

Introduction to Special Issue

The evolution of geomicrobiology: perspectives from the mineral–bacteria interface

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This issue of *Geobiology* provides a glimpse into the state of geomicrobiology with research presented spanning from molecular-scale cellular metal interactions to field studies of elemental cycling. The broad link between all of these papers presented here is the interconnectivity between minerals and microbial ecology and metabolisms. This issue was organized and solicited from the session ‘Bacteria–mineral interface’ at the International Mineralogical Association meeting in Kobe, Japan, 2006.

From its origins, perhaps some 4 billion years ago, biology has had a profound effect on shaping our planet. The ‘higher’ organisms, multicellular eukaryotes, are restricted for the most part to the Earth’s surface, while the ubiquitous nature of prokaryotic organisms has allowed them to extend from polar icecaps to the hottest desert, from the most acid acidic mine waste to salty and highly alkaline lakes, and from atmospheric dust particles to oceanic trenches, hydrothermal ocean vents and a myriad of subterranean environments. Indeed, it would be necessary to penetrate several kilometres into the crust where temperatures are outside the physiochemical limits for life to find a sterile environment. Not only are prokaryotes widespread in the Earth’s crust, but throughout the biosphere, microbial populations are intimately involved in transforming both inorganic and organic compounds to meet their metabolic and energetic requirements, and in doing so, they have modified almost every aspect of the Earth’s biosphere (see Konhauser, 2007).

Geomicrobiological research has been conducted under various guises (e.g. microbial ecology, low-temperature geochemistry, environmental engineering, economic geology, chemical oceanography) for many years but perhaps the true blossoming of the science followed the MSA short course and volume by Banfield & Neelson in (1997). Since this time, the discipline has grown into a multidisciplinary science that

links microbiologists, genome scientists, geochemists, physicists, biochemists, and analytical chemists together, and has essentially generated a subfield of molecular geomicrobiology which has garnered significant attention (e.g. Banfield *et al.*, 2005). Of course, much of this focus has led to the development of large environmental or single organism genomic databases, which are still substantially separated from pairing the genetic basis to their biogeochemically relevant metabolic pathways. Molecular geomicrobiology, in this case, also refers to the increased use and utility of spectroscopic techniques to study nanoscale processes at the bacteria–mineral interface (e.g. Jiang *et al.*, 2004). Opportunities abound for continuing on with molecular geochemistry via further deconstruction using model organisms (e.g. DiChristina *et al.*, 2005) and the use of artificial membranes or colloids in spectroscopic studies (e.g. Boyanov *et al.*, 2007). However, there still remains a need for system-based science in geomicrobiology. The relevance of gene expression, and what are considered biogeochemical relevant genes, will remain unknown, unless they are evaluated in the context of interdependent communities, chemical gradients, and typical transport mechanisms in near-surface geological settings. Here we present a number of papers that, in their own way, attempt to adjust to the biocomplexity of these natural settings by: using the microbes’ ecological settings as models for laboratory-based studies; molecularly characterizing the surface chemistry of native mineral–bacteria composites or actively metabolizing bacteria; and by studying mesoscale and end-member geomicrobiological settings to isolate microbial influences on, and function within, near-surface geological settings.

CELL SURFACE REACTIVITY

One of the uniquely characteristic features of microorganisms is their large surface area to volume ratios. This, coupled with highly reactive charged surfaces, leads to significant metal partitioning onto microbial biomass. Many of the metals bound serve physiological functions, but interestingly, many

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cells seem to act as cation scavengers, accumulating a litany of trace metals. Some of the areas of current interest include assessing whether reactive functional groups are consistent between different species, why microorganisms bind different metals with different degrees of fidelity, how experimental studies on microbial surface reactivity can be applied to natural systems, and how microorganisms can be effectively employed in metal bioremediation.

Here in this issue, two papers examined the role of surface reactivity of bacterial cells and associated minerals. Johnson *et al.* examined the effect of bacterial metabolism on the adsorption of Cd onto Gram-positive and Gram-negative bacterial cells. The authors demonstrated that Gram-positive cells showed a marked difference in adsorption between metabolizing and nonmetabolizing cells attributed to the presence or absence of proton motive force, while Gram-negative cells displayed no systematic difference because metal binding is likely focused on a region of the cell wall that is not reached, or is unaffected by this proton flux. Importantly, the results suggest that biosorption remediation strategies that involve Gram-positive bacterial species may be more efficient at metal removal from natural solutions if their metabolism was in some way inhibited during the sorption process.

