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Recent progress in understanding the ecology and molecular genetics of soil mineral weathering bacteria

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1 **TITLE:** RECENT PROGRESS IN UNDERSTANDING THE ECOLOGY AND MOLECULAR
2 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 ?

23 **ABSTRACT**

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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.

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

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

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

94 **Rhizosphere:** the volume of soil under the root influence.

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

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

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100

101

102 1) INTRODUCTION

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

123

124 2) DIVERSITY OF MINERAL WEATHERING BACTERIA

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

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

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

143 144 **3) RESOURCE AVAILABILITY DETERMINES THE DISTRIBUTION OF MINERAL** 145 **WEATHERING BACTERIAL COMMUNITIES**

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

152 153 **a) Regulation by plant root exudates**

154 Root exudation is considered an essential mechanism used by plants to adapt to low nutrient
155 availability and to regulate the composition and the function of their associated microbiota for
156 their benefit through the metabolites realised [25-27]. As stated by metabolomics analyses, the
157 composition of exudates depends on the plant species, the season, and the soil conditions and
158 consequently, the concentrations of saccharides, amino/organic acids and secondary metabolites
159 can strongly vary between plant species and from one site to another [28-29]. Glucose (up to
160 ~40–50% of the total constituents), ribose, fructose, and saccharose are considered the main
161 saccharides found in these exudates and in the soil [28-31]. The screening of various collections
162 of bacterial strains isolated from the rhizosphere of different plants and from the surrounding soil
163 revealed an enrichment of MWe bacteria in the rhizosphere, confirming the importance of the C

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

169

170 **b) Importance of C and N substrates**

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

184

185 **c) Availability of inorganic nutrients**

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

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

198

199 **d) Selective effect of minerals**

200 The selective effect of minerals (*i.e.*, **mineralosphere** effect) [23,24] on bacteria has now been
201 evidenced in various metagenomic studies [42-47]. Comparisons of different mineral types
202 incubated in different soils and under different land covers have clearly showed the link that
203 exists among mineral chemistry, soil properties, and the distribution of the mineral-associated
204 bacterial communities. Such conclusions fit well with prior studies on rock outcrops or aquifers
205 from the '90s that proposed that bacteria use rocks and minerals as sources of nutrients [23,48].
206 Comparatively, less is known on how the function of those bacteria is affected. From culture-
207 dependent studies, we know that a significant proportion of mineral-associated bacteria are
208 effective at weathering. Compared to the surrounding bulk soil (BS), 50 to 90% of the
209 mineralosphere-bacteria tested are effective at weathering while only 20% in BS. All these
210 studies highlighted that higher frequencies of MWe bacteria are observed on less weatherable
211 (e.g., **obsidian**) and weathered minerals (**calcite**) than on highly weatherable minerals [42-47,49].
212 In addition, bacteria isolated from the mineralosphere appeared characterized by lower metabolic
213 abilities and a lower range of substrates metabolized than those from the surrounding bulk soil,
214 suggesting that mineralosphere-enriched bacteria are more adapted to oligotrophic conditions
215 [47].

216

217 **4) DIFFERENT MOLECULAR MECHANISMS AND GENES INVOLVED**

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

224

225 **a) An active role for proton mediated reactions**

226 **Acidolysis** has been regarded for a long time as the main microbial MWe mechanism
227 explaining [6,24,73,98]. Consequently, one may expect that all the physiological processes
228 allowing the release of protons (*e.g.*, enzymatic reactions, NH₄⁺ assimilation) and organic (*e.g.*,
229 gluconate, oxalate, citrate, acetate or fumarate) and inorganic (*e.g.*, sulfuric and carbonic) acids in
230 the extracellular environments of bacteria to be involved in MWe [50]. This is notably the case
231 for glucose metabolism. Metabolism of glucose usually occurs through glycolysis and the
232 pentose phosphate (PP) pathways, but many bacteria also use alternative pathways, such as the
233 Entner-Doudoroff (ED) and direct oxidative (DO) pathways (Box 1). The real role of these
234 alternative metabolic pathways remains undetermined, as they produce far less energy than the
235 main metabolic routes (glycolysis or PP) but allow stronger acidification. While most bacteria are
236 capable of metabolizing glucose, many are not effective at weathering, suggesting that MWe
237 effectiveness depends on specific pathways or regulatory mechanisms. The DO pathway may be
238 used by bacteria to adapt to nutrient limitations, to mobilize poorly soluble nutrients entrapped in
239 rocks and minerals [51,52]. Such demonstration was done for iron. Indeed, by comparing a
240 *Pseudomonas* strain growing in Fe-depleted and Fe-repleted conditions, Sasnow *et al.* [51]
241 confirmed that most of the C derived from glucose is converted to gluconic acid (ca 50%) and
242 only a small portion is converted to biomass (ca 10%) under Fe-depleted conditions, while it is
243 mostly converted to biomass (ca. 55%) and few to gluconic acid (ca. 2%) in Fe-repleted condition
244 [51]. Recent studies performed on *Pseudomonas* and *Collimonas* provide a better understanding
245 of this metabolic pathway and the link between **GDH** and mineral weathering (Box 1) [53,54].

246

247 *b) Direct and indirect roles of chelators*

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

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

264

265 **c) Electron transfer through phenazines**

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

276

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

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

288 wollastonite (CaSiO₃) through the addition of purified CA. The dissolution observed would result
289 from the action of the protons produced during HCO₃⁻ formation [66].

