

# Chapter 3

## The Biological Path to Rock Breakdown

**Abstract** Biological weathering is exerted through both, biophysical and biochemical corridors. Considering the recent scientific advances in applied microbiology, it is now possible to attain a more accurate view on the role of biology in the breakdown of minerals and rocks in the Earth's material cycle. Roots, lichens, mosses, algae, and bacteria are significant agents in mineral and rock breakdown, even exerting in some cases a comminuting action that promotes further the ensuing bio- or geochemical effect. Microorganisms tackle such action by producing aggressive substances (e.g., organic acids) that dissolve minerals and produce secondary solid and soluble phases which participate, through their riverine exportation to world oceans, in the process of continental denudation. The role of bacteria in dissolving metal sulfides, as in tailing impoundments resulting from mining operations, is particularly important to contribute to the understanding of the interaction of biota with the inorganic realm.

**Keywords** Biological weathering · Critical zone · Biophysical weathering · Biochemical weathering · Microbes · Bacteria · Lichens · Algae · Mosses · Fungi

### 3.1 Introduction

Weathering processes occur at the intersection of the biosphere with the remaining Earth's spheres: atmosphere, lithosphere, and hydrosphere. This is the zone where rock meets life and it is increasingly known as the *critical zone* (e.g., Anderson et al. 2007). Therefore, the role of living organisms in the process of material breakdown is so characteristic that it must be recognized as a separate category, identifying biophysical and biochemical processes as accepted subdivisions. Decaying organic matter, plant roots, mosses, microbes (algae, fungi, lichens, and bacteria) are biological agents that actively participate in mineral and rock collapse (Fig. 3.1).

**Fig. 3.1** Rocks profusely colonized by lichens and moss at Wulaia Bay, Navarino Island (Tierra del Fuego, Chile,  $\sim 55^\circ$  S  $68^\circ$  W). Photograph by P.J. Depetris



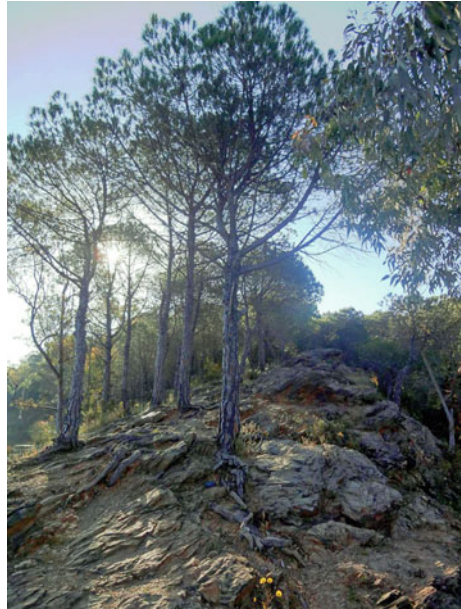
Two main pathways are used by living matter to support mineral and rock breakdown: they may apply physical stress through, for instance, the expansion and contraction of plants or roots, or they may produce substances such as carbon dioxide, several acids (inorganic or organic), complexing agents, protons, and electrons, all of which are part of their life processes.

### 3.2 Biophysical Weathering

Seedlings sprouting in crevices and plant roots may exert physical pressure as well as providing a pathway for water infiltration. Frequently expressed ideas imply that, as roots grow, they press against the rock and put stress on the joints they are growing in. Over time, this stress breaks rocks apart. Some authors, however, argue that the **effect of roots** is far from efficient in as much as effective tensile stress is set up by radial pressure which, in the case of roots is only 1/3–1/4 of the axial amount, typically of the order of three MPa, only sufficient to fracture some weak rocks (Bland and Rolls 1998). Other authors have demonstrated that some tracks and holes in minerals that have been mistakenly attributed to the action of roots were, in fact, produced by chemical dissolution mechanisms (Sverdrup 2009). At any rate, the mechanical role of roots appears as still open to discussion although visual evidence appears to support their significance (Fig. 3.2).

