Planta (2024) 259:25
https://doi.org/10.1007/s00425-023-04290-1

SHORT COMMUNICATION

Resilience of *Xanthoria parietina* under Mars-like conditions: photosynthesis and oxidative stress response

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Received: 23 September 2023 / Accepted: 13 November 2023 / Published online: 18 December 2023

Abstract

Main conclusion ***Xanthoria parietina*** **survivability in Mars-like conditions was supported by water-lysis efficiency recovery and antioxidant content balancing with ROS production after 30 days of exposure.**

Abstract *Xanthoria parietina* (L.) Th. Fr. is a widespread lichen showing tolerance against air pollutants and UV-radiation. It has been tested under space-like and Mars-like conditions resulting in high recovery performances. Hereby, we aim to assess the mechanisms at the basis of the thalli resilience against multiple space stress factors. Living thalli of *X. parietina* were exposed to simulated Martian atmospheric conditions (Dark Mars) and UV radiation (Full Mars). Then, we monitored as vitality indicator the photosynthetic efficiency, assessed by in vivo chlorophyll emission fluorescence measurements (F_M; F_V/F_0). The physiological defense was evaluated by analyzing the thalli antioxidant capacity. The drop of F_M and F_V/F_0 immediately after the exposure indicated a reduction of photosynthesis. After 24 h from exposure, photosynthetic efficiency began to recover suggesting the occurrence of protective mechanisms. Antioxidant concentrations were higher during the exposure, only decreasing after 30 days. The recovery of photosynthetic efficiency in both treatments suggested a strong resilience by the photosynthetic apparatus against combined space stress factors, likely due to the boosted antioxidants at the beginning and their depletion at the end of the exposure. The overall results indicated that the production of antioxidants, along with the occurrence of photoprotection mechanisms, guarantee *X. parietina* survivability in Mars-like environment.

Keywords Adaptation · Antioxidant · Lichen · Photosynthesis · Space environment

Abbreviations

DM	Dark Mars condition
FM	Full Mars condition
ECd/w	Dried/wetted External Controls
$F_{O/M}$	Basal/maximum fluorescence of dark-adapted samples
F_V/F_O	Maximum water-lysis efficiency
F_V/F_M	Maximum quantum yield of dark-adapted samples
OEC	Oxygen evolving complex

Communicated by Dorothea Bartels.

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Introduction

The study of life's limits in extreme environments is a hot topic in astrobiology, which investigates the physiological and biochemical response of living organisms to stressful exoplanetary conditions (Horneck et al. 2016; de la Torre Noetzel et al. 2020). In particular, our research investigates the potential of adaptation of ubiquitous early colonizer terrestrial organisms, such as lichens (Lorenz et al. 2023), in the perspective of environmental change and colonization of extra-terrestrial habitats, such as Mars' surface and exoplanets (Wassmann et al. 2010). Lichens' features of poikilohydry and anhydrobiosis allow them to colonize most of the extreme habitats on Earth's surface. For this reason, lichens and their secondary substances are topics of interest in space biology. Our study involved the lichen species *Xanthoria parietina* (L.) Th. Fr.—already tested in space-like and Mars-simulated conditions—that has proven to have high survival performances due to poikilohydry and anhydrobiosis features, hyphal matrix, thallus structure and lichen secondary substances (Solhaug and Gauslaa 2004; Solhaug et al. 2010; Gauslaa et al. 2012, 2017; Lorenz et al. 2022, 2023). Lorenz et al. (2023) provide a mainstream photosystem II (PSII) activity analysis using F_V/F_M as a photochemical indicator. The hereby paper aims to monitor the recovery of physiological performance in *X. parietina* thalli after Mars-simulated environment exposure using as photosystem healthy proxies, two additional fluorescence parameters linked to photoprotection and photodamage of PSII, namely F_M and F_V/F_0. The combined assessment of both indexes allows us to evaluate how harsh conditions may affect the oxygen-evolving complex (OEC) activity and thus the resume of PSII photochemical reactions. Furthermore, we extend the analysis to evaluate the cells' capacity to scavenge the increase of ROS formation following Mars-like conditions exposure, analyzing the antioxidant capacity. The changes in the antioxidant pool provide valuable information on the dynamics of ROS production and scavenging, which is related to the stress-resistance of *X. parietina* in Mars simulated conditions with implications for its survival capacity and acclimation to space extreme environments.

