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1 **Microorganisms Meet Solid Minerals: Interactions and Biotechnological Applications**

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13

14 **Abstract**

15 In natural and engineered environments, microorganisms often co-exist and interact with
16 various minerals or mineral-containing solids. Microorganism-mineral interactions contribute
17 significantly to environmental processes including biogeochemical cycles in natural
18 ecosystems and biodeterioration of materials in engineered environments. In this mini-
19 review, we provide a summary of several key mechanisms involved in microorganism-
20 mineral interactions, including (i) solid minerals serve as substrata for biofilm development,
21 (ii) solid minerals serve as an electron source or sink for microbial respiration, (iii) solid
22 minerals provide microorganisms with macro- or micro-nutrients for cell growth, and (iv)
23 (semi)conductive solid minerals serve as extracellular electron conduits facilitating cell-to-
24 cell interactions. We also highlight recent developments in harnessing microbe-mineral
25 interactions for biotechnological applications.

26 **Keywords:** biofilm, solid mineral, microorganism-mineral interaction, bioleaching,
27 bioweathering, anaerobic digestion

28

29 **Introduction**

30 In natural and engineered environments, microorganisms often co-exist and, in many cases,
31 interact with solid minerals (Fig. 1). The interaction of microorganisms with solid minerals in
32 subsurface environments is generally considered a key factor in shaping and altering the
33 physicochemical characteristics of the minerals (Gadd 2010). Indigenous microbial
34 communities associated with rocks such as granite and black shale have been found to be
35 involved in the bioweathering of the minerals present in these rocks (Frey et al. 2010;
36 Gleeson et al. 2005; Gleeson et al. 2006; Matlakowska et al. 2010; Matlakowska et al. 2012).
37 Certain microorganisms interact with minerals to scavenge essential elements which have
38 low bioavailability (Ehrlich 1996). Consequently, microorganism-mineral interactions in
39 natural ecosystems contribute significantly to environmental processes including
40 biogeochemical cycling and metal/mineral transformations.

41 Microorganisms also play an active role in the deterioration of engineered materials such as
42 concrete in anthropogenic environments (Bertron 2014). The interaction of microorganisms
43 with solid minerals is a major contributor to the deterioration of cultural heritage sites.
44 Colonization of bacteria, fungi and cyanobacteria on stones may cause discolouration and
45 mineral dissolution, resulting in the deterioration of monuments and frescoes (Cappitelli et al.
46 2009; Cappitelli et al. 2007; Crispim and Gaylarde 2005; Fernandes 2006). Similarly, certain
47 microorganisms promote corrosion and damage building materials such as concrete (Bertron
48 2014), which compromises the integrity of important infrastructures such as sewer pipes
49 (Santo Domingo et al. 2011). On the other hand, microorganism-mineral interactions can be
50 exploited in biotechnological applications, including anaerobic digestion, bioelectrochemical
51 applications, metal recovery, repair of building materials and pH control. The interaction of
52 microorganisms and minerals in natural and engineered environments has emerged as an

53 exciting field of research that allows us to better understand environmental bioprocesses and
54 to develop novel biotechnological applications.

55 In this mini-review, we provide a summary of the different mechanisms involved in
56 microorganism-mineral interactions. In addition, we also highlight recent developments in
57 biotechnological applications of microorganism-mineral interactions.

58 **Microorganism-mineral interactions**

59 *Biofilm formation on solid minerals*

60 Mineral surfaces provide a stable environment for the attachment and development of
61 surface-associated microbial communities encased by an extracellular matrix comprising of
62 extracellular polymeric substances (EPS), known as biofilms (Costerton et al. 1995; Ding et
63 al. 2014; Papida et al. 2000). Biofilms on solid minerals often form at the solid-air (subaerial
64 biofilms) or solid-liquid (subaquatic biofilms) interfaces (Gorbushina 2007; Jenkinson and
65 Lappin-Scott 2001; Spiers et al. 2003). Examples are subaerial biofilms on natural rocks and
66 man-made stone monuments (Gorbushina 2007; Polo et al. 2012). Similarly, the majority of
67 minerals, soil aggregates and sediment-water interfaces in aquatic environments are
68 colonized by epilithic subaquatic biofilms (Gorbushina 2007; Lünsdorf et al. 2000).
69 Subaquatic biofilms play important roles in carbon cycling and contribute significantly to
70 primary production in oligotrophic lakes (Bartrons et al. 2012). The surface of solid minerals
71 may provide microorganisms in biofilms with a favorable environment, facilitating extraction
72 of inorganic nutrients directly from the mineral (Warren 2005).

