Mineral weathering and element cycling in soil-microorganism-plant system

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Soil is an essential part of the critical zone, and soil-microbe-plant system serves as a key link among lithosphere, biosphere, atmosphere and hydrosphere. As one of the habitats with the richest biodiversity, soil plays a critical role in element biogeochemistry on the earth surface (weathered crust). Here we review the soil biological processes that are relevant to mineral weathering, element cycling, and transformation, with an emphasis on rock weathering mediated by soil microbes, plant root and the rhizosphere.

soil, plant, microorganism, geobiology

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Soil is a natural body that forms from the interaction of the atmosphere, lithosphere, biosphere, and hydrosphere. Its formation, development, and functions profoundly influence the sustainability of ecosystem. The unique characteristics of soil make it one of the key subjects of geology and biogeochemistry.

Critical Zone (CZ) is the near surface environment in which rock, soil, water, air, and living organisms have complex interactions and regulate the natural habitat. The soil biological system, containing plants (especially roots), microorganisms, and soil inorganic components, belongs to an important part of the Critical Zone. Within the soil system, complex interactions between soil biota and soil abiotic components (organic compounds, minerals, water and various ions) are developed. There exist many geochemical pro-

cesses in soil-plant systems, including the interaction of minerals and life, transformation and transportation of elements. In comparison to traditional soil science, modern geology pays more attention to the dynamics in biogeochemical processes, and highlights the biological driving force of various geochemical processes. The studies of soil-plant system with geobiological methods would greatly enhance our understanding of soil science and contribute to sustainable agriculture.

1 The effects of soil microbes on rock

1.1 Weathering of rock by microbes

The weathering of rock occurs when it is exposed to rain and oxygen or it experiences temperature variations. Rock weathering is a fundamental geochemical process on the

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surface of the earth (Barker et al., 1998). During the long geological evolution, rock on the surface of the earth disintegrated and broke down, becoming small grit or loose structure, i.e., weathering crust as the parent soil. Parent soil from rock weathering represents the initial stage of soil formation, gradually turning to the soil for plant growth. Microbes play a crucial role in soil evolution and formation due to their characteristics such as rapid growth, wide distribution, tremendous phylogenetic and metabolic diversity, and the strongest adaption and colonization to extreme environments. Nothing on the surface of earth is uncorrelated or unaffected by microbes. Numerous investigations demonstrate that mineral decomposition is quite different between the presence and absence of bacteria. The rate of mineral decomposition and rock weathering are virtually enhanced by the existence of microbes.

Rock weathering by soil microbes is achieved via the functions of their metabolic products, extracellular secretion, and redox exchange. The mechanisms are reviewed as the following aspects:

1.1.1 Acidification

Acidification on rock surface leads to the replacement of cations with protons. Fungi excrete citric acid, oxalic acid, and gluconic acid; bacteria excrete formic acid, acetic acid, lactic acid, succinic acid, pyruvic acid, and other types of organic acid. The alkali cations such as Na^+ , K^+ and Ca^{2+} on rock surface can easily release by exchange of those organic acids with protons. Minerals on the rock are dissolved under the acidic microenvironments induced by bacteria. Some organic acid molecules, i.e., citric acid, oxalic acid, and tartaric acid, prefer to chelate metal ions (Fe, Al, Cu, Zn, Mn, etc) by forming strong chemical bonds, and thus the chelating effect dramatically increases the mobility of these elements (Xiao et al., 2012).

1.1.2 Chelation reactions

Microbes are adhered on the surface of the rock by forming biofilm or gel layer with excreted extracellular polymeric substances (EPS) as the mediator. EPS contains plenty of carboxyl groups, having high ability of adhesions to organic and inorganic ions. Some chemical bonds in crystal lattice of minerals were broken by the adhesion of EPS, improving weathering of minerals (Uroz et al., 2009). Studies show that silicate weathering by bacteria has a strong relationship with extracellular metabolites such as EPS or low molecular weight organic acid (Bennett et al., 2001). The formation of co-complexes of bacteria and minerals by chelating reaction enhanced the dissolution of silicate.