Materials and methods

Experimental conditions

The experiment was performed at PASLAB (Department of Planetary Laboratories at DLR, Berlin, Germany). Lichen material was exposed to Mars-like conditions for 1 day, 7 days and 30 days. The atmospheric composition of the chamber was a dry gas mixture of 95% CO_2, 4% N_2 and 1% O_2 at 600 Pa. The temperature ranged between − 55 °C (night) and 16 °C (day) and relative humidity ranged between 100% (night) and 0.1% (day). A Xe-UV lamp was employed to simulate the Martian solar spectrum (200–2200 nm) and it was daily turned on for 16 h and switched off for 8 h. The UV average irradiances and the average UV cumulative absorbed doses were 16.5 W m^{-2} and 0.95 MJ m^{-2} for 1 day, 15.1 W m^{-2} and 5.7 MJ m^{-2} for 7 days, 14.2 W m^{-2} and 24.5 MJ m^{-2} for 30 days, respectively. Full Mars (FM 1d, FM 7d, FM 30d) samples were exposed to atmospheric conditions plus UV radiation. Dark Mars (DM 1d, DM 7d, DM 30d) samples were exposed only to atmospheric conditions. External Controls (ECw 30d) and exposed samples (FM and DM) in recovery phase were kept in a growing chamber at 25 °C, with 12 h dark and 12 h light at 50 µmol m^{-2} s^{-1} PAR photons and daily wetted. Additional External Controls (ECd 30d) were added to the original design, and were kept air-dried for 30 days. See Lorenz et al. (2023) for more details.

Chlorophyll *a* fluorescence analysis

The imaging PAM instrument (red LED Imaging-PAM M-series, Heinz Walz GmbH, Effeltrich, Germany), was used to assess the photobiont photochemical efficiency before, after and in the following 8 days after the exposure to Mars-like conditions as described in Lorenz et al. (2023). The LED-array platform was mounted at a working distance of 7 cm above the samples. Chlorophyll fluorescence measurements were performed hydrating the samples and keeping them in dark-adapted conditions for 10 min, covering the Petri dish with a black cloth (Bianchi et al. 2019; Lorenz et al. 2022). The Imaging PAM retrieved F_0 and F_M fluorescence average values of the selected area on the sample. F_0 indicates the basal fluorescence of dark-adapted samples, showing the energy loss during the electron transfer from the harvesting complex to the PSII reaction center, depending on light intensity and electron transfer efficiency. In addition, Pfündel (1998) reported that PSI contributes up to 30% of F_0 value. F_M indicates the maximal fluorescence, reached when every electron acceptor of PSII is reduced and reaction centers are temporarily closed (Baker and Rosenqvist 2004).

We calculated F_V (as $F_V = F_M - F_0$) indicating the variable fluorescence of dark-adapted samples depending on the maximum quantum efficiency of PSII. In addition, we retrieved F_V/F_0 as maximum efficiency parameter of water lysis by PSII donor. Considering the physiological meaning of the F_V/F_0 ratio, it may be considered a good indicator of oxygen production too, the OEC being highly sensitive to electron transport chain activity (Pereira et al. 2000).

Antioxidant analysis

Dried lichen material was stored at – 18 °C, as reported in Lorenz et al. (2023), and thawed for the antioxidant assay. The water-soluble fraction of antioxidants was evaluated following the procedure described by Biswas et al. (2019), using the Sigma-Aldrich Antioxidant Assay kit (CS0790) (Miller et al. 1995). The analysis was performed using four replicates for each treatment: FM 1d, DM 1d, FM 7d, DM 7d, FM 30d, DM 30d, ECd 30d and ECw 30d (Lorenz et al. 2023). The assay's principle is forming a ferryl myoglobin radical from metmyoglobin and hydrogen peroxide, which oxidizes the ABTS (2,2′-azino-bis-3-ethylbenzthiazoline-6-sulphonic acid) to generate a radical cation, $ABTS^{\bullet+}$, a soluble chromogen that is green in color and can be measured spectrophotometrically at 405 nm. Frozen lichen samples were powdered with liquid nitrogen and homogenized with an ice-cold 1 × assay buffer. Samples were then centrifuged for 20 min, at 18.000g at 4 °C. The pellet was discarded and the supernatant was kept on ice. The assay reaction was performed in a 96-well microplate by adding the kit reagents to the samples and Trolox, used as standard. Briefly, after loading the Trolox standard solution (10 µL of a Trolox standard and 20 µL of myoglobin working solution), test samples (10 µL of the test sample and 20 µL of myoglobin working solution) were loaded, adding ABTS substrate working solution (150 µL) to each well. Then all samples were incubated for 5 min at room temperature. Finally, a stop solution (100 µL) was added to each well to stop the reaction. The endpoint absorbance was read at 405 nm using a microplate reader spectrophotometer (BioTek Synergy HTX Multimode Reader, Software: Gen5). The antioxidant concentration was expressed in mM relative to the concentration of the Trolox standard.

