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TITLE: RECENT PROGRESS IN UNDERSTANDING THE ECOLOGY AND MOLECULAR
GENETICS OF SOIL MINERAL WEATHERING BACTERIA

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Highlights:

- Environmental distribution and effectiveness of mineral weathering bacterial communities depend on nutrient availability, the C sources and the type of mineral.
- Mineral weathering ability is conserved in some taxa and very variable in others
- Bacteria engage a large set of molecular mechanisms related to nutrient access and transport during the mineral weathering process
- Omics highlighted differential regulation of molecular mechanisms involved in acidification and iron acquisition according to nutrient availability and mineral presence

OUTSTANDING QUESTIONS:

- Do other extrinsic factors (e.g., drought frequency, climate change) determine the distribution and functioning of the MWe bacterial communities? Based on this knowledge, is it possible to develop models that predict MWe by bacteria?
- Are the molecular mechanisms engaged by the MWe bacteria the same whatever the mineral or rock considered? Is there a differential regulation ?
- Are the molecular mechanisms and the genes the same whatever the taxa? And is it possible to use the genes identified on model strains as probes to investigate *in situ* distribution of the MWe function including non-culturable taxa ?
- Is there an alternation across seasons or any environmental fluctuation of the action of MWe bacteria, from mineral weathering to mineral stabilization/precipitation ? Can we consider MWe bacteria as active players of the C sequestration on mineral surfaces ?
- Can we manipulate the soil microbiota to increase the frequency of effective MW bacteria and promote plant growth ?

ABSTRACT

Mineral weathering bacteria play essential roles in nutrient cycling and plant nutrition. However, we are far from having a comprehensive view of the factors regulating their distribution and the molecular mechanisms involved. In this review, we highlight the extrinsic (i.e., nutrient availability, carbon source) factors and the intrinsic properties of minerals explaining the distribution and functioning of these functional communities. We also present and discuss the progress made in understanding the molecular mechanisms and genes that are used by bacteria during the mineral weathering process or regulated during their interaction with minerals that have been recently unravelled by omics approaches.

54

55 **Glossary:**

56 **Acidolysis:** mineral dissolution owing to acidification of the medium.

57 **Basalt:** Volcanic rock rich in magnesium and iron.

58 **Base cations:** It corresponds to exchangeable ammonium, calcium, magnesium, potassium, and

59 sodium, by opposition to acid cations (i.e., aluminium and protons)

60 **Calcite:** Mineral from the carbonate group formed as calcium carbonate (CaCO_3).

61 **Cofactor:** It is a non-protein compound or metallic ion that is required to permit the activity of an

62 enzyme. In bacteria different cofactors are used such as PQQ (pyrroloquinoline quinone), FAD

63 (flavine adenine dinucleotide), NAD (nicotinamide adenine dinucleotide) or NADP

64 (nicotinamide adenine dinucleotide phosphate)

65 **Chemolithotrophic bacteria:** It refers to bacteria that can use the oxidation of inorganic

66 substances as a source of energy for cell biosynthesis and maintenance.

67 **Complexolysis:** mineral dissolution owing to chelation of ions.

68 **Direct oxidative pathway (DO):** Metabolic pathway by which bacteria allow the transformation

69 of the glucose transported in periplasmic space into D-glucono-1,5-lactone which is then

70 converted into GA and protons

71 **GDH:** The glucose dehydrogenase catalyses the conversion of glucose to D-glucono-1,5-lactone.

72 Different types of GDH exist which vary in their metabolic role and in their cofactors (PQQ,

73 FAD, NAD).

74 **GMC oxidoreductase:** The glucose-methanol-choline oxidoreductases are FAD-dependent

75 flavoproteins oxidoreductases.

76 **Mineral weathering:** dissolution and transformation of a mineral. The term biocorrosion is also

77 used when mineral weathering is related to metals.

78 **Mineralosphere:** the volume of soil under the influence of the nutritive and toxic elements

79 contained in minerals.

80 **Nutrient availability:** It refers to the nutritive elements directly available for the biosphere. Here

81 it corresponds mainly to base cations, nitrogen forms and P.

82 **Obsidian:** Naturally occurring volcanic glass formed when lava cools rapidly with minimal

83 crystal growth.

Omics: The term refers to large-scale data generated by proteomics, genomics, transcriptomics, metabolomics and aiming at the genetic and molecular characterization and quantification of biological molecules that translate into the structure, function, and dynamics of an organism or organisms.

Phyllosilicates: group of minerals formed by parallel sheets composed of SiO_4 tetrahedral crystals combined with other sheet-like grouping of cations (Mg^{2+} , Fe^{2+} , Al^{3+}) in octahedral coordination. The most common phyllosilicates are muscovite, biotite, serpentine and clay minerals.

Proteomics: It refers to the technologies used to study the entire set of proteins produced or modified by an organism (i.e, its proteome) according to its environment.

Rhizosphere: the volume of soil under the root influence.

Siderophore: small molecules produced and secreted by plants and microorganisms that chelate iron with a very high and specific affinity

Transcriptomics: It refers to the technologies used to study the RNA transcripts produce by an organism (i.e, its transcriptome) according to its environment.