Extending this work to natural samples and field settings, Lalonde *et al.* compared the surface reactivity of native microbial communities and ferric oxyhydroxide minerals (HFOs) from several hot springs at Yellowstone National Park, USA. HFOs from acidic spring waters displayed surface functional groups typical of previously reported synthetic HFO and bound more cations, while neutral spring water HFOs were characterized by a lower functional group density and retained more arsenic. When microbial biomass samples from acidic springs were analysed, it became apparent that some algal mats behaved similarly to HFO samples on a dry weight basis, while other thermophilic S⁰-rich mats were considerably less reactive. This work highlighted the fact that variation in sorptive properties can exist between different microbial populations and mineral surfaces in close proximity. Overall, these results demonstrate the importance of chemical parameters, such as surface functional group concentrations and pK_a distributions, in accounting for complex sorption phenomena, which in turn, will lead to a better understanding of the microbial role in element partitioning in environmental systems.

BIOMINERALIZATION

Microorganisms' reactive cell walls also facilitate the precipitation of a variety of authigenic mineral phases. Some minerals, such as magnetite in magnetotactic bacteria, or silica in diatoms, serve biological functions which require the organisms to expend energy on its formation. However, in most cases biomineralization is apparently incidental, recording the interactions between the activity of the microorganisms and their surrounding environment. While it is still unknown whether indirect

extracellular biomineralization is in any way fortuitous to the encrusted microbial cells, this process, in combination with geochemical parameters can record microbiological metabolic processes in the precipitated phase.

Leveille *et al.* examined the role of microbiological activity in carbonate and clay mineralization in basaltic sea caves in Kauai, Hawaii, USA. Isotope and major element geochemistry combined with flow-path modelling revealed that two different processes may control carbonate precipitation in the microenvironment. In droplets and thin films, evaporation likely drives precipitation of the mineral magnesite, while many of the Ca carbonates occur in intimate association with microbial mats containing cyanobacteria and exhibit elevated ¹³C signatures, indicative of photosynthetic metabolic activity. Significantly, these data and the holistic study undertaken by the authors, emphasize the utility of studying modern biogeochemical systems to fully understand biosignatures so they can be properly applied and interpreted in ancient and perhaps extraterrestrial systems.

MINERAL WEATHERING

While microbial metabolism can play a role in mineral precipitation, it can also significantly alter mineral equilibria causing dissolution, sometimes with environmental and ecological implications. For example, the ability of bacteria to oxidize metal sulfides has caused significant environmental problems, e.g. acid mine drainage. Growth of the main culprits, such as *Thiobacillus*, however, also has economic advantages, and if harnessed, it can assist in the biorecovery of trace metals from mining spoil. Reduced iron, as well as other trace metals, in silicate minerals is also an important energy source for microorganisms, and given their common occurrence in the Earth's crust, their weathering may be a key energy source for subsurface microbial populations.

In this volume, Kulczycki *et al.* examined the role of the extracellular copper-binding compound excreted by methanotrophs, methanobactin, in the dissolution of copper-bearing silicate glasses. Copper availability regulates enzyme expression by type II methanotrophs, impacting rates of bacterial methane oxidation. As copper is typically limiting in solution, this study examined the ability of methanobactin to sequester copper from primary minerals, such as silicates. Results demonstrate that methanobactin promotes glass dissolution and copper release; however, the magnitude of this process is impacted by concentrations of methanobactin and solid-phase copper. As these experiments were done in the absence of bacteria, it is speculated that the addition of a vital effect (i.e. metabolizing cells) may catalyse this process through bacterial copper uptake. Methanotrophs therefore may access copper from refractory phases, such as silicates, with the production of a chalkophore (e.g. methanobactin), and importantly, this mode of microbial weathering may play a key role in regulating the rate of methane oxidation in microbially active systems.

