vegetative cells) at Elefantera beach, Fildes Peninsula King George Island (62°11'57,07" S; 58° 59'42,48"W). Samples were transported to the laboratory in the station "Base Profesor Julio Escudero" where they were cultured in bottles (TR6000, TrueLine, USA) using "Snow Algae" media standardized according to protocols defined by the culture Collection of algae of The University of Texas at Austin (UTEX). The samples were kept at a temperature of 5 °C with a photoperiod of 18:6 D:L, at irradiance of 4.7 µmol m⁻² s⁻¹. The samples were transferred to the Photobiology Laboratory of the Universidad Austral de Chile, in Valdivia, where Chlorella sp. was isolated by successive dilutions and repeated subcultures [28]. The clonal stock culture (now coded as ChlaP7MSA) was kept at a temperature of 5 °C under a 12:12 L:D light regime at 4.7 μ mol m⁻² s⁻¹. These culture conditions were maintained to achieve the exponential growth phase, determined through daily cell counts, with an optical microscope using a Neubauer chamber. Cultures were photographed under Olympus BX51TF epifluorescence microscope (model CKX41SF; Olympus, Japan) equipped with a digital camera (QImaging Micro Plublisher 5.0 RTV; software QCapture pro) under bright-field as well as visualizing chlorophyll as orange-red autofluorescence according to the methodology described by Huovinen and Gómez [29] with the U-MWBV2 mirror unit (Olympus) (excitation 400-440 nm, detection of emission from 475 nm) (Fig. 1). Experiments were performed with the clonal stock culture in the exponential growth phase.

Measurement of solar radiation and temperature in the snowpack

In situ spectral irradiance was measured during a sunny day (February 13, 2015 at noon) using an underwater hyperspectral radiometer (RAMSES-ACC2-UV–Vis, TriOs Optical Sensors, Rastede, Germany) through the snow column down to a depth of 40 cm (8 and 19 measurements per depth). According to the President Eduardo Frei Montalva Metereological Station's records,



this day had 10 % cloud cover, and moderate breeze from the Northwest at 3 m/s. At the same time, a set of HOBO UA-002-64 dataloggers (Onset Computer Corporation, Bourne, MA, USA) was programmed to record temperature and solar irradiance (PAR) at 0, 10, 20 and 30 cm depth in the snow column every 5 min for 15 days during the study period.

Exposures to temperature and UV radiation

Samples from *Chlorella sp.* clonal culture (3500 cell/ ml, exponential growth phase) were put in cell culture plates without aeration and exposed to PAR, PAR + UV-A and PAR + UV-A + UV-B radiation treatments for 12 h under a 4 temperature conditions (5, 10, 15 and 20 °C), followed by a 12-h recovery period in dim light without UV. A thermoregulated waterbath (Digit-Cool, Selecta, Spain) was used to set the different temperatures, whilst illumination was provided by three types of fluorescent lamps: UV-B-313 emitting UV-B; UV-A-340 emitting UV-A (Q-Panel, USA) and and TL-D 36 W/54-765 emitting PAR (Philips, Thailand). Three UV treatments were obtained by covering the cell culture with different cut-off filters: Ultraphan 295 (Digefra, Germany) for PAR + UV-A + UV-B condition, Ultraphan 320 for PAR + UV-A, and Ultraphan 400, for PAR treatment. The experimental UV irradiances were set at 0.25 W m⁻² for UV-B and 0.95 W m⁻² for UV-A, whilst the PAR irradiance was of 10 μ mol m⁻² s⁻¹. Total radiation dose during the 12 h exposure was 10.8 kJ m⁻² for UV-B and 40.5 kJ m⁻² for UV-A. The radiation levels were measured using the RAMSES-ACC2-UV–Vis hyperspectral radiometer.

