Bacterial use of siderophores increases olivine dissolution rates by nearly an order of magnitude
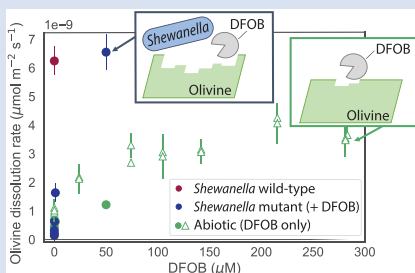
A. Lunstrum[1]*, M. Van Den Berghe[1], X. Bian[1], S. John[1], K. Nealson[1], A.J. West[1]

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Abstract

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Mafic minerals, such as olivine, are an important source of metals and alkalinity to Earth's surface, impacting the planet's long term carbon cycle and climate. Yet, environmental controls on their dissolution rates remain poorly understood. Recent studies show that exogenous siderophores can enhance olivine dissolution abiotically, but it remains unclear how important siderophores are in microbially enhanced dissolution. Here, we isolated the effect of microbial siderophores on olivine dissolution using the bacteria *Shewanella oneidensis*, including both wild type and a mutant strain incapable of siderophore production. We show that *S. oneidensis* required siderophores to access mineral bound Fe, without which dissolution was not enhanced above background abiotic rates. Furthermore, dissolution rates with the bacteria were eight fold higher than those in abiotic solutions with the same concentrations of exogenous siderophores, implying a synergy between siderophores and other biotic mechanisms. After reaching stationary phase, dissolution in the *S. oneidensis* wild type treatment slowed, whereas that in the mutant + siderophore treatments continued at high rates. These results suggest that while siderophores are critical for biotically enhanced olivine dissolution, other microbe-related mechanisms magnify their effect.

Introduction

The chemical weathering of silicate minerals is an important control on global biogeochemical cycling and climate *via* the release of metal cations and alkalinity (White and Brantley, 1995). Improved understanding of the environmental controls on silicate dissolution is thus important for characterising the climate-weathering feedback (Berner *et al.*, 1983), and for informing engineered "enhanced weathering" efforts to mitigate climate change (Hartmann *et al.*, 2013). In this regard, olivine ($(Mg^{2+},Fe^{2+})_2SiO_4$) and olivine-rich rocks (such as basalt) are often studied as model silicates due to their high solubility, abundance, and resulting large contribution to earth's weathering flux (Dessert *et al.*, 2003; Hartmann *et al.*, 2009).

At Earth's surface, olivine dissolution kinetics can vary by orders of magnitude as a function of both abiotic and biotic environmental factors. The effect of abiotic conditions such as temperature, solution pH, and solution chemistry are relatively well constrained (Rimstidt *et al.*, 2012; Oelkers *et al.*, 2018). The effects of biology on dissolution rates, on the other hand, are less clear. While the net effect of biology on mineral dissolution is typically assumed to be positive, observed biotic effects range from inhibition to enhancement (Schwartzman and Volk, 1989).

Low molecular weight, multi-dentate ligands known as siderophores may be important drivers of microbially enhanced olivine dissolution. Siderophores are secreted by many bacteria, fungi, and grasses in response to Fe limitation. While they are structurally diverse, siderophores typically contain multiple metal-binding ligands that collectively result in exceptionally high binding affinity with Fe^{3+} (log $K_f > 30$), preventing its loss from solution *via* Fe oxide precipitation (Hider and Kong, 2010). Significant research has shown that siderophores can *abiotically* enhance dissolution rates for a range of Fe^{3+} and Al^{3+}-containing minerals, including Fe oxides (Cheah *et al.*, 2003; Kraemer, 2004; Reichard *et al.*, 2007), Fe containing phyllosilicates (Rosenberg and Maurice, 2003; Haack *et al.*, 2008; Shirvani and Nourbakhsh, 2010; Ferret *et al.*, 2014; Bray *et al.*, 2015), and hornblende (Kalinowski *et al.*, 2000; Liermann *et al.*, 2000; Buss *et al.*, 2007). Olivine, in contrast, contains Fe almost exclusively in the +2 oxidation state, which is more weakly bound by siderophores (*e.g.*, for the siderophore deferoxamine B, log $K_f = 30$ for Fe^{3+} *vs.* 10 for Fe^{2+}) (Dhungana and Crumbliss, 2005). Nonetheless, recent research has shown that siderophores also increase olivine dissolution rates by nearly an order of magnitude (Torres *et al.*, 2019). An important distinction, however, is that these studies use purified siderophores at high micromolar concentrations, whereas environmental concentrations are consistently much lower (pico- to nanomolar) (Kraemer, 2004). Thus, there remains a disconnect between our understanding of catalyst driven and biology driven mineral dissolution, and uncertainty as to whether siderophores are ultimately important drivers of dissolution in the environment (Brantley *et al.*, 2006).