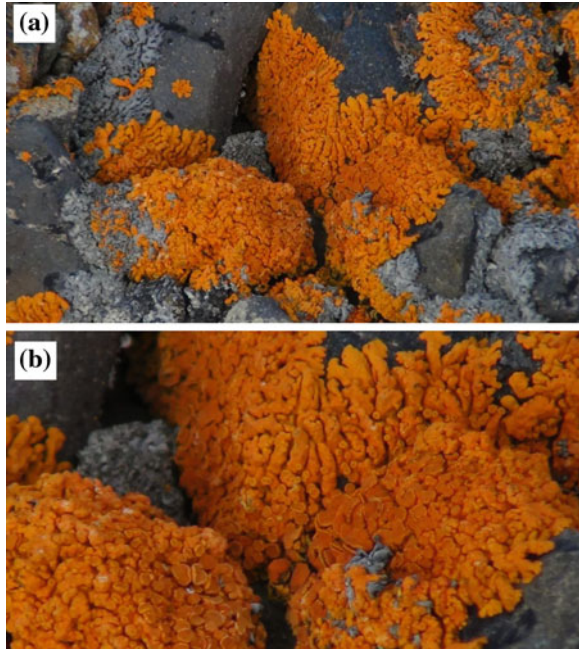
The mechanical effect of roots seems to be more effective in regolith, soils, and unconsolidated sediments. Li et al. (2006) have shown that in China's loess plateau, plant roots have stronger effects on soil physical properties than on chemical characteristics; the role of plant roots in controlling soil weathering and leaching increases in the following order: infiltration enhancement > increased flow of bioactive substances > stabilization of soil structure.

**Fig. 3.2** Trees growing in schists and phyllites from “Pizarroso-Cuarcítico” Devonian Group in Sotiel Coronada, Huelva, Spain. Photograph by K.L. Lecomte



**Lichens** are composite organisms, consisting of fungi and algae harmonically growing together (e.g., Purvis 2000). Lichens are capable of physically breaking down rocks, by the penetration of hyphae (whose growth-induced stress may exceed the tensile strength of most rocks), and by increasing their water content (typically between 150 and 300 %), thus reaching damaging levels of tensile stress by volume increase (Chen et al. 2000). The physical effects of lichens are also reflected by the mechanical disruption of rocks caused by expansion and contraction of lichen thallus, and the swelling action of organic and inorganic byproducts originating from lichen activities (Chen et al. 2000). Lee and Parsons (1999) have shown the significant weathering effect of the crustose lichen *Rhizocarpon geographicum* by both, biomechanical and biochemical means, on a Lower Devonian granite. Biomechanical weathering is mediated by fungal hyphae that enter the rock via mineral boundaries at a rate  $\geq 0.002\text{--}0.003 \text{ mm y}^{-1}$ . Once inside the rock, hyphae make use of intragranular pores along weak planes in biotite, alkali, and plagioclase feldspar. Biotite grains exposed at the lichen–granite interface have been fragmented by biomechanical action in less than 122 years. After extensive biomechanical weathering (e.g., outcrop surfaces exposed for  $\sim 10$  Kyr), sub-mm sized fragments of biotite (which show the clearest evidence for biochemical weathering) and plagioclase feldspar abound in the lower parts of the lichen’s thallus (Lee and Parsons 1999). The relative significance of weathering by lichens appears as substantial in extremely cold environments, like in Antarctica (Fig. 3.3), where they act mechanically and chemically (Jie and Blume 2002).

**Fig. 3.3** **a** Lichens growing on pebbles and cobbles in a large ice-free area in the James Ross Island (Antarctica's NW). **b** Detail of **a**. Photographs by K.L. Lecomte



The effectiveness of **algae** as agents of mechanical weathering also shows significance in cold climates. Studies have revealed that the algal mucilage that surrounds algal cells would incorporate a large quantity of water during wet periods (e.g., 20 times the volume of the dry state), thus producing an expansionary force sufficient to separate already-weakened rock pieces. Observations performed on a number of *nunataks* of the Juneau Icefield in Alaska indicate that algae play a significant role in the breakdown of granitic rock. Data gathered at Juneau by Hall and Otte (1990) suggested that the average mass of material loss could be as high as  $562 \text{ g m}^{-2} \text{ yr}^{-1}$ .

To conclude with the biophysical aspects of weathering, it is worth mentioning that an experimental approach has shown that **microbes** promote physical weathering. The use of a combination of physical and biological processes in several experiments with building stones has shown that the extent of decay in limestone was significantly enhanced when compared with the physical or biological agents acting alone (Papida et al. 2000).