Chlorophyll fluorescence measurements

The photosynthetic performance of *Chlorella* was measured before and after exposure to different temperatures and radiation treatments using an amplitude modulation fluorometer (Water PAM, Walz, Effeltrich, Germany). After a 12-h exposure, as well as after a 12-h recovery period, the samples were kept for 10 min in darkness and the maximum quantum yield (F_v/F_m) was subsequently measured.

The P-I curves were based on electron transport rate vs. irradiance (ETR-I) curves by exposing the *Chlorella* samples to a gradient of PAR irradiances (0 to 446 µmol photon $m^{-2} s^{-1}$) under the four temperatures described above. The relative electron transport rate (rETR) was estimated relating the effective quantum yield (Φ_{PSII}) and the intensity of actinic radiation [30], as follows:

$$rETR = \Phi_{PSII} \times E_{PAR} \times 0.5$$

where E_{PAR} is the incident actinic irradiance. The 0.5 factor comes from the assumption that 4 of the 8 electrons required to assimilate one CO₂ molecule are provided by the PSII. The ETR parameters were defined through a modified non-linear function proposed by Jassby and Platt [31]:

$$ETR = rETR_{max} * tanh (\alpha * E/rETR_{max})$$

where rETR_{max} is the maximum electron transport rate, tanh is the hyperbolic tangent function, α is the efficiency of electron transport (initial slope of the rETR vs. irradiance curves), and E is the incident irradiance. The saturation irradiance for electron transport (E_k) was calculated as the intersection between α and the rETR_{max} values.

The effect of UV radiation and temperature was assessed by comparing the inhibition of F_v/F_m , that was calculated as the percentage of decrease between the values measured in PAR + UV-A and PAR + UV-A + UV-B and values measured in samples exposed only to PAR. Likewise, the recovery was estimated by comparing the F_v/F_m values of the samples treated with UV radiation with those treated only with PAR.

Statistical analysis

The variation in the incident solar radiation of UV-B, UV-A and PAR at different depths (0, 10, 20, 30, 40 cm) was compared using nonparametric analysis of variance (Kruskal-Wallis). The variation in the responses of the photosynthetic parameters to the UV radiation exposure and recovery at different temperatures, were compared through a two-way variance analysis (ANOVA). Posthoc comparisons were carried out using Tukey HSD test. In both analyses, the ANOVA assumptions (variance homogeneity, normal distribution) were examined through the Levene's and Kolmogorov-Smirnov tests, respectively.

Results

In situ solar irradiance and temperature

The weather conditions at King George Island during the study period was characterized by cloudy days. In this line, maximal PAR values normally did not exceed 400 μ mol m⁻² s⁻¹ (Table 1). For a sunny day (10 % could

| Table 1 Maximum Photo | osynthetically Active Radiation (PAR) |
|--------------------------|---------------------------------------|
| levels, measured in snow | column, during the study period |

| Depth (cm) | 0 | 10 | 20 | 30 | |
|-------------|--|-----|-----|----|--|
| Date | PAR (μ mol photon m ⁻² s ⁻¹) | | | | |
| 3-Feb-2015 | 357 | 134 | 27 | 13 | |
| 4-Feb-2015 | 281 | 54 | 14 | 7 | |
| 5-Feb-2015 | 740 | 73 | 18 | 10 | |
| 6-Feb-2015 | 311 | 35 | 9 | 5 | |
| 7-Feb-2015 | 212 | 50 | 11 | 5 | |
| 8-Feb-2015 | 459 | 191 | 61 | 33 | |
| 9-Feb-2015 | 198 | 191 | 121 | 41 | |
| 10-Feb-2015 | 560 | 54 | 14 | 8 | |
| 11-Feb-2015 | 510 | 191 | 38 | 18 | |
| 12-Feb-2015 | 459 | 96 | 54 | 25 | |
| 13-Feb-2015 | 1276 | 331 | 122 | 60 | |
| 14-Feb-2015 | 342 | 60 | 15 | 8 | |
| 15-Feb-2015 | 459 | 45 | 12 | 6 | |
| 16-Feb-2015 | 255 | 49 | 12 | 6 | |
| 17-Feb-2015 | 383 | 134 | 49 | 27 | |
| 18-Feb-2015 | 153 | 121 | 89 | 30 | |

