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# Mineral weathering by bacteria: ecology, actors and mechanisms

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**Soil microbes play an essential role in the environment by contributing to the release of key nutrients from primary minerals that are required not only for their own nutrition but also for that of plants. Although the role of fungi in mineral weathering is beginning to be elucidated, the relative impact of bacteria in this process and the molecular mechanisms involved remain poorly understood. Here, we discuss the ecological relevance of bacterial weathering, mainly in the soil and especially in acidic forest ecosystems, which strongly depend on mineral weathering for their sustainability. We also present highlights from recent studies showing molecular mechanisms and genetic determinants involved in the dissolution of complex minerals under aerobic conditions. Finally, we consider the potential applications of genomic resources to the study of bacterial weathering.**

## From geochemical to microbial weathering

Exposure of minerals to rainwater, temperature changes and oxidative conditions results in weathering reactions, including dissolution and crystallization of minerals. All these events have driven the genesis of sediments, soils and landscapes, determining soil fertility and water quality. Plants and microbes are also involved in formation and destruction of minerals. For example, microorganisms contribute to precipitation of new minerals and to carbonate production (or biocalcification, in the case of calcite formation) [1–3]. Whereas carbonate precipitation strongly impacts global carbon cycling, a second biological process on which we will focus here – mineral weathering (see Glossary) – plays a fundamental role in the environment by influencing the bioavailability of chemical elements that can be either beneficial or toxic to living organisms. Microbial mineral weathering is a widespread key process, not only because of its ecological significance but also because it affects human health, as well as architectural and artistic patrimony (Figure 1). Moreover, bacterial mineral weathering is used by industries to recover scarce metals from ore (for a review, see Refs [4,5]), and fungi might be useful for bioremediation of asbestos-rich soils [6]. Another exciting possibility is the future use of efficient mineral-weathering bacteria to replace chemical fertilization; these microbes are able to promote the growth of

plants by releasing trapped mineral nutrients [7–9]. This biofertilization might result in a reduction of both economical cost and environmental impact of crop production.

Plants, lichens, fungi and bacteria (Figure 2) can colonize mineral surfaces, especially pores and cracks, but their relative impacts on natural weathering are difficult to evaluate and separate from purely abiotic processes. Nevertheless, it is now established that mineral weathering can be accelerated, or even initiated, by microorganisms [10,11]. Although the role of fungi in these processes has long been recognized, the relative importance of bacteria and the molecular mechanisms involved remain poorly understood. In this article, we discuss the ecological relevance of bacterial weathering and review the known molecular mechanisms and genetic determinants involved in the dissolution of complex minerals, mainly focussing on aerobic environments.

## Bacterial weathering of minerals: different actors in different environments

Several bacterial strains from diverse genera have been reported to have mineral-weathering abilities (Table 1). They can impact mineral stability alone or in association with other microorganisms, forming complex microbial communities that colonize mineral surfaces. Although most functional studies have been focused on bacteria isolated from soil (see below), first we examine other environments to offer a wider perspective of the subject.

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### Glossary

**Acidic forest**: forest with a soil characterized by low pH ($<4.5$) and poorly weatherable minerals.
**Acidolysis**: mineral dissolution owing to acidification of the medium.
**Apatite**: a calcium phosphate mineral.
**Biotite**: a mica-type mineral containing potassium, iron and magnesium.
**Complexolysis**: mineral dissolution owing to chelation of ions.
**Endolithic**: an organism growing inside a rock or in the pores between the mineral grains of a rock.
**Epilithic**: an organism living on rocks or other mineral surfaces.
**Goethite**: iron-bearing oxide mineral found in soil and other low-temperature environments [FeO(OH)].
**Hematite**: mineral form of iron (III) oxide ($Fe_2O_3$).
**Mineral weathering**: dissolution and transformation of a mineral.
**Mycorrhizal fungi**: fungi growing in symbiosis with a plant, forming mycorrhizae.
**Mycorrhizosphere**: volume of soil under the influence of mycorrhizae.
**Phyllosilicate**: a type of mineral containing $SiO_4$ tetrahedral crystals.
**Rhizoplane**: surface of plant roots.
**Rhizosphere**: the volume of soil under the root influence.

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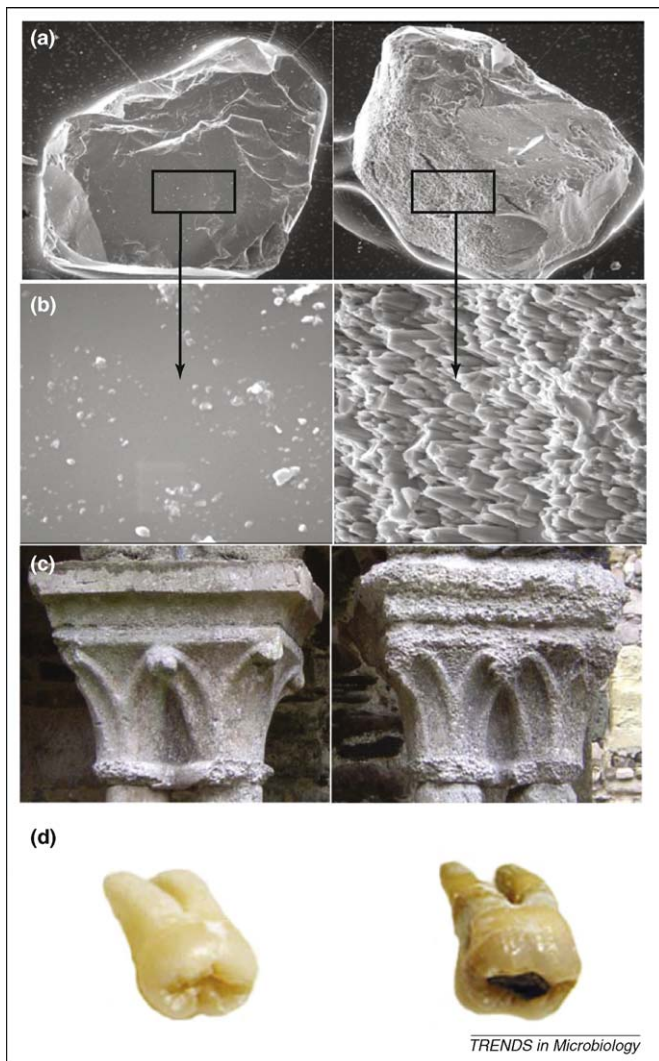*Corresponding author:* Uroz, S. (uroz@nancy.inra.fr)