### 3.3 Biochemical Weathering

The zone dominated by plant roots is referred to as the *rhizosphere* (probably the most effective weathering microenvironment), where **roots** may bring about material breakdown, particularly through biochemical paths. Roots are systems

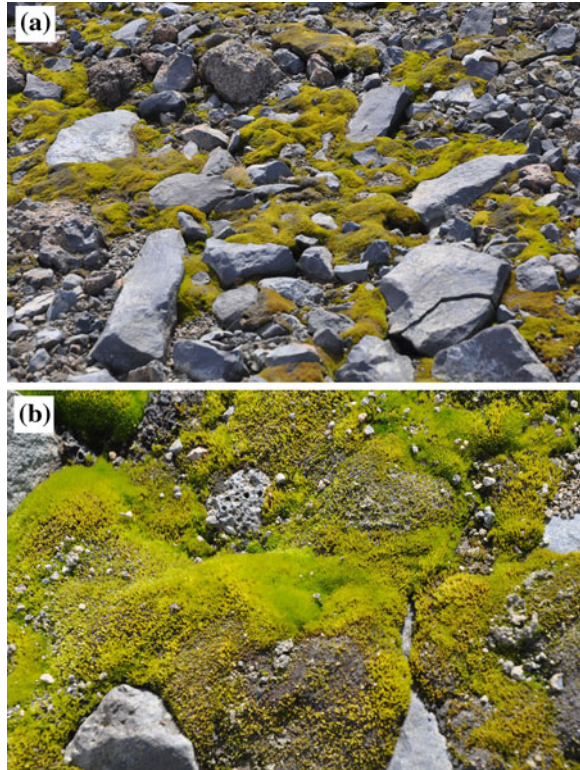
that, as part of a complex life-sustaining process, emit and absorb components. The tip of the main root releases organic acids of low-molecular-weight (e.g., citric, lactic, and tartaric acid), along with protons and electrons, which contribute to mineral decay through the delivery and mobilization of iron and aluminum in chelate-like compounds. Experimental work using polished marble tablets has shown that root etching occurs across grains and at grain boundaries, and emerges as more severe at the junction of root networks (Mottershead et al. 2003). More recently, Calvaruso et al. (2006) have shown that on the basis of column experiments with a quartz-biotite substrate, for example, pine roots significantly increased biotite weathering by a factor of 1.3 for magnesium and 1.7 for potassium. They demonstrated as well that the inoculation of *Burkholderia glathei* significantly increased biotite weathering by a factor of 1.4 for magnesium and 1.5 for potassium in comparison with the pine alone.

In the Ouachita Mountains (Arkansas, USA.), Phillips et al. (2008) gathered evidence on the rapid initial rate ( $5\text{--}10\text{ mm yr}^{-1}$ ) of soil production, which is facilitated by aggressive vegetation colonization, along with a favorable regional climate and sediment accumulation. Plant establishment (i.e., it takes  $<10$  yr of pedogenic maturation in the case of trees) accelerates local weathering rates.

After the stage of physical weathering (i.e., disaggregation and fragmentation) of the rock in immediate contact with **lichens**, the ensuing chemical weathering is fundamentally due to the excretion of organic acids. As a result, many rock-forming minerals exhibit extensive surface corrosion. Moreover, the specific literature points out that oxalic acid and so-called “lichen acids” (e.g., physolic and lobaric acids) are considered biomolecules particularly active as weathering agents; chelation of metallic cations is also important (e.g., Chen et al. 2000). In regions with extreme climate, such as the Qinghai-Tibet Plateau, the gathered evidence indicated that the assumed dominance of physical weathering processes on granite, such as freeze-thaw was in fact, attributable to the action of lichens (Hall et al. 2005). It is also important to underline that the effectiveness of lichens as biochemical weathering agents appears as significant on different rock substrates. Besides granite, lichens have also proved successful as weathering agents on Lanzarote’s lava flows (Stretch and Viles 2002), on a mica-schist mini-watershed ( $<1\text{ m}^2$ ) (Aghamiri and Schwartzman 2002), and on a Calabrian granodiorite from the Sila uplands (Scarciglia et al. 2012). Chen et al. (2000) have produced an interesting review, mainly on the effect of lichens on different rock substrates and on the weathering byproducts that they generate. Almost concurrent, Adamo and Violante (2000) published an extensive review contributing to the knowledge on the characteristics of lichen-induced weathering and, also, on the likely formation of oxalate/“lichen acid”-derived minerals.

