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The Geomycology of Elemental Cycling and Transformations in the Environment

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1 **The geomycology of elemental cycling and transformations in the environment**

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21

22 **Running Title: Geomycology of elemental cycling**

23 **Keywords:** Geomycology, geomicrobiology, elemental cycling, metal-mineral

24 transformations, bioremediation, biomineralization

25 **SUMMARY**

26 Geomicrobiology addresses the roles of microorganisms in geological and geochemical
27 processes and geomycology is a part of this topic focussing on the fungi. Geoactive roles of
28 fungi include organic and inorganic transformations important in nutrient and element
29 cycling, rock and mineral bioweathering, mycogenic biomineral formation, and metal-fungal
30 interactions. Lichens and mycorrhizas are significant geoactive agents. Organic matter
31 decomposition is important for cycling of major biomass-associated elements, e.g. C, H, N,
32 O, P and S as well as all other elements found in lower concentrations. Transformations of
33 metals and minerals are central to geomicrobiology, and fungi effect changes in metal
34 speciation, as well as mediate mineral formation or dissolution. Such mechanisms are
35 components of biogeochemical cycles for metals as well as associated elements in biomass,
36 soil, rocks and minerals, e.g. S, P, and metalloids. Fungi may have the greatest geochemical
37 influence within the terrestrial environment. However, they are also important in the aquatic
38 environment and significant components of the deep subsurface, extreme environments and
39 habitats polluted by xenobiotics, metals and radionuclides. Applications of geomycology
40 include metal and radionuclide bioleaching, biorecovery, detoxification, and bioremediation,
41 and the production of biominerals or metal(loid) elements with catalytic or other properties.
42 Adverse effects include biodeterioration of natural and synthetic materials, rock and mineral-
43 based building materials (e.g. concrete), cultural heritage, metals, alloys and related
44 substances, and adverse effects on radionuclide mobility and containment. The ubiquity and
45 importance of fungi in the biosphere underlines the importance of geomycology as a
46 conceptual framework encompassing the environmental activities of fungi.

47

48 **INTRODUCTION**

49 The significance of fungi in natural environments is extensive and profound. Their most
50 obvious roles are as decomposers of organic materials, and as animal and plant pathogens and
51 symbionts. It is therefore obvious that they are of major importance in the global carbon cycle
52 through such activities and as important determinants of plant growth and productivity.
53 However, their importance in terms of nutrient and element cycling greatly extends beyond
54 this core activity and they are involved in the biogeochemical cycling of many other elements
55 and substances, as well as many other related processes of environmental significance. The
56 growing discipline of geomicrobiology addresses the roles of microorganisms in geological
57 and geochemical processes (1,2), and geomycology can be considered to be a part of this
58 topic that focusses on the fungi (3,4). The often clear demarcation between mycological and
59 bacteriological research has ensured that the geoactive properties and significance of fungi
60 have been unappreciated in wider geomicrobiological contexts. The range of prokaryotic
61 metabolic diversity found in archaea and bacteria, including their abilities to use a variety of
62 different terminal electron acceptors in respiration and effect redox transformations of many
63 metal species (5,6), has also contributed to a narrow overall view of the significance of
64 eukaryotic organisms in important biosphere processes. A recent collection of
65 geomicrobiology review articles managed to completely exclude fungi (as well as algae),
66 even to the extent of defining “microbes” as being only bacteria and archaea (7).
67 Nevertheless, appreciation of fungi as agents of geochemical change is growing, and their
68 significance is being discovered even in locations not usually regarded as prime fungal
69 habitats, e.g. rocks, acid mine drainage, deep aquatic sediments, hydrothermal vents and the
70 igneous oceanic crust (8-11). Their significance as bioweathering agents of rocks and
71 minerals is probably better understood than bacterial roles (12), and this ability is of prime
72 importance in the weathering of human structures in the built environment and cultural
73 heritage (13-15). On the positive side, the geoactive properties of fungi can be used for

74 human benefit and several aspects may contribute to providing solutions to several important
75 global challenges. Geomycology is relevant to reclamation and revegetation of polluted
76 habitats, bioremediation, nuclear decommissioning and radionuclide containment,
77 biorecovery of important elements, and the production of novel biomaterials. This chapter
78 outlines important geoactive properties of fungi in relation to important environmental
79 processes, their positive and negative applications and impact on human society.

80

81 **THE FUNGAL HABITAT**

82 Fungi are ubiquitous components of the microbial communities of any terrestrial
83 environment, including such hostile habitats as the Arctic, hot deserts, and metal-rich and
84 hypersaline soils (16). They are significant inhabitants of the aquatic environment as
85 decomposers of organic matter but are also involved in other elemental cycles, e.g.
86 Manganese oxidation (17). Fungi are ubiquitous in habitats polluted by xenobiotics, toxic
87 metals and radionuclides, both terrestrial and aquatic, as well as leachates and other solid or
88 liquid wastes (18). In such habitats, fungi may exhibit a variety of mechanisms that determine
89 tolerance and survival, and which are also components of elemental cycles for pollutant
90 elements (18). These “extreme” locations may also act as a reservoir of novel organisms with
91 unusual properties. For example, acid mine drainage is now known to harbor fungal
92 communities, the preponderance of earlier research on this habitat being devoted to
93 prokaryotes, and some isolates possess unusual element bioaccumulation properties. New
94 species include *Fodinomyces uranophilus* and *Coniochaeta fodinicola* from uranium mine
95 locations that can bind mobile uranium (10,19) and a *Penidiella* sp. from an acidic abandoned
96 mine location that was capable of accumulating rare earth elements such as dysprosium (Dy)
97 (20). A global fungal role in biogeochemical cycling of the elements (e.g. C, H, N, O, P, S,
98 metals, metalloids) is therefore obvious and interlinked with the ability to adopt a variety of

99 growth, metabolic and morphological strategies, adaptive capabilities to environmental
100 extremes and, their symbiotic associations with animals, plants, algae and cyanobacteria
101 (16,21,22). The ability of many fungi to grow oligotrophically by scavenging nutrients from
102 the air and rainwater helps them survive on stone and rock surfaces which are considered to
103 be an inhospitable environment (9,23). In addition, organic and inorganic residues on
104 mineral surfaces or within cracks and fissures can act as nutrient sources in the sub-aerial
105 rock environment (24). One of the most successful means for fungi to survive in the extreme
106 sub-aerial environment is underpinned by their symbiotic associations with algae and
107 cyanobacteria as lichens where the phototrophs provide a source of carbon and protection
108 from light and irradiation (24,25). Lichens enable colonization of a wide range of
109 environments including those at climatic extremes such as the Arctic and Antarctic, exposed
110 rock surfaces and dry deserts.

