Weathering and soil formation in hot, dry environments mediated by plant–microbe interactions

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Weathering and soil formation in hot, dry environments mediated by plant–microbe interactions

Blanca R. Lopez[1,2] · Macario Bacilio[1]

Abstract

Bioweathering in arid lands is a complex set of processes comprising a wide variety of organisms, all contributing to soil formation. Weathering starts with outcrop fragmentation by physical forces, later thermal stress and salts produce propagation of cracks that allow colonization by lithobiontic communities. Growth and development of primary colonizers produce pools of C and N available for further establishment of non-vascular plants when moisture is available. Furthermore, plants capable of living in crevices establish interactions with microbial communities and together optimize rock resources (organic or inorganic), enhance nutrient cycling, and accelerate soil development. Cacti and succulents are frequent rock colonizers in hot deserts. These plants exhibit numerous adaptations that enable them to survive in deserts including CAM biochemistry, physiological adaptations, and interactions with their associated microbiome. The associated microbiomes include plant growth-promoting microorganisms that increase essential nutrient supply (N and P) to the plants. We propose a conceptual model of weathering where microbial associates induce higher root exudation of organic acids in succulents. This model has to be experimentally tested; however, it involves several challenges, such as: (a) the difficulty of collecting exudates from the field or emulating experimental conditions similar to nature, and (b) selecting appropriate temporal scales to detect measurable changes since most cacti exhibit remarkably slow growth rates. Therefore, innovative approaches are in order.

Keywords Plant colonization of rocks · Bioweathering for pedogenesis · Cacti root exudates · Plant growth-promoting microorganisms of arid lands · Lithobionts of arid lands

Introduction

The Earth's crust is always changing. Throughout geological evolution, rocks on the Earth's surface have been exposed to physical and biological agents that modify their structure and chemistry. Weathering is the process of rock decomposition occurring in the Earth's critical zone, defined as the permeable layer of Earth where water, air, and life interact (Anderson 2019). Weathering and erosion are the fundamental processes of soil development and the basis for productive terrestrial ecosystems and crops growing on soils (Frings and Buss 2019).

Arid and hyper-arid regions, characterized by evapotranspiration rates that are higher than annual rainfall rates, cover nearly 20% of the Earth's surface (Wierzchos et al. 2012). Patterns of rock weathering in arid landscapes reflect the environmental variability due to fluctuations in temperature and ephemeral water availability (Warke 2013). Physical, chemical, and biological weathering processes have been extensively studied across all types of climates. However, many studies are exploratory (Smith 2009) and discipline-specific, focusing on highly specific processes and sometimes generating misconceptions about global processes operating in arid environments.

In the current scenario of climate change and critical problems of land degradation and desertification (Mapelli et al. 2012), there is a need for interdisciplinary studies that explain weathering processes at different spatial and temporal scales

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and design approaches for recovering soils and managing rock and mineral resources. In this review, we discuss the distinctive processes of rock weathering in dry landscapes, highlighting the contribution of living organisms to soil formation in each successive stage of weathering. We then focus on the influence of the rhizosphere, particularly regarding the role of organic acids, and plant–microbe interactions in rock weathering, with an emphasis on plants colonizing rocks in hot deserts. We follow this with a conceptual model of rock weathering, which includes succulents and their microbial associates. Finally, we present various perspectives on weathering research and suggest innovative applications of rock weathering. This review does not explore the well-known mechanisms of weathering in depth but rather brings together various elements to demonstrate the complexity of factors that accelerate rock weathering and build-up of soils in arid lands.

The typical model of weathering and pedogenesis

In general terms, weathering is a combination of geophysical, geochemical, and biological processes responsible for the alteration of parent rocks. Physical weathering begins when masses of rock are eroded from an overlying rock and exposed as outcrops (Earle 2015) (Fig. 1a). Then, differences in temperature usually break the rocks into smaller fragments, which are more prone to chemical attack (Fig. 1b). This changes the structure of rocks and leads to the production of secondary minerals and gravel particles susceptible to further weathering (Dolui et al. 2016). Bioweathering is a set of processes by which the growth and development of biota (microorganisms, plants, and animals) produce mechanical forces and metabolic compounds, such as organic acids and chelators, that alter rock-forming minerals (Brantley et al. 2012; Field and Little 2009; Leake et al. 2008; Uroz et al. 2009) (Fig. 1b–g).

According to the typical chronosequence model, bioweathering begins by the action of chemolithoautotrophic bacteria, which use mineral compounds as electron donors (oxidation) and change the structure of primary minerals (Fig. 1c). The metabolic activity of different taxa such as Cyanobacteria and other free-living N-fixing bacteria together with more complex microbial communities, such as lichens, produces parent materials (defined as the relatively unweathered minerals or organic material from which soil develop, [Mocek and Owczarzak 2011], Fig. 1d), that substantially increase the amount of N and facilitates the establishment of unrooted plants, such as mosses (Fig. 1d, e). Growth and exudation by rhizoids and microorganisms lead to an accumulation of organic matter and N over time, forming a shallow original soil that retains nutrients. The strong interaction between the original soil and non-vascular vegetation during the

weathering process makes more nutrients available for higher plants (Zhu et al. 2014) (Fig. 1e). The active growth of plants accelerates the evolution of the original soil and stimulates the formation and differentiation of mature soil (Fig. 1f, g). In general, humid regions follow this simplified model. However, in arid environments, weathering is a more complex set of processes strongly determined by the native features of rocks and subject to environmental variability. Therefore, these environments are characterized by lower rates of pedogenesis. In cold deserts, Borin et al. (2010), found that in sites released from permanent glacier ice, the mineral weathering mediated by chemolithoautotrophic bacteria contributed to create specific microenvironments for plant colonization, enabling an accelerated phenomenon of pedogenesis.

