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Review article

Gypsophytes and the use of Martian Gypsum: A review of their potential for agriculture on Mars

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ABSTRACT

Gypsophytes are plants that thrive on gypsum soils on Earth. They possess some adaptive traits that could constitute pre-adaptations to the conditions for potential cultivation in a controlled habitat on Mars. Martian agriculture should utilize substrates obtained directly from the planet itself. However, the detection of perchlorates in the soil of Mars raises doubts about this possibility. These molecules are distributed globally and in concentrations toxic to both humans and plants. The polar winds may preserve some Martian gypsum outcrops from the effects of perchlorates. If so, using this Martian gypsum as a growing substrate for gypsophytes may be a viable option. In the medium term, implementing gypsophyte adaptations on staple crops would also be possible using CRISPR-Cas9 and/or other gene-editing technologies. According to the literature reviewed, *Gypsophila struthium* subsp. *struthium* shows a high degree of colonization capacity and high resistance to drought. This taxon serves as an ecological facilitator for other species, and its germination appears to be favored by the presence of gypsum. Several experimental results suggest it would be worthwhile to test the cultivation of this and other plants on reliable simulants or Martian gypsum through sample return missions or on a mission that would perform the cultivation on Mars itself.

1. Challenges regarding the development of agriculture on Mars

The development of agriculture on Mars is crucial if a permanent or long-term human presence on that planet is intended. This presence would be much safer if based on the strategy of in situ resource utilization ISRU (Muscatello and Santiago-Maldonado, 2012). Using native soils would make it easier and less expensive to establish a self-sufficient base (Wamelink et al., 2014).

Extreme conditions, complex dynamics, and the combined influence of astronomical and atmospheric factors shape the current climate of Mars. The planet's obliquity (25,2°) and the significant eccentricity of its orbit (0.0934) lead to pronounced seasonal and latitudinal variations, which drive the global cycles of dust, carbon dioxide (CO_2), and water (H_2O). These cycles, involving radiative and dynamic atmospheric processes, regulate Mars' present climate (Martinez et al., 2017). As a result of all these factors, Mars' current surface environment is extremely cold (an average annual temperature of -60°C) and dry. The soil is chemically active, and the surface is subject to high levels of ultraviolet and ionizing radiation. The low atmospheric pressure (600 N/m^2) would also pose an obstacle for future human explorers (Boston, 2010). Any controlled habitat on Mars, whether intended for plants or humans, must be suitably adapted to meet each and every one of these challenges.

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In the case of plants, researchers have proposed multiple strategies to design habitats suitable for cultivating plants in warm environments with reduced exposure to ultraviolet (UV) radiation. One promising approach involves the use of greenhouses constructed with silica aerogels. Notably, silica aerogels are transparent to visible light while effectively blocking UV radiation at wavelengths between 20 and 400 nm (Wordsworth et al., 2019). Under mid-latitude Martian environmental conditions, a 2–3 cm thick layer of this material would shield against harmful UV radiation while allowing adequate light transmission for photosynthesis and achieving temperature differentials exceeding 45 K under a solar flux of 150 W/m^2. Another alternative (while not excluding the previous one) involves the use of artificially illuminated greenhouses (Poulet et al., 2014). On Earth, light-emitting diodes (LEDs) have proven to be efficient light sources in horticultural applications, offering reduced energy consumption and investment costs (Singh et al., 2015). Their application covers extraterrestrial settlements without continuous access to natural sunlight, including lava tubes (Boston, 2010; Mari et al., 2021; Romio, 2022) and polar outposts (Cockell, 2001; Rüede et al., 2019). To recreate Earth-like growing conditions, habitats must be pressurized to at least 0.8 bar, resulting in a pressure differential of approximately 80,000 Pa. This pressure differential imposes considerable mechanical stress on greenhouses, which must be absorbed by structural components with high tensile strength (Rüede et al., 2019).

Despite the above, the availability of a suitable growing substrate remains a fundamental requirement in order to develop a Martian Agricultural Life Support System. This review critically evaluates the suitability of gypsophytes for cultivation in a controlled habitat on Mars using an ISRU growth substrate. The development of new Martian and lunar regolith simulants made experimentation in this field possible (Allen et al., 1998; Rickman et al., 2007). Earlier research results suggest that a mixture of Martian regolith simulant and organic matter may be a suitable growing substrate (Wamelink et al., 2014). However, the authors were extremely cautious about this, highlighting the need to continue investigating crucial aspects of the soil, such as the representativeness of the simulants, the water-holding capacity, and the influence of Martian gravity or light (Wamelink et al., 2014).

The results of direct analyses conducted in situ presented a less flattering picture for a Martian regolith-based agriculture. The first probes to land on the surface of Mars, the 1970s Viking 1 and 2 landers, inferred perchlorates (ClO_4^-) in both Utopia Planitia and Chryse Planitia (Navarro-González et al., 2010). Later, direct detections of these molecules were made both at the Phoenix probe landing site and at Gale Crater (Hecht et al., 2009; Glavin et al., 2013). Other measurements obtained from orbit by the Mars Odyssey Gamma Ray Spectrometer point to a global presence of ClO_4^- in the first tens of centimeters of the regolith (Davila et al., 2013). The presence of perchlorates would pose a significant obstacle to the development of Martian agriculture, as these chemical compounds are toxic to both plants and humans (Diamond et al., 2008). Oze et al. (2021) conducted a series of experiments using a Martian simulant (a regolith analogue of the Gusev Crater) and a control soil (a mixture of recycled forest products, composted materials, and lime) to investigate the effects of perchlorate on plant growth. In these experiments, no plant could germinate in Martian soil simulant when exposed to perchlorate (Oze et al., 2021). These results underscore the magnitude of the problem caused by the presence of perchlorates in the Martian regolith.