111

112 In the deep subsurface, the research emphasis is mostly on prokaryotes, but the presence of
113 fungi is now well known (11, 26-28). Fungi occur in abundance and high diversity in such
114 varied environments as deep-sea sediments (29), hydrothermal vents (30,31), and methane
115 cold-seeps (29,32). They are now also known as abundant inhabitants of the igneous oceanic
116 crust which has consequently been described as the largest fungal habitat on Earth (11).
117 Fungi seem to play an important ecological role in the igneous oceanic crust as they exist in
118 symbiosis with chemolithotrophic prokaryotes, decompose organic matter, dissolve and form
119 minerals, and therefore are involved in the cycling of elements (11,33,34). Fossilized
120 microorganisms have been observed in drilled cores and dredged samples from the ocean
121 floor with a majority of these findings representing fungi (34,35). These fungi existed in a
122 close symbiotic-like relationship with two types of prokaryotes, which appeared to use the
123 structural framework of the mycelium for their growth (34). It therefore seems clear that

124 geomycological processes are significant in a wide range of biosphere habitats, including
125 those traditionally thought to be inimical to fungal growth and development (36).

126

127 **ORGANIC MATTER DECOMPOSITION AND BIOGEOCHEMICAL CYCLING OF** 128 **COMPONENT ELEMENTS**

129 Organic matter decomposition is the attribute most commonly associated with fungi, and is a
130 major contribution to global biogeochemistry as well as the spoilage of foodstuffs and
131 organic materials (21,36). In fact, fungal processes represent a potential control point in the
132 global carbon cycle (37). To some extent, research on this aspect of chemoorganotrophic
133 metabolism has obscured the wider global implications of decomposition in terms of the
134 cycling of other elements and nutrients, and also contributed to a lack of attention to fungal
135 roles in wider geochemical cycles.

136

137 Most biogeochemical attention on fungi has been given to carbon and nitrogen cycles, and
138 the ability of fungi to utilize a wide spectrum of organic compounds is well known. Simple
139 compounds such as sugars, organic acids, and amino acids can easily be transported into the
140 cell while more complex molecules are first broken down to smaller molecules by
141 extracellular enzymes before cellular entry. Such compounds include natural substances such
142 as cellulose, pectin, lignin, lignocellulose, chitin and starch to anthropogenic products like
143 hydrocarbons, pesticides, and other xenobiotics (21,37). Organometals (compounds with at
144 least one metal-carbon bond) can also be attacked by fungi. Degradation of organometallic
145 compounds can be carried out by fungi either by direct enzymic action or by facilitating
146 abiotic degradation, e.g. by alteration of external pH through metabolite excretion. Tributyltin
147 oxide and tributyltin naphthenate may be degraded to mono- and dibutyltins by fungal action,
148 inorganic Sn(II) being the final degradation product (38). Organomercury compounds may be

149 detoxified by conversion to Hg(II) by fungal organomercury lyase, the Hg(II) being
150 subsequently reduced to Hg(0) by mercuric reductase, a system analogous to that found in
151 mercury-resistant bacteria.

152

153 Some fungi have remarkable degradative properties and ligninolytic fungi, like the white rot
154 *Phanerochaete chrysosporium*, can degrade many xenobiotics including aromatic
155 hydrocarbons, chlorinated organics, polychlorinated biphenyls, nitrogen-containing aromatics
156 and many other pesticides, dyes and xenobiotics (39,40). Such activities are of importance in
157 polluted habitats and have been applied in bioremediation where ligninolytic fungi have been
158 used to treat soil contaminated with substances like pentachlorophenol (PCP) and polynuclear
159 aromatic hydrocarbons (PAHs) (21, 41-43). In many cases, xenobiotic-transforming fungi
160 need additional utilizable carbon sources for co-metabolism because although capable of
161 degradation, they cannot adequately utilize these substrates as an energy source. Inexpensive
162 utilizable lignocellulosic wastes such as corn cobs, straw and sawdust can therefore be used as
163 nutrient additions for enhanced pollutant degradation. Wood-rotting and other fungi have also
164 received considerable attention for the bleaching of dyes and industrial effluents, and
165 biotreatment of various agricultural wastes such as forestry, pulp and paper by-products,
166 sugar cane bagasse, coffee pulp, sugar beet pulp, apple and tomato pulp, and cyanide (42).

167

168 As mentioned, fungi are highly important in the degradation of naturally-occurring complex
169 molecules in terrestrial and aquatic habitats. Since around 95% of plant tissue is composed of
170 carbon, hydrogen, oxygen, nitrogen, phosphorus and sulfur, decomposition activities of fungi
171 are clearly important in relation to redistribution of these elements between organisms and
172 environmental compartments. As well as C, H, O, N, P, and S, another 15 elements are
173 typically found in living plant tissues - K, Ca, Mg, B, Cl, Fe, Mn, Zn, Cu, Mo, Ni, Co, Se,

174 Na, Si. However, all 90 or so naturally-occurring elements may be found in plants, mostly at
175 low concentrations although this may be highly dependent on environmental conditions.
176 These include toxic and inessential metals and metalloids including As, Hg, Pb and U. Some
177 plants accumulate relatively high concentrations of metals like Ni and Cd. Plant metal
178 concentrations may reflect environmental conditions and provide a bioindicator of toxic
179 metal pollution or a metalliferous substrate. Metal-accumulating plants are also receiving
180 attention in bioremediation (=phytoremediation).