Weathering in arid landscapes

Landscapes in all environments arise as a combined result of small-scale processes that occur at the mineral-grain scale (Frings and Buss 2019). In most environments, all types of weathering processes operate together but usually one dominates over others. This generally depends on temperature and rainfall (Gabler et al. 2009). Physical weathering predominates in deserts and arid landscapes, which often exhibit cracked surfaces representing the initial stage of rock disintegration (Gabler et al. 2009; McFadden et al. 2005; Smith 2009). The widespread conception that temperature is the main driver of physical weathering in hot deserts is supported by a large body of literature describing field observations of cracks caused by thermal stress related to diurnal heating and cooling. However, few studies have systematically analyzed this phenomenon. McFadden et al. (2005) analyzed several types of cracks in the Mojave, Sonoran, and Chihuahuan Deserts and the high desert of central New Mexico. They found that longitudinal, surface-parallel, fabric-related, and meridional cracks are solar generated and are explained by heating and cooling due to the diurnal cycles of solar paths. This causes the expansion and contraction of rocks and the rapid breakdown of subaerially exposed rocks, similar to the effect of the freezing-thawing cycles in cold deserts. Once micro-cracks are formed, salt weathering causes them to grow and expand. Crystallization and the differential expansion or hydration of salts deposited into pre-existing cracks induces internal stresses that eventually lead to fracture formation (Amit et al. 1993; McFadden et al. 2005).

In addition to the significant role of physical processes in shaping the landscape of arid and hyper-arid lands, other environmental and biotic factors synergistically contribute to weathering and soil formation (Smith 2009; Warke 2013). Even though water is limited in arid climates, contrary to common belief, moisture is available in deserts from rainfall, dew, and fog, particularly during the night (Smith 2009). This
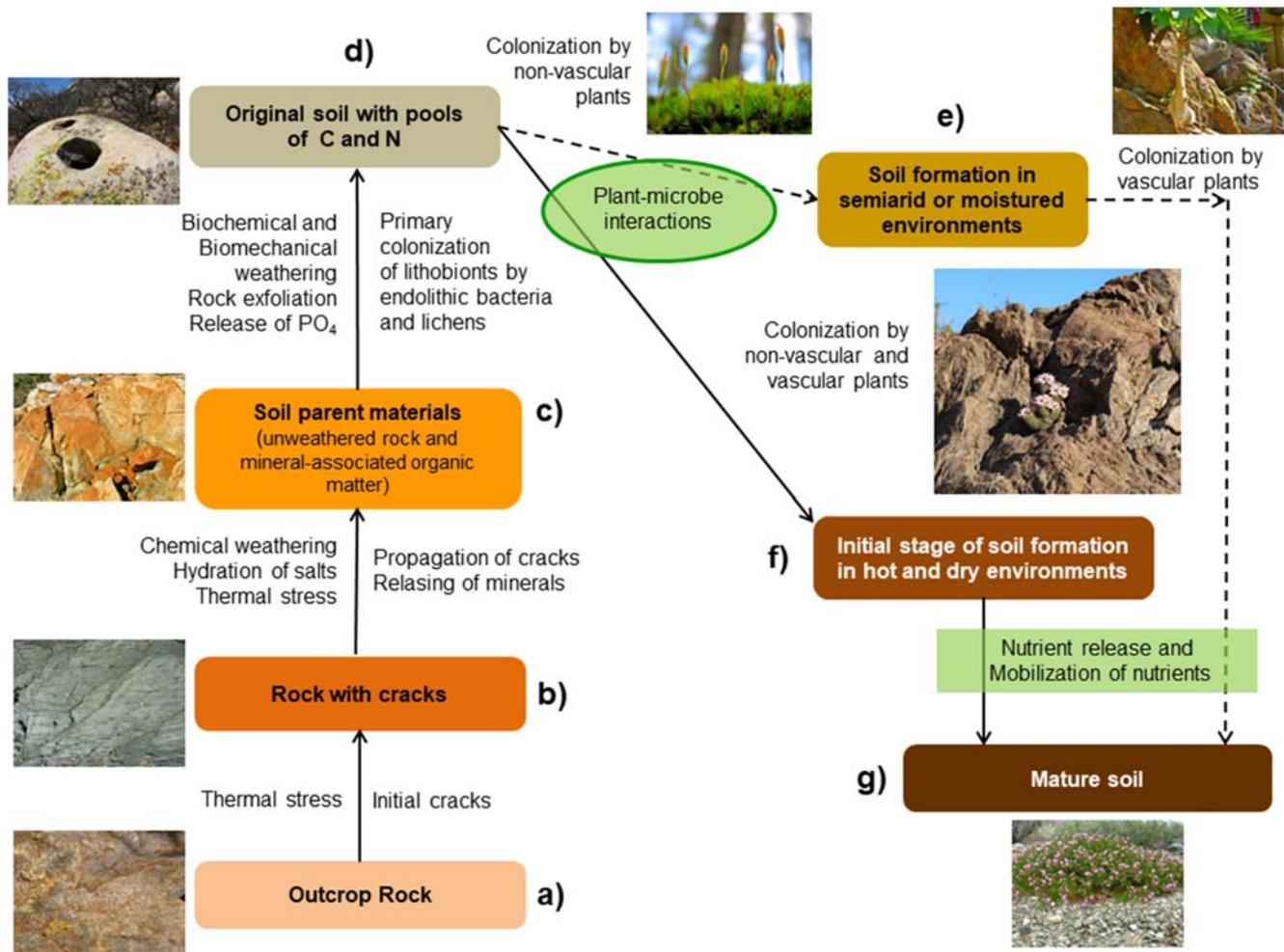
Fig. 1 Sequential stages of rock weathering for soil formation and evolution in arid and semi-arid environments. Physical weathering is the initial stage of outcrop fragmentation. Thermal stress and salts produce propagation of cracks and loose materials that allow colonization by lithobiontic communities. Growth and development of primary colonizers produce pools of C and N available for further establishment of non-vascular plants when moisture is available. Alternatively, plants able to live in crevices establish interactions with microbial communities and together optimize the minimum soil resources (organic and inorganic). Plant–microbe interactions, enhance nutrient cycling, and lead to soil development. The basic model of weathering was modified from Zhu et al. (2014)

not only causes chemical reactions such as salt hydration but also facilitates the generation of parent materials and the development of soils through bioweathering.