A solution to this could be to remove the perchlorates by flow-through reactors. Again, Oze et al. (2021) tested this approach through a series of experiments using the regolith simulant and the control soil. These experiments involved passing a constant flux (1.5 mL h^{-1}) of ultra-pure water through sealed tubes containing the different samples. One of their conclusions was that removal by washing or volatilization should be coupled with enhancement of the regolith with organic matter to promote structure and nutrient cycling (Oze et al., 2021). Other alternatives include phytoremediation (Susarla et al., 1999; Misra et al., 2021) or the elimination of perchlorates through the decomposition of the molecule into chlorine and oxygen, facilitated by enzymes (Okeke and Frankenberger, 2003; Davila et al., 2013). Phytoremediation is a promising method for in situ decontamination of large volumes of polluted soil and water on Earth. In a laboratory study, Susarla et al. (1999) evaluated the perchlorate removal capabilities of thirteen terrestrial, aquatic, and wetland species from aqueous solutions. Only three showed high performance: *Bacopa caroliniana, Salicornia virginica*, and *Myriophyllum aquaticum*. Some are suitable for contaminated water bodies or engineered systems, while *Liquidambar styraciflua, Populus deltoides*, and *Salix nigra* are effective for perchlorate-contaminated soils in upland areas. Extracts of *Artemisia dracunculus sativa* may be applied in mechanized continuous-flow systems for water treatment (Susarla et al., 1999). However, on Mars, water availability and plant survival impose significant limitations that require further investigation. Misra et al. (2021) conducted a comprehensive review of phytoremediation and microbial remediation using rhizosphere microorganisms and extremophiles. Given the harsh Martian environment, extremophiles are promising candidates for successful microbial remediation on the planet. Nevertheless, even if perchlorates are efficiently removed, their influence on soil metal ion availability requires careful consideration. In this sense, perchlorates have an ambivalent effect. Although they can mobilize nutritional cations like Ca^{2+}, Mg^{2+}, and K^+ (Karmarkar et al., 1991), they also solubilize toxic heavy metals (Kumarathilaka et al., 2016), which increases the risk of contamination, plant toxicity, and human health problems. This effect has been observed for Ni and Co in laterite (Senanayake et al., 2011) and for Fe in goethite and hematite (Majima et al., 1985).

These findings highlight the potential of perchlorates to alter metal availability, potentially rendering the Martian regolith phytotoxic despite their removal (Oze et al., 2021). Regardless of the remediation strategy employed, it would be essential to evaluate whether plants cultivated in treated Martian regolith (if possible) are safe for human consumption. The availability of a perchlorate-free substrate on Mars could mitigate, or even eliminate, several of these challenges.

2. Towards a possible alternative

2.1. Gypsum and gypsophytes

This study examines the use of Martian gypsum as a cultivation substrate and the plants that can grow in it, the gypsophytes, as an alternative to regolith. Some evidence suggests that significant outcrops of this mineral may be free of perchlorates (see below). If this evidence is confirmed, its use as an agricultural substrate would not require more or less complex processing procedures to remove those chemicals. This material, along with other hydrated calcium sulfate phases, has been detected in several locations on the Martian surface (Langevin et al., 2005). Although soils with high concentrations of calcium sulfates are not ideal environments for most plants on Earth, some species can tolerate and thrive in them, known as gypsophiles (also referred to as gypsophytes). These plants inhabit the gypsum steppes of various parts of the world (Parsons, 1976; Mota et al., 2016), often in extreme climates that include periods of severe aridity. Such environments have generated selective pressures that have compelled these organisms to develop a diverse range of adaptations tailored to these habitats. These could enable them to grow on a Martian gypsum-based substrate. The authors of this study acknowledge that their research is also applicable to a hypothetical process of terraforming Mars, but that question falls beyond the scope of the present study. The comprehensive work by Pérez-García et al. (2018) provides valuable insights into the diversity of gypsophytes. This inventory could serve as a foundational resource for identifying potential species that may be adapted to Martian gypsum soil conditions. Besides utilizing information from laboratory-based testing (e.g., cold and UV-radiation tolerance), results generated using ecological niche models can provide valuable, complementary information,

serving as a starting point or exploratory analysis to guide such experiments.

An important characteristic of gypsum soils is a resistant physical and/or biological surface crust, which could prevent rooting by constituting an impassable barrier for the tender radicles of some species (Gil de Carrasco and Ramos Miras, 2011; Escudero et al., 2015). A multitude of organisms, including eukaryotic algae, cyanobacteria, and fungi, populate the biological crust, which plays a crucial yet complex role in soil ecology for plant life (Escudero et al., 1999). Another important issue for gypsophilic plants is the competition between Ca^{2+} and Mg^{2+} ions, which can affect the uptake of Mg^{2+} (Alves et al., 2021). Gypsophytes, however, have developed a wide range of adaptations to face all these challenges, which we will discuss below. This study concludes that all those traits, together with the well-established presence of gypsum on Mars, make these plants suitable candidates for growing on substrates obtained in situ on the planet.