Data analysis

F_V/F_0 data over the recovery time period were analyzed fitting linear mixed-effects models (LMEM) in a repeated measurements ANOVA design, using sample identity as a random factor to account for the temporal correlation of observations. Time was used as an ordinal variable because the relationship between F_V/F_0 and time was not a simple linear regression. F_V/F_0 was used as response variable and the treatment conditions and time of recovery as explanatory variables in a full factorial design. ANOVA type II Wald Chi-square test method was used to verify significance of the fixed effects and of associated interaction factors. Data normality of the residuals was checked with the Shapiro–Wilk test (Lorenz et al. 2023).

Antioxidant data were compared performing one-way ANOVA to check for significant differences between treatments. A Tukey's HSD post-hoc test was run to analyze differences in mean levels.

All the analyses were carried out with the open-source software RStudio v. 2023.03.0 + 386. ANOVA computations were performed using the *aov* function (in base R) for one-way ANOVA test. LMEM computations were performed using the *lmer* function of the *lme4* package version 1.1–12 for fitting the models.

Results

F_V/F_M results are reported in Lorenz et al. (2023). Specifically, after the exposure we detected a significant decrease of F_V/F_M ratio in FM and DM sampled of 85% (0.096 ± 0.042) and 46% (0.339 ± 0.083) compared to the initial values, respectively. After 24 h, FM and DM F_V/F_M values reached 0.418 ± 0.023 and 0.546 ± 0.122. After 192 h of exposure, FM and DM F_V/F_M values were 0.541 ± 0.007 and 0.614 ± 0.058, respectively, reaching the 86% and 97% of the beginning values.

F_M values (maximal chlorophyll fluorescence) were measured by an Imaging PAM fluorometer (see the section "Materials and methods") (Fig. 1; Table S1). ANOVA results indicated no significant difference among treatments, specifically, Full Mars (FM) and Dark Mars (DM) conditions (Table S2, $P < 0.1$). After the 30-day exposure period, we observed a drop in F_M values, with 0.152 ± 0.065 (mean ± SD) for FM and 0.189 ± 0.031 for DM. Then, the samples did not reach more than 0.219 ± 0.111 (FM, after 96 h) and 0.251 ± 0.139 (DM, after 168 h). The ratio of variable to basal chlorophyll fluorescence F_V/F_0 was calculated using the data retrieved during the recovery period of the simulation described in Lorenz et al. (2023). The kinetic of F_V/F_0 recovery is shown in Fig. 2 and Table S3. The F_V/F_0 values changed significantly after the treatment in both the experimental conditions through time (Table S4, $P < 0.001$). FM and DM's F_V/F_0 significantly decreased by 94% and 69%, respectively, compared to pre-exposure values. DM reached the drop-down fall value of 0.529 ± 0.203. Instead, FM reached a lower value of 0.107 ± 0.049. Once the recovery period started, F_V/F_0 values increased significantly depending on the treatments. After 24 h, F_V/F_0 values reached 42% (0.719 ± 0.067) for FM, and 76% (1.300 ± 0.543) for DM, of the pre-exposure values. For both treatments, samples showed similar recovery trends, with DM values achieving the maximum at 1.765 ± 0.355 (after_96h). Nevertheless, after 72 h of recovery, FM did not increase more than 1.179 ± 0.034 (after_192h). Consequently, FM samples were not able to reach similar levels as the initial F_V/F_0 values. Conversely, control samples F_V/F_0 values ranged between 1.884 ± 0.167 (pre_exp) and 1.461 ± 0.295 (after_192h). Antioxidant assay results are

