# Bacterial and fungal geomicrobiology: a problem with communities?

G. M. GADD

*Division of Molecular and Environmental Microbiology, College of Life Sciences, University of Dundee, Dundee, DD1 5EH, Scotland, UK*

I first met Terry Beveridge at the International Symposium on Microbial Ecology in Ljubljana in 1986, and got to know him better at that conference during an organized day-trip to Venice. I was of course familiar with his published work long before then particularly that relating to metal binding by bacteria cell walls and outer layers (Beveridge & Murray, 1976, 1980; Beveridge & Koval, 1981; Beveridge *et al.*, 1982). During my early research, I was interested in metal interactions with fungi especially uptake and transport phenomena, and the research on the characterization of metal binding sites in bacterial cell walls and surfaces was a great stimulus, the Beveridge group being one of only a handful worldwide who I felt directly appealed to my own proclivities, namely the cellular biology and physiology of metal–microbe interactions but within an ecological or environmental context. I was rather slow to appreciate the wider geochemical significance of such work, such as in biomineral formation, but Beveridge *et al.* (1983) became one of my favourite papers and a major influence on my growing interest in biomineralization. I met Terry again in the flesh at a 1988 SGM conference in Warwick at which we were both speaking. I was a co-editor of the symposium volume (Poole & Gadd, 1989) and Terry provided a chapter (Beveridge, 1989). I remember that one of my slides stuck in the projector, causing abandonment of the morning session and a reconvening of the session after a tea break. The subject matter of the slide was a manganese deposit within a vacuole of a Mn-tolerant yeast strain and I had just mentioned toxic effects. My ordeal eventually over, but with the awful university conference lunch to come, a voice boomed out from the lengthening queue – 'I thought your talk was a little disjointed, Geoff!' said Terry, a big grin on his face. On another occasion after a scientific meeting, I went on a camping holiday, with my wife Julie, to the Peak District of England, and while in one of the picturesque Derbyshire

towns, was amazed to encounter Terry and his wife Jan striding across the square. I thought he was so busy and famous he could not possibly be having any spare time away from the lab, while I felt he might think badly of me as a youngster, having time off and not working every minute for the good of microbiology and my career! Latterly, we became good friends, corresponded regularly, and met at many meetings around the world. I soon realized from Terry that you need a life as well as the science! We had some nice times together and I especially remember us driving to a nice river in New England during a 1995 Environmental Microbiology Gordon Conference on a beautiful sunny day. I had a few casts with my fishing tackle and to my surprise caught a small trout about 10 cm long. Terry was suitably unimpressed, but my work was done so we lay down in the river to cool down and chew the fat. Terry said midstream 'Do you like red wine?' I of course replied in the affirmative thinking he was about to discourse at length on the mysteries of the grape but instead he directed me to a bottle of wine, opener and glasses that he had secreted in the car! So we drank some wine, immersed in the river. In 2001/2, I was awarded a Burroughs Wellcome Fund Visiting Professorship in the Microbiological Sciences to visit and work with Terry at the University of Guelph, sponsored by the ASM, and this was a great time in getting to know Terry, think about microbiology, meet other great workers, and also go fishing near his home in Elora. On a small isolated stream a few miles from his house, I hooked a small fish and simultaneously was accosted through the trees on the other bank by someone I took to be a farmer. I thought I was in trouble until the voice said 'Are you the guy who's come to stay with Terry?' 'Good grief (or similar), the guy is famous round here, too!' I thought. During my visit, I also introduced Terry to the Monty Python lumberjack song which he pretended never to have heard! He was an honoured plenary speaker at a SGM Geomicrobiology Conference I

organized in the UK in 2005 and again contributed a fine chapter (Phoenix *et al.*, 2005) to the symposium volume (Gadd *et al.*, 2005). More recently, in December 2006, Terry chaired the External Review Panel for my Division of Environmental and Applied Biology in the University of Dundee and characteristically did a thorough and precise job, one outcome of the review being the creation of a new Division of Molecular and Environmental Microbiology with me as Head. Thanks Terry! All the time I knew him, Terry was always positive and humourous about life and our conversations were always full of jokes: in serious vein, he always gave me support and encouragement. Without his example and the stimulus his work always gave me, I doubt very much if my career would have developed along the lines it did.