Bioweathering of rocks and soil formation in arid and hyper-arid regions

The old assumption that deserts are inaccessible environments with few life forms has led to the perception that bioweathering does not make an important contribution to shaping the landscape in these regions. However, an increasing number of studies support the claim that bioweathering in arid lands is a complex set of processes comprising a wide variety of organisms (Warke 2013), all contributing to soil formation. Since the 1960s, studies have emphasized the importance of lithobiontic microorganisms in the early stages of rock weathering. Today, we know that rock-surface microbial communities play an important role in regulating weathering, soil stability, and hydrological and nutrient cycles (Pointing and Belnap 2012). These uniquely adapted communities to cold or hot deserts, consist of desiccation-tolerant Cyanobacteria, algae, fungi, and lichens inhabit the surface (epilithic), underside (hypolithic), and inside (endolithic) of rocks (DiRuggiero et al. 2013; Warke 2013). These environments provide microorganisms of substrate and protection against severe environmental conditions, such as high radiation and desiccation, common in hot deserts (Hall et al. 2008). Due to the great diversity of adaptive strategies of lithobionts, endolithic habitats are further classified into cryptoendolithic (natural pore spaces within the rock), chasmoendolithic (fissures and cracks), and hypoendolithic (underside of the rock, in contact with soil habitats) (Wierzchos et al. 2012; Wierzchos et al. 2018).

Cyanobacteria are the initial photoautotrophic colonizers of bare rocks in hot deserts, such as the Sinai, Mojave, Sonoran, and Negev Deserts (Friedmann 1980). Büdel et al. (2004) reported that extensive areas of the Clarens sandstone formations in South Africa exhibit landscapes with light and dark patches of different shades caused by sequential exfoliation of the upper rock layers. During the exfoliation process, sandstone flakes about 2 mm thick, detach from the rock surface along the blue-green cryptoendolithic zone. Quantitation of photosynthesis, respiration, and pH shift in cultures of endolithic Cyanobacteria and microsensor measurements in a model system profile indicated that the weathering of silica was induced by the growth of crypotoendolithic Cyanobacteria through substratum alkalization. Bioalkalization resulted from photosynthetic activity where accumulation of OH^- is part of the activation of a CO_2 concentrating mechanism characteristic in Cyanobacteria to alleviate CO_2 limitation. OH^- is then excreted to the pores of sandstones where carbonate ions combine with cations and precipitate as carbonates within the zone of Cyanobacterial colonization, thus preventing cementation of silica grains and resulting in flake exfoliation. Based on small-scale quantifications of short-term measurements, these authors estimated a flake detachment rate at an average of 24 kg of rock material per 100 m^{-2} per year, representing 2.4 tons per hectare per year. These estimations suggest that exfoliation processes may occur within a human life timescale. During the last decade, culture-independent molecular methods have revealed a great diversity of endolithic communities inhabiting rocks. In the Atacama Desert, DiRuggiero et al. (2013) took a multiphasic approach consisting of remote-sensing techniques, geological analysis, microscopy investigations, and high-throughput sequencing of chasmoendolithic habitats consisting of fissures and cracks. These authors described diverse microbial communities dominated by Cyanobacteria associated with less abundant heterotrophic bacteria. Moreover, diversity was related to greater availability of water and the particular mineral composition of certain micro-environments, which represent refuges called "islands of life" in the desert.

Lichens are another prominent component of lithobiontic communities in hot deserts. These are mutualistic symbioses of fungus and algae or Cyanobacteria (Nash III et al. 2002). Lichens are well-known inhabitants of rocks and participate in weathering through the mechanical disruption of rocks caused by the hyphal penetration, expansion, and contraction of lichen tallus. The mutualistic interaction between heterotrophic N_2-fixing Cyanobacteria and lichen fungi in the presence of a C source can enhance the release of organic acids and improve the solubilization of the mineral substrate (Seneviratne and Indrasena 2006). For instance, oxalic acid effectively dissolves minerals and chelate metallic cations (Chen et al. 2000). In the Sonoran Desert, Garvie et al. (2008) analyzed environmental data, along with mineralogical, anatomical structure and isotopes, to explain the possible mechanisms of adaptation of the lichen *Verrucaria rubrocincta*. In a cross-section of rock, this lichen exhibits an anatomical zonation where the upper layer consists of micrite, then the photobiont (algal clusters) and the fungal structures towards the bottom layer, in contact with the rock surface composed originally of caliche. When the lichen grows, it actively degrades its substrate and produces precipitated micrite. This microcrystalline calcite is highly reflective and acts as an efficient sunscreen against harmful UV-radiation and also helps to trap moisture. According to these authors, this lichen survives by combining biodeterioration with biomineralization thus facilitating its adaptation to colonize endolithic habitats.

