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Microbial Catalysis for CO_2 Sequestration: A Geobiological Approach

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One of the greatest threats facing the planet is the continued increase in excess greenhouse gasses, with CO_2 being the primary driver due to its rapid increase in only a century. Excess CO_2 is exacerbating known climate tipping points that will have cascading local and global effects including loss of biodiversity, global warming, and climate migration. However, global reduction of CO_2 emissions is not enough. Carbon dioxide removal (CDR) will also be needed to avoid the catastrophic effects of global warming. Although the drawdown and storage of CO_2 occur naturally via the coupling of the silicate and carbonate cycles, they operate over geological timescales (thousands of years). Here, we suggest that microbes can be used to accelerate this process, perhaps by orders of magnitude, while simultaneously producing potentially valuable by-products. This could provide both a sustainable pathway for global drawdown of CO_2 and an environmentally benign biosynthesis of materials. We discuss several different approaches, all of which involve enhancing the rate of silicate weathering. We use the silicate mineral olivine as a case study because of its favorable weathering properties, global abundance, and growing interest in CDR applications. Extensive research is needed to determine both the upper limit of the rate of silicate dissolution and its potential to economically scale to draw down significant amounts (Mt/Gt) of CO_2. Other industrial processes have successfully cultivated microbial consortia to provide valuable services at scale (e.g., wastewater treatment, anaerobic digestion, fermentation), and we argue that similar economies of scale could be achieved from this research.

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GLOBAL CLIMATE CHANGE

Human-driven global climate change is increasingly apparent, with global impacts accelerating during the last decade (Dreyfus et al. 2022). Over geological time, the global carbon cycle has regulated Earth's climate via silicate chemical weathering and carbonate formation (Fig. 1; Renforth and Henderson 2017). Weathering of silicate minerals causes uptake and storage of excess atmospheric CO_2 in various forms, including soluble dissolved inorganic carbon (DIC) and insoluble minerals like calcite. Today, the release of anthropogenic greenhouse gas (GHG) emissions derives from diverse human activities such as the burning of fossil fuels, deforestation, land use, cement production, etc. The rate of release of GHGs like carbon dioxide (CO_2) and methane are currently far too high to be buffered by both short-term (e.g., biological processes) and long-term (e.g., mineral weathering) carbon cycles, thereby pushing the Earth to multiple climate tipping points (Lenton et al. 2019).

Mitigating global climate change requires the cessation of the use of fossil fuels, which will slow the accumulation of GHGs in the atmosphere. Despite some incremental progress, this has proven to be a difficult social and political task (Arora and Mishra 2021). Further, cessation of fossil fuel use is not enough to curb global warming. It is estimated that the concentration of CO_2 in the atmosphere will not decline for centuries (Cawley 2011), thereby leading to continuous, severe impacts even if emissions cease. Additionally, the transition to a green economy will require burning fossil fuels for some time into the future. Thus, major carbon dioxide removal (CDR) and storage (sequestration) efforts are necessary to limit global warming to 1.5°C–2°C more than preindustrial levels (National Academies of Sciences, Engineering, and Medicine 2022). To avoid the worst impacts of climate change, CDR methods must extract >1000 gigatonnes of CO_2 ($GtCO_2$) by 2100 (Campbell et al. 2022). To this end, a number of solutions have been suggested and modeled to be economically and operationally sustainable (Dreyfus et al. 2022).

GEOCHEMICAL CDR AND ENHANCED WEATHERING

In parallel to other CDR methods, we suggest that a global effort to accelerate the removal of

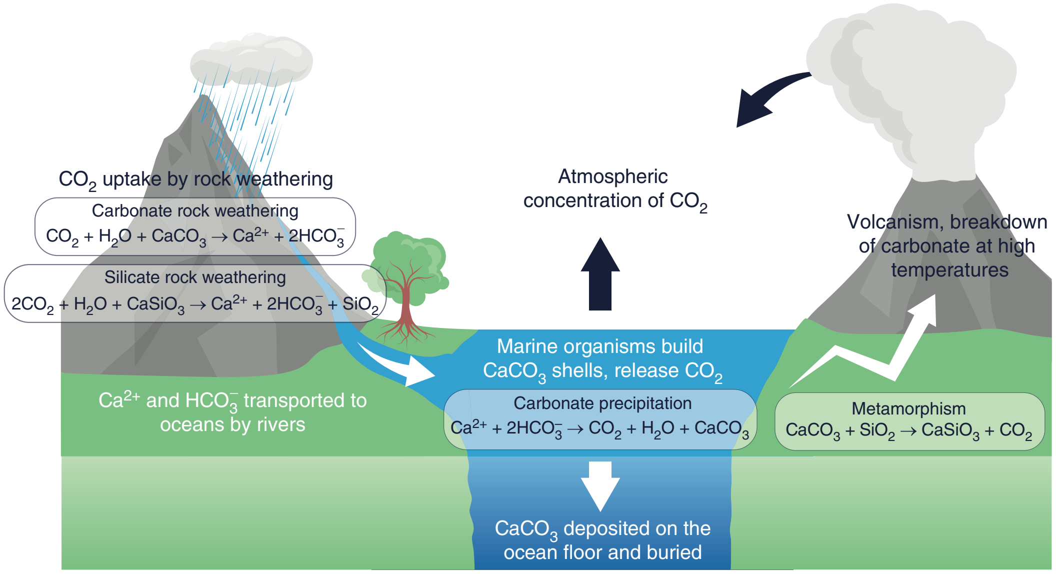

Figure 1. The carbonate–silicate cycle. CO_2 is sequestered in the form of HCO_3^- by rock weathering, transported to oceans, and eventually precipitated as $CaCO_3$ by marine organisms.