cover), the daily course of solar irradiation and temperature measured at 0, 10, 20 and 30 cm depths in the snow column is shown in Fig. 2. The surface irradiance reached values of 1300 µmol m⁻² s⁻¹ around midday and was attenuated by 70 % at 10 cm (decreasing to less than 350 μ mol m⁻² s⁻¹). This value matches the light requirements for saturation of photosynthesis (E_k) measured for Chlorella sp. (see Table 1). The number of hours at which algae remain under saturating irradiance (H_{sat}) at the surface was close to 12-13 h, decreasing with increasing depth (Fig. 2a). Temperature in the snow pack varied within the ranges of minimum and maximum air temperature registered by the Presidente Eduardo Frei Meteorological Station (Fig. 2b). Maximal temperature at 10 cm depth was close to 4 °C with a positive correlation between the solar irradiation and the temperature at each depth (r > 0.9; p < 0.05). Under 10 cm, temperature was close to 2 °C and varied less in the course of the day. The spectral profiles of UV radiation and PAR indicated strong decreases of UV-A and UV-B below 10 cm depth (Fig. 2c; Table 2).

Photosynthetic responses

The ETR-I curves indicated lower photosynthesis in samples incubated to 5 °C compared to higher temperatures (Fig. 3, Table 3). Mean values of ETR_{max} ranged between 50.6 at 5 °C and 71.6 at 10 °C. Similarly, the light requirements for photosynthesis (E_{k}) were lower in algae incubated to 5 °C (204.7 µmol e⁻ m⁻² s⁻¹) compared to the other temperatures where E_{k} varied between 259

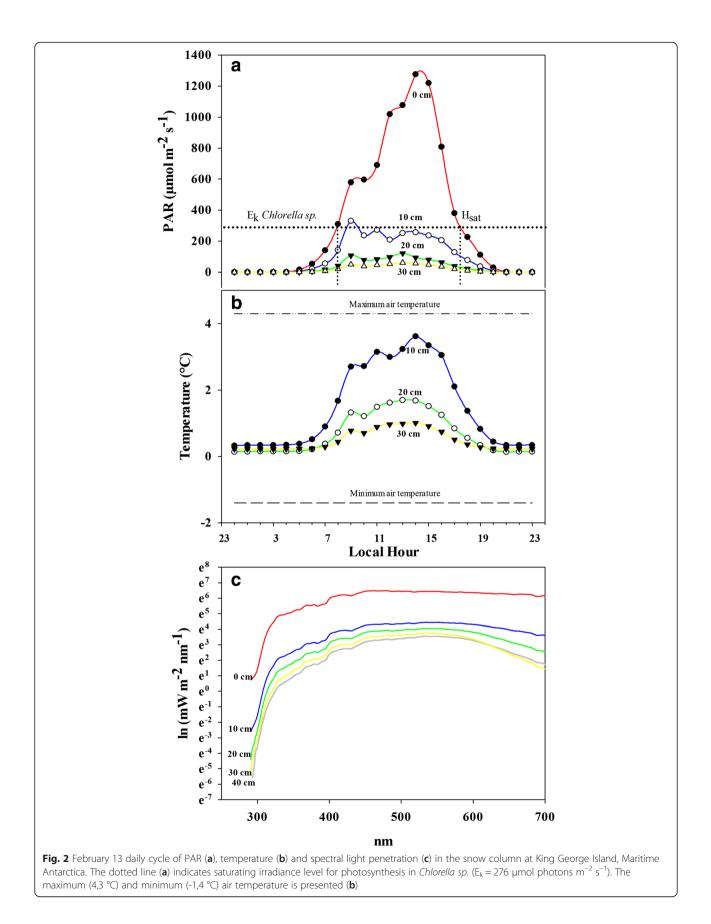


Table 2 Levels of solar UV radiation ($W m^{-2}$) in the snow column at different depths measured using a RAMSES hyperspectral radiometer. Values correspond to 8-19 measurements per depth. The spectral characteristics are shown in Fig. 2c