The role of **fungi** in the weathering processes occurring in forest ecosystems is also well-established, where biological activity in general and fungi in particular are significant drivers of organic matter decomposition, cycling of nutrients, mineral formation, and metal dynamics. The mineral soil horizons of boreal forest are intensively colonized by mycorrhizal mycelia (forming symbioses with forest trees) which

**Fig. 3.4** **a** Antarctic volcanic rocks blanketed by mosses (James Ross Island). **b** Blown up detail of **a**. Photograph by K.L. Lecomte

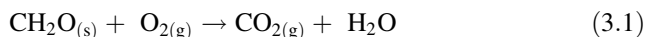


transfer organic metabolites and protons to mineral surfaces, resulting in mineral dissolution and mobilization of nutrients and metal cations (Finlay et al. 2009).

Although the weathering effect of **mosses** has been less investigated than the one exerted by lichens, algae, or fungi, it is now clear that their function in dissolving rocks is significant nowadays and was even more important in the geological past. Lenton et al. (2012), for example, probed into their role during the Ordovician, when nonvascular plants appear to have affected the weathering rate and, hence, climate, significantly lowering ambient temperature. The weathering “amplification factor” due to the presence of moss was significant for Al, Ca, Fe, K, and Mg from silicates. The spreading out of nonvascular land plants during the Ordovician accelerated chemical weathering and may have drawn down enough atmospheric CO<sub>2</sub> to activate the growth of ice sheets. There are recent case studies that have looked into the current role of nonvascular plants and lichens in their relative significance in the control of weathering in cold climates (e.g., Zakharova et al. 2007; Guglielmin et al. 2012). Figure 3.4 shows mosses growing on volcanic rocks in Antarctica peninsula.

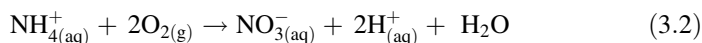
**Bacteria** are uni- or multicellular microscopic organisms that have been active in the Earth’s surface for perhaps 3,100 million years are found in both, aerobic and anaerobic environments. They may be *heterotrophic* (i.e., feed on organic

molecules), *autotrophic* (i.e., are sustained by simple inorganic compounds), or *mixotrophic* (i.e., use both nutrient sources). In biologically active soils,  $\text{CO}_2$  may be concentrated by 10–100 times the amount expected from equilibrium with atmospheric  $\text{CO}_2$  (i.e., almost 0.004 %), yielding  $\text{H}_2\text{CO}_3$  and  $\text{H}^+$  via dissociation. The result is a lowering of the pH of soil solutions (i.e., typically to 4 or 5) and the ensuing increase of weathering reactions through a biochemical pathway. In the following equations, organic matter is represented by the generalized formula for carbohydrate,  $\text{CH}_2\text{O}$ .



The respiration of soil organic matter has, as it will be seen in the next chapter, a major impact on the chemical weathering of minerals.

*Nitrification* is a substantial part of a larger chemical sequence known as the *nitrogen cycle*, and it is the general term to describe the conversion of ammonium ions (products of the bacterial processing of dead organic matter) to nitrites and nitrates. The significance of this process in biochemical weathering is that it involves the release of protons:



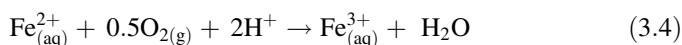
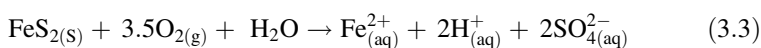
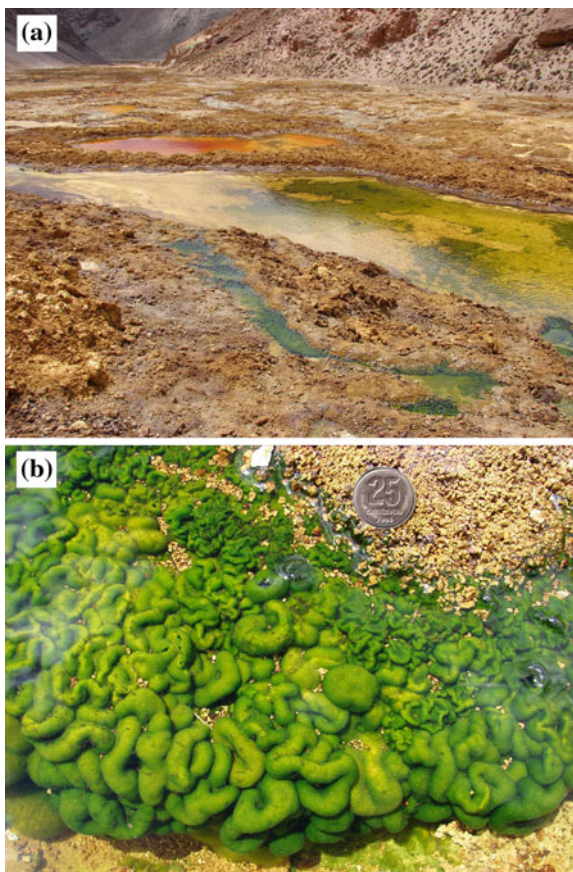
As a result of this bacteria-mediated reaction, two hydrogen ions are produced for every ammonium ion and acidification occurs, thus affecting the weathering rate.

Several laboratory experiments have been carried out to prove the occurrence of biologically-induced mineral dissolution. Ullman et al. (1996) obtained experimental evidence for silicate minerals dissolution mediated by microbes, proving that some microbial metabolites enhanced dissolution rates by a factor of ten above the expected nonbiological alteration. Barker et al. (1998) reported the increased release of cations from biotite (Si, Fe, Al) and plagioclase (Si, Al) by up to two orders of magnitude by microbial activity compared to abiotic controls. Song et al. (2007) analyzed the effect of *Bacillus subtilis* on granitic rocks, concluding that bacteria have a strong influence in the granite weathering by forming pits at as rate 2.4 times faster than bacteria-free specimen.

The role of bacteria in biochemical weathering may be emphasized further by mentioning their participation in the oxidation of metals, as it happens with sulfides when they are transformed into water-soluble metal sulfates. Oxidation happens at a slow rate in very acid waters; below pH 3.5, iron oxidation is catalyzed by the iron bacterium *Thiobacillus thiooxidans*. At pH 3.5–4.5 oxidation is catalyzed by *Metallogenium*. Clearly, acid conditions foster microbial alteration raising significantly their reaction rates when compared to nonbiological mechanisms. Figure 3.5 shows an acidic environment-type and the associated colonies of acidophilus bacteria and algae.

The oxidation of iron pyrite to ferric sulfate is an example of the above mentioned mechanism:

**Fig. 3.5** **a** Extreme acidic environment in Amarillo River (La Rioja, Argentina,  $\sim 29^\circ$  S  $\sim 67^\circ$  30' W). **b** Associated colonies of acidophilus algae and bacteria. Photographs by K.L. Lecomte



Bacteria use iron compounds to obtain energy for their metabolic demand [i.e., such as the oxidation of Fe(II) to Fe(III)]. Since these bacteria derive their energy from the oxidation of inorganic matter, they thrive where organic matter is rare or missing, using  $\text{CO}_2$  as a source of carbon. However, energy is not obtained efficiently from iron oxidation and approximately 220 g of  $\text{Fe}^{2+}$  must be oxidized to produce 1 g of carbon. It is not surprising then that large deposits of Fe(III) oxide develop in areas where iron-oxidizing bacteria endure.