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CO_2 via enhanced silicate weathering should be initiated. Silicate weathering is widely recognized as one of the primary natural processes that regulates long-term atmospheric CO_2 concentrations (Renforth and Henderson 2017). Increasing the rate of weathering of silicate minerals (in this case, focusing on olivine) would accelerate naturally occurring geologic drawdown and storage of atmospheric CO_2. Collectively, terrestrial and marine silicate weathering are estimated to have the potential to sequester tens of billions of tonnes of CO_2/year (Renforth 2019; Campbell et al. 2022; National Academies of Sciences, Engineering and Medicine 2022). Both terrestrial and marine applications can have the potential to be more permanent and scalable carbon removal solutions than other widespread carbon removal approaches (e.g., afforestation) (Campbell et al. 2022), particularly because of the long residence time of DIC in the oceans (>10,000 yr) (Middelburg et al. 2020). Accordingly, ocean DIC is the largest DIC pool on Earth. In its 2021–2022 ocean-based CDR report, The National Academies of Sciences, Engineering and Medicine (2022) called for a rapid increase in research on ocean alkalinity enhancement (OAE) methods, inclusive of silicate-based CO_2 removal to help sequester >1000 $GtCO_2$ by 2100.

CO_2 drawdown from silicate weathering is principally controlled by the generation of alkalinity. Anions released into solution from mineral dissolution act as a proton sink (Eq. 1), neutralizing acidity present in an environment. In most natural aqueous environments, carbonic acid, resulting from the presence of atmospheric CO_2, is the dominant form of acidity. Hence, the generation of alkalinity in the marine environment induces the drawdown of atmospheric CO_2 following air–sea equilibration (He and Tyka 2022) to form DIC, principally as bicarbonate and carbonate ions:

$$\begin{aligned}&Mg_{2-x}Fe_xSiO_4 + 4CO_2 + 4H_2O \rightarrow \\ &\quad 2 - xMg^{2+} + xFe^{2+} + 4HCO_3^- + H_4SiO_4.\end{aligned} \tag{1}$$

Bicarbonate ions (HCO_3^-) in seawater can have residence times in excess of 10,000 yr (Middelburg et al. 2020), therefore qualifying as a highly permanent method for CO_2 removal and storage. Subsequently, marine calcification processes can convert DIC and alkalinity into solid carbonate species, such as calcite, aragonite, and vaterite. Although these secondary carbonate reactions decrease CO_2 removal efficiencies, they represent another permanent form of CO_2 sequestration as solid carbonate. Thus, both seawater DIC and carbonate precipitates ultimately offer an effective form of permanent storage.

Although various highly reactive hydroxide salts such as brucite also generate alkalinity and capture carbon effectively, they are not widely available in large enough quantities to contribute to gigatonne-scale CDR (Power et al. 2013). The most useful silicates are those that can both effectively capture the most protons per mole of silicate dissolution and dissolve the fastest. These include mafic–ultramafic neso-, soro-, and inosilicates minerals such as olivine and pyroxenes, as well as some hydrated clays. Of these, the minerals that have some of the highest dissolution rates are olivine, serpentine, and wollastonite (Hartmann et al. 2013; Bullock et al. 2022). They are globally abundant and occur in areas easily accessible to humans. Combined, the CDR potential of their known reserves is estimated to be in the tens of thousands of $GtCO_2$ (Lackner 2002; Power et al. 2013), orders of magnitude greater than what is needed to permanently sequester anthropogenic CO_2 emissions. The questions surrounding methods of carbon capture via ultramafic minerals therefore relate to the scientific, engineering, political, and economic logistics of implementation at large scales, which we explore below.

Olivine

Olivine is considered to be one of the most favorable silicate minerals for CDR, as it weathers quickly under Earth surface conditions (Rimstidt et al. 2012; Hartmann et al. 2013). This reactivity, along with its structure of silicate tetrahedra isolated by only two cations (Mg^{2+}, Fe^{2+}), makes olivine dissolution both relatively simple and highly energetically favorable. Additionally, olivine dissolution generates more alkalinity (prin-

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cipally HCO_3^-) than other common silicate minerals, with up to 4 mol of CO_2 sequestered per mol of olivine, equivalent to ~1 tonne CO_2 per tonne of olivine dissolved (Eq. 1). Hence, olivine ($Mg_{2-x}Fe_xSiO_4$) has been proposed as a scalable mineral for CDR applications, as it is a globally abundant, naturally occurring ultramafic silicate mineral (Beerling et al. 2021).