2.2. Gypsum on Mars

As mentioned above, the exploration of Mars' surface has revealed that it is rich in sulfur, a finding that is relevant regarding several geological processes (King and McLennan, 2010). Most of this sulfur exists in the form of sulfates, among which gypsum, also known as calcium sulfate dihydrate ($CaSO_4{\cdot}2H_2O$), is the most prevalent. Analyses have identified this mineral at multiple sites on Mars, including Olympia Undae (Szumila et al., 2013), Meridiani Planum (Grotzinger et al., 2005; Squyres et al., 2012), Noctys Labyrinthus (Weitz et al., 2013), and Gale Crater (Vaniman et al., 2018). Bassanite, another form of calcium sulfate ($CaSO_4{\cdot}½H_2O$), has been identified at Mawrth Vallis (Wray et al., 2010). The spectral characteristics of both minerals are well known, allowing for their remote detection by orbiting space probes (Bishop et al., 2014). However, in situ detections have also been performed by landers and rovers, such as the gypsum veins discovered in the Endeavour Crater by the Opportunity rover (Squyres et al., 2012).

The boreal polar region of Mars could be a significant source of calcium sulfates, including gypsum. One area where it is especially abundant is Olympia Undae, a vast field of dunes near the northern polar region of the planet (Szumila et al., 2013). Gypsum can also be found much further south, even at latitudes slightly lower than 5° south of the equator. There is the large crater Gale, with an approximate diameter of 155 km, at the center of which rises Aeolis Mons, an elevation approximately 5 km high composed of highly varied sediments. Among them, in its lower part, are clayey strata underlying sulfate-rich ones with various degrees of hydration (Vaniman et al., 2018). Evidence strongly indicates the presence of gypsum on Mars across a wide range of latitudes, and significant reserves may be present in the boreal polar zone. However, the crucial question of whether any of these outcrops is free of perchlorates remains unanswered.

3. Findings from previous studies

3.1. Are there gypsum deposits free of perchlorates on Mars?

To the authors' knowledge, Olympia Undae, a vast dune field in the northern region hosts some of the most significant gypsum reserves on Mars (Szumila et al., 2013). Although concentrations of perchlorates are similar everywhere in the global soil unit, due to the widespread mixing caused by planet-wide dust storms (Clark and Kounaves, 2016), there is some evidence suggesting an absence or at least a limited presence of perchlorates in Olympia Undae. The dune field pattern formation exhibits two generations of crest lines (Fig. 1). While the oldest generation forms are transverse to the circumpolar easterly winds, the younger generation of crest lines emerged in response to both the circumpolar easterly winds and NE winds (Ewing et al., 2010). These crest-lines correspond closely to springtime katabatic winds driven by the Coriolis force (Spiga and Smith, 2018). Although the Phoenix polar mission

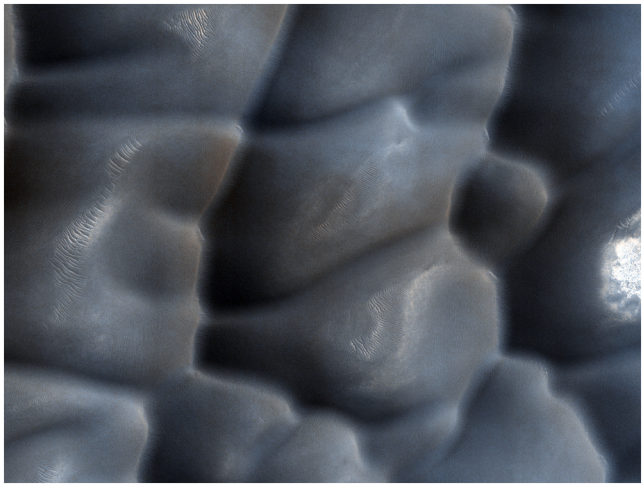


Fig. 1. Dune field in Olympia Undae. The two distinct generations of crest line formations are visible. The older generation is oriented transversely to circumpolar easterly winds, while the younger generation developed under the influence of both circumpolar easterly and northeasterly winds. This photograph was taken on December 9th, 2006, by the Mars Reconnaissance Orbiter mission. The center of the image is at 80.2°N latitude and 191.2°E longitude. The distance to the target was 316.4 km, and the projected image scale is 25 cm/pixel. At the time the image was captured, the Sun was 21° above the horizon. Image: NASA/JPL-Caltech/UArizona.

detected perchlorates at 68° N latitude, the majority of Olympia Undae extends northward of 80° latitude. This region is under the influence of the North Polar Vortex. Martian polar vortices are regions of cold, isolated air over the poles, circumscribed by powerful westerly jets which can act as barriers to the transport of dust, water, and chemical species (Streeter et al., 2021). Thus, it seems reasonable to assume that both the katabatic winds and the westerly jets associated with the polar vortex could have prevented transportation of materials from lower latitudes, including perchlorates.

3.2. Which species to use and why

Gypsophytes have received extensive scientific attention, and a wealth of literature exists on them. The information covers their biochemistry, physiology, ecology, and anatomical adaptations, among other biological aspects. Many of these studies highlight the remarkable germination, colonization, and survival capacity of *Gypsophila struthium* subsp. *struthium.* The genus *Gypsophila* is likely to have originated in the steppes of the Irano-Turanian region and the Caucasus Mountains (Barkoudah, 1962). They are mostly steppe plants able to cope with extreme edaphic and climatic conditions, and this species is no exception. The following points outline why *G. struthium* subsp. *struthium.* (Fig. 2**a**) may be considered a highly appropriate taxon for future research in this field.

a. Oxygen production and CO_2 uptake — Like any plant, *G. struthium* subsp. *struthium* has an autotrophic photosynthetic nutrition based on water photolysis. It can produce oxygen and remove CO_2 from the atmosphere to fix it into glucose molecules. In this sense, these organisms can serve as an alternative or a supplement to other methods of obtaining oxygen, such as solid oxide electrolysis from CO_2 (Hoffman et al., 2023) or water electrolysis (Tobias et al., 2011).