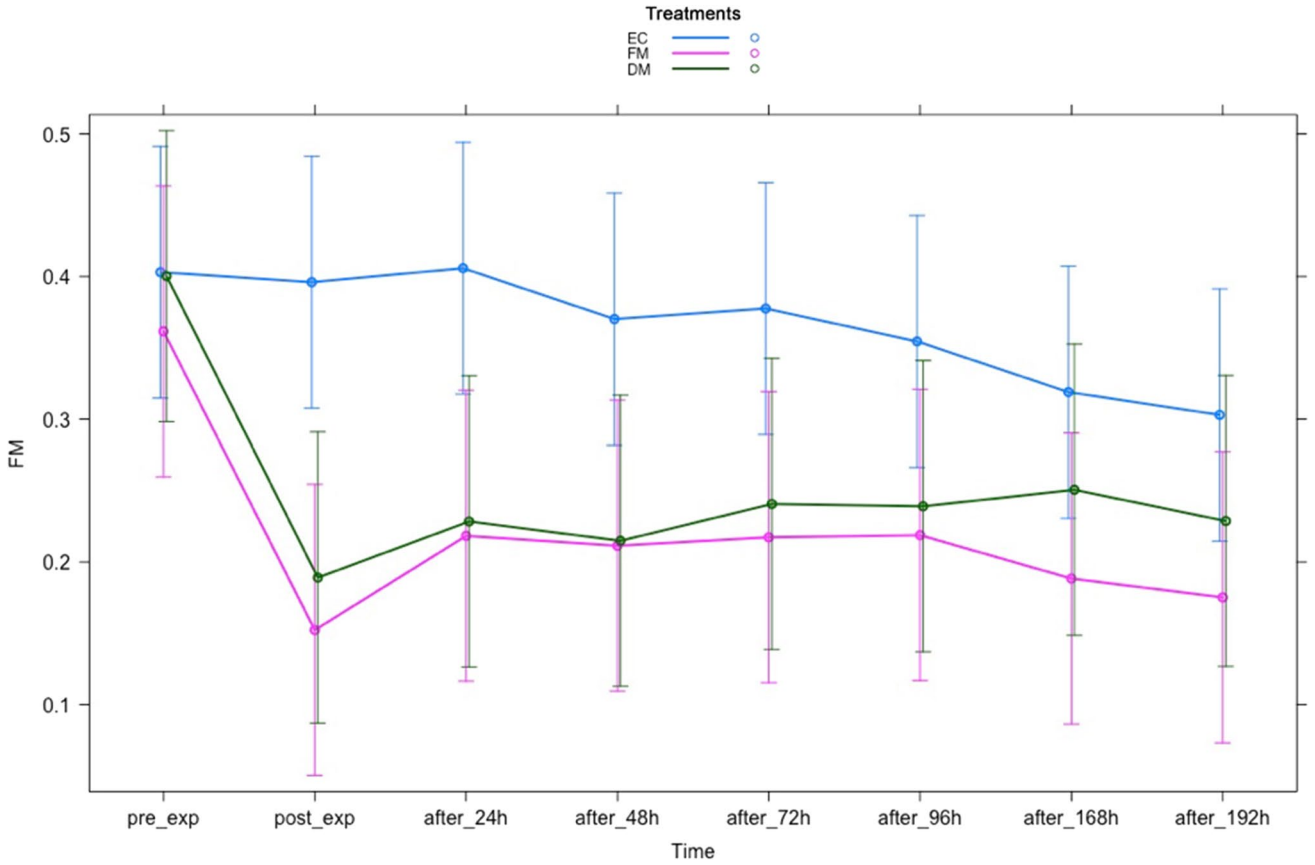

Fig. 1 Variation of F_M values before (pre_exp), after (post_exp) and 24 h, 48 h, 72 h, 96 h, 168 h and 192 h after the exposure of 30-day simulation. Blue line = external control (EC); magenta line = full Mars (FM); green line = dark Mars (DM). Error bars stand for confidence intervals. See Table S1 for F_M values and Table S2 for ANOVA results

shown in Fig. 3, which describes the comparison between FM 1d and DM 1d with 7d and 30d samples, along with the air-dried External Controls for 30 days (ECd 30d) and the daily wetted ones for 30 days (ECw 30d). Specifically, we found a not statistically significant difference among each condition in the same day, but a significant difference between days (Fig. 3; Table 1; Table S5, $P < 0.001$). In addition, we observed an increase of variance between FM 1d and DM 1d (4.357 ± 0.167 and 4.368 ± 0.211, respectively) and FM 7d and DM 7d (4.668 ± 0.614; 4.594 ± 0.595, respectively) (Fig. 3; Table 1). After 30 days, there was a significant decrease for both treatments (FM 30d, 3.520 ± 0.440 and DM 30d, 3.761 ± 0.315) compared to 1d and 7d samples (Fig. 3; Table 1).

