

Living at the edge: mechanisms, evolution and threats for plant life on gypsum soils

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Premio a la Investigación de la Academia 2022. Sección de Naturales

Abstract

Gypsum soils are some of the most restrictive environments for plant life on Earth, yet these atypical substrates host singular ecosystems that are home to unique vascular and cryptogamic floras worldwide. The analysis of the mechanisms displayed by plants to survive the limiting conditions of gypsum can help improve crops and management of some of the most vulnerable regions of the planet. It can also inform on the best practices for the management and conservation of these remarkable ecosystems. This review is an invitation to discover gypsum ecosystems, with a special focus on the most recent advances on the plant diversity they host, the mechanisms displayed by plants to cope with the main limitations of these environments and the current global threats that make these ecosystems extremer than ever.

Plant life in extreme environments

What are the limits for plant life? Extreme environments have restrictive conditions that pose challenges to the life of most plants (Boyd *et al.*, 2016). Among extreme environments for plant life we find, for example, those in which extreme temperatures, water, light or nutrient availability, or the presence of toxic substances, limit the metabolism and, consequently, the life of plants. Examples of this type of environments are polar regions, alpine areas, deserts or atypical soils (such as saline soils, serpentines or soils rich in gypsum).

Despite the limiting conditions that prevail in extreme environments, many plant species have been able to develop, throughout evolution, different biochemical, physiological, anatomical and ecological solutions to survive in them. The analysis of these mechanisms constitutes one of the priority fields of plant science. Since its origins, plant scientists have tried to identify the mechanisms that allow plants from extreme or highly stressful environments to cope with environmental limitations (Lambers *et al.*, 2008). These analyses have been decisive for the advancement of agronomy and the selection of traits in cultivated species (Lambers *et al.*, 2008). They also have important applications in ecological restoration and decontamination (Boyd *et al.*, 2016). On the other hand, extreme environments are usually rich in endemic species, with low tolerance to environmental changes (Doi and Kikuchi, 2009; Verboom *et al.*, 2017). These species are increasingly threatened by the effect of global change (Doi and Kikuchi, 2009). The study of the mechanisms that make plant life possible in extreme environments helps to better understand the limits for plant life and is a key aspect for the conservation of these unique plants.

Gypsum soils are extreme environments

Gypsum is a hydrated salt formed by calcium sulphate and water (i.e. $\text{CaSO}_4 \cdot 2\text{H}_2\text{O}$). This rock-forming mineral can also be present in soils when arid conditions prevail. Gypsum soils extend over 200 million Ha worldwide (Eswaran and Gong, 1991; Casby-Horton, 2015). They are present in 112 countries (Pérez-García *et al.*, 2017), being prevalent in arid and semi-arid areas of the planet (Watson, 1999). For example, they affect ca. 40%, 75% and

25% of the total surface of Africa, Western and Central Asia, respectively (Escudero *et al.*, 2015). Within Europe, gypsum soils occur mainly in Spain (where they are widespread throughout the Eastern side of the country) and, with minor extent, in Italy, Cyprus and Turkey (FAO, 1990). Gypsum is also a key water-holding mineral of Mars (Langevin *et al.*, 2005) and, as such, has been extensively studied as a Martian analogue.

Owing to the restrictive conditions they impose on plant life, gypsum soils are considered extreme environments (Cera *et al.*, 2022a). This is due to the atypical physico-chemical features of gypsum, but also to the dry conditions that unavoidably surround gypsum soils. The formation of gypsum soils from gypsum bedrock requires dry conditions, since gypsum is easily leached off the soil. From the Mediterranean conditions of gypsum soils in Spain, Turkey or Western Australia, to the hyper-arid climate of gypsum-rich deserts like the Namib, Atacama or Lut, and including monsoon-like weather conditions like those in the Chihuahuan Desert, plants living on gypsum soils face dry conditions during part of the year (Pérez-García *et al.*, 2018). Consequently, water is, unavoidably, a limiting resource for plants growing on gypsum soils.