b. Source of antioxidants — On the Martian surface, living cells of Earth visitors, human or plant, face high radiation doses. These doses cause radiolysis of cytoplasmic water molecules (Gómez et al., 2021), producing dangerously high levels of reactive oxygen species (ROS). Various abiotic factors also generate oxidative stress in habitats with gypsiferous soils through the production of ROS. A

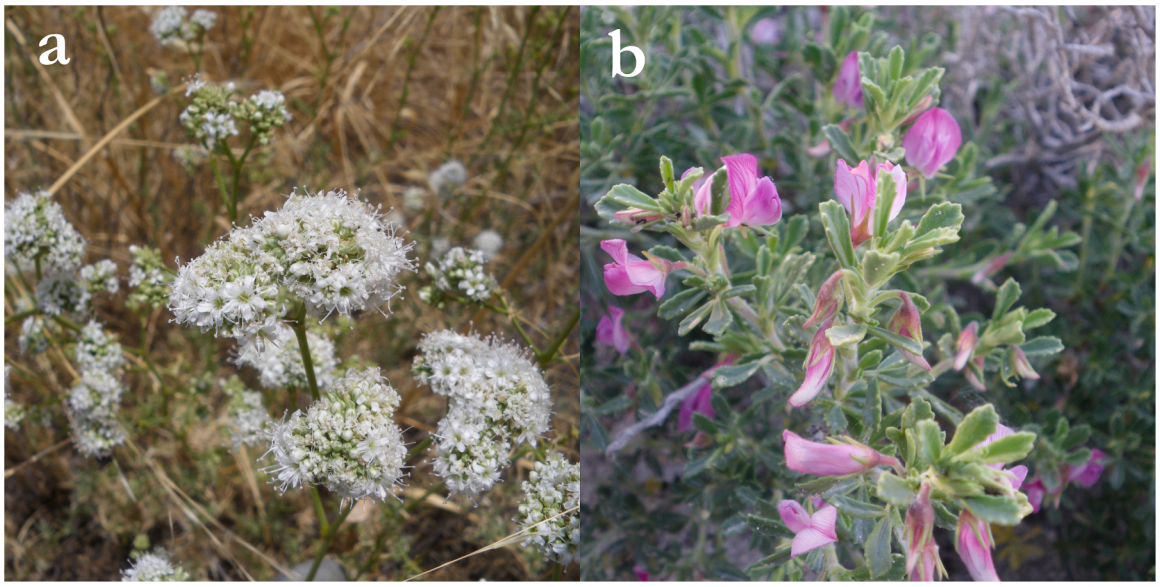


Fig. 2. Gypsophytes suitable for experimentation on Martian soils, according to our results. a. G. struthium subsp. struthium. b. Ononis tridentata. Gypsum steppes of the central region of the Iberian Peninsula (Alcarria plateau). Credit: M. de L.

protective response that activates antioxidant systems has evolved in gypsophytes. Flavonoids and other phenolic compounds are among the antioxidant molecules involved in this response and are essential for adaptation to gypsum soils (Boscaiu et al., 2010; Çekiç et al., 2018; Sekmen et al., 2012). Flavonoids are substances found naturally in fruits, grains, roots, stems, and flowers in many angiosperm species. They are currently considered fundamental in various medical and pharmacological applications, as they are credited with antioxidant, anti-inflammatory, antimutagenic, and anticarcinogenic properties (Panche et al., 2016). Other compounds, such as saponins (steroid or triterpenoid glycosides), exhibit not only detergent properties but also anticarcinogenic and immunomodulatory effects (Rao and Sung, 1995; Cheikh-Ali et al., 2019). All these substances would therefore offer significant benefits to the crew of a Mars base.

The genus *Gypsophila* is known for its diverse saponin profiles and for being the most diverse source of these molecules (Cheikh-Ali et al., 2019). These plants offer significant potential for bio-regenerative cultivation on Mars. For example, their saponins could enhance plant resilience in the harsh Martian environment. The chemical complexity of saponins in *Gypsophila* may help the plant adapt to stressors such as low gravity and limited resources (Cheikh-Ali et al., 2019). They also ease abiotic stresses — such as drought, salinity, and temperature extremes — by stabilizing cell membranes and reducing oxidative damage. Saponins promote plant growth and protect against pathogens, such as fungi and bacteria, due to their antimicrobial properties, playing a crucial role in plant survival and resilience under challenging conditions (Cheikh-Ali et al., 2019; Kayabas and Yildirim, 2022). Gypsophila's saponins could enhance soil health and nutrient cycling, which is crucial for sustainable Martian agriculture (Fons et al., 2003).

c. Ecological facilitator — The habitats with gypsiferous soils have often been affected by the exploitation of this mineral. Some studies of their restoration propose the recolonization of abandoned quarries by gypsophyte plants. In such interventions, a strategy based on the high colonizing power of *G. struthium* is proposed (Mota et al., 2004). However, this plant seems to be more than just a diligent colonizer of abandoned quarries. Plant ecologists have also studied its role in facilitating the establishment of other species. Such research suggests that *G. struthium* decreases soil compaction and softens temperature extremes under its canopy. These effects enable the establishment and development of other species, highlighting a role as ecosystem engineers or nurse plants and facilitating the restoration processes of these habitats (Foronda et al., 2017; Mota et al., 2023). These qualities could also be applicable in the successful colonization of new environments.

d. Germination — The seeds of *G. struthium* subsp. *struthium* matures in late summer, when annual high summer temperatures give way to milder ones. The minimal duration or absence of a dormancy period allows for germination with the first autumn rains. If the seeds are subjected to a period of low temperatures to simulate the passage of winter, they do not enter a dormant state either. These seeds are ready to germinate as soon as temperatures are favorable and there is sufficient water to do so (Merlo et al., 1997; Moruno et al., 2011). This behavior is known as an opportunistic germination strategy. These qualities make this species highly competitive in colonizing new habitats.