At the time I first met Terry, I was deeply interested in all metal–microbe interactions (Gadd & Griffiths, 1978) but my earlier research concentrated on fungal systems and their interactions with toxic metals mostly from the perspective of toxicity, uptake and tolerance (Gadd & White, 1985). I now rather mildly regret that yeasts became an experimental model, perfect for experimentation on transport (White & Gadd, 1986, 1987), but probably of little relevance to the natural environment and biogeochemistry. However, the differences in perspective between bacterial and fungal research in the area of metal–microbe interactions and the relative imbalances in knowledge regarding several important topics were striking, and in many cases still are. I was often asked by Terry why did people either work on bacteria or on fungi and rarely on both, even when considering aerobic terrestrial locations and this is a question I have thought about a lot over the years. In soil, for example, bacteria and fungi always co-exist yet a prokaryotic/eukaryotic demarcation exists, which sometimes I have found also reflected in the attitudes of certain scientists and even their societies. Some may be a result of the evolution of microbiology as a rigorous and central biological discipline while mycology was positioned as some kind of botanical curiosity. We did produce a joint contribution that detailed both bacterial and fungal metal–mineral transformations (Glasauer *et al.*, 2004), and over the years I also developed a strong interest in bacterial geomicrobiology even to the extent of working with sulfate-reducing bacteria (e.g. Smith & Gadd, 2000; Hockin & Gadd, 2003, 2006) as did Terry (Fortin & Beveridge, 1997; Fortin *et al.*, 1994; 1995). Terry's group even published a paper on metal sorption by fungal systems (Mullen *et al.*, 1989)! However, anaerobiosis is something most fungi do not do very well so we were still not addressing bacterial and fungal activities in the same location. It seems clear that in the field of geomicrobiology, a broad appreciation of fungi as agents of biogeochemical change is lacking, and apart from a fixation with the carbon (and perhaps to a lesser extent the nitrogen) cycle, they are frequently neglected in contrast to bacteria in terrestrial and subsurface ecosystems, as well as freshwater and marine environments, where fungi are also found widely. Most work in relation to the latter concentrates on

decomposition, pathogenicity, and systematics. I prefer, like Terry, to have a broad view of geomicrobiology and appreciate the importance of all kinds of organisms in aerobic and anaerobic parts of the biosphere, while still being able to work on my own personal favourites. The wider significance of microbial metal and mineral transformations in global biogeochemistry is now widely appreciated and Terry's pioneering work was instrumental in this awareness (Beveridge & Doyle, 1989). It is no surprise that geomicrobiologists are found in Earth Science/Geology Departments in many Universities around the world, and of course many former students and associates of Terry occupy such positions. It is also no surprise that microbiological research is widely presented at almost all the established geological, geochemical and mineralogical conferences. I have to thank Terry for cementing (biomineralizing?) my own perspective on the fundamental roles of microorganisms in biogeochemical processes. In the remainder of this tribute, I will outline a few other thoughts on bacterial and fungal activities which, in line with Terry's original question, may help understanding and appreciation across these fundamental divisions of life and of microbiologists.

It is commonly stated that bacteria and archaea are highly significant geochemical agents because of their incredible metabolic diversity and this is undoubtedly true (Table 1). Anaerobes, $N_2$-fixers, methanogens, metal-reducing bacteria, sulfate reducers, arsenate respirers, etc., are among the many groups of organisms commonly thought of in terms of geomicrobiology and global biogeochemistry, and the anaerobic deep subsurface is where many peculiarly prokaryotic processes are located. Eukaryotes are commonly thought of as being aerobic heterotrophs (fungi), oxygenic phototrophs (algae) or heterotrophic phagotrophs (protozoa), each group of course possessing their own communities of scientists and research priorities. However, all these groups exhibit some major biogeochemical activities. Algae are important regarding global primary productivity, $CO_2$ fixation, with some groups highly involved in Ca (coccolithophores) and Si cycling (diatoms) for example, with protozoa being regarded as prime determinants of bacterial populations as well as roles in biomineralization (e.g. radiolarians and foraminiferans, as in the white radiolarian/foraminiferan cliffs of Dover, England). Characteristic geochemical activities of fungi, that will be elaborated on later, include mineral dissolution, mineral formation, organic matter decomposition and nutrient cycling (Table 1; Fig. 1) (Gadd, 2006, 2007). Fungi are of course usually associated with aerobic locations. However, apart from several yeasts and a relatively small number of other fungi that can grow anaerobically, several other species are now found in quite 'prokaryotic locations', e.g. the anaerobic deep subsurface, deep-sea sediments, etc. (Reitner *et al.*, 2006). What are these fungi doing there? How are they interacting with the archaea and bacteria and what are they living on? Are they particularly important? Could a lack of appreciation of fungi be due to the reluctance of mycologists (or microbiologists who work with fungi) to look at environments where they

**Table 1** Comparison of selected important fungal and bacterial/archaeal activities in geobiological transformations. Broad areas of generality are clear with biggest differences relating to significance of growth form, chemolithotrophy and anaerobiosis. Anaerobic fungi, including several yeast species, have received little attention in a biogeochemical context. Many fungi are capable of sulfur compound oxidation and metal sulfide deposition, though the significance of this in relation to much more widespread prokaryotic activities is unclear. Not indicated in this Table are differences in environmental tolerances that can be marked between pro- and eukaryotes in terms of, e.g. temperature, pH, toxic metals, nutrient limitation, etc. In general terms, it may be concluded that the metabolic versatility of prokaryotes ensures more obvious survival and success in 'extreme' environments although extremophiles tolerant to extremes of temperature, acidity, alkalinity, oligotrophy, toxicants, etc. are also widely found in the eukaryotes.