In addition to the arid conditions that prevail on gypsum soils, this type of substrates have special physico-chemical properties that make them particularly restrictive for plant life and agriculture. One of the most distinct features of gypsum soils is the remarkably high calcium (Ca) and sulphate concentrations in the soil solution (FAO, 1990; Guerrero Campo *et al.*, 1999). Even when compared to other alkaline soils with high Ca content such as calcareous soils, gypsum soils have higher Ca cation activity, due to the higher solubility of gypsum and the relatively lower pH of gypsum soils (FAO, 1990). Both excess Ca and sulphate ions in the soil solution can be toxic for plants (Ernst, 1998; Nakata, 2003). In addition to these toxicity issues, the saturation of the soil cation exchange complex with Ca drastically decreases nutrient availability for plants (FAO, 1990). Therefore, gypsum soils are inherently nutrient poor for essential elements like P, N and, to a minor extent, K. Available P levels in gypsum soils often fall below the detection limit of standard soil analytical procedures, e.g. (Muller *et al.*, 2017). Gypsum-rich soils have a moderate salinity, which is not considered to lead to strong osmotic issues in plants (Herrero and Porta, 2000). However, gypsum soils are often mixed with other salts, like halite, which may increase the osmotic stress on plants.

On top of these chemical features, gypsum soils show also specific physical properties that limit plant life. One of them is the development of extremely hard surface physical crusts, which may restrict the establishment of plant seedlings (Meyer, 1986; Romao and Escudero, 2005). Gypsum soils are also mechanically unstable, due to a lack of plasticity, cohesion and aggregation (Bridges and Burnham, 1980). Finally, in certain areas, gypsum soils show low porosity, which may limit the growth of certain plant roots (Guerrero Campo *et al.*, 1999).

As a result of the above restrictive conditions, gypsum soils frequently host open landscapes, with sparse vegetation patches that show a remarkable similar appearance across the world (Fig. 1). The present review will address current knowledge on the mechanisms displayed by plants to cope with the restrictive conditions of gypsum soils, with a special focus on two of its most remarkable features: the strong nutrient imbalance and the scarcity of water.

Gypsum ecosystems as singular habitats

Despite the restrictive conditions of gypsum soils, these substrates host singular ecosystems, home to a unique and highly diversified flora, rich in endemic and rare species. A preliminary assessment of the global plant checklist of gypsum soils indicates over 1200 plant taxa across the world seem to have high affinity for gypsum soils (Rudov, Palacio *et al.*, un published data), most of them being restricted to this type of substrate. Many of these species have narrow distribution areas, being local endemics and rare plants. For example, in the Chihuahuan Desert, where the gypsum flora is particularly diverse, gypsum endemics comprise over 300 taxa, which account for 7.5% of the total endemic flora of the region (Flores Olvera *et al.*, 2018). Gypsum endemic species occur in all continents and belong to distantly related floras that have evolved independently, often under different climatic conditions (Pérez-García *et al.*, 2018). Accordingly, the restriction to gypsum soils seems to have emerged several times in the evolution of plants, although some plant lineages are especially rich in gypsum endemic species (Moore *et al.*, 2014). Preliminary data indicate the plant species with high affinity for gypsum detected worldwide belong to