73 Microbial biofilms on solid minerals often contain bacteria, fungi and algae. Table 1 shows
74 various microbial communities that have been identified on minerals in natural and man-
75 made environments. Airborne microorganisms may settle and colonize the exposed mineral

76 surfaces to form biofilms at the solid-air interfaces (Abrusci et al. 2005; Borrego et al. 2010).
77 Although chemolithotrophic, chemoorganotrophic and phototrophic microorganisms can be
78 found in subaerial biofilms, chemo-organotrophs that trap minerals and organic substances
79 from the air are often the first to colonize exposed surfaces (Viles and Gorbushina 2003). In
80 addition, algae have been reported to be associated with green subaerial patinas on
81 monuments while black fungi have been shown to be the dominant microorganisms in black
82 patinas (Polo et al. 2012). Subaquatic biofilms consist of prokaryotic and eukaryotic
83 microorganisms with cyanobacteria and algae being important taxa (Bartrons et al. 2012;
84 Lyautey et al. 2005).

85 Surface adhesion is the initial step in biofilm formation (Hori and Matsumoto 2010). The
86 attachment of microbial biofilms to mineral surfaces is mediated by an EPS matrix which
87 consists of extracellular polymers and high molecular weight cell surface compounds
88 secreted by the microorganisms (Welch et al. 1999). The EPS protects the cells from
89 mechanical damage and plays fundamental roles in the interactions of microorganisms with
90 mineral surfaces (Tuson and Weibel 2013). High molecular weight acidic polysaccharides in
91 EPS increases mineral weathering by chelating metal ions derived from minerals as well as
92 providing protons which react with the mineral surface, resulting in proton-promoted
93 dissolution (Welch et al. 1999). Batch reactor experiments demonstrated that Al and Si
94 release to the bulk solution from feldspar dissolution under acidic conditions (pH 4.0) was
95 enhanced up to 100-fold in the presence of commonly produced microbial acidic
96 polysaccharides, such as gum xanthan, pectin, low, medium and high molecular weight
97 alginates (Welch et al. 1999). Similarly, biofilms of cyanobacterium *Nostoc punctiform* and
98 ascomycete *Knufia petricola* enhanced leaching of Ca and Mg from carbonate and silicate
99 minerals (Seiffert et al. 2014). Biofilms of bacteria isolated from black shale enhanced the
100 release of K, P, Cu and As from shale into the aqueous phase, which resulted in partial

101 dissolution and changes to the shale surface such as pitting (Matlakowska et al. 2012).
102 Matlakowska et al. (2012) proposed that the mobilization of elements was facilitated by the
103 production of siderophores as well as metabolites.

104 Biofilms also contribute to the biomechanical deterioration of solid minerals. The EPS matrix
105 is hydrophilic and absorbs water to prevent microbial communities from drying out (Papida
106 et al. 2000). The presence of moisture in the EPS maintains diffusion pathways and supplies
107 microbial cells with readily available nutrients at low water potential, enabling cells to
108 survive periods of desiccation (Chenu and Roberson 1996; Papida et al. 2000). It was shown
109 that the diffusion of glucose in clay was significantly facilitated by EPS at low water
110 potentials (Chenu and Roberson 1996). Thus, trapping of moisture by the EPS may help to
111 preserve the physiological activity of the microorganisms even during desiccation events,
112 increasing the time available for mineral hydrolysis by microbial action and contributing to
113 the acceleration of weathering (Chenu and Roberson 1996; Ercole et al. 2007). During
114 repeated wetting and drying cycles, water absorption by the EPS also causes expansion of the
115 biofilm matrix while water evaporation causes its contraction, resulting in mechanical stress
116 which widens fissures in minerals (Papida et al. 2000; Warscheid and Braams 2000).

117 *Solid minerals as electron acceptors and donors for respiration*

118 Metals in solid minerals may have important biological functions in microorganisms as
119 terminal electron acceptors and donors for respiration (Ehrlich 1996; Gadd 2010; Karlsson et
120 al. 2012) (Fig. 2). Insoluble minerals like oxides of iron and manganese are among the most
121 abundant terminal anaerobic electron acceptors in the Earth's subsurface environments
122 (Richardson et al. 2013) (Fig. 2A). Mineral respiration constitutes one of the most widespread
123 respiratory processes in anoxic zones and has significant influence on the balance of several
124 biogeochemical cycles such as the nitrogen, sulphur and carbon cycles (Fredrickson and

125 Gorby 1996; Lovley et al. 2004; Nealson and Myers 1992). The reduction of metals for
126 energy generation is coupled to the oxidation of carbon substrates such as acetate or inorganic
127 electron donors such as hydrogen (Fredrickson and Gorby 1996; Nealson and Myers 1992)
128 and is the main contributor to degradation of organic matter in aquatic sediments (Lovley
129 1991; Thamdrup 2000). Bacteria from diverse taxonomic groups such as *Shewanella*,
130 *Pseudomonas*, *Bacillus*, *Arcobacter* and *Colwellia* capable of reducing manganese and
131 oxidising organic carbon substrates have been isolated from the Black Sea and manganese
132 oxide-rich marine sediments, suggesting that these bacteria may play a pivotal role in carbon-
133 linked Mn (IV) reduction in these anoxic environments (Nealson et al. 1991; Vandieken et al.
134 2012). Similarly, Fe (III) reduction is responsible for the anaerobic oxidation of organic
135 carbon in freshwater and marine sediments (Lovley et al. 2004). In addition to manganese
136 and iron, bacteria of the *Shewanella* genus have been found to be able to reduce an array of
137 electron acceptors such as uranium, chromium, technetium, neptunium, plutonium, selenite,
138 tellurite and vandate (Fredrickson et al. 2008). Microbial respiration on solid minerals
139 increases the solubility of these minerals in the environment and accelerates mineral
140 weathering (Gadd 2010).