Also relevant are the results on the influence of gypsum on the germination of different species. These studies have demonstrated that gypsum in the soil enhances the germination of specific plant species (Cañadas et al., 2014). Calcium (Ca^{2+}) germination tests revealed not only the highest germination rates for *Gypsophila struthium* subsp. *struthium*, but also shorter dormancy periods, 6 days or fewer, than other gypsophile species, with calcium concentrations of between 350 and 450 ppm being optimal for germination (Merlo et al., 1997).

e. Seeds — The seeds of *G. struthium* maintain a high viability when preserved in an atmosphere of low relative humidity or under freezing conditions. In these cases, seeds maintain their viability for two years in the seed bank (Moruno et al., 2011), a period longer than that required to reach Mars using current technology. As they are small seeds (less than 2 × 2 mm), a spacecraft could transport large quantities of them without significantly increasing the weight of the mission payload.

f. Photosynthetic efficiency under stress — In a comparative study of three gypsophyte species, researchers found that the stress of warmer, drier months affected them unequally. Among these species, *G. struthium* was found to exhibit the most stable quantum efficiency of Photosystem II under harsh conditions, and was the least sensitive to soil type (Merlo et al., 2009). Recent research also shows that

some species of the genus can utilize calcium oxalate (CaOx) crystals as a dynamic internal carbon pool, which can be utilized during periods of low atmospheric CO_2 availability, thereby aiding photosynthesis while conserving water (Tooulakou et al., 2016; Kayabas and Yildirim, 2022). This mechanism allows *Gypsophila* to adjust its metabolic processes in response to water scarcity, enhancing its survival in extreme habitats.

g. Usage of crystallization water from the gypsum structure — In a hypothetical base on the surface of Mars, it would be important to minimize water expenditure. Although several researchers have proposed strategies to obtain water, some of these approaches are complex and challenging to implement. For example, extracting water from subsurface ice through drilling or mining techniques (Changela et al., 2021) presents significant technical challenges. Mining water from gypsum crystallization could offer a feasible alternative (Van Der Gaag, 2008; van Susante et al., 2021). In any case, obtaining water would involve a certain amount of energy and technological cost, and could be a limiting factor. However, there is evidence that some gypsophytes may obtain gypsum crystallization water by themselves. Studies show that the crystalline water of gypsum (which can account for about one-fifth of gypsum's weight) can be a significant water source for plants (Palacio et al., 2014). This crystallization water uptake reaches its maximum during the summer (as soil heating enhances gypsum dehydration), which may hinder its use of gypsum as a water source on Mars. However, gypsophytes can obtain crystallization water molecules from gypsum through non-temperature-dependent processes (Palacio et al., 2014). Plants and associated microorganisms can access gypsum's crystallization water through chemical and biological mechanisms. Roots and microbes modify soil pH by releasing organic acids and protons, thereby facilitating gypsum dissolution (Palacio et al., 2014). Additionally, cyanobacteria can form biofilms on gypsum surfaces, inducing local dissolution and conversion to anhydrite, which releases structurally bound water (Huang et al., 2020; de la Puente et al., 2022).

h. Morphological and anatomical key adaptations to cope with various types of stress in extreme environments — the presence of waxes and microstructural features on the leaf surface enhances water retention. This minimizes water loss, allowing the plants to survive in arid conditions. Such adaptation is crucial for maintaining hydration in environments with limited water availability. Gypsophytes, including *Gypsophila* species, generally exhibit a conservative water use strategy, characteristic of isohydric behavior. For this reason, *Gypsophila* species exhibit xeromorphic traits, including rough leaf surfaces and a strategic distribution of stomata, as well as low stomatal conductance, which help reduce transpiration and optimize water use (Kayabaş and Yildirim, 2022). As a result, they can conserve water during droughts and continue photosynthesis in the dry season by taking advantage of sporadic rains. This strategy involves tightly regulating the stomatal opening to maintain stable leaf water potential and minimize water loss (León Sánchez, 2016).

i. Low water requirements and broad climatic niche — Ecological Niche Models (ENMs) facilitate the quantification and visualization of the ecological preferences of an organism in a geographical or environmental space. Sometimes, it is more useful to represent niches in the predictor variable hyperspace rather than in the geographic space, as niche topology does not directly match a species' distribution (Guisan et al., 2014). We performed dimension reduction using Principal Component Analysis (de Luis et al., 2019; Janžekovič and Novak, 2012), which defines the environmental space by the first two PCA axes and divides it into an r × r grid of unique environmental conditions. This method, proposed by Broennimann et al. (2012), facilitates a visual comparison of niche extent, particularly when plotting two taxa simultaneously (Fernández-López, 2017). Data on the localities of occurrence of the studied species are available from the Global Biodiversity Information Facility (GBIF, https://www.gbif.org/). Researchers can access data on climatic variables through the WorldClim portal (Worldclim, https://www.worldclim.org). When we use precipitation in the driest month as the only predictor variable, the observed response of *G. struthium* subsp. *struthium* is remarkable. This taxon shows one of its maxima of density of occurrence near to 0, indicating that this species can thrive even in almost no rainfall during the driest month (de Luis et al., 2019). These results are consistent with the summer stress values measured for this species (Merlo et al., 2009). In the representation of the niches in their environmental space (Fig. 3), the wider niche of *G. struthium* subsp. *struthium* (de Luis et al., 2018b) is also clear when compared with that of closely related species such as *G. bermejoi* (López González, 1984). This indicates that *G. struthium* can occupy a wide range of environments, which aligns with its generalist ecological strategy and makes it more likely to colonize novel environments. Such behavior could facilitate the creation of suitable environmental conditions in a greenhouse or reduce the associated costs. For instance, if the plants tolerate lower temperatures, this could reduce some of the energy needed to heat the habitat.