Microbial Catalysis of Olivine Dissolution

The rate of alkalinity generation during enhanced weathering is, in part, determined by the rate of silicate mineral dissolution (Rimstidt et al. 2012; Oelkers et al. 2018). Many studies of olivine (or other silicate minerals) conducted under laboratory conditions clearly indicate that weathering rates can be increased by grinding minerals to small particle sizes to increase the surface-to-volume ratio (Rosso and Rimstidt 2000). However, accelerated dissolution rates are difficult to sustain in abiotic closed laboratory systems, as demonstrated by us (Fig. 2) and others (Oelkers et al. 2015, 2018); and for reasons not yet clear, rates slowed significantly over time. Prior research showed that a nanometer-thick layer of ferric oxyhydroxide can form around the olivine as it weathers, acting as an impediment to further weathering (Schott and Berner 1983; Oelkers et al. 2018). Utilizing catalysts or implementing open-system applications like coastal enhanced weathering (Meysman and Montserrat 2017; Montserrat et al. 2017) may be able to accelerate the dissolution of olivine and other silicate minerals, thereby improving the feasibility and potential scale of CDR efforts based on enhanced weathering.

Despite the tremendous potential of silicate weathering for CDR, natural silicate dissolution needs to be greatly accelerated to limit global warming to 2°C more than preindustrial levels by the end of this century. Current estimates of natural, abiotic olivine dissolution place the half-life of a sand-sized olivine grain in the range of decades, nearing an asymptotic 100% dissolution of more than two centuries (Montserrat et al. 2017). Alternatively, using microbes as catalysts has the potential to reduce the mineral half-life to a few years, nearing an asymptotic 100% dissolution of ~50 yr (Berghe et al. 2021). A handful of studies tested the biological enhancement of weathering, and preliminary evidence demonstrates both fungi and bacteria can accelerate silicate dissolution via several mechanisms (Campbell et al. 2022 and references therein). Our experiments (Fig. 3) and those of others (e.g., Torres et al. 2014, 2019; Lunstrom et al. 2023) point to significant catalysis by Fe-binding organic ligands known as siderophores produced by several different bacterial groups. Whereas us-

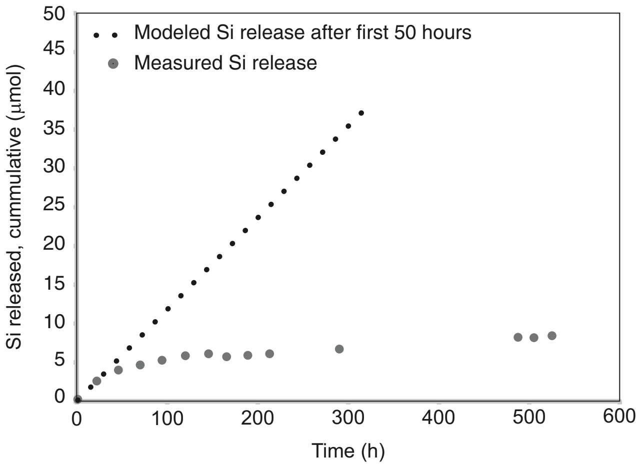

Figure 2. Modeled abiotic olivine dissolution rates in the first 50 h can be more than an order of magnitude greater than empirical dissolution rates over longer timescales, which become asymptotic.

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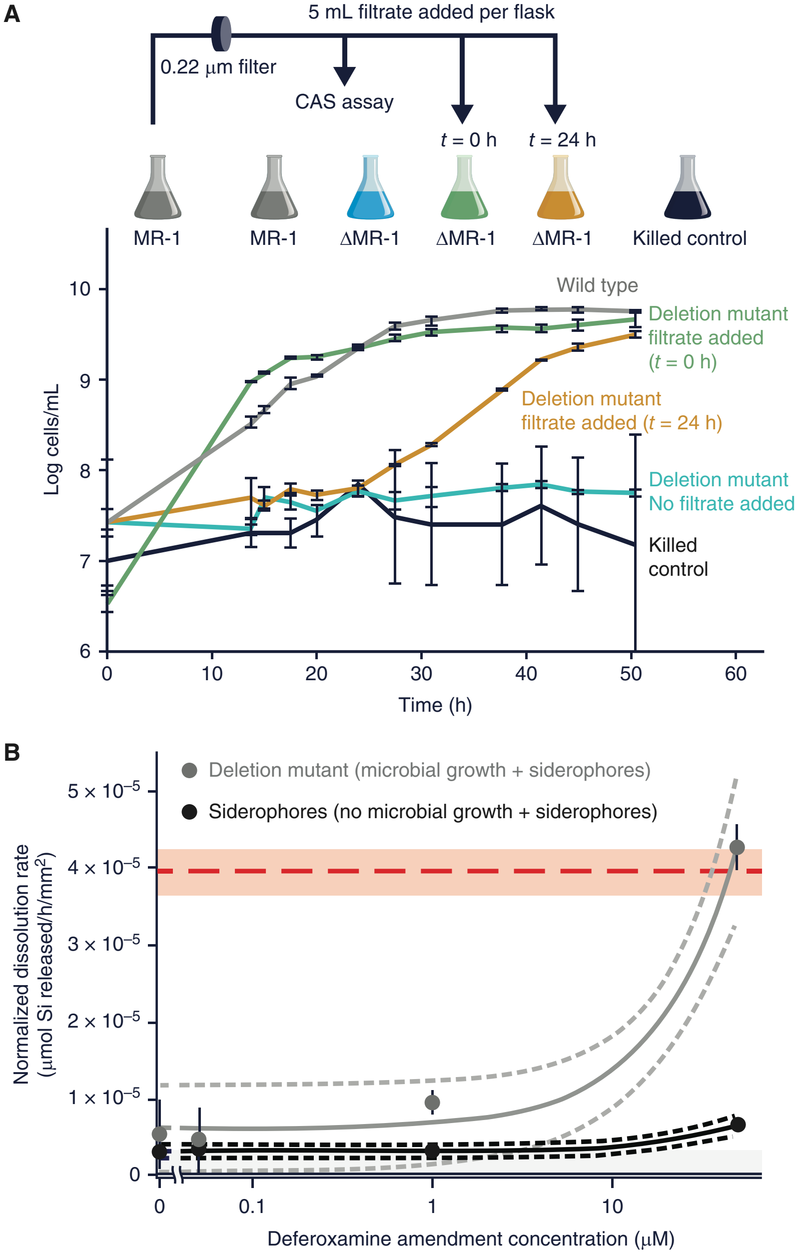