This study attempts to clarify whether siderophores enhance olivine dissolution in biotic conditions (*i.e.* when actively utilised by microbes), and if so, if they are a requisite

1. Department of Earth Sciences, University of Southern California, Los Angeles, CA 90089, USA
* Corresponding author (email: lunstrum@usc.edu)

component of biotically enhanced dissolution. Specifically, we use sub-micromolar concentrations of siderophores — which do not significantly increase dissolution abiotically — to assess whether their active use by microbes increases mineral dissolution rates. While previous studies have found that siderophores are indeed critical for microbes to access or use mineral bound Fe, they have not linked this dependency quantitatively to mineral dissolution rates (Dehner *et al.*, 2010; Ferret *et al.*, 2014; Van Den Berghe *et al.*, 2021). Here, we focus specifically on this link between microbial use of siderophores and rates of mineral dissolution. To do so, we measured olivine dissolution rates in the presence of the bacteria *Shewanella oneidensis* (MR-1) wild type, and in the presence of a gene-deletion mutant of MR-1 incapable of producing siderophores (ΔMR-1) plus varying concentrations of the exogenous siderophore, deferoxamine B (DFOB). We furthermore compare these dissolution rates to abiotic rates with DFOB alone. While MR-1 is often studied for dissimilatory metal reduction, it was used in this study only due to availability of the siderophore gene-deletion mutant; dissimilatory Fe reduction was not a concern, as olivine bound Fe is almost exclusively in the +2 oxidation state (Van Den Berghe *et al.*, 2021).

Siderophores are Required for Biotically Enhanced Olivine Dissolution

In the absence of DFOB, ΔMR-1 could not access olivine bound Fe at rates fast enough to support growth, and correspondingly did not enhance mineral dissolution above well established abiotic rates (Figs. 1–3, S-1, Table S-1) (Rimstidt *et al.*, 2012). *S. oneidensis* has the capacity to take up Fe through alternative pathways not involving siderophores — including direct uptake of Fe^{2+} and/or ligand bound Fe^{3+} transport — so a dependence on siderophores for microbial growth is not obvious *a priori* (Liu *et al.*, 2018). Furthermore, alternative microbial processes, such as decreased pH or production of low molecular weight organic acids could also facilitate mineral dissolution to feed microbial growth (Wogelius and Walther, 1991). However, these processes may be insufficient to drive dissolution alone: ligand

facilitated dissolution has been shown to be significant only at high ligand concentrations (typically >1 mM), which may not be achieved by slow growing microbes (Reichard *et al.*, 2007), and pH gradients in biofilms may not be severe enough to facilitate dissolution (Liermann *et al.*, 2000).

Similar studies using mutant *Pseudomonas* sp. grown in the presence of Fe^{3+} oxides and clays also found reduced growth rates in the absence of siderophores (Dehner *et al.*, 2010; Kuhn *et al.*, 2013; Ferret *et al.*, 2014). In contrast to our study, however, microbial growth was detectable without siderophores, indicating that alternative dissolution facilitating processes may be sufficient to facilitate some amount of microbial growth on Fe oxides and clays. The insignificant growth and dissolution in our ΔMR-1 (0 DFOB) treatment, on the other hand, indicates that siderophores are required to access olivine bound Fe. This difference suggests that Fe^{2+} bound within the olivine structure may be more difficult for microbes to access without siderophores than Fe^{3+} in oxides or clays.