j. Nutrients — The elemental composition of *Gypsophila* species, characterized by high calcium and sulfur accumulation, reflects their adaptation to gypsum soils. This atypical chemical profile supports their growth in nutrient-poor environments (Ruiz et al., 2003; Merlo, 2019; Cera et al., 2023). It is supposed that several transporters, described in different plant species, would allow the introduction of these ions into cell vacuoles**.** In this manner, they would not interfere with sensitive metabolic processes, and the plant would avoid toxicity because of excessive calcium or sulfate in the cytoplasm. These ions could aid in regulating osmotic balance and function as osmoprotectants in dry and saline environments (Kaiser et al., 1989).

k. Mycorrhiza — Mycorrhizal fungi form symbiotic relationships with *Gypsophila struthium* susbp. *struthium*, which helps it to access essential nutrients like phosphorus and nitrogen that are often scarce in gypsum soils (Alguacil et al., 2009). On Mars, the soil is also poor in these and other nutrients. These fungi could also enhance water retention and soil stability, which are crucial for agriculture on Mars. The unique mycorrhizal associations might enhance plant resilience, making them a strong candidate for sustainable Martian agriculture.

3.3. The potential of gypsophytes for Martian cultivation: are gypsophytes pre-adapted to Martian gypsum?

The evidence presented above strongly suggests that the unique traits and adaptations of gypsophytes, developed over their evolutionary history, could be instrumental for their survival in a controlled habitat on Mars. Their ability to thrive in highly arid conditions, where specific nutrients are scarce, and their production of various antioxidant molecules, are clear examples of this. The specific case of *G. struthium* subsp. *struthium*, with its opportunistic germination strategy and the stability of its photosynthetic molecular machinery under stress conditions, is particularly noteworthy. Were it so, this would constitute one of the most extreme examples of pre-adaptation, as it would facilitate the successful establishment and colonization of another planet. On Earth, this plant is one of the best colonizers of degraded gypsum environments. However, the question remains: could any gypsophyte species grow on a gypsum substrate from Olympia Undae? Forecasting how these plants will perform on Mars is a complex, multifaceted challenge that requires rigorous experimental validation. A crucial step is selecting the taxa with the highest likelihood of thriving in a Martian gypsum substrate. It is important to note that this work focuses on cultivating plants in a greenhouse with controlled environmental conditions, thereby shielding them from the extreme Martian climate. Martian gypsum, yes; Martian weather, no.

In scientific literature, *G. struthium* subsp. *struthium* stands out in terms of physiology, secondary metabolism, and ecology. However,