141 Minerals can also function as electron donors for lithotrophic bacteria, which have been
142 reported to oxidize a variety of inorganic substrates (e.g., sulphide, metal, ammonium, nitrite)
143 in the generation of ATP during respiration (Tolli and King 2005). Acidophilic S and Fe
144 oxidising bacteria such as *Thiobacillus* sp. and *Acidithiobacillus* sp. have been isolated from
145 mine tailings (Baker and Banfield 2003; Wakelin et al. 2012). The oxidation of sulphide and
146 iron by chemolithotrophic bacteria accelerates the dissolution of sulphide minerals such as
147 pyrite, arsenopyrite, chalcopyrite, marcasite and sphalerite and significantly impacts rates of
148 weathering (Baker and Banfield 2003). Chemolithotrophs obtain their energy from the
149 oxidation of certain inorganic compounds, which can occur in the presence or absence of

150 light. In contrast, photolithotrophs, such as green and purple sulphur bacteria, which oxidize
151 elemental sulphur as well as reduced sulphur compounds (e.g., sulphides and thiosulphates),
152 obtain their energy from sunlight (Frigaard and Dahl 2008; Imhoff 1995; Madigan and Jung
153 2009). Sulphur oxidising bacteria are widely distributed in anoxic aquatic environments and
154 are important for the cycling of sulphur as well as sulphide detoxification (Madigan and Jung
155 2009).

156 *Solid minerals as reservoirs for macro and/or micronutrients*

157 Solid minerals are also sources of macro and/or micronutrients such as cobalt, nickel and iron
158 (Fig. 3). Cobalt is an important co-factor of methyltransferases while nickel is essential for
159 the activity of several hydrogenases in methanogenic microorganisms (Karlsson et al. 2012).
160 Iron is a macronutrient that is a key component of metalloenzymes such as cytochromes,
161 nitrogenases and monooxygenases (Konhauser et al. 2011). Hence, microorganisms interact
162 with minerals to acquire these essential macro and micronutrients. Microbial metabolites
163 including organic acids, siderophores and cyanide cause the leaching of metal ions and
164 contribute to mineral solubilisation. Carboxylic acids provide protons for protonolysis as well
165 as metal chelating anions while oxalic acids form oxalate complexes with metal ions (Gadd
166 2010; Uroz et al. 2009). Siderophores are organic ligands which chelate and sequester iron.
167 They are produced by a wide range of environmental microorganisms, especially under
168 conditions with low soluble iron levels (Cabaj and Kosakowska 2009; Neilands 1995).
169 Cyanide solubilizes metals by forming complexes with them (Frey et al. 2010). The
170 production of these metal chelating metabolites which facilitate metal ion acquisition has
171 been frequently reported in microorganisms isolated from rocks. Microorganisms isolated
172 from black shale at the Lubin copper mine produced siderophores during growth on medium
173 lacking soluble iron so as to facilitate the mobilization of Fe^{3+} ions from added insoluble

174 iron-containing compounds (Matlakowska and Sklodowska 2009). Likewise, a positive
175 correlation was observed between the production of oxalate and cyanide and iron release
176 from granite when bacterial isolates from a glacier forefield were cultivated in the presence of
177 granite powder (Frey et al. 2010).

178 *Solid minerals as electron transfer conduits facilitating intercellular interactions*

179 Conductive or semiconductive iron oxide minerals such as pyrite, magnetite and hematite are
180 abundant in soil and sediments and can function as natural electron conduits (Kato et al.
181 2012b). These conductors connect spatially separated biogeochemical redox processes by
182 transferring electrons between microorganisms. Unlike large crystals, these iron oxide
183 particles are often small enough to fit into the intercellular spaces of microbial communities
184 in soil and sediments and form electron conduits between cells (Kato et al. 2010) (Fig. 4).
185 Interspecies electron transfer (IET) was observed in a magnetite and hematite supplemented
186 anaerobic co-culture of the soil bacteria *Geobacter sulfurreducens* and *Thiobacillus*
187 *denitrificans* containing acetate and nitrate as the electron donor and acceptor, respectively.
188 IET in the hematite supplemented culture was mostly mediated by iron redox cycles whereas
189 magnetite served as an electron conduit between the two bacteria (Kato et al. 2012b). IET via
190 (semi)conductive iron oxide minerals in microbial communities can also accelerate
191 methanogenesis (Kato et al. 2012a).

