



# Microbial Interactions in Soil Formation and Nutrient Cycling

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## 1 Introduction

The soil is the outer layer covering the earth surface called pedosphere. Soil serves as a medium for plant growth, alters the earth's atmosphere through the liberation of the volatile substances, stores, supply and purifies water and it is a niche for organisms that in turn alter the soil. Soil formation involves physical, chemical and biological processes through which the parent rock materials are weathered or broken down into smaller particles. The broken rock materials combine with the organic matters produced by living organisms. Thus soil consists of organic and inorganic compounds, mineral particles and weathered pieces of rocks (Dominati et al. 2010). The major factors influencing the soil formation include the nature of the parent material, living organisms, climate, topography and time (Paul and Clark 1996). The interactions between these factors result in soil formation.

All the components of soil biota live and function in their habitat comprised of soil pore network, physiochemical constituents of components, biotic communities and environmental factors such as temperature and moisture. Biota in soil structure plays a pivotal role in soil function emphasizing the interaction between organisms and the physical construction of their environment called soil architecture. A primary physiochemical factor governing soil community structure is the individuals with different pH optima (Fierer and Jackson 2006). Soil moisture optima for the belowground biota vary between organism types as they rely on moisture films for their transport through the soil matrix while for mycorrhiza, it is not constrained (Augé 2004).

Bioweathering is an important process involving the dissolution or break down of rocks and minerals by soil microorganisms and plants via physical and chemical

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mechanisms (Gadd 2007). This process contributes to soil formation and enhances the plant growth in different habitats and climate (Gulati et al. 2008; Mapelli et al. 2011). The soil stability and their formation are directly related with clay mineralogy and dissolution process, the occurrence of binding sources such as root exudates and fungal hyphae (Deneff and Six 2005; Rillig and Mummey 2006). Soil microorganisms play a critical role in the formation of soil as they are involved in the biological transformations and develop most of the stable nutrients pools like carbon (C), nitrogen (N) and other vital nutrients (Schulz et al. 2013). Microbial symbioses like the lichens are important as they are the initial colonizers of rocks and therefore initialize the process of bioweathering and involve in early stages of soil mineral formation (Gadd 2017).

Mineralization by soil micro-organisms plays an important role in the environment as it releases trapped mineral nutrients [phosphorus (P), potassium (K), magnesium (Mg), calcium (Ca), and iron (Fe)] required for plant growth. Some of the living organisms such as mosses, cyanobacteria, microfungi and lichen present in the uppermost or top of the soil constitute biological soil crusts or biocrusts (Garcia-Pichel et al. 2003). These biocrusts develop mostly in dry or bare land and serve as a reservoir for C and N (Belnap et al. 2001). They are also formed in the wide space in between the vascular plants. Besides their role in C and dinitrogen (N<sub>2</sub>) fixation, biocrusts also improve the soil stability, prevents soil erosion, soil water relationship, seed germination and make available nutrients to the plants (Kuske et al. 2012).

The intimate contact between the plant roots and microorganisms associated with the soil constitutes the rhizosphere. The microbial interaction in the rhizosphere is critical as microbes tend to modify the physical and chemical process during soil formation (Gregory et al. 2007). In the rhizosphere region, microorganisms remain active with higher microbial activity and soil factors affect the microbes that in turn contribute to nutrient cycling (Lambers et al. 2009). Mycorrhizal and saprophytic fungi and bacteria are responsible for mineral weathering in rhizosphere through acidification. The weathering and acidification processes lead to diverse weathering characteristics in mineral grains and thus supplying mineral nutrients for mycorrhizal plants in the rhizosphere (Koele et al. 2014). Mycorrhiza denotes a symbiotic relationship between plant root and the soil fungi (Smith and Read 2008). Apart from its role in plant growth promotion; mycorrhizal fungi have a key role in soil aggregation and improvisation of soil structure (Rillig and Mummey 2006). Soil management practices could change the physical and chemical characteristics of soil and microbiota dynamics.

Soil micro-organism constitutes bacteria, actinomycetes, fungi, protozoa, yeast, algae, worms and insects. Certain bacteria and all fungi being heterotrophic, depend on the organic matter and obtain nutrients and minerals by decomposing them. Therefore they have different roles in nutrient cycling that keeps the soil in good and healthy condition for plant growth. The substrate in the soil increase the bacterial populations that feed on them and recycles the nutrients important for both plants and other soil organisms (Kuske et al. 2012). The expansion of bacterial population supports protozoa that predate bacteria. The increasing protozoan population, in turn, triggers the activity of mites which feed on protozoans. The substrate arrival expands

the fungal population and the competition among the fungal species. Nematodes are prompted to feed on fungi and other nematodes species. Some nematophagous fungi are also capable of trapping and feeding on nematodes. In general, fungi consume and store more nutrients than bacteria due to the different proportions of C and N and thereby maintain the soil health (Paul and Clark 1996). A gram of soil may consist of several kilometers of fungal hyphae (Young and Crawford 2007). However, plant roots host diverse microorganisms (bacteria and fungi) that can stimulate each other forming specific interface between soil and plants. The nutrients stored in the cells of the micro-organisms prevent nutrient loss by leaching. This act as agents of nutrient exchange and helps to maintain the soil structure.

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## 2 Microbial Activities in Soil Formation

One of the mechanisms for involvement of biota in soil formation and its functioning is the influence of higher plants, micro and mesofauna and microflora on the mineral decomposition (Sokolova 2011). The importance of mineral dissolution through the activities of microorganisms can be compared to that of the absorption of CO<sub>2</sub> by plants and atmospheric N<sub>2</sub> fixation by soil microbial communities (Schulz et al. 2013). Soil biota plays an important role in the degradation and decomposition of organic matters and contributes to humus formation. Microorganisms decompose the organic remnants and substances in the soil surfaces such as senesced plant leaves and other litter. The organic matters are utilized by the microbes as an energy source and thus increase their population in the soil. These microbes degrade the digestible materials leaving those that are not decomposed easily. This results in the formation of humus that holds the primary soil particles (clay, silt and sand) and forms secondary aggregates. Soil biota and humus aids in the soil formation and development of soil horizons (Martin and Haider 1971).

Due to their widespread distribution, rapid growth, metabolic diversity and colonization and adaption to extreme conditions, microorganisms occupies a central role in soil evolution and formation (Zhu et al. 2014). The litter decomposition process is intimately linked with microbial activities that modify the chemical structure of litter and manage soil C and N dynamics (Berg and McLaugherty 2014). Microorganisms play a key role in plant litter decomposition and formation of soil through their enzymatic activities (Helfrich et al. 2015). The microbial growth and their resulting biomass and necromass change the chemical composition of soil organic matter, as perceived in nutrient immobilization (Wanek et al. 2010; Cotrufo et al. 2013). Moreover, the transformations of microbial necromass and biomass influence soil stability, formation and fertility (Six et al. 2006; Fontaine et al. 2011). The microbial growth and decomposition could also be measured by amino acids and amino sugars and biomolecules which are very rich in microorganisms than in plant litter (Tremblay and Benner 2006). In addition, amino acids and amino sugars are essential constituents for N immobilization and C sequestration in the soil (Liang et al. 2007).

Microbial weathering is a geological process occurring on the Earth's surface that fundamentally refers to the microbial growth and reproduction (Bin et al. 2008). The microbial metabolites promote the dissolution of some substances from the rock due to the influence of microbial enzymes on the natural degrading rate of minerals. Microbial weathering alters the composition of minerals and rocks and thus leads to the liberation of elements such as, silica (Si), Fe, manganese (Mn), aluminium (Al) from silicates, oxides, carbonates that changes the proportion and contents of soil minerals (Bin et al. 2008). Calcareous rocks are mainly subject to chemical weathering (acidic dissolution of the calcium carbonate) whereas; siliceous rocks are mainly fractured as a consequence of freezing-thawing cycles. Siliceous rocks contain a number of minerals which contain essential elements and hence support microbial life. In contrary, the weathering of calcareous rocks liberates only a few elements which stimulate the growth of microbes. Serpentine rocks may even release toxic compounds such as, nickel (Ni) and cadmium (Cd) which prevents the establishment of plant life and could also hinder microbial activities (Bratteler et al. 2006).

Microorganisms contribute to mineral weathering both through direct and indirect ways (Sokolova 2011). The direct effect of soil microflora occurs when microbial cells are directly in contact with the mineral surface. The adhesive property of microbes on the mineral particles may be due to their fixation on earlier absorbed compounds. On the other hand, the indirect effect of soil microbes includes varying products of soil microorganism's functioning that consist of chelating agents, bases and acids (Sokolova 2011). Microbial activity accelerates the release of P and sulphur (S) elements from the bedrock to supply living organisms with P and S, whereas C and N are not part of the mineral composition and are scarce in the initial soils. Soil aggregation is most crucial in controlling the structure and function of microorganisms and plant life (Kobierska et al. 2011). Thus, it is clear that the initial processes of soil formation and input of nutrients rely on the activity of microorganisms. The foremost principles of soil biota are biological weathering of the bedrock material and the formation of interfaces for nutrient turnover at vegetation free site.