1) INTRODUCTION

Mineral weathering (MWe) is an important process by which nutrients are released from minerals and rocks. This process depends not only on the intrinsic parameters of the minerals (*i.e.*, their physicochemical properties) [1], but also extrinsic ones (*i.e.*, pH, water circulation, biotic activity). Mineral weathering has several essential roles in our environment. In soil, it contributes to pedogenesis and is considered the main buffer against ecosystem acidification through releasing cations from **phyllosilicates** [2]. It also regulates the availability of nutrients, some of which are essential for plant nutrition (e.g., Mg, K and P) [3,4] while others are toxic elements (Al, As) [5]. In recent decades, investigations on interactions between minerals and microorganisms in different environments (*i.e.*, soil, aquifer) have revealed that MWe is attributed not only to abiotic processes [6-11], but also to microorganisms (bacteria and fungi) that effectively contribute to and even increase mineral weathering and plant growth [6-11]. Based on these properties they have been proposed to be used as biological fertilizers in agriculture [12,13] and as bioactive agents to manage building construction materials (*i.e.*, asbestos) [14]. However, field experiments and microbial inoculations gave contrasting results, evidencing the need to have a better understanding of the ecology of the MWe bacteria and to characterize the associated genetic basis in order to effectively control and utilize them. In this article, we present and discuss the progress made in our understanding of the molecular mechanisms and genes known or suspected to explain the MWe ability of bacteria and propose an integrated view by combining ecological and molecular studies done in aerobic conditions and terrestrial environments.

2) DIVERSITY OF MINERAL WEATHERING BACTERIA

In the absence of known genes related to MWe function, isolation and functional screening of collections of bacteria have been the main ways to investigate the identity and role of MWe bacteria. A broad range of bacteria representative of different genera and lineages (Gram-negative and positive) has now been identified as effective at weathering minerals such as biotite, apatite, serpentine or chrysotile (Table 1) [15]. Some of them were also shown to improve plant nutrition when inoculated alone or in consortia [16,17]. MWe bacteria have been reported in different environments (desert, forest soil, mangrove, aquifer, rock surface, etc.), especially in the **rhizosphere** of annual and perennial plants. More recently, effective MWe bacteria have been

found on the surface of minerals and inside limestone rocks colonized by tree roots [18]. The enrichment of effective MWe bacteria in such interfaces suggests that these communities play a key role in the mobilisation of **base cations** and phosphorous.

From these screenings, several very effective taxa have been identified, such as *Arthrobacter*, *Burkholderia-Caballeronia-Paraburkholderia*, *Collimonas*, *Janthinobacterium*, *Kitasatospora*, *Leifsonia*, *Polaromonas* and *Streptomyces* (Table 1) [19-21]. These functional screenings revealed that the MWe ability is conserved in some genera (e.g., *Collimonas*) [22] or that taxonomically related strains of the same genus/species can be very effective at weathering or not effective at all (e.g., *Arthrobacter*, *Burkholderia-Caballeronia-Paraburkholderia* or *Janthinobacterium*)[19-21].

3) RESOURCE AVAILABILITY DETERMINES THE DISTRIBUTION OF MINERAL WEATHERING BACTERIAL COMMUNITIES

Recent functional screening studies have shown that the distribution and functioning of MWe bacteria in soil are based on deterministic processes linking extrinsic factors (*i.e.*, plant exudates, C and N sources, **nutrient availability**, pH) and intrinsic properties of minerals (*i.e.*, composition, weatherability) [23]. Such evidences have been proposed previously on various ecosystems [10,24], but not with the resolution provided by current metagenomic tools and environmental microbiology approaches.

a) Regulation by plant root exudates

Root exudation is considered an essential mechanism used by plants to adapt to low nutrient availability and to regulate the composition and the function of their associated microbiota for their benefit through the metabolites realised [25-27]. As stated by metabolomics analyses, the composition of exudates depends on the plant species, the season, and the soil conditions and consequently, the concentrations of saccharides, amino/organic acids and secondary metabolites can strongly vary between plant species and from one site to another [28-29]. Glucose (up to ~40–50% of the total constituents), ribose, fructose, and saccharose are considered the main saccharides found in these exudates and in the soil [28-31]. The screening of various collections of bacterial strains isolated from the rhizosphere of different plants and from the surrounding soil revealed an enrichment of MWe bacteria in the rhizosphere, confirming the importance of the C

substrates released by the plants [18,21]. Noticeably, seasonal variations were observed, and higher frequencies of effective MWe bacteria were reported in the rhizosphere at periods when the plant nutritional requirements were higher [32]. All these observations suggest that plants control the distribution and function of the MWe bacteria in their rhizosphere according to their nutritive requirements.

b) Importance of C and N substrates

The nature and concentration of C and N substrates are important factors determining the MWe effectiveness of bacteria. Glucose is the C source conferring the highest weathering effectiveness to bacteria compared to other carbohydrates and derivatives (e.g., arabinose, cellobiose, gluconate, mannitol, sucrose, trehalose) [22,33-34]. While glucose is considered among the most abundant sugar in soil [30-31], it is also the most degradable. Consequently, its absorption and metabolism are very fast [35]. Similarly, the form of nitrogen can also affect the MWe effectiveness. Indeed, bacteria can have a preferential N form (NO_3^- or NH_4^+) that improves their growth and metabolic activities. Ammonium uptake can induce dissolution of minerals through the proton extrusion mechanism [34,36]. Such a difference may be explained by the use of different metabolic pathways for each substrate, the regulation of different physiological processes, and/or by lower growth rates. Notably, experimentation in soil microcosms showed that the addition of nitrogen and/or glucose modified the relative abundance of MWe bacteria but also the phosphatase activity involved in organic P mobilization [37,38].

c) Availability of inorganic nutrients

In nutrient-poor environments, the ability to mobilize base cations and P from minerals is an ecological advantage, but it also requires metabolic expenditures to produce active MWe compounds [18-20]. Bennett and colleagues [24] were among the first to evidence the importance of the nutritive requirements of MWe bacteria and the impact of nutrient availability on the distribution and taxonomic composition of mineral-associated bacterial communities [24]. In soils, those characterized by acidic and nutrient-poor conditions are usually characterised by higher frequencies of effective MWe bacteria than in nutrient-rich conditions [39-41]. However, this functional distribution can be modified through mineral amendments [37,41]. For instance, a low input of K or Mg in a soil naturally poor in K and Mg can quickly decrease the frequency of

bacteria capable of weathering minerals as their effectiveness, while they remained high in non-amended soil [41]. These results highlight how reactive MWe bacteria are to the variations in the concentrations of base cations and nutrients potentially released from soil minerals.