192 **Biotechnological applications of microbe-mineral interactions**

193 Microbe-mineral interactions have been exploited in several recent biotechnological
194 applications, including the improvement of anaerobic digestion (AD) performance,
195 bioelectrochemical performance, metal recovery, repair of concrete and carbonate stone, and
196 pH control (Fig. 5).

197 *Improvement of anaerobic digestion (AD) performance*

198 The addition of minerals such as metal oxides has been shown to improve the performance of
199 anaerobic digesters. During the AD of dairy wastewater, methane generation and organic
200 degradation was significantly enhanced in reactors supplemented with semiconductive ferric
201 oxyhydroxide and conductive magnetite, with the greatest improvement observed in a reactor
202 treated with magnetite. Similarly, the degradation efficiency and methane yields of plant
203 biomass were increased in the presence of the iron oxides goethite, hematite and magnetite.
204 In both cases, it is likely that these iron oxides facilitated direct IET (electric syntrophy)
205 between methanogens and electroactive iron-reducing bacteria, thus resulting in more
206 acidogenic substrates (e.g. volatile fatty acids) for methanogenesis (Baek et al. 2015; Ma et
207 al. 2015).

208 Other minerals have also been shown to improve AD. The sulfate-containing mineral gypsum
209 promotes the growth of sulfate reducing bacteria (SRB) by enabling their decomposition of
210 organic compounds. Mere addition of hematite or gypsum accelerated removal of total
211 organic carbon (TOC) from beef extract and peptone (Chen et al. 2014). Simultaneous
212 addition of gypsum and hematite promoted both TOC degradation and formation of FeS and
213 CaCO₃. In other studies, anaerobic digestion processes of swine manure were improved by
214 the addition of zeolite which decreased the inhibitory effect of ammonia on methanogenesis
215 by ammonium adsorption to the mineral particles, thus resulting in an improvement in
216 methane production (Lin et al. 2013; Montalvo et al. 2005).

217 *Bioelectrochemical applications*

218 Electrochemically active bacteria are capable of exchanging electrons with extracellular
219 (semi)conductive minerals. The bioelectrochemical interaction between bacteria and

220 (semi)conductive minerals can be harnessed to enhance the performance of
221 bioelectrochemical devices such as microbial fuel cells. The performance of microbial fuel
222 cells can be improved by the addition of (semi)conductive solid minerals to establish
223 electrically conductive networks. For example, supplementation of an electrochemical cell
224 containing rice paddy soil bacteria with hematite, magnetite and ferrihydrite enhanced the
225 current density and Coulombic efficiency of the culture (Kato et al. 2010). In another study,
226 coating ruthenium oxide on the anode of a microbial fuel cell enhanced bioelectrochemical
227 performance by 17 times, in which the mechanism remains unknown (Lv et al. 2012). For a
228 detailed summary of conductive mineral (e.g., metal oxides) enabled high performance
229 bioelectrochemical devices, the audience may refer to several recently published reviews on
230 the fundamentals and applications of bioelectrochemical systems (Ge et al. 2014; Lovley and
231 Nevin 2013; Sun et al. 2015; Wang and Ren 2013; Yong et al. 2015).

232 *Metal recovery*

233 High value, critical, and scarce metals as well as rare earth elements (REE) can be recovered
234 by bioleaching from ores or electronic wastes for subsequent industrial reuse. Such metals are
235 usually locked in sulphide and iron minerals. Several bacteria species with potential metal
236 bioleaching capacities such as acid and siderophore production have been isolated from
237 mineral ores and mining environments (Curutchet et al. 2001; Matlakowska and Sklodowska
238 2009). Immobilized biofilms of the acidophilic bacterium *Thiobacillus ferrooxidans*, which
239 produce sulphuric acid (promoter of mineral dissolution) and Fe (III) (oxidant), have been
240 developed for metal recovery from the dissolution of sulphide minerals. Treatment of a low-
241 grade sulphur ore with sulphuric acid and Fe (III) produced by the bacteria resulted in the
242 recovery of 69.7% of copper, 39.5% of zinc and 99.5% of manganese after 75 days
243 (Curutchet et al. 2001). Another acidophilic bacterium, *Acidithiobacillus ferrooxidans* has

244 been shown to be able to leach copper from printed circuit boards as well as cobalt and
245 lithium from spent lithium ion batteries (Mishra et al. 2008; Yang et al. 2009).

246 Organic acids produced by filamentous fungi have been demonstrated to be able to leach
247 REEs from ores such as bauxite residue and monazite sand (Brisson et al. 2016; Qu and Lian
248 2013). Citric acid produced by *Penicillium tricolor* was shown to have the potential for
249 recovering REEs and radionuclides from bauxite residue by the formation of soluble
250 complexes. Leaching efficiencies ranging from 20 to 40% were achieved (Qu and Lian
251 2013). *Aspergillus niger* and two newly isolated strains, *Aspergillus terreus* strain ML3-1 and
252 *Paecilomyces* spp. strain WE3-F were found to be able to use monazite as their sole
253 phosphate source and hence, were able to solubilize phosphate to release REEs (Brisson et al.
254 2016).

