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Perchlorate-Rich Martian Regolith Analogs: Effects on Terrestrial Cereal Proxies and Implications for Surface Habitability and Bioregenerative Life-Support Systems

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ABSTRACT: A better understanding of Martian surface chemistry and its implications for habitability and in-situ resource utilization is required for long-term human Mars exploration and settlement. Perchlorate salts, especially magnesium perchlorate, are most limiting geochemical constraints for the Martian surface, impact water stability, oxidation potential and the ability of any biological system placed on the Martian regolith. The Martian regolith analog in this case was made by altering terrestrial soil to mimic important physicochemical properties of the Martian surface material, such as having a high pH, low organic carbon, low bulk density, and being contaminated with perchlorate.

The limits of biological activity in perchlorate-bearing substrates were defined using two terrestrial cereal species that are known to be stress-tolerant, Pennisetum glaucum and Setaria italica. Biological stress was measured as growth, chlorosis, water uptake, and survival time and magnesium perchlorate was applied in controlled environmental conditions of closed bioregenerative habitats at 0.1-0.6% (w/v). High and strong perchlorate biological inhibition was found, with perchlorate concentration greater than 0.3% causing severe physiological impairment. The findings suggest that perchlorate contamination is a significant chemical obstacle to sustained biological activity on Mars, and highlight the importance of pre-treatment of regolith for future mission architectures and habitat design

1. INTRODUCTION

The most promising spot for future manned space exploration and settlement in the Solar System is Mars. However, its surface is a harsh physicochemical environment with low organic carbon content, high mineral reactivity, high radiation, low atmospheric pressure and the presence of abundant perchlorate salts. The Viking, Phoenix, Pathfinder and Mars Exploration Rover missions have all shown that perchlorates exist throughout the Martian regolith and dust (Davila et al., 2013). The role of these salts in Martian geochemical processes involving water stability, oxidation reduction reactions and long-term

preservation and degradation of organic molecules is central. The interactions between living organisms and contaminated regolith with perchlorate are therefore a very fundamental question in planetary science and astrobiology.

The salts of magnesium and calcium are highly soluble, strongly oxidizing. The addition of these would alter the hygroscopic properties of Martian soil and facilitate the formation of transient brines, as well as greatly influence the physicochemical conditions that would be available to any introduced biological system. Right now, one of the most important chemical constraints on the biological activity on the Martian surface is the presence of perchlorates (Davila et al., 2013); and perchlorates have been proposed as in-situ sources of oxygen and propellant. Therefore, it is crucial to quantify the biological tolerance to perchlorate exposure to limit Mars habitability models and design bioregenerative life-support systems.

Regeneration of oxygen, carbon, humidity and food in the closed ecological systems for long missions and planetary surface bases, is based on biological processes. Processed Martian regolith is a potential growth medium for these systems, but there is a lack of direct biological response of complex multicellular organisms to perchlorate contamination, and most previous testing has been performed in hydroponic or aqueous exposure systems, not in regolith systems.

In this work, the biological responses of two terrestrial cereal species (proxy models) are studied to help resolve the extent of biological activity in Martian regolith analogs perchlorate. This study models essential physicochemical characteristics of Martian soil, and includes controlled concentrations of magnesium perchlorate for experimental constraints on Martian surface chemistry and for evaluation of planetary habitability for future bioregenerative life support systems.

2. MATERIALS AND METHODS

2.1 Chemicals and Reagents

The main chemical stressor used to mimic perchlorate toxicity found in Martian regolith was magnesium perchlorate hexahydrate (analytical grade). The chemical was obtained from a recognized supplier and stored in sealed containers to prevent moisture from getting into the containers. All treatment solutions were prepared in double distilled water, and the new solution was made at the start of each experiment to allow for repeatability and chemical stability to prevent interference of the dissolved ions and/or contaminants. The regolith analog was designed to mimic the high pH, low organic carbon content and low bulk density of Martian fines and simulants as reported by Clark et al. (1982), Stirzaker et al. (1996), and Zeng et al. (2015).