Figure 3. Plots showing *Shewanella oneidensis* growth dynamics and olivine dissolution rates across various experimental treatments. (*A*) Plot showing *S. oneidensis* growth from siderophore-based iron acquisition of olivine minerals, with the siderophore synthesis deletion mutant growing only when given exogenous siderophores. (Plot adapted with permission from Van Den Berghe et al. 2021, © 2021 John Wiley & Sons Ltd.) (*B*) Plot comparing normalized olivine dissolution rates as a function of siderophore concentrations and microbial activity. The red dashed line denotes wild-type *S. oneidensis* dissolution rates (native siderophore concentration/production unknown). The light gray line denotes olivine dissolution rates of microbial growth of the *S. oneidensis* deletion mutant as a function of added concentrations of siderophores. The black line denotes olivine dissolution rates as a function of increasing siderophore concentrations with no microbial growth. Dashed line with color background represents 95% confidence intervals on the regression lines.

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ing microbes as catalysts offers a promising path forward, mineral dissolution rates must be characterized and measured against microbial carbon cycling and net carbon fluxes to fully characterize CDR potential. Here, we suggest a path for a sustainable CO_2 sequestration program using siderophores as a case study for one potentially promising mechanism to facilitate microbial catalysis of silicate weathering.

Siderophores are organic ligands with extremely high binding affinity for Fe^{3+} and intermediate affinities for Fe^{2+}, Mn^{3+}, and many other transition metals (Hider and Kong 2010). There is a wide variety of structures produced by many different bacteria and fungi as a component of their high-affinity Fe uptake systems, particularly in aerobic marine environments, where the solubility of iron is calculated to be 10^{-16} M.

Given that the formation constants for many siderophores are 10^{30} and higher, it is a microbial mechanism that is very prevalent in the ocean, in soils, and in at least a significant fraction of the microbes in the human (Manck et al. 2022). In the ocean, iron availability has a clear and direct impact on primary productivity (Hutchins and Boyd 2016), despite being absolutely insoluble in oxic environments ($K_{sp} = 10^{-37}–10^{-44}$; Guerinot and Yi 1994). This points to evolutionary mechanisms of microbial nutrient acquisition from insoluble mineral phases (Manck et al. 2022). In fact, this is what led to previous experimental efforts to apply ocean iron fertilization as a means for CDR (Williamson et al. 2012), whereby particulate Fe-containing materials can act as sources of scarce micronutrients, promoting primary productivity and microbial growth.

Experiments by us and others have shown that the addition of siderophores to olivine particles enhances the rate of the reaction (Torres et al. 2014, 2019; Berghe et al. 2021). Although this work was encouraging, the concentrations of siderophores required to sustain the reaction were high and likely prohibitively expensive for any large-scale CDR operations. Subsequent studies (Berghe et al. 2021; Lunstrum et al. 2023), however, showed that microbes that produce siderophores can obtain nutrients from olivine, resulting in sustained growth as a function of olivine weathering (Fig. 3A). Specifically, *Shewanella oneidensis* obtained nutrients for growth from olivine particles only during the production of its siderophore, putrebactin (Ledyard and Butler 1997). This live system resulted in significantly higher rates of olivine dissolution relative to those previously seen with the addition of exogenous siderophores alone (Fig. 3B).

FUTURE DIRECTIONS

Prior experiments demonstrated increases in olivine dissolution rates by more than an order of magnitude via siderophore synthesis, but several key biological and engineering questions remain before CDR by microbially mediated mineral dissolution can be implemented at scale. Below, we outline important areas of research necessary to understand the full potential of microbially enhanced weathering.