Among other adaptive mechanisms to survive in extreme environments, microorganisms develop biofilms that create micro-habitats differing markedly from their surrounding environment (Gorbushina 2007). Bacterial biofilms are formed by communities embedded in a self-produced matrix of hydrated extracellular polymeric substances (EPS), consisting mainly of polysaccharides, proteins, nucleic acids, and lipids (Flemming et al. 2016). Biofilms have emergent properties that mediate adhesion of three-dimensional polymers, provide stability to biofilm, improve water retention, and act as an external digestive system that enables cells to metabolize dissolved colloidal and solid biopolymer (Flemming and Wingender 2010; Flemming et al. 2016). In vitro biofilm formation by microbial isolates and natural in situ colonization engineering experiments on glass or even rock surfaces are widely known (Anderson et al. 2006). However, given the high energetic cost of production and maintenance of biofilms, their existence in rocks has been challenging to demonstrate but recently recognized as an essential form of life that allows microorganisms to grow in extreme arid, cold, or oxygen-limited environments (Flemming et al. 2016). Increasing studies report microbial biofilms formed in native rock matrices, fracture zones, or even in continental subsurface rocks where there is no oxygen, water is limited, and life is supported mainly by anaerobic metabolisms (Anderson et al. 2006; Escudero et al. 2018). Subaerial biofilms develop on solid mineral surfaces exposed to the atmosphere. In rocks, these biofilms consist of adjacent soil or dust and extracellular polymeric substances that serve as evaporation barriers, stabilizing the rock surface by coating and protecting the weathered front (Gorbushina 2007; Wieler et al. 2019). Although biofilms are considered anti-erosion agents, they also play a role in weathering by counteracting biodeterioration with bioprotection (Wieler et al. 2019).

Discussion persists about the impact of bioweathering on soil formation in deserts. However, new insights by Mergelov et al. (2018) revealed that the alteration of contemporary rocks in the cold desert of east Antarctica by subaerial endolithic systems (comprised of endolithic microorganisms, mineral environment and in situ organo-mineral by products)

represents one of the initial pathways for the beginning of soils on Earth. In this model, over geological time scales, cryptic niches occupied by endolithic microorganisms (Cyanobacteria, fungi, lichen) interact with silicates, generated organo-mineral complexes and stabilizing organic materials (e.g., polysaccharides, proteins, nucleic acids, and lipids), and develop soils through similar processes to those known for modern soils of various climates. In general, microorganisms are responsible for most biological transformations and drive the development of stable and labile pools of C, N, and other nutrients that facilitate the establishment of plants (Schulz et al. 2013) (Fig. 1d).

Primary succession by endolithic communities also contributes to rock weathering by breaking down minerals and intergranular bonds. This creates subsurface weaknesses that can be subjected to other types of weathering (Warke 2013), such as biophysical and biochemical mechanisms imposed by non-vascular plants or even higher plants that colonize barren rocks (Bashan et al. 2002) (Fig. 1f). Microcosm approaches indicate that biochemical weathering by non-vascular plants, such as mosses, liverworts, and hornworts, occurs through the action of acids on minerals (Porada et al. 2016); however, it has been difficult to quantify their impact on a global scale. Using a spatial modeling approach, Porada et al. (2016) simulated global silicate weathering during the Late Ordovician (approximately 450 million years ago) and found that predecessors of today's bryophytes caused high weathering rates similar to bioweathering in today's biosphere and that non-vascular vegetation at that time reduced the levels of CO_2, causing a global cooling effect on the biosphere.

Following the typical scheme of soil formation in chronosequence, after initial weathering by lithobionts, vascular plants colonized lands through to the development of woody root systems and symbiotic interactions with microorganisms such as arbuscular mycorrhizal fungi. Consequently, they established an intimate association with rocks, gaining access to rock-derived nutrients and accelerating the rate of weathering (Porder 2019). Plants are recognized as the primary drivers of biotic weathering since they colonized land (Leake et al. 2008) and have significantly contributed to reducing the CO_2 levels of the atmosphere at higher rates than in previous ages in Earth's geological past (IPCC 2013). However, debate is ongoing about the impact of higher plants on the initial stages of weathering through biomechanical processes. As Pawlik et al. (2016) pointed out, in the multiple examples of rocks split by tree roots, roots tend to concentrate in the upper layer of soil, which implies that biochemical processes acted before tree establishment. Bashan et al. (2006) conducted a field survey in the Sonoran Desert in Mexico of succulent trees of *Pachycormus discolor* covering large areas of volcanic flows consisting of granite and basalt boulders. The fractures were explained by mechanical forces imposed by roots and their possible association with rock-weathering microorganisms. However, this phenomenon

deserves deeper assessment. While roots generate radial pressures (0.51–0.9 MPa) below the tensile strength of rocks (1–25 MPa) (Pawlik et al. 2016), it is likely that, over decades, subcritical cracking (fracture propagation at low rates) coupled with the undisputed biochemical interactions in the rhizosphere may promote rock fracture (Eppes and Keanini 2017; Anderson 2019). For long-living cacti, such as the giant cardon (*Pachycereus pringlei*), this could happen in one generation of plants, presumably decades, although estimating the age of this plant has been challenging because cacti do not produce annual rings of wood. Field surveys and models indicate that the giant cardon has an average growth rate of 0.098 m year^{-1} (Delgado-Fernández et al. 2016). Long-term studies and new approaches are required to understand the role of cacti and succulents in soil formation in rocky habitats.

Historical or accumulated stresses are essential in determining the susceptibility of rocks to weathering. Rocks that have undergone long periods of chemical weathering in wetter phases may be more susceptible to eolian abrasion, while rocks with a history of thermal cycling are susceptible to breakdown by physical forces (Warke 2013). Viles et al. (2018) performed a four-stage experiment involving different physical and chemical stresses to analyze their effect on basalt weathering and found that stress histories can explain patterns and styles of rock breakdown and partly explain the distinctive spatial variability of arid landscapes. In addition to stress histories, the primary degradation of rocks could be crucial for providing not only mineral sources but also N to the rhizosphere of rock-dwelling plants. Contrary to conventional assumptions, present-day rocks not only provide inorganic nutrients. Recent evidence from Houlton et al. (2018) suggest that up to 17% of N in natural systems may be derived from modern-day rocks. This N comes from mineral-associated organic matter from different sources, such as the activity and decomposition of endolithic biota. In the past, mineral-associated organic matter was considered a vital but relatively passive source of N. However, emerging research in biogeoscience suggests that minerals are crucial mediators of soil N availability for plants and microorganisms (Jilling et al. 2018). Therefore, biochemical weathering induced by plants or microorganisms can mobilize N from both minerals and associated organic soil matter through destabilization pathways consisting of modifications of organo–mineral interactions (e.g., by root exudates). Another explanation for colonization on "barren rocks" is that the accumulation of parental materials (dust deposition) and organic debris (from animals and plants) in cracks and crevices provides an additional source of nutrients and anchorage for plants. However, this topic needs to be systematically addressed.