1.1.3 Redox reactions

As an engine of mass circulation in soil and mineral weathering, the cycling of elements on earth has a direct relationship with redox reactions. Oxidation-reduction reactions are derived mostly by organisms, especially microbes, although

they could occur automatically. Microbial respiration is a substantial redox reaction, which occurs not only intercellular but also extracellular. Mineral weathering can be improved by oxidation-reduction of microorganisms. For example, in order to obtain enough phosphate for growth, microbes weather Fe-P or Al-P minerals via redox reaction. The dilution of phosphate from minerals is utilized to support microbial growth (Bennett et al., 2001). Microorganisms gain their energy for growth by coupling the reduction of metals in the minerals as terminal electron acceptor and oxidation of ambient organic compounds as electron donor (Weber et al., 2006).

1.2 Microbial Fe oxidation and reduction

The redox reaction mediated by microbes is a typical process of soil formation and evolution. Iron is the most abundant transition element with 5.1% chemical abundance in the earth crust. Fe minerals are rich in soil environment, such as Fe oxides, Fe carbonates, Fe silicates and Fe sulfides (Zhao et al., 2002). As an essential nutrition element for most prokaryotes and all eukaryotes, iron participates in various physiological processes of living microbes. In order to obtain sufficient iron from minerals to support their growth, microorganisms evolved several kinds of pathways to oxidize or reduce iron in the environment. Iron redox in rock has great impacts on rock weathering and other geochemical processes in soil, e.g., decomposition of organic matter, dissolution and erosion of minerals, formation of geological minerals, and mobilization and fixation of metal ions (Weber et al., 2006).

Iron-reducing bacteria are distributed widely in the soil environment. The best studied iron-reducing bacteria are *Geobacter* and *Shewanella*, both of which belong to the gamma Proteobacteria. These dissimilatory iron-reducing bacteria can reduce iron oxides through various strategies. Three primary strategies have been proposed to facilitate the electron transfer between microorganisms and solid Fe(III) oxide surfaces. (1) Direct contact of bacteria with the iron oxide surface, where electrons are directly transferred from cells to solid iron minerals through the redox proteins in the cell membrane. (2) Soluble endogenous or exogenous chemicals such as humic acid, quinoline, phenazine, and riboflavin, which serve as an electron shuttle to mediate electron transfer to solid-phase Fe(III) oxides. These shuttles are able to deliver electrons to minerals within a short distance due to the low diffusion efficiency (Lovley, 2006). (3) The production of nanowires (conductive extracellular appendages) can facilitate electron transfer to long-distance targets, even conducting interspecies electron transfer and coupling two different metabolism systems (Malvankar and Lovley, 2012). During the reduction of iron oxides, the secondary minerals are formed concomitantly. Ferrous minerals such as vivianite ($\text{Fe}_3(\text{PO}_4)_2$), siderite (FeCO_3), and Fe(II)-Fe(III) oxides such as magnetite (Fe_3O_4) are the most commonly

observed secondary minerals in soil, whose formation is facilitated by redox bacteria (Borch et al., 2010). For example, during the reduction of nontronite by *Shewanella* species, electron shuttle is excreted and transfers montmorillonite to illite (Liu et al., 2011; 2012). The reduction of iron oxides also can release other ions (phosphate and arsenate), which tend to be absorbed or co-precipitated on the surface of iron minerals (Huang et al., 2012; Wang et al., 2009a; 2009b).

Both aerobes and anaerobes are able to oxidize Fe(II) ions. In a neutral pH environment, ferrous ions can be oxidized by aerobes and oxygen. In anaerobic or acidic environment, microorganisms play a key role in Fe(II) oxidation. The mechanisms of Fe(II) oxidation by bacteria in anaerobic environments remain unclear. The main microbial communities involved in Fe(II) oxidation are aerobic acidophilic and neutrophilic iron oxidizing bacteria, phototrophic bacteria, and nitrate dependent iron oxidizing bacteria. In anoxic environments, microbial Fe(II) oxidation has been demonstrated to couple with the reduction of nitrate, perchlorate or chlorate. Fe(II) oxidation forms Fe(III) hydroxides which coprecipitate with phosphate, decreasing the phosphate mobility (Lake et al., 2007). The formation of vivianite and Fe(II)-phosphorus minerals also fix the bioavailability of phosphate.