Discussion

F_V/F_M results reported in Lorenz et al. (2023) highlighted that FM samples did not reach the initial values after the 8-day recovery period. Conversely, DM samples reached 97% of the initial values, possibly indicating the almost total restoration of PSII photochemical efficiency compared to FM samples. UV radiation may have caused a delay in photosynthetic electron flow reactivation or possible chlorophyll structural damages (Kranner et al. 2008), as indicated by F_V/F_M ratio reduction in FM samples.

Our previous results allow us to suppose that the significant difference between FM and DM treatments in F_V/F_0 (Fig. 2) may be due to the combined effects of UV radiation and atmospheric conditions experienced by FM samples (de Vera et al. 2004; Sancho et al. 2007; Kranner et al. 2008; Lorenz et al. 2022). Specifically, F_M decrease and the lack of recovery in FM and DM conditions may be related to a lower capacity of PSII acceptors to come back in the reduced status after the stress was imposed by exposure (Krause and Weis 1991; Oxborough and Baker 1997). In these thalli, a decline in F_0 was also observed (Lorenz et al. 2023). Since F_0 variations are primarily dependent on the chlorophyll contents of the light-harvesting complexes (Butler 1978; Malkin and Fork 1981; Baruffo and Tetriach 2007), F_V/F_0 ratio is an effective proxy of the structural integrity of the PSII photosystem (Li et al. 2006) and in particular, the water lysis efficiency and the OEC functionality (Pereira et al. 2000;