Role of the rhizosphere in pedogenesis

Plant roots and microbial activities that rely on root-derived C (Lambers et al. 2009) in the rhizosphere contribute

significantly to bioweathering processes. The rhizosphere is a narrow microenvironment in the soil–root interface where plant–microbe associations occur and where the soil is under the biochemical influence of plant roots (Hartmann et al. 2008). The rhizosphere is characterized by high microbial activity, higher turnover rates of organic and inorganic compounds, and a distinctive microbiome compared to bulk soils, which is the portion of soil that is not influenced by the rhizodeposition (Pawlik et al. 2016; Vieira et al. 2019). Two distinctive processes relevant for mineral weathering take place in the rhizosphere: (1) rhizodeposition of cells debris, sloughed cells, mucilage, and diverse root exudates; and (2) enhanced chemical weathering by low-molecular-weight organic acids (Gregory 2006). Both processes accelerate mineral alteration and dissolution. Plants release nearly 40% of their photosynthates in the form of root exudates (Neumann and Römheld 2007), which contain diverse compounds, including sugars, vitamins, amino acids, organic acids, nucleosides, phenolic and aldonic acids, terpenoids, inorganic ions (such as HCO_3^-, OH^-, and H^+), and gases (such as CO_2 and H_2) (Dakora and Phillips 2002; Igamberdiev and Eprintsev 2016). In the past, it was thought that the majority of root exudates were passively lost from the root and then used by rhizosphere-dwelling microorganisms. However, recent studies indicate that root exudation mostly occurs and is regulated at the root tip and that concentration of primary metabolites in root exudates is modulated by microbial stimuli (Canarini et al. 2019). Moreover, soil properties, particularly soil texture, water content, and soil type, have a strong influence on the composition of root exudates and, consequently, on the selection of microbial communities in the rhizosphere (Vieira et al. 2019). Furthermore, bacterial communities are shaped by the stage of pedogenesis of desert barren substrates. Mapelli et al. (2018) analyzed changes in bacterial diversity in bulk soils and rhizosphere of a pioneer plant across a High Arctic glacier chronosequence. Illumina 16S rRNA sequencing and network analysis showed that the bacterial community in the rhizosphere is strongly modulated by the developmental stage of soil (Mapelli et al. 2018).

Profiles of root exudates differ according to many factors including the photosynthetic pathways of CO_2 fixation; amino acids and organic acids are distinctively high in C4 plants, whereas carbohydrate concentrations are higher in C3 plants (Nabais et al. 2011). While a range of low-molecular-weight compounds, such as monosaccharides, amino acids, organic acids, and phenols, participate in nutrient mobilization in the rhizosphere (Zhu et al. 2014), organic acids are the most important chemical forms participating in mineral dissolution. Moreover, regardless the type of photosynthesis, diurnal rhythms of root exudation influence the taxonomical configuration of the rhizosphere microbiome with changes coinciding with functional genes involved in carbohydrate and amino acid metabolism, therefore indicating strong interaction between exudation in the rhizosphere and its microbiome (Baraniya et al. 2018). Organic acids are mainly produced in the tricarboxylic acid cycle during photosynthesis of C3, C4, and the Crassulacean Acid Metabolism plants (CAM) (Sharma et al. 2016). They represent the transitory or stored forms of fixed C and play an important role in maintaining energy and redox balance, supporting ionic gradients on membranes and, therefore, the acidification of extracellular spaces (Igamberdiev and Eprintsev 2016). One of the main roles of organic acids in the rhizosphere is the mobilization of essential nutrients from the rhizosphere to plants by, for example, dissolving poorly soluble P-containing compounds and increasing P supply. Organic acids are recognized for their participation in mineral weathering and plant nutrition. However, some of them exert negative effects in plant–microbe interactions and, therefore, in the beneficial impact of the rhizosphere microbiota (Zhou et al. 2018). In Bornean tropical forests with poor P substrates, organic acids exuded by both roots and microorganisms promote the solubilization and uptake of P bonded to aluminum and iron oxides (Fujii 2014). Although organic acid exudation is assumed to help plants to counter nutritional stress in arid lands, there is scarce information regarding root exudates in these environments. The study by Abrahão et al. (2014) described that the cacti *Discocactus placentiformis* exhibits a sand-binding root specialization with rhizosheath of mucilage that protects the root tip against dehydration, contributes to soil aggregation, and, according to Ahmed et al. (2018), also mitigates hydric stress of certain rhizosphere microbial communities.

Plant organic acids and rock weathering

Organic acids have been the primary cause of soil formation by rock weathering throughout geological times. Weathering by plants is a biospheric phenomenon that has changed the Earth's crust and formed soil since bryophytes colonized land. It was continued by rooted plants, which reduced atmospheric CO_2 and contributed significantly to rock weathering by the root excretion of organic acids using photosynthetically fixed C (Igamberdiev and Eprintsev 2016).

Whereas CAM plants temporarily store malate (as their main carboxylate), C4 plants use it as an intermediate transporter from mesophyll to bundle sheaths, and C3 plants release citrate and malate from vacuoles during the night for transportation to mitochondria to support respiration (Meyer et al. 2010). Even though malate and citrate are the most accumulated organic acids in plants (Igamberdiev and Eprintsev 2016), some plants excrete large amounts of oxalate (Meyer et al. 2010). The CAM photosynthetic pathway is fundamental in the ecophysiology of the vast majority of succulents (Griffiths and Males 2017). Among the 407 species known to exhibit this metabolism (mostly Crassulaceae,

Cactaceae, Bromeliaceae, and Aizoaceae; Sayed 2001), only three species have been explored for root exudations patterns; therefore, research on exudation in CAM plants is still scarce (Vranova et al. 2013).