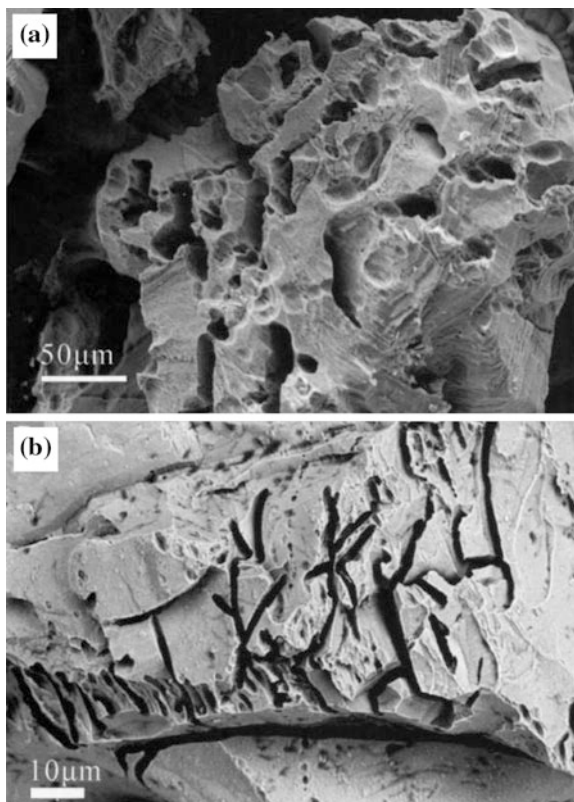
Investigations in acid mine drainage have produced a wealth of information on the interaction of metal sulfides and bacteria, where their relationships may be complex; Ehrlich (1996) reported several satellite microorganisms that live in close association with *Acidithiobacillus ferrooxidans*. More recent data (e.g.,



**Fig. 3.6** Scanning electron micrographs of corrosion etches on sulfide minerals caused by surface-attached *Acidithiobacillus ferrooxidans* cells.

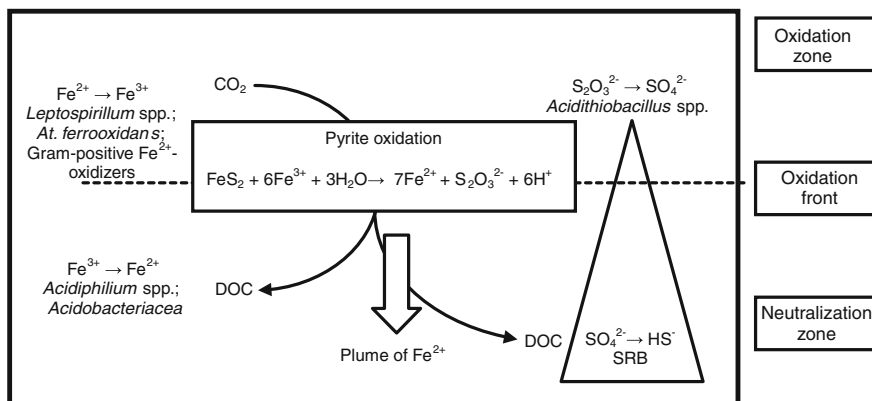
**a** Arsenopyrite particles bio-oxidized for 15 days.

**b** Broken surface of pyrite particles bio-oxidized for 36 days (Lu and Wang 2012). Reproduced with permission, Mineralogical Society of America



Halinen et al. 2009; Ziegler et al. 2009) show complex communities structures in pyrite oxidation and bioleaching operation (Fig. 3.6). It is nowadays recognized that complex ecological interactions control the biogeochemical element cycles in acid environments, like in the Tinto River, in Spain (G-Toril et al. 2003). *Leptospirillum ferrooxidans* (Edwards et al. 1998; Diaby et al. 2007; Rawlings and Johnson 2007), heterotrophic bacteria, green algae, fungi, yeasts, mycoplasma, and amoebae have all been reported from acid mine waters.

The model of Fig. 3.7 sums up the observed changes within tailing impoundments proposed by Diaby et al. (2007). As the water level inside the impoundment decreases, oxygen promotes the oxidative dissolution of sulfide minerals (e.g., pyrite), chiefly by *Leptospirillum* spp. acidophiles (*Sulfobacillus* spp. and *At. ferrooxidans*) add to this process by generating  $H_2SO_4$ , as well as by oxidizing Fe(II). *Lysates* and exudates (mainly dissolved organic carbon or DOC that leaches out from the pores of injured tissue) from autotrophic acidophilus sustain the growth of heterotrophic acidophilus (iron-reducing *Acidiphilium* and *Acidobacterium*-like bacteria, and sulfate-reducing *prokaryotes*) while oxidation products of the primary producers [Fe(III) and sulfate] act as terminal electron acceptors for the heterotrophs where oxygen is limiting or absent. Below the oxidation front,



