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## Assessing biological soil crusts as agents of Ca–Mg silicate dissolution and CO<sub>2</sub> sequestration

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### ABSTRACT

Biological soil crusts (BSCs) monitored over a 25-year period enhance the dissolution of the Ca-silicate plagioclase and the Mg-silicate olivine at Sonoran Desert and Colorado Plateau, USA, study sites. This first measured biological enhancement of weathering (BEW) for plagioclase is a mean of  $2.3 \pm 0.4$  and  $3.0 \pm 0.4$  for the Organic Pipe, Arizona and Moab, Utah study sites; and it is  $4.9 \pm 0.8$  and  $3.9 \pm 0.3$  for olivine at these respective sites. These BEWs are low compared to other biological agents such as lichens, tree roots, termites and especially ants. If these modern BEW for BCSs reflect the magnitude of BEW in Archean soil crusts, then the presence of abundant BSCs covering an Archean Earth surface would not contradict available evidence for no substantial atmospheric CO<sub>2</sub> decline in Earth's early atmosphere. The relatively low BEW value for BCSs indicates that BSCs would not be a useful geoengineering solution to high levels of atmospheric carbon dioxide.

### KEYWORDS

carbon dioxide; drawdown; Earth's habitability; faint sun hypothesis; in situ weathering

### Tribute

*Discussions with Luna Leopold in 1980 over the importance of long-term monitoring experiments and then with Anthony Orme in 1983 over different possible agents of mineral decay led to a 25-year-long field experiment to monitor the in situ dissolution of Ca–Mg silicate minerals, olivine and plagioclase. In particular, Tony was curious about the relative importance of ants and cryptobiotic crusts, now called biological soil crusts (BSCs), because BSCs might have covered the earth's land surface prior to other forms of life and because ants underwent a great diversification and expansion at the onset of Cenozoic global cooling. Frankly, I had never given ants nor BSCs any thought as potential agents of mineral dissolution before Tony mentioned them. Hence, when I started my field experiments, I made sure to include BSCs and ants. Tony was spot on about ants and their possible role in Cenozoic cooling. The finding that eight different ant species enhance mineral dissolution by ~50–300× over controls and hence is the most powerful known BEW was published elsewhere (Dorn, 2014). I think that Tony would have been fascinated to learn that BSCs are not major biological enhancement of weathering (BEW) agents, at least not the studied modern analogs to the Precambrian cover that Tony considered.*

## Introduction

Earth's habitability over geological time scales is best explained by the slow drawdown of atmospheric CO<sub>2</sub> despite increasing solar irradiance (Schwartzman, 2002, 2017; Schwartzman & Volk, 1989, 1991, 1992) through the Urey reaction (Urey, 1952) generalized as:

CO<sub>2</sub> + CaSiO<sub>3</sub> (Ca-silicate, e.g., plagioclase) → CaCO<sub>3</sub> (limestone) + SiO<sub>2</sub> (e.g., clays) (1)

CO<sub>2</sub> + MgSiO<sub>3</sub> (Mn-silicate, e.g., olivine) → MgCO<sub>3</sub> (dolomite) + SiO<sub>2</sub> (e.g., clays) (2).

Biotic enhancement of Ca–Mg-silicate dissolution has been particularly important in CO<sub>2</sub> drawdown (Arens & Kleidon, 2011; Cochran & Berner, 1992; Dontsova et al., 2020; Dorn, 2014; Drever, 1994; Finlay et al., 2020; Moulton, 2000; Porada et al., 2016; Schwartzman, 2002, 2017; Schwartzman & Volk, 1989).

Field measurements are increasingly being used to quantify the BEW of Ca–Mg silicates (Azam et al., 2019; Brantley, 2005; Brantley & Velbel, 1993; Navarre-Sitchler & Brantley, 2007; Pacheco & Alencao, 2006; Rosenstock et al., 2019; Swoboda-Colberg & Drever, 1993; White & Brantley, 2003). A common strategy to understand BEW through field observations is to use the solute load of rivers: comparing lichen-covered (Aghamiri & Schwartzman, 2002) and non-lichen covered drainages (Moulton, 2000); comparing pine-covered and deforested drainages (Arthur & Fahey, 1993); and comparing bare rock versus meadows in alpine drainages (Drever & Zobrist, 1992).