255 Microorganisms also produce metal chelating compounds which can be used in metal
256 recovery. Cyanogenic bacteria produce cyanide which forms complexes with metal ions and
257 can also be employed to recover high-value metals such as gold from electronic wastes.
258 *Chromobacterium violaceum* has been investigated in the recovery of gold from electronic
259 waste. Metabolically engineered *C. violaceum* strains which produced 1.5 times more cyanide
260 than the wild-type, made possible 3 times more gold biorecovery from electronic scrap metal
261 (Tay et al. 2013). Likewise, mutant strains of *C. violaceum* have been generated by random
262 mutagenesis were shown to cause 2-fold improvement of gold recovery from electronic scrap
263 metal (Natarajan and Ting 2014).

264 In addition to bioleaching, microorganisms can also be employed to mobilize critical and
265 scarce metals and remove them from contaminated sites during bioremediation. These scarce
266 elements are essential in many industries ranging from electronics to healthcare. However,
267 they may also accumulate in the environment and cause pollution (Nancharaiah et al. 2016).

268 Bacterial recovery and recycling of these elements by immobilization is potentially safer and
269 more efficient than current practice makes possible. Tellurium, one of the rarest elements in
270 the Earth's crust (0.00001%), has multiple applications in antimicrobials, photovoltaic (PV)
271 modules and thermoelectric generators. A hydrothermal vent bacterium *Pseudoalteromonas*
272 sp. strain EPR3 has been shown to be able to reduce and methylate tellurium into insoluble
273 metallic tellurium particles and gaseous tellurium species respectively from various
274 tellurium-containing compounds such as cadmium telluride, bismuth telluride, autoclave slime
275 and tellurium dioxide (Bonificio and Clarke 2014). This concentrates the scarce element for
276 downstream recovery processes.

277 Selenium, chromium and uranium from anthropogenic sources such as wastewater can
278 contaminate the environment. These metals are also widely used in the industry and by the
279 military. Hence, they should be recovered to meet industrial needs besides being removed in
280 bioremediation. Microbial conversion of soluble selenium, chromium and uranium into the
281 insoluble elements may be exploited in the biological treatment of wastewaters. Soluble
282 oxyanions of selenium (SeO_4^{2-} , SeO_3^{2-}) can be reduced by microorganisms to insoluble
283 selenium which lowers its bioavailability in the environment (Nancharaiah and Lens 2015).
284 The dissimilatory metal-reducing bacterium *Shewanella oneidensis* MR-1 can reduce soluble
285 chromium (VI) to insoluble chromium (III) precipitates which accumulate in the extracellular
286 matrix (Belchik et al. 2011). Soluble uranium (VI) species in the environment may be
287 extracted by microbial processes such as biosorption onto cells, intracellular
288 bioaccumulation, bioprecipitation to hydrogen uranyl phosphate ($\text{H}_2\text{UO}_2\text{PO}_4$) and
289 bioreduction as uranite (UO_2) (Nancharaiah et al. 2016). Enzymatic bioprecipitation of U(VI)
290 to uranium phosphate precipitates is a recent attractive approach for bioremediation of
291 uranium as the precipitates are not susceptible to changes in oxidation state, thus functioning

292 as a stable long term sink for uranium (Kulkarni et al. 2013). The insoluble particles of these
293 elements may then be recovered and used in industrial applications.

294 *Repair of concrete and carbonate stone*

295 Bacteria capable of biomineralization can be used for the biological repair of small cracks in
296 concrete as well as the development of self-healing concrete (DeJong et al. 2006; Seifan et al.
297 2016). Alkali resistant *Bacillus* sp. which precipitates calcium carbonate as calcite, aragonite
298 and vaterite minerals, have been investigated as potential healing agents (Jonkers and
299 Schlangen 2008; Van Tittelboom et al. 2010; Wiktor and Jonkers 2011). In addition, *Bacillus*
300 sp. form thick walled spores, which can be viable for more than 200 hundred years in dry
301 conditions (Schlegel 1993). *Bacillus* sp. have been reported to be able to survive when
302 incorporated in cement and hence, are potential candidates in the development of self-healing
303 concrete (Jonkers 2007). The EPS produced by the biofilms of calcifying bacteria trap
304 calcium ions, thus facilitating calcium carbonate mineralization and healing of the cracks
305 (Ercole et al. 2012). Bacteria can be externally applied or incorporated into concrete as a
306 healing agent for the filling of cracks and the production of self-healing concrete respectively
307 (Jonkers and Schlangen 2008; Van Tittelboom et al. 2010). As compared to conventional
308 methods of concrete repair which pose environmental and health hazards, bacterial induced
309 calcium carbonate precipitation is a pollution free alternative (Van Tittelboom et al. 2010). It
310 has been shown that precipitation of calcium carbonate in the presence of calcium by
311 externally applied *B. sphaericus* resulted in complete filling of 10 mm deep cracks, similar to
312 the results observed when the cracks were traditionally treated with epoxy. The calcium
313 carbonate crystals formed may also contribute to a further decrease in water permeability
314 observed in cracks treated with active bacteria as compared to autoclaved bacteria. In another
315 study it was shown that the incorporation of high numbers of *Bacillus pseudofirmus* (5.8×10^8)