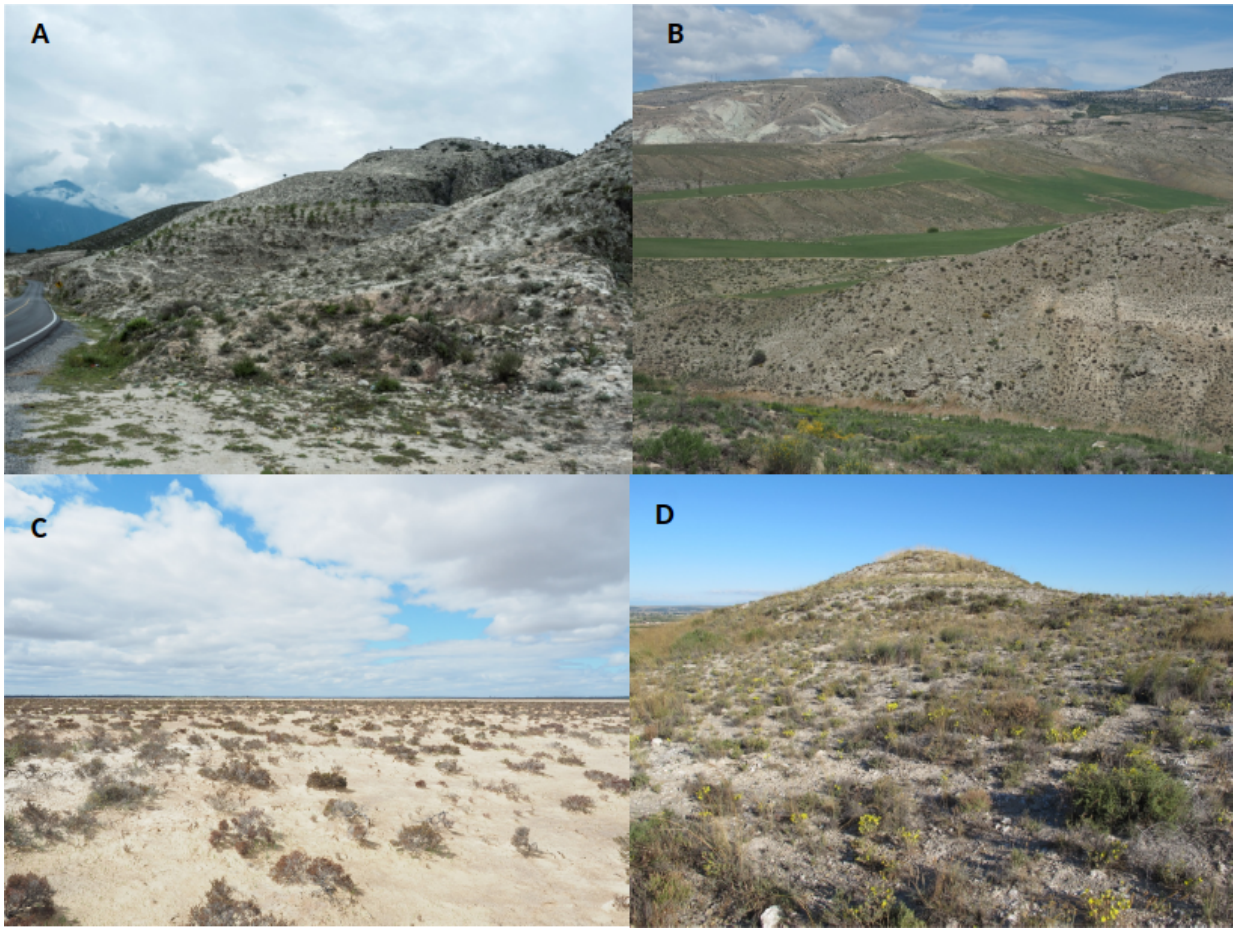


Figure 1: Gypsum ecosystems from different regions of the world. A) Zaragoza, Cohauila, Mexico; B) Central Anatolia, Turkey; C) Lake Mollerin, Western Australia, Australia; D) Villamayor de Gállego, Zaragoza, Spain. Foto credits by Sara Palacio.

88 different taxonomic families, with *Asteraceae*, *Fabaceae*, *Chenopodiaceae* and *Brassicaceae* being the most prominent plant families, each belonging to a different plant order (Rudov, Palacio et al., un published data).

In addition to vascular plants, gypsum soils are also home to a highly diversified cryptogamic flora. These organisms make part of extensive biological soil crusts (BSCs), small scale ecosystems formed by lichens, mosses, and free living algae, fungi and bacteria (Belnap *et al.*, 2016), which cover extensive areas amongst plant patches in gypsum ecosystems (Escudero *et al.*, 2015). BSCs are key components of the ecosystem (Bowker *et al.*, 2008, 2013). They regulate most biogeochemical cycles (including those of water, carbon and nitrogen) and affect plant emergence and establishment, mediating plant community composition (Bowker *et al.*, 2013; Sánchez *et al.*, 2022). The biodiversity behind BSCs on