Digital image processing of back-scattered electron (BSE) microscope imagery allows the study of field-based mineral dissolution at a vastly different scale, orders of magnitude smaller areas than drainage basins (Dorn, 1995). For example, lichens can be compared to uncolonized rock surfaces just a few centimeters away (Brady et al., 1999). This technique has been used to analyze olivine and plagioclase placed in ant colonies, termite colonies and plant root mats (Dorn, 2014). The BSE approach of measuring porosity of Ca-silicates is the method, thus, that is most appropriate to study the impact of biological soil crusts (BSCs) on mineral decay, because the thickness of BSCs is on the scale of a few millimeters at most. With the BSE method of measuring *in situ* dissolution (Dorn, 1995), it is possible to obtain quantitative measurements from sand-sized samples placed directly into the middle of BSCs.

BSCs are widespread phenomena globally (Belnap et al., 2001; Rodriguez-Caballero et al., 2018), but tend to be more studied in arid and semi-arid regions (Belnap, 2003, 2006; Bowker et al., 2008; Faist et al., 2017; Garcia-Pichel & Belnap, 2003; Garcia-Pichel et al., 2003). Metting (1991) claimed that BSC organisms accelerate rock weathering, but unfortunately did not provide insight into the magnitude of the hypothesized acceleration or insight into the role of BSCs on dissolution of Ca–Mg silicates. The author is not aware of any other prior scholarship on the role of BSCs on BEW – the goal of this research.

This paper's structure starts with the methods employed in the field and laboratory and then presents results that BSCs do enhance BEW somewhat, but at accelerations nowhere near others studied biological agents such as ants or tree roots. The discussion section then turns towards an evaluation of the implications for modern carbon sequestration and for a solution to a paradox associated with Archean carbon sequestration.

## Methodology

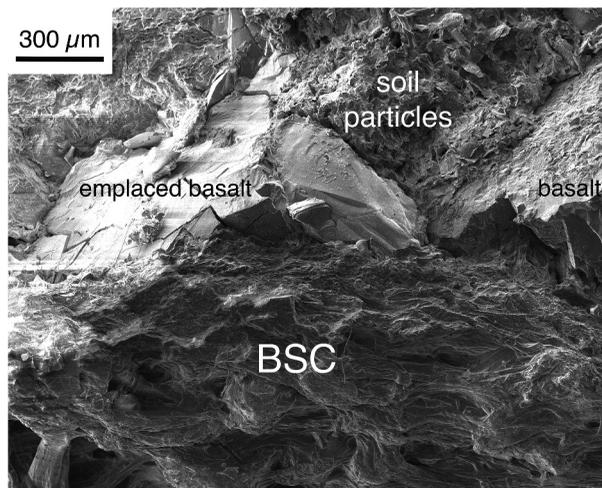
### Overview

A fundamental difficulty in quantifying the impacts of BSCs on Ca–Mg-silicate dissolution involves the issue of dormancy associated with desiccating events (Angel & Conrad, 2013; Rajeev et al., 2013). Another difficulty rests in obtaining data from samples directly in contact with BSCs. Both of these complications can be handled by the general strategy used in Dorn (2014): grind up recent (unweathered) Hawaiian basalt material that is foreign to a field setting and emplace sand-sized grains directly inside BSCs. Hawaiian basalt contains both Ca-rich plagioclase and Mg-rich olivine. Thus, the basic approach employed here rests in obtaining statistically significant data by emplacing hundreds of sand-sized grains directly into BSCs and then recollecting samples every 5 years. Dissolution of minerals is then measured directly with the BSE method (Dorn, 1995).

### Field sites

The first step in this research involved collection of basalt from the A.D. 1800–1801 Kaupulehu flow of Hualalai Volcano, Hawaii with the second step measuring the initial state of intra-crystal porosity for 200 Ca-plagioclase grains at  $0.002 \pm 0.002\%$  and for 200 Mg-olivine grains at  $0.001 \pm 0.001\%$  using the BSE method (Dorn, 1995). The third step involves crushing the basalt, followed by sieving to keep just 0.5 mm grains. This material was prepared for this BSC research, as well as research on ant colonies, termite colonies and tree root maps reported previously (Dorn, 2014).