| | Fungi | Bacteria/Archaea |
|---|---|---|
| Growth form | Unicellular, filamentous, and multicellular structures | Unicellular |
| | Lichens | |
| | Mycorrhizas | |
| | Biofilms; consortia; endoliths; endophytes; symbionts; pathogens etc. | |
| Metal solubilization mechanisms | Chemoorganotrophic leaching mechanisms – $H^+$ and ligand mediated; siderophores (Fe(III)); organic and inorganic metabolites; $CO_2$ (carbonic acid) | |
| | – | Chemolithotrophic leaching – $H^+$, Fe(III), $SO_4^{2-}$ |
| | Aerobic/anaerobic reductive solubilization, e.g. Fe(III) to Fe(II); Mn(IV) to Mn(II) | |
| Metal immobilization mechanisms | Sorption; redox reactions; uptake and accumulation; intracellular sequestration; organic and inorganic metabolites; secondary mineral nucleation; secondary mineral precipitation | |
| | Organellar localization | – |
| | Oxalates | – |
| | –? | Anaerobic redox reactions |
| | –? | Anaerobic sulfide precipitation |
| Other metal/metalloid transformations | Redox transformations; methylation | |
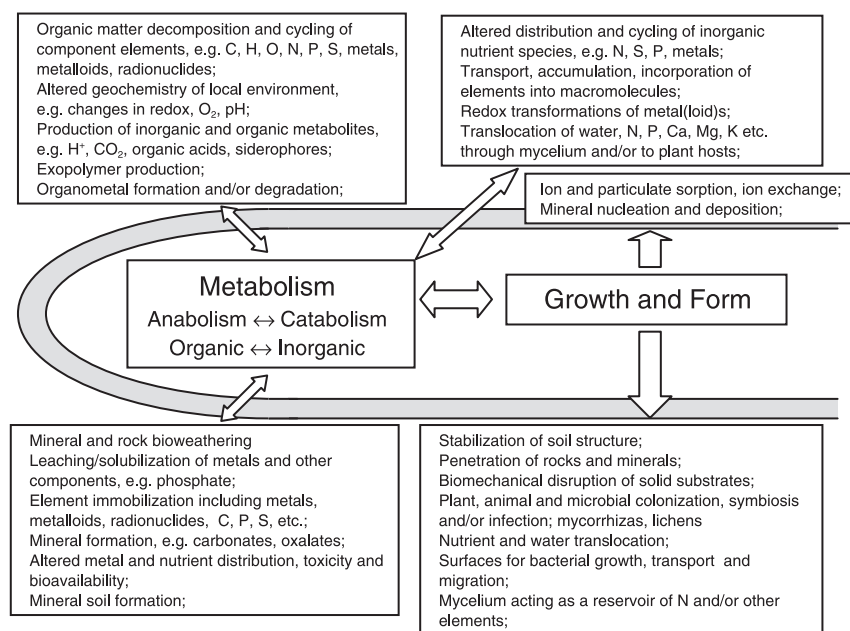


**Fig. 1** Some of the important roles and activities of fungi in biogeochemical processes. Such activities take place in aquatic and terrestrial ecosystems, as well as in artificial and man-made systems, their relative importance depending on the populations present and physicochemical factors that affect activity. The terrestrial environment is the main locale of fungal-mediated biogeochemical change, especially in mineral soils and the plant root zone, and on exposed rocks and mineral surfaces. By comparison, there is a limited amount of knowledge on fungal biogeochemistry in freshwater and marine systems, sediments, and the deep subsurface. Note that most if not all of these roles are interlinked, almost all directly or indirectly depending on the mode of fungal growth (including symbiotic partnerships) and accompanying chemoorganotrophic metabolism, in turn dependent on a utilizable carbon source for biosynthesis and energy, and other essential elements, such as N, O, P, S and many metals, for structural and cellular components.

think fungi might not be found? Or a reluctance of bacteriologists and archaeaologists (in the archaeal organism research sense) to accept that fungi may be present and perhaps even active in such locations? Similar questions could probably be asked about other 'exotic' or 'extreme' locations.