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### 3 Plant-Microbe Interaction

Microbiological activity is greater in the rhizosphere than in soil away from the plant roots. Plant-microbe interactions contribute to several soil processes such as nutrient cycling, C sequestration and ecosystem services. Plants play an important role in soil development and display a nutrient hotspot at initial sites of soil formation in terms of C, as they provide up to 40% of the photosynthetically fixed C to the microorganisms (Miniaci et al. 2007; Towe et al. 2010; Duc et al. 2009). In exchange, soil microbes provide N, P and other essential nutrients to the plant and also defend them against herbivores or parasites (Butler et al. 2003).

Plant roots secrete important compounds, which have a major role in the physical, chemical and biological interaction between plant roots and the rhizosphere (Moore et al. 2015). Alterations in the secondary metabolites released by the plants

could influence the soil microbial communities (Bressan et al. 2009). The root exudates influence the biological and chemical activities of the soil thereby improves soil fertility (Altieri 2004). The root exudates supply a huge amount of C which activates the soil aggregate formation. The mucilaginous root exudates adhere to the soil particles and lead to short-term soil aggregation (Morel et al. 1991). The rhizosphere region usually has increased CO<sub>2</sub> and lower pH level and oxygen. Depending on the nutrients taken up by the plant roots from the soil, exudates could make the rhizospheric soil more alkaline or acidic. Rhizosphere activity modifies mineral surfaces; attack mineral structures, and also take up the weatherable soil minerals. All these activities stimulates mineral weathering and directs the formation of soil which makes rhizosphere the most dynamic environment in the soil. This intensification of mineral weathering is dependent on pH in addition to exudate and microbial communities in the rhizosphere. The capacity of soil microbial communities in mineral weathering is well documented (Favero-Longo et al. 2005; Uroz et al. 2007; Calvaruso et al. 2006).

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## 4 Lichens in Soil Formation

Lichens play a vital role in soil formation. Lichens that inhabit rocks are referred to as saxicolous that include different morphology namely, foliose, crustose and fruticose (de los Rios et al. 2002). Several studies have shown the significant role of lichens in mineral and rock weathering and in soil formation (Chen et al. 2000; Begonha 2009). The close contact of fungi with the substratum and presence of algae on outer layers of the lichen thallus suggest that weathering capacity is critically due to the mycobionts (Chen et al. 2000). The deteriorating ability of rocks by lichens varies according to their growth form (de los Rios et al. 2002). For example, foliose lichens exert pressure on the rocks via fixation structures, whereas the thallus of crustose lichen gets fully developed and incorporated within the lithic substrate. The alterations in the volume of the thallus brought about by the lichens due to the expansion and narrowing by drying or freezing results in the mechanical breakdown of rocks (Ascaso et al. 2002).

During the metabolic activity, lichens produce organic acids that have a significant impact on weathering and decomposing the parent rocks (Belnap and Lange 2003). They have the capacity to break down the rock into smaller particles at a faster rate. Lichen undergoes both physical and chemical process during weathering of rocks. The physical process involves a mechanical breakdown of rocks through penetration of hyphae, expansion and contraction of lichen thallus and swelling of inorganic and organic salts generated during lichen activity. In the chemical weathering, lichens secrete organic acids, specifically oxalic acid, which efficiently break down minerals and chelate the metallic cations (Chen et al. 2000). In addition, lichens stimulate secondary mineral formation through turgor pressure and production of exopolysaccharide. These secondary minerals react with the cations of rock and cause disintegration and flaking of outer rock surface (Ranalli et al. 2009). The minerals formed by weathering of rocks by lichens possess enhanced surface

corrosion. *Lecidea atrobrunnea*, *Rhizocarpon geographicum* and *Sporastatia testudinea* are capable of weathering the serpentinized rocks in alpine environments (Favero-Longo et al. 2005).

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## 5 Bacteria in Mineral Weathering

Bacteria are not only involved in the biological processes such as biogeochemical cycles, providing nutrients to the plants, enhancing plant growth and in controlling plant pathogens (Hayat et al. 2010); they also have a crucial role in the initial stage of soil formation via modification of parental rock and in soil structuring (Paul and Clark 1996). Unlike other organisms, bacteria can adapt or tolerate extreme environmental conditions. The mineral particle forms a microenvironment to protect bacteria from stress conditions. Thus, bacteria obtain inorganic phosphate and energy from the mineral matrix or through the activities of other microbes. The mechanisms involved in mineral weathering include oxidoreduction reactions and production of organic acids and chelating agents (Uroz et al. 2007). Several bacteria that are involved in weathering of rocks and minerals, release large amounts of beneficial minerals from rocks to the plants, organic acids and fix N<sub>2</sub> and condense the rock particles thus forming mineral soil (Puente et al. 2009). These bacteria either in combination with other microbes or alone could mineralize through formation of complex microbial communities that associate with mineral surface (Uroz et al. 2009). For example, the species belonging to the genera *Bradyrhizobium*, *Collimonas*, and *Anabaena* are capable of mineral weathering (Männistö and Häggblom 2006; Calvaruso et al. 2009; Collingnon et al. 2011). The bacteria inhabiting the rock surfaces are different from those residing in the surrounding soil (Certini et al. 2004). The mineral particles that are colonized by bacterial communities commonly include quartz, granite, limestone or apatite (Gleeson et al. 2005; Carson et al. 2009). The chief elements such as Al, Ca or Si present in the mineral particles influence the structure of the bacterial communities. This lead to a new concept called 'mineralosphere', where certain microbes are selected for their capacity to utilize the inorganic nutrients that are released by soil minerals. Bacteria isolated from the rhizosphere soil and mineralosphere could supply nutrients to the plants in the nutrient-poor soil (Uroz et al. 2009). For example, one of the mineral weathering bacterial strain *Burkholderia glathei* PML1 promoted the growth of pine tree under nutrient stress condition in the presence of biotite (Calvaruso et al. 2006).

The composition of bacterial communities gets modified in the presence or absence of arbuscular mycorrhizal (AM) fungal hyphae (Marschner and Baumann 2003; Rillig et al. 2006). Moreover, the potential effect of bacterial hyphal colonizers on AM fungi and the AM fungal symbiosis is high. Several types of interactions between bacteria and AM fungi have been described (see Bonfante and Anca 2009). Bacteria could also enhance the rate of mineral dissolution and the ability of bacteria involved in mineral weathering varies according to the habitat they occupy (Huang et al. 2014). Mostly mineral weathering bacteria are isolated from the rhizosphere of trees and the ectomycorrhizosphere that forms tree root-soil boundary

where nutrient exchange takes place (Calvaruso et al. 2007). The bacterial isolates isolated from the mycorrhizosphere region of the ectomycorrhizal fungus *Scleroderma citrinum* had higher mineral weathering capacity when compared to those isolated from bulk soil. The fungi select a bacterial community with greater mineral weathering ability in the bulk soil through carbon metabolism (Uroz et al. 2007). Likewise, Collignon et al. (2011) also reported the presence of potential mineral weathering bacteria (*Pseudomonas*, *Rhizobium*, *Burkholderia*, *Bacillus*) in tree rhizosphere of *Fagus sylvatica* and *Picea abies* was higher than in the bulk soil and the mineral weathering efficacy changes depending upon the seasons (Collignon et al. 2011). A Gram-negative, aerobic and motile mineral weathering bacterium, *Rhizobium yantingense* isolated from the surface of weathered rock was shown to possess high mineralization activity (Chen et al. 2015).

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## 6 Non Mycorrhizal Endophytes in Mineral Weathering

Non mycorrhizal endophytes include both bacteria and fungi that colonize the plant tissues without causing any adverse effect to the host (Wilson 1995). These endophytes have the capability to transfer complex compounds (Wang and Dai 2011). Phosphate solubilization, rock degradation and N<sub>2</sub> fixation contributes to efficient rock-weathering bacterial endophytes (Lopez et al. 2011). Endophytic bacteria (*Bacillus* sp.) isolated from cactus roots have been reported as an efficient rock weathering microbe. This bacterial endophyte helps in the weathering of igneous rocks in nutrient-poor regions upon colonization of the plant roots (Puente et al. 2009). The bacterial endophytes, *Azotobacter vinelandii*, *Bacillus megaterium* and *Pseudomonas putida* isolated from roots of *Mammillaria fraileana* are capable of N<sub>2</sub> fixation and weathering of rocks into smaller particles (Lopez et al. 2011).