d) Selective effect of minerals

The selective effect of minerals (*i.e.*, **mineralosphere** effect) [23,24] on bacteria has now been evidenced in various metagenomic studies [42-47]. Comparisons of different mineral types incubated in different soils and under different land covers have clearly showed the link that exists among mineral chemistry, soil properties, and the distribution of the mineral-associated bacterial communities. Such conclusions fit well with prior studies on rock outcrops or aquifers from the '90s that proposed that bacteria use rocks and minerals as sources of nutrients [23,48]. Comparatively, less is known on how the function of those bacteria is affected. From culture-dependent studies, we know that a significant proportion of mineral-associated bacteria are effective at weathering. Compared to the surrounding bulk soil (BS), 50 to 90% of the mineralosphere-bacteria tested are effective at weathering while only 20% in BS. All these studies highlighted that higher frequencies of MWe bacteria are observed on less weatherable (e.g., **obsidian**) and weathered minerals (**calcite**) than on highly weatherable minerals [42-47,49]. In addition, bacteria isolated from the mineralosphere appeared characterized by lower metabolic abilities and a lower range of substrates metabolized than those from the surrounding bulk soil, suggesting that mineralosphere-enriched bacteria are more adapted to oligotrophic conditions [47].

4) DIFFERENT MOLECULAR MECHANISMS AND GENES INVOLVED

Various physiological processes and genes have been demonstrated or proposed to play a direct or indirect role in MWe by bacteria (Figure 1). From this diversity, we can wonder if the processes identified are linked or not, and if the MWe ability is determined by a single gene or an association of genes. To allow a comprehensive view, we classified the genes into different categories related to acidification, chelation, mineral/bacteria interactions, physiological adaptation or unexpected functions, and summarized the genes identified in Table 2.

a) An active role for proton mediated reactions

Acidolysis has been regarded for a long time as the main microbial MWe mechanism explaining [6,24,73,98]. Consequently, one may expect that all the physiological processes allowing the release of protons (*e.g.*, enzymatic reactions, NH_4^+ assimilation) and organic (*e.g.*, gluconate, oxalate, citrate, acetate or fumarate) and inorganic (*e.g.*, sulfuric and carbonic) acids in the extracellular environments of bacteria to be involved in MWe [50]. This is notably the case for glucose metabolism. Metabolism of glucose usually occurs through glycolysis and the pentose phosphate (PP) pathways, but many bacteria also use alternative pathways, such as the Entner-Doudoroff (ED) and direct oxidative (DO) pathways (Box 1). The real role of these alternative metabolic pathways remains undetermined, as they produce far less energy than the main metabolic routes (glycolysis or PP) but allow stronger acidification. While most bacteria are capable of metabolizing glucose, many are not effective at weathering, suggesting that MWe effectiveness depends on specific pathways or regulatory mechanisms. The DO pathway may be used by bacteria to adapt to nutrient limitations, to mobilize poorly soluble nutrients entrapped in rocks and minerals [51,52]. Such demonstration was done for iron. Indeed, by comparing a *Pseudomonas* strain growing in Fe-depleted and Fe-repleted conditions, Sasnow *et al.* [51] confirmed that most of the C derived from glucose is converted to gluconic acid (ca 50%) and only a small portion is converted to biomass (ca 10%) under Fe-depleted conditions, while it is mostly converted to biomass (ca. 55%) and few to gluconic acid (ca. 2%) in Fe-repleted condition [51]. Recent studies performed on *Pseudomonas* and *Collimonas* provide a better understanding of this metabolic pathway and the link between **GDH** and mineral weathering (Box 1) [53,54].

b) Direct and indirect roles of chelators

Complexolysis occurs through a combination of direct (*i.e.*, surface dissolution through ligand-promoted dissolution) and indirect (*i.e.*, modification of the solution equilibrium through chelation of the ions in solution) actions of metabolites presenting chelating activity [6,55]. Their MWe ability was demonstrated with organic acids (*e.g.*, acetate, citrate, or oxalate) and **siderophores** (*e.g.*, desferrioxamine B) through abiotic experiments [56]. Comparatively, few studies have been performed to demonstrate their role in a cellular context. One difficulty is that many of these molecules present both chelating and acidifying abilities depending on the solution pH. They are also concomitantly produced with other acidifying metabolic by-products, making it difficult to disentangle their chelating action from other mechanisms (described in this section).

The use of mutants that were selectively affected in the production of chelators permitted a robust demonstration of their role in the MWe process in a cellular context. In *Enterobacter cloacae*, S71 mutants that were affected in acetate production were less effective at weathering than the WT strain [57]. Similarly, mutants affected in the production of siderophores in *Pseudomonas aeruginosa* (pyoverdine-deficient mutant) or *Collimonas pratensis* (malleobactin-deficient mutant) were far less effective at weathering than the WT strains, but only when acidifying metabolism was limited [58-61].

c) Electron transfer through phenazines

Electron transfer is another mechanism involved in MWe. While it is a direct process under anaerobic conditions (see the section on iron-reducing and iron-oxidizing bacteria), under aerobic conditions, such a phenomenon is known to occur through shuttle molecules such as phenazines. Phenazines were initially described for their broad-spectrum antibiotic action and later as redox-active molecules [62]. The demonstration of their role in extracellular electron transfer has been clearly linked to biocorrosion [63]. Phenazine-defective mutants of *Pseudomonas* were less effective at weathering iron and manganese oxides than the WT strain [63,64]. Such an effect was also observed *in situ* after inoculation of *Pseudomonas synxantha* strain 2-79 and its phenazine-defective mutant in the rhizosphere of wheat, where an increase in the accessibility of iron and its transfer to the plant was only observed for the WT strain [65].

d) A potential role of carbonic anhydrase (CA)?