In the main, however, it is true that fungal activities are aerobic and heterotrophic and that the largest fungal populations and their prime geochemical significance occur in locations such as the soil, the plant-root zone, rock and mineral surface layers, plant surfaces, etc. (Gadd, 2007). Although they might be metabolically less diverse than prokaryotes, the majority of fungi are filamentous, and use their explorative mycelium to sense and probe their habitat, translocate nutrients, and even effect mineral transformations by biochemical and biophysical mechanisms (Boswell *et al.*, 2002). How much does this difference in morphology contribute to a divergence in microbiological specialization? In relation to environmental success, the growth form of fungi is of paramount importance but fungi

also exhibit considerable physiological diversity, for example growth over quite large pH ranges, and characteristically thriving under acidic conditions where they often dominate. They can also grow under extreme conditions including high ultraviolet radiation, high radioactivity, high salinity, oligotrophic conditions, the presence of organic and inorganic toxicants, etc. and although perhaps not matching the most extremophilic of the archaea and bacteria, still exhibit a wealth of survival responses and resistance strategies, many analogous to those found in prokaryotes (Gadd *et al.*, 1984; Gadd, 1993). Bacteria are mainly unicellular, and many are motile which enables them to sense and locate more favourable locations in their environment, providing there is enough water about. Sensory and translocatory mechanisms at hyphal tips and through the mycelium serve such a role in fungi and the growing mycelial front can be considered to be a form of motility especially as older parts of the mycelium may become moribund and die. It might be rather startling for some to visualize great swathes of advancing fungal mycelium rapidly spreading through forest soil in this way. Even more startling may be the fact that such organisms may be the world's largest living things, even dwarfing blue whales, the giant redwood and the mighty Scots pine!

Another significant adaptation of geochemical significance is the fungal habit for symbiosis. Lichens, a fungal growth form, are composed of a fungus as well as an alga and/or cyanobacterium, while mycorrhizal associations with plant roots are found in over 90% of plant species. Perhaps such complex systems are a step too far for prokaryotic researchers and both systems have their own large scientific communities. However, some reports hint at 'helper' bacteria and other tripartite interactions between the root-inhabiting bacteria, fungi and the plant hosts but these are few. For mycorrhizas, the dogma is that they are responsible for increased phosphate solubilization and uptake by the plant partner. Since phosphate is associated with metals, then these symbiotic fungi must be responsible for global amounts of metal and P cycling. These metals may be essential as well as toxic. Are these systems ever properly included in the usual element cycle diagrams found in (micro)biology text books? Mycorrhizal fungi can be involved in proton- and ligand-promoted metal mobilization, metal immobilization and extracellular precipitation of mycogenic oxalates. Indeed, it has been shown that such organisms can also respond to the various silicate and phosphate minerals encountered in the plant-root zone. Lichens are probably the most successful means for fungi to survive in extreme environments and colonize fresh rock outcrops. The significance of lichens as pioneer organisms in the early stages of mineral soil formation should be widely appreciated. Lichens can grow in almost all terrestrial surface environments and occupy an estimated 6% of the Earth's surface. Globally, they are involved in the cycling of all major elements found in the substratum, and can also accumulate metals from the substratum. Other symbioses may occur with wood-boring and other insects where fungal partners aid digestion and decomposition of plant materials.

On the subject of decomposition, fungi and bacteria are the prime organisms of importance with fungi especially being associated with the decomposition of plant materials. However, the range of organic substances used by fungi is huge and ranges from simple sugars to complex macromolecules, including xenobiotics. Degradation of the latter is relevant to environmental reclamation and bioremediation, and it is now realized by some that bacterial and fungal interactions are significant in effecting certain xenobiotic transformations in contaminated environments. However, a prokaryotic–fungal divide also exists in the biodegradation field. A collaborator once complained that during a search for xenobiotic-degrading bacteria, the enrichment cultures were routinely overgrown with fungi and bacteria could not be isolated. The idea to use the fungi instead was clearly too revolutionary but may have been more interesting! A further geochemical point is that the majority of elements can be associated with biomass in varying amounts. For example, about 95% of plant tissue is composed of C, H, O, N, P, and S while another 15 elements are typically found including K, Ca, Mg, B, Cl, Fe, Mn, Zn, Cu, Mo, Ni, Co, Se, Na and Si. After this, practically all 90 or so other elements may be found depending on what the organisms have been exposed to in their environment, e.g. As, Hg, Pb and U. A similar situation occurs in other life forms including microorganisms. Humble decomposition processes can therefore lead to a variety of element transformations and movements between environmental compartments. Any decomposition or degradative activity is therefore linked to cycling of all constituent elements on local and global scales (Fig. 2) (Gadd, 2004).

Apart from organic materials, fungi are also involved in attack of inorganic materials. They are well suited to bioweathering of rocks and minerals because of their morphological and physiological attributes and also through their symbiotic relationships (Sayer *et al.*, 1999; Burford *et al.*, 2003a,b; Gadd, 2007). Subaerial rock surfaces may be considered inhospitable but many species can deal with extremes of light, salinity, pH, water potential, and over considerable time periods. It seems fungi are ubiquitous components of all rock types, even in the harshest environments. In such locations they must often co-exist and interact with bacteria within biofilms, such interactions contributing to the formation of patinas, films, crusts, varnishes, and the like, on rocks and on mineral surfaces (Gorbushina, 2007). How much work at all is there on mixed fungal and bacterial biofilms in any context? Biomechanical attack may occur through hyphal penetration, burrowing, turgor pressure, cellular expansion, etc. and aided by sensory responses like thigmotropism (Bowen *et al.*, 2007). Accompanying biochemical attack may be through metabolite excretion including $H^+$, carboxylic acids, $CO_2$, siderophores, amino acids and phenolic compounds (Gadd, 1999, 2007).