gypsum is largely unexplored, but they are likely to host a remarkable “hidden” diversity. A recent survey on the lichen diversity on gypsum ecosystems collected over 6000 records of lichen species occurring on gypsum worldwide (Prieto, Personal Communication). Just in Spain, ca. 160 species of lichens, 7 of them being exclusive to these substrates, and more than 100 species of liverworts and mosses have been found on gypsum (Mota *et al.*, 2011). Knowledge on the cryptogamic component of gypsum ecosystems in other parts of the world is largely unexplored, even though BSCs can have a dominant role in the ecosystem. For example, a recent expedition to the hyperarid gypsum deposits of the Namib Desert, where lichen fields often dominate gypsum landscapes, found 47 lichen species from 21 different families (Siebert *et al.*, Submitted). The numbers of cryptogamic taxa linked to gypsum soils are likely to increase in the future. In the case of lichens, many of the groups occurring on gypsum have taxonomic issues that are difficult to solve by morphological traits. New species are likely to be described with the incorporation of molecular tools and novel prospections of poorly explored gypsum areas of the world.

Owing to their singularity, gypsum ecosystems have been identified as an international conservation priority. In Spain, 77 taxa are gypsum endemic and half of them are protected under local, regional or national regulations (Mota *et al.*, 2011). In the European Union, the Habitats 2000 Directive specifically listed gypsum ecosystems as of “community interest” (European Community, 1992), underpinning the singularity of gypsum habitats as a whole. Indeed, a recent analysis on the conservation status of the world gypsophilic flora indicated that almost one third of the plants included in the preliminary global gypsum checklist had been listed in red lists or scientific conservation reports (Bueno *et al.*, 2022). The study also showed that one out of every four gypsum-loving species were under a certain degree of protection (as threatened, rare or protected) (Bueno *et al.*, 2022). These figures are remarkable, particularly if we take into account that most gypsum regions of the world have been poorly explored from a botanical perspective. Accordingly, large areas rich in gypsum and with highly diversified floras, like central Asia, Southern America or Southern Africa are mostly unexplored for gypsum plants. In some cases, this oblivion comes from a lack of interaction between soil and plant sciences. For example, in the whole Flora of China, there is only mention to three plants potentially linked to gypsum soils (Pérez-García *et al.*, 2017). A surprisingly low amount of plants if we consider the richness and diversification of the Chinese flora and the extent of the gypsum deposits of this country.

Certainly, the global figures of taxa restricted to gypsum are likely to increase as scientific interest on these special substrates arises within the scientific community. Similarly, the degree of vulnerability of the world gypsum flora is expected to be largely underestimated at present, owing to the remarkably high number of narrow endemics and recently described taxa that compose the world gypsophilic flora.

Plant ecological strategies on gypsum

Depending on their specificity for gypsum soils, plants can be grouped into gypsum endemics, also named gypsophiles, i.e. plants that only grow on gypsum; and non-endemics, also named gypsovags, which can grow both on and off gypsum soils (Meyer, 1986). Some authors further consider two groups within gypsophiles owing to the extent of their distribution area: wide gypsophiles (i.e. those plants restricted to gypsum with a broad distribution area within a given region), and narrow gypsophiles (i.e. plants restricted to gypsum but with a very limited distribution area) (Palacio *et al.*, 2007). This categorization within gypsum endemics is supported by the observation that widely distributed gypsophiles show distinct traits typical of plants specialized to atypical soils, such as a distinct elemental composition similar to that of gypsum soils (Palacio *et al.*, 2007; Cera *et al.*, 2022c). Wide gypsum endemics from different geographical origins have remarkably high Ca, S and Mg foliar concentrations, sometimes more than one order of magnitude higher than those of gypsovags or narrowly distributed gypsophiles (Muller *et al.*, 2017; Palacio *et al.*, 2022). Contrastingly, the foliar elemental composition of narrow gypsum endemics is closer to that of gypsovags (Palacio *et al.*, 2007, 2022). This group of plants may include species with different ecological strategies, ranging from young lineages recently evolving towards a specialization on gypsum, to stress tolerant plants, not specifically adapted to gypsum soils, which find refuge from competition from other faster growing species on these extreme environments. Finally, gypsovags frequently include plants with broad ecological amplitudes, commonly stress tolerant species, more or less widely distributed within a given region, although narrowly distributed gypsovags also occur. Gypsovag species often are taxa adapted to xeric conditions, like desert or Mediterranean species, and to soil

nutrient unbalances, like halophytic or calcareous plants (Mota *et al.*, 2011). Despite not being specialized to gypsum soils, gypsovag species can be quite prevalent on gypsum, and sometimes dominate gypsum plant communities.