The Biological Underpinnings of Mineral Dissolution

The precise mechanisms involved in the microbial acquisition of particulate-bound nutrients are not yet fully understood. Siderophores can play a crucial role in transforming mineral-phase iron (esp. oxidized iron) into a bioavailable form, which can remove a thin (nanometer-thick) layer of oxidized iron deposited along the surface of olivine grains. This process enabled microbial exponential growth for siderophore-producing bacteria, whereas bacteria incapable of producing siderophores proved to be unable to grow in the same conditions (Berghe et al. 2021). This accelerated dissolution seemed to be most pronounced during microbial exponential growth, which would be the period of maximal demand for new iron entering the biological pool.

Siderophore activity can be augmented by other, complementary microbial processes related to the formation of biofilms along mineral surfaces. Bacteria can form thick, redox-active biofilms along mineral surfaces (Fig. 4) that can support abundant and dense growth (Hall-Stoodley et al. 2004). Although some studies have suggested that biofilms can inhibit mineral dissolution (Oelkers et al. 2015), the success of these biofilms in sustaining growth in environ-

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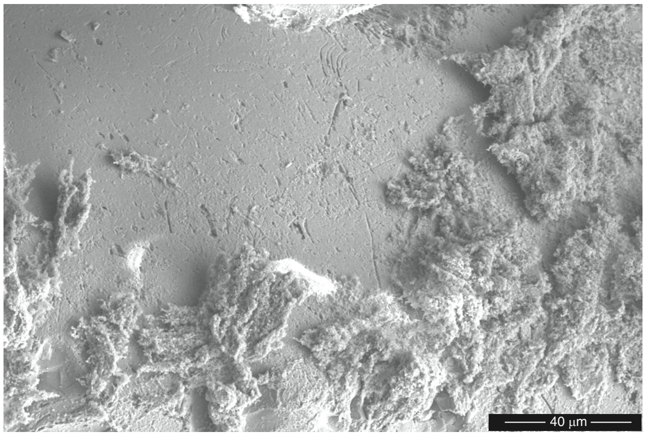

Figure 4. Scanning electron microscope (SEM) secondary electron imagery showing *Pseudomonas aeruginosa* biofilm growth atop olivine grains in an iron-deplete medium. Accelerated weathering features are clearly visible on the mineral surface (middle of the image) after only 48 h. Scale bar, 40 μm.

ments where dissolved nutrients are limiting suggests active mechanisms of nutrient acquisition directly from mineral phases. Biofilms can host a wide range of metabolic activities. If this activity can be channeled toward mineral-phase nutrient acquisition, the sheer density and intimate proximity of biofilms to mineral surfaces can have a profound effect on mineral dissolution rates, as observed in prior studies (Berghe et al. 2021; Campbell et al. 2022). In addition to siderophore activity, respiration can significantly lower the pH along the mineral surface, further enhancing mineral dissolution rates. Bacteria can also produce significant amounts of organic acids within the confines of biofilms (e.g., lactate, pyruvate, citrate; Rogers et al. 2013), which can have significant effects on localized pH and are often excellent cation sorbents that can further help promote mineral dissolution (Pokrovsky et al. 2009).

Here, we propose that a genetic and physiological understanding of mineral dissolution mechanisms would critically inform the utilization and application of microbially enhanced dissolution reactions. Identification of genetic synthesis pathways and their regulators would inform engineering efforts to improve dissolution. Particularly, a mechanistic understanding would drive the selection of promising organisms for large-scale dissolution systems, the application of genetic engineering to maximize dissolution, and the design of culture environments and reactor systems.

The Upper Limit of Microbially Mediated Dissolution and Biosynthetic Production

Sustaining microbially accelerated mineral dissolution requires the continuous maintenance of an environment that favors both a specific metabolic activity from a microbiome and the kinetics and thermodynamics of mineral dissolution and carbon drawdown. Scientific and technological advancements have transformed these challenges into engineering questions rather than scientific barriers. For example, maintaining an environment in a steady geochemical state to promote a specific reaction is done routinely (and at scale)—for example, in water treatment plants and breweries. Similarly with microbes, impressive advances in the field of synthetic biology now allow us to more easily genetically engineer non-model strains, although the future goals are to control entire microbiomes (Brophy et al. 2018; Lawson et al. 2019; Lee et al. 2020).

Microorganisms may also add separate economic value beyond the generation of alkalinity from mineral dissolution. These can include the biosynthesis of lipids, vitamins, and other bio-

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molecules that have societal and economic value in industries such as pharmaceuticals or agriculture and aquaculture (Włodarczyk et al. 2020). Alternatively, certain substrates introduced into the reactors can promote the growth of a specific strain or metabolism, such as certain degradable plastics (e.g., polyhydroxyalkanoates [PHAs] and polyhydroxybutyrates [PHBs]) as a carbon source for biofilm-forming heterotrophs (Suzuki et al. 2021). Not only would such specific substrates select for specific, desired microbial activity, they can offer a sustainable means to manage plastic wastes while replacing the costs of adding a carbon source to the reactor. Last, the dissolution of large quantities (i.e., gigatonnes) of minerals will release significant amounts of trace metals associated with ultramafic materials, most notably nickel, cobalt, and chromium. These metals are particularly valuable, as they play a critical role in the transition away from fossil fuels and toward an electricity-based economy (Diallo et al. 2015).