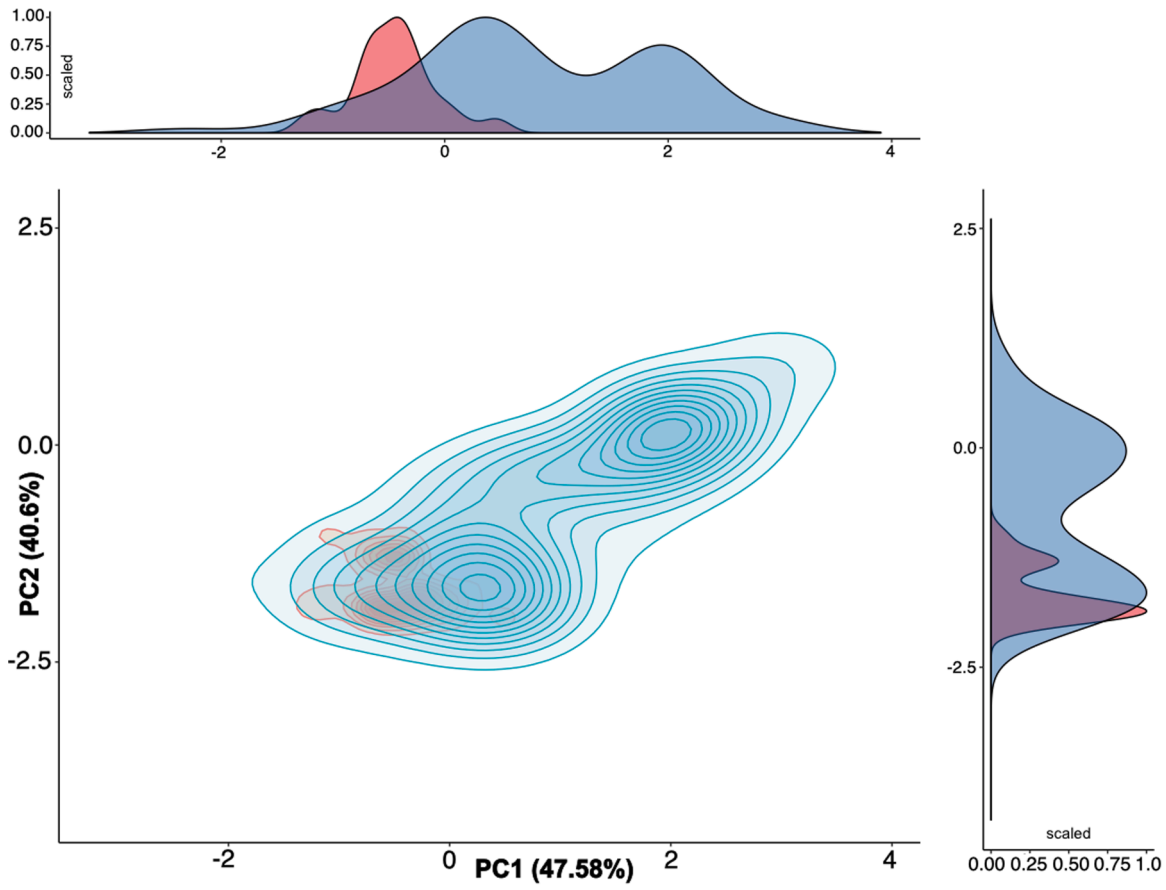


Fig. 3. Climatic niche modeling for species selection. Representation of the ecological niches of two taxa of the genus Gypsophila sp. in the environmental space. The first two axes of Principal Component Analysis define the environmental space, and the minimum and maximum environmental values bound it across the entire study area. Contour lines indicate the density of the species' occurrence. The different taxa have been plotted in pairs to facilitate easier comparison. The density of occurrence values ranges from 0 to 1, and the side graphs show a "side view" of these functions from both axes. This plot reveals that G. struthium subsp. struthium (blue) can thrive in a much wider range of environmental conditions than G. bermejoi (red). For these models, the predictor variables were: Annual Mean Temperature (bio1), Temperature Seasonality (bio4), Minimum Temperature in the Coldest Month (bio6), Temperature Annual Range (bio7), Annual Precipitation (bio12), Precipitation Seasonality (bio15), and Precipitation in the Driest Quarter (bio17). These variables are available from WorldClim. (Modified from de Luis et al., 2018b).

certain aspects of the soil, such as substrate texture and composition, should also be taken into consideration. It is possible to perform an analysis based on the granulometric data from Olympia Undae. The OMEGA (Observatoire pour la Minéralogie, l'Eau, les Glaces et l'Activité) instrument detected soil rich in gypsum deposits in 2006, according to Langevin et al. (2005). In some areas of this sea of dunes, the results showed values of 35% pure gypsum grains, a few microns in diameter, mixed with 65% coarser grains (millimeter-sized) of the same mineral. In the mixture, there would be some dark inclusions that could be basaltic grains trapped in the gypsum or magnetite formed by the alteration of iron-, sulfide-, and calcium-rich pyroxene sand grains (Fishbaugh et al., 2007). These dark inclusions could be of great interest for a growing medium, perhaps providing essential elements in plant nutrition such as iron and magnesium. It is important to note that these grain sizes are averages from a distribution of sizes. The sample exhibited a bimodal grain size distribution. On Earth, *Gypsophila struthium* inhabits gypsiferous soils with a wide range of gypsum contents, ranging from 7% to over 95% (mean = 56.3), and variable textures with a predominance of fine fractions, with silt + clay percentages greater than 80% (Merlo et al., 2009; Salmerón-Sánchez et al., 2014). In these soils, gypsum particles are distributed heterogeneously and are predominantly microscopic, ranging in size from 1 to 10 μm (Vieillefon, 1979). This ecological tolerance reflects a notable edaphic plasticity, suggesting thatgypsophile species like this could adapt to similar substrates on Mars. Interestingly, *G. struthium* subsp. *struthium* also thrives in abandoned quarries, growing on pure crystalline gypsum. Here, these plants show an abundance of floral scapes, indicative of a perfect nutritional status (Fig. 4). In Olympia Undae, although, processes such



Fig. 4. Gypsophila struthium subsp. struthium thrives in abandoned quarries, growing on pure crystalline gypsum. Here, these plants show an abundance of floral scapes, indicative of a perfect nutritional status. Credit: J.M.

as surface gypsum dissolution and reprecipitation—common in terrestrial systems like the Ebro Basin—do not occur, other mechanisms modify fine particles: sublimation and deposition of ice, aeolian erosion of Martian dust, and past aqueous alteration phases that allowed gypsum formation in evaporitic environments. Despite the different geochemical dynamics, fine or powdery gypsum crystals suggest textural conditions compatible with those tolerated by gypsophile plants on Earth.

3.4. Nitrogen fixation and biological crusts

If the Martian habitat where these plants grow maintains an Earth-like atmosphere (greenhouses would facilitate this), it is essential to have nitrogen-fixing plants. Nitrogen (N) is a major, crucial plant nutrient and a significant limiting factor for many crop species. Biological nitrogen fixation (BNF) allows the transformation of atmospheric N_2 into plant-assimilable forms of N. Accordingly, some Earth gypsum-loving plants are capable of performing this function. *Ononis tridentata* L. *(Fabaceae)* is a plant considered as an indicator of gypsiferous soils (Mota et al., 2009) and grows in a wide variety of soils, such as those with crusts, saccharoid soils, and gypsiferous loams (Fig. 2**b**). It can also flourish in those with low gypsum content, such as the washed soils of the Supramediterranean floor (Mota et al., 2004; Ferrandis et al., 2005)). The above role of ecological facilitator of *G. struthium* subsp. *struthium* would facilitate the combined cultivation of the two plant taxa.