**Figure 1**. Impact of mineral weathering on diverse substrates. Images on the left correspond to unweathered surfaces, whereas those on the right represent weathered surfaces. **(a,b)** Scanning electron micrographies of apatite particles before (left) or after (right) four years of incubation in the rhizosphere of an 80-year-old beech tree forest. Reproduced, with permission, from Ref. [79]. **(c)** Stone capital after or before restoration. **(d)** Healthy or decayed teeth (reproduced, with permission, from M.B. Ecole-plus.com).

## The buccal cavity: lessons to be learnt?

For soil microbiologists, the buccal cavity might be considered as an exotic environment. However, it is a niche where mineral weathering plays an important part and which has been extensively studied. Therefore, knowledge of the buccal cavity might be useful to guide research on mineral weathering in more complex environments such as soils. In the buccal cavity, the minerals are our teeth, which are biominerals composed of hydroxylapatite ($Ca_5[OH|(PO_4)_3]$). Bacteria can adhere and grow on the heterogeneous surface of the teeth, forming complex biofilms – approximately 1000 different bacterial species have been identified using molecular techniques [12,13]. Our teeth are continuously bathed in saliva, which keeps the conditions at approximately pH 7, but bacterial metabolism (particularly aerobic and anaerobic production of organic acids from sugars) creates a locally low pH ($<5$) [12]. In addition, bacterial biofilms induce the development of dental plaque, a microenvironment in which the saliva is not able to buffer the medium and remineralize dentin damage. Because the crucial pH for enamel demineralization is approximately pH 5.5 [12], all of these events lead to a localized dissolution of calcium and phosphorus from the tooth enamel (i.e. caries). Often, the microbes involved in this process are acidogenic and aciduric (i.e. acid-tolerating) *Streptococcus* and *Lactobacillus* bacteria [13]. A functional analysis of bacteria isolated from the caries should permit an estimate of their mineral-weathering potential.

## Rock surfaces

Because of their exclusive mineral composition, stones can be considered as primary ecosystems where only a few adapted microbes, with mineral-weathering abilities, can survive and grow. These pioneer microorganisms might release the inorganic nutrients necessary for the establishment of other organisms, such as plants. However, to our knowledge, there are no studies on microbial weathering combining functional and taxonomic investigations for these environments. To date, it is generally accepted that lichens (symbiotic associations between fungi and photosynthetic algae or cyanobacteria) are the first weathering pioneer organisms [14]. They are capable of colonizing and weathering the same mineral spot on the surface of a rock or monument for decades. Interestingly, complex microbial communities (in addition to the two symbiotic partners) have been identified in lichens, including bacteria from different genera such as *Anabaena*, *Bradyrhizobium*, *Burkholderia* and *Collimonas* [15–18]. However, their relative
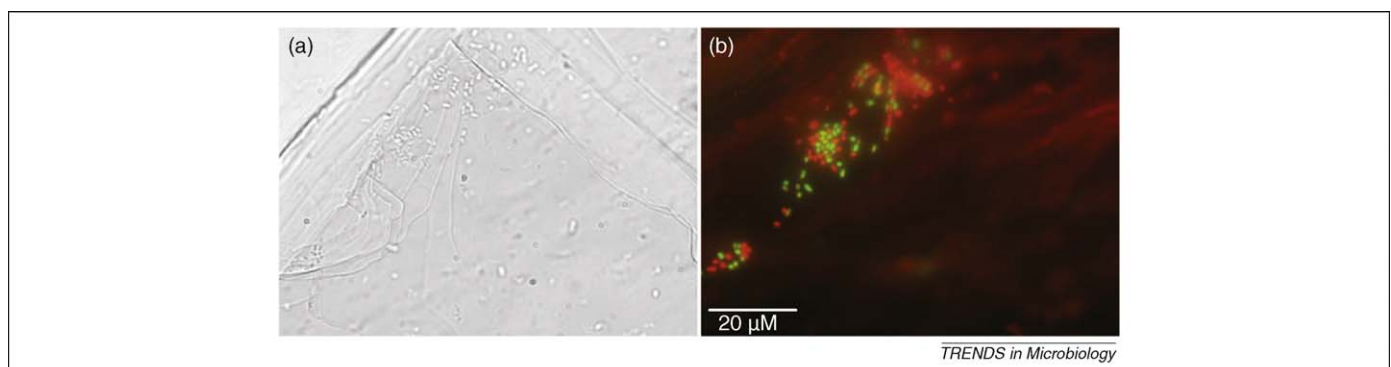


**Figure 2**. Bacteria colonizing biotite particles. Biotite particles (phyllosilicate) were incubated over 48 h with an efficient mineral-weathering bacterium, *Burkholderia glathei* strain PML1(12). Samples were then treated with a mixture of two fluorescent dyes (LIVE/DEAD® and Invitrogen) and observed at a magnification of 1000 using **(a)** light transmission or **(b)** epifluorescence. Viable bacteria (with intact cell membranes) appear in a green colour, whereas those with damaged membranes stain red.

