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The role of bacterial extracellular polymeric substances in geomicrobiology

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ABSTRACT

The last two decades have seen geomicrobiology evolve into a broad field encompassing a wide range of environmentally significant processes such as proton and metal adsorption onto cell surfaces, and the effect of microbes on mineralisation, redox cycling, and contaminant transport. Within this sphere, research groups have conducted studies using bacteria, fungi, diatoms and sludges, all of which can play a part in geochemical processes. Here, we review research on the role played by microbial extracellular polymeric substances (EPS), focussing on bacterial and cyanobacterial EPS. We conclude by outlining future research directions in order to investigate unresolved questions in the field.

The effect of EPS on metal adsorption is complex; whereas some studies report an increase in metal adsorption when cells contain EPS, some report no differences; yet others report a decrease. These discrepancies may reflect differences in molecular and functional group composition of the EPS. EPS provides a template for adsorption of metal cations to which carbonate ions are attracted to induce local mineral supersaturation. This may be behind observed changes in both crystal polymorphism favouring formation of less stable polymorphs, and crystal morphology where the presence of EPS promotes the formation of rounded, smoothed crystals or spheroids. The role of EPS in mineral dissolution, bioleaching and corrosion is equivocal. EPS alone appears to have little effect on mineral dissolution, bioleaching or biocorrosion. Instead, it appears that EPS increases rates of mineral weathering and leaching by forming complexes with metallic ions released by the mineral surface, which may themselves catalyse bioleaching in the case of sulphides. EPS in biofilms forms effective barriers to the transport of particulate phases, and exerts important controls on the transport and deposition of natural and engineered nanoparticles.

Much less is known about the role of EPS in the cycling of redox-sensitive trace metals. Intuitively, and as observed in microbial mats with sulphate reducing bacteria, EPS is a labile electron donor for microbial metabolism that could affect metal biogeochemistry but this remains to be conclusively demonstrated in laboratory experiments. Hence, in this and other areas, further studies are required to develop a mechanistic basis for including the effects of EPS in biogeochemical models.

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1. Introduction and context

The roles of microbes such as bacteria, fungi and algae in metal biogeochemistry have been the subject of intense research interest in recent years. In particular, the abilities of cell walls to participate in metal adsorption reactions, and potentially mediate mineral precipitation and dissolution reactions, have been studied extensively. The overall objective of such investigations is to develop a predictive framework for microbial mediation of biogeochemical processes that is applicable to a range of environmental conditions, leading to a better understanding of geochemical cycles and transport of metals in the environment, as well as of preservation of traces of early life on Earth.

Biogeochemically, bacterial cells and other microbes may exert influence over metal cycling by four principle processes:

- cell surface adsorption, the non-metabolic uptake of metal ions and other solutes to the cell surfaces of bacteria and other microscopic organisms such as fungi, archaea and algae;
- metabolic uptake, which may lead to the sequestration of metals within the cell interior. Bioessential metals are required for cell metabolic processes, particularly the manufacture of enzymes;
- biomineralisation, the precipitation of minerals within a microbial cell, on the cell surface or in close association with the cell. Biomineralisation may be categorised as either biologically-induced or biologically-controlled, depending upon the mechanism of mineral precipitation;
- microbial oxidation and reduction of metal species, which may occur as a consequence of cell metabolic processes. Metals are often utilised both as electron donors and as terminal electron acceptors by bacteria. The consequent change in oxidation state of the metal may result in precipitation if the resulting species is insoluble (Francis et al., 2000; Abdelouas et al., 2005). In most environments, microbes have a significant or even controlling influence over the cycling of redox-sensitive metals.