Biotic Dissolution Rates exceed Abiotic Rates at the same Siderophore Concentration

It has been established that siderophores, independent of live culture, stimulate the dissolution of many Fe containing minerals, including olivine (Torres *et al.*, 2019). We show here, however, that live bacteria enhance this dissolution even further, beyond the rates expected for siderophore associated dissolution alone (Fig. 2, Table S-1). In all ΔMR-1 treatments where microbial growth was detectable (DFOB > 0.2 μM), dissolution rates exceeded those in abiotic conditions at the same DFOB concentration: at 1 μM DFOB addition, dissolution with ΔMR-1 exceeded the abiotic rate by three fold, and at 50 μM DFOB addition, this increased to eight fold. The enhanced dissolution observed in the biotic treatments implies that *S. oneidensis* does not simply benefit from passive use of siderophores, but rather, magnifies their efficiency.
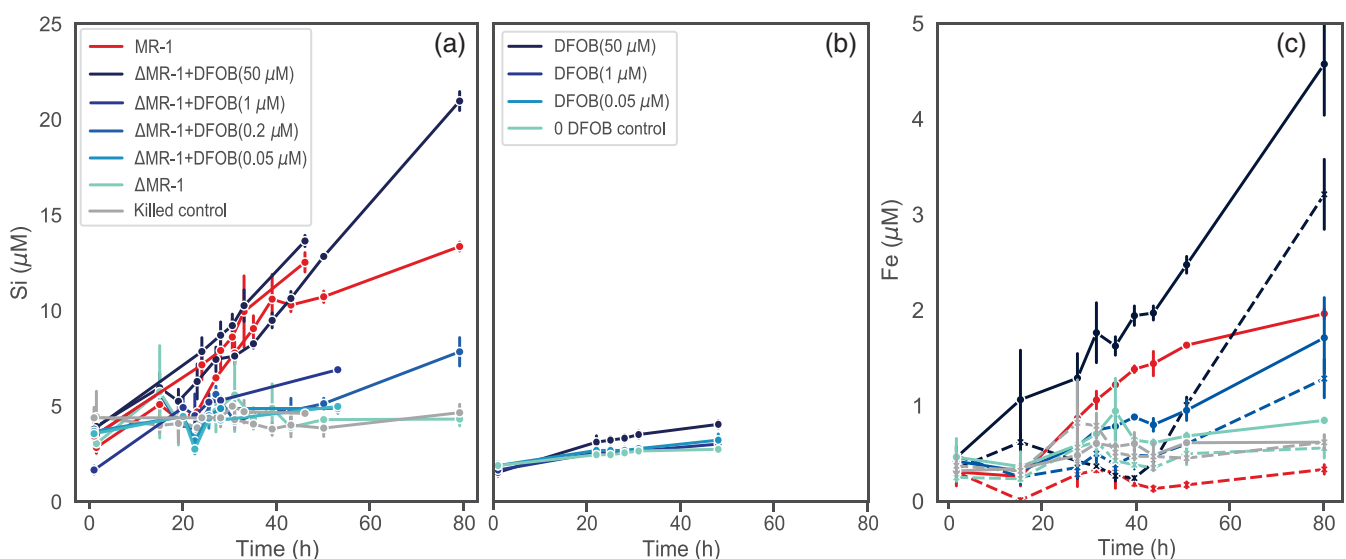

Figure 1 Dissolved Si measured in **(a)** biotic and **(b)** abiotic experiments, and **(c)** dissolved and total Fe in the biotic experiments (mean ± s.d.). Colours in all figures correspond to the same concentration of exogenous DFOB. Dashed lines in **(c)** represent dissolved concentrations, while solid lines are total concentrations.
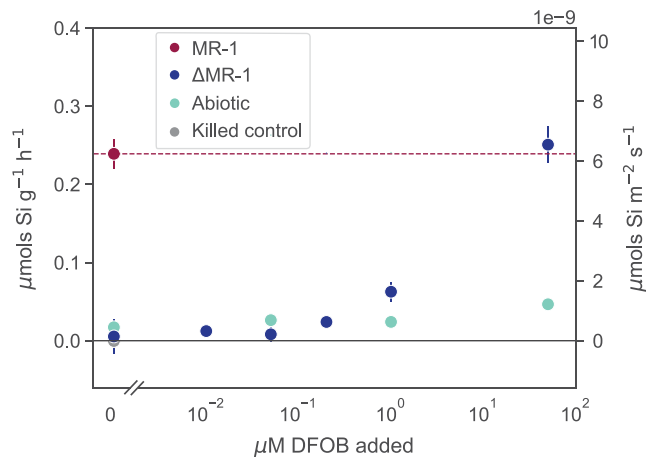
Figure 2 Olivine dissolution rates (based on Si release) as a function of DFOB addition. Dissolution rates in biotic treatments (ΔMR-1) exceed abiotic treatments at the same DFOB addition for DFOB > 1 μM. At 50 μM DFOB addition, biotic dissolution rates exceed abiotic rates by 8 fold. Dashed line represents dissolution rate for MR-1, with no exogenous siderophore addition.