We propose that microorganisms can be genetically engineered for large-scale mineral dissolution processes, specifically for production of siderophores, formation of biofilms, production of valuable biomolecules, and growth on renewable substrates. Identification of the genetic networks responsible for these phenotypes represents the enabling technology to enhance or tune strain performance.

Siderophore synthesis pathways have been identified in many organisms through both experiments and bioinformatics (Hider and Kong 2010; Garber et al. 2020, 2021). Several pathways have been expressed and further engineered in the model organism *Escherichia coli*, with the goal of producing siderophores as therapeutic antibiotics (Fujita and Sakai 2013; Fujita et al. 2018). To our knowledge, there have been limited efforts to enhance the production of endogenous siderophores, to date. Siderophores are typically produced in bacteria by nonribosomal peptide synthesis and secretion, which are both resource- and energy-intensive processes (Hider and Kong 2010). Enhanced production may require the constitutive expression of siderophore biosynthesis systems both endogenously and heterologously, metabolic engineering for increased availability of siderophore precursors, or alterations of the bacterial secretion complex. Although transcriptomic studies have been performed on siderophore-producing organisms under iron-limiting conditions (Manck et al. 2020), the biological bottleneck for the production of siderophores is sparingly known and often complex. For example, *Staphylococcus aureus* can produce both staphyloferrin A (SA) or B (SB), both of which are citrate-based siderophores; down-regulation of the tricarboxylic acid (TCA) during Fe limitation limits the production of SA because of decreased citrate synthase activity. An alternate citrate synthase up-regulated by Fe limitation supports the synthesis of SB, however. This system provides a natural inspiration to transcriptionally and metabolically maintain enhanced siderophore synthesis (Sheldon et al. 2014). Enhanced or constitutive secretion of siderophores could shed light on the possible upper limit of siderophore-mediated silicate dissolution and contribute to the broader understanding of engineered synthesis and production of complex natural products. There is also the point that siderophores are not a chemical monolith, but rather a functional category composed of highly diverse chemical structures and backbones, which influences their bioavailability, chemical behavior in water, and photoreactivity (Barbeau et al. 2003). Exploring the specific interactions between siderophores and olivine will better inform possible designer siderophores that are both metabolically cheap to produce and optimized for catalyzing dissolution.

Genetic engineering may also enhance other mechanisms of mineral dissolution, such as biofilm formation, citrate production, and local acidification. Biofilm formation in the context of pathogenesis, for example, has been studied extensively both genetically and physiologically, resulting in a range of therapeutics and drugs that disrupt biofilm formation (Jiang et al. 2020). Biofilms could be used industrially for olivine dissolution and other applications such as microbe–electrode interactions, but engineering and controls of film formation and architecture remain difficult (Angelaalincy et al. 2018; Mukherjee et al. 2020).

Many of the phenotypes described here, such as siderophore production and biofilm for-

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mation, are difficult to engineer rationally because of their complex genetics. In the system proposed here, however, microbial growth is coupled to the harvesting of iron from olivine and other silicate minerals. It may be possible, therefore, to perform large-scale selection of mutants for enhanced harvesting of nutrients from minerals. High-throughput selections or screens could reveal key targets for rational genetic engineering and identify high-performing gain-of-function mutations that have immediate industrial utility.

Bottom-up genetic engineering and synthetic biology can improve the performance of coculture or consortia systems (Lawson et al. 2019). For operation at large scales, the stability of a multicomponent living system is challenging, especially in complex, nonsterile mediums. Mutual dependencies between microbial organisms have been extensively described in natural systems and applied to synthetic systems at laboratory scale (Schink 2002; Goers et al. 2014; Chen et al. 2019). To date, synthetic microbial consortia have not been implemented at industrial scale, however. The olivine dissolution system described here, specifically, offers a novel solution for synthetic mutual dependency.

Finally, metabolic engineering and synthetic biology have been extensively applied to synthesize valuable biomolecules at high titers in engineered hosts. These include biomass components such as lipids, complex natural products, biofuels, and medicines (Chemler and Koffas 2008; Courchesne et al. 2009; Adrio and Demain 2010; Choi et al. 2020). Similar techniques are applied to enhance the growth of microorganisms on renewable feedstocks, such as lignocellulose, or plastic polymers as discussed earlier (Huang et al. 2014). One additional microbial application of olivine dissolution is the uptake and concentration of valuable trace metals. Metal uptake by bacteria has been studied in the context of heavy metal remediation (Gadd 1990; Valls and Lorenzo 2002) and plant–microbe interactions (Kidd et al. 2017). A system for microbial dissolution of minerals provides a uniquely useful platform with which to study the uptake and harvesting of valuable metals.