316 cm⁻³ cement stone) did not significantly decrease the compressive strength of concrete
317 (Jonkers and Schlangen 2008). Calcium carbonate precipitation by bacteria may also be a
318 method to protect monuments and sculptures made of carbonate stone (Mapelli et al. 2012).
319 Hence, the use of calcifying bacteria such as *Bacillus* sp. is a promising tool for concrete and
320 carbonate stone repair.

321 *pH control*

322 Calcite and silicate minerals can also be used for pH control in biological systems. Both
323 calcite and silicate minerals are easily obtainable from natural environments. Calcium
324 carbonate may potentially be used as a neutralizing agent in microbial biotechnological
325 applications such as anaerobic fermentation to produce acetic and lactic acid or in wastewater
326 treatment plants (Salek et al. 2015). Calcium carbonate is 60-80% cheaper than the current
327 neutralizing agent sodium carbonate, translating to a reduction in operational costs (Halmann
328 and Steinfeld 2006). In addition, active pH control is not required as the use of calcium
329 carbonate forms a self-regulating pH system in which the pH will not exceed 8.5 due to the
330 nature of calcium carbonate (Salek et al. 2015). pH control is required in lactic acid
331 fermentation processes as the decrease in pH with increasing lactic acid production will result
332 in feedback inhibition, inhibiting further production of lactic acid by the microorganisms.
333 Although ammonia, sodium hydroxide and potassium hydroxide are efficient neutralizers in
334 lactic acid fermentation, ammonia toxicity can result in lowering of the final acid yield and
335 cell concentration. The use of calcium hydroxide results in high lactic acid yields but also
336 generates calcium sulphate as a solid waste in the extraction process. Hence, a method for the
337 production of lactic acid was developed using recycled calcium carbonate as a neutralizing
338 agent without the generation of calcium sulphate (Yang et al. 2015). It was reported that
339 recycled calcium carbonate can maintain a higher pH at higher lactate concentrations as

340 compared to that of original calcium carbonate in a fermentation culture of *Lactobacillus*
341 *lactis*, leading to improved lactic acid yields. This was due to the small particle size and
342 increased surface area of the recycled calcium carbonate which resulted in higher dissolution
343 rates. In addition, *Lactobacillus lactis* was adsorbed to the rough surface of the recycled
344 calcium carbonate and formed holes on the particles, which enables them to function as
345 favourable microenvironments for microbial growth and production of lactic acid (Yang et al.
346 2015). Other studies have demonstrated the buffering potential of nepheline, an
347 aluminosilicate mineral, in acid mine water (Kleiv and Sandvick 2000).

348 Recent studies examined the use of silicates as long term pH buffering agents to maintain pH
349 in acidified groundwater during bioremediation. Chlorinated ethenes such as
350 tetrachloroethene (PCE) and trichloroethene (TCE) are common groundwater contaminants
351 in industrialized countries (Lacroix et al. 2014a). A cost-effective method of bioremediation
352 of chlorinated ethenes is the dechlorination of these compounds by organohalide-respiring
353 bacteria (OHRB) in organohalide respiration (OHR) to form non-toxic ethene (Lee et al.
354 1998). However, substrate fermentation and OHR generate acids which acidify the
355 groundwater. This drastically inhibits OHR as OHRB are inactivated at decreased pH
356 (Lacroix et al. 2014b). Circulation of sodium bicarbonate or sodium carbonate solutions is
357 commonly used to adjust the pH of groundwater during OHR (Robinson et al. 2009).
358 However, this only has a short term effect and requires constant monitoring with frequent
359 injections. In comparison, the dissolution of silicate minerals is relatively slow which enables
360 them to function as long term sources of alkalinity. Formate dehydrogenation, an alternative
361 method of pH control which generates only bicarbonate without acid production, may be
362 insufficient in cases of high dechlorination rates (Philips et al. 2013). Additionally, the
363 dissolution of silicate minerals is stimulated by acidity, thus avoiding pH overshooting and
364 wastage of buffering material (Marini 2006). Silicate minerals forsterite, diopside and fayalite

365 maintained pH in the neutral range in batch cultures of OHRB, facilitating complete
366 dechlorination of chlorinated ethenes to ethene (Lacroix et al. 2014a; Lacroix et al. 2014b).
367 Hence, silicates may be potential good buffering agents in the bioremediation of acidified
368 groundwater.