Possible Mechanisms for Magnification of Siderophore Effects

One possible mechanism explaining higher rates in biotic *vs.* abiotic conditions is simply the microbial recycling of siderophores. In abiotic conditions, siderophores in solution can become saturated with chelated Fe. Active microbial populations, however, can transfer Fe to biomass, thus freeing siderophores for reuse. Our total *vs.* dissolved Fe data (Fig. 1c) support this mechanism, as Fe is almost entirely shunted into biomass, with no accumulation of chelated Fe in solution for the first 40 h of the ΔMR-1 experiments, and for the entirety of the MR-1 experiment. Even at 50 μM DFOB addition, which exceeds the concentration needed for maximum growth of ΔMR-1 (approximately 5 μM; Van Den Berghe *et al.,* 2021), chelated Fe does not accumulate in solution until well after stationary phase is reached, suggesting highly efficient siderophore use and shuttling of siderophore bound Fe into biomass.

However, mineral dissolution does not necessarily scale with siderophore *concentration*, but rather is known to scale with siderophores *adsorbed to the mineral surface*. As a result, dissolution rates plateau according to an adsorption isotherm. For DFOB, this has been well documented on olivine, Fe oxides and Fe containing phyllosilicates (Cheah *et al.,* 2003; Kraemer, 2004; Haack *et al.,* 2008; Torres *et al.,* 2019). Considering the relationship between olivine dissolution and DFOB concentration published by Torres *et al.* (2019) — which was derived at experimental conditions similar to ours (30 °C, pH 7.5) — dissolution rates plateau at >100 μM DFOB (Fig. 3). However, our measured dissolution rates for MR-1 and ΔMR-1 with only 50 μM DFOB addition are well above the bounds of the isotherm, suggesting that siderophore recycling alone does not fully explain biotic dissolution rates. Some other biotic mechanism likely facilitates increased siderophore efficiency. Siderophore adsorption to mineral surfaces is thought to be limited by both steric hindrance and charge repulsion (Cocozza *et al.,* 2002), so microbial secretion of surfactants or negatively charged ligands could increase adsorption efficiency (Carrasco *et al.,* 2007). Alternatively, small ligands like oxalate can interact synergistically with siderophores by liberating surface bound Fe when the saturation state of surrounding solution is lowered by siderophore mediated chelation

of dissolved Fe (Cheah *et al.,* 2003; Reichard *et al.,* 2007). Of course, it is possible that a combination of these mechanisms collectively magnify siderophore efficiency.

Biotically Enhanced Dissolution persists with DFOB Addition, but Slows with Wild Type

When comparing the dissolution trends of MR-1 wild type and ΔMR-1 + DFOB (50 μM) treatments, three key observations stand out. First, dissolution rates are similar, despite ΔMR-1 achieving only 50 % of the wild type planktonic cell density (Figs. S-1, S-2). Second, dissolution in the wild type treatment slows after stationary phase is reached, whereas dissolution rates are constant in the ΔMR-1 treatments (Fig. 1a). And third, dissolved Fe begins to accumulate in the ΔMR-1 treatments during stationary phase, whereas dissolved Fe is completely absent in the wild type treatments (Fig. 1c). The fact that dissolution slows in the presence of MR-1 wild type can be explained by down regulation of siderophore production in response to Fe availability, a well established biofeedback mechanism in siderophore producers. In contrast, the unabated dissolution and accumulation of dissolved Fe in ΔMR-1 + DFOB experiments indicate that exogenous siderophores stimulate dissolution in excess of bacterial nutritional needs. Because dissolution continues at rates much higher than the abiotic DFOB rate, it can be inferred that the mechanism responsible for siderophore "magnification" is not limited by the same processes that down regulate siderophore production upon reaching stationary phase. Note that by the end of the experiment, dissolved Fe in the ΔMR-1 + DFOB (50 μM) treatment is only 3 μM. If not limited by other mechanisms, enhanced dissolution would likely continue until siderophores become saturated with Fe, *i.e.* up to 50 μM (Reichard *et al.,* 2007).