Fundamental to almost all of these mineral transformations are metal movements and reactions and Terry uniquely connected the two processes in much of his bacterial work. This also proved to be an inspiration for my work with fungal
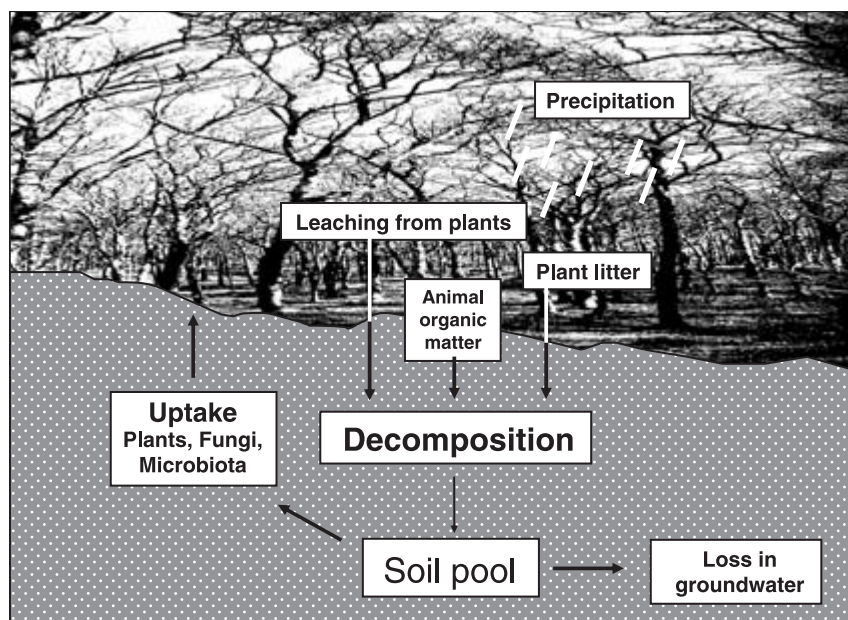
systems. As mentioned above, uptake may be a prelude to mineral formation but this also limits metal bioavailability. The biosorptive influence of both bacteria and fungi on metal bioavailability in natural ecosystems may be underrated (de Rome & Gadd, 1987; Mullen *et al.*, 1989, 1992; Walker *et al.*, 1989; Morley & Gadd, 1995; White *et al.*, 1995). Some fungal pigments like melanin can greatly enhance binding and it seems that a high proportion of fungal biomass is melanized in the natural environment. The formation of mycogenic minerals has been mentioned previously and this, together with other metal immobilization mechanisms, is analogous or similar to processes found in prokaryotes. Fungi are also capable of mobilization of metals from rocks, minerals, soil components by a variety of mechanisms including acidification, siderophores, metabolites, reductive dissolution and methylation, the latter leading to volatilization, and again all processes found in the prokaryotic world. Oxalate can leach metals that form soluble oxalate complexes, e.g. Fe(III) and Al(III), while some fungi can also reduce Hg(II) to Hg(0), the characteristic resistance mechanism of mercury-resistant bacteria!

The role of bacteria in effecting secondary mineral formation is widely appreciated (Ferris *et al.*, 1986, 1987, 1988, 1989; Beveridge, 1989; Urrutia & Beveridge, 1994; Schultze-Lam *et al.*, 1996; Fortin *et al.*, 1997). Some of our early results on, e.g. silver or thorium accumulation by fungi (Gadd & White, 1989) gave electron micrographs that looked like those produced in the Beveridge lab, albeit with bacteria and other metals, and this triggered a lasting interest in mineral deposition around cells (Burford *et al.*, 2006). Some of our fungi were examined in Terry's facility at Guelph, as in fact were some bacterial deposits (Hockin & Gadd, 2003, 2006). It is now clear that, like bacteria, fungi can also precipitate, nucleate or otherwise deposit crystalline (and amorphous) material in
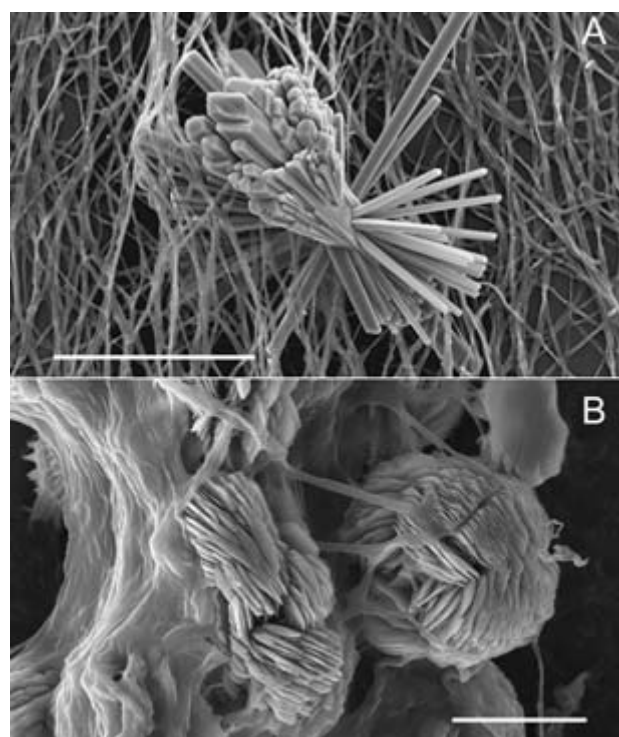