369 **Conclusion and future perspectives**

370 Microorganisms interact with minerals in various ways and these interactions play vital roles
371 in natural and engineered environments by mediating biological and geochemical processes.
372 Solid minerals provide a surface for the stable attachment of biofilms, function as electron
373 acceptors and donors, as reservoirs for macro and/or micronutrients as well as electron
374 transfer conduits facilitating intercellular interactions. Microbe-mineral interactions are major
375 contributors to the biodeterioration of engineered materials, resulting in degradation of
376 cultural heritage sites and infrastructures. On the other hand, the interactions between
377 microorganisms and solid minerals have been exploited for various biotechnological
378 applications such as improvement of anaerobic digestion performance, enhancement of
379 bioelectrochemical performance, metal recovery, repair of concrete and carbonate stone, and
380 pH control in microbial fermentation.

381 Although extensive studies have been conducted in elucidating microorganism-mineral
382 interactions in natural and engineered environments, our understanding of biofilm formation
383 on mineral surfaces is limited. While most studies have focussed on the effects of biofilm
384 formation on minerals and their significance, the molecular mechanisms involved in biofilm
385 development on mineral surfaces are not well understood. Whether and how interactions with
386 mineral surfaces influence the genetic regulation networks of the biofilm lifestyle is an
387 interesting research topic to explore. Further understanding of the genetic regulation of

388 biofilm formation on solid minerals may be exploited for other novel biotechnological
389 applications in the future.

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398

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661

662 **Table 1.** A summary of some microbial communities on minerals in natural and engineered environments.

Type of biofilm	Location	Microorganisms	Classification	References		
Subaerial	Granite	<i>Arthrobacter</i> sp.	<i>Actinobacteria</i>	(Frey et al. 2010)		
		<i>Leifsonia</i> sp.				
		<i>Rhodococcus erythropolis</i>				
		<i>Frigoribacter</i> sp.			<i>Alphaproteobacteria</i>	
		<i>Rhizobium caulinodans</i>				
		<i>Pimetobacter simplex</i>				
		<i>Bradyrhizobium</i> sp.				
		<i>Paenibacillus</i> sp.				<i>Bacilli</i>
		<i>Janthinobacterium</i> sp.				
		<i>Oxalobacter</i> sp.				
		<i>Paucibacter steynii</i>				
		<i>Polaromonas</i> sp.				
		<i>Variovoras</i> sp.				
		<i>Nitrosomonas oligotropha</i>				(Gleeson et al. 2006)
		<i>Pedobacter steynii</i>			<i>Bacteroidetes</i>	(Frey et al. 2010)
		<i>Pseudomonas</i> sp.			<i>Gammaproteobacteria</i>	(Gleeson et al. 2006)
<i>Xylella fastidiosa</i>						
<i>Zymobacter palmae</i>						

Type of biofilm	Location	Microorganisms	Classification	References
Subaerial	Granite	<i>Gleotheca</i> sp. <i>Microcystis</i> sp. <i>Porpidia hydrophila</i> <i>Bellemeria alpine</i> <i>Lecidea lapicida</i> <i>Buellia triseptata</i> <i>Rhizocarpon reductum</i> <i>Botryosphaeria ribis</i>	<i>Cyanobacteria</i> <i>Fungi</i>	(Gleeson et al. 2005)
Subaerial	Black shale	<i>Pseudomonas</i> sp. <i>Acinetobacter</i> sp. <i>Bacillus</i> sp.	<i>Gammaproteobacteria</i> <i>Firmicutes</i>	(Matlakowska and Sklodowska 2009)
Subaerial	Stone heritage buildings	<i>Microbacterium</i> sp. <i>Janthinobacterium</i> sp. <i>Marmoricola</i> sp. <i>Actinobacterium</i> <i>Acidobacteria</i> <i>Proteobacterium</i> <i>Cyanobacterium</i>	<i>Actinobacteria</i> <i>Oxalobacteraceae</i> <i>Actinomycetales</i> <i>Acidobacteria</i> <i>Proteobacteria</i> <i>Cyanobacteria</i>	(Polo et al. 2012)

Type of biofilm	Location	Microorganisms	Classification	References
		<i>Paenibacillus validus</i>	<i>Bacilli</i>	
		<i>Paenibacillus</i> sp.		
		Cyanobacteria	<i>Cyanobacteria</i>	
		<i>Capnobotryella</i> sp.	<i>Fungi</i>	
		<i>Exophiala</i> sp.		
		<i>Penicillium</i> sp.		
		<i>Lecanoromycetes</i>		
		<i>Umbilicaria</i> sp.		
		Chlorophyta	<i>Chlorophyta</i>	
Subaquatic	Concrete sewer pipes	<i>Alkaliflexus</i> spp.	<i>Bacteroidetes</i>	(Santo Domingo et al. 2011)
		<i>Desulfobacter</i>	<i>Deltaproteobacteria</i>	
		<i>Desulfomicrobium</i>		
		<i>Desulfovibrio</i>	<i>Gammaproteobacteria</i>	
		<i>Acidithiobacillus</i> sp		(Magniont et al. 2011; Santo Domingo et al. 2011)
		<i>Rhodanobacter</i>		(Santo Domingo et al. 2011)
		<i>Lysobacter</i>		
		<i>Thiomonas</i> sp.	<i>Betaproteobacteria</i>	(Santo Domingo et al. 2011)