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## 7 Role of Fungi in the Weathering Process

Fungi are prominent geoactive agents that are involved in the transformation of metals and minerals that in turn modify the chemistry and surface structure of rocks and minerals (Gadd 2017). Fungal communities that are capable of mineral weathering and dissolution include saprophytic fungi, lichen-forming fungi and mycorrhizal fungi (Hoffland et al. 2004). Symbiotic fungi or free-living fungi inhabit the outer surface of rocks and are recognized as one of the potential deteriorates of rocks and minerals (Warscheid and Braams 2000). The microcolonial fungi (black melanized colonies) that inhabit the exposed rock surfaces are tolerant to environmental stresses and produce filamentous hyphae that may penetrate into the rocks. These interactions may give rise to different types of surface coatings and secrete polysaccharides forming micropits in the rock surfaces. They may also form mutualistic relationship with algae on rock substrate in order to acquire C (Gorbushina 2007).



The colonization of fungi could lead to physical and biochemical changes in rocks. Fungi enter the solid materials through physical and chemical methods. The fungal hyphae penetrate along the weak points or spots on the surface of the rocks. The hyphae thus form ridges and grooves as the result of surface contours. At these spots, fungi weather the minerals by physical and chemical process. The exudates diffusion into the soil is prevented by these processes and thus enhances weathering mediated by fungi and result in the tunnel formation (Hoffland et al. 2002). Chemical weathering by fungi include the production of proton and ligand-based weathering agent. The hyphal tip growth involves the production of carbonic acids that aids in the breakdown of weak spots of rock surface and comprises proton based agents. Production of siderophores, polyphenolic and polysaccharide acids and organic anions are ligand based weathering mediators (Hoffland et al. 2004).

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## 8 Mycorrhiza: Mineral Weathering

Mycorrhizal fungi play a major role in mineral weathering and in the formation of soil. The mechanism involved in weathering of rocks by the mycorrhizal fungi is well documented (Wallander and Thelin 2008; Brantley et al. 2011; Thorley et al. 2015). Taylor et al. (2009) suggested mechanisms through which mycorrhizal fungi influence the mineral weathering processes. This includes (a) disintegration of minerals through secretions like  $H^+$  and organic chelators of low molecular weight; (b) respiration of plant roots and mycorrhizal fungi enhance  $CO_2$  presence in the soil solution; (c) organic matter decomposition elevates the concentrations of high molecular weight organic acids and organic chelators in the soil solution, that are further utilized by heterotrophs to fuel respiration and hence returning base cations to the soil solution from the biota; and (d) the transpiration increase the water flow consisting of nutrients and base cations to plants. The adsorbed soil particles on to the plant roots and mycorrhizal hyphae decrease the soil erosion thus contributing to the soil development continuously. As symbiotic plant partners, mycorrhizal fungi extend into soils and act as biosensors for nutrients that are taken up by them and supplied to their host plants (Bücking and Kafle 2015). The mycorrhizal hyphae force mechanically and chemically alter the minerals to obtain the nutrient elements (Bonneville et al. 2009). The organic acids produced by mycorrhizal hyphae acidify their environment that helps in the breakdown of minerals (Uroz et al. 2011).

The mycorrhizal group, both AM and ectomycorrhizal fungi are actively involved in weathering of rocks (Koele et al. 2014). Mycorrhizal fungi mostly target the minerals that consist of essential and needful plant nutrients during the weathering process (Remiszewski et al. 2016). Arbuscular mycorrhizal fungi may impact the mineral weathering through respiration and proton release and extraradical mycelium efficiently bind soil particles and influence soil aggregation (Bago et al. 1996; Smith and Read 2008). Ectomycorrhizal fungi forms a layer of fungal material around the root tip and the hyphae growing outside the layer penetrates into the soil acting as the nutrient scavenger (Landeweert et al. 2001). A positive correlation was reported between densities of root tip of ectomycorrhizal fungi and tunnel frequency



suggesting that ectomycorrhizal fungi may participate in the formation of mineral tunnels (Hoffland et al. 2002). The ectomycorrhizal fungi produce low molecular organic compounds and proton that might enhance the mineral weathering even under P deficiency (Smits et al. 2012). Arbuscular mycorrhizal fungi are capable of weathering biotite through which they contain acquire mineral elements (Sanz-Montero and Rodríguez-Aranda 2012).

In the zone of mineral–microbial contact, mineral dissolution, precipitation and clay mineral formation is influenced by the presence of the microbial cells and low molecular weight organic compounds produced by them. The organic compounds that are generated by the fungi impact the weathering process beneath the contact zone (Banfield et al. 1999). The ectomycorrhizal fungi enable weathering activity depending upon the chemical activity and colonization of the mycelia in the soil (Wallander et al. 1997). Acidification by the fungal hyphae due to the liberation of respired CO<sub>2</sub>, the release of organic acids, biomineral precipitation, the occurrence of extracellular acidic polymer substances and proton efflux constitute the chemical activity of mycelia (Gadd 2007; Burford et al. 2003). The capability of ectomycorrhizal fungi in weathering has been investigated to P, K and Mg in mineral form (Fomina et al. 2006; Rosling et al. 2009). However, the process of induced weathering in relation to P availability in ectomycorrhizal fungi is yet to be determined. In a study, Quirk et al. (2012) reported that ectomycorrhizal fungi associated with gymnosperm released two folds more Ca from the weathering of silicate surface when compared to AM associated angiosperms.

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## 9 Mycorrhiza and Soil Structure

Mycorrhizal fungi are intimately associated with plant roots, colonizing the root cortex as well as the surrounding soil. Mycorrhizal fungi are dominant among the fungal community in mineral soils (Lindahl et al. 2007). They play essential roles in terrestrial ecosystems serving as a sink for nutrient and carbon cycles. It is estimated that around 80% of plant N and P are acquired through mycorrhizal fungi (van der Heijden et al. 2015). The extensive extraradical hyphae facilitate the fungi to colonize and utilize nutrient-rich substrates in the soil and to absorb and translocate nutrients like P and C in soils contributing to plant fitness and soil quality (Ritz 2006).

As mycorrhizal colonization usually influences the soil structure, AM fungi may also probably affect soil water relations and therefore, the water relations of the host plants (Rilling and Mummey 2006). The extramatrical mycelia of ectomycorrhizal fungi obtain C from the soil through enzymatic breakdown of organic matter and from tree photosynthates. This contributes to the association between weathering of minerals in the soil and photosynthetically-assimilated C acquired from trees. Mycorrhizal plants may be considered as efficient competitors as they decrease the mineralizing populations in a scarcity of N and P or change the quality of the decomposing litter. In addition, ectomycorrhizal fungi modify the environment through acidification, organic acid exudation by hyphae (Rosling et al. 2009) and siderophores (Winklemann 2007).

Besides several beneficial aspects, mycorrhizal fungi also contribute to soil structure through soil aggregation (Rillig and Mummey 2006). Mycorrhizal fungi, plant roots and organic matter are considered as important traits in the development of soil structure (Daynes et al. 2013). Aggregation helps to maintain the soil porosity, biogeochemical cycle and water infiltration (Diaz-Zorita et al. 2002). Arbuscular mycorrhizal fungal hyphae are regarded as the primary soil aggregators thus, exhibiting a positive correlation between the AM fungal hyphae and aggregate stability (Borie et al. 2008). Soil aggregates are broadly classified as microaggregates (<250  $\mu\text{m}$  in diameter) and macroaggregates (>250  $\mu\text{m}$  in diameter) (Rillig and Mummey 2006). Microaggregates are formed by fungal hyphae and plant roots bounded by polysaccharides whereas extraradical fungal hyphae of AM fungi and fine plant roots associate to constitute macroaggregates by releasing a large amount of polysaccharides (Snyder and Vázquez 2005). Fungi can either influence the soil aggregation directly by combining the extracellular compounds produced by the fungi or indirectly by maintaining the soil particles through the hyphal network (Borie et al. 2008). As AM fungi dominate the soil component through constitution of around 30% of the soil microbial biomass (Olsson et al. 1999), they provide much more C when compared to saprobic fungi due to longer existence in the soil even after the removal of host plant. Therefore, AM fungi tend to be crucial component in relating biotic influences on soil aggregation (Borie et al. 2008).