**Fig. 3.7** Model of the microbial impact on geochemical dynamics observed at Piuquenes tailings impoundment. *DOC* dissolved organic carbon. *SRB* sulfate-reducing bacteria (Diaby et al. 2007). Reproduced with permission, John Wiley and Sons

dissimilatory reduction of Fe(III) and sulfate is considered to be the leading geochemical processes, both of which are eventually limited by the availability of these oxidized species or by electron donors. The oxidation front will continue to migrate downwards, depending on the rate at which the water table falls. In due course, if and when the impoundment is completely drained, the mineral debris could become essentially fully oxidized, resulting in the dissolution of significant quantities of waste sulfide minerals from the mining operation and the generation of metal-rich acid effluents. Johnson (2009) produced an excellent review on the nature of extremely acid environments and on the biodiversity of microorganisms found within them. At any rate, all these biochemical mechanisms end up playing a role in continental wearing down.

The influence of microorganisms persists throughout the occurrence of regolith processes that affect all the materials that will be eventually removed from the continents. Reith et al. (2009) have produced a comprehensive review on the impact of microorganisms on regolith that should be examined by all those interested in probing into the chain of processes that intervene in continental denudation.

## Glossary

**Autotrophic:** Any organism capable of self-nourishment by using inorganic materials as a source of nutrients and using photosynthesis (photoautotrophs) or chemosynthesis (lithoautotrophs) as a source of energy as most plants and certain bacteria and protists. Autotrophs can reduce carbon dioxide to make organic compounds, creating a store of chemical energy.

**Chelation:** A particular way that ions and molecules bind metal ions.

**Critical zone:** System of coupled chemical, biological, physical, and geological processes operating together to support life at the Earth's surface.

**Heterotrophic:** An organism that cannot synthesize its own food and is dependent on complex organic substances for nutrition. This contrasts with autotrophs, such as plants and algae.

**Lysates:** Solutions produced when cells are destroyed by disrupting their cell membranes.

**Mixotrophic:** Any organism capable of existing as either an autotroph or heterotroph. Mixotrophs can be either eukaryotic or prokaryotic.

**Nitrification:** The substitution of a nitro group for another group in an organic compound. The biological oxidation of ammonia with oxygen into nitrite followed by the oxidation of these nitrites into nitrates.

**Nitrogen cycle:** Continuous sequence of events by which atmospheric nitrogen and nitrogenous compounds in the soil are converted, as by nitrification and nitrogen fixation into substances that can be utilized by green plants. Then substances return to the air and soils as a result of the decay of plants and denitrification. This transformation can be carried out through both biological and physical processes.

**Nunataks:** Areas of rock emerging above ice sheets and glaciers.

**Prokaryotes:** A group of organisms whose cells lack a membrane-bound nucleus (karyon).

**Rhizosphere:** Is the narrow region of soil that is directly influenced by root secretions and associated soil microorganisms.

## References

- Adamo P, Violante P (2000) Weathering of rocks and neogenesis of minerals associated with lichen activity. *Appl Clay Sci* 16:229–256
- Aghamiri R, Schwartzman DW (2002) Weathering rates of bedrock by lichens: a mini watershed study. *Chem Geol* 188:249–259
- Anderson SP, von Blackenburg F, White AF (2007) Physical and chemical control on the critical zone. *Elements* 3:315–319
- Barker WW, Welch SA, Chu S et al (1998) Experimental observations of the effects of bacteria on aluminosilicate weathering. *Am Mineral* 83:1551–1563
- Bland W, Rolls D (1998) Weathering: an introduction to the scientific principles. Arnold, London
- 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. *Appl Environ Microbiol* 72(2):1258–1266