**Table 1. Some bacteria characterized for their ability to solubilize minerals**

| Microorganism | Solubilized material (mechanism) | Origin of microorganism | Refs |
|---|---|---|---|
| **α-Proteobacteria** | | | |
| *Agrobacterium* | Phosphate | Rhizosphere of pine | [44] |
| *Aminobacter* | Biotite | Spruce–*Scleroderma citrinum* mycorrhizosphere | (S.U. *et al.*, unpublished) |
| *Azospirillum* | Phosphate (production of gluconic acid) | Rhizosphere of sugarcane | [66] |
| *Labrys* | Biotite | Spruce–*Scleroderma citrinum* mycorrhizosphere | (S.U. *et al.*, unpublished) |
| *Rhanella* | Hydroxyapatite (production of gluconic acid) | Rhizosphere of soybean | [65] |
| *Rhizobium* | Phosphate | Agricultural soil | [65] |
| *Sphingomonas* | Biotite<br>Phosphate, iron[a] | Oak–*Scleroderma citrinum* mycorrhizosphere | [19,20] |
| **β-Proteobacteria** | | | |
| *Achromobacter* | Phosphate | Not available | [68] |
| | Phosphate | Rhizosphere of beech | [44] |
| *Burkholderia* | Biotite<br>Phosphate, iron[a] | Oak–*Scleroderma citrinum* mycorrhizosphere | [19,20] |
| | Phosphate (production of gluconic acid) | Rhizosphere of mung bean | [54] |
| | Phosphate | Not available | [68] |
| | Granite | Isolated from the white-rot fungus *Phanerochate chrysoporium* | [57] |
| *Collimonas* | Biotite<br>Phosphate, iron[a] | Oak–*Scleroderma citrinum* mycorrhizosphere | [19,20] |
| *Janthinobacterium* | Biotite | Rotting *Agaricus bisporus* | (S.U. *et al.*, unpublished) |
| **δ-Proteobacteria** | | | |
| *Acinetobacter* | Phosphate | Rhizosphere of soybean | [68] |
| *Azotobacter* | Pyrite, glauconite, olivine, goethite, limonite, hematite (production of dihydroxybenzoic acid and siderophore) | Alberta soil | [51,69] |
| *Geobacter* | Iron [reduction of Fe(III)] | Sediment | [70] |
| **γ-Proteobacteria** | | | |
| *Acidithiobacillus* | Pyrite<br>Cristal | Acid mine drainage | [71] |
| *Citrobacter* | Phosphate<br>Rock | Rhizoplane of cactus | [32] |
| *Dyella* | Biotite | Spruce–*Scleroderma citrinum* mycorrhizosphere | (S.U. *et al.*, unpublished) |
| *Enterobacter* | Phosphate (production of gluconic acid) | Compost | [56] |
| | Phosphate | Not available | [68] |
| *Frateuria* | Biotite | Spruce–*Scleroderma citrinum* Mycorrhizosphere | (S.U. *et al.*, unpublished) |
| *Pseudomonas* | Biotite | Forest soil | [20] |
| | Phosphate, iron[a] | Douglas Fir–*Laccaria bicolor* S238N mycorrhizosphere | [35] |
| | Phosphate (production of gluconic acid) | Compost | [56] |
| | Phosphate, rock | Rhizoplane of cactus | [32] |
| *Serratia* | Phosphate (production of gluconic acid) | Compost | [56] |
| | | Rhizosphere of *Dendrocalamus strictus* | [72] |
| *Shewanella* | Smectite<br>Iron [reduction of Fe(III)]<br>Calcite, dolomite | Anoxic sediment | [73–76] |
| **Gram positive** | | | |
| *Arthrobacter* | Hornblende (production of organic acids and siderophore) | Adirondacks soil | [53] |
| *Bacillus* | Phosphate, rock | Rhizoplane of cactus | [56] |
| | Granite | Not available | [77] |
| *Mycobacterium* | Biotite | Oak–*Scleroderma citrinum* mycorrhizosphere | (S.U. *et al.*, unpublished) |
| *Paenebacillus* | Biotite | Forest soil | (S.U. *et al.*, unpublished) |
| | Bauxite | | [78] |
| *Staphylococcus* | Biotite | Oak–*Scleroderma citrinum* mycorrhizosphere | (S.U. *et al.*, unpublished) |
| *Streptomyces* | Hornblende (production of siderophore) | Adirondacks soil | [52] |

[a]The ability to mobilize iron was tested using the Chromazurol S *in vitro* assay. This assay is used to highlight the production of siderophores.

impact on the mineral-weathering process is poorly understood. An indirect effect of *Bradyrhizobium elkanii* on the mineral-weathering ability of a lichen has been reported [18]: rather than directly weathering the mineral substrate, the bacterium fixes and supplies nitrogen to the fungus, enhancing fungal organic acid production. Nevertheless, on the basis of what has been demonstrated in the tree mycorrhizosphere [19,20], it is tempting to hypothesize that lichens could associate with selected bacterial communities to access atmospheric nitrogen and, perhaps, inorganic nutrients trapped in the rock. A functional analysis of bacteria associated with the lichen and the surrounding stone surface should permit an estimate of their mineral-weathering potential. Future studies comparing the impact of axenic and non-axenic lichen cultures on a mineral will shed some light on the relative contribution of lichens and their associated bacteria in the mineral-weathering process.

*Aquifers*

Several inorganic nutrients are also scarce in many groundwater systems, such as aquifers [21]. To survive in these ecosystems, microorganisms must extract these nutrients from minerals. One might suspect that the more efficient mineral-weathering microorganisms will dominate the consortia colonizing mineral surfaces. Bennett and colleagues [22] were among the first to try to estimate *in situ* the impact of microorganisms on silicate weathering. By placing sterile silicates in an aquifer for periods of months to years, they evidenced (by scanning electron microscopy) distinct colonization and weathering patterns, depending on the mineral type. Their analyses mainly evidenced the presence of anaerobic bacteria belonging to either the family *Geobacteraceae* or the genus *Geothrix*. However, the relative impact of these bacterial communities on the weathering process remains unknown [21].