Apart from the role of AM fungal hyphae in soil aggregation, AM fungi are well known to produce a non-water soluble and highly persistent glycoprotein called glomalin (Wright and Upadhyaya 1996) that have an important role in maintaining the soil structure and fertility (Fokom et al. 2012). Glomalin is also known as glycosylated glycoprotein (Gillespie et al. 2011). This glycoprotein is produced in cell walls of mycorrhizal fungi and persists in soil even after the death of the fungal hyphae (Driver et al. 2005). Glomalin commonly occurs in soils rich in insoluble humus or mineral fractions (Wright and Upadhyaya 1996). Owing to its adhesive properties, glomalin produces soil aggregates by combining fine soil particles together that aids in soil aeration (Purin and Rillig 2007). A positive correlation has been reported between C sequestration, soil aggregation and AM fungal density in a field study (Wilson et al. 2009). The amount of C and N from glomalin contributes to respectively 3% and 5% of soil C and N pools (Lovelock et al. 2004). Polyphenolic compounds such as humic acid and soil tannins have also been extracted along with glomalin (Whiffen et al. 2007; Jonathan and Javier 2006). Glomalin protects the fungal hyphae during translocation of nutrients to the hyphal tip from plants and to the plant from soil (Pal and Pandey 2014). The capability of AM fungal isolate to influence glomalin content and to the formation of extensive mycelial networks in the soil could impact the stability of soil aggregates through hyphal entrapment of soil particles. This suggests the need for the selection of potential AM fungal isolates that could be used for the improvement of soil quality and restoration of degraded lands (Bedini et al. 2009). Wu et al. (2012) studied the spatial distribution and relationship of glomalin with soil aggregates and root mycorrhization in the rhizosphere of *Citrus unshiu* and reported a positive correlation between glomalin related soil protein and plant roots. The study also revealed the fact that the

secretion of glomalin decreased with increasing soil depth. Rillig and Steinberg (2002) observed an increased production of glomalin by *Rhizophagus intraradices* (= *Glomus intraradices*) under unfavorable environmental condition by facilitating the soil structure in lacking adequate soil pores.

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## 10 Nutrient Cycling

Soil mineral weathering contributes in providing input of plant nutrients to ecosystems, thus preventing nutrient limitations (Chadwick et al. 1999). Moreover, the cations produced through mineral weathering neutralize the soil acidification, thereby enhancing the nutrient availability to plants (van Breemen et al. 1983). Clay particles formed as a result of weathering product contribute to the cation exchange capacity of the soil, decreasing the leaching of nutrients like K and ammonium and also positively correlates with soil organic matter and water holding capacity (Sollins et al. 1996). Weathering of rocks composed of silicate minerals releases a large amount of Ca and Mg that play a vital role in the C cycle as they are locked up as carbonates (Hartmann and Moosdorf 2011). The interaction between the process of geological leaching of plant nutrients and biological cycle that includes bioaccumulation process usually results in pedogenesis. The nutrients released during weathering processes are utilized by plants for their growth. In biological cycling, plants uptake specific nutrients from parent materials, atmosphere and water, thus through photosynthesis prepare organic matter, which is returned in the form of leaf or root residues to the soil. The decomposed organic matters from plant litters constitute an essential part of soil humus that enhances soil fertility (Zhu et al. 2014).

Nutrient cycling is an important ecological function that involves a defined, typically bounded, compartment which nutrients enter and leave via a range of pathways, and within which they are transformed via a myriad of chemical and biochemical reactions. In soil systems, a large proportion of these transformations are mediated by biota. Microbial communities play a crucial role in the nutrient cycle as they degrade organic materials; liberate inorganic nutrients that are taken up by plants; influence plant growth, availability of nutrients through several processes such as, chelation, oxidation, solubilization and reduction; stores and releases nutrients from microbial biomass (Marschner 2007). Microbes involved in N or P cycling are  $N_2$ - fixers, AM fungi and P- mobilizers.

Nitrogen cycling involves three important processes,  $N_2$  fixation, denitrification and nitrification. Microorganisms take part in these processes as  $N_2$  fixers, denitrifiers and nitrifiers (Stein and Klotz 2016). The  $N_2$ - fixing bacteria and AM fungi represent the most significant beneficial symbionts associated with nutrient cycling (Dos Santos et al. 2012; Schüßler and Walker, 2011). The capability of microorganisms to convert atmospheric N to ammonia is limited to bacteria that contain nitrogenase enzyme which combines hydrogen and N to form ammonia (de Bruijn 2015). The  $N_2$  fixers are either free-living or symbiotic bacteria are commonly known as diazotrophs (Dixon and Khan 2004). The rhizobia bacteria can fix  $N_2$  with leguminous plant through mutual symbiotic association, whereas, some of the

actinomycetes fix  $N_2$  and form nodules on the roots, that is known as actinorrhizal plants (Olivares et al. 2013). Other  $N_2$  fixing bacteria include *Azotobacter*, *Bacillus*, *Clostridium*, *Frankia*, etc. The ammonium is converted into nitrate through soil bacteria such as *Nitrosomonas*, *Nitrobacter* etc. The last process of N cycling involves denitrification that are carried out by denitrifiers like, *Pseudomonas* and *Clostridium* through which nitrates are converted to  $N_2$  (Hayatsu et al. 2008).

Phosphorus is stored in the soils, bedrock and sediments and is not available directly to organisms (Ruttenberg 2002). Microorganisms including bacteria, fungi and actinomycetes have the capacity to solubilize and mineralize P (Alori et al. 2017). The most prominent soil bacteria involved in P are the species of *Agrobacterium*, *Pseudomonas*, *Acetobacter* and *Bacillus* (Babalola and Glick 2012; Kumar et al. 2014; David et al. 2014). Acidification, chelating organic acids, and siderophore production is involved in solubilizing Fe, Ca and aluminium phosphate from the soil (Marschner 2008). Phosphate solubilizers enhance the amount of orthophosphate leaving the nutrient to be absorbed by the plant roots (Richardson et al. 2009). Phosphatase enzymes are utilized by fungi and bacteria in mineralizing P (Jorquera et al. 2008). Some of the efficient fungal P solubilizers include *Fusarium*, *Cladosporium*, *Rhizoctonia*, and *Alternaria* (Sharma et al. 2013). Some fungi decompose and degrade the wood thus producing large amounts of oxalic acids. These oxalic acids might have a secondary effect on the release of P from the soil (Dutton and Evans 1996; Fransson et al. 2004).

Arbuscular mycorrhizal fungal symbioses are significant for the continual nutrient cycling in the plant community and thus avoid nutrient sequestration. During root colonization, the fungus grows in the surrounding soil of roots to establish a network of hyphae called extraradical mycelium. The extraradical mycelium uptake the nutrient from the soil with help of branched absorbing structures and transfer to a long distance of about 25 cm (Jansa et al. 2003). Arbuscular mycorrhizal fungi rely on the host plant for C compounds for their growth and metabolism, in return for mineral nutrients (especially P) that the extraradical mycelium takes up from the soil and transport to the root. For the growth and metabolism, AM fungi rely on the host plant for C sources and in return, the extraradical mycelium provides mineral nutrient from the soil to plant roots. This symbiotic relation of extraradical mycelium and intraradical mycelium is important for translocation, distribution and movement of mineral nutrients in the plant-soil environment (Richardson et al. 2009). The AM fungal contribution to plant nutrition through P uptake by mycelium is considered as the extension of the root system. AM fungi influence the uptake of other nutrients such as K, Ca, Zn, Cu or Fe (Liu et al. 2000).

Arbuscular mycorrhizal fungi stimulate the inorganic phosphate transporters which are present in the periarbuscular membrane (Xie et al. 2013). These genes are considered as functional markers for the AM symbiosis (Harrison 2012). Therefore, mycorrhizal plants absorb P directly via root epidermis and through the AM fungal pathway) that delivers P to the root cortex (Smith and Smith 2011). It is proposed that mycorrhizal N uptake is similar to  $P_i$  uptake pathway. The C transfer to fungi from the plant is transferred to plant sink organs, distributed at the arbuscular interface and are further hydrolyzed by cell walls (Ferrol and Pérez-Tienda 2009). Mycorrhizae can also influence the uptake of a range of elements by plants,

including S, B, K, Ca, Mg, Na, Zn, Cu, Mn, Fe, Al and Si (Clark and Zeto 2000). Bacteria may generate various metabolites necessary for mineral weathering with the available nutrients (Bennett et al. 2001). Photoautotroph organisms fix C and penetrate into the soil through root deposition, specifically through soluble exudates that originate from growing roots at a faster rate and slowly by cells and tissue depositions. The senesced plants parts are accumulated on the soil surface and these organic matter in the soil are transformed by soil organisms during the assimilation of energy for growth and reproduction. Through this, the compounds are additionally transformed and cycled between the compartments (Paul 2007). This process yields stable soil organic matter which contributes to structural development.

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## 11 Conclusion

It is clear that soil biota's as the biological engine carry out the myriad of the process which underpins soil function via biochemical pathways. Soil biota is involved in many aspects of soil functioning and delivery of the full range of ecosystem goods and services that soils support. Nevertheless, the virtual role of biota in soil production varies between systems. Soil organisms exist in the presence of other populations and the diverse members of biomass. Thus, emerging interactions persuade the community structure within soils having strong impact on growth and functions of individual organisms. The process of mineral weathering via microorganisms and thereby providing nutrients to plants is well documented. Nevertheless, the microbial enzymes, genes in the mineral weathering process are yet to be investigated. The transfer of electron and genes involved in interaction between microbes and minerals is still obscure. The information on the distribution of microorganisms on the mineral surface and its chemistry could help in better understanding of mineral weathering processes. Compared to the microcosm experiments, mesh bag incubation studies could be performed to determine the dissolution rate of minerals. The interaction between plants and microbes and the microbes and mineral particles constitute a major role in soil formation.