Controlled environments could be enriched with biological crusts, such as those described by Li et al. (2024), highlighting the potential of extremotolerant desert mosses, like *Syntrichia caninervis*, as pioneer plants for colonizing extraterrestrial environments. Incorporating diverse microorganisms, as explored by Fučíková et al. (2024), could further enhance soil health and the resilience of the entire biocenosis in Martian soil conditions.

3.5. Gypsophilization?

If gypsum-tolerant plants can be grown on Martian substrates, the next logical step could be to provide these adaptations to plants of clear nutritional, medicinal, or other interest. This process, a process we term 'gypsophilization,' could be a game-changer. New biotechnologies applied to plants, such as gene regulation, multiple gene editing, mutagenesis, and directed evolution technologies, hold the potential to make this goal a reality in the medium term. Various strategies are currently employed to enhance crop resistance to soil salinity. A key approach involves overexpressing genes that encode proteins excluding Na^+ (such as PM-ATPase, SOS1 antiporter, and HKT1 transporter) and compartmentalizing them in vacuoles via V-H^+ ATPase, V-H^+ PPase, and NHX antiporter. Proteins such as aquaporins and dehydrins also mitigate water deficits caused by salt stress (Kotula et al., 2020). Many studies focus on gene transfer related to salt exclusion and Na^+ compartmentalization, with roles of transporters established across plant species. For instance, in *Arabidopsis thaliana*, the SOS1 gene codes for a plasma membrane Na^+/H^+ antiporter that expels sodium to maintain ion balance (Shi et al., 2002). In *Mesembryanthemum crystallinum*, the Mitr1 and Mitr2 genes, along with NHX-type transporters, facilitate Na^+ exclusion in roots and vacuolar sequestration in leaves (Chauhan et al., 2000). In *Oryza sativa* (rice), tolerant varieties, such as FL478, regulate genes including OsCHX11, OsCNGC1, OsCAX, and OsTPC1 to reduce Na^+ uptake, maintain low Na^+: K^+ ratios, and limit apoplastic transport, highlighting their potential for breeding salt-tolerant crops (Senadheera et al., 2009). Halophilic species, such as *Salicornia europaea* and *Atriplex dimorphostegia*, have been utilized as gene donors for crops like wheat (*Triticum aestivum*) and rice, respectively (Kotula et al., 2020). NASA proposed this research direction over a decade ago (The National Aeronautics and Space Administration, 2013). However, traditional genetic engineering methods (e.g., *Agrobacterium*-mediated transformation or mutation breeding) are slow and difficult to control (Wang and Doudna, 2023). CRISPR-Cas9 technology enables precise genome editing, potentially enhancing yields, disease resistance, and herbicide resistance, as well as accelerating domestication (Zhu et al., 2020; Wang and Doudna, 2023).

Regarding the adaptation of gypsophytes, their ability to accumulate sulfur (S), calcium (Ca), and magnesium (Mg) is critical. Sulfur transporters from the SULTR family are vital: SULTR1;2 absorbs sulfate from soil, while tonoplast-localized SULTR4;1 and SULTR4;2 aid sulfate storage in the vacuole, with expression modulated by sulfate availability, drought, and salinity (Takahashi, 2019; Gallardo et al., 2014). Calcium homeostasis under stress involves transporters like CAX1/3 (vacuolar) and ACA8/10 (extracellular) (Zhou et al., 2024). Magnesium transporters MGT1 and MGT2 in *Arabidopsis* mobilize Mg^{2+} from vacuoles to the cytosol under deficiency, while MGT10, MGR8, and MGR9, in the chloroplast inner membrane, regulate Mg^{2+} homeostasis and photosynthesis (Tang et al., 2022; Dukic et al., 2023). By analogy with the work performed with halophilic species, these transporters could be potential targets for implementing gypsophily in staple crops.

4. Future perspectives

Considering the risk to human life a mission to Mars involves, ensuring viable cultivation on Martian substrate is a critical step which must not be overlooked. Thus, the *plants-first* strategy gains relevance, implying that the first earthlings to live on Mars should be plants, and, according to the reviewed evidence, gypsophytes could be the perfect candidate. Within this framework, a sample return mission to Olympia Undae could constitute a necessary milestone. Such a phase would enable experimentation using an actual Martian substrate and/or the development of reliable soil simulants.

Given the uncertainty regarding the effects of the low gravitational field strength and other variables relevant to plant physiology, it seems logical that experimentation in situ would be crucial. If some plants thrive on the material, the next step would involve cultivating them on Mars, using a robotic laboratory deployed on Olympia Undae. Such an installation would have to be able to solve the problem of irrigation water supply and obtain the substrate for growing plants independently. If this option were implemented, the study's authors consider that specimens of the species *G. struthium* subsp. *struthium* and *Ononis tridentata* would be very suitable candidates for inclusion among the first terrestrial organisms to inhabit Mars. The soil could already be there!

CRediT authorship contribution statement

Miguel de Luis: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Jordi López-Pujol:** Writing – review & editing, Investigation. **Juan Mota:** Writing – review & editing, Investigation. **M. Encarna Merlo:** Writing – review & editing, Investigation. **Julio Álvarez-Jiménez:** Writing – review & editing. **Jose Ignacio Aparicio:** Writing – review & editing. **Carmen Bartolomé:** Writing – review & editing. **Jens Ormö:** Writing – review & editing. **Laura M. Parro:** Writing – review & editing.

Declaration of competing interest

The authors declare no competing interests.

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