From the exudation profiles of *Ananas comosus* and *Sedum alfredii*, we know that CAM plants produce malic, citric, and succinic acids (Vranova et al. 2013). Carboxylate-releasing cluster roots in *Discocactus placentiformis* (Cactaceae) are capable of mobilizing P from P-impoverished habitats consisting of sandy soils named *campos rupestres* (Abrahão et al. 2014). In addition, these authors found that *D. placentiformis* exuded oxalic acid, malic, citric, lactic, succinic, fumaric, and malonic acids.

Rock and mineral weathering mediated by plant–microbe interactions

Plants and microorganisms have been associated since the bryophytes colonized lands. They co-evolved for the benefit of both partners and have persisted until today (Porder 2019). The basic idea behind these interactions in rocky substrates is that C compounds produced by plants serve as a C source for microorganisms, which, in exchange, provide plants with N and other nutrients dissolved from primary minerals and thus promoting plant growth. Plant growth-promoting bacteria (PGPB) are free-living soil, rhizosphere, rhizoplane, endophytic, and phylosphere bacteria that under some conditions are beneficial for plants (Bashan and Holguin 1998; Santoyo et al. 2016). PGPBs promote plant growth in two ways: (a) directly affecting the metabolism of plants by providing them with phytohormones and essential nutrients such as N and P compounds that are usually in short supply and (b) indirectly inducing plant tolerance to stresses, such as drought, high salinity, metal toxicity, and biocontrol against phytopathogenic microbes (Bashan et al. 2008; Berendsen et al. 2018).

In most environments, especially acidic soils in forests, experimental approaches have shown that roots and their associated microorganisms increase the rate of rock and mineral weathering (Calvaruso et al. 2006). In both cases, the root–rock interface represents the initial stage of a rhizosphere and, therefore, the site where formation of soil starts (Lambers et al. 2009), while the bulk soil has less influence (Uroz et al. 2009). Accelerated rock weathering by plants and microorganisms improves the physical and chemical properties of original soils, increasing depth and loosening, structuring, water retention, aeration, gas exchange, and higher availability of organic and inorganic compounds (Lambers et al. 2009). Despite the abundant literature on the mechanisms that induce bioweathering (e.g., acidification, chelation reactions, redox reactions, and siderophores), rock weathering, and soil formation mediated by plants have received little attention and knowledge of these processes is still speculative (Beerling

and Butterfield 2012; Brantley et al. 2012; Puente et al. 2004a; Thorley et al. 2015). Thus, the extent to which plant–microbe interactions speed up weathering in drylands and hot deserts remains questionable, mainly because it is difficult to quantify the enhancement in real conditions (Frings and Buss 2019). For instance, weathering rates are often faster in the laboratory than in the field (Brantley 2003). Moreover, it has been difficult to distinguish the contribution of roots from that of their associated weathering microbes (Mapelli et al. 2012).

Rock colonization by succulents and some trees is common in the Baja Peninsula, Mexico. Bashan et al. (2002, 2006) and Puente et al. (2004a) have reported that the giant cactus (*Pachycereus pringlei*), pitaya (*Stenocereus thurberi*), nipple cactus (*Mammillaria fraileana*), cholla (*Cylindropuntia cholla*), elephant tree (*Pachycormus discolor*), and fig tree (*Ficus petiolaris*; syn. *F. palmeri*) grow on rocks and cliffs of volcanic rocks almost without soil and participate in rock fragmentation. These authors isolated rhizoplane bacteria (N-fixing, thermo-tolerant, and rock-weathering) and used scanning electron microscopy to show abundant populations of bacteria colonizing the rhizoplane of all species. Increased phosphate solubilization and rock-degradation allowed authors to conclude that these bacteria are involved in chemical weathering in hot, subtropical deserts. Puente et al. (2004b) inoculated *Pachycereus pringlei* with rhizoplane bacteria (*Pseudomonas* spp. and *Bacillus* spp.) and achieved a plant-growth-promoting effect by increasing the supply of N, soluble P, and other essential minerals such as P, K, Mg, Fe, Cu, and Zn to the plant.

Among small cacti, *Mammillaria fraileana* can colonize rocks or live preferentially on shallow soils. This endemic plant almost exclusively colonizes cracks rhyodacite rocks in the southern arid region of the Baja Peninsula in Mexico (Lopez et al. 2009). The ecological advantage of exploiting rocks has been explained by several mechanisms, including the specialization of root systems, which allows them to explore a large surface area (Poot and Lambers 2008); physiological advantages, such as efficient water storage in stems; and their association with beneficial microbial communities, especially rock-degrading bacteria, mineral solubilizers, and N fixers colonizing the rhizoplane and the endosphere (Lopez et al. 2011; Puente et al. 2004a, 2004b; Puente et al. 2009). Lopez et al. (2011, 2012) investigated if endophytic bacteria with the capacity to fix N, degrade rhyodacite, and solubilize phosphate in vitro participate in mobilizing mineral from rocks to plants and assist them in establishing on rocks. In this study, seedlings of *M. fraileana* obtained in axenic conditions were inoculated with their native endophytes and grown on different rocky substrates in micro-growth chambers kept under greenhouse conditions for 8 months. Similar to the effects reported in *Pachycereus pringlei*, these endophytes increased N content and biomass and mobilized elements depending on the chemical composition of the rocks and the relative

abundance of elements. This indicates that the mobilization of elements is not a straightforward or simple phenomenon. Moreover, it was confirmed that endophytes enhanced the CAM photosynthetic metabolism, even in such slow-growing plants (~0.5 cm height).