Plant nutrition on gypsum soils: how do plants cope with excess S and Ca in the soil?

One of the most distinct features of gypsum soils is their remarkable sulphate, Mg and Ca concentrations. In the case of Ca, the cation (Ca^{2+}) activity of gypsum soils is even higher than in other calcareous substrates, such as those derived from carbonates (FAO, 1990). Consequently, plants growing on gypsum face abnormally high Ca^{2+} and sulphate concentrations, but also remarkably low availability of key elements such as P, N and K.

Calcium is an essential element for plant life (White and Broadley, 2003). As a key second messenger, the Ca ion (Ca^{2+}) takes part in a huge variety of cell signaling processes, affecting all stages of cell life and several key metabolic processes (Xu *et al.*, 2022). Excess intracellular Ca levels can also lead to P deficiency through the formation of calcium phosphate precipitates (Hayes *et al.*, 2019). Consequently, excess Ca in the soil can lead to toxicity problems in plants and intracellular Ca concentrations have to be kept low at all times to avoid cell damage (Lux *et al.*, 2021). Similarly, excess sulphate in the soil can become toxic for some plants (Ernst, 1998). Plants growing on gypsum soils show different mechanisms to cope with the high soil Ca and S concentrations typical of gypsum. Gypsovag species block S uptake at the fine root level (Cera *et al.*, 2022c), likely by the presence of apoplastic and/or symplastic barriers to the movement of ions (Sattelmacher, 2001; Davidian and Kopriva, 2010; Hawkesford *et al.*, 2012). Contrastingly, widely distributed gypsophiles accumulate remarkable concentrations of Ca, S and Mg throughout the plant (Cera *et al.*, 2022c), even when cultivated off gypsum soils (Cera *et al.*, 2022b). Recent studies indicate the increased accumulation of S, Mg and, to a minor extent, Ca, of wide gypsophiles is a convergent trait across different plant lineages linked to plant specialization to gypsum soils (Palacio *et al.*, 2022). However, how do these plants manage such high elemental concentrations without interfering with the normal cell metabolism?

Plants show various mechanisms to accumulate excess elements without interfering with the normal cell metabolism. One of the most widespread is compartmentalization, i.e. accumulating excess elements in organelles such as the vacuole. Ca accumulation inside the cell vacuole has been repeatedly described in plants (Kinzel, 1989), and most plants accumulate S as sulphate in the cell vacuole (Rennenberg, 1984). In gypsum plants, recent studies show most S accumulation is in the form of sulphates, likely inside the cell vacuole (Cera *et al.*, 2022c). Plants may also detoxify excess elements by including them in molecules or compounds that do not interfere with cell functioning. For example plants belonging to lineages with oxalic acid metabolism, like *Caryophyllaceae* or *Lamiaceae*, can detoxify excess Ca^{2+} through the formation of calcium oxalate crystals, by the combination of Ca cations with oxalic acid (Nakata, 2003), a process that has been described in gypsum plants (Palacio *et al.*, 2014a). Plants belonging to the *Brassicaceae* may also incorporate excess S in organic compounds (Ruiz *et al.*, 2003) such as glucosinolates, which have been shown to increase in plants growing on gypsum soils (Tuominen *et al.*, 2019) Other S-rich compounds with detoxifying potential are thiosulfinates (typical of *Allium sp.*) or flavone sulfates (Ernst, 1998).