The processes of iron redox by microbes are often accompanied with the immobilization or mobilization of heavy metals. The mobility of heavy metals was reduced by co-precipitated Fe(II) oxidation (Richmond et al., 2004) or absorbed on the surface of secondary iron minerals. Recent studies have confirmed the coupled mechanism of nitrate-iron-arsenic reaction (Chen et al., 2008; Hohmann et al., 2009). During the processes of iron oxidation, arsenite is oxidized to arsenate, and then absorbed on the surface of generated iron oxides (Wang et al., 2011). Some bacteria, such as *Dechlorosoma suillum* PS, can generate different iron oxides when treated with different Fe(II) oxidation rates. U(VI) and Co(II) ion were found to also have the ability to be absorbed on iron oxide surfaces (Lack et al., 2002). Therefore, Fe redox microorganisms significantly contribute to Fe(II) oxidation or coprecipitation with Fe(III) minerals, and have a significant influence on the fate of heavy metals. The microbially mediated iron redox cycle coupled with the formation and transformation of Fe, P and As minerals is shown in Figure 1.

2 The interactions between soil and root

As early as 1845, Ebelmen speculated that organic acids secreted from plant roots promote the weathering of soil minerals. Until recently, interactions between soil and plants have gradually attracted attention from geologists. There are various interactions between soil and plants, which are detailed below.

2.1 The role of plants in mineral weathering and soil formation

The growth and reproduction of microorganisms on the surface of soil parent materials gradually accumulate organic matter and nitrogen in the parent materials. Microbe and lower plants can produce large amounts of secretions. These secretions play a pioneering role in soil formation, such as eroding rock, accelerating the process of rock weathering, changing the properties of the parent material, and improving soil fertility. With the action of secretions over periods of time, shallow original soil is gradually formed. Biological growth on the surface of original soil can prevent nutrient leaching during weathering processes, so that the nutrients are preserved in the original soil. With large populations of moss, the interaction between organisms and rock is increasingly strengthened, and the original soil constantly develops, which provides the possibility for higher plant growth. The growth of higher plants on original soil accelerated the process of soil formation, and prompted the formation and differentiation of mature soil. The role of organisms on the transformation process from rocks, to parent material and eventually to soil, can be summarized as follows:

Plants play a crucial role in the processes of soil formation and development. Pedogenesis is actually the interactive process of geological cycling of plant nutrients (geological leaching processes) and biological small cycle (bio-accumulation process). During the geological cycle, the weathered surfaces of rocks release a variety of nutrients for plant growth. During the biological small cycle, plants take up nutrients selectively from parent materials, water and atmosphere, and make organic matter through photosynthesis. The organic matter is then returned to the soil as a form of leaf or root residual. Organic matter decomposed from plant litter forms the most important component of soil "humus", which promotes the formation of soil fertility. Geological cycling prepares the conditions for the formation of soil, and soil biological small cycle provides humus for soil. Biological small cycle depends on the geological cycle, while without the biological cycle, parent material cannot form fertile soil.

2.2 Influence of plant roots on soil development

Nutrient cycling between pedosphere and biosphere is an

Figure 1 The microbially mediated iron redox cycle.

important aspect of the interactions between soil and plant. Plants exert significant impacts on the cycle of mineral nutrients between soil and biosphere. Based on annual mass balances, White et al. (2012) analyzed the mineral nutrient cycling between the biotic/abiotic interfaces. They found the impacts of plant on the cycling of different mineral nutrients were different. Above the biotic/abiotic (A/B) interface, K and Ca exhibit seasonal variability with plants, whilst there was no seasonal variability beneath the A/B interface, indicating closed nutrient cycling within the root zone. As for Mg, because of lower plant nutrient requirements, it exhibited downward leakage from biotic to abiotic zone. In addition, plant roots have a major impact on the formation and differentiation of soil. For example, plants can maintain or change the physical structure and chemical composition of soil. Plants have an irreplaceable function on maintaining the ecological functions and agricultural production of pedosphere.