| 0 | | | |
|------------|---------------|-----------------|-----------------|
| | UV-A | UV-B | PAR |
| Depth (cm) | | Mean ± S.D. | |
| 0 | 15.8 ± 0.97 | 0.35 ± 0.01 | 163.7 ± 14.72 |
| 10 | 1.31 ± 0.33 | 0.018 ± 0.00 | 19.0 ± 4.12 |
| 20 | 0.69 ± 0.07 | 0.007 ± 0.00 | 11.5 ± 1.55 |
| 30 | 0.30 ± 0.01 | 0.002 ± 0.00 | 6.5 ± 0.34 |
| 40 | 0.42 ± 0.06 | 0.003 ± 0.00 | 7.6 ± 1.72 |
| - | | | |

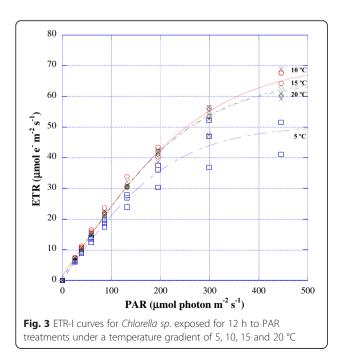
and 276 μ mol e⁻ m⁻² s⁻¹ (Table 3). The initial slope (α) did not varied between temperature treatments (Table 3).

The exposure to UV radiation caused F_v/F_m inhibition in *Chlorella sp.* (Fig. 4; p < 0.001; ANOVA; Table 4;). PAR + UV-A radiation was responsible for 5.8 % inhibition, but when UV-B was added (PAR + UV-A + UV-B) F_v/F_m decreased by 15.8 %. The temperature factor did not promote F_v/F_m differences. After the period of darkness, the F_v/F_m recovery varied between 80 to 100 %, with an increase in the recovery level associated to an increase in temperature (Fig. 4; p < 0.001; ANOVA; Table 4).

Discussion

Photosynthetic characteristics and the light environment

Our results show that at the sampling location in Fildes Peninsula, 10 cm below the snow surface



| | ETR _{max} | | E _k | | α | |
|---------------|--------------------|------|----------------|-------|-------|------|
| | Means | SD | Means | SD | Means | SD |
| 12-h Exposure | | | | | | |
| 5 °C | 50.63 | 2.30 | 204.74 | 29.43 | 0.27 | 0.02 |
| 10 ℃ | 71.64 | 2.40 | 276.29 | 24.86 | 0.30 | 0.02 |
| 15 ℃ | 65.86 | 0.60 | 259.18 | 11.93 | 0.29 | 0.00 |
| 20 °C | 66.87 | 2.10 | 261.12 | 63.66 | 0.30 | 0.02 |