Previous studies also highlighted the presence of gypsum crystals inside the cells of widespread gypsum endemics, which was suggested as evidence of a potential de-toxifying mechanisms by the compartmentalization of excess Ca and S inside the cell vacuole leading to the precipitation of crystals due to oversaturation (Palacio *et al.*, 2014a). Nevertheless, a recent study evaluating the presence of gypsum crystals by XR-diffraction in wide gypsophile species revealed no presence of gypsum crystals in intact fresh leaves (Cera *et al.*, In prep.). Interestingly, gypsum crystals appeared fast and progressively in leaves processed for standard biomineral analyses, e.g. sliced fresh similar to processing for microscopic analyses, and dried similar to processing for FTIR spectroscopy. These results seem to indicate previous observations of gypsum crystals in widespread gypsophiles were the result of the fast precipitation of dissolved gypsum when the osmotic conditions inside leaf cells were altered by sample processing. The fast formation of gypsum crystals points at this salt being accumulated at over-saturation, likely compartmentalized inside the cell vacuole. What mechanism may prevent the precipitation of such over-saturated gypsum solutions? Gypsum plants are remarkable Mg accumulators (Palacio *et al.*, 2022), and the Mg cation is a strong inhibitor of the nucleation and growth kinetics of calcium sulphate crystals,

even at low concentrations (Rabizadeh *et al.*, 2017). Consequently, gypsophiles may be detoxifying excess Ca by combining it with excess sulfates to form gypsum that would be stored at over-saturation by the anti-crystalizing effect of Mg.

High cytosolic Ca^{2+} concentrations may precipitate with phosphate, decreasing P assimilation by plants. Consequently, the increased ability of wide gypsophiles to detoxify excess Ca may also have benefits for their P assimilation, being P one of the most limiting nutrients in gypsum soils (Muller *et al.*, 2017; Cera *et al.*, 2021a). Accordingly, wide gypsophiles have a lower reliance on arbuscular mycorrhizal fungi (AMF), one of the best-known symbiotic associations by plants promoting P uptake, than gypsovags (Palacio *et al.*, 2012; Cera *et al.*, 2021a). Taken together, these results indicate differential nutritional strategies between gypsophiles and gypsovags. Wide gypsophiles seem to rely on an intensive nutrient uptake by roots, showing mechanisms to deal with excess Ca and S through detoxification by the formation of gypsum, compartmentalization inside the cell vacuole, and anti-crystallization by high Mg contents. Contrastingly, gypsovags may have more difficulties for root nutrient uptake on gypsum, since the blockage of Ca and S uptake may also interfere with other nutrients uptake, which may render them more dependent on symbionts, like AMF (Cera Rull, 2021).

Other than contributing to detoxify excess Ca and S in the soil, the increased S accumulation of wide gypsophiles may also play an ecological role. Several S-rich compounds are known to have a potential anti-herbivore role (Ernst, 1990). Gypsum ecosystems are open landscapes where herbivores frequently graze and gypsum plants may have evolved under moderate grazing pressures. Accordingly, recent studies have shown that grazing increased gypsophile presence in gypsum plant communities (Cera *et al.*, 2022b), and wide gypsophiles were more resilient to grazing than gypsovags (Cera *et al.*, 2022a). Moreover, foliar S concentrations of gypsum plants increased with higher grazing, pointing at a potential anti-herbivore role of S accumulation in these species (Cera *et al.*, 2022b).

Water use by gypsum plants: how do plants cope with water scarcity in gypsum soils?

Water is one of the most limiting resources for plants growing on gypsum soils. Accordingly, plants show a variety of mechanisms to uptake water, often leading to a segregation of hydrological niches during the dry periods, which promotes plant coexistence and diversity (Palacio *et al.*, 2017; de la Puente *et al.*, 2021, submitted). Such segregation is frequently related to root depth and access to different water sources, so that plants with deeper root systems have access to more reliable water sources like the water table, whereas shallow rooted species rely on more superficial and also ephemeral water sources (Palacio *et al.*, 2017; de la Puente *et al.*, submitted). Noteworthy, some plants from gypsum ecosystems have been described to have remarkably deep root systems, sometimes exceeding several meters depth (Mota *et al.*, 2011).