The role of CA in mineral weathering was recently proposed [66]. Bacteria possess different genetic families of CA (α -, β -, and γ -CA). α -CA is periplasmic or extracellular and converts CO₂ to bicarbonate and protons ($\text{CO}_2 + \text{H}_2\text{O} \rightleftharpoons \text{H}^+ + \text{HCO}_3^-$) through a reversible reaction. In *Bacillus mucilaginosus*, β - and γ -CA are cytoplasmic and involved in pH homeostasis and the supply of CO₂ to carboxylase enzymes. Random mutagenesis never indicated the role of CAs in any known MWe bacterial strain, possibly because of the specific conditions required to demonstrate the activity of these enzymes and due to the presence of several copies in their genome. *B. mucilaginosus* possesses 5 putative CAs in its genome, and the expression analyses revealed up-regulation of all the CAs under low concentrations of CO₂ and low availability of calcium. Interestingly, one of them (PCA4) was experimentally demonstrated to amplify the dissolution of

wollastonite (CaSiO_3) through the addition of purified CA. The dissolution observed would result from the action of the protons produced during HCO_3^- formation [66].

e) Role of extracellular polymeric substances and biofilm formation

In addition to the mineral weathering mechanisms involving a constant contact with mineral surfaces, bacteria can also form transitory or permanent interactions with minerals using extracellular polymeric substances (EPS) and flagella [67-69]. However, determining the effect of biofilm formation of minerals remains difficult, as colonization of mineral surfaces by bacteria depends on the mineral type, the electrostatic charge of the surface, the environmental conditions (i.e., pH, nutrient availability), and the bacteria considered. Abiotic experiments done in the presence or absence of polysaccharides (e.g., gum xanthan, pectin or alginate) clearly show the inhibiting effect of such molecules on feldspar dissolution [68]. In *Bacillus subtilis*, EPS have been shown to adsorb on minerals, with differential adsorption of EPS-C, -N and -P according to the type of mineral, but their role in MWe was not determined. *In situ* experiments revealed that biofilm formation can inhibit [70] and in other cases intensify MWe [71], differences explained by the different types of minerals considered and the environmental conditions. At the genetic level, a mutant with defective flagella synthesis of the strain *Rhizobium pusense* S41 presented a lower MWe ability than that of the WT strain [72].

f) Genes with unexpected roles in MWe

Random mutagenesis or genomic libraries have permitted the identification of other genes playing a role in MWe, but the real mechanisms involved remain to be determined. Some of the identified genes were obtained through heterologous expression in *Escherchia coli*, which is known to be poorly effective at weathering. This low effectiveness is explained by the absence of the genes coding for the **cofactor** PQQ in its genome, and this function can be restored by heterologous expression of *pqq* genes. Notably, several genomic regions with no homology with the *pqq* or *gdh* genes have also been shown to restore *E. coli* GDH and P solubilizing activities (Table 2) [73-75]. Other genes related to metabolism or the formation of disulfide bonds were also shown in their native context to affect the MWe ability of *Pseudomonas fluorescens* strain F113 [76].

319 *f) Lessons learned from iron-reducing (FeRB) and iron-oxidizing (FeOB) bacteria*

320 **Chemolithotrophic** bacteria can use redox-active minerals containing iron, sulphur, copper
321 or manganese as electron donors or acceptors, conducting their dissolution [77,78]. This is the
322 case for oxy/hydroxides such as pyrite, hematite or rocks containing high amounts of iron such as
323 **basalt**. Electron transfer occurs between the cell surface and the minerals, allowing the reduction
324 or oxidation of the metals and provoking the dissolution of the minerals or, in contrast, the
325 precipitation of new structures. For some taxa, electron transfer involves pili and nanowires, but
326 it can also be done using extracellular shuttle molecules (e.g., antibiotics, quinones, extracellular
327 cysteines) [78,79]. For FeOB, such as *Acidithiobacillus ferrooxidans*, iron is used as an electron
328 donor, and the oxidation of FeII to FeIII is catalyzed by *c*-type cytochrome oxidases (e.g., aa3
329 and cbb3 types) [80]. For FeRB, such as *Geobacter metallireducens* or *Shewanella oneidensis*,
330 iron is used as a terminal electron acceptor, and the reduction of FeIII to FeII also involves
331 contact between the cell and minerals and the action of *c*-type cytochromes [78]. The implication
332 of FeOB in granite dissolution [81] and the effectiveness at recovering metals from minerals
333 containing copper, gold and uranium [82] of FeRB suggest that both groups must be considered
334 MWe agents.

335
336 **5) USING OMICS TO UNRAVEL MINERAL/BACTERIA INTERACTION**
337 **MECHANISMS**

338 **Transcriptomics** and **proteomics** (*i.e.*, **omics**) represent complementary approaches to the
339 gene-centred approach described above by providing a global view of the molecular mechanisms
340 regulated. Omics methodologies have been applied to address different questions on how bacteria
341 [83-89], and in some cases, how fungi [90-92], react to low nutrient availability or to the
342 presence/absence of minerals in their environment. They provide a good opportunity to determine
343 which molecular mechanisms are activated and what the genetic bases of mineral weathering are.
344 Based on the conclusions obtained, we propose a hypothetical functional model that describes the
345 different steps involved in mineral weathering by bacteria (Box2).