- Chen J, Blume HP, Beyer L (2000) Weathering of rocks induced by lichen colonization—a review. *Catena* 39:121–146
- Diaby N, Dold B, Pfeifer H-R et al (2007) Microbial communities in a porphyry copper tailings impoundment and their impact on the geochemical dynamics of the mine waste. *Environ Microbiol* 9(2):298–307
- Edwards KJ, Schrenk MO, Hamers R et al (1998) Microbial oxidation of pyrite: experiments using microorganisms from extreme acidic environment. *Am Mineral* 83:1444–1453
- Ehrlich HL (1996) *Geomicrobiology*. Dekker, New York
- Finlay R, Wallander H, Smits M et al (2009) The role of fungi in biogenic weathering in boreal forest soils. *Fungal Biol Rev* 23:101–106
- G-Toril E, L-Brossa E, Casamayor EO et al (2003) Microbial ecology of an extreme acid environment: the Rio Tinto river. *Appl Environ Microbiol* 69:4853–4865
- Guglielmin M, Worland MR, Convey P et al (2012) Schmidt Hammer studies in the maritime Antarctic: application to dating Holocene deglaciation and estimating the effects of macrolichens on rock weathering. *Geomorphology* 155–156:34–44
- Halinen AK, Rahunen N, Kaksonen AH et al (2009) Heap bioleaching of a complex sulfide ore. Part I: effect of pH on metal extraction and microbial composition in pH controlled columns. *Hydrometallurgy* 98(1–2):92–100
- Hall K, Otte W (1990) A note on biological weathering on nunataks of the Juneau Icefield, Alaska. *Permafrost Periglac Process* 1:189–196
- Hall K, Arocena JM, Boelhouwers J et al (2005) The influence of aspect on the biological weathering of granites: observations from the Kunlun Mountains, China. *Geomorphology* 67:171–188
- Jie C, Blume HP (2002) Rock-weathering by lichens in Antarctic: patterns and mechanisms. *J Geo Sci* 12(4):387–396
- Johnson DB (2009) Extremophiles: acidic environments. In: Schaechter M (ed) *Encyclopedia of microbiology*. Elsevier, Amsterdam
- Lee MR, Parsons I (1999) Biomechanical and biochemical weathering of lichen-encrusted granite: textural controls on organic–mineral interactions and deposition of silica-rich layers. *Chem Geol* 161(4):385–397
- Lenton TM, Crouch M, Johnson M et al (2012) First plants cooled the Ordovician. *Nat Geosci* 5:86–89
- Li Y, Zhang Q, Wan G et al (2006) Physical mechanisms of plant roots affecting weathering and leaching of loess soil. *Sci China Ser D Earth Sci* 49(9):1002–1008
- Lu X, Wang H (2012) Microbial oxidation of sulfide tailing and the environmental consequences. *Elements* 8(2):119–124
- Mottershead DN, Baily B, Collier P et al (2003) Identification and quantification of weathering by plant roots. *Build Environ* 38:1235–1241
- Papida S, Murphy W, May E (2000) Enhancement of physical weathering of building stones by microbial populations. *Int Biodeterior Biodegrad* 46:305–317
- Phillips JD, Turkington AV, Marion DA (2008) Weathering and vegetation effects in early stages of soil formation. *Catena* 72:21–28
- Purvis W (2000) *Lichens*. Smithsonian, Washington
- Rawlings DE, Johnson DB (2007) *Biomining*. Springer, Berlin
- Reith F, Dürr M, Welch S et al (2009) Geomicrobiology of regolith. In: Scott KM, Pain CF (eds) *Regolith science*. Springer, Dordrecht
- Scarciglia F, Saporito N, La Russa ML et al (2012) Role of lichens in weathering of granodiorite in the Sila uplands (Calabria, southern Italy). *Sed Geol*. doi:10.1016/j.sedgeo.2012.05.018
- Song W, Ogawa N, Oguchi CT et al (2007) Effect of *Bacillus subtilis* on granite weathering: a laboratory experiment. *Catena* 70(3):275–281
- Stretch RC, Viles HA (2002) The nature and rate of weathering by lichens on lava flows on Lanzarote. *Geomorphology* 47:87–94
- Sverdrup H (2009) Chemical weathering of soils and minerals and the role of biological processes. *Fungal Biol Rev* 23:94–100

- Ullman WJ, Kirchman DL, Welch SA et al (1996) Laboratory evidence for microbially mediated silicate mineral dissolution in nature. *Chem Geol* 132: 11–17
- Zakharova EA, Pokrovsky OS, Dupré B et al (2007) Chemical weathering of silicate rocks in Karelia region and Kola Peninsula, NW Russia: assessing the effect of rock composition, wetlands and vegetation. *Chem Geol* 242:255–277
- Ziegler S, Ackermann S, Majzlan J et al (2009) Matrix composition and community structure analysis of a novel bacterial pyrite leaching community. *Environ Microbiol* 11(9):2329–2338