The fact that dissolved Fe does not accumulate in the MR-1 wild type treatment suggests that this bacterium uses siderophores extremely efficiently, shunting all *chelated* Fe into biomass. Considering the stoichiometry of total metal release,
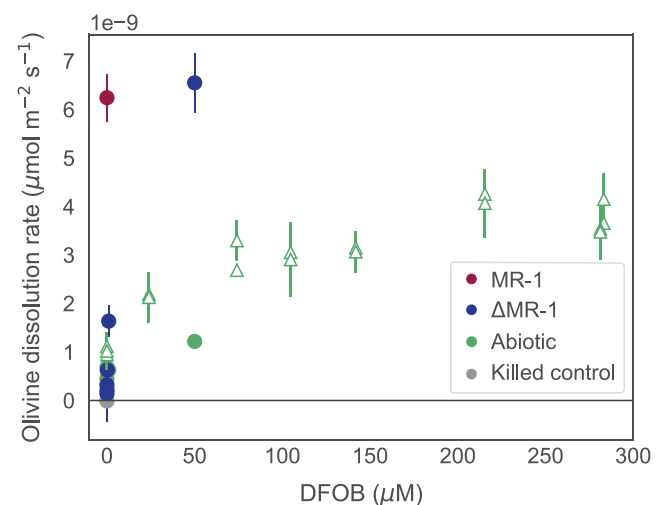

Figure 3 Olivine dissolution rates as a function of DFOB addition. Filled circles are from this study; hollow triangles are from Torres *et al.* (2019), adjusted to pH 7.2 as *per* the abiotic rate equations in Rimstidt *et al.* (2012). At 50 μM DFOB addition, our abiotic rate is reasonably characterised by (and slightly lower than) the abiotic adsorption isotherm. In contrast, the MR-1 and ΔMR-1 rates are significantly above the isotherm.

however, total Fe recovery in MR-1 was only 60 % of expected (based on Si release) at the end of the experiment, indicating that some dissolved Fe may escape chelation and be lost to secondary mineral precipitation (Fig. S-4). In contrast, the ΔMR-1 + DFOB treatments had full Fe recovery. The reduced Fe recovery and lack of dissolved Fe in MR-1 wild type experiments together suggest that siderophore production is low and/or localised at the microbe-mineral interface, with little siderophore loss to solution. Furthermore, a conundrum persists in that our previous research confirmed the presence of siderophores in MR-1 solution (using chrome-azurol S), and an experiment with ΔMR-1 fed filtrate from MR-1 exhibited normal growth patterns (Van Den Berghe *et al.*, 2021). It is possible that extremely low concentrations of *Shewanella*'s native siderophore putrebactin are sufficient to maintain the bacteria's growth and mineral dissolution needs, and that structural differences between putrebactin (a cyclic dihydroxamate) and DFOB (a tris-hydroxamate) allow for more efficient use in the former. The fact that MR-1 grows to stationary phase cell densities double those of ΔMR-1, yet dissolution rates are lower, further suggests that MR-1 uses available (chelated) Fe more efficiently with putrebactin.

Conclusions and Further Considerations

In conclusion, *Shewanella* does not use siderophores passively to enhance dissolution, but rather increases their efficiency to rapidly access mineral bound Fe. The observed biotically enhanced dissolution rates may not persist long term in natural conditions as they require the active biosynthesis of siderophores, which likely peak during exponential growth. Thus, significantly enhanced dissolution in the environment may be characteristic of non-stationary conditions, *e.g.*, when populations experience Fe limitation or other environmental perturbation (Reichard *et al.*, 2007). On the other hand, the continued high dissolution rates observed in the ΔMR-1 + DFOB treatments suggest that dissolution could persist in environments in which siderophores are present in excess of a given microbial group's growth needs, *e.g.*, when supplied by other bacteria, fungi, or plants. Similarly, the addition of exogenous siderophores, and/or microbes with altered genetic capabilities, may help maintain high dissolution rates in engineered conditions. These findings may be useful for engineering biotically mediated enhanced weathering systems, a nascent but potentially useful approach to increasing mineral dissolution rates. If dissolution rates can be maintained at 10× above abiotic rates, with minimal energy inputs, such geobiological approaches may be efficient methods for effective carbon dioxide sequestration.

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Additional Information

Supplementary Information accompanies this letter at https://www.geochemicalperspectivesletters.org/article2315.

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