181

182 Similar concepts of element cycling also relate to animal and microbial biomass. Animals
183 also contain multiple elements in varying amounts. The human body (like other organisms) is
184 mostly water and around 99% of the mass comprises oxygen, carbon, hydrogen, nitrogen,
185 calcium and phosphorus. However, many other elements are present in lower amounts
186 including substances taken up as contaminants in food and water. It follows that
187 decomposition, degradative and pathogenic activities of fungi are linked to the redistribution
188 and cycling of all these constituent elements on local and global scales. There must be a
189 fungal component therefore in the biogeochemical cycles of virtually all biomass-associated
190 elements (3,21). The release of elements and nutrient moieties through degradation makes
191 them available to other microorganisms and plants, and also chemical interaction with the
192 environmental pool of different chemical species.

193

194 **FUNGAL INTERACTIONS WITH THE INORGANIC ENVIRONMENT: ROCKS,** 195 **MINERALS AND METALS**

196

197 **Bioweathering**

198 Rocks and minerals represent a vast reservoir of elements, many essential for life, and such
199 elements must be released in forms that may be assimilated by the biota. These include essential
200 metals as well as elements like S and P (3,44). Many important microbial processes are
201 influenced by minerals including nutrient acquisition, cell adhesion and biofilm formation (45).
202 Essential nutrients and environmental contaminants sorbed to mineral surfaces can be acquired
203 or removed by organisms including metals and organic compounds (46,47). Other elements
204 and nutrients may be released from minerals as a result of bioweathering, and fungi have
205 notable activities in this context (3,16,24,48).

206

207 Bioweathering can be defined as the erosion, decay and decomposition of rocks and minerals
208 mediated by living organisms. Fungi are well suited as geoactive weathering agents since they
209 possess a variety of growth, metabolic and morphological strategies and can be resistant to a
210 range of environmental extremes such as metal toxicity, UV radiation, and desiccation. Their
211 mutualistic associations with plants (mycorrhizas), algae and cyanobacteria (lichens) are
212 particularly significant geoactive agents (3,16,24,48). The ability of fungi to translocate water,
213 ions and nutrients within the mycelial network is another important feature for exploiting
214 heterogeneous environments (49-51).

215

216 Fungi appear to be ubiquitous components of the microbiota of all rocks, building stone and
217 concrete, and have been reported from a wide range of rock types, e.g. limestone, marble,
218 granite, sandstone, basalt, gneiss, dolerite and quartz, even from the most extreme
219 environments (9,16,48). Rock surfaces may be subject to moisture deficit and nutrient
220 limitation although many species can tolerate extremes of UV irradiation, salinity, pH, and
221 water potential (16,24,25,48,52). Nutrients can be scavenged from the atmosphere and
222 rainwater, and they also use organic and inorganic residues on surfaces or within cracks and

223 fissures, waste products of other microorganisms, decaying plants and insects, dust particles,
224 aerosols and animal faeces as nutrient sources (24). Fungi may receive protection from
225 environmental extremes by the presence of melanin pigments and mycosporines in their cell
226 walls, and by the production of mucilaginous exopolymeric substances that may entrap
227 inorganic particulates, e.g. clay minerals, providing further protection (9,53). Fungal
228 interactions with rock-mineral substrates can result in dissolution and biodeterioration but also
229 the formation of patinas, films, varnishes, and crusts (3,9). In soil, fungus-mineral interactions
230 are also an integral component of environmental cycling of elements and nutrients (4,21).

231

232 Biomechanical deterioration of rocks and minerals can occur through hyphal penetration and
233 burrowing into decaying material and along crystal planes in, e.g. calcitic and dolomitic rocks
234 (3,24,54). Intracellular turgor pressure may be a significant factor in biomechanical disruption
235 (55,56). Spatial exploration of the environment to locate and exploit new substrates is
236 facilitated by a range of sensory responses that determine the direction of hyphal growth such
237 as thigmotropism (or contact guidance) (57). Biochemical weathering of rocks and minerals
238 can occur through excretion of geoactive metabolites (58,59), and this is believed to be a more
239 significant process than mechanical degradation although a combination of mechanisms is
240 often likely. This can result in pitting and etching of surfaces to complete dissolution of mineral
241 grains (60-62). Bioweathering is a highly significant process and has direct consequences not
242 only for rock and mineral dissolution, but the mobilization and immobilization of metals,
243 nutrient release, and the formation of secondary minerals (2,3).

244

245 **Metal mobilization**

246 Metal mobilization from rocks, minerals, soil and other substrates can be a consequence of
247 protonolysis, carbonic acid formation from respiratory CO₂, complexation by Fe(III)-binding

248 siderophores and other excreted metabolites, e.g. amino acids, phenolic compounds, and
249 organic acids, and methylation (for e.g. Hg, Se and As) which can result in volatilization.
250 Fungal-excreted carboxylic acids can attack mineral surfaces providing protons as well as a
251 metal-chelating anion, e.g. citrate (58). Oxalic acid can leach metals that form soluble oxalate
252 complexes, e.g. Al and Fe (63). Solubilization mechanisms can result in metal mobilization
253 from toxic metal containing minerals, e.g. pyromorphite ($\text{Pb}_5(\text{PO}_4)_3\text{Cl}$), contaminated soil and
254 other solid wastes (64-66). Fungi may also mobilize metals and attack mineral surfaces by
255 redox transformations: Fe(III) and Mn(IV) solubility is increased by reduction to Fe(II) and
256 Mn(II) respectively. Fungal reduction of Hg(II) to volatile elemental Hg(0) has also been
257 recorded (67). As discussed earlier, metals may be mobilized from organic substrates during
258 decomposition (21).

259

260 **Metal immobilization**

261 Fungi are effective accumulators of metals and related substances. Important mechanisms
262 include biosorption to cell walls, pigments and exopolymers, intracellular transport,
263 accumulation and sequestration, or bioprecipitation on and/or around hyphae (3,53,68-76).
264 Living or dead fungal biomass are effective biosorbents for a variety of metals including Ni,
265 Zn, Ag, Cu, Cd and Pb as well as actinides, e.g. U, Th, with a variety of functional groups
266 being involved (24,53,76). The presence of chitin, and pigments like melanin, may enhance the
267 ability of fungal biomass to act as a biosorbent. Fungal biomineralization processes lead to
268 metal immobilization as biominerals or elemental forms, as described below (3).