**Bacterial weathering of minerals in soil**

Soils have been the focus of most functional studies regarding the abilities of bacteria for mineral weathering. These environments are complex and composed of diverse niches (Figure 3). For example, rock surfaces seem to be colonized by specific bacteria that are different to those inhabiting the surrounding soil [23]. Moreover, the surface and the inside of soil mineral particles seem to be inhabited by dissimilar communities: in limestone, the endolithic bacterial community seemed to be composed mainly of

Gram-positive bacteria and acidobacteria, whereas the epilithic population was composed of approximately 50% proteobacteria [24].

Because mineral particles are composed of inorganic nutrients that can potentially be used by microbes, mineral composition is another key factor influencing bacterial communities. Colonization of mineral particles by bacteria was reported for different primary minerals such as granite, limestone, apatite, plagioclase, quartz or a mix of phlogopite and quartz [25–27] (S.U. *et al.*, unpublished). Gleeson *et al.* [26] showed that the fingerprints of bacterial communities colonizing granite were different depending on the type of mineral inclusion (muscovite, plagioclase, K-feldspar and quartz) and that the mineral chemistry altered individual bacterial ribotypes. Major elements contained in these minerals – such as aluminium, silica and calcium – seemed to have a significant impact on the structure of the bacterial community.

All these observations show that mineral composition affects the structure of the associated bacterial communities. This prompts us to propose a new concept, the mineralosphere, to qualify the surroundings of soil minerals, where microorganisms are selected for their ability to preferentially use the inorganic nutrients released by soil minerals. Further research will be needed to compare the mineral-weathering potentials of bacteria from the mineralosphere to those of the soil and rhizosphere isolates to characterize this unexplored niche, which might serve as a crucial reservoir for plant nutrition in nutrient-poor soils.
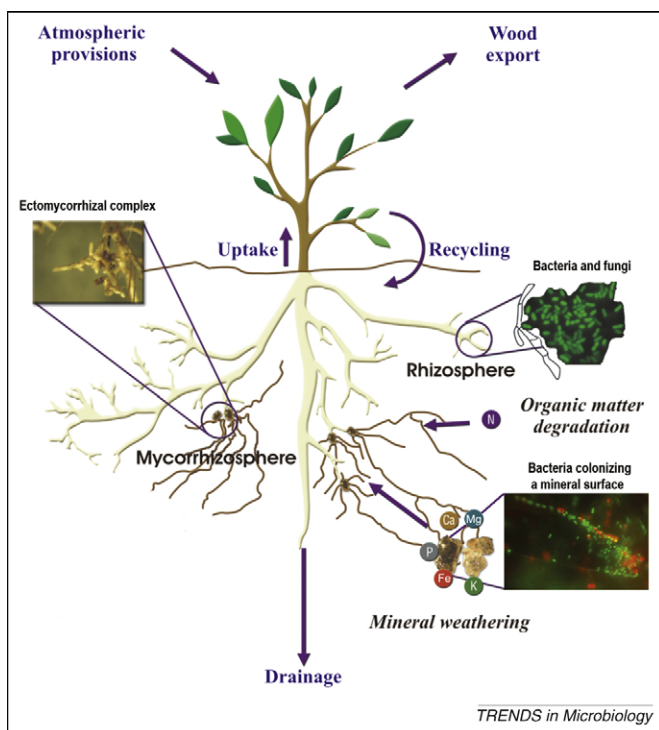
*The soil and the rhizosphere*

The soil (and, in particular, the close environment around plant roots termed 'the rhizosphere') is influenced by the biological weathering of minerals. Mineral weathering is more rapid in the rhizosphere than in bulk soil without roots [28]. This intensification of the mineral-weathering process can be linked to the pH status of the rhizosphere, which is generally different to that of bulk soil. This variation in pH and the mineral-weathering intensification can be due to the plants themselves: their growing roots might physically disrupt the mineral particles, exposing new surface areas to weathering, and/or the exuded metabolites (such as organic acids and protons) might act directly on mineral-weathering kinetics [11]. The real impact of organic acids on the soil mineral particles remains unclear because of the underestimation of their concentrations in the soil solution [29].

The intensification of mineral weathering in the rhizosphere can also be attributed, in part, to root-associated fungal and bacterial communities (Figure 3). There is increasing evidence that indicates that mineral weathering by soil fungi and bacteria affects ion cycling and plant nutrition [7,9,30]. Until recently, mineral-weathering ability had been mainly documented in mycorrhizal fungi. However, the presence of weathering bacteria was reported in the rhizosphere or rhizoplane of several plants, including mangrove trees [31], cactus [32], desert plants (*Helianthus annus jaegeri* and annual sunflower) [8] and tree species from temperate forests [19,20,33,34] (Table 1). These observations support the hypothesis that plants can



**Figure 3**. Involvement of soil microorganisms in nutrient cycling and in forest tree nutrition. Nutrient cycling in forest ecosystems is composed of five main components: uptake, recycling, atmospheric supplies, wood export and drainage. Two of them (uptake and recycling) are strongly influenced by soil microoganisms from different niches: the rhizosphere (soil surrounding non-mycorrhizal roots), the mycorrhizosphere (soil surrounding mycorrhizal roots) and the mineral surfaces (mineralosphere). Tree roots, bacteria and fungi affect the stability of mineral particles, leading to the release of inorganic nutrients. This dissolution locally modifies the physicochemical properties of the soil and influences the nutrition and the physiological activities of bacteria, fungi and plants.