irradiance does not exceed 350 μ mol m⁻² s⁻¹, which matches well the average light required for saturation of photosynthesis determined in this study for Chlorella sp. (276 μ mol m⁻² s⁻¹). Using the number of hours per day at which algae are exposed to saturating irradiances (the so-called H_{sat}), one can argue that photosynthesis of these microalga is not limited by at least for 10 h at a depth of 10 cm and 12-13 h at the surface of the snowpack, during sunny conditions. In general, these light requirements are in the lower ranges described for Chlamydomonas from Giant Mountains, Czech Republic [25] and clearly lower than light requirements of 523-826 μ mol photons m⁻² s⁻¹ measured in an Arctic population of Chlamydomonas *nivalis* [32]. In contrast to *Chlorella sp.*, the high E_k values determined in Chlamydomonas are indicative of that these algae are exposed to photoinhibitory levels of PAR, which could have negative effects on photosynthesis. In fact, it is well documented in this genus that excess of irradiation results in the formation of robust, red pigmented cysts [33-35], which are also mostly located at the surface of the snowpack [36]. Although we did not perform in situ measurements of photosynthesis, the high levels of solar radiation recorded during midday in a sunny day at Fildes Peninsula (exceeding 1200 μ mol photons m⁻² s⁻¹) suggest that Chlorella can suffer considerable photoinhibition of photosynthesis, at least when exposed to high irradiances close to the snow surface. This is exacerbated by snow reflecting most of the long wavelength radiation [37], directly affecting the light extinction patterns, mostly due to the changes in phase transitions of water [38]. It must be emphasized that in our laboratory study, levels of PAR used in the incubations were considerably lower than current irradiances measured in the field (PAR was maintained low to avoid photoinhibition and mask UV effects) and thus we cannot evaluate the impact of high PAR on the physiology of this alga.

Effects of temperature on UV stress tolerance

Due to its ubiquitous character, many species of *Chlorella* have been described as eurythermal microorganisms, which can inhabit all type of freshwater and soil environments [22]. This capacity to cope with different

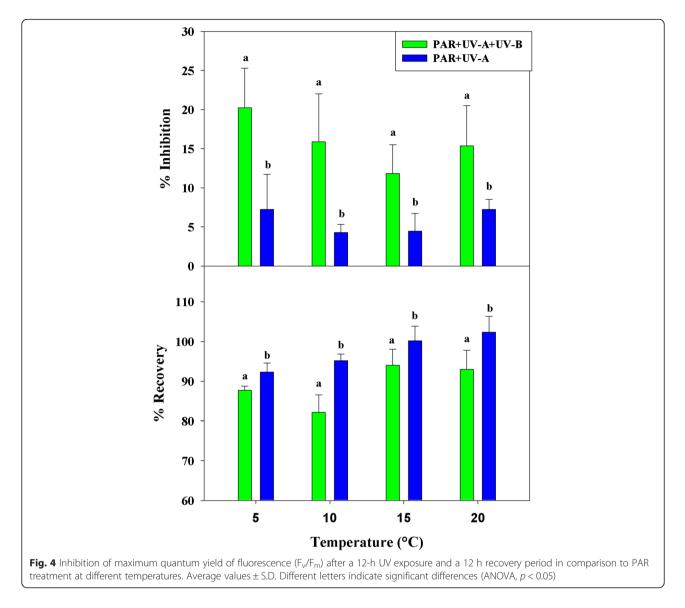


Table 4 Effects of the experimental treatments on maximum quantum yield (F_v/F_m) analysed by two-way ANOVA

| | Fv/Fm | 1 | | |
|-------------------------|-------|--------|-------|---------|
| Source | d.f. | MS | F | Р |
| 12-h Exposure | | | | |
| Temperature | 3 | 33.00 | 2.01 | 0.153 |
| Radiation | 1 | 604.51 | 36.87 | < 0.001 |
| Temperature x Radiation | 3 | 11.03 | 0.67 | 0.581 |
| 12-h Recovery | | | | |
| Temperature | 3 | 131.18 | 10.95 | < 0.001 |
| Radiation | 1 | 412.87 | 34.47 | < 0.001 |
| Temperature x Radiation | 3 | 21.04 | 1.76 | 0.196 |

thermal conditions has also been recognized for isolated strains of Chlorella sp. from Antarctic [19]. In our study, Chlorella sp. was visually more abundant below 10 cm where temperatures along the day ranged between 0 and 3.8 °C. Apparently, in this environment, algae find a more stable microhabitat with lesser temperature variations [39]. This allows us to argue that excess UV radiation at strata close to the surface would be the key factor limiting the proliferation of Chlorella sp. at depths < 10 cm. In fact, our results indicate that Chlorella sp. is sensitive to UV radiation but not to temperature. Regarding the levels of UV radiation recorded at depths below 10 cm (0.01 W m⁻² for UV-B and 1.3 W m^{-2} for UV-A), it could be argued that microalgae were not exposed to detrimental UV conditions. For example, in situ measurements carried out in the snowfields of the Rocky Mountains, Wyoming, with

abundant populations of *Chlamydomonas nivalis* indicated that maximal transmittance of UV-B radiation was close to 4 cm [24].