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## References

- Alori, E. T., Glick, B. R., & Babalola, O. O. (2017). Microbial phosphorus solubilization and its potential for use in sustainable agriculture. *Frontiers in Microbiology*, 8, 971. <https://doi.org/10.3389/fmicb.2017.00971>.
- Altieri, M. A. (2004). Linking ecologists and traditional farmers in the search for sustainable agriculture. *Frontiers in Ecology and the Environment*, 2, 35–42.
- Ascaso, C., Wierchos, J., Souza-Egipsy, V., & De los RÃaos A. (2002). In situ evaluation of the biodeteriorating action of microorganisms and the effects of biocides on carbonate rock of the Jeronimos Monastery (Lisbon). *International Biodeterioration Biodegradation*, 49, 1–12.
- Augé, R. M. (2004). Arbuscular mycorrhizae and soil/plant water relations. *Canadian Journal of Soil Science*, 84, 373–381.
- Babalola, O. O., & Glick, B. R. (2012). The use of microbial inoculants in African agriculture: Current practice and future prospects. *Journal of Food, Agriculture and Environment*, 10, 540–549.

- Bago, B., Vierheilig, H., Piché, Y., & Azcón-Aguilar, C. (1996). Nitrate depletion and pH changes induced by the extraradical mycelium of the arbuscular mycorrhizal fungus *Glomus intraradices* grown in monoxenic cultures. *The New Phytologist*, *133*, 273–280.
- Banfield, J. F., Barker, W. W., Welch, S. A., & Taunton, A. (1999). Biological impact on mineral dissolution: Application of the lichen model to understanding mineral weathering in the rhizosphere. *Proceedings of the National Academy of Sciences of the United States of America*, *96*, 3404–3411.
- Bedini, S., Pellegrino, E., Avio, L., Pellegrini, S., Bazzoffi, P., Argese, E., & Giovannetti, M. (2009). Changes in soil aggregation and glomalin-related soil protein content as affected by the arbuscular mycorrhizal fungal species *Glomus mosseae* and *Glomus intraradices*. *Soil Biology and Biochemistry*, *41*, 1491–1496.
- Begonha, A. (2009). Mineralogical study of the deterioration of granite stones of two Portuguese churches and characterization of the salt solutions in the porous network by the presence of diatoms. *Materials Characterization*, *60*, 621–635.
- Belnap, J., & Lange, O. L. (2003). Biological soil crusts: Structure, function, and management. In I. T. Baldwin, M. M. Caldwell, G. Heldmaier, O. L. Lange, H. A. Mooney, E.-D. Schulze, & U. Sommer (Eds.), *Ecological studies series 150* (Vol. 150, pp. 1–503). Berlin: Springer.
- Belnap, J., Büdel, B., & Lange, O. L. (2001). Biological soil crusts: Characteristics and distribution. In J. Belnap & O. L. Lange (Eds.), *Biological soil crusts: Structure, function, and management* (Ecological studies analysis and synthesis, Vol. 150, pp. 3–30). Berlin/Heidelberg: Springer.
- Bennett, P. C., Rogers, J. R., Choi, W. J., & Hiebert, F. K. (2001). Silicates, silicate weathering, and microbial ecology. *Geomicrobiology Journal*, *18*, 3–19.
- Berg, B., & McLaugherty, C. (2014). Decomposition as a process: Some main features. In B. Berg & C. McLaugherty (Eds.), *Plant litter: decomposition, humus formation, carbon sequestration* (pp. 11–34). Berlin/Heidelberg: Springer.
- Bin, L., Ye, C., Lijun, Z., & Ruidong, Y. (2008). Effect of microbial weathering on carbonate rocks. *Earth Science Frontiers*, *15*, 90–99.
- Bonfante, P., & Anca, I. A. (2009). Plants, mycorrhizal fungi, and bacteria: A network of interactions. *Annual Review of Microbiology*, *63*, 363–383.
- Bonneville, S., Smits, M. M., Brown, A., Harrington, J., Leake, J. R., Brydson, R., & Benning, L. G. (2009). Plant-driven fungal weathering: Early stages of mineral alteration at the nanometer scale. *Geology*, *37*, 615–618.
- Borie, F., Rubio, R., & Morales, A. (2008). Arbuscular mycorrhizal fungi and soil aggregation. *Journal of Soil Science and Plant Nutrition*, *8*, 9–18.
- Brantley, S. L., Megonigal, J. P., Scatena, F. N., Balogh-Brunstad, Z., Barnes, R. T., Bruns, M. A., & Yoo, K. (2011). Twelve testable hypotheses on the geobiology of weathering. *Geobiology*, *9*, 140–165.
- Bratteler, M., Lexer, C., & Widmer, A. (2006). Genetic architecture of traits associated with serpentine adaptation of *Silene vulgaris*. *Journal of Evolutionary Biology*, *19*, 1149–1156.
- Bressan, M., Roncato, M. A., Bellvert, F., Comte, G., Haichar, F. Z., Achouak, W., & Berge, O. (2009). Exogenous glucosinolate produced by *Arabidopsis thaliana* has an impact on microbes in the rhizosphere and plant roots. *The ISME Journal*, *3*, 1243–1257.
- Bücking, H., & Kafle, A. (2015). Role of arbuscular mycorrhizal fungi in the nitrogen uptake of plants: Current knowledge and research gaps. *Agronomy*, *5*, 587–612.
- Burford, E. P., Fomina, M., & Gadd, G. M. (2003). Fungal involvement in bioweathering and biotransformation of rocks and minerals. *Mineralogical Magazine*, *67*, 1127–1155.
- Butler, J. L., Williams, M. A., Bottomley, P. J., & Myrold, D. D. (2003). Microbial community dynamics associated with rhizosphere carbon flow. *Applied and Environmental Microbiology*, *69*, 6793–6800.
- Calvaruso, C., Turpault, M. P., & Frey-Klett, P. (2006). Root-associated bacteria contribute to mineral weathering and to mineral nutrition in trees: A budgeting analysis. *Applied and Environmental Microbiology*, *72*, 1258–1266.



- Calvaruso, C., Turpault, M. P., Leclerc, E., & Frey-Klett, P. (2007). Impact of ectomycorrhizosphere on the functional diversity of soil bacterial and fungal communities from a forest stand in relation to nutrient mobilization processes. *Microbial Ecology*, *54*, 567–577.
- Calvaruso, C., Mareschal, L., Turpault, M. P., & Leclerc, E. (2009). Rapid clay weathering in the rhizosphere of Norway spruce and oak in an acid forest ecosystem. *Soil Science Society of America Journal*, *73*, 331–338.
- Carson, J. K., Campbell, L., Rooney, D., Clipson, N., & Gleeson, D. B. (2009). Minerals in soil select distinct bacterial communities in their microhabitats. *FEMS Microbiology Ecology*, *67*, 381–388.
- Certini, G., Campbell, C. D., & Edwards, A. C. (2004). Rock fragments in soil support a different microbial community from the fine earth. *Soil Biology and Biochemistry*, *36*, 1119–1128.
- Chadwick, O., Derry, L., Vitousek, P., Huebert, B., & Hedin, L. (1999). Changing sources of nutrients during four million years of ecosystem development. *Nature*, *397*, 491–497.
- Chen, J., Blume, H.-P., & Beyer, L. (2000). Weathering of rocks induced by lichen colonization – A review. *Catena*, *39*, 121–146.
- Chen, W., Sheng, X.-F., He, L.-Y., & Huang, Z. (2015). *Rhizobium yantingense* sp. nov., a mineral-weathering bacterium. *International Journal of Systematic and Evolutionary Microbiology*, *65*, 412–417.
- Clark, R. B., & Zeto, S. K. (2000). Mineral acquisition by arbuscular mycorrhizal plants. *Journal of Plant Nutrition*, *23*, 867–902.
- Collignon, C., Uroz, S., Turpault, M. P., & Frey-Klett, P. (2011). Seasons differently impact the structure of mineral weathering bacterial communities in beech and spruce stands. *Soil Biology and Biochemistry*, *43*, 2012–2022.
- Cotrufo, M. F., Wallenstein, M. D., Boot, C. M., Deneff, K., & Paul, E. (2013). The Microbial Efficiency-Matrix Stabilization (MEMS) framework integrates plant litter decomposition with soil organic matter stabilization: Do labile plant inputs form stable soil organic matter? *Global Change Biology*, *19*, 988–995.
- David, P., Raj, R. S., Linda, R., & Rhema, S. B. (2014). Molecular characterization of phosphate solubilizing bacteria (PSB) and plant growth promoting rhizobacteria (PGPR) from pristine soils. *International Journal of Innovative Science Engineering and Technology*, *1*, 317–324.
- Daynes, C. N., Field, D. J., Saleeba, J. A., Cole, M. A., & McGee, P. A. (2013). Development and stabilisation of soil structure via interactions between organic matter, arbuscular mycorrhizal fungi and plant roots. *Soil Biology and Biochemistry*, *57*, 683–694.
- de Bruijn, F. J. (2015). Biological nitrogen fixation. In B. Lugtenberg (Ed.), *Principles of plant-microbe interactions* (pp. 215–224). Cham: Springer International.
- De los Ríos, A., Wierzychos, J., & Ascaso, C. (2002). Microhabitats and chemical microenvironments under saxicolous lichens growing on granite. *Microbial Ecology*, *43*, 181–188.
- Deneff, K., & Six, J. (2005). Clay mineralogy determines the importance of biological versus abiotic processes for macroaggregate formation and stabilization. *European Journal of Soil Science*, *56*, 469–479.
- Díaz-Zorita, M., Perfect, E., & Grove, J. H. (2002). Disruptive methods for assessing soil structure. *Soil and Tillage Research*, *64*, 3–22.
- Dixon, R., & Kahn, D. (2004). Genetic regulation of biological nitrogen fixation. *Nature Reviews. Microbiology*, *2*, 621–631.
- Dominati, E. J., Patterson, M. G., & Mackay, A. D. (2010). A framework for classifying and quantifying the natural capital and ecosystem services of soils. *Ecological Economics*, *69*, 1858–1868.
- Dos Santos, P. C., Fang, Z., Mason, S. W., Setubal, J. C., & Dixon, R. (2012). Distribution of nitrogen fixation and nitrogenase-like sequences amongst microbial genomes. *BMC Genomics*, *13*, 162–162.
- Driver, J. D., Holben, W. E., & Rillig, M. C. (2005). Characterization of glomalin as a hyphal wall component of arbuscular mycorrhizal fungi. *Soil Biology and Biochemistry*, *37*, 101–106.
- Duc, L., Noll, M., Meier, B. E., Burgmann, H., & Zeyer, J. (2009). High diversity of diazotrophs in the forefield of a receding alpine glacier. *Microbial Ecology*, *57*, 179–190.