**Fig. 3** Mycogenic minerals associated with fungal biomass after growth in laboratory microcosms on various mineral substrates. (A) Strontium oxalate dihydrate ($Sr(C_2O_4) \cdot 2H_2O$) on biomass of *Serpula himantioides*. Bar = 100 μm. (B) Moolooite ($Cu^{2+}(C_2O_4) \cdot nH_2O$) (n < 1) on biomass of *Beauveria caledonica*. Bar = 20 μm (Fomina, Burford & Gadd, unpublished).

and around cell walls and surface layers (Figs 1 and 3). Such mycogenic minerals can include carbonates and oxalates, but hydroxides, phosphates and sulfides may also occur (Burford *et al.*, 2003a,b, 2006). Carbonate formation may be

a significant contribution to the global $CO_2$ sink especially if lichens are considered. Oxalate may serve as a reservoir for calcium, but also influences phosphate availability. Reduced metal and metalloid species, e.g. Ag, Au, Se, Te, Cr, can be precipitated by many fungi. Fungi can oxidize Mn(II) and Fe(II) and precipitate them as oxides. The oxidized metal layer called desert varnish is also believed to be of microbial origin with some fungal involvement. Among the secondary minerals that have been associated with fungi are birnessite, ferrihydrite, forsterite, goethite, hydrocerussite, and moolooite (Fig. 3).

In general terms therefore and in the context of geomicrobiology, bacteria and fungi exhibit a range of similarities and differences over a wide spectrum of morphological and physiological attributes (Table 1). Clearly the filamentous hyphal growth form of the majority of fungi is a major difference between the majority of unicellular bacteria apart from those select bacterial groups that exhibit filamentation. The ability to form symbiotic relationships is also pronounced in the fungi with lichens and mycorrhizas representing global biogeochemical entities. Certain prokaryotes can form symbiotic $N_2$-fixing relationships with plants: $N_2$ fixation of course is not found in fungi or other eukaryotes. Regarding metals and minerals, many mechanisms of solubilization or immobilization are found in bacteria and fungi. $H^+$ and ligand-mediated solubilization, complexation by metabolites, reductive dissolution and others are common, while for immobilization, sorption, transport, intracellular sequestration, secondary mineral formation, reductive immobilization, are similarly ubiquitous. Obviously the greatest metabolic differences occur within the aerobic or anaerobic framework and the wide variety of chemolithotrophic metabolisms that bacteria and archaea are capable of (Table 1). Fungi, as mentioned are aerobic in the main, so the use of the many different electron acceptors in anaerobic environments and accompanying geochemical transformations do represent a major prokaryotic influence on the biosphere. It therefore seems that the greatest demarcation between bacterial and fungal geomicrobiology occurs between aerobic and anaerobic metabolism, the complexities of growth form, differences in the relative amounts of research activity associated with the different systems, and mindsets of varying openness depending on the kind of microbial apprenticeship served. However, it should be clear to all that free-living and symbiotic fungi are of major significance in the aerobic lithosphere, the soil, the plant-root zone, and surfaces of rocks and minerals, where they generally co-exist and interact with prokaryotes (Fig. 1) (Gadd, 2006). They are also likely to be important in other locations that so far have not received detailed studies in a geobiological context. Perhaps there will never be a true synthesis of pro- and eukaryotic geomicrobial processes but all workers should take a step back and try a more global view. Or indeed attempt to engineer interesting collaborations. Geomycology can be considered a subset of geomicrobiology or geobiology, and defined as the role that fungi have played and are playing in fundamental geological processes (Burford *et al.*, 2003a,b; Gadd, 2006,

2007). The microorganisms that have determined and influence all parts of the biosphere and our everyday lives comprise bacteria, archaea and eukaryota and that should be appreciated by all. I thank Terry Beveridge above all for leading and encouraging my broad perspective of geomicrobial processes and their significance, for enhancing my love of microbiology, and his friendship.

## References

Beveridge TJ (1989) Interactions of metal ions with components of bacterial cell walls and their biomineralization. In *Metal–Microbe Interactions* (eds Poole RK, Gadd GM). IRL Press, Oxford, UK, pp. 65–83.