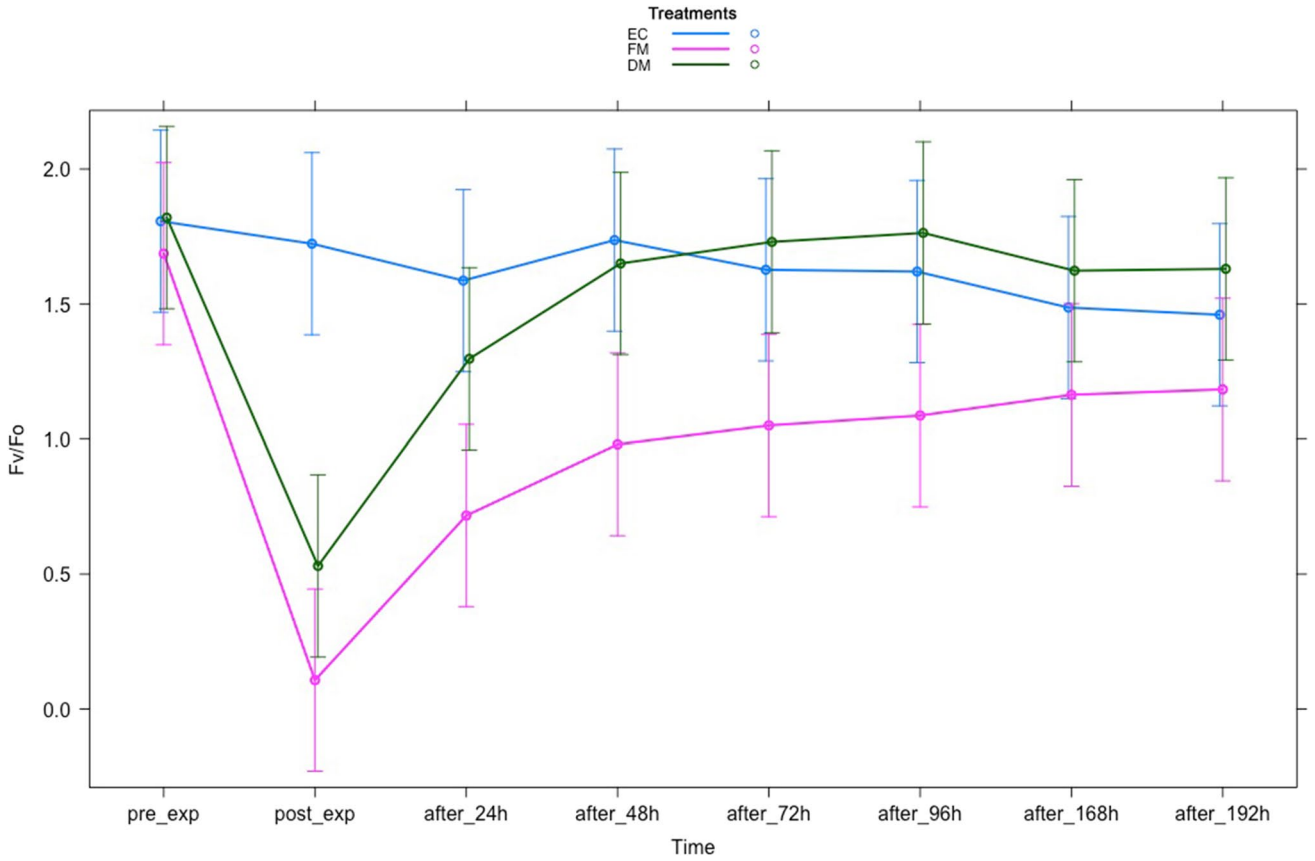

Fig. 2 Variation of F_V/F_0 values before (pre_exp), after (post_exp) and 24 h, 48 h, 72 h, 96 h, 168 h and 192 h after the exposure of 30-day simulation. Blue line = external control (EC); magenta line = full Mars (FM); green line = dark Mars (DM). Error bars stand for confidence intervals. See Table S3 for F_V/F_0 values and Table S4 for ANOVA results

Gupta 2020). Our results indicated that FM and DM conditions may have inhibited or reduced the OEC activity. Desiccation stresses—as the applied day and night cycle—can affect OEC structure leading to water molecules depletion and ROS production by photo-excited pigments (Nabe et al. 2007).

Based on these results, we may assume that maximum fluorescence (F_M) is similarly affected in both treatments, possibly indicating the atmosphere and the thermophysical conditions as driver stressors in determining the F_M decline. However, the similar trends observed for F_V/F_M and F_V/F_0 suggest a comparable recovery pattern in both the treatments, even if FM seems to be the most severe condition. As reported in Lorenz et al. (2023), the highlighted difference between recovery in F_M and F_V/F_M, F_V/F_0 values may be associated with F_0 kinetics that showed a decreasing trend over the recovery time. Since PSI may contribute up to the 30% of F_0 value and since that low F_0 values are noteworthy associated to PSII good functionality (Krause and Weis 1991; Pfündel 1998), we interpreted F_M decline after the exposure as a loss of the electron transfer efficiency among light-harvesting pigments together with a reduced efficiency of plastoquinone and other electron transport acceptors (Krause and Weis 1991; Oxborough and Baker 1997). Consequently, based on the lack of F_M recovery after Mars-like condition exposure, we may hypothesize an impairment of PSII. However, we suppose that, since F_0 values decreased after exposure and stay low over the recovery time, the reduction of basal fluorescence may have strongly contributed to F_V/F_M and F_V/F_0 recovery for both treatments, indicating a reprise of both PSII and OEC efficiency and functionality.

In addition, since the OEC contributes to generating electron gradients by charge separation from water molecules into electrons, protons and dioxygen using light energy, OEC components are easily exposed to ROS (Kranner et al. 2008; Tyystjärvi 2013). Generally, stress effects may be reduced by the anhydrobiotic state, involving a multifaceted system of photobiont protection (Kranner et al. 2008). This may help the high recovery performances of the photosynthetic activity (F_V/F_M) (Lorenz et al. 2023). However, all abiotic stresses are reported to enhance ROS formation, determining an impairment of photosynthesis (Meeßen et al. 2017). The extreme environmental conditions used in our experiment