The fourth step placed these basalt fragments directly into BSCs. This was done by hand, by gently pushing the grains in the middle of the BSCs (e.g., Figure 1). Sand grains were emplaced into BSCs in 30 different spots in the same local area of a few tens of



**Figure 1.** Secondary electron image of a sample extracted from the Moab site after 20 years of exposure to BSCs. The sample was gently “dug out” of the BSC, placed carefully in epoxy to preserve the structure, and then placed on an SEM stub for this image prior to polishing.

square meters. The idea was to insert equivalent samples to recollect every 5 years. In addition to the BSC-emplaced grains, control samples were placed inside plastic pipes receiving only infiltrating precipitation.

The samples were placed into BSCs in a field setting in the lower Sonoran Desert and another field setting in the Colorado Plateau. The lower Sonoran Desert setting is on Bureau of Land Management land on the northern border of Organ Pipe National Monument (N 32.302 W 112.756). This is in the same general area as the late Quaternary piedmont setting studied by Nagy et al. (2005). The rugose crusts are characterized by cyanobacteria and fungi with patches of lichens and mosses (Belnap, 2006). Nagy et al. (2005) focused their study on the prokaryotic diversity, and they found the most common members to be Cyanobacteria, Proteobacteria, Actinobacteria and Acidobacteria. Bacterioidetes; Chloroflexi and Gemmatimonadetes were not abundant, but were present (Nagy et al., 2005).

The Colorado Plateau field site is located the same general setting studied by Garcia-Pichel et al. (2003) in the Moab area of the Colorado Plateau (N 38.569 W 102.467). The BSC studied here is same the “light” type of pinnacled crust with abundant lichen and moss cover; light crusts represent a relatively early stage of BSC formation, in this case, on sandy soils (Garcia-Pichel et al., 2003).

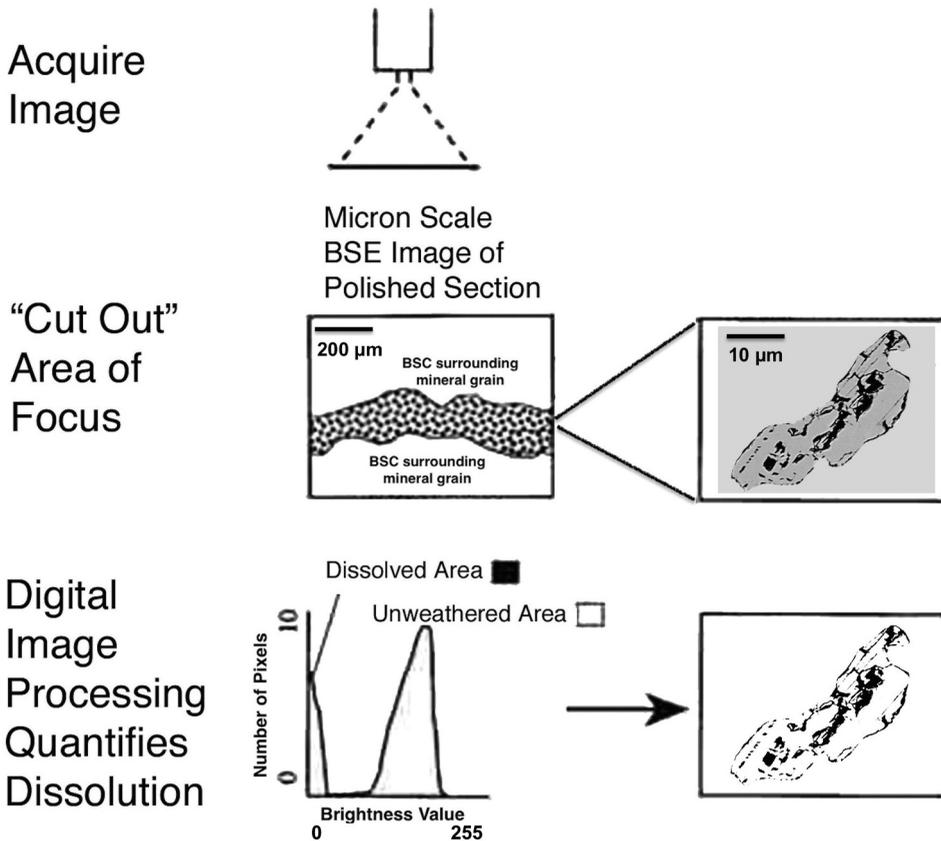
Emplaced samples were recollected from five of the emplacement locations after 5 years. Then, another five emplaced locations were collected at 10, 15, 20 and 25 years from both the BSCs and the control plastic pipes. Because Hawaiian basalt is very different in appearance from soil material at each of the field sites, the basalt grains were easy to identify in the BSC samples with a 10–45× stereomicroscope in the field. The samples were then inserted directly into an epoxy mold to preserve *in situ* relationships (e.g., Figure 1).