2.2 Plant Material

Pearl millet and foxtail millet were chosen as biological models for drought and salinity stress tolerance for extraterrestrial agriculture under controlled conditions for planetary growth-simulation experiments due to their short life cycle, high germination rate and their tolerance to environmental stress including drought and salinity (Ashraf and McNeilly, 1992; Serraj et al., 2005; Sreenivasulu et al., 2000; Sobhanian et al., 2010; Lapuimakuni et al., 2018; Jha et al., 2022). Both species are also food and fodder crops, and their nutritional profile is favourable, further supporting their role as potential crops for closed agricultural systems (Saleh et al., 2013). The seeds used were uniform and certified from agriculture research supplier that had uniform size and viability.

2.3 Seed Sterilization

Seeds were surface sterilized before being used in the experiment. First the seeds were dipped in 70% ethanol for 1 minute to remove the surface lipids and microbial contaminants, followed by dips in 1% sodium hypochlorite for 5 minutes. To wash away traces of sterilizing solution that might adversely affect germination or growth, the seeds were then washed five times with sterile distilled water

2.4 Perchlorate Treatment Solutions

A stock solution of magnesium perchlorate was prepared followed by the preparation of final concentrations of 0% (control), 0.1%, 0.3% and 0.6% (w/v) table 1. These concentrations represent a realistic range of possible perchlorate concentrations in Martian regolith and a dose-dependence for toxicity (Hecht et al., 2009; Kounaves et al., 2010). For all treatment solutions, all treatment solutions were made in advance of experimental run.

Table 1. Magnesium perchlorate treatment concentrations used to establish the dose-response series

Treatment	$Mg(ClO_4)_2$ concentration (% w/v)	Rationale
Control	0.0	Untreated regolith analog; baseline growth reference
T1	0.1	Low, sub-inhibitory perchlorate loading
T2	0.3	Threshold concentration for onset of severe stress
T3	0.6	Upper bound of Martian-relevant perchlorate abundance

2.5 Germination Experiment

Germination tests were carried out in plastic trays, lined with autoclaved filter paper and filled with sterile soil. Twenty sterilized seeds of each species were evenly spread out on the moistened filter paper and exposed to 10 mL of the perchlorate solution for each tray. Triplicates were used for all treatments. The trays were kept in a controlled growth chamber at 25 ± 2 °C, with 16 h light / 8 h dark photoperiod, with water refilled occasionally to prevent dehydration with a relative humidity of 60%. After 7 days, the radicle of a seed was deemed to be germinated if it had reached a length of 2 mm or more and the percentage germination was calculated as the number of germinated seeds divided by the number of sown seeds.

2.6 Seedling Growth Conditions

Germinated seedlings were then transplanted into plastic pots filled with sterile quartz sand figure 1 (as an inert growth medium) and subjected to the same conditions they experienced during germination, but with the perchlorate solutions for a 21-day growth period. The seedlings were planted at a density of 50 plants per square meter. Seedlings were planted.



Figure 1. Seedling growth trays used for the perchlorate dose-response experiment, showing the multi-well tray design with a ventilated cover lid used to regulate humidity and limit contamination.

2.7 Morphological and Physiological Measurements

At the end of experimental period harvest was conducted of the plants and morphological parameters were recorded. The root and shoot length were measured using digital caliper. During the experiment the following visual stress symptoms were noted; chlorosis, wilting, decrease in vigor or necrosis, the fresh biomass was measured immediately after harvest with an analytical balance and the dry biomass was measured after 48 hours of drying at 60 ° C. Water uptake and general turgidity were recorded periodically. Photographs were shot of samples to demonstrate changes in form.