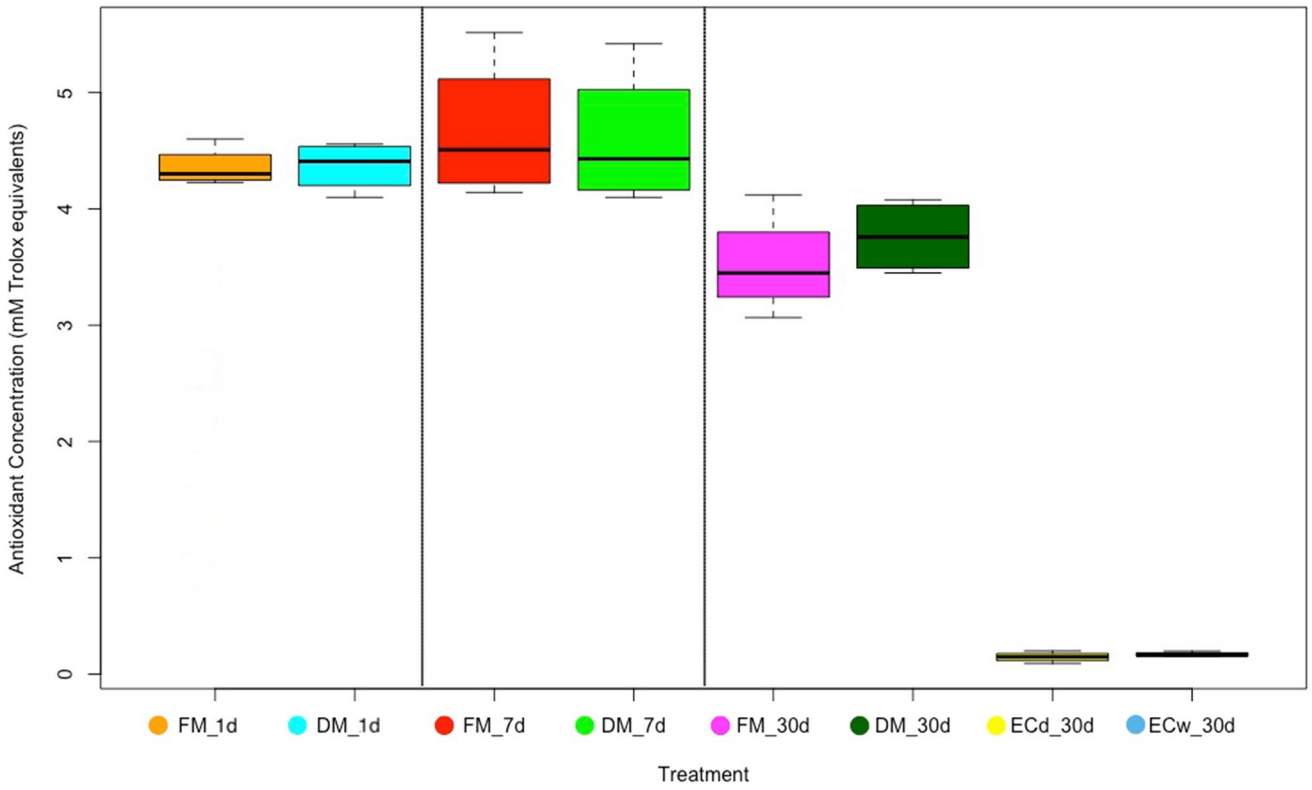

Fig. 3 Antioxidant concentrations' boxplots of each treatment: Full Mars for 1d (FM 1d, orange), Dark Mars for 1d (DM 1d, cyan), Full Mars for 7d (FM 7d, red), Dark Mars for 7d (DM 7d, light green), Full Mars for 30d (FM 30d, magenta), Dark Mars for 30d (DM 30d, dark green), External Control air-dried for 30d (ECd 30d, yellow) and External Control daily wetted for 30d (ECw 30d, light blue). See Table 1 for antioxidant concentrations values and Table S5 for one-way ANOVA results

Table 1 Antioxidant concentrations (mM Trolox equivalents) for each treatment. Four replicates (*n*) for each treatment. The values stand for mean ± SD

Treatment ($n=4$)	Antioxidant Concentrations mM
FM 1d	4.357 ± 0.167
DM 1d	4.368 ± 0.211
FM 7d	4.668 ± 0.614
DM 7d	4.594 ± 0.595
FM 30d	3.520 ± 0.440
DM 30d	3.761 ± 0.315
ECd 30d	0.169 ± 0.021
ECw 30d	0.147 ± 0.045