Utilization of genetically engineered organisms for large-scale mineral dissolution requires consideration of the ethical and ecological impacts. One advantage of the proposed system is the potential for physical containment on top of genetic controls. Furthermore, engineering controls may protect against unwanted mutation or ecosystem proliferation. Recently reported organisms with a reduced genetic code may be less likely to acquire natural genetic material that could confer new phenotypes and contribute synthetic genetic material to the natural gene pool (Lau et al. 2017; Robertson et al. 2021). Novel kill switches and synthetic auxotrophy may also restrict the activity and replication of engineered organisms to controlled environments (Stirling et al. 2018, 2020; Whitford et al. 2018; Stirling and Silver 2020). In 2022, the Engineering Biology Research Consortium released a road map for the application of synthetic biology to climate and sustainability that urges the identification, assessment, and open communication of benefits and risks associated with research efforts (Chen et al. 2022). Early examples of deployment of engineered organisms such as engineered crops with resistance to pests or drought provide a framework within which new technologies may be evaluated (Scheben and Edwards 2017; Smyth 2020).

In short, physical, chemical, and genetic conditions may be engineered to optimize metabolic functions, as well as the thermodynamics and kinetics of mineral dissolution and carbon capture. Such cultivation systems can be operated within a broader existing economic and industrial infrastructure, in which they can act not only as systems of large-scale carbon capture, but also offer sustainable means of waste management and/or production of valuable by-products.

Considerations for Mineral Feedstocks and Industrial Cultivation

Large-scale (Mt/Gt) CDR reactors will require large inputs of water, nutrients, and mineral feedstock and will require downstream processing to recover valuable added products. Industrial infrastructure and scientific knowledge already exist to implement such reactors at scale. Com-

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bined, the mining and construction sectors produce >8 Gt/yr of mineral waste materials with CDR potential >8 Gt/yr (Renforth 2019; Bullock et al. 2022). The remaining questions then relate to finding the upper limits of dissolution and carbon capture rates that such reactors can offer, while identifying the operating conditions that will sustain these at scale.

Some of the key questions that remain include identifying the conditions for maximal mineral dissolution and carbon capture rates. Reaching these maxima will involve experimenting with a wide range of physical and chemical constraints, as these help manage the baseline thermodynamic environment of mineral dissolution. As discussed, silicate dissolution rates can be difficult to constrain over periods of years. There is a significant bias in the literature, within which quantified measures of dissolution have focused on short time periods of hours to days (Fig. 2; Oelkers et al. 2018), which may not be representative of long-term steady state dissolution rates. Figure 2 shows a modeled dissolution rate derived from the first 300 h of dissolution versus empirical dissolution data over several weeks. Moreover, characterizing mineral dissolution over months can, however, be challenging, as dissolution can be nonstoichiometric, and different proxies (i.e., dissolved silicon vs. nickel) can give different quantified estimates of dissolution rates (Montserrat et al. 2017).

Additionally, a comprehensive characterization of mineral substrates and their geochemistry is key. As discussed, a mineral's dissolution rate and potential to generate alkalinity are critical characteristics in determining the carbon capture potential. In this respect, ultramafic minerals such as olivine and serpentine are of great interest (Bullock et al. 2022). However, associated reactions can negatively impact carbon capture efficiency, such as the oxidation of iron. As a major component of olivine and many ultramafic minerals, ferrous iron will oxidize readily during mineral dissolution, a reaction that releases free protons and neutralizes the alkalinity generation congruent to silicate dissolution. Choosing ultramafic minerals with low iron content would be important in abiotic conditions. However, in the context of bioreactors that promote microbial iron acquisition, it is unclear what iron concentration will maximize dissolution rates. Furthermore, the processes involved in the microbial acquisition of iron (i.e., ligand exchange reactions between siderophores and ferric iron, ferric reduction involved in iron cellular absorption, along with photoreduction of ligand-bound iron) are all proton-sensitive reactions and can impact pH and thus alkalinity generation to some extent (Barbeau et al. 2002; Dhungana and Crumbliss 2005). Characterizing this process will help constrain system design for maximal carbon capture.

Another critical component in estimating net CO_2 fluxes relates to the fate of carbon held in the organic pool. Characterizing the fluxes and fate of carbon across processes like biological assimilation, biofilms, mineral dissolution, and secondary precipitation in a dense environment is a challenging yet exciting and meaningful scientific endeavor. Although the single most important metric for a bioreactor might be net carbon fluxes and associated carbon capture rates, it will be important to characterize the fate of carbon and all its forms. This implies steep geochemical and metabolic gradients, forcing a wide range of reactions that can impact the form and fate of carbon. The main forms of carbon flowing out of bioreactors will be dissolved as well as particulate organic and inorganic phases. Being able to account for all their relative abundances will be valuable, not only as an additional means to measure carbon capture and potentially useful biomolecule production, but also to inform on strategies around reactor design, engineering, and permanent carbon storage.

Inorganic carbon fluxes are highly dependent on a system's carbonate saturation and precipitation as secondary mineral phases (Fuhr et al. 2022). As per Equation 1, the most efficient form of carbon capture is in the form of bicarbonate (also referred to as dissolution trapping). An ideal bioreactor system should therefore maintain conditions below carbonate and silicate saturation to limit the precipitation of secondary minerals. Although the precipitation of carbonates still produces a net sink of stored carbon (also referred to as mineral trapping or carbonation), the acidity simultaneously generated in this reac-

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tion decreases the efficacy of the process significantly (Fuhr et al. 2022). The flexibility of an engineered system offers the possibility to promote and effectively manage carbonate precipitation as a form of long-term storage.