2.8 Statistical Analysis and Experimental Design

The experimental design was completely randomized with three replications per treatment. Data are presented as means ± SD. Assumptions of normality and variance homogeneity were checked for each set of data with the Shapiro-Wilk and Levene tests, respectively, prior to analysis; all data were found to be normally distributed and have homogenous variance ($p > 0.05$) indicating the validity of parametric analysis. One-way analysis of variance (ANOVA) was used to statistically compare groups with $p < 0.05$ and post hoc was used to compare treatment groups.

3. RESULTS AND DISCUSSION

3.1 Germination and Early Growth

The germination rate reaches 80% to 100% within 14 days. The early growth rate is high figure 2. In both proxy species, treatments, including the highest concentration of magnesium perchlorate tested (0.6%), were successful in producing radicle emergence after 24-36 hours, suggesting that perchlorate exposure did not acutely prevent the early emergence of radicles. On the third day of growth, however, distinct differences were observed between seedlings grown in control and perchlorate-treated substrates -- seedlings grown in perchlorate-enriched substrates had smaller shoots, slower leaf growth and less water uptake. These early physiological changes increased in severity with the concentration of perchlorate. On watering, the highly soluble, hygroscopic magnesium perchlorate was visibly reactive at the soil surface, consistent with its documented deliquescence and brine-forming behaviour in Mars-relevant conditions (Kang et al., 2006; Quinn et al., 2013).



Figure 2. Surface reaction of the magnesium perchlorate-amended regolith analog on watering, showing foam and a shiny salt deposition at the wetting front.

3.2 Morphological Separation of Treatments

Beginning on day 4, (figure 3) differences in the morphology of the treatments were apparent. Seedlings grown under control conditions continued to grow normally, while those in the perchlorate continued to be progressively inhibited in their growth. Seedling growth was essentially unchanged at 0.1 perchlorate, and shoot elongation was definitely diminished at 0.3 perchlorate and greatly reduced at 0.6 perchlorate.

Stress symptoms were apparent by day 6 with a decrease in shoot elongation rate and water absorption capacity, and leaves became chlorotic with yellowing and leaf narrowing. As the concentration of perchlorate increased, the growth of the plants was arrested to a greater extent. By day 6, no growth was observed for plants exposed to 0.6% perchlorate.

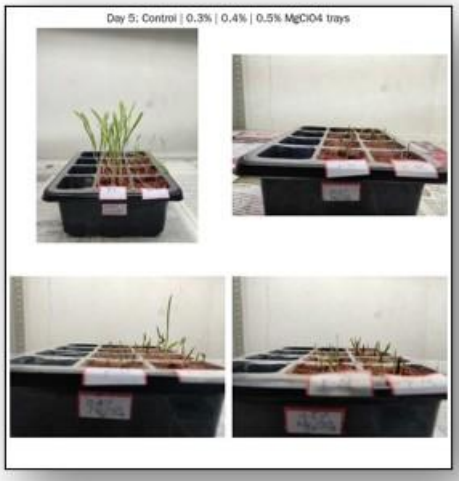


Figure 3. Comparative seedling growth on Day 5 across treatments: control and 0.3%, 0.4%, and 0.5% (w/v) magnesium perchlorate, illustrating the progressive dose-dependent reduction in vigor and onset of chlorosis**.**

3.3 Water Uptake

As the concentration of perchlorate increased, the uptake of water decreased. Table 2, Figure 4 shows the water uptake by the control plants was roughly 5 mL/well during the experiment. Those that were grown with 0.3% perchlorate (as a component of the nutrient solution) took up the water in smaller amounts, reaching about 4.0 mL by day 6 and 3.0 mL by day 10. Water uptake was further reduced at 0.4% and 0.5% perchlorate to ~2.5 mL and 2.0 mL by day 10 respectively, with negligible uptake by plants at 0.6% perchlorate by day 10. The pattern suggests that at higher concentrations of perchlorate, there is significant impairment of root metabolic activity and transpiration.