346
347 *a) Does P availability drive mineral weathering ability?*

348 Under high P availability, bacteria usually exhibit a decreased MWe ability, but the
349 regulations observed vary from one strain to another [83]. In *Burkholderia multivorans* WS-FJ9,

an increase in P availability comes with decreased production of pyruvic acid, constant production of gluconic acid, and down-regulation of genes related to P sensing, transport and transcriptional regulation as well as glucose metabolism and transport (*i.e.*, glycerate kinase, 2-oxoglutarate dehydrogenase, ABC transporter) [83,84], including the FAD-GDH described in Box 1. In contrast, up-regulation of the genes related to motility, enzymes involved in mannose metabolism, solute transporters and regulation processes and signal transportation were observed with increasing P concentrations [83]. For the strain *Paenibacillus sonchi* SBR5, higher concentrations of oxoglutarate are produced under high P availability, while acetic and gluconic acids represent the main acids produced under low P availability [85]. When P was directly available, up-regulation of genes coding for 2-oxoglutarate dehydrogenase, trehalose-6P hydrolase, glycogen synthase, iron acquisition/metabolism and P transport was reported, while genes related to motility, thiamine and capsule synthesis appeared down-regulated. Although strain SBR5 possesses a GDH, it was expressed only in the total absence of P and not under low or high P concentrations. Together, these results show how P availability induces important modifications in MWe bacteria, in the metabolites produced, and in the transcriptomic response and how the regulation can differ between bacteria.

b) Does mineral presence induce regulation mechanisms?

The introduction of the mineralosphere changed the paradigm that considered minerals as inert substrates for bacteria. From this discovery, we can wonder whether minerals can induce physiological changes in bacteria during the first steps of interaction between bacteria and mineral particles, before any biofilm establishment. The potential physiological response of bacteria to the presence of mineral in their vicinity was addressed considering the effective MWe *Caballeronia mineralivorans* strain PML1(12) incubated in culture conditions amended or not with biotite $K(Mg,Fe)_3(OH,F)_2(Si_3AlO_{10})$ and varying in the carbon source used [86]. Strain PML1(12) appeared very effective at weathering biotite with glucose as the sole C source but not with mannitol [22]. Gluconic acid was the main organic acid produced in the presence of glucose, but its concentration appeared lower in the presence of biotite. Chelating activity was detected under nutrient-depleted conditions, but only in the absence of biotite and regardless of the C source. The dual transcriptomics and proteomics approach highlighted that functions associated with ion transport (porins), iron access and storage (e.g., siderophore production,

381 deferrochelataase), sugar metabolism and starvation mechanisms (e.g., glycogen debranching
382 enzyme, **GMC oxidoreductase** and pqq-dependent enzymes) were up-regulated in the absence
383 of biotite and under nutrient-deprived conditions. In contrast, the presence of biotite allowed an
384 increased expression of the functions related to motility (e.g., flagella synthesis, chemotaxis),
385 monosaccharides and by-product metabolism (e.g., glycosyl transferases, GMC oxidoreductase).
386 The use of mannitol instead of glucose as C source clearly evidenced that the response of strain
387 PML1(12) at the early step of interaction with biotite differed, as seen by the down-regulation of
388 genes involved in transport and mobilization of iron (e.g., bacterioferritin, deferrochelataase) or
389 encoding GMC oxidoreductases (e.g., FAD-dependent GADH and GDH), cytochrome oxidases
390 (e.g., ubiquinol oxidase and DsbD types).

391
392 *c) Do minerals represent a source of nutrients or stress?*

393 Another important point to consider is whether the bacterial response to the presence of
394 minerals reflects a nutritive strategy or stress adaptation. Indeed, some of the chemicals contained
395 in minerals can be toxic such as aluminium, arsenic, nickel and many others. As an example,
396 aluminium represents a dominant cation released through the weathering of aluminosilicates in
397 acidic soils and Al^{3+} stress can be important for plants and microorganisms. To determine
398 whether genes related to stress response were activated or not in presence of a mineral, the strain
399 *Cupriavidus* sp. CH34 was incubated in iron-rich (MM+Fe) or iron-depleted (MM-Fe) conditions
400 either amended or not with basalt [87,88]. The production of a siderophore (i.e., staphyloferrin B)
401 was detected in the culture supernatant but only in nutrient-deprived conditions and not in
402 MM+Fe or MM-Fe+basalt. Transcriptomics confirmed these results, revealing an up-regulation
403 of the genes encoding the siderophore and its receptors only in MM-Fe. When added to MM+Fe,
404 basalt induced the up-regulation of several genes related to solute transport (ABC transporters,
405 permeases, porins), motility (chemotaxis, flagella synthesis) and heavy metal resistance (*czs* and
406 *hmy* detoxication or *cop* systems; Cd,Zn,Co,Ni, Cu). Noticeably, the up-regulation of
407 detoxication-related genes observed by transcriptomics and proteomics clearly shows that the
408 mineral allowed physiological stress responses in strain CH34, highlighting that the most
409 important regulatory factor was not nutrient limitation, but the presence of the mineral.

411 *d) Is there a differential suite of mechanisms activated during mineral weathering and*
412 *carbonation?*

413 Understanding the different steps of interaction between bacteria and minerals is essential, as
414 the molecular mechanisms engaged probably vary between the early and late steps. In particular,
415 minerals and/or conditions where precipitation occurs, as is the case for serpentine, can allow the
416 activation of very different mechanisms during dissolution and precipitation. Serpentine
417 dissolution by *Bacillus subtilis* is considered an active process engaged by this strain to access
418 magnesium, a limiting nutrient in its environment. Following the dynamic dissolution of a nickel-
419 containing serpentine $[(\text{Mg,Fe,Ni})_3\text{Si}_2\text{O}_5(\text{OH})_4]$ during a 7-day incubation, Liu *et al.* [89] clearly
420 revealed two steps: i) a first step corresponding to a rapid increase in magnesium in the solution,
421 and ii) a second step after 5 days corresponding to the formation of carbonates. Comparing the
422 differential proteomic responses between these two stages provides information on the cellular
423 processes regulated. The first stage corresponded to the activation of different enzymes (e.g.,
424 oxidoreductases) and pathways related to organic acid biosynthesis and inorganic cation
425 transmembrane transporter activity, suggesting an active metabolism related to acidification and
426 nutrient transport is involved in MWe. During the second stage (*i.e.*, carbonate formation), the
427 transport of ions from the cell to the solution is massively activated by *Bacillus subtilis*. Part of
428 these transport systems corresponds to nickel transporters activated to limit intracellular
429 concentrations of this toxic element and to glycine/betaine ABC transporters that regulate both
430 ammonium transport and osmotolerance. Such conditions change the solution saturation and
431 allow the pH to increase, resulting in the formation of secondary minerals such as carbonates
432 (*i.e.*, MgCaCO_3) and struvite (NH_4MgPO_4). Notably, high-resolution mass spectrometry analyses
433 revealed that the secondary minerals formed contained a high content of proteins and organic
434 compounds identified as carbohydrates, lipids, unsaturated hydrocarbons, and tannins.