Gypsum landscapes are often covered by soft hills intermingled by flatlands and saline depressions (Fig. 1), where plant communities may show a sharp zonation linked to water, salts and nutrient availability (Braun-Blanquet and Bolòs, 1957; Guerrero Campo *et al.*, 1999). Plants dominating these communities have been shown to use different water sources depending on their root depth and their position along the topographic gradient (Palacio *et al.*, 2017). For example, plant communities from the top and high slope of gypsum hills do not have access to the water table, feeding mainly on superficial sources. Contrastingly, plants from lower slope areas, flatlands or depressions show an increasing use of the water table during dry periods. In the case of low slope areas and flatlands, access to the water table is restricted to deep root plants, whereas plants growing in saline depressions feed on underground water throughout the year, irrespectively of their root depth (Palacio *et al.*, 2017).

The differential use of water sources has important consequences for plant access to nutrients and salts. Plants feeding from superficial water sources rely on comparatively less stable water, but have access to increased nutrient availability than plants tapping from the water table (Querejeta *et al.*, 2021). Similarly, plants growing on saline depressions have good water availability throughout the year, by the up flow of underground water (Palacio

et al., 2017). However, the intense evaporation at gypsum soils leads to a remarkable concentration of dissolved salts in such up flowing water, leading to increased salinity, toxic for most plants (Guerrero Campo *et al.*, 1999). Consequently, plants thriving on these saline depressions are frequently halophytes or gypso-halophytes, suited with specific mechanisms to cope with high salt concentrations (Braun-Blanquet and Bolòs, 1957; Guerrero Campo *et al.*, 1999).

In addition to free water, gypsum, as a hydrated salt, holds water in its crystalline structure. Every gypsum molecule has two molecules of water that may be released under natural conditions, depending on the temperature, pressure, and dissolved electrolytes or organics (Freyer and Voight, 2003; Carbone *et al.*, 2008). The crystallization water can account for up to 20.8% of gypsum weight (Bock, 1962), and gypsum de-hydration has been recorded at temperatures above 40°C (Freyer and Voight, 2003), which are often reached in gypsum soils worldwide (Grande López *et al.*, 1967; Berstein, 1979; Herrero and Porta, 2000). Studies analyzing the stable isotope composition of the xylem sap of gypsum plants indicate that the crystalline water of gypsum can be a significant water source for plants during summer (Palacio *et al.*, 2014b). This is not restricted to gypsophile species, but seems to be widespread across shallow-rooted plants growing on gypsum soils, irrespectively of their affinity for gypsum soils (de la Puente *et al.*, 2021). Similarly, cyanobacteria growing in gypsum crystals in the Atacama Desert have been reported to use gypsum crystalline water to survive the extreme hyperarid conditions (Huang *et al.*, 2020). Although the mechanisms behind the use of gypsum crystalline water by plants remain elusive, all these findings point at the existence of a new water source for plants, with crucial implications for the search of life in other planets (Palacio *et al.*, 2014b).

Conservation threats for gypsum ecosystems

Despite the relevance of gypsum ecosystems for their widespread occurrence, the unique biodiversity they host and the exceptional mechanisms displayed by the organisms that thrive on them, gypsum ecosystems are severely threatened. Today, the pervasive effects of global change drivers make life on gypsum soils extremer than ever. Around the world, gypsum ecosystems face intensive degradation through increased habitat destruction by

mining, urban development, cropping and over-grazing. In Europe, the acknowledgement of the need to preserve gypsum habitats by the European Commission by their inclusion in the Habitat 2000 directive (European Community, 1992), contrasts with the intensive destruction of vast gypsum flatlands subsidized by the same organism through Common Agricultural Policy (CAP) aids to promote cropping. Gypsum mining is also a widespread activity worldwide and, despite the proved efficiency of relatively inexpensive restoration practices (Mota *et al.*, 2004; Ballesteros *et al.*, 2012, 2014), habitat restoration is not undertaken in most gypsum mining countries. In countries where gypsum soils are home to highly populated rural communities, like in Iran and certain areas of central Anatolia, overgrazing by livestock is a serious threat to the conservation of these ecosystems (Akhani, 2015). Contrastingly, gypsum ecosystems in depopulated areas of Spain face degradation by shrub encroachment after grazing abandonment (Cera *et al.*, 2022b). The damaging effects of habitat destruction may be exacerbated by climate change. Temperatures and drought events are forecasted to increase remarkably in future decades in drylands, including gypsum soils (IPCC, 2014).