(1) Plant roots play an important role in soil and water conservation, especially in mountainous and desert areas. Plant root systems can greatly increase the anti-erosion ability of soil, which can reduce or prevent soil loss, weathering or landification. In addition, living roots can provide secretions, and dead roots can provide organic matter for soil, which serve as a cementing agent for soil pellets. Moreover, the penetration and winding of fibrous root system can also greatly enhance soil and water conservation.

(2) Plants can shade soil, keeping soil at low temperature, thus slowing evaporation; conversely, through transpiration, plants can also promote soil moisture loss, regulating water

cycling between pedosphere and atmosphere. Plants can synthesize and secrete new chemicals, which can break or form soil particles, thus changing the soil structure. On the other hand, soil properties can significantly affect the growth of plants, such as soil density, clay, chemical composition, pH, temperature, and humidity, etc.

(3) Plant taproots can penetrate several meters in soil, through different layers of the soil, while fine roots can spread extensively in the shallow soil layer. Plant taproots and fine roots can greatly facilitate material exchange and water cycle in the soil, both longitudinally and horizontally.

(4) Plants can affect soil organic carbon and nitrogen contents. Plants can make organic carbon through photosynthesis by using solar radiation. After plants die, plant litter accumulates at the soil surface. Through the transformation and decomposition by microorganisms, the organic carbon in plant litter is returned to the soil. The influence of different vegetation on soil organic carbon content is different. Detwiler et al. (1986) found that modifying forest to cropland resulted in 40% loss of average organic carbon, whereas modifying forest to grassland resulted in 20% loss of organic carbon. Symbiotic nitrogen-fixing legume roots can fix nitrogen in the air and thus increase the nitrogen content of the soil.

(5) Plants exert a significant effect on mineral release. Root exudates of low molecular weight compounds, such as monosaccharide, amino acids, organic acids and phenols, etc., can greatly mobilize nutrients in the rhizosphere, including Ca, P, K, Se, etc. Under P deficiency, plants can increase the secretion of low molecular weight organic acids,

and promote the dissolution of poorly soluble soil phosphorus-containing compounds, releasing phosphate and improving P supplying status of the rhizosphere, thereby increasing crop yields and improving the quality of agricultural products. For example, Johnson et al. (1996) found that under P deficiency, white lupin (*Lupinus albus* L.) developed clustered tertiary lateral roots, which exuded large amounts of citric acid. On one hand, citric acid can reduce the pH of rhizosphere, and thus increase phosphate desorption from goethite, kaolinite and other minerals. On the other hand, citric acid can counteract with Al, Fe, Ca, Zn, and other metal ions, and thus greatly increase the release of phosphate from Al-P, Fe-P, Ca-P or Zn-P complexes, thereby increasing phosphorus availability in the rhizosphere (Gardner et al., 1983; Dinkelaker et al., 1989). Houben et al. (2012) demonstrated that root activity of Italian ryegrass (*Lolium multiflorum* Lam.) accelerated the weathering of smithsonite (ZnCO_3), and promoted the release of Zn. Chardot-Jacques et al. (2013) showed that the growth of nickel hyperaccumulator (*Leptoplax emarginata*) increased chrysotile dissolution by more than 2-fold, which promoted the release of nickel. Salehi and Tahamtani (2012) found that the growth of wheat and oats can promote Mg release from Mg-rich mineral palygorskite, providing sufficient Mg for the growth of plants supplied with Mg-free nutrient solution. Christophe et al. (2013) studied the effect of Scots pine roots on the dissolution of apatite grains. They found that Scots pines significantly increased the release of Ca, P, As, Sr, Zn, U, Y, and rare earth elements such as Ce, La, and Nd from apatite, compared to control abiotic treatment. Scanning electron microscopy observations confirm traces of apatite dissolution in contact of roots. In addition, most dissolved elements were taken up by Scots pine roots, i.e., approximately 50% of Ca, 70% of P, 30% of As, 70% of Sr, 90% of Zn, and 100% of U, Y, and rare earth elements.