Beveridge TJ (1989) Role of cellular design in bacterial metal accumulation and mineralization. *Annual Review of Microbiology* **43**, 147–171.

Beveridge TJ, Doyle RJ, eds (1989) *Metal Ions and Bacteria*. Wiley, New York.

Beveridge TJ, Koval SF (1981) Binding of metals to cell envelopes of *Escherichia coli* K12. *Applied and Environmental Microbiology* **42**, 325–335.

Beveridge TJ, Murray RGE (1976) Uptake and retention of metals by cell walls of *Bacillus subtilis*. *Journal of Bacteriology* **127**, 1502–1518.

Beveridge TJ, Murray RGE (1980) Sites of metal-deposition in the cell wall of *Bacillus subtilis*. *Journal of Bacteriology* **141**, 876–887.

Beveridge TJ, Forsberg CW, Doyle RJ (1982) Major sites of metal binding in *Bacillus licheniformis* walls. *Journal of Bacteriology* **150**, 1438–1448.

Beveridge TJ, Meloche JD, Fyfe WS, Murray RGE (1983) Diagenesis of metals chemically complexed to bacteria: laboratory formation of metal phosphates, sulfides, and organic condensates in artificial sediments. *Applied and Environmental Microbiology* **45**, 1094–1108.

Boswell GP, Jacobs H, Davidson FA, Gadd GM, Ritz K (2002) Functional consequences of nutrient translocation in mycelial fungi. *Journal of Theoretical Biology* **217**, 459–477.

Bowen AD, Davidson FA, Keatch R, Gadd GM (2007) Induction of contour sensing in *Aspergillus niger* by stress and its relevance to fungal growth mechanics and hyphal tip structure. *Fungal Genetics and Biology* **44**, 484–491.

Burford EP, Fomina M, Gadd GM (2003a) Fungal involvement in bioweathering and biotransformation of rocks and minerals. *Mineralogical Magazine* **67**, 1127–1155.

Burford EP, Kierans M, Gadd GM (2003b) Geomycology: fungal growth in mineral substrata. *Mycologist* **17**, 98–107.

Burford EP, Hillier S, Gadd GM (2006) Biomineralization of fungal hyphae with calcite ($CaCO_3$) and calcium oxalate mono- and dihydrate in carboniferous limestone microcosms. *Geomicrobiology Journal* **23**, 599–611.

Ferris FG, Beveridge TJ, Fyfe WS (1986) Iron-silica crystallite nucleation by bacteria in a geothermal sediment. *Nature* **320**, 609–611.

Ferris FG, Fyfe WS, Beveridge TJ (1987) Bacteria as nucleation sites for authigenic minerals in a metal-contaminated lake sediment. *Chemical Geology* **63**, 225–232.

Ferris FG, Fyfe WS, Beveridge TJ (1988) Metallic ion binding by *Bacillus subtilis*: implications for the fossilization of microorganisms. *Geology* **16**, 149–152.

Ferris FG, Schultze S, Witten TC, Fyfe WS, Beveridge TJ (1989) Metal interactions with microbial biofilms in acidic and neutral pH environments. *Applied and Environmental Microbiology* **55**, 1249–1257.

Fortin D, Beveridge TJ (1997) Microbial sulfate reduction within sulfidic mine tailings: formation of diagenetic Fe-sulfides. *Geomicrobiology Journal* **14**, 1–21.

Fortin D, Southam G, Beveridge TJ (1994) Nickel sulfide, iron-nickel sulfide and iron sulfide precipitation by a newly isolated *Desulfotomaculum* species and its relation to nickel resistance. *FEMS Microbiology Ecology* **14**, 121–132.

Fortin D, Davis B, Southam G, Beveridge TJ (1995) Biogeochemical phenomena induced by bacteria within sulfidic mine tailings. *Journal of Industrial Microbiology* **14**, 178–185.

Fortin D, Ferris FG, Beveridge TJ (1997) Surface-mediated mineral development by bacteria. *Reviews in Mineralogy* **35**, 161–180.

Gadd GM (1993) Interactions of fungi with toxic metals. *New Phytologist* **124**, 25–60.

Gadd GM (1999) Fungal production of citric and oxalic acid: importance in metal speciation, physiology and biogeochemical processes. *Advances in Microbial Physiology* **41**, 47–92.

Gadd GM (2004) Mycotransformation of organic and inorganic substrates. *Mycologist* **18**, 60–70.

Gadd GM, ed. (2006) *Fungi in Biogeochemical Cycles.* Cambridge University Press, Cambridge, UK.

Gadd GM (2007) Geomycology: biogeochemical transformations of rocks, minerals, metals and radionuclides by fungi, bioweathering and bioremediation. *Mycological Research* **111**, 3–49.

Gadd GM, Griffiths AJ (1978) Microorganisms and heavy metal toxicity. *Microbial Ecology* **4**, 303–317.