Table 2. Water uptake (mL/well) at Day 6 and Day 10 across perchlorate treatments.

Concentration	Day 6 (mL)	Day 10 (mL)
Control	~5.0	~5.0
0.3%	4.0	3.0
0.4%	n.d.	2.5
0.5%	n.d.	2.0
0.6%	n.d.	Negligible

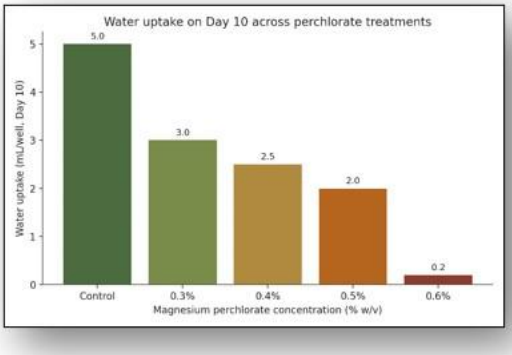


Figure 4. Water uptake on Day 10 across magnesium perchlorate treatments, showing the dose-dependent decline in root water absorption. n.d. = not determined at this time point.

3.4 Survival

It was found that as the concentration of perchlorate increased, the survival time decreased. For both proxy species, the control samples remained viable for over 20 days (table 3, figure 5). Increasing perchlorate concentration led to a drop in survival time: pearl millet had a survival time of about 15 days at 0.1%, 14 days at 0.2%, and about 11 days at 0.3%; foxtail millet had a survival time of about 14 days at 0.1%, 12 days at 0.2%, and 11 days at 0.3%. In both species, further reductions in survival were found at 0.4% and 0.5% perchlorate, while complete mortality was found by day 6 at 0.6% perchlorate. Pearl millet exhibited a higher tolerance to perchlorate stress, with consistently longer survival time compared to foxtail millet in all treatments, up to one to two days.

Table 3. Survival time (days) of pearl millet and foxtail millet across perchlorate treatments

Concentration	Pearl millet (days)	Foxtail millet (days)
Control	>20	>20
0.1%	15	14
0.2%	14	12
0.3%	11	11
0.6%	≤6 (complete mortality)	≤6 (complete mortality)

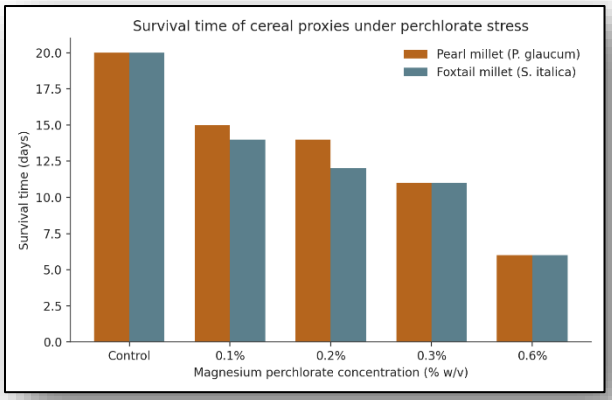


Figure 5. Survival time of pearl millet and foxtail millet under increasing magnesium perchlorate stress. Values for 0.4% and 0.5% are omitted pending verification against the original data set.

3.5 Shoot and Root Growth

A quantitative assessment of growth was performed on day 10 of treatments where plants were still alive. There was a clear dose-response relationship for shoot growth (table 4,5 figure 6). For pearl millet, the shoot length was reduced to 4.5 cm, 3.6 cm and 2.2 cm at 0.3%, 0.4% and 0.5%, respectively, of the control with a total reduction of about 86.7% at the highest surviving application rate. Foxtail millet was more sensitive, showing a reduction in shoot length from 14.7 cm to 2.5 cm, 2.3 cm and 1.35 cm at 0.3%, 0.4% and 0.5%, respectively, which is about 90.8%.