435
436 **6) CONCLUDING REMARKS AND FUTURE PERSPECTIVES**

437 In this review, we have provided a comprehensive view of the different intrinsic and extrinsic
438 processes explaining the distribution and functioning of MWe bacteria at both community and
439 cellular levels [23,24]. At the community level, the enrichment of effective MWe bacteria in the
440 mineralosphere or in the rhizosphere fits with the idea that the MWe ability provides a
441 competitive advantage [21,41,45,48]. Higher abundance effective MWe bacteria in nutrient-poor

ecosystems highlights the importance of nutrient availability [21,48]. At the strain and cellular levels, the physiological regulations observed in the presence of minerals revealed that bacteria can perceive the presence of minerals in their environment and adapt their metabolism and physiology [59, 69,86-89]. Regardless of the scale considered (i.e., community or cellular), the C source used by bacteria plays a central role in their MWe ability, as it determines the metabolic pathways and the main mechanisms engaged. The integration of genetic and omics approaches with geochemistry has greatly improved our understanding of the genetic bases of MWe in bacteria, of how bacteria regulate mechanisms to promote dissolution and ion transport, and of the different steps occurring during MWe. From the occurrence of the MWe in very different taxa, we predict that new genes and pathways will be identified. Further studies combining environmental genomics and microbiology, metabolomics, geochemistry, microscopy and mineralogy will be necessary to advance our understanding of the mineral weathering mechanisms involved, their conservation among bacteria and their regulation as several questions (see Outstanding Questions) remain unanswered yet. The conservation of these molecular mechanisms in other microorganisms (such as fungi) capable of weathering minerals deserves also to be investigated as the weathering mechanisms may differ [105]. At last, the interactions between bacteria and fungi need to be considered as they may play an important role in the mineral weathering process.

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FIGURES, TABLES AND BOX

Table 1: Overview of some of the most reported bacterial taxa effective at mineral weathering and their ecological origin

Ecological origin	Habitat	Taxa	References
Soil	Soil horizons	<i>Achromobacter</i> <i>Brachybacterium</i> <i>Caulobacter</i> <i>Chryseobacterium</i> <i>Enterobacter</i> <i>Exiguobacterium</i> <i>Flavobacterium</i> <i>Granulicatella</i> <i>Massilia</i> <i>Microbacterium</i> <i>Mitsuaria</i> <i>Novosphingobium</i> <i>Ochrobactrum</i> <i>Phyllobacterium</i> <i>Pseudoxanthomonas</i> <i>Serratia</i> <i>Solibacillus</i>	[19, 39]

		<i>Sphingomonas</i> <i>Vogesella</i>	
Forest soil	Mycorrhizosphere (Oak, beech, spruce)	<i>Caballeronia</i> , <i>Collimonas</i> , <i>Paraburkholderia</i> , <i>Pseudomonas</i> , <i>Sphingomonas</i> , <i>Streptomyces</i>	[18,21]
	Hyphosphere of <i>Rhizophagus</i> <i>irregularis</i>	<i>Burkholderia</i> <i>Dyella</i> <i>Erwinia</i> <i>Rhanella</i> <i>Rhizobium</i>	[93]
	Mineralosphere	<i>Caballeronia</i> , <i>Collimonas</i> <i>Paraburkholderia</i> ,	[46,47]
Desert	Cactus rhizosphere	<i>Bacillus</i> <i>Citrobacter</i>	[94]
	Mangrove	<i>Bacillus</i>	[95]

	rhizosphere	<i>Enterobacter</i> <i>Kluyvera</i> <i>Paenibacillus</i> <i>Pseudomonas</i> <i>Xanthobacter</i>	
Alpine glacier	Granite sand	<i>Arthrobacter</i> <i>Leifsonia</i> <i>Janthinobacterium</i> <i>Polaromonas</i>	[20]

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485 **Table 2: List of genes with a demonstrated role in MW.**

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Bacterial strain	Gene(s)	Function	Accession number	Molecular mechanism	Mineral tested	Reference
<i>Burkholderia</i> group						
<i>Burkholderia cenocepacia</i> strain 71-2	<i>eno</i>	phosphopyruvate hydratase / convert 2-phospho-D-glycerate (2-PGA) to phosphoenol pyruvate (PEP)	X82400.1	Metabolism	TriCalic phosphate	[101]
<i>Burkholderia cepacia</i> E-37	<i>gabY</i>	Histidine ABC transporter permease HisQ	U10242	Pi solubilisation, GA production, decrease of pH	TriCalic phosphate	[75]
<i>Pseudomonas</i>						
<i>Pseudomonas fluorescens</i> strain F113	<i>dsbA</i>	Formation of disulfide bonds of periplasmic proteins	GQ202032	Pi solubilisation, GA production, decrease of pH	TriCalic phosphate	[76]
	<i>pqqB</i> <i>pqqE</i>	Genes involved in PQQ synthesis	GQ202029	Pi solubilisation, GA production, decrease of pH	TriCalic phosphate	[76]
	<i>gcd</i>	<i>gcd</i> encodes a PQQ-	GQ202031	Pi solubilisation, GA	TriCalic	[76]