269

270 **Biomineralization**

271 Biomineralization refers to the processes by which organisms form minerals. Biologically-
272 induced mineralization (BIM) is where the organism modifies the local microenvironment

273 creating conditions amenable for extracellular chemical precipitation of mineral phases. The
274 organism does not appear to control the biomineralization process in BIM while a great degree
275 of control over biomineralization is exerted in biologically-controlled biomineralization
276 (BCM), e.g. the complex cellular biomineral structures found in certain other eukaryotes like
277 diatoms (77). Fungal biomineralization therefore usually refers to biologically-induced
278 mineralization. This can result from the bioweathering mechanisms discussed previously such
279 as redox transformations and metabolite excretion (78,79) and organic matter decomposition
280 where released substances re-precipitate with metals in the microenvironment, and *vice versa*
281 (4,21,80-82). As mentioned, fungal surfaces provide many reactive sites for sorption (\equiv
282 biosorption) and this can also lead to the formation of mineral precipitates (2,71,83).

283

284 **Common Mineral and Biomineral Transformations by Fungi**

285 Fungi are involved in many environmental mineral transformations at differing scales (84-86).
286 They are clearly a very important group of geoactive organisms especially when considering
287 their ubiquity and capacity for production of mineral-transforming metabolites, their symbiotic
288 associations, and the aforementioned consequences of their major significance in organic
289 matter decomposition (4,5).

290

291 **Carbonates** Insoluble carbonates may be broken down by fungal attack, usually the result of
292 acid formation (87-89). Such activity is particularly evident on limestones and marble used in
293 building construction, but can also occur in natural limestone (88,90). Fungal attack on
294 carbonates (dolomites and limestones) can result in transformation of these substrates to
295 dolomite ($\text{CaMg}(\text{CO}_3)_2$), glushinskite ($\text{MgC}_2\text{O}_4 \cdot 2\text{H}_2\text{O}$), weddellite ($\text{CaC}_2\text{O}_4 \cdot 2\text{H}_2\text{O}$),
296 whewellite ($\text{CaC}_2\text{O}_4 \cdot \text{H}_2\text{O}$), and possibly struvite ($\text{NH}_4\text{MgPO}_4 \cdot 6\text{H}_2\text{O}$) (91).

297

298 Certain fungi can deposit calcium carbonate extracellularly (92-95). Calcite (CaCO_3) and
299 calcium oxalate monohydrate (whewellite; $\text{CaC}_2\text{O}_4 \cdot \text{H}_2\text{O}$) was precipitated on hyphae of
300 *Serpula himantioides* when grown in simulated limestone microcosms (93). Urease-positive
301 fungi degrade urea liberating carbonate (96). This process results in the precipitation of metal-
302 containing carbonates which provides a means of metal immobilization and biorecovery (94).
303 Incubation of *Neurospora crassa* in urea-containing media resulted in the formation of calcite,
304 as well as carbonates containing other metals. When a carbonate-laden *N. crassa* culture
305 supernatant was mixed with CdCl_2 , the Cd was precipitated in the form of highly pure otavite
306 (CdCO_3) (94). After incubation in media containing urea and CaCl_2 and/or SrCl_2 ,
307 *Pestalotiopsis* sp. and *Xepiculopsis graminea* (syn. *Myrothecium gramineum*), isolated from
308 calcareous soil, precipitated calcite (CaCO_3), strontianite (SrCO_3), vaterite in different forms
309 [CaCO_3 , $(\text{Ca}_x\text{Sr}_{1-x})\text{CO}_3$] and olekminskite [$\text{Sr}(\text{Sr},\text{Ca})(\text{CO}_3)_2$] suggesting that urease-positive
310 fungi could play an important role in the environmental fate, bioremediation or biorecovery of
311 Sr or other metals and radionuclides that form insoluble carbonates (95). *Paecilomyces*
312 *javanicus* mediated the formation of an unknown lead mineral phase after incubation in liquid
313 media with lead shot. After 2 weeks incubation, precipitated mineral phase particles were found
314 to contain plumbonacrite ($\text{Pb}_{10}(\text{CO}_3)_6\text{O}(\text{OH})_6$). However, after 4 weeks incubation, the lead
315 particles that accumulated inside the fungal pellets were transformed into a white mineral phase
316 composed of lead oxalate (PbC_2O_4), hydrocerussite ($\text{Pb}_3(\text{CO}_3)_2(\text{OH})_2$) and a new lead
317 hydroxycarbonate mineral species, thus revealing novel steps in lead carbonation by fungi (97).
318

319 **Oxalates** Calcium oxalate is the most common form of oxalate in the environment, occurring
320 as the dihydrate ($\text{CaC}_2\text{O}_4 \cdot 3\text{H}_2\text{O}$, weddellite) or the more stable monohydrate ($\text{CaC}_2\text{O}_4 \cdot \text{H}_2\text{O}$,
321 whewellite) (59,79). Calcium oxalate can be associated with free-living, pathogenic and plant
322 symbiotic fungi, and lichens, and is formed by precipitation of soluble calcium as the oxalate