Comparatively, root growth was less affected. In pearl millet, root length decreased by approximately 22.4% from the control level, to 4.75 cm at 0.3%, 4.15 cm at 0.4% and further reduction at 0.5%. For foxtail millet, the root length was reduced by about 25.8% under the same treatments as the control (4.45 cm, 3.85 cm, 3.6 cm, respectively). The results in this study suggest aerial tissues were more sensitive to the perchlorate stress than root tissues, a pattern also reported for other perchlorate- and salt-stressed crops where photosynthetic tissue shows disproportionate oxidative injury relative to the root system (Meharg and Hartley-Whitaker, 2002; Calderón et al., 2014; Tan et al., 2004).

Table 4. Shoot growth analysis (length, cm) on Day 10

Millet strain	Control (cm)	0.3% (cm)	0.4% (cm)	0.5% (cm)
Pennisetum glaucum	16.5 – 16.8	4.1 – 4.9	3.3 – 3.8	2.1 – 2.4
Setaria italica	14.5 – 14.9	2.4 – 2.6	2.2 – 2.4	1.3 – 1.4

Table 5. Root growth analysis (length, cm) on Day 10

Millet strain	Control (cm)	0.3% (cm)	0.4% (cm)	0.5% (cm)
Pennisetum glaucum	5.3 – 5.4	4.7 – 4.8	4.5 – 4.6	4.1 – 4.2
Setaria italica	4.8 – 4.9	4.4 – 4.5	3.8 – 3.9	3.5 – 3.7

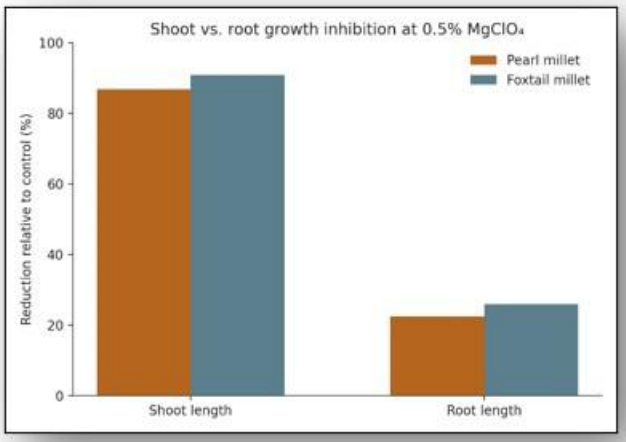


Figure 6. Percentage reduction in shoot and root length relative to control at 0.5% (w/v) magnesium perchlorate, showing the greater sensitivity of shoot tissue in both species.

Perchlorate was found to have a statistically significant effect on both shoot and root growth for both species by one-way ANOVA ($p < 0.05$). Shoot growth was extremely responsive to perchlorate stress compared to root growth, and interspecies differences were significant over all treatments; pearl millet had longer shoots and roots than foxtail millet, consistent with its ability to withstand perchlorate stress.

Overall, these results suggest that perchlorate-containing regolith analogs are strongly, dose-dependently inhibited from biological activity. Growth was not greatly affected by perchlorate initially, but progressive physiological stress became apparent after day 3 and growth was significantly inhibited at concentrations higher than 0.3% perchlorate and completely inhibited at 0.6% perchlorate. Pearl millet's relative resistance to perchlorate compared to other crops that were tested reflects species-specific variation in perchlorate resistance among candidate crops for growing on other planets.

3.6 Discussion

The results of these experiments show that magnesium perchlorate is a major abiotic factor that limits the potential for ongoing biological activity in Martian regolith models. The observed, dose-dependent inhibition is consistent with previous reports that perchlorates are potent oxidizing salts that disrupt plant metabolism, nutrient uptake and photosynthesis, as well as other environmental toxicology literature related to perchlorate occurrence, reactivity and remediation (Coates and Achenbach, 2004; Rao, 2010; Niziński et al., 2021; Kumar et al., 2023). The delayed onset of toxicity, only after initial germination, suggests perchlorate is not metabolically deactivating itself during the initial metabolic activation, but rather gradually impacts biological function over time with continued exposure. This trend is analogous to previous studies investigating the disruption of

chloroplast function and induction of oxidative stress due to perchlorate exposure in plants which showed time-dependency (Xie et al., 2009; Xie et al., 2014).