3 Soil-microorganism-root interactions

3.1 Mycorrhizal symbiosis

Generally there are no pure roots, as plant roots are commonly associated with soil microorganisms. Mycorrhizal symbiosis is a representative association formed between plant roots and soil fungi. Among different fungal groups, arbuscular mycorrhizal fungi (AMF) are the oldest symbiotic fungi, which first appeared in the Devonian about 400 million years ago, almost simultaneous with the emergence of terrestrial plants (Remy et al., 1994). By contrast, ectomycorrhizal fungi (EMF) together with angiosperms first appeared in the Cretaceous about 100 million years ago (Moyersoen et al., 2006). In total, more than 90% of plant families in the world form symbiosis with either AMF or EMF (Smith and Read, 2008). Many studies have demonstrated that mycorrhizal fungi play an important role in both mineral weathering and biogeochemical cycling of mineral

nutrients.

Taylor et al. (2009) proposed five mechanisms underlying the mycorrhizal effects on mineral weathering processes: (1) Dissolution of minerals by secretions such as H^+ and low molecular weight organic chelators; (2) Respiration of plant roots and mycorrhizal fungi increases CO_2 pressure in soil solution; (3) Decomposition of organic matter increases the concentration of high molecular weight organic acids and low molecular weight organic chelators in the soil solutions, which are further used by heterotrophs via fuel respiration and thus returning base cations from the biota to the soil solution; (4) Plant transpiration increases the water flow bearing base cations and other nutrients to plants, and influences soil water residence times and rainfall on a regional scale; (5) The sorption of soil particles by plant roots and mycorrhizal hyphae reduces soil erosion, thus allowing continued soil development. These five processes involve both AMF and EMF; however, different mycorrhizal types function differently in mineral weathering.

3.2 AMF

Unlike EMF, it is commonly recognized that AMF are not directly involved in mineral weathering; however, there is some evidence showing accelerated mineral weathering by AMF. AMF can influence mineral weathering via respiration and proton release, and influence soil pH by acquisition of nitrate and ammonium (Johanson et al., 1993; Bago et al., 1996). Besides, extraradical mycelium of AMF can effectively bind soil particles and affect soil aggregation (Tisdall and Oades, 1982; Six et al., 2004; Smith and Read, 2008). Glomalin related proteins secreted by AMF (Wright and Upadhyaya, 1996) may play important roles in mineral weathering by increasing the amount of soil aggregates, or enhancing biological and chemical weathering between small soil particles. Furthermore, glomalin related proteins could also form an aquifuge on the surface of minerals to block interactions between water and minerals (Kleber et al., 2007).

Both lab experiment and field trials supported silicate and carbonate dissolution by AMF (Glowa et al., 2003; Kollo and Claeys, 2005). Sanz-Montero and Rodríguez-Aranda (2012) found that AMF can weather biotite, through which they can obtain mineral nutrients. Arocena et al. (2012) also found that inoculation with AMF could accelerate biotite weathering and further form low-potassium clay minerals. All in all, AMF influence mineral weathering mainly by modifying soil chemo-physical properties, improving plant mineral nutrition, growth and transpiration, and by regulating soil aggregation dynamics.

3.3 EMF

EMF can absorb nutritional elements from weathering rocks, including P from phosphate rocks (Finlay et al., 2009). Smit

et al. (2012) found that EMF-plant interactions enhanced weathering of apatite. EMF was also found to be sensitive to minerals enriched in Mg and K (Paris et al., 1996; Glowa et al., 2003; Arocena et al., 2004). The EMF weathering of minerals might have a profound influence on the growth of plants and the cycling of base cations in soil ecosystem. Jongmans et al. (1997) observed large amounts of fungal hyphae in pores of feldspars and hornblendes, which were presumably formed by secretion of organic acids from hyphal tips of mycorrhizal or saprotrophic fungi. Usually, these low molecular weight organic compounds do not decrease soil pH in the rhizosphere, but can potentially accelerate mineral weathering through chelation (Kinraide 1991; Ochs, 1996).

The frequency of micro tunnels in mineral grains can be used as a tool to quantify the intensity of EMF weathering. Hoffland et al. (2003) observed a positive correlation between EM root tip density and tunnel frequency, suggesting that EMF might involve the formation of mineral tunnels. Van Schöll et al. (2006a; 2006b) provided further evidence that EMF can accelerate mineral weathering through exudation of organic anions, but their contribution to mineral weathering at ecosystem level remains unknown. Van Breemen et al. (2000) estimated the contribution of EMF to mineral weathering via mineral tunneling alone to be 50%. However, Sverdrup et al. (2002) estimated the contribution of organic ligands to total mineral weathering to be 15%, whereas the contribution of all soil biota could be maximally 2%. These studies implied the importance of using improved methods for evaluating the EMF capacity in mineral weathering.