Recent studies indicate gypsum plants are able to adapt to changing conditions, including increased drought and warmer temperatures (Luzuriaga *et al.*, 2020; Blanco-Sánchez *et al.*, 2022). However, studies on the effect of fragmentation through habitat destruction shed worrying forecasts on the conservation of gypsum plants. Gypsum plants from small habitat fragments are more vulnerable to climate change effects than those from large fragments (Matesanz *et al.*, 2009), and such vulnerability is inherited from generation to generation, so that plants grown from seeds from mother plants from smaller fragments are weaker than those from plants from larger fragments (Pias *et al.*, 2010).

However, probably the largest current threat to gypsum ecosystem across the world is their perception by local populations as “degraded” areas or “wastelands”. Alike other open landscapes deprived from trees (Bond *et al.*, 2019; Silveira *et al.*, 2020), gypsum ecosystems are frequently perceived as of “low value” by society, especially when compared to forests or woodlands (Palacio, 2022). Consequently, the extent of gypsum ecosystems subjected to any degree of protection is remarkably low. This perception is far from reality since, as indicated before, gypsum ecosystems are singular habitats that host a unique biodiversity. Unfortunately, open habitats perceived as “degraded” are key targets for current climate

change mitigation policies based in large-scale afforestation programs. Similar to other naturally open landscapes, a new threat looms over gypsum ecosystems: that of massive tree plantations. While of high importance for the recovery of truly degraded areas previously occupied by woodlands, massive afforestation programs can be a severe threat for the conservation of naturally open ecosystems, like gypsum soils (Bond *et al.*, 2019; Silveira *et al.*, 2020; Palacio, 2022). Tree plantation implies ploughing, altering the soil profile and destroying BSCs. It also involves the plantation of tree species, often exotic, which may out-compete shade-intolerant gypsum plants. It is, hence, urgent to understand the differences between naturally open areas and those that are truly degraded and require afforestation (Bond *et al.*, 2019; Silveira *et al.*, 2020), so that climate change mitigation policies do not interfere with the conservation of unique ecosystems like gypsum soils (Palacio, 2022).

Conclusions

Gypsum soils are widespread extreme environments that host unique ecosystems of global conservation concern. Despite being open landscapes with low plant cover, these ecosystems harbor remarkable arrays of specialized plant, fungi and cryptogam taxa. These species show unique eco-physiological mechanisms to cope with the extreme conditions typical of gypsum environments. Plants specialized to gypsum soils accumulate large amounts of Ca, S and Mg across their tissues through compartmentalization inside the cell vacuole, and detoxification with different compounds. Gypsum plants show also remarkable strategies to obtain water, including the use of gypsum crystallization water. Notwithstanding the relevance of gypsum ecosystems, these habitats are severely threatened across the world. Particularly because they are often perceived as “degraded” ecosystems of low natural value. There is, consequently, a pressing need to make different sectors of the society aware of the huge ecological value of gypsum ecosystems worldwide. Only then, will the conservation of these unique habitats and the remarkable biodiversity they host be guaranteed.

Acknowledgements

Andreu Cera provided useful comments to an earlier version of this manuscript. SP greatly acknowledges funding from Fundación San Valero as part of the Research Prize from the Royal Sciences Academy of Zaragoza. Her research was also funded by the European Union's Horizon 2020 research and innovation program (Project H2020-MSCA-RISE-GYPWORLD GA No. 777803), the Spanish Ministry of Science and Innovation (MICINN, PID2019-111159GB-C31), the Spanish Ministry of Economy and competitiveness (MINECO, CGL2015-71360-P) and CSIC (projects: I-LINK1110, I-COOPB20231, I-COOPB20464, COOPB22018 and 202230I206).

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