Mycorrhizae are considered essential symbionts for plants as they actively weather minerals and transport photosynthates through the mycelial systems, which form tunnels inside mineral grains (Leake et al. 2008). Arbuscular mycorrhizae (AM) are common in developed soils of arid lands. In developed soils in the Sonoran Desert, AM grow profusely below patches of vegetation called resource islands. In these islands, an autocatalytic cycle of plant–soil interaction occurs, whereby the fungi improve plant growth by enhancing nutrient uptake and the plants provide the substrate for the fungus (Carrillo-Garcia et al. 1999). However, to the best of our knowledge, mycorrhizal colonization, ectomycorrhiza (intercellular growth) or endomycorrhiza (intracellular growth), or even saprotrophs, have rarely been reported in plants colonizing rocks in hot and dry environments. Endophytic growth appears to be a convenient association for plants living in harsh environments such as cold or hot deserts. Endophytes are ubiquitous microorganisms, bacteria, or fungi that live inside the plant tissue without causing apparent disease to plants and instead they usually establish mutualistic associations with their host (obligate or facultative) (Nisa et al. 2015; Rosenblueth and Martínez-Romero 2006). One of the few studies of endophytic fungi in arid environments is that of Pereira et al. (2019), who surveyed populations of the perennial grass *Festuca rubra subsp. pruinosa*, a chamaephyte (plants living in rock crevices) that colonizes sea cliffs on the Atlantic coasts of Europe. They found that the core mycobiome contained halotolerant elements such as the culturable fungal endophyte *Epichloë festucae* related to the adaptation of this grass, mainly regarding salinity. Moreover, dark-septate endophytic fungi have been found in various cold hostile environments such as in plant roots from high-elevation sites in the Andes and the Rocky Mountains at about 5391 m.a.s.l (Schmidt et al. 2008).

Proposal of a conceptual model of weathering by succulents and their microbial associates

Succulent plants are widely distributed and reach their highest diversity in arid and semi-arid regions, although agave, cacti, and other xerophytes represent the keystone species of these environments exclusively in the American continent (Hernández-Hernández et al. 2014). The success of cacti in arid environments is related to morphological adaptations, such as modified leaves in the form of spines, succulent stems, a dual root system that allows them to acquire water in moisture-limiting conditions (Nobel 1997), and root–stem junctions that operate as hydraulic safety valves by quickly conducting water while also avoiding water loss (Kim et al.

2018). Physiological strategies involve (1) root shrinkage during drought (Nobel 1997); (2) mucilaginous exudation, which forms a soil sheath around roots and prevents desiccation during drought (Huang et al. 1993); (3) CAM photosynthesis, which means that C fixation occurs at night, preventing losses by evapotranspiration during the day; and (4) stomata that remain closed during the day but open at night to absorb carbon dioxide, which is then stored in the vacuoles as malate (Nobel 2002).

In spite of the low overall productivity of CAM plants, they can be highly productive under certain circumstances. For instance, the effect of their microbial associates (rhizoplane, rhizosphere, endophytic) can induce increased photosynthesis and biomass production (Lopez et al. 2012). The molecular characterization of seed-borne bacteria of cacti from hot, dry arid lands supports the claim that these microbial symbionts are vertically inherited and can promote plant growth and drought tolerance for the fitness of the cacti holobiont (Fonseca-García et al. 2016).

The prevailing scheme of soil formation in arid environments involves the active participation of non-vascular plants during the initial stages of soil formation (Fig. 1a–e); however, there is increasing evidence that plants growing in barren rocks participate actively in rock and mineral weathering (Fig. 1f). Here, we propose a conceptual model for arid lands where cacti in native conditions exudate organic acids to the external medium as an alternative to vacuolar accumulation. This strategy may represent another ecological advantage of rock-pioneering cacti, allowing them to weather rock minerals from seedling emergence throughout their entire life cycle (Fig. 2). During germination, seedlings can impact the surrounding environment. Cereal seeds excrete acid from the scutellum and aleurone layer to the endosperm to provide acidic conditions for the breakdown of starch (Ma et al. 2016). If seedlings can modify their rhizosphere and take advantage of the microenvironment represented by rock fissures or cracks, they can establish and participate in the early development of soil due to their long-life cycle. Moreover, beneficial bacteria residing in the rhizosphere, rhizoplane, or endophytic populations can increase the rate of photosynthesis and, therefore, of organic acid exudation and phosphate dissolution and uptake (Lopez et al. 2009, 2012). It is expected that the increased metal mobilization of elements by cacti inoculated with native populations of plant growth-promoting bacteria is related to abundant organic acids, which form complexes with micronutrients and metals.

Our proposal is hypothetical and must be systematically tested. To understand the links between primary metabolite exudation by plant–microbe interactions and their contribution to rock weathering and soil formation in hot arid environments, we face several challenges, such as the common difficulty of collecting exudates from plants. Traditionally, root exudate collection was obtained in hydroponic (sterile) environments, but it has the
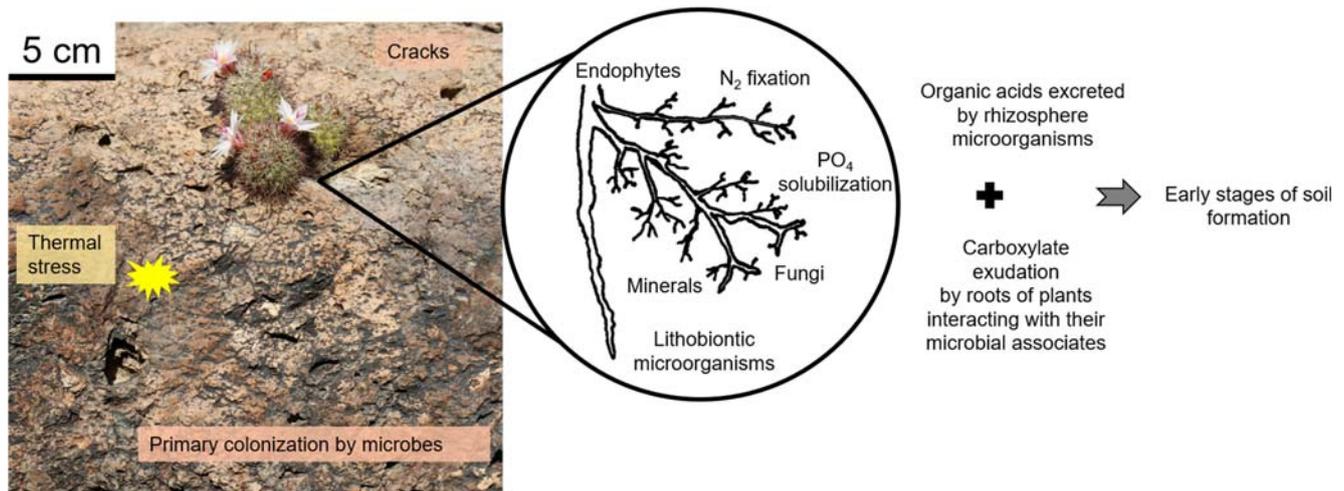
Fig. 2 Weathering mediated by plant–microbe interactions in the Sonoran Desert. The circle indicates the elements and processes in the rhizosphere participating in bioweathering. The combined effect of the organic acids (carboxylates) produced by CAM plants (such as cacti) and microbial populations enhances mineral dissolution and release of nutrients (P, K), deposition of C and N, thereby accelerating formation of the initial shallow soil