The initial and persistent symptom was chlorosis, which was noted at 0.3% perchlorate and higher. Previous work has shown chlorosis to be associated with a disruption of chlorophyll synthesis and degradation of photosynthetic pigments and has shown the effect of perchlorate exposure on chlorophyll fluorescence parameters (Xie et al., 2009) and the ability to accumulate biomass and metabolically function. In the present study, soil nutrient analyses did not show any N deficiency as a cause of the chlorosis observed, suggesting that the perchlorate toxicity is responsible for the observed chlorosis directly, rather than indirectly via nutrient deficiencies. The resulting physiological decline is typical of the degradation of photosynthetic ability and results in decreased respiration, decreased energy production and eventual plant death.

The reduction in water uptake seen with increasing amounts of perchlorate treatment also suggests that the root metabolic function was disrupted, as water uptake is closely coupled with root respiration, membrane transport and transpiration. The reduction in water flow and root activity before has been reported with perchlorate amended culture media and in perchlorate concentration studies on aquatic and terrestrial plants conducted on a field-scale level (He et al., 2013; Tan et al., 2004; Calderón et al., 2014; Bulaeva et al., 2015). Taken together, these findings suggest that perchlorate toxicity affects a variety of plant processes, including photosynthesis and root, leading to a disruption of the system.

One of the important findings of this study is that the root tissues are less sensitive than the shoot tissues and shoot growth is found to be more inhibited. Similar trends have been observed in other plant stress responses, such as increased susceptibility of aerial tissues to oxidative stress because of the increased metabolic activity and reliance on photosynthesis (He et al., 2013; Meharg and Hartley-Whitaker, 2002). The relative stability of the root systems suggest that some biological activity in the roots may be sustained at the subsurface level in the presence of perchlorate stress, and can be directly applied to future designs for extraterrestrial cultivation systems.

The two proxy species, pearl millet and foxtail millet, were compared and it was found that pearl millet was more tolerant of perchlorate stress than foxtail millet, consistent with previous agronomic and physiological studies that demonstrated pearl millet is a highly stress-tolerant cereal, with a high capacity to withstand drought and adverse soil conditions (Serraj et al., 2005; Ashraf and McNeilly, 1992; Jha et al., 2022). This inter-species variability in stress tolerance could be due to genetic and physiological differences in antioxidant capacity, osmotic regulation, stress responsive metabolic pathways and other mechanisms as observed in salt and drought stressed millets and other halophytic grasses (Sreenivasulu et al., 2000; Sobhanian et al., 2010; Lapuimakuni et al., 2018).

In planetary science terms, these findings also provide further evidence that perchlorate contamination is one of the most critical chemistry issues that calls into question the possibility of life on Mars. Perchlorates occur globally in the Martian surface regolith, and are an important part of the surface geochemistry and oxidation processes (Davila et al., 2013; Hecht et al., 2009; Glavin et al., 2013; Clark and Kounaves, 2016). Perchlorates are also toxic, posing a serious challenge for any biologic system that may be applied in long duration missions, but could potentially be used as an in-situ resource to generate oxygen and propellant, along with other Mars-derived volatiles and reactive salts (Hepp et al., 1993; Sanders and Larson, 2011).

The results also have implications for life detection and astrobiology. Partly, the low abundance of organic material found at the Martian surface could be explained by the tendency for organic molecules to be destroyed by oxidation and by the ability of perchlorates to both oxidizing organic molecules and complicating detection of a biosignature during thermal analysis (Glavin et al., 2013; Quinn et al., 2013). The harsh reduction of multicellular biological activity found in this study is in line with the general idea that the near-surface environments on Mars that are not shielded and not chemically modified, are inhospitable to complex life.