Smits et al. (2005) quantified the contribution of EMF mineral tunneling to total weathering via image analysis, and found that mineral tunneling accounted for less than 0.5% of total feldspar weathering in the upper 2 cm of the mineral soil. Therefore, tunneling is likely only one part of EMF weathering. Subsequent studies by Smits et al. (2012) showed significant surface weathering through oxalate exudation by EMF, and the intensity of surface weathering was one order higher than weathering through tunneling. Modeling predication also indicated that EM exudation of oxalate alone could account for 3% of microcline surface (2 cm) weathering and 4% of plagioclase surface (2 cm) weathering. In addition, EMF can also exude protons and other low molecular weight organic compounds such as citrate which could stimulate weathering. Under nutrient deficiency, ECM could produce more exudates, which could subsequently enhance mineral weathering. Van Hees et al. (2006) found that EMF induced weathering of potassium-containing minerals was 3–10 times faster compared to natural weathering.

Not all EMF show the same ability to weather minerals, and various factors can affect mineral weathering processes. Van Schöll et al. (2006b) found that the ability of EMF in mineral weathering depended on the fungal species. Ability

of EMF to acidify substrate varies with species (Casarin et al., 2003; Rosling et al., 2004) and mineral type (Rosling et al., 2004). EMF species also varies in organic ligand exudation (Casarin et al., 2003) and differs in their colonization ability (Dickie et al., 2002; Rosling et al., 2003). Under field conditions, individual trees normally support different EMF assemblages, and their P demand increases with increasing EMF diversity (Baxter and Dighton, 2001). Therefore, weathering capacity for individual EMF species identified under lab conditions may not reflect the overall weathering potential by EMF assemblages under natural conditions.

In conclusion, compelling evidence has shown that EMF is a major contributor to mineral weathering. EMF can affect mineral weathering through the exudation of organic compounds, formation of mineral tunneling, and also plant growth and respiration. Potential mechanisms underlying the mycorrhizal effects on mineral weathering processes are summarized in Figure 2.

3.4 Soil structure-biota interaction

Soil structure is a key property of soil fertility, determining the retention and transport of water, gas and solute in soil, and providing the habitat of plant growth and soil organism activity. Good soil structure can improve soil resistance to erosion and enhance soil productivity. Soil structure formation and stabilization interrelate with soil biological, chemical and physical processes. Of them, the soil structure-biota interaction has received more attention.

Biotic factors of soil structure formation involve plant roots, soil fauna, and microbes, while abiotic factors include tillage, wetting and drying cycle, and freezing and thawing cycle. Soil structure is also dependent on intrinsic soil properties (i.e., soil texture, clay mineral, and Fe/Al oxides) and on external stresses (i.e., temperature and rainfall) (Díaz-Zorita et al., 2002; Bronick and Lal, 2005; Six et al., 2004). According to the importance of biota at different scales, Tisdall and Oades (1982) proposed an aggregate hierarchical concept. In this concept, plant roots, fungi, microbial and plant derived polysaccharides are the main binding agents of macroaggregates (>250 μm), while humified organic matter and polyvalent metal cations are the main agents of microaggregates (<250 μm). This model has been verified in soils of various temperatures in the last three decades, but not in tropical and subtropical soils rich in sesquioxides. Due to the difficulty in extraction of plant and microbial derived exudates, their role in soil structure formation was limited to simulation experiments in laboratory (Czarnes et al., 2000; Peng et al., 2011). Applying to different analogues of biotic exudates, Peng et al. (2011) found that soil aggregation depended much on their physical features (i.e., viscosity and surface tension). Xanthan with highest viscosity increased the soil mechanical strength most, whereas lecithin with the lowest surface tension improved aggregate stability through the enhanced water