**Box 1. Mineral weathering in soils: a key to sustainability in acidic forest ecosystems?**

How does one explain forest growth? It might seem surprising to ask such a question, but it is actually not easy to answer. Among terrestrial ecosystems, acidic forests are among those less altered by man and the less amended, as compared to farmland. Therefore, we should wonder about the origin of the inorganic nutrients necessary for the sustainable growth of these extensive ecosystems. Aside from the contributions of rainwater, atmospheric deposits and the recycling of elements contained in falling leaves and dead roots, soil minerals (primary and secondary minerals) constitute the main reservoir of inorganic nutrients for the long-lasting functioning of these ecosystems. However, because of the soil conditions (low pH), the remaining minerals are poorly weatherable. The example of the Fougères forest (west of France) presented in Figure I is representative of all temperate forests with acidic soils. The figure illustrates a paradoxical situation: despite an important stock of inorganic nutrients contained in soil minerals, only a limited amount of cations are accessible to the tree roots. Nevertheless, during a 150-year time period, the trees are able to accumulate a considerable stock of nutrients in their biomass, which suggests the involvement of an active mineral-weathering process that releases nutrients from soil minerals. How does this mineral weathering work? What are the relative contributions of abiotic and biotic reactions? In forest ecosystems, rhizosphere microorganisms such as symbiotic fungi [38,39] and bacteria [19,20] cooperate with the plant to release the inorganic nutrients required for their growth. However, understanding the mechanisms involved in the evolution of mineral-weathering abilities in these microorganisms and the relative contribution of bacteria in the weathering process is still a scientific challenge.
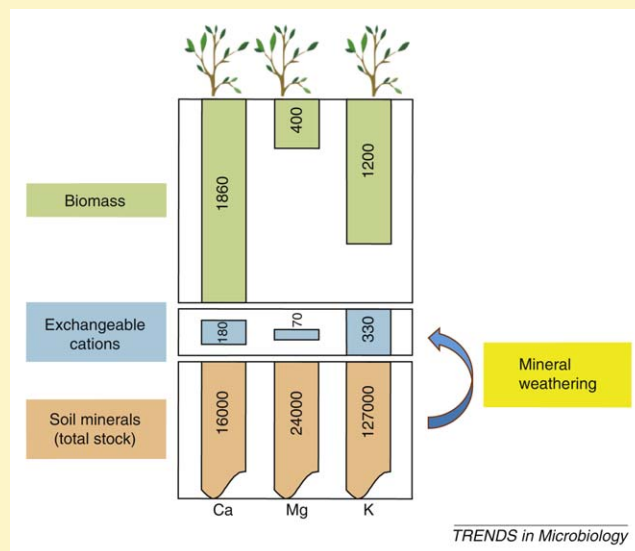


**Figure I**. Nutrient contents of a beech tree planting after 150 years. Nutrient contents are indicated in kilograms per hectare (Nys C., personal communication).

select beneficial bacterial communities to improve their own nutrition [35]. Moreover, the detected presence of weathering bacteria in extreme environments such as deserts highlights the potential role of these microbes on plant establishment and survival in poor-nutrient environments.

*The forest ecosystem*
Among terrestrial ecosystems, acidic forests are among those less influenced by mankind, unlike farmland. They are also characterized by an important stock of inorganic nutrient entrapped in soil minerals and, hence, not easily accessible to tree roots. In other words, trees are placed into 'famine in a land of plenty' [36]. The mineral-weathering process is, thus, of great importance in acidic forest ecosystems (Box 1). For decades, biological mineral weathering in forests was mainly attributed to mycorrhizal symbiotic fungi, which are known to participate in tree nutrition and in mobilizing essential nutrients directly from soil minerals [37]. These fungi colonize the tree roots and form a specific structure, the mycorrhiza (Figure 3). Several mycorrhizal fungi have been reported to be involved in releasing phosphorus and potassium from apatite and biotite, respectively [30,38,39]. In older soils (podzolic soil) the presence of tunnels inside mineral grains was attributed to fungal hyphae activity [40]. However, the contribution of tunnelling to mineral weathering was suggested to be important mainly in these older soils, and its impact remained globally low in other soils [41].

Although the impact of the mycorrhizal symbiosis on mineral-weathering and tree nutrition processes has been clearly demonstrated, the relative importance of the associated bacterial community has been poorly documented. However, several studies have highlighted the presence of complex bacterial communities in and around the mycorrhizal complex [35,42], suggesting a possible impact on mycorrhizal symbiosis and tree nutrition. For instance, populations of *Pseudomonas fluorescens* associated with the Douglas fir (*Laccaria bicolor*) symbiosis were shown to be significantly more efficient in extracting iron and phosphorus from inorganic stocks than the *P. fluorescens* isolates from the surrounding soil [35]. Similarly, the proportion of bacteria capable of weathering biotite and extracting iron or phosphorus from inorganic stocks was significantly higher in the mycorrhizosphere of an ubiquitous forest symbiotic fungus, *Scleroderma citrinum*, than in the surrounding soil [19,20]. Interestingly, the proportion of mineral-weathering bacteria in the mycorrhizosphere might vary among different tree species. A comparison between the culturable bacterial communities associated with the *S. citrinum* ectomycorrhizae among spruce or oak stands and those from the surrounding soil revealed that the structure of the mineral-weathering bacterial community varied significantly for the oak species; however, this effect was not observed for the spruce species (Calvaruso *et al.*, unpublished). Interestingly, mainly because of their nitrogen nutrition, some tree species (such as spruce, but not oak) are able to acidify the rhizosphere soil by themselves, causing the release of inorganic nutrients from soil mineral particles [43]. These results suggest a possible functional complementation between the tree, the symbiotic fungi and the bacterial communities. One could hypothesize that the selection of an efficient mineral-weathering bacterial community does not occur in the rhizosphere of trees such as spruce, which are independently capable of acidifying the rhizosphere soil and releasing the nutrients required for their growth.