- Dutton, M. V., & Evans, C. S. (1996). Oxalate production by fungi: Its role in pathogenicity and ecology in the soil environment. *Canadian Journal of Microbiology*, *42*, 881–895.
- Favero-Longo, S. E., Turci, F., Tomatis, M., Castelli, D., Bonfante, P., Hochella, M. F., Piervittori, R., & Fubini, B. (2005). Chrysotile asbestos is progressively converted into a non-fibrous amorphous material by the chelating action of lichen metabolites. *Journal of Environmental Monitoring*, *7*, 764–766.
- Ferrol, N., & Pérez-Tienda, J. (2009). Coordinated nutrient exchange in arbuscular mycorrhiza interface. In C. Azcon-Aguilar, J. M. Barea, S. Gianinazzi, & V. Gianinazzi-Pearson (Eds.), *Mycorrhizas: Functional processes and ecological impact* (pp. 73–87). Berlin/Heidelberg: Springer.
- Fierer, N., & Jackson, R. B. (2006). The diversity and biogeography of soil bacterial communities. *Proceedings of the National Academy of Sciences of the United States of America*, *103*, 626–631.
- Fokom, R., Adamou, S., Teugwa, M. C., Boyogueno, A. D. B., Nana, W. L., Ngonkeu, M. E. L., Tchamen, N. S., Nwaga, D., Tsala Ndzomo, G., & Amvam Zollo, P. H. (2012). Glomalin related soil protein, carbon, nitrogen and soil aggregate stability as affected by land use variation in the humid forest zone of south Cameroon. *Soil and Tillage Research*, *120*, 69–75.
- Fomina, M., Charnock, J. M., Hillier, S., Alexander, I. J., & Gadd, G. M. (2006). Zinc phosphate transformations by the *Paxillus involutus*/pine ectomycorrhizal association. *Microbial Ecology*, *52*, 322–333.
- Fontaine, S., Henault, C., Aamor, A., Bdioui, N., Bloor, J. M. G., Maire, V., Mary, B., Revault, S., & Maron, P. A. (2011). Fungi mediate long term sequestration of carbon and nitrogen in soil through their priming effect. *Soil Biology and Biochemistry*, *43*, 86–96.
- Fransson, A.-M., Valeur, I., & Wallander, I. (2004). The wood-decaying fungus *Hygrophoropsis aurantiaca* increases P availability in acid forest humus soil while N addition hampers this effect. *Soil Biology and Biochemistry*, *36*, 1699–1705.
- Gadd, G. M. (2007). Geomycology: Biogeochemical transformations of rocks, minerals, metals and radionuclides by fungi, bioweathering and bioremediation. *Mycological Research*, *111*, 3–49.
- Gadd, G. M. (2017). Fungi, rocks, and minerals. *Elements*, *13*, 171–176.
- Garcia-Pichel, F., Johnson, S. L., Youngkin, D., & Belnap, J. (2003). Small-scale vertical distribution of bacterial biomass and diversity in biological soil crusts from arid lands in the Colorado Plateau. *Microbial Ecology*, *46*, 312–321.
- Gillespie, A. W., Farrell, R. E., Walley, F. L., Ross, A. R. S., Leinweber, P., Eckhardt, K.-U., Regier, T., & Blyth, R. I. R. (2011). Glomalin-related soil protein contains non-mycorrhizal-related heat-stable proteins, lipids and humic materials. *Soil Biology and Biochemistry*, *43*, 766–777.
- Gleeson, D. B., Clipson, N. J. W., Melville, K., Gadd, G. M., & McDermott, F. P. (2005). Mineralogical control of fungal community structure in a weathered pegmatitic granite. *Microbial Ecology*, *50*, 360–368.
- Gorbushina, A. A. (2007). Life on the rocks. *Environmental Microbiology*, *9*, 1613–1631.
- Gregory, A. S., Watts, C. W., Whalley, W. R., Kuan, H. L., Griffiths, B. S., Hallett, P. D., & Whitmore, A. P. (2007). Physical resilience of soil to field compaction and the interactions with plant growth and microbial community structure. *European Journal of Soil Science*, *58*, 1221–1232.
- Gulati, A., Rahi, P., & Vyas, P. (2008). Characterization of phosphate-solubilizing fluorescent pseudomonads from the rhizosphere of seabuckthorn growing in the cold deserts of Himalayas. *Current Microbiology*, *56*, 73–79.
- Harrison, M. J. (2012). Cellular programs for arbuscular mycorrhizal symbiosis. *Current Opinion in Plant Biology*, *15*, 691–698.
- Hartmann, J., & Moosdorf, N. (2011). Chemical weathering rates of silicate dominated lithological classes and associated liberation rates of phosphorus on the Japanese Archipelago-implications for global scale analysis. *Chemical Geology*, *287*, 125–157.
- Hayat, R., Ali, S., Amara, U., Khalid, R., & Ahmed, I. (2010). Soil beneficial bacteria and their role in plant growth promotion: A review. *Annales de Microbiologie*, *60*, 579–598.