In the last 15–20 years, there have been a large number of studies on the surface chemical reactivity of bacterial cells, with the objective of determining whether a single set of protonation parameters can be used to represent the surface chemistry of a wide range of different bacterial species, under varying experimental conditions (Fein et al., 1997; Fowle and Fein, 1999; Yee and Fein, 2001; Borrok et al., 2004a, 2004b, 2005; Fein, 2006). Developing a set of adsorption constants that are applicable to a wide range of bacterial species and environmental conditions would greatly facilitate prediction of metal-microbe interactions in a given setting, and also enable better understanding of the extent to which microbes influence biogeochemical cycling of metals under different conditions. However, this cannot be done until the effects of a range of experimental variables can be understood and accurately quantified. Studies have investigated the contributions to proton and metal adsorption of variables such as presence of other metal species (Macaskie and Basnakova, 1998; Chatellier and Fortin, 2004; Takahashi et al., 2005; Tsuruta, 2006; Claessens and van Capellen, 2007), ligand composition (Fein and Delea, 1999; Fein et al., 1999; Daughney et al., 2001; Sheng and Fein, 2013; Dunham-Cheatham et al., 2014), ionic strength (Daughney and Fein, 1998; Small et al., 2001; Borrok and Fein, 2005; Kenward et al., 2006; Ams et al., 2013), bacterial strain (Haas et al., 2001; Yee and Fein, 2001; Ngwenya et al., 2003; Borrok et al., 2004a, 2004b; Burnett et al., 2006a, 2006b; Hetzer et al., 2006; Burnett et al., 2007; Heinrich et al., 2007; Johnson et al., 2007), metabolic state (Chubar et al., 2013) and adsorption temperature (Wightman et al., 2001; Aksu, 2002; Takahashi et al., 2005; Gorman-Lewis et al., 2006; Ginn and Fein, 2009; Gorman-Lewis, 2009, 2011).

These studies have generally concluded that the effects of these variables are small, and the applicability of a ‘universal’ surface complexation model to a range of both gram-positive and gram-negative bacterial species has been demonstrated (Yee and Fein, 2001; Ngwenya et al., 2003; Borrok et al., 2004a, 2004b, 2005; Johnson et al., 2007), based on minimal variation in adsorption behaviour between different species (Fig. 1). Furthermore, the similarity of stability constants obtained from multi-metal systems to constants obtained for the same metals in single-metal systems (Fowle and Fein, 1999; Burnett et al., 2007; Ngwenya et al., 2009) suggests that laboratory-derived stability constants may be applicable to more complex settings.

However, it seems that varying growth conditions, or bacterial adaptation to extreme or perturbed environments, may lead to observable differences in cell surface chemistry and hence adsorption characteristics (Daughney et al., 2001; Sharma et al., 2003; Borrok et al., 2004b, 2004c; Haas, 2004; Hong and Brown, 2006; Guine et al., 2007; Ginn and Fein, 2009; Gorman-Lewis et al., 2013; Harrold and Gorman-Lewis, 2013). Specifically, variations in growth conditions can induce the production of extracellular polymeric substances (EPS), in planktonic cells but particularly in biofilms (Zisu and Shah, 2003; Kives et al., 2006; Eboigbodin et al., 2007; Noghabi et al., 2007). These polymers may be soluble, contributing to the dissolved organic carbon component in a system (Sheng et al., 2010). Soluble organic matter contains fractions that may be highly significant complexing agents of dissolved species. Consequently, the production of EPS by bacterial cells affects the transportation and bioavailability of metals in aqueous environments (Czajka et al., 1997; Van Hullebusch et al., 2003; Jensen-Spaulding et al., 2004; Yang et al., 2013). Although a number of studies have characterised the proton and metal binding properties of extracted EPS (Loaec et al., 1997; Guibaud et al., 2004, 2005a; Comte et al., 2006a, 2006c), the effects of an in-situ EPS layer on the surface properties of bacterial cells is a relatively unexplored area of research. Furthermore, it is unclear what role bacterial EPS plays in metal biomineralisation as well as redox cycling, although progress is also being made in these areas (e.g. Kang et al., 2014).

This review summarises the current state of knowledge about the role of EPS in cell surface mediated processes of significant