However, if the presence of efficient weathering bacteria was highlighted in forest soils, their relative contribution in the mineral-weathering process remains poorly docu-
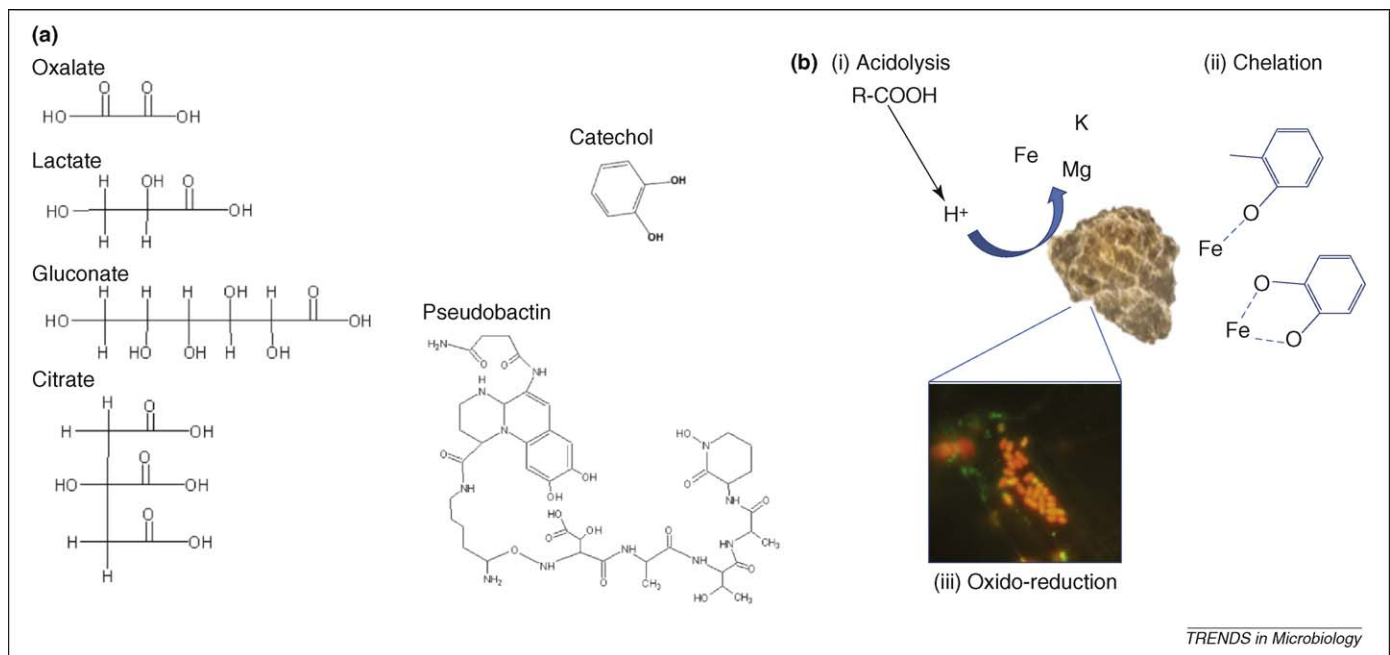
**Figure 4**. Microbial molecules and mechanisms involved in mineral weathering. **(a)** Structure of some common organic molecules, which can act as mineral-weathering agents, produced by microorganisms. **(b)** Putative mechanisms of action of these molecules on biotite: (i) acidolysis, (ii) chelation, (iii) oxidoreduction. (i) The protons associated with organic acid molecules decrease the pH of the solution and, therefore, induce the releasing of cations such as iron, potassium and magnesium. (ii) Chelating molecules might increase the dissolution rates of cations by forming strong bonds with them or with mineral surfaces. (iii) Oxidoreduction reactions occurring at the surface of complex minerals, such as silicates, require direct contact of the bacterial membrane and the mineral surface to occur. The epifluorescence picture presents bacteria colonizing biotite particles. Aerobic oxidation of elemental sulphur of various mineral sulphides such as pyrite ($FeS_2$) to the corresponding metal sulphate is an example in which oxidoreduction leads to mineral dissolution; a similar process might also be involved in biotite weathering.

mented. This gap is clearly linked to the complexity of the microbial communities, the high proportion of non-culturable bacteria in soil, and the difficulties in establishing simplified microcosms to answer this question. Nevertheless, a recent study has demonstrated that it is possible to quantify the relative contribution of mineral-weathering bacteria in a simplified system containing a plant and a model bacterial strain. Using a mineral-weathering budget approach, Calvaruso *et al.* [7] confirmed that a selected bacterial isolate from the *S. citrinum*–oak mycorrhizosphere was a true actor in mineral weathering. This isolate significantly multiplied the weathering of biotite (a phyllosilicate) by a factor of 1.5 for potassium compared with the effect of a non-inoculated plant [7]. Other experiments testing co-inoculation of an efficient weathering bacterial strain with a mycorrhizal fungus showed no increase of weathering compared with single inoculations [44]. These observations highlight that mineral weathering in soil is not the sum of the respective contributions of the different actors (plant, fungi and bacteria) but that other factors, such as the microbial interactions or the ecological origin of the microorganisms, are involved. Taking into account these factors and developing relevant microcosms will be the next challenges to better understand these processes.

## What do we know about the mechanisms of bacterial mineral weathering?

Bacteria are remarkable for their tremendous phylogenetic and metabolic diversity, for their ability to adapt and colonize extreme environments not tolerated by other organisms, and for their ability to develop biofilms [12,15]. The attachment to mineral surfaces creates microenvironments that protect bacteria against environmental stresses. In these microenvironments, bacteria extract inorganic nutrients and energy directly from the mineral matrix and/or from the surrounding microorganisms. Known and potential weathering mechanisms include several oxidoreduction reactions and the production of weathering agents, such as organic acids and chelating molecules (Figure 4).