### **BSE *in situ* measurement of dissolution**

The fifth step in the methods quantified *in situ* dissolution of plagioclase and olivine using digital image processing of backscattered electron microscope imagery (Dorn, 1995). In total, 150 Ca-plagioclase grains and 150 Mg-olivine grains were analyzed for each time period, composed of 30 randomly selected basalt grains from each of five emplaced BSC and control. This strategy made it possible to better understand intra-site variability for each time interval.

Sample preparation involved the same techniques used in previous *in situ* studies (Dorn, 1995; Brady et al., 1999, 2014). An epoxy mold was polished using progressively smaller grit sizes ending with 0.1 μm aluminum paste. This small size provides a polish appropriate for BSE imagery.

Figure 2 summarizes the BSE method. A BSE detector acquires images of basalt grains emplaced in the BSCs. BSE images consist of a grayscale where material with higher atomic number producing brighter pixels. Since dissolution areas show up as black in the BSE image, thresholding using the public domain software NIH Image (<https://imagej.nih.gov/nih-image/>) yields information on the percent of the dissolved area of each plagioclase and olivine mineral grain. A key assumption, confirmed during method development (Dorn, 1995), is that the two-dimensional cross-section produces a result that is statistically indistinguishable from a 3D analysis; this test was done by making



**Figure 2.** The BSE method of measuring in situ mineral dissolution (modified from Dorn, 1995) uses an electron microscope with a BSE detector to acquire an image of a polished section. Then, individual minerals are manually “cut out”. Thresholding with the NIH image software then yields a percentage of porosity for the mineral. The bimodal nature of the brightness values – very low for dissolved areas and then much brighter for mineral material. This is a common digital image processing strategy.

multiple polished cross-sections of the same minerals – imaging and polishing, repeatedly, with multiple iterations.

### Data analysis

The study compiles 1200 measurements of mineral porosity for olivine and plagioclase minerals in controls exposed only to precipitation and minerals exposed to BSCs. Acquired data were compiled in a structure of rows and columns. The 150 rows of data consist of 30 minerals dissolution measurements for each of the five sampling sites. Data are placed in eight columns: Organ Pipe control for plagioclase minerals; Moab control for plagioclase minerals; Organic Pipe control for olivine minerals; Moab control for olivine minerals; Organ Pipe BSC for plagioclase minerals; Moab BSC for plagioclase minerals; Organic Pipe BSC for olivine minerals; and Moab BSC for olivine minerals.

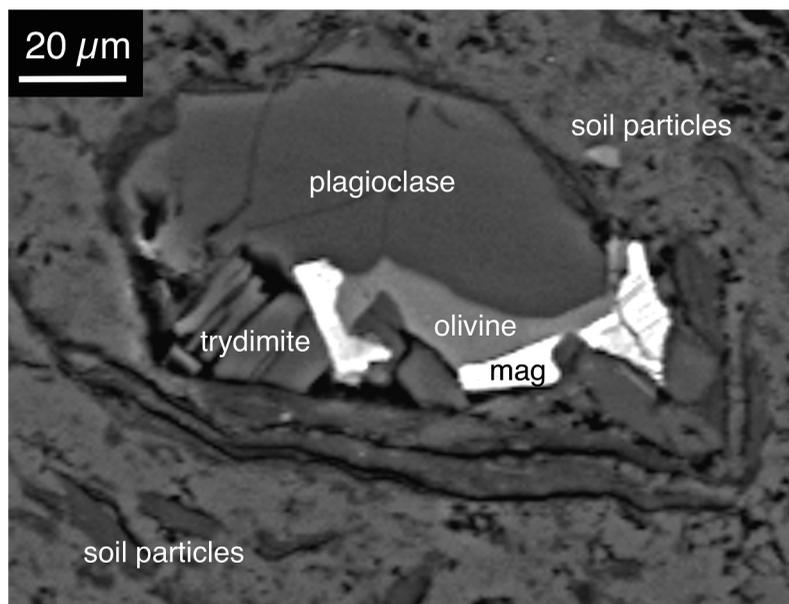
Mean and median measurements of central tendency were then calculated for each sampling site based on 30 mineral measurements. This produced five separate means and