- Hayatsu, M., Tago, K., & Saito, M. (2008). Various players in the nitrogen cycle: Diversity and functions of the microorganisms involved in nitrification and denitrification. *Soil Science & Plant Nutrition*, *54*, 33–45.
- Helfrich, M., Ludwig, B., Thoms, C., Gleixner, G., & Flessa, H. (2015). The role of soil fungi and bacteria in plant litter decomposition and macroaggregate formation determined using phospholipid fatty acids. *Applied Soil Ecology*, *96*, 261–264.
- Hoffland, E., Giesler, R., Jongmans, T., & van Breeman, N. (2002). Increasing feldspar tunneling by fungi across a North Sweden podzol chronosequence. *Ecosystems*, *5*, 11–22.
- Hoffland, E., Kuyper, T. W., Wallander, H., Plassard, C., Gorbushina, A. A., Haselwandter, K., Holmström, S., Landeweert, R., Lundström, U. S., Rosling, A., Sen, R., Smits, M. M., van Hees, P., & van Breemen, N. (2004). The role of fungi in weathering. *Frontiers in Ecology and the Environment*, *2*, 258–264.
- Huang, J., Sheng, X. F., Xi, J., He, L. Y., Huang, Z., Wang, Q., & Zhang, Z. D. (2014). Depth-related changes in community structure of culturable mineral weathering bacteria and in weathering patterns caused by them along two contrasting soil profiles. *Applied and Environmental Microbiology*, *80*, 29–42.
- Jansa, J., Mozafar, A., & Frossard, E. (2003). Long-distance transport of P and Zn through the hyphae of an arbuscular mycorrhizal fungus in symbiosis with maize. *Agronomie*, *23*, 481–488.
- Jonathan, J. H., & Javier, M. G. (2006). Bradford reactive soil protein in Appalachian soils: Distribution and response to incubation, extraction reagent and tannins. *Plant and Soil*, *286*, 339–356.
- Jorquera, M. A., Hernández, M. T., Rengel, Z., Marschner, P., & Luz Mora, M. (2008). Isolation of culturable phosphobacteria with both phytate-mineralization and phosphate-solubilization activity from the rhizosphere of plants grown in a volcanic soil. *Biology and Fertility of Soils*, *44*, 1025–1034.
- Kobierska, F., Jonas, T., Magnusson, J., Zappa, M., Bavay, M., Bosshard, T., Paul, F., & Bernasconi, S. (2011). Climate change effects on snow melt and discharge of a partly glacierized watershed in Central Switzerland (Soil Trec Critical Zone Observatory). *Applied Geochemistry*, *26*, 60–62.
- Koele, N., Dickie, I. A., Blum, J. D., Gleason, J. D., & de Graaf, L. (2014). Ecological significance of mineral weathering in ectomycorrhizal and arbuscular mycorrhizal ecosystems from a field-based comparison. *Soil Biology and Biochemistry*, *69*, 63–70.
- Kumar, S., Baudhdh, K., Barman, S. C., & Singh, R. P. (2014). Amendments of microbial bio fertilizers and organic substances reduces requirement of urea and DAP with enhanced nutrient availability and productivity of wheat (*Triticum aestivum* L.). *Ecological Engineering*, *71*, 432–437.
- Kuske, C. R., Yaeger, C. M., Johnson, S., Ticknor, O. L., & Belnap, J. (2012). Response and resilience of soil biocrust bacterial communities to chronic physical disturbance in arid shrublands. *The ISME Journal*, *6*, 886–897.
- Lambers, H., Mougél, C., Jaillard, B., & Hinsinger, P. (2009). Plant–microbe–soil interactions in the rhizosphere: An evolutionary perspective. *Plant and Soil*, *321*, 83–115.
- Landeweert, R., Hoffland, E., Finlay, R. D., Kuyper, T. W., & van Breemen, N. (2001). Linking plants to rocks: Ectomycorrhizal fungi mobilize nutrients from minerals. *Trends in Ecology & Evolution*, *16*, 248–254.
- Liang, C., Zhang, X., & Balsler, T. C. (2007). Net microbial amino sugars accumulation process in soil as influenced by different plant material inputs. *Biology and Fertility of Soils*, *44*, 1–7.
- Lindahl, B. D., Ihrmark, K., Boberg, J., Trumbore, S. E., Hogberg, P., Stenlid, J., & Finlay, R. D. (2007). Spatial separation of litter decomposition and mycorrhizal nitrogen uptake in a boreal forest. *The New Phytologist*, *173*, 611–620.
- Liu, A., Hamel, C., Hamilton, R. I., Ma, B. L., & Smith, D. L. (2000). Acquisition of Cu, Zn, Mn and Fe by mycorrhizal maize (*Zea mays* L.) grown in soil at different P and micronutrient levels. *Mycorrhiza*, *9*, 331–336.
- Lopez, B. R., Bashan, Y., & Bacilio, M. (2011). Endophytic bacteria of *Mammillaria fraileana*, an endemic rock-colonizing cactus of the Southern Sonoran Desert. *Archives of Microbiology*, *193*, 527–541.

- Lovelock, C. E., Wright, S. E., & Nichols, K. A. (2004). Using glomalin as an indicator for arbuscular mycorrhizal hyphal growth: An example from a tropical rainforest soil. *Soil Biology and Biochemistry*, *36*, 1009–1012.
- Männistö, M. K., & Häggblom, M. M. (2006). Characterization of psychrotolerant heterotrophic bacteria from Finnish Lapland. *Systematic and Applied Microbiology*, *29*, 229–243.
- Mapelli, F., Marasco, R., Rizzi, A., Baldi, F., Ventura, S., Daffonchio, D., & Borin, S. (2011). Bacterial communities involved in soil formation and plant establishment triggered by pyrite bioweathering on Arctic moraines. *Microbial Ecology*, *61*, 438–447.
- Marschner, P. (2007). Plant microbe interactions in the rhizosphere and nutrient cycling. In P. Marschner & Z. Rengel (Eds.), *Nutrient cycling in terrestrial ecosystems* (Soil biology series, pp. 159–182). Heidelberg: Springer.
- Marschner, P. (2008). The role of rhizosphere microorganisms in relation to P uptake by plants. In P. J. White & J. Hammond (Eds.), *The ecophysiology of plant-phosphorus interactions series: Plant ecophysiology* (Vol. 7, pp. 165–176). Dordrecht: Springer.
- Marschner, P., & Baumann, K. (2003). Changes in bacterial community structure induced by mycorrhizal colonisation in split-root maize. *Plant and Soil*, *251*, 279–289.
- Martin, J. P., & Haider, K. (1971). Microbial activity in relation to soil humus formation. *Soil Science*, *111*, 54–63.
- Miniaci, C., Bunge, M., Duc, L., Edwards, I., Burgmann, H., & Zeyer, J. (2007). Effects of pioneering plants on microbial structures and functions in a glacier forefield. *Biology and Fertility of Soils*, *44*, 289–297.
- Moore, J. A. M., Jiang, J., Courtney, M., Patterson, C. M., Melanie, A., Mayes, M. A., Wang, G., & Classen, A. T. (2015). Interactions among roots, mycorrhizas and free-living microbial communities differentially impact soil carbon processes. *Journal of Ecology*, *103*, 1442–1453.
- Morel, J. L., Habib, L., Plantureux, S., & Guckert, A. (1991). Influence of maize root mucilage on soil aggregate stability. *Plant and Soil*, *136*, 111–119.
- Olivares, J., Bedmar, E. J., & Sanjuán, J. (2013). Biological nitrogen fixation in the context of global change. *Molecular Plant-Microbe Interactions*, *26*, 486–494.
- Olsson, P. A., Thingstrup, I., Jakobsen, I., & Baath, F. (1999). Estimation of the biomass of arbuscular mycorrhizal fungi in a linseed field. *Soil Biology and Biochemistry*, *31*, 1879–1887.
- Pal, A., & Pandey, S. (2014). Role of glomalin in improving soil fertility. *International Journal of Plant and Soil Science*, *3*, 112–129.
- Paul, E. A. (2007). Soil microbiology, ecology and biochemistry in perspective. In E. A. Paul (Ed.), *Soil microbiology ecology and biochemistry* (3rd ed., pp. 3–24). San Diego: Academic.
- Paul, E. A., & Clark, F. E. (1996). *Soil microbiology and biochemistry* (2nd ed.). San Diego: Academic.
- Puente, M. E., Li, C. Y., & Bashan, Y. (2009). Rock-degrading endophytic bacteria in cacti. *Environmental and Experimental Botany*, *66*, 389–401.
- Purin, S., & Rillig, M. C. (2007). The arbuscular mycorrhizal fungal protein glomalin: Limitations, progress, and a new hypothesis for its function. *Pedobiologia*, *51*, 123–130.
- Quirk, J., Beerling, D. J., Banwart, S. A., Kakonyi, G., Romero-Gonzalez, M. E., & Leake, J. R. (2012). Evolution of trees and mycorrhizal fungi intensifies silicate mineral weathering. *Biology Letters*, *8*, 1006–1011.
- Ranalli, G., Zanardini, E., & Sorlini, C. (2009). Biodeterioration including cultural heritage. In M. Schaechter (Ed.), *Encyclopedia of microbiology* (3rd ed., pp. 191–205). Oxford: Elsevier.
- Remiszewska, K. A., Bryce, J. G., Fahnestock, M. F., Pettitta, E. A., Blichert-Toft, J., Vadeboncoeur, M. A., & Bailey, S. W. (2016). Elemental and isotopic perspectives on the impact of arbuscular mycorrhizal and ectomycorrhizal fungi on mineral weathering across imposed geologic gradients. *Chemical Geology*, *445*, 164–171.
- Richardson, A. E., Barea, J. M., McNeill, A. M., & Prigent-Combaret, C. (2009). Acquisition of phosphorus and nitrogen in the rhizosphere and plant growth promotion by microorganisms. *Plant and Soil*, *321*, 305–339.
- Rillig, M. C., & Mummey, D. L. (2006). Mycorrhizas and soil structure. *The New Phytologist*, *171*, 41–53.