323 (59,61,87,98,99). Fungal calcium oxalate can exhibit a variety of crystalline forms (tetragonal,
324 bipyramidal, plate-like, rhombohedral or needles) (100). Calcium oxalate has an important
325 influence on soil biogeochemistry, acting as a calcium reservoir, and can also influence
326 phosphate availability. Fungi can produce many other metal oxalates on interacting with a
327 variety of different metals and metal-bearing minerals, e.g. Ca, Cd, Co, Cu, Mg, Mn, Sr, Zn,
328 Ni and Pb (3,59,64,79,101-103). The formation of toxic metal oxalates may contribute to
329 fungal metal tolerance (53,102). In many arid and semi-arid regions, calcareous soils and near
330 surface limestones (calcretes) are secondarily cemented with calcite (CaCO_3) and whewellite
331 (calcium oxalate monohydrate, $\text{CaC}_2\text{O}_4\cdot\text{H}_2\text{O}$) and the presence of fungal filaments
332 biomineralized with these substances has been reported (52). Calcium oxalate can also be
333 degraded to calcium carbonate, and this may again cement pre-existing limestones (104). Other
334 experimental work has demonstrated fungal precipitation of secondary calcite, whewellite, and
335 glushkinskite ($\text{MgC}_2\text{O}_4\cdot 2\text{H}_2\text{O}$) (3,16,48,93). Fungal attack on a dolomitic and seawater
336 substrate resulted in the formation of Ca-oxalates (weddellite, $\text{CaC}_2\text{O}_4\cdot 2\text{H}_2\text{O}$; whewellite,
337 $\text{CaC}_2\text{O}_4\cdot\text{H}_2\text{O}$) and glushinskite ($\text{MgC}_2\text{O}_4\cdot 2\text{H}_2\text{O}$) (105).

338

339 **Oxides** Several fungi can oxidize Mn(II) to Mn(IV) O_2 including *Acremonium* spp.
340 (17,106,107). Fungal oxidation is probably non-enzymatic in many cases although
341 involvement of laccase and/or multicopper oxidases have been shown in ascomycetes (17,106).
342 Non-enzymatic microbial Mn^{2+} oxidation may be effected through production of organic acids
343 such as citrate, lactate, malate, gluconate, or tartrate. Some fungi can oxidize Mn(II) and Fe(II)
344 in metal-bearing minerals such as siderite (FeCO_3) and rhodochrosite (MnCO_3) resulting in
345 their precipitation as oxides (108). Manganese and iron oxides are major components (20–
346 30%) along with clay (~60%) and various trace elements in desert varnish (9,108). Oxidation
347 of Fe(II) and Mn(II) by fungi can lead to the formation of dark patinas on glass surfaces (109).

348 Manganese-reducing microbes may mobilize oxidized manganese, releasing it into the aqueous
349 phase. Most of those fungi that reduce Mn(IV) oxides reduce them indirectly (non-
350 enzymatically) with the likely mechanism being the production of metabolic products that act
351 as reductants for Mn(IV) such as oxalate (1,103).

352

353 **Phosphates** Phosphorus occurs primarily as organic phosphate esters and inorganic forms,
354 e.g. calcium, aluminium, and iron phosphates. Organic phosphates are broken down by
355 phosphatases which liberate orthophosphate during the microbial decomposition of organic
356 material. Fungi also mobilize orthophosphate from insoluble inorganic phosphates by
357 producing acids or chelators, e.g. gluconate, citrate, oxalate, and lactate, which complex the
358 metal resulting in dissociation. Phosphate-solubilization is very important in the plant
359 mycorrhizosphere (110). Microbes can also play a role in the formation of phosphate minerals
360 such as vivianite ($\text{Fe}_3(\text{PO}_4)_2 \cdot 8\text{H}_2\text{O}$), strengite ($\text{FePO}_4 \cdot 2\text{H}_2\text{O}$), and variscite ($\text{AlPO}_4 \cdot 2\text{H}_2\text{O}$).
361 The orthophosphate may be derived from organic phosphate degradation while Fe or Al may
362 arise from solubilization of other minerals. Such formation of phosphate minerals is probably
363 most common in soil (1). Fungal biodeterioration of metallic lead can result in pyromorphite
364 ($\text{Pb}_5[\text{PO}_4]_3\text{X}$ [X= F, Cl or OH]) formation (111-113). Many fungi can solubilize uranium
365 oxides and depleted uranium and reprecipitate secondary uranium phosphate minerals,
366 uramphite and/or chernikovite, which can encrust fungal hyphae to high accumulation values
367 (73,74,114). These minerals appear capable of long-term U retention (73,74,114,115).
368 *Aspergillus niger* and *Paecilomyces javanicus* precipitated U-containing phosphate
369 biominerals when grown with an organic P source with the hyphal matrix acting to localize the
370 uranium minerals. The uranyl phosphates identified included potassium uranyl phosphate
371 hydrate ($\text{KPUO}_6 \cdot 3\text{H}_2\text{O}$), meta-ankoleite [$(\text{K}_{1.7}\text{Ba}_{0.2})(\text{UO}_2)_2(\text{PO}_4)_2 \cdot 6\text{H}_2\text{O}$], uranyl phosphate
372 hydrate [$(\text{UO}_2)_3(\text{PO}_4)_2 \cdot 4\text{H}_2\text{O}$], meta-ankoleite ($\text{K}(\text{UO}_2)(\text{PO}_4) \cdot 3\text{H}_2\text{O}$), uramphite

373 (NH₄UO₂PO₄·3H₂O) and chernikovite [(H₃O)₂(UO₂)₂(PO₄)₂·6H₂O] (80). These organisms
374 could also mediate lead bioprecipitation during growth on organic P substrates (81). These
375 minerals were identified as pyromorphite (Pb₅(PO₄)₃Cl) which was only produced by *P.*
376 *javanicus*, and lead oxalate (PbC₂O₄), which was produced by *A. niger* and *P. javanicus* (81).
377 Several yeasts could also mediate lead bioprecipitation when utilizing an organic phosphorus-
378 containing substrate (glycerol 2-phosphate, phytic acid) as sole phosphorus source. The
379 minerals precipitated here included lead phosphate (Pb₃(PO₄)₂), pyromorphite (Pb₅(PO₄)₃Cl),
380 anglesite (PbSO₄), and the lead oxides massicot and litharge (PbO). All yeasts examined
381 produced pyromorphite, and most produced anglesite (82).