Treatments are Full Mars for 1d (FM 1d), Dark Mars for 1d (DM 1d), Full Mars for 7d (FM 7d), Dark Mars for 7d (DM 7d), Full Mars for 30d (FM 30d), Dark Mars for 30d (DM 30d), External Control air-dried for 30d (ECd 30d) and External Control daily wetted for 30d (ECw 30d)

may have led to high ROS formation and, consequently, activate ROS scavenging processes, mediated by an antioxidant content increase (Kranner et al. 2008; Sharma et al. 2012; Beckett et al. 2021). Specifically, the higher antioxidant concentrations found in 1d (FM 1d and DM 1d) and 7d (FM 7d and DM 7d) exposures likely represent the early response of thalli to the oxidative stress induced at the beginning of the simulation (Riley 1994). In addition, the observed increase of variance between FM 1d and DM 1d, as well as FM 7d and DM 7d may be associated to a different response to the harsh conditions related to different samples. Since antioxidants act as O_2 scavengers and free radical terminators (Sánchez-Moreno et al. 1999; Kranner et al. 2008), we assume a continuous ROS-depletion activity on the basis of antioxidant concentrations decline after 30 days of simulation (FM 30d and DM 30d). Indeed, FM and DM samples showed higher and similar Trolox equivalents, significantly different from external controls (ECd 30d and ECw 30d).

Thus, the significant reduction of the antioxidant content in response to the increasing duration of exposure in FM and DM samples suggests the permanence of the oxidative stress and the consumption of water-soluble antioxidants in cell detoxification, as reported in plants and fungi exposed to ionizing radiation (Arena et al. 2013; Mami et al. 2013). Nevertheless, we may assume that both exposure conditions (FM and DM) have caused a general decrease in PSII

acceptors reduction capacity (F_M), and post-exposure drops with subsequent recovery in PSII photoefficiency (F_V/F_M) and in OEC functionality (F_V/F_0). In light of this, ROS formation may have similarly involved samples under both conditions. On the other hand, given F_V/F_0 and F_V/F_M results, the higher antioxidant concentrations in FM and DM samples, may have efficiently removed ROS, allowing the performing recovery of F_V/F_0 and F_V/F_M.

Conclusion

In conclusion, we use the F_M and F_V/F_0 ratio as efficient proxies of lichen survival capability under simulated Martian conditions. Light-induced water lysis efficiency and OEC functionality were recovered as reported by F_V/F_0 values, following a similar trend to F_V/F_M (Lorenz et al. 2023), explaining the reprise of the photosynthetic apparatus after exposure in both treatments. Nevertheless, F_M showed a general reduction in both treatments, indicating a lower reduction capacity of PSII acceptors that may be related to damages due to the applied conditions. The kinetics of stress and recovery of photochemical indicators used in this study together with the widely applied F_V/F_M analysis reported in Lorenz et al. (2023) provide us with an overview on the PSII photosystem functionality and photochemical resilience of *Xanthoria parietina* after Mars-like conditions exposure. The additional information about the modulation of *X. parietina* antioxidant capacity indicate that at the beginning of the exposure a significant oxidative stress occurred, and that the scavenging system of this species promptly reacts, as first aid, enabling the recovery and lichen survival. Thus, the over production of antioxidants, along with the occurrence of photoprotection mechanisms within photosystems, may explain the resilience of *Xanthoria parietina* and its persistence in many extreme ecosystems on Earth.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00425-023-04290-1.

Acknowledgements C. L. and JR. B. acknowledge ASI/INAF 2023-3-HH.0 agreement. G. P. acknowledges support by Centre National d'Études Spatiales (CNES). M. B. acknowledges support from the Deutsche Forschungsgemeinschaft (DFG—German Research Foundation), Grant 426601242, project RaBioFAM.

Author contributions Contributions listed according to authorship credits. CL: conceptualization, experimental design, specimens retrieving, data retrieving (performing all the analyses/measurements), data analysis, investigation, data interpretation, writing (original draft, review and editing). CA: conceptualization, experimental design, investigation, data interpretation, writing (review and editing). EV: data retrieving, investigation, data interpretation, writing (review and editing). EB: data interpretation, investigation, writing (review and editing). GP: writing (review and editing). GA: contribution to IR spectroscopy measurements. RB: writing (review and editing). JRB: writing (review and editing). SG: responsible for Mars Simulation Facility-Laboratory. JH: responsible for IR spectroscopy laboratory. SL: writing (review and editing). AL: responsible for Mars Simulation Facility-Laboratory. AM: responsible for IR spectroscopy laboratory. AP: writing (review and editing). J-PV data interpretation, investigation, writing (review and editing). MB: data interpretation, investigation, writing (review and editing). All authors read, edited and approved the final manuscript.

Data availability Data is available under reasonable request to the corresponding author.

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