		dependent glucose dehydrogenase		production, decrease of pH	phosphate	
<i>P. fluorescens</i>	Heterologous expression of <i>gltA</i> and <i>citC</i>	GltA encodes a citrate synthase from <i>E. coli</i> and <i>citC</i> encodes a citrate transporter from <i>Salmonella typhimurium</i>	NA	Acidification	Rock phosphate	[102]
<i>P. fluorescens</i> *	Heterologous expression of <i>oah</i> and <i>fpOAR</i>	Introduction of genes encoding <i>Aspergillus niger</i> oxaloacetate acetyl hydrolase (<i>oah</i>) and <i>Fomitopsis plaustri</i> oxalate transporter (FpOAR)	NA	Acidification and chelation	Rock phosphate	[103]
<i>Pseudomonas</i> F77	<i>gdh</i> <i>gad</i> <i>adh</i> <i>fimA</i> <i>ecpD</i> <i>pilO</i> <i>glk</i> <i>gntK</i>	Gdh encodes a PQQ-dependent glucose dehydrogenase; <i>gad</i> encodes gluconate 2-dehydrogenase from the GMC family; <i>adh</i> gene encoding adhesin major subunit pilin; <i>fimA</i> encodes	AQT92806 AQT91766 AQT92815 AQT92094 AQT92093 AQT92110 AQT96247 AQT96106	Mineral solubilisation, GA production, decrease of pH	biotite	[53]

		fimbrial protein; <i>ecpD</i> and <i>pilO</i> are involved in pilus assembly; <i>glk</i> encodes a glucokinase; <i>gntK</i> encodes a gluconokinase				
<i>Pseudomonas aeruginosa</i> PAO1	<i>pvdA</i> and <i>pvdC</i>	Pyoverdine synthesis	Q51548.2	Iron chelation	ChromazurolS	[59]
	<i>pchEF</i>	Pyochelin synthesis	PA4225	Iron chelation		[59]
<i>Pseudomonas chlororaphis</i> PCL1391	<i>phzB</i> <i>phzH</i>	phenazine biosynthesis phenazine modifying enzyme	BBN57311 PA0051	Reduction/dissolution	Iron and manganese oxides	[64]
<i>Collimonas</i>						
<i>Collimonas pratensis</i> PMB3(1)	<i>mbaA</i>	Encodes a Non-ribosomal peptide synthetase module	NKI69295.1	Chelation and hematite dissolution	Hematite, ChromazurolS	[61]
<i>Collimonas pratensis</i> PMB3(1)	<i>gmc</i>	Encodes a cytochrome c subunit of a Glucose/Gluconate/Sorbitol 2-dehydrogenase	NKI70796	Mineral solubilisation, GA production, decrease of pH	Biotite, TriCalic phosphate	[54]

<i>Collimonas pratensis</i> PMB3(1)	<i>tatB</i>	Part of the TatABC operon (Twin arginine system)	NKI71758	Protein transport / Mineral solubilisation, GA production, decrease of pH	Biotite, TriCalic phosphate	[54]
<i>Collimonas pratensis</i> PMB3(1)	<i>resB</i>	involved in cytochrome c biogenesis /maturation	NKI71673	synthesis of cytochrome / Mineral solubilisation, GA production, decrease of pH	Biotite, TriCalic phosphate	[54]
<i>Enterobacter</i>						
<i>Enterobacter cloacae</i> S71	<i>pta</i> <i>ackA</i> <i>poxB</i>	<i>Pta</i> encodes a phosphotransacetylase; <i>ackA</i> encodes a acetate kinase that converts acetyl- CoA to acetate and one molecule of adenosine triphosphate; <i>poxB</i> encodes a pyruvate oxidase	MG991822, MG991823, MG991821,	Metabolism and chelation	biotite	[57]
<i>Paenibacillus</i>						
<i>Paenibacillus</i> <i>mucilaginosus</i> K02	<i>ca4</i>	Encodes a carbonic anhydrase	YP_006193233	Proton attack of wollastonite during HCO ₃ ⁻ formation	wollastonite	[66]
<i>Rhizobium</i>						
<i>Rhizobium pusense</i> S41	<i>fliG</i>	Flagellar biosynthesis/type III secretory pathway	QKJ89976.1	Mobility	Biotite	[72]

		M-ring (FliF/YscJ)				
<i>Serratia</i>						
<i>Serratia marcescens</i>	Plasmid with 6 genes	Open reading frames presenting homology with transcriptional regulators, porin, transglycosylase or coding hypothetical proteins	AY028915	Pi solubilisation, GA production, decrease of pH	TriCalic phosphate	[73]
<i>Other</i>						
Metagenomic library	Fosmids with different genes	Genes encoding for PQQ, the Pho or Pst systems, some porins or hydrolases	JQ970523-JQ970528	Pi solubilisation, GA production, decrease of pH	TriCalic phosphate	[74]