382

383 **Silicates** Silicates comprise 30% of all minerals and about 90% of the Earth's crust (116)
384 (1,60,116). Many species of fungi play a role in the dissolution of silicates and therefore in the
385 formation of clay minerals, and in soil and sediment formation (54, 87, 117-122). The presence
386 of clay minerals can be a typical symptom of rock bioweathering by lichens and
387 ectomycorrhizas (118,119). Bioweathering is mainly indirect, through the production of
388 metabolites together with biomechanical effects (123,124). Geoactive metabolites may be
389 excreted into the bulk phase but may also be produced by adhering organisms on silicate
390 surfaces resulting in etching (125,126). After colonization of sheets of muscovite, a
391 phyllosilicate mineral, by *Aspergillus niger*, dissolution was evident by a network of fungal
392 "footprints" that reflected coverage by the mycelium (126). New biominerals resulted from
393 fungal interactions with both zinc silicate and zinc sulfide, largely resulting from organic acid
394 excretion. Zinc oxalate dihydrate was formed and mineral surfaces showed varying patterns of
395 bioweathering and biomineral formation (127). Silicate dissolution may release limiting
396 nutrients like bound P and Fe. In lichen bioweathering of silicates, calcium, potassium, iron,
397 clay minerals and nanocrystalline aluminous iron oxyhydroxides become mixed with fungal

398 organic polymers (118), while biotite ($\text{K}(\text{Mg,Fe(II)})_3\text{AlSi}_3\text{O}_{10}(\text{OH,O,F})_2$) was penetrated by
399 fungal hyphae along cleavages, partially converting it to vermiculite
400 ($(\text{Mg,Fe(II),Al})_3(\text{Al,Si})_4\text{O}_{10}(\text{OH})_2 \cdot 4\text{H}_2\text{O}$) (117). The fungal partner has also been reported to
401 be involved in formation of secondary silicates, such as opal ($\text{SiO}_2 \cdot n\text{H}_2\text{O}$) and forsterite
402 (Mg_2SiO_4), in lichen thalli (128). The transformation rate of mica and chlorite to clay minerals
403 was pronounced in ectomycorrhizosphere soil and probably a result production of organic acids
404 and direct extraction of K^+ and Mg^{2+} by fungal hyphae (119). Fungal-clay mineral interactions
405 also play an important role in soil development, aggregation and stabilization (16,129).
406 Interactions between clay minerals and fungal biomass alters the sorptive properties of both
407 clay minerals and fungal hyphae (130,131) and also affect the size, shape and structure of
408 mycelial pellets (132).

409

410 **Reduction or oxidation of metals and metalloids** Many fungi can precipitate reduced forms
411 of metals and metalloids, e.g. Ag(I) reduction to elemental silver Ag(0); selenate [Se(VI)] and
412 selenite [Se(IV)] to elemental selenium [Se(0)]; tellurite [Te(IV)] to elemental tellurium
413 [Te(0)] (133-135). Reduction of Hg(II) to volatile Hg(0) can also be mediated by fungi (67,68).
414 Increased arsenate reduction contributed to tolerance in an *Aspergillus* sp. (136,137). Mn
415 oxidation/reduction has been described above.

416

417 **Other mycogenic minerals** A range of minerals other than those mentioned above have been
418 found in association with fungi (2,3,73,74,77,80-82,114). Mycogenic secondary minerals
419 associated with fungal hyphae and lichen thalli include desert varnish (MnO and FeO),
420 ferrihydrite ($5\text{Fe}_2\text{O}_3 \cdot 9\text{H}_2\text{O}$), iron gluconate, calcium formate, forsterite, goethite (α -
421 $\text{Fe}^{3+}\text{O}(\text{OH})$), moolooite ($\text{Cu}(\text{C}_2\text{O}_4) \cdot 0.4\text{H}_2\text{O}$), halloysite ($\text{Al}_2\text{Si}_2\text{O}_5(\text{OH})_4$), and hydrocerussite
422 ($\text{Pb}_3(\text{CO}_3)_2(\text{OH})_2$) (16,48,52,108,120,128,138). Another biogenic mineral (tepius) has been

423 identified in association with a lichen carpet occurring in high mountain ranges in Venezuela
424 (128).

425

426 **Halide transformations** Several fungi have the ability to produce a variety of atmospheric
427 methyl halides. This ability is widespread in both free-living and symbiotic fungi, and is
428 dependent on substrate concentration and community composition (139,140). The production
429 of chloromethane (CH₃Cl) by wood-rotting fungi, e.g. *Phellinus* spp., may be particularly
430 significant with one estimate of annual global input to the atmosphere from this source being
431 160 000 t of which 75% is released from tropical and subtropical forests (139). Filamentous
432 fungi may also contribute to the global circulation of stable iodine and also the long-lived
433 radioiodine, ¹²⁹I (half-life: 1.6 x 10⁷ years), released from nuclear facilities (141).

434

435 **FUNGAL SYMBIOSES IN GEOMYCOLOGY**

436 Many fungi form partnerships with plants (mycorrhizas) and algae or cyanobacteria (lichens)
437 that are significant geoactive agents. In general terms, the mycobiont is provided with carbon
438 by the photobionts, while the mycobiont may protect the symbiosis from harsh environmental
439 conditions (e.g., desiccation, metal toxicity), and provide increased access to inorganic
440 nutrients such as phosphate and essential metals.

441

442 Lichens are fungi that exist in facultative or obligate symbioses with one or more
443 photosynthesizing partners occurring in almost all surface terrestrial environments (142).

444 Lichens play important roles in retention and distribution of nutrient (e.g. C, N) and trace
445 elements, in soil formation, and rock bioweathering (54,87,143). Lichens can accumulate
446 metals such as lead (Pb) and copper (Cu), and many other elements, including radionuclides
447 (144). They also form a variety of metal-organic biominerals, e.g. oxalates, especially during

448 growth on metal-rich substrates (98,143). On copper sulfide bearing rocks, precipitation of
449 copper oxalate (moolooite) can occur within lichen thalli (145,146).

450

451 The majority of terrestrial plants depend on symbiotic mycorrhizal fungi (147,148).

452 Mycorrhizal fungi can mediate metal and phosphate solubilization from mineral sources,
453 extracellular precipitation of metal oxalates, and immobilize metals within biomass
454 (65,66,149-157). Such activities lead to changes in the physico-chemical characteristics of the
455 root environment and enhanced bioweathering of soil minerals (55,157,158). Furthermore,
456 ectomycorrhizal mycelia may respond to different soil silicate and phosphate minerals (e.g.
457 apatite, quartz, potassium feldspar) by regulating growth and metabolic activity (159,160).