For crewed missions, any perchlorate found in regolith-grown food would also have to be removed from the crop before consumption, as there is much literature on the impact of perchlorate on human health, specifically its interference with human use of iodine and thyroid function (Wolff, 1998; Blount et al., 2007; Steinmaus et al., 2010; Gonsioroski et al., 2020). This introduces a food-safety component to the agronomic limits of tolerance reported herein, and strengthens the argument for pre-treating regolith, rather than relying on crop tolerance.

Finally, the experimentally determined tolerance limits are used for designing bioregenerative life-support systems. It is likely that future Martian cultivation substrates will require biological pre-treatment (microbiological reduction of perchlorate,

leaching, or engineered cultivation media) to allow sustained microbial growth, for example microbial reduction of perchlorate (Waller et al., 2004; Coates and Achenbach, 2004). Microbial soil amendment/inoculation approaches are worth evaluating as an adjunct to substrate pre-treatment and have previously been demonstrated to work with perchlorate-tolerant cyanobacteria at concentrations relevant to Mars, as well as to form beneficial associations with plant roots under salt stress conditions (Rzymski et al., 2022; Singh et al., 2022; Cuddy et al., 2013).

More broadly, sustained crop production on the Moon and Mars will require an integrated substrate-engineering and crop-selection strategy validated across simulants and growth systems (Wamelink et al., 2014; Onsay et al., 2019; Poulet et al., 2022; Duri et al., 2022). A steady progression towards the integration of planetary science, astrobiology and habitat engineering will be required to support the human presence on Mars for longer periods.

4. CONCLUSION

The study shows that magnesium perchlorate is a strong geochemical limitation to prolonged biological activity in Martian regolith analogues. Germination was not directly inhibited, but as plants continued to grow, progressive physiological stress caused progressive growth inhibition, chlorosis, decreased water uptake, and increased early mortality as perchlorate concentrations increased. A dose-response effect was observed, with significant inhibitory activity occurring at greater than 0.3% perchlorate with complete growth inhibition occurring at 0.6%. These findings indicate that pre-treatment of Martian regolith or habitat cycling would be necessary to allow for long-term biological activity in that environment.

All aerial tissues were more sensitive to perchlorate stress than roots, suggesting a greater susceptibility to oxidative damage in photosynthetic tissues. Pearl millet exhibited higher stress tolerance than foxtail millet, highlighting the importance of stress tolerance by species when choosing candidate organisms for future bioregenerative life-support systems. Engineering and identifying stress-tolerant organisms, potentially in combination with perchlorate-tolerant microbial soil amendments, will thus be an important part of future Mars life-support strategies (Verseux et al., 2016; Rzymski et al., 2022).

The results presented offer experimentally derived constraints applicable to resource utilization, astrobiology and surface habitability management on Mars. Perchlorates are toxic to life, but they could also provide oxygen and propellants on Mars; the presence of perchlorates on Mars is a challenge and an opportunity. Toxicity will need to be addressed with technologies such as microbial reduction, leaching and engineering of substrates before the sustainable use of biological systems can be realized. This work further advances knowledge of planetary surface chemistry and biological sustainability, which is fundamental to closed ecological life-support systems and long-term planetary surface exploration and habitation in the Solar System.

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AUTHOR CONTRIBUTIONS

AM and SRS contributed to conceptualization, methodology, investigation, supervision. formal analysis and writing the original draft. AA was responsible for data curation, investigation and validation. DR contributed to methodology, editing All authors contributed to manuscript revision and approved the final version.

CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

ETHICS STATEMENT

Ethical approval was not required for this study.

DATA AVAILABILITY STATEMENT

Data supporting the findings of this study are available from the corresponding author upon reasonable request.

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