Rosling *et al.* also investigated the microbial acquisition of nutrients from mineral sources, examining the ability of fungi to release the macronutrient, phosphorus (P), from apatite as a function of P concentration in solution. Using fungal isolates from a grassland in northern California, USA, the authors identified three fungi-mediated modes of dissolution including acidification, moderate acidification, and no acidification. Acidifying isolates, identified as *Zygomycetes* in the order Mucorales, induce fluorapatite dissolution by producing oxalic acid while growing in the presence of P. In contrast, the non-acidifying isolate, identified as *Ascomycetes* belonging to the family Trichocomaceae, lowered the solution pH and induced fluoroapatite dissolution without the production of low molecular weight organic acids under P-limited conditions. Results from this study stress the significance of soil mineralogy as a source of essential nutrients, such as phosphorus, which is limiting in many soil environments.

ELEMENTAL CYCLING

All of Earth's major biogeochemical cycles are also effected by microbial metabolism. Some cells couple the oxidation of organic material with the dissolution of mineral phases (e.g. ferric iron reduction) or dissolved solutes (e.g. sulfate reduction), whereas other cells have evolved the metabolic capacity to oxidize inorganic substances for autotrophic carbon fixation. In either case, microorganisms simply catalyse reactions that are thermodynamically favoured, yet kinetically hindered. In sediments, the reductive–oxidative processes work in tandem, with the by-products of one metabolic guild the substrate for another. This invariably leads to biochemical stratification, and although the fundamentals underlying biogeochemical zonation are established, it is now becoming apparent that complex recycling in microniches may impart significant heterogeneity on the overall system. Recent advances in sampling both pore-water geochemistry and microbiological populations, using for example, signature lipid biomarkers or nucleic acid sequence analysis of genes, are providing new insights into characterizing microbial community structure and nutritional status.

Here in this issue, two papers focused on the environmental ramifications of metal reduction. Rowland *et al.* investigated the control exerted by organic matter on microbially mediated Fe(III) reduction and arsenic(III) release in sediments from a shallow alluvial aquifer in Cambodia. Using natural sediments and various types of organic carbon, the authors showed that the rate and magnitude of Fe(III) reduction and As(III) release under anaerobic conditions were enhanced after the addition of acetate and AQDS (used in the study as an analogue for humic substances) when compared to autoclaved-control systems. The presence of AQDS, hydrocarbons and finer grained sediments enhanced As release associated with the amorphous and crystalline Fe and Al fractions of the sediments. The native microbial community was initially

complex and involved in various metabolic processes, but the addition of acetate and AQDS to the microcosms led to a predominance of microorganisms closely related to metal-reducing *Geobacter* species. The role of *Geobacter* in the mobilization of As remains unclear, but the authors proposed that dissolution of ferric oxides was likely responsible for the release of As. This study highlights the role of heterogeneity in sediment geochemistry and carbon source in differentiating microbial communities resulting in unique geomicrobiological conditions.

Wilkens *et al.* provide an intriguing view of the grand challenges associated with scaling the study of Fe, U, and Tc reduction in the laboratory to natural systems. The authors discovered that Fe(III)-reducing microorganisms in the Drigg site sediments (currently operated by British Nuclear Fuels) effectively removed both U(VI) and Tc(VII) from the aqueous phase while continuing to immobilize radium in the sediments. With the onset of denitrifying conditions, an organism closely related to *Pseudomonas stutzeri*, dominated the bacterial community structure and leads to nitrite production. The reoxidation and the introduction of nitrate to the system facilitated the remobilization of U(VI), whereas Tc remained in an insoluble form. Ultimately, this work stresses the need for site-specific information on a variety of scales in order to accurately predict radionuclide mobility and potential bioremediation outcomes for the long-term stability of contaminated sites.

All of the studies included in this issue emphasize the broad implications of geomicrobiology in modern environments, but they have relevance for the geological past as well. Indeed, the events that led to the emergence of life and evolution of the biosphere can only really be elucidated by studying modern ecosystems along with the fossil and stratigraphic records. Complimentary modern ecosystem studies provide a means to understand the biogeochemical processes by which life interacted with its environment through time, and ultimately how biosignatures are recorded in the geological record. Furthermore, these geomicrobiological investigations at the complex laboratory scale and the mesoscale in the field are perhaps our best opportunities for insight into novel microbial metabolic pathways and ecosystem function of particular groups of organisms, thereby providing crucial linkages between geochemical and microbiological evolution in subsurface environments.

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