458

459 Mycorrhizal fungi often excrete bioweathering agents such as low molecular weight
460 carboxylic acids and siderophores (65,161). Ectomycorrhizal fungi can also form narrow
461 pores in weatherable minerals in podzol E horizons, probably by dissolution of Al silicates
462 (162,163). Such excretions can also release elements from apatite and wood ash (K, Ca, Ti,
463 Mn, Pb) (164). Ericoid mycorrhizal and ectomycorrhizal fungi can dissolve several
464 cadmium, copper, zinc and lead-bearing minerals including metal phosphates
465 (65,66,152,161,165). Mobilization of phosphorus from inorganic and organic phosphorus
466 sources is generally regarded as one of the most important functions of mycorrhizal fungi,
467 and this can also result in redistribution of incorporated metals, and the formation of other
468 secondary minerals including other metal phosphates. The ericoid mycorrhiza *Oidiodendron*
469 *maius* can solubilize zinc oxide and phosphate (161). Many ericoid mycorrhizal and
470 ectomycorrhizal fungi are able to solubilize zinc, cadmium, copper phosphates and lead
471 chlorophosphate (pyromorphite) releasing phosphate and component metals (65,152). An
472 association of arbuscular mycorrhizal fungi (AMF) with *Lindenbergia philippensis*, sampled

473 from a Zn-contaminated settling pond at a zinc smelter, enhanced Zn accumulation in Zn-
474 loaded rhizosphere sediment compared to treatments that suppressed AMF colonization. A
475 significant proportion of Zn was present as crystalline and other solid materials that were
476 associated with the root mucilaginous sheath (166). Such results may indicate a role for AMF
477 in enhancing Zn immobilization in the rhizosphere of plants that successfully colonize Zn
478 mining and smelting disposal sites (153,166,168).

479

480 **ENVIRONMENTAL AND APPLIED SIGNIFICANCE OF GEOMYCOLOGY**

481 The kinds of processes detailed previously can impact upon human society not only through
482 their environmental significance and biotechnological applications, but also in deleterious
483 contexts such as biodeterioration and biocorrosion. The biodeterioration of stone and mineral
484 artefacts represents a loss of cultural heritage (13,14). Materials used to stabilize building
485 blocks (mortar) and to coat surfaces prior to painting (plaster or stucco) are also susceptible
486 to biodeterioration (13). Highly deteriorated stone surfaces provide a “proto-soil” for
487 colonization by mosses, ferns and higher plants (14). Mechanisms of stone deterioration are
488 complex and include most of the direct and indirect mechanisms previously discussed for
489 mineral dissolution (13,169). Extracellular polymeric substances (EPS) are also capable of
490 metal complexation and weakening of mineral lattices through wetting and drying cycles, as
491 well as the production of efflorescences, i.e. secondary minerals produced through reaction of
492 anions from excreted acids with cations from the stone (170). Physical damage may be
493 caused by hyphal penetration of weakened areas (88,138). Lichens cause damage due to
494 penetration by their rhizines, composed of fungal filaments, and expansion/contraction of the
495 thallus on wetting/drying (171). “Lichen acids”, mainly oxalic acid, cause damage at the
496 stone/lichen interface, and lichen thalli may accumulate up to 50% calcium oxalate,
497 depending on the substrate (172,173). In addition, carbonic acid formed in the lichen thallus

498 can solubilize calcium and magnesium carbonates in calcareous stone (174). Fungal
499 biodeterioration of ancient ivory (natural apatite; walrus tusk) was accompanied by
500 widespread etching and tunneling by hyphae and extensive formation of calcium oxalate
501 monohydrate, whewellite (175). Concrete and cement can be biodeteriorated and in some
502 environments, fungi dominate the concrete-deteriorating microbiota (13,14,176-178).
503 Microbial attack on concrete is mediated by protons, inorganic and organic acids and the
504 production of hydrophilic slimes leading to biochemical and biomechanical deterioration
505 (13,75,169). Several species of microfungi were able to colonize samples of the concrete used
506 as radioactive waste barrier in the Chernobyl reactor and leached iron, aluminium, silicon and
507 calcium, and re-precipitated silicon and calcium oxalate (75).

508

509 Mineral and metal solubilization mechanisms enable metal removal from industrial wastes,
510 low-grade ores, and metal-bearing minerals. This may have application in bioremediation,
511 metal biorecovery and recycling (58,68,179,180). Metals can be solubilized from fly ash
512 (originating from municipal solid waste incineration), contaminated soil, electronic scrap and
513 other waste materials by fungal activity (179,181). Although fungal systems cannot compare
514 with the efficiency of bacterial bioleaching, they may be more suited to specific bioreactor
515 applications (58). A variety of fungal mechanisms result in metal immobilization such as
516 biosorption, bioaccumulation and bioprecipitation. Biosorption is a physico-chemical
517 process, and is a property of both living and dead organisms (and their components), and
518 fungi are effective agents for removal of metals, radionuclides and other substances from
519 solution (69,70,71,76,130,182-193). Urease-positive fungi can be used to precipitate metal-
520 containing carbonates, some in nanoscale dimensions, thus providing a means of metal
521 biorecovery as well as potentially useful nanoscale biomineral products (94,95). Similarly,
522 the formation of other insoluble metal compounds by fungi or their metabolites could also be

523 considered as a means to biorecover metals, metalloids and radionuclides, e.g. oxalates,
524 oxides, oxalates, and phosphates, as well as the production of elemental metal or metalloid
525 forms (2,78). Some biomineral and elemental products, including those of nanoscale
526 dimensions, are of relevance to the production of novel advanced biomaterials with
527 applications in metal and radionuclide bioremediation, antimicrobial treatments (e.g. nano-
528 silver), solar energy and electrical battery applications, and microelectronics (194). In a novel
529 approach, urease-positive *Neurospora crassa* was used to precipitate manganese carbonate.
530 After thermal treatment at 300°C, the carbonized biomass-manganese oxide composite
531 material was used in lithium-ion batteries (LiB) and supercapacitors where it was found to
532 exhibit excellent electrochemical properties. In LiB, around 90% charge capacity was
533 retained after 200 charge-discharge cycles (195).