Hence, a comprehensive characterization of accelerated mineral dissolution geochemistry under a wide range of conditions will be critical to maximize carbon capture, and the forms of carbon must be fully characterized to best manage its permanent storage. Carbonate precipitates can be easy to store permanently because they are relatively unreactive in the natural environment. Bicarbonate and DIC, however, need to be stored in vast, well-buffered basins such as the world's oceans to remain stable and not outgas CO_2 back into the atmosphere. Organic forms of carbon (particulate and dissolved) will need to be stored in an environment where it will avoid reoxidation, which might involve specific containment strategies.

Techno-Economic Viability

The total CDR potential of known, global reserves of ultramafic minerals lies in the range of several tens of thousands of $GtCO_2$, orders of magnitude greater than what is required to sequester anthropogenic CO_2 emissions (Lackner 2002; Power et al. 2013). Although geochemical CDR thus offers tremendous potential, implementing it at scale carries economic constraints that must be taken into account. Techno-economic analyses of large-scale reactors are critical in guiding research and development, highlighting constraints that are not always obvious in a laboratory or small-scale setting.

By estimating the dimensions and requirements of a reactor at scale, one can infer the costs and logistical constraints of such an operation. Namely, these will include the costs of building the reactors, excavating and grinding the ultramafic minerals, the costs of fertilizers and other substrates, accessing and treating the water used in reactors, and total energy requirements. The economic potential of carbon capture also offers a unique opportunity for industries that use microbial catalysis as a process of chemical engineering. Some industries have been extremely successful (i.e., fermentation and the alcoholic beverages industry), and some have struggled to remain competitive (i.e., algae farms and biofuels industry) (Hoffman et al. 2017). Carbon capture reactors, however, sell, at their core, carbon credits. The recovery of additional, valuable by-products like metals could serve to subsidize the cost of carbon capture and will further help integrate CDR efforts into the broader economy, by providing a source of valuable commodities to other sectors including agriculture and aquaculture, pharmaceuticals, and other industries. This represents an unprecedented opportunity to connect the accelerated weathering of the ultramafic minerals to rapidly growing carbon markets projected to surpass \$1 trillion in 2050, as net-zero pledges from countries and companies continue to skyrocket (Liu et al. 2022).

Thus far, our techno-economic analyses show that industrial-scale bioreactor systems for enhanced weathering are comparable to common water treatment facilities and can thus benefit from existing infrastructure and engineering capabilities. With the scientific proof of concept already established (Berghe et al. 2021), our analyses indicate that methodological and technological improvements to scale bioreactors as described above have the potential to achieve net cost of carbon capture (including capex, opex, energy and carbon costs, substrate inputs) of ~\$100/tonne. Because of these valuable, additional products, this process not only has the potential to be inherently profitable, but could be considered a simultaneous carbon capture and mining and resource extraction process.

CONCLUSION

Because of inaction for broad decarbonization coupled to continuous anthropogenic GHG emissions, there is a global consensus that large-scale CDR will be needed to remove $GtCO_2$ over the next several decades. CDR will also be necessary to remove further CO_2 emissions required for the transition to a decarbonized, green economy. Accelerating Earth's inorganic carbon cycle through the weathering of silicate minerals like olivine offers a promising path to removing and storing gigatonnes of at-

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mospheric CO_2. Because of the sheer amount of CO_2 that needs to be sequestered, however, multiple weathering approaches must be pursued simultaneously. Although grinding minerals into sand-sized particles can accelerate weathering rates of olivine minerals in coastal environments (i.e., coastal enhanced weathering), half-lives of olivine grains are on the order of decades. Hence, we suggest that microbial catalysis to accelerate mineral dissolution rates must be explored alongside other CDR methods. We have shown that microbes have the potential to significantly increase weathering rates leading to olivine grain half-lives of several years. By using micronutrients like Fe in olivine, microbes can use these mineral substrates for exponential growth, thereby offering a path to scale the cultivation of microbiomes growing on silicate minerals. Indeed, other industries have successfully cultivated microbes to perform specific, valuable functions including wastewater treatment and fermentation. Further research to examine the biological mechanisms of microbial–mineral interactions, biofilm formation, and large-scale cultivation will provide critical insights that can galvanize global efforts in silicate dissolution for CDR. It will also create a step change in our understanding of fundamental microbial processes particularly in biofilm formation and the synthesis of complex natural products, while also opening the door to novel approaches to engineer microbiomes. These research endeavors naturally integrate the fields of CDR, synthetic biology, geochemistry, climate science, engineering, and economics and will provide new models that can yield various outputs from the sustainable biosynthesis of valuable products to the removal and long-term storage of excess atmospheric CO_2. Although many of these fundamental processes have been happening worldwide for billions of years, we are only taking the initial steps along the pathway toward understanding how these mechanisms can help turn the tide on the climate crisis.

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