* plant nutrition and growth improved

Box 1: Direct oxidative (DO) pathway of glucose and role in MWe

The DO pathway allows the transformation of glucose transported in the periplasmic space into D-glucono-1,5-lactone, which is then converted into gluconic acid (GA) through the action of gluconolactonase or via spontaneous hydrolysis of the lactone group [96]. Depending on the taxa considered, GA is the final product or can be converted to different derivatives (2KGA, 5KGA and 2,5KGA) (Figure I) [92]. Part of these metabolites and the associated protons are then exported outside of the cell and contribute to MWe mainly through acidolysis [53,54,98]. Another part can be used in the intracellular compartment in different metabolic pathways. One of the strongest organic acids produced by bacteria is 2KGA ($pK_a = 2.5$), while 5KGA and GA have pK_a values ranging from ca. 3.2 to 3.6, respectively. Historically, MWe was attributed to the action of quinoproteins known as GDH and GADH, localized in the periplasmic space and associated with the intracellular membrane. The activity of these enzymes depends on a cofactor named PQQ (pyrroloquinoline quinone). Genomic analyses revealed that the organization and number of PQQ-encoding genes strongly vary among bacteria [11,76]. For many taxa (e.g., *Pseudomonas*), the DO pathway involves only PQQ-dependent enzymes, while in other taxa, different types of enzymes have been identified [76,54]. In *Gluconobacter*, the conversion of GA to 2KGA or 5KGA was shown to depend on different membrane-bound GADHs [99]. The first is a FAD-dependent GADH that converts GA to 2KGA. It belongs to the glucose-methanol-choline (GMC) oxidoreductase family and is formed by 3 subunits: a small subunit, a large subunit and a cytochrome-C subunit. The second is a PPQ-dependent GADH, which converts GA to 5KGA. *Gluconobacter* can also convert 2KA to 2,5KGA through a second FAD-dependent GMC oxidoreductase (2KGADH). *Erwinia* have both a PQQ-GDH and a FAD-GADH [100]. Recently, genomic analyses demonstrated that *Collimonas* do not possess PQQ genes or genes related to PQQ-dependent enzymes [54], and organic acid production and weathering analyses confirmed that strain PMB3(1) use an FAD-dependent GDH from the GMC family to convert glucose to GA and weather minerals [54]. Mutagenesis and bioinformatics evidenced a key role of the cytochrome-C (GdhC) and TAT-dependent small (GdhS) subunits of GMC oxidoreductase [54]. These observations show that different GDH types are involved in the MWe ability of bacteria.

Figure I of Box 1: Direct oxidative pathway of glucose and role in the MWe ability of bacteria. Abbreviations: GA, gluconic acid; 2KGA, 2 ketogluconic acid; 2,5KGA: 2,5

ketogluconic acid; GDH: glucose dehydrogenase; GADH: gluconic acid dehydrogenase; 2KGADH: 2 ketogluconic acid dehydrogenase. The enzymes involved are presented in green and the byproducts released in the extracellular medium are presented in red. The mineral presented in a biotite particle. The elements released from biotite by MWe are presented in red.

Figure 1: Overview of the putative and demonstrated molecular mechanisms involved in MWe by bacteria

The figure presents an integrative view of the different molecular mechanisms currently identified by genetic (i.e., gene-centred approach; section 4 of the manuscript) or omic (i.e., global view; section 5 of the manuscript) approaches. To help the reader, the main mechanisms have been numbered as follows: 1, Acidification; 2, Ion uptake/transport; 3, Chelation; 4, Metabolism; 5, Osmoprotectant production ; 6, Motility and biofilm formation ; 7, Electron transfer. The activation of these different mechanisms by bacteria depends on intrinsic factors of the minerals (presence and physicochemical properties) and extrinsic factors (nature of C and N substrates, nutrient availability (P, K, Mg), solution pH, O₂ and CO₂ concentrations). CA, Carbonic anhydrase; Glc, glucose; Fru, fructose; INV, invertase; GA, gluconic acid; 2KGA, 2ketogluconic acid; TCA, tricarboxylic acid cycle; PP, pentose phosphate; ED, Entner-Doudoroff; IM, inner membrane and PM, periplasm membrane. The enzymes involved are presented in green and the different pathways are presented in blue with the Direct Oxidative pathway pointed by a blue window.

Box 2: Mechanistic scheme of the different stages of mineral weathering by bacteria. The hypothetical functional model presented here is based on data extracted from different studies performed on heterotrophic bacteria and fungi interacting with minerals and/or cultivated under variable nutrient availability conditions [85-92,104]. Though these studies are based on microcosm experiments without solution circulation, each step corresponds to a situation that may occur *in situ*. To help the reader, each step has been presented as a continuum according to a decrease of the main C source metabolized (i.e., glucose) and nutrient availability (K, Mg, Fe, etc)(Figure II). However, the order can change according to the solution conditions (nutrient availability, pH), the mineral type, the type and concentration of the C source metabolized and

the bacterial strain. Nutrient availability (e.g., K, Mg, Fe, P) is symbolized by a triangle on the bottom right of each panel, in which colour indicates nutrient availability (white: nutrient depleted and black: nutrient repleted).

Step 1: Under nutrient depletion (e.g., Fe, Mg) and in the absence of minerals, bacteria produce organic acids from the metabolized C source and siderophores and a lower investment in biomass production.

Step 2: In the presence of minerals and at very early stages of interaction, the produced siderophores scavenge iron. Iron and other divalent or trivalent cations are captured by siderophores and become limiting factors in solution.

Step 3: Organic acids and protons, due to the activation of enzymes, induce acidolysis of the minerals and the release of nutrients (Fe, K, Mg, etc.) into the solution. The production of siderophores is progressively stopped, and the cell biomass increases.

Step 4: Upon the release of iron into the medium, chemotaxis and motility are induced, and the bacteria move towards the iron source (i.e., the mineral). Transitory or permanent interactions with minerals occur.

Step 5: Upon the increase in nutrients in solution, complex gene expression regulation occurs. Enzyme activities and metabolism are regulated according to nutrient and C availability. Transporters of ions are activated, and bacteria adapt to variations in the concentration of cations inside and outside of the cell through the production of osmoprotectants.

Step 6a: This corresponds to the moment when the main C source has been fully metabolized and mineral acidolysis is progressively stopped due to a metabolic switch to an alternative C source for the bacteria.

Step 6b: This corresponds to the moment when the solution saturation reaches a level compatible with the neoformation of secondary minerals. Depending on the CO₂ conditions and the salt concentrations, the formation of carbonates and oxides/hydroxides occurs on mineral surfaces and in the solution.

Figure II of Box 2: Different stages of mineral weathering by bacteria according to nutrient availability. Each box corresponds to potential situation occurring during the interactions between bacteria, their local environment and the minerals/rocks.

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