Figure 2 The six key mechanisms of mineral weathering induced by plants and their mycorrhizal fungi. I: Exudates include reactive species such as H^+ and low molecular weight organic chelators. II: Respiration increases the PCO_2 of the soil solution. III: Decomposition increases the concentration of high molecular weight organic acids and low molecular weight organic chelators in the soil solution, fuels respiration by heterotrophs, and returns base cations from the biota to the soil solution. IV: Evapotranspiration increases the flow of water bearing base cations and other nutrients to plants, and affects soil water residence times and the amount of rainfall on a regional scale. V: Small tubular pores in the minerals formed by root tips or extraradical hyphae. VI: Erosion is reduced due to the binding of soil particles by roots and mycorrhizal hyphae, allowing continued soil development.

repellency. The roles of polygalacturonic acid and dextran on aggregation were moderate between the two exudates as mentioned above. Relative to bacteria, fungi, particularly arbuscular mycorrhizal fungi (AMF), have received more attention on soil structure. Fungi promote soil aggregation through physical entanglement. On the other hand, the water repellency of mycelium of fungi can maintain water-stable aggregate longer (Rillig and Mummey, 2006). Plant roots have three roles on soil structure. Firstly, root growth and penetration may compact soil structure; secondly, plant roots intensify wetting and drying cycles and consequently promote soil structure formation; thirdly, the decay of plant roots creates new pores. Burrowing activity of macrofauna forms macropores network, improving aeration and water transport. Earthworm cast and termite nest are sequester of C and N and stabilize aggregates. In brief, the roles of biotic factors on stabilizing soil structure are scale-dependent. Exudates from bacteria, fungi and roots generally form aggregate scale, whereas the roots penetration and macrofauna burrowing impact macropore structure at core scale. A number of biotic factors on aggregation have been reported in previous studies; however, their interaction is scarce. How to develop a feasible methodology to isolate their contributions to soil structure needs our further efforts. The knowledge of the feedback of soil structure on diversity and activity of microbes is also poor.

Soil structure is a dynamical soil feature. Change in soil structure may be faster and greater than any other soil prop-

erty. Until now, the dynamics of soil structure has concentrated mainly on aggregate scale, which is often indicated by aggregate water stability. For example, Abiven et al. (2008) demonstrated the temporal change in aggregate stability during the decomposition of soil organic matter. Plaza-Bonilla et al. (2013) reported seasonal change in aggregate stability under different fertilization practices. These works may help us understand the dynamics of aggregate stability, but cannot explain what happens between aggregates, and how soil fauna and roots impact soil structure (Bronick and Lal, 2005). We further do not know how aggregates form larger ones and the turnover of aggregates due to the limited knowledge of aggregation pathway. The change of soil structure at core scale should be faster and more intensive than the structure at aggregate scale. Relative to aggregate structure, the soil structure should also be more sensitive to climate change and human activity. Owing to the opacity of soil, however, we have little knowledge of three-dimensional soil structure in solid phase and/or in pore phase. As Young and Crawford (2004) pointed out, the quantification of soil structure and its interaction with biotic factors is still a challenge.

4 Perspectives

The weathering of minerals involves comprehensive processes. The study of mineral weathering by microbes needs

to be strengthened by combined approaches in mineralogy, biology, and chemistry, especially in the following aspects.

(1) Microbial mineral weathering is a key process and is widespread, not only because of its ecological significance but also because of its effects on human health, as well as architectural and artistic patrimony. From a mechanistic point of view, we still know very little about the microbial genes, enzymes and metabolites involved in mineral weathering, especially the mechanisms and processes of electron transfer between microbes and minerals. Studies regarding *in situ* characterization of mineral weathering need to be improved.

(2) Most research about the mineral weathering by plant is still qualitative. Quantitative analysis is scarce and usually conducted at laboratory scale. How much plants contribute to the whole weathering process in comparison to physico-chemical and microbial weathering is still unclear. New techniques need to be developed to investigate the efficiency of weathering by plant roots *in situ* and the effects on the biogeochemical cycling.

(3) The interactions between soil, microorganisms and plant roots make the soil weathering process more complex. Plants, mycorrhizal fungi, and bacteria interact with each other. The next step should be to develop microcosm studies by taking into account all these factors using *in situ* measurements and imaging, therefore providing new insights about the processes at micro-scale.

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