### Oxidoreduction reactions

In contrast to eukaryotes that use oxygen for respiration, some bacterial taxa excel in using alternative terminal electron acceptors for their energetic and metabolic needs. The majority of these electron acceptors are soluble, including nitrate and sulphate. By contrast, other acceptors, such as the iron contained in minerals such as goethite or hematite, are insoluble and need direct contact with the mineral surface [45]. For both goethite and hematite, the mechanism by which the electrons are transferred remains unclear. It was suggested that this transfer could occur by excreted and membrane-associated molecules such as quinones, extracellular cysteines or heteropolymers of melanin [46,47]. In theory, the reduction or oxidation of a chemical compound entrapped in a complex structure should result in instability of the mineral crystal and, therefore, its dissolution (Figure 4). However, to date, there is no clear evidence that this process single-handedly induces bacterial mineral weathering of complex minerals such as silicates.

### Acidolysis and chelation reactions

Another major mechanism involved in mineral weathering is acidification. Minerals are known to be susceptible to various biological by-products of bacterial metabolism, including protons, organic acids and more complex mol-

ecules [48]. For example, gluconic acid is a metabolite frequently reported for its ability to induce phosphate solubilization (Table 1, Figure 3). Mineral dissolution can also be due to carbonic acid formed from $CO_2$ by bacterial respiration or to nitric and nitrous acid produced by nitrifying bacteria [11,49].

Organic acids and chelating molecules have a triple action on mineral weathering: (i) they adhere to mineral surfaces and extract nutrients from mineral particles by electron transfer; (ii) they break the oxygen links; and (iii) they chelate ions present in solution through their carboxyl and hydroxyl groups, indirectly accelerating the dissolution rate of the mineral by creating an imbalance between cation and anion concentrations in the solution [50]. Chelating ability is also characteristic of another group of molecules containing carbonyl structures with a strong affinity for iron, the siderophores (Figure 4). They are excreted into the medium by some bacteria under iron-deficiency conditions, in which they chelate and transport iron ions into bacterial cells. Interestingly, catechol derivatives produced by *Azotobacter* sp. or *Streptomyces* sp. are suspected to increase dissolution of, respectively, iron-containing minerals (olivine, glauconite and goethite) or hornblende [51–53].

Acidolysis and complexolysis processes can be used simultaneously by bacteria to impact mineral stability. *Agrobacterium* and *Bacillus* strains were described for their ability to weather phlogopite via aluminium chelation and acidic dissolution of the crystal network [44]. Bacteria can also produce gluconic acid, which harbours both acidifying and chelating functions, as reported for a strain of *Burkholderia* [54]. However, its impact on complex minerals, such as phyllosilicates, still needs to be demonstrated.

### Impact of carbon, nitrogen and phosphorus sources on mineral-weathering mechanisms

Depending on the available nutrients, bacteria can produce different metabolites with weathering potential [21]. As expected, a functional heterogeneity exists among bacteria. For instance, certain isolates are more active in mineral solubilization when xylose (a sugar common in wood) or glucose are available, whereas the weathering activity of other bacteria is increased in the presence of lactose or mannitol (a sugar common in plants, algae and fungi) [20,55,56]. The nitrogen source might also impact the weathering efficacy of bacteria, some being more efficient with nitrate or ammonium and others being more efficient with a mix of ammonium and nitrate [55,57]. One might suspect that in natural soils, the weathering activities of bacteria are influenced by both plant and fungal exudates. Taken together, these data highlight a link between microbial metabolism, soil conditions, biotic interactions and mineral weathering by soil bacteria.

### Genomics: a valuable resource to better understand the mechanisms of bacterial mineral weathering

During the past decade, the study of bacteria with specific weathering abilities (such as sulphate reduction and iron oxidation) has led to the identification of key microbial processes involved in mineral weathering. However,

genetic and biochemical analyses of these microorganisms are still in their infancy, and little is known about the molecular mechanisms involved. Nevertheless, the current progress in genomics constitutes an excellent opportunity to help characterize these microbes and to develop molecular tools to study bacterial mineral weathering *in situ*. For example, the available genomic sequences of *Acidithiobacillus ferrooxidans*, *Desulfovibrio vulgaris*, *Geobacter sulfurreducens* and *Shewanella oneidensis* represent a valuable resource for the elucidation of the ecology and the metabolic potential of these metabolically remarkable bacterial species [58–60]. Genomic sequencing of other relevant bacterial species will open new perspectives for industrial applications, particularly for the extraction of scarce ore in mining and for sustainable management of the environment.

The genomic sequencing of *A. ferrooxidans* generated a list of candidate genes likely to encode pathways specific to this microorganism (e.g. the ability to oxidize iron) [60]. Interestingly, it has been suggested that the availability of electron donors (sulfur or iron) might affect the relative expression of the 11 cytochrome C genes uncovered in the genome [61]. Complex regulatory mechanisms are expected to be involved in the control of weathering activities. Comparing aerobic and denitrifying (anoxic) conditions, Beller *et al.* [62] demonstrated by microarray analysis that genes of *Thiobacillus denitrificans* related to iron acquisition and oxidoreduction (e.g. siderophore-related genes and cytochrome oxidase genes) were upregulated in aerobic conditions. By contrast, genes involved in the denitrification cycle and the oxidation of sulfur compounds were upregulated in anoxic conditions. These data suggest that *T. denitrificans* could impact mineral stability through different weathering mechanisms, depending on the oxygen concentration in its environment.