disadvantage of missing the effect of microorganisms and soil particles (Oburger and Jones 2018). The quantity and quality of these exudates are usually limiting factors to assess root exudation in natural conditions and even more difficult in arid environments. Another challenge is that root exudates reflect the overall plant metabolism, the strong relationship root–microbiome, and the effect of the environment. Therefore, there is a need for innovative approaches for collecting exudates from the field or design experimental systems emulating natural conditions (rocky substrates with almost no soil) and appropriate temporal scales to detect measurable changes since most cacti have remarkable slow growth rates. New methods for root exudate collection in drought conditions and analyses by metabolomics (Gargallo-Garriga et al. 2018) and high-resolution microscopy represent promising approaches to assess the response of belowground plant tissues to water-limited conditions. Methodological challenges need to be addressed to advance and strengthen our comprehension of the importance of root exudates in rocks weathering processes mediated by plant–microbe interactions of arid lands.

Perspectives

After half a century of research, we are now beginning to understand the existence of complex relationship between weathering and soil formation in deserts. The significant environmental variability (spatial and temporal) of these habitats gives rise to distinctive combinations of weathering systems within which physical, chemical, and biological processes contribute to rock weathering and breakdown to differing extents (Warke 2013). From an ecological perspective, deep exploration of microbe associated with rock-dwelling plants is required to provide an understanding of the relevance of this ecological interaction in rocky habitats and its role in weathering and to identify the elements of plant–microbe adaptation in hot and dry environments.

Interdisciplinary studies and polyphasic approaches to specific models, such as those of succulents and their associates, would increase our understanding of the complexity of weathering in arid lands. Those approaches might include modeling and field studies of measurable change (e.g., metabolomics of root exudation and isotope labeling of organic compounds) carried out over an extended period. Studies of long-term significance should take into account previous geological stresses and the long-term history of rock outcrops (Smith 2009). Bridging the spatial and temporal boundaries that separate the short-term effects at the microscale from their cumulative impact on the landscape is another challenge. From a hydrologic point of view, the mechanisms governing root–rock interactions regarding plant adaptations and rooting patterns are only beginning to be investigated. More studies are required to investigate root growth and water circulation in cracks and crevices, the dynamics of water recharge and depletion in weathered bedrock, and C deposition deep in the regolith (Lambers et al. 2009).

In addition to its geological and ecological importance, the management of rock weathering is an innovative technology. Powdered rocks have been shown to be a sustainable and cost-effective alternative to chemical fertilizers and the basis for an environmental technology for amending highly weathered soils, known as "geotherapy" (Goreau et al. 2014; Manning and Theodoro 2018). Enhanced weathering involving plants and microbes is now becoming recognized as a promising dioxide-removal technology. This approach consists of applying powdered silicate rock to soils to enhance weathering. Similar to the natural geologic biochemical weathering process, silicate minerals are dissolved in a reaction with

atmospheric CO_2 and water causing the release of cations such as Ca^{+2} and Mg^{+2} and bicarbonate ions, which are transported to oceans and stored or "sequestered" in sediments (Andrews and Taylor 2019). Researchers are currently assessing its potential efficacy in real systems.

Conclusions

Arid lands (cold or hot) exhibit similar patterns of weathering that reflect the ephemeral availability of water and temperature fluctuations. The rate of bioweathering depends on historical factors imposed by climate (historical stresses) but also on the ability of microorganisms to colonize lithic niches and establish cooperative relationships with other organisms. In some arid areas, primary colonization of rocks by higher plants occurs with incipient accumulation of parent materials. Although rock weathering is typically explained by the action of rock-degrading microbes associated with rock-dwelling plants, beneficial bacteria can occupy other plant microsites and improve plant growth by increasing nutrient acquisition and protecting them against abiotic stress.

We propose a conceptual model of rock weathering for soil formation by cacti. The basis of our model relies on the ecological advantages of cacti as rock pioneers, allowing them to participate in the early development of soil due to their long-life cycle and its association with beneficial microbial communities residing in the rhizosphere, rhizoplane, or endosphere. In this model, microbes would improve plant growth by increasing the rate of photosynthesis, and therefore exudation of organic acids that degrade minerals and increase nutrient uptake. Together, plants and microbes intensify weathering and cover a broader spectrum of mineralization. The challenge to test this model involves experimental models at appropriate temporal scales to detect measurable changes. Polyphasic approaches and innovative techniques will allow a better understanding of the complexity of bioweathering by succulents and their associates in deserts.

Understanding bioweathering mediated by plants and microbes in arid lands will contribute to developing environmental technologies aimed to enhance soil formation in arid lands and counteract desertification.

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