Type of biofilm	Location	Microorganisms	Classification	References
				2011; Vollertsen et al. 2008)
		<i>Aspergillus albertensis</i>	<i>Fungi</i>	(Santo Domingo et al. 2011)
Subaquatic	River pebbles	<i>Olisthodiscus luteus</i>	<i>Chrysophyceae</i>	(Lyautey et al. 2005)
		<i>Nostoc punctiforme</i>	<i>Cyanobacteria</i>	
		<i>Deinococcus radiodurans</i>	<i>Deinococcus-Thermus</i>	
		<i>Flectobacillus major</i>	<i>Bacteriodetes</i>	
		<i>Spirosoma linguale</i>	<i>Betaproteobacteria</i>	
		<i>Brachymonas denitrificans</i>	<i>Betaproteobacteria</i>	
		<i>Hydrogenophilus thermoluteus</i>	<i>Betaproteobacteria</i>	
		<i>Aeromonas scubertii</i>	<i>Betaproteobacteria</i>	
		<i>Nitrospira moscoviensis</i>	<i>Nitrospirae</i>	
Subaquatic	Marine sediment	<i>Paenibacillus</i> sp.	<i>Bacilli</i>	(Kerfahi et al. 2014)
		<i>Bacillus</i> sp.	<i>Bacilli</i>	
		<i>Haloplasma</i> sp.	<i>Haloplasmataceae</i>	
		<i>Pseudomonas</i> sp.	<i>Gammaproteobacteria</i>	
		<i>Acinetobacter</i> sp.	<i>Gammaproteobacteria</i>	

Type of biofilm	Location	Microorganisms	Classification	References
		<i>Halomonas</i> sp.	<i>Gammaproteobacteria</i>	
		<i>Pseudoalteromonas</i> sp.	<i>Gammaproteobacteria</i>	
		<i>Idiomarina</i> sp.	<i>Gammaproteobacteria</i>	
		<i>Ferrimonas</i> sp.		
		<i>Vibrio</i> sp.		
		<i>Photobacterium</i> sp.	<i>Vibrionaceae</i>	
		<i>Enterobacter</i> sp.	<i>Enterobacteriaceae</i>	
		<i>Buttiaxuella</i> sp.		
		<i>Lutibacter</i> sp.	<i>Bacteroidetes</i>	
		<i>Eudoraea</i> sp.		
		<i>Georgenia</i> sp.	<i>Actinobacteria</i>	

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Figure Captions

667 **Fig. 1.** Ubiquitous presence of microorganism-mineral interactions in natural and built
668 environments. Microbial biofilms can form at solid-air or solid-liquid interfaces. Biofilms on
669 buildings, monuments and pipes cause discolouration and corrosion which result in
670 deterioration of these structures. In natural environments such as lakes, microorganism-
671 mineral interactions on sediment, pebbles and rock are vital for biogeochemical cycling such
672 as carbon and iron cycling.

673 **Fig. 2.** Minerals function as electron acceptors and donors for respiration in microorganisms.
674 A. Metal ions (*e.g.*, Mn^{4+} and Fe^{3+}) in metal oxides are reduced during anaerobic mineral
675 respiration. B. In chemolithotrophic and photolithotrophic respiration, microorganisms obtain
676 electrons from elements and ions (*e.g.*, S, S^{2-} , $\text{S}_2\text{O}_3^{2-}$, Fe^{2+}).

677 **Fig. 3.** Minerals function as reservoirs for macro and/or micronutrients. Macro and
678 micronutrients function as co-factors for enzymes and are essential for microbial function. To
679 acquire these essential nutrients, microorganisms in biofilms produce metabolites such as
680 organic acids, siderophores and cyanide which cause leaching of metal ions and contribute to
681 mineral solubilisation. Some of the leached metal ions will be used by the microorganisms
682 while the remainder will be released into the environment.

683 **Fig. 4.** (Semi)Conductive solid minerals such as hematite and magnetite can function as
684 electron transfer conduits facilitating intercellular interactions. These conduits connect
685 spatially separated biogeochemical redox processes by transferring electrons between
686 microorganisms. Interspecies electron transfer (IET) via hematite and magnetite nanoparticles
687 couple acetate oxidation to nitrate reduction and accelerate thermodynamically unfavourable
688 reactions such as methanogenesis from acetate and ethanol.

689 **Fig. 5.** Examples of biotechnological applications by harnessing the power of
690 microorganism-mineral interactions in the last 10 years.

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