- Rillig, M. C., & Steinberg, P. D. (2002). Glomalin production by an arbuscular mycorrhizal fungus: A mechanism of habitat modification? *Soil Biology and Biochemistry*, *34*, 1371–1374.
- Rillig, M. C., Mummey, D. L., Ramsey, P. W., Klironomos, J. N., & Gannon, J. E. (2006). Phylogeny of arbuscular mycorrhizal fungi predicts community composition of symbiosis-associated bacteria: AMF-associated bacterial communities. *FEMS Microbiology Ecology*, *57*, 389–395.
- Ritz, K. (2006). Fungal roles in transport processes in soils. In G. M. Gadd (Ed.), *Fungi in biogeochemical cycles* (pp. 51–73). Cambridge: Cambridge University Press.
- Rosling, A., Roose, T., Herrmann, A. M., Davidson, F. A., Finlay, R. D., & Gadd, G. M. (2009). Approaches to modelling mineral weathering by fungi. *Fungal Biology Reviews*, *23*, 1–7.
- Ruttenberg, K. C. (2002). The global phosphorus cycle. In A. S. Goudie & D. J. Cuff (Eds.), *The encyclopedia of global change* (Vol. 2, pp. 241–245). Oxford: Oxford University Press.
- Sanz-Montero, M. E., & Rodríguez-Aranda, J. P. (2012). Endomycorrhizae in Miocene paleosols: Implications in biotite weathering and accumulation of dolomite in plant roots (SW Madrid Basin, Spain). *Palaeogeography Palaeoclimatology Palaeoecology*, *333–334*, 121–130.
- Schulz, S., Brankatschk, R., Dumig, A., Kogel-Knabner, I., Schloter, M., & Zeyer, J. (2013). The role of microorganisms at different stages of ecosystem development for soil formation. *Biogeosciences*, *10*, 3983–3996.
- Schübler, A., & Walker, C. (2011). Evolution of the ‘plant-symbiotic’ fungal phylum, Glomeromycota. In S. Pöggeler & J. Wöstemeyer (Eds.), *Evolution of fungi and fungal-like organisms* (pp. 163–185). Berlin: Springer.
- Sharma, S. B., Sayyed, R. Z., Trivedi, M. H., & Gobi, T. A. (2013). Phosphate solubilizing microbes: Sustainable approach for managing phosphorus deficiency in agricultural soils. *Springer Plus*, *2*, 587.
- Six, J., Frey, S. D., Thiet, R. K., & Batten, K. M. (2006). Bacterial and fungal contributions to carbon sequestration in agroecosystems. *Soil Science Society of America Journal*, *70*, 555–569.
- Smith, S. E., & Read, D. J. (2008). *Mycorrhizal symbiosis* (3rd ed.). New York: Academic.
- Smith, S. E., & Smith, F. A. (2011). Roles of arbuscular mycorrhizas in plant nutrition and growth: New paradigms from cellular to ecosystems scales. *Annual Review of Plant Biology*, *63*, 227–250.
- Smits, M. M., Bonneville, S., Benning, L. G., Banwart, S. A., & Leake, J. R. (2012). Plant-driven weathering of apatite-The role of an ectomycorrhizal fungus. *Geobiology*, *10*, 445–456.
- Snyder, V. A., & Vázquez, M. A. (2005). Structure. In D. Hillel, J. H. Hatfield, D. S. Powlson, C. Rosenzweig, K. M. Scow, M. J. Singer, & D. L. Sparks (Eds.), *Encyclopedia of soils in the environment* (pp. 54–68). Oxford: Elsevier/Academic.
- Sokolova, T. A. (2011). The role of soil biota in the weathering of minerals: A review of literature. *Eurasian Soil Science*, *44*, 56–72.
- Sollins, P., Homann, P., & Caldwell, B. A. (1996). Stabilization and destabilization of soil organic matter: Mechanisms and controls. *Geoderma*, *74*, 65–105.
- Stein, L. Y., & Klotz, M. G. (2016). The nitrogen cycle. *Current Biology*, *26*, 94–98.
- Taylor, L. L., Leake, J. R., Quirk, J., Hardy, K., Banwart, S. A., & Beerling, D. J. (2009). Biological weathering and the long-term carbon cycle: Integrating mycorrhizal evolution and function into the current paradigm. *Geobiology*, *7*, 171–191.
- Thorley, R. M., Taylor, L. L., Banwart, S. A., Leake, J. R., & Beerling, D. J. (2015). The role of forest trees and their mycorrhizal fungi in carbonate rock weathering and its significance for global carbon cycling. *Plant, Cell & Environment*, *38*, 1947–1961.
- Towe, S., Albert, A., Kleinedam, K., Brankatschk, R., Dumig, A., Welzl, G., Munch, J. C., Zeyer, J., & Schloter, M. (2010). Abundance of microbes involved in nitrogen transformation in the rhizosphere of *Leucanthemopsis alpina* (L.) Heywood grown in soils from different sites of the Damma glacier forefield. *Microbial Ecology*, *60*, 762–770.
- Tremblay, L., & Benner, R. (2006). Microbial contributions to N-immobilization and organic matter preservation in decomposing plant detritus. *Geochimica et Cosmochimica Acta*, *70*, 133–146.

- Uroz, S., Calvaruso, C., Turpault, M. P., Pierrat, J. C., Mustin, C., & Frey-Klett, P. (2007). Effect of the mycorrhizosphere on the genotypic and metabolic diversity of the soil bacterial communities involved in mineral weathering in a forest soil. *Applied and Environmental Microbiology*, *73*, 3019–3027.
- Uroz, S., Calvaruso, C., Turpault, M. P., & Frey-Klett, P. (2009). Mineral weathering by bacteria: Ecology, actors and mechanisms. *Trends in Microbiology*, *17*, 378–387.
- Uroz, S., Turpault, M. P., van Scholl, L., Palin, B., & Frey-Klett, P. (2011). Long term impact of mineral amendment on the distribution of mineral weathering associated bacterial communities from the beech *Scleroderma citrinum* ectomycorrhizosphere. *Soil Biology and Biochemistry*, *43*, 2275–2282.
- van Breemen, N., Mulder, J., & Driscoll, C. T. (1983). Acidification and alkalization of soils. *Plant and Soil*, *75*, 283–308.
- van der Heijden, M. G. A., Martin, F. M., Selosse, M.-A., & Sanders, I. R. (2015). Mycorrhizal ecology and evolution: The past, the present and the future. *The New Phytologist*, *205*, 1406–1423.
- Wallander, H., & Thelin, G. (2008). The stimulating effect of apatite on ectomycorrhizal growth diminishes after PK fertilization. *Soil Biology and Biochemistry*, *40*, 2517–2522.
- Wallander, H., Wickman, T., & Jacks, G. (1997). Apatite as a P source in mycorrhizal and non-mycorrhizal *Pinus sylvestris* seedlings. *Plant and Soil*, *196*, 123–131.
- Wanek, W., Mooshammer, M., Blöchl, A., Hanreich, A., & Richter, A. (2010). Determination of gross rates of amino acid production and immobilization in decomposing leaf litter by a novel <sup>15</sup>N isotope pool dilution technique. *Soil Biology and Biochemistry*, *42*, 1293–1302.
- Wang, Y., & Dai, C. C. (2011). Endophytes: A potential resource for biosynthesis, biotransformation, and biodegradation. *Annales de Microbiologie*, *61*, 207–215.
- Warscheid, T., & Braams, J. (2000). Biodeterioration of stone: A review. *International Biodeterioration and Biodegradation*, *46*, 343–368.
- Whiffen, L. K., Midgley, D. J., & McGee, P. A. (2007). Polyphenolic compounds interfere with quantification of protein in soil extracts using the Bradford method. *Soil Biology and Biochemistry*, *39*, 691–694.
- Wilson, D. (1995). Endophyte – the evolution of the term, a clarification of its use and definition. *Oikos*, *73*, 274–276.
- Wilson, G. W., Rice, C. W., Rillig, M. C., Springer, A., & Hartnett, D. C. (2009). Soil aggregation and carbon sequestration are tightly correlated with the abundance of arbuscular mycorrhizal fungi: Results from long-term field experiments. *Ecology Letters*, *12*, 452–461.
- Winkelmann, G. (2007). Ecology of siderophores with special reference to the fungi. *Biometals*, *20*, 379–392.
- Wright, S. F., & Upadhyaya, A. (1996). Extraction of an abundant and unusual protein from soil and comparison with hyphal protein of arbuscular mycorrhizal fungi. *Plant and Soil*, *198*, 97–107.
- Wu, Q. S., He, X. H., Zou, Y. N., He, K. P., Sun, Y. H., & Cao, M. Q. (2012). Spatial distribution of glomalin-related soil protein and its relationships with root mycorrhization, soil aggregates, carbohydrates, activity of protease and  $\beta$ -glucosidase in the rhizosphere of *Citrus unshiu*. *Soil Biology and Biochemistry*, *45*, 181–183.
- Xie, X., Huang, W., Liu, F., Tang, N., Liu, Y., Lin, H., & Zhao, B. (2013). Functional analysis of the novel mycorrhiza-specific phosphate transporter AsPT1 and PHT1 family from *Astragalus sinicus* during the arbuscular mycorrhizal symbiosis. *The New Phytologist*, *198*, 836–852.
- Young, I. M., & Crawford, J. W. (2007). Interactions and self organisation in the soil-microbe complex. *Science*, *304*, 1634–1637.
- Zhu, Y. G., Duan, G. L., Chen, B. D., Peng, X. H., Chen, Z., & Sun, G. X. (2014). Mineral weathering and element cycling in soil-microorganism-plant system. *Science China Earth Sciences*, *57*, 888–896.