534

535 The ability of fungi and bacteria to transform metalloids has been successfully used for
536 bioremediation of contaminated land and water. Selenium methylation results in
537 volatilization and this has been used to remove selenium from the San Joaquin Valley and
538 Kesterson Reservoir, California (196). Mycorrhizal associations may have application in
539 phytoremediation (197,198), the use of plants to remove or detoxify environmental pollutants
540 (199), by metal phytoextraction or by acting as a biological barrier (200-202). Glomalin, an
541 insoluble glycoprotein, is produced in copious amounts on hyphae of arbuscular mycorrhizal
542 fungi and can sequester metals such as Cu, Cd and Pb (203). Arbuscular mycorrhizal fungi
543 can also decrease U translocation from plant roots to shoot (204-206). For ericaceous
544 mycorrhizas, the fungus prevents translocation of Cu and Zn to host plant shoots
545 (147,207,208). The development of stress-tolerant plant-mycorrhizal associations may be a
546 promising strategy for phytoremediation and soil amelioration (161,209,210).

547

548 Some of the geomycological processes detailed previously may have consequences for
549 abiotic soil treatment processes, notably the immobilization of toxic metals by phosphate
550 formation. Apatite $\text{Ca}_5(\text{PO}_4)_3(\text{F},\text{Cl},\text{OH})$, pyromorphite $\text{Pb}_5(\text{PO}_4)_3\text{Cl}$, mimetite
551 $\text{Pb}_5(\text{AsO}_4)_3\text{Cl}$ and vanadinite $\text{Pb}_5(\text{VO}_4)_3\text{Cl}$ are the most common prototypes of the apatite
552 mineral family. Such minerals hold promise for stabilization and recycling of industrial and
553 nuclear waste and have been explored for treatment of lead-contaminated soils and waters
554 (211-216). The stability of these minerals is therefore of interest in any soil remediation
555 strategy seeking to reduce the effects of potentially-toxic elements, like Pb, V and As. For
556 example, pyromorphite is a highly insoluble lead phosphate mineral under a wide range of
557 geochemical conditions and has often been suggested as a means to reduce Pb bioavailability.
558 However, solubilization of pyromorphite and formation of lead oxalate by several free-living
559 and symbiotic fungi demonstrates that pyromorphite may not be as effective at immobilizing
560 lead as some previous studies have suggested (64,65). Similarly, despite the insolubility of
561 vanadinite, fungi exerted both biochemical and biophysical effects on the mineral including
562 etching, penetration and the formation of new biominerals (217). Lead oxalate was
563 precipitated by *Aspergillus niger* during the bioleaching of vanadinite and mimetite which
564 implies a general fungal mechanism for the transformation of lead-containing apatite group
565 minerals (e.g. vanadinite, pyromorphite, mimetite) (217,218). This pattern of fungal
566 bioweathering of lead apatites could be extended to other metal apatites, such as calcium
567 apatite $[\text{Ca}_5(\text{PO}_4)_3(\text{OH},\text{F},\text{Cl})]$. Here, the formation of monohydrated (whewellite) and
568 dihydrated (weddelite) calcium oxalate can be accomplished by many different fungal
569 species (79,93,99,175,219,220). The ability of free-living and mycorrhizal fungi to transform
570 toxic metal-containing minerals should therefore be taken into account in risk assessments of
571 the long-term environmental consequences of *in situ* chemical remediation techniques,
572 revegetation strategies or natural attenuation of contaminated sites. The bioweathering

573 potential of fungi has been suggested as a possible means for the bioremediation of asbestos
574 rich soils. Several fungi could extract iron from asbestos mineral fibres (e.g. 7.3% from
575 crocidolite and 33.6% from chrysotile by a *Verticillium* sp.), thereby removing the reactive
576 iron ions responsible for DNA damage (221).

577

578 **CONCLUSIONS**

579 The geoactive roles of fungi have often received scant attention in geomicrobiological
580 contexts but they are of clear importance in several key areas. These include a variety of
581 organic and inorganic transformations important in nutrient and element cycling, rock and
582 mineral bioweathering, mycogenic biomineral formation, and metal-fungal interactions.
583 Lichens and mycorrhizas are of special significance as geoactive agents. Organic matter
584 decomposition is important for the cycling of major biomass-associated elements, e.g. C, H,
585 N, O, P and S as well as all other elements that may be found in lower concentrations.
586 Transformations of metals and minerals are central to many geomicrobial processes, and
587 fungi can effect changes in metal speciation, toxicity and mobility, as well as mediate mineral
588 formation or dissolution. Such mechanisms are important components of natural
589 biogeochemical cycles for metals as well as associated elements in biomass, soil, rocks and
590 minerals, e.g. S and P, and metalloids, actinides and metal radionuclides. It is within the
591 terrestrial environment where fungi have the greatest abundance and geochemical influence.
592 However, they are also important in aquatic habitats and are now recognized as significant
593 components of aquatic sediments and the deep subsurface. Geomycological processes can
594 have beneficial or detrimental consequences in a human context. Beneficial applications in
595 environmental biotechnology include metal and radionuclide bioleaching, biorecovery,
596 detoxification, and bioremediation, and in the production of biominerals or metal(loid)
597 elements with catalytic or other properties in nanoparticle, crystalline or colloidal forms. The

598 latter may be relevant to the development of novel biomaterials. Adverse effects include
599 biodeterioration and destruction of natural and synthetic materials, rock and mineral-based
600 building materials (e.g. concrete), cultural heritage, biocorrosion of metals, alloys and related
601 substances, and adverse effects on radionuclide speciation, mobility and containment. The
602 ubiquity and importance of fungi in biosphere processes underlines the importance of
603 geomycology as a conceptual framework encompassing the environmental activities of fungi,
604 their impact, and their applied significance.

605

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616

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