The inhibition of the maximum quantum yield (F_v/F_m) of Chlorella sp. was wavelength dependent. Under PAR + UV-A + UV-B treatment, fluorescence values decreased by 15 % after exposures of 5 to 20 °C. For the PAR + UV-A treatment, inhibition of F_v/F_m did not exceed 7 %. However, the recovery of the samples exposed to PAR + UV-A was in the range of 90-100 % relative to PAR control, while recovery in algae exposed to PAR + UV-A + UV-B varied between 80 and 95 %. These results highlight the tolerance of *Chlorella* to the UV exposure, at least for periods close to 12 h and high UV-B:UV-A ratio. Studies carried out with UMACC 237, another Antarctic Chlorella strain, revealed a higher tolerance to UV-B compared to strains of the same genus isolated from temperate and tropical regions [40]. Apparently, exposure to enhanced UV radiation in snow living populations of Chlorella stimulates the activity of antioxidant enzymes, such as catalases and superoxide dismutase [23, 41] or enhance the synthesis of protective compounds like secondary carotenoids (e.g. in Chlorella zofingiensis) or mycosporine-like amino acids (MAAs) [14]. However, when algae were exposed to higher temperatures, repair processes in Antarctic strains increase significantly [27]. This could be a confirmation that elevated temperatures can ameliorate the detrimental impact of UV radiation as has been reported in Antarctic macroalgae [42].

Implications for snow algal ecology in scenarios of climate change

Recent reviews dealing with the ecology of snow algae and in general of extreme cold-adapted organisms [2, 21] emphasize the urgent need for physiological and molecular studies that allow identifying the adaptive and acclimative strategies that snow algae exhibit in response to environmental factors beyond their tolerance threshold. Based on a scenario of extended melt periods in maritime Antarctica [43] with concomitant higher impact of elevated temperature and UV radiation, the examination of stress tolerance mechanisms is essential to understand and predict near-future impacts of climate change especially in polar regions where snowfields and their algal communities have an important role on the biogeochemical fluxes [44]. Snow algae are probably the most sensitive biological indicators of present and future scenarios of regional warming and meltdown in vast sectors of Antarctica, especially at ecologically relevant (seasonal and interannual) scales. In addition to their important role as primary producers, polar extremophiles are involved in exchange of reactive gases with the atmosphere (e.g. N_2 , CO_2 , dimethyl sulfoxide, etc.) [2, 45] and in snowfields in the maritime Antarctica, they play important subsidiary roles through the melting runoff, food web and degradation products [7, 8]. The impact that these processes will have on in the biogeochemical cycles of the whole coastal system in this region is unknown and prompt for further research.

Conclusions

Overall, our findings revealed that *Chlorella sp.* isolated from a snow microalgal community in maritime Antarctic not only shows high photosynthetic efficiency at ambient conditions, but also exhibits tolerance to solar radiation under higher temperatures. Avoiding the highly UV exposed snow surface and possessing a capacity for recovery after inhibition of photosynthesis by UV radiation appear as two important strategies of *Chlorella sp.* in these ecosystem . However, it remains open how these algae will endure the future Antarctic summer, characterized by warmer temperatures and less snow, in which they will exposed to high solar radiation.

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

Framing hypotheses/experimental design: CR, NN, PH, IG. Laboratory or field work: CR, NN. Data analysis and interpretation: CR, NN, PH, IG. Manuscript preparation: CR, NN, PH, IG. All authors read and approved the final manuscript.

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