Gadd GM, White C (1985) Copper uptake by *Penicillium ochro-chloron*: influence of pH on toxicity and demonstration of energy-dependent copper influx using protoplasts. *Journal of General Microbiology* **131**, 1875–1879.

Gadd GM, White C (1989) The removal of thorium from simulated acid process streams by fungal biomass. *Biotechnology and Bioengineering* **33**, 592–597.

Gadd GM, Chudek JA, Foster R, Reed RH (1984) The osmotic responses of *Penicillium ochro-chloron*: changes in internal solute levels in response to copper and salt stress. *Journal of General Microbiology* **130**, 1969–1975.

Gadd GM, Semple K, Lappin-Scott H, eds (2005) *Microorganisms in Earth Systems: Advances in Geomicrobiology.* Cambridge University Press, Cambridge, UK.

Glasauer S, Beveridge TJ, Burford EP, Harper FA, Gadd GM (2004) Metals and metalloids, transformations by microorganisms. In *Encyclopedia of Soils in the Environment* (eds Hillel D, Rosenzweig C, Powlson DS, Scow KM, Singer MJ, Sparks DL, Hatfield J). Elsevier, Amsterdam, pp. 438–447.

Gorbushina AA (2007) Life on the rocks. *Environmental Microbiology* **9**, 1613–1631.

Hockin S, Gadd GM (2003) Linked redox-precipitation of sulfur and selenium under anaerobic conditions by sulfate-reducing bacterial biofilms. *Applied and Environmental Microbiology* **69**, 7063–7072.

Hockin S, Gadd GM (2006) Removal of selenate from sulphate-containing media by sulphate-reducing bacterial biofilms. *Environmental Microbiology* **8**, 816–826.

Morley GF, Gadd GM (1995) Sorption of toxic metals by fungi and clay minerals. *Mycological Research* **99**, 1429–1438.

Mullen MD, Wolf DC, Ferris FG, Beveridge TJ, Flemming CA, Bailey GW (1989) Bacterial sorption of heavy metals. *Applied and Environmental Microbiology* **55**, 3143–3149.

Mullen MD, Wolf DC, Beveridge TJ, Bailey GW (1992) Sorption of heavy metals by the soil fungi *Aspergillus niger* and *Mucor rouxii*. *Soil Biology and Biochemistry* **24**, 129–135.

Phoenix VR, Korenevsky AA, Matias VRF, Beveridge TJ (2005) New insights into bacterial cell-wall structure and physico-chemistry: implications for interactions with metal ions and minerals. In *Microorganisms in Earth Systems – Advances in Geoicrobiology* (eds Gadd GM, Semple K, Lappin-Scott H). Camridge University Press, Cambridge, UK, pp. 85–108.

Poole RK, Gadd GM, eds (1989) *Metal-Microbe Interactions.* IRL Press, Oxford, UK.

Reitner J, Schumann G, Pedersen K (2006) Fungi in subterranean environments. In *Fungi in Biogeochemical Cycles* (ed. Gadd GM). Cambridge University Press, Cambridge, UK, pp. 377–403.

de Rome L, Gadd GM (1987) Copper adsorption by *Rhizopus arrhizus, Cladosporium resinae* and *Penicillium italicum*. *Applied Microbiology and Biotechnology* **26**, 84–90.

Sayer JA, Cotter-Howells JD, Watson C, Hillier S, Gadd GM (1999) Lead mineral transformation by fungi. *Current Biology* **9**, 691–694.

Schultze-Lam S, Fortin D, Davis BS, Beveridge TJ (1996) Mineralization of bacterial surfaces. *Chemical Geology* **132**, 171–181.

Smith WL, Gadd GM (2000) Reduction and precipitation of chromate by mixed culture sulphate-reducing bacterial biofilms. *Journal of Applied Microbiology* **88**, 983–991.

Urrutia MM, Beveridge TJ (1994) Formation of fine-grained metal and silicate precipitates on a bacterial surface (*Bacillus subtilis*). *Chemical Geology* **116**, 261–280.

Walker SG, Flemming CA, Ferris FG, Beveridge TJ, Bailey GW (1989) Physicochemical interaction of *Escherichia coli* cell envelopes and *Bacillus subtilis* cell walls with two clays and ability of the composite to immobilize heavy metals from solution. *Applied and Environmental Microbiology* **55**, 2976–2984.

White C, Gadd GM (1986) Uptake and cellular distribution of copper, cobalt and cadmium in strains of *Saccharomyces cerevisiae* cultured on elevated concentrations of these metals. *FEMS Microbiology Ecology* **38**, 277–283.

White C, Gadd GM (1987) The uptake and cellular distribution of zinc in *Saccharomyces cerevisiae*. *Journal of General Microbiology* **133**, 727–737.

White C, Wilkinson SC, Gadd GM (1995) The role of microorganisms in biosorption of toxic metals and radionuclides. *International Biodeterioration and Biodegradation* **35**, 17–40.