It is worth mentioning that the study of genetic material isolated from environmental samples (metagenomics) can also provide valuable insights into metabolic pathways of complex microbial communities [63]. Combining *in silico* analysis with functional screening might help uncover genes coding for new activities involved in mineral weathering.

The recent genomic data complement the information already acquired on a small number of genes by more conventional genetic techniques. Classical genetics highlighted the role of secondary metabolites produced by some *Pseudomonas* strains in the dissolution of mineral oxides; these metabolites included humic substances, quinones, phenazines and riboflavin. The disruption of the *phz*B gene, which is normally involved in the synthesis of the antibiotic carboxamide-1-phenazine, suppresses the ability of *Pseudomonas chlororaphis* strain PCL1391 to dissolve iron and manganese oxides [46]. The authors suggested that the metabolite might act by reducing iron or manganese, inducing the separation of the metals from their oxides, particularly under low-oxygen conditions.

Few genes involved in mineral weathering under aerobic conditions have been identified, with the main exception of genes for the synthesis of gluconic acid [64–66]. Bacterial gluconic acid is produced by direct oxidation of glucose via a glucose dehydrogenase, which uses pyrrolo-

quinoline quinine (PQQ) as a coenzyme. Mutation of genes necessary for PQQ formation suppresses gluconic acid production and phosphate solubilization, as shown on artificial media [64]. However, the real impact of these genes on the weathering of complex minerals, such as phyllosilicates, has not been demonstrated so far. More generally, one would expect that any genes encoding enzymes involved in the synthesis of either organic acids or siderophores could be relevant for mineral-weathering processes. Interestingly, gluconic acid seemed to inhibit fungal growth, demonstrating that this molecule can have additional roles in the microbial world [67]. From this observation, one should ask whether any mineral-weathering mechanisms are specifically dedicated to mineral dissolution or, alternatively, whether they result from cross-reactions required for the bacterial metabolism.

## Concluding remarks and future directions
Because minerals are present in a myriad of environments, more bacterial species with mineral-weathering ability, as well as additional molecular mechanisms involved in this process, will continue to be discovered in the future. In this article, we aimed to emphasize that multidisciplinary studies of weathering bacteria, linking biogeochemistry to ecology and genetics, are required if we want to understand these processes in their natural environments. Many questions remain unanswered and should stimulate further research in the coming years (Box 2). From a mechanistic point of view, we still know

very little about the microbial genes, enzymes and metabolites involved in mineral weathering. From an ecological point of view, we need to evaluate the relative impact of the different organisms that coexist in soils, and that of their interactions, on mineral weathering. Moreover, advancing our knowledge in this field will not simply contribute to a better understanding of complex natural processes; it might also help develop new industrial applications, as well as sustainable and environmentally friendly practices in agriculture.

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**Box 2. Questions for future research**

- Is it possible to develop a 'universal' weathering assay to screen for weathering abilities of bacteria isolated from various environments?
- What is the importance of the origin of bacteria on their weathering potential? Does this potential differ among various soil compartments (different mineralospheres, mycorrhizospheres, rhizospheres and bulk soils)?
- How can we evaluate the impact of non-culturable bacteria on the mineral-weathering processes?
- Can we clearly identify the mechanisms used by bacteria to weather complex minerals such as silicates?
- Do bacteria mobilize different weathering mechanisms depending on the mineral type? How specific are these mechanisms? Are they strictly dedicated to mineral weathering or are they side-effects of basal metabolism?
- How can we quantify the relative contribution of each actor (plant roots, fungi and bacteria)? Is it relevant to separate these actors when studying mineral-weathering processes? How important are the interactions among different microbes and between microbes and plants?
- How can we develop useful mathematical or conceptual models to study mineral weathering? What are the key factors involved?
- Is it possible to develop methods combining molecular and isotopic approaches, such as stable-isotope probing of nucleic acids, to identify mineral-weathering organisms and quantify their relative contributions? Is it possible to combine fluorescent *in situ* hybridization, ion microprobe and micro-autoradiographic methods to highlight weathering bacteria *in situ* in relevant niches?
- More studies are needed to identify additional microbial genes, enzymes and metabolites involved in mineral weathering. Are the weathering mechanisms driven by these biomolecules general (widespread among bacterial genera) or specific (restricted to some taxonomic groups)? What are the environmental factors regulating the expression of these genes?

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## Celebrating Darwin: Evolution of Hosts, Microbes and Parasites

To commemorate the 200th anniversary of Charles Darwin's birthday (12th February, 1809), *Trends in Microbiology* is featuring several articles with evolutionary themes in the course of 2009, along with *Trends in Parasitology* and *Cell Host & Microbe.*

Although it is commonly assumed that Darwin had nothing to say about microbes, he did in fact say quite a lot. However, Darwin's impact on microbiological thinking of the late nineteenth century was negligible. These topics are the focus of an Opinion article by Maureen O'Malley, entitled 'What did Darwin say about microbes, and how did microbiology respond?', published in this issue of *Trends in Microbiology* (August 2009).

See also 'Evolution of the Apicomplexa: where are we now?' by David Morrison in the August issue of *Trends in Parasitology.* The author examines how little we know about the biodiversity of the Apicomplexa, a large taxonomic group whose members are entirely parasitic.

In the next issue of *Trends in Microbiology* (September 2009), Ramiro Logares and colleagues have an article entitled 'Infrequent marine-freshwater transitions in the microbial world'. Similar to what has been reported before for macroorganisms, marine and freshwater microbes are usually not closely related, often grouping into distinct marine and freshwater phylogenetic clusters. This suggests that transitions between the two types of environments have been rare events during the diversification of microbes, and that most of these transitions occurred a long time ago in evolutionary terms.

**All the articles in the series are collected in the following webpage:**
**http://www.cell.com/trends/microbiology/Darwin**