290

291 *e) Role of extracellular polymeric substances and biofilm formation*

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

306

307 *f) Genes with unexpected roles in MWe*

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

318

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,

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

366

367 ***b) Does mineral presence induce regulation mechanisms?***

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

381 deferrochelatase), 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, deferrochelatase) 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.

410

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 [(Mg,Fe,Ni)₃Si₂O₅(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.*, MgCaCO₃) and struvite (NH₄MgPO₄). 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.

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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

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

460

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469 manuscript.

470

FIGURES, TABLES AND BOX

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472 **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 plaustris</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</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]

487 * plant nutrition and growth improved

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

492 The DO pathway allows the transformation of glucose transported in the periplasmic space into
493 D-glucono-1.5-lactone, which is then converted into gluconic acid (GA) through the action of
494 gluconolactonase or via spontaneous hydrolysis of the lactone group [96]. Depending on the taxa
495 considered, GA is the final product or can be converted to different derivatives (2KGA, 5KGA
496 and 2.5KGA) (Figure I) [92]. Part of these metabolites and the associated protons are then
497 exported outside of the cell and contribute to MWe mainly through acidolysis [53,54,98].
498 Another part can be used in the intracellular compartment in different metabolic pathways. One
499 of the strongest organic acids produced by bacteria is 2KGA (pka = 2.5), while 5KGA and GA
500 have pka values ranging from ca. 3.2 to 3.6, respectively. Historically, MWe was attributed to the
501 action of quinoproteins known as GDH and GADH, localized in the periplasmic space and
502 associated with the intracellular membrane. The activity of these enzymes depends on a cofactor
503 named PQQ (pyrroloquinoline quinone). Genomic analyses revealed that the organization and
504 number of PQQ-encoding genes strongly vary among bacteria [11,76]. For many taxa (e.g.,
505 *Pseudomonas*), the DO pathway involves only PQQ-dependent enzymes, while in other taxa,
506 different types of enzymes have been identified [76,54]. In *Gluconobacter*, the conversion of GA
507 to 2KGA or 5KGA was shown to depend on different membrane-bound GADHs [99]. The first is
508 a FAD-dependent GADH that converts GA to 2KGA. It belongs to the glucose-methanol-choline
509 (GMC) oxidoreductase family and is formed by 3 subunits: a small subunit, a large subunit and a
510 cytochrome-C subunit. The second is a PPQ-dependent GADH, which converts GA to 5KGA.
511 *Gluconobacter* can also convert 2KA to 2.5KGA through a second FAD-dependent GMC
512 oxidoreductase (2KGADH). *Erwinia* have both a PQQ-GDH and a FAD-GADH [100]. Recently,
513 genomic analyses demonstrated that *Collimonas* do not possess PQQ genes or genes related to
514 PQQ-dependent enzymes [54], and organic acid production and weathering analyses confirmed
515 that strain PMB3(1) use an FAD-dependent GDH from the GMC family to convert glucose to
516 GA and weather minerals [54]. Mutagenesis and bioinformatics evidenced a key role of the
517 cytochrome-C (GdhC) and TAT-dependent small (GdhS) subunits of GMC oxidoreductase [54].
518 These observations show that different GDH types are involved in the MWe ability of bacteria.

519
520 **Figure I of Box 1: Direct oxidative pathway of glucose and role in the MWe ability of**
521 **bacteria.** Abbreviations: GA, gluconic acid; 2KGA, 2 ketogluconic acid; 2.5KGA: 2.5

522 ketogluconic acid; GDH: glucose dehydrogenase; GADH: gluconic acid dehydrogenase;
523 2KGADH: 2 ketogluconic acid dehydrogenase. The enzymes involved are presented in green and
524 the byproducts released in the extracellular medium are presented in red. The mineral presented
525 in a biotite particle. The elements released from biotite by MWe are presented in red.

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527

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

530 The figure presents an integrative view of the different molecular mechanisms currently
531 identified by genetic (i.e., gene-centred approach; section 4 of the manuscript) or omic (i.e.,
532 global view; section 5 of the manuscript) approaches. To help the reader, the main mechanisms
533 have been numbered as follows: 1, Acidification; 2, Ion uptake/transport; 3, Chelation; 4,
534 Metabolism; 5, Osmoprotectant production ; 6, Motility and biofilm formation ; 7, Electron
535 transfer. The activation of these different mechanisms by bacteria depends on intrinsic factors of
536 the minerals (presence and physicochemical properties) and extrinsic factors (nature of C and N
537 substrates, nutrient availability (P, K, Mg), solution pH, O₂ and CO₂ concentrations). CA,
538 Carbonic anhydrase; Glc, glucose; Fru, fructose; INV, invertase; GA, gluconic acid; 2KGA,
539 2ketogluconic acid; TCA, tricarboxylic acid cycle; PP, pentose phosphate; ED, Entner-
540 Doudoroff; IM, inner membrane and PM, periplasm membrane. The enzymes involved are
541 presented in green and the different pathways are presented in blue with the Direct Oxidative
542 pathway pointed by a blue window.

543

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

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

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

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

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

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

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

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

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

579
580 **Figure II of Box 2: Different stages of mineral weathering by bacteria according to nutrient**
581 **availability.** Each box corresponds to potential situation occurring during the interactions
582 between bacteria, their local environment and the minerals/rocks.

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