**Table 1.** Twenty-five years of dissolution of olivine and plagioclase observed at the moab and organ pipe BSC sites. Each number represents the mean of 30 measured minerals in a subsample site location, along with the average and standard deviation of five sites.

Sample	Mean dissolution ratio to control					Ave $\pm$ SD
	Site 1	Site 2	Site 3	Site 4	Site 5	
Organ Pipe BSC olivine	4.6	5.7	5.1	3.7	5.5	4.9 $\pm$ 0.8
Organ Pipe BSC plagioclase	2.4	1.7	2.0	2.5	2.8	2.3 $\pm$ 0.4
Moab BSC olivine	3.6	4.0	4.4	3.6	3.8	3.9 $\pm$ 0.3
Moab BSC plagioclase	3.2	2.6	2.8	2.9	3.7	3.0 $\pm$ 0.4

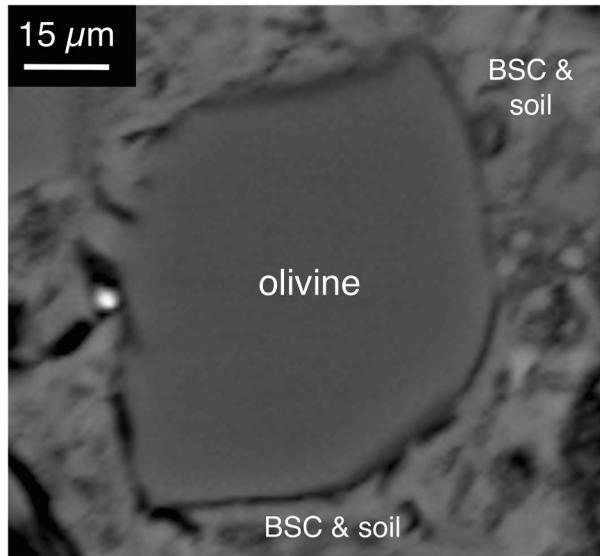
**Table 2.** Twenty-five years of dissolution of olivine and plagioclase observed at the moab and organ pipe BSC sites. Each number represents the median of 30 measured minerals in a subsample site location, along with the average and standard deviation of five sites.

Sample	Mean dissolution ratio to control					Ave $\pm$ SD
	Site 1	Site 2	Site 3	Site 4	Site 5	
Organ Pipe BSC olivine	11.0	9.3	7.5	3.8	6.0	7.5 $\pm$ 2.8
Organ Pipe BSC plagioclase	3.0	4.0	3.5	3.0	3.0	3.3 $\pm$ 0.4
Moab BSC olivine	6.5	3.0	10.5	4.3	4.3	5.7 $\pm$ 3.0
Moab BSC plagioclase	3.2	3.8	3.3	5.0	5.5	4.2 $\pm$ 1.0



**Figure 3.** Plagioclase and olivine show very little dissolution, even after 25 years of exposure to BSCs. Dissolution shows up as black holes this BSE image of a polished cross-section of basalt emplaced in organ pipe BSCs. The dark hole on the far-left side of the plagioclase mineral is one of the larger dissolution areas observed in this study. This image shows a cross-section of a basalt fragment surrounded by soil matrix – all enveloped in rugose BSC. This basalt cross-section shows Ca-rich plagioclase, Mg-rich olivine, mag (magnetite) and trydimite. The various platelets seen in the soil matrix are clay minerals.

medians for the eight types of samples: plagioclase control (Organ Pipe Boundary and Moab area sites); olivine control (Organ Pipe and Moab); plagioclase in contact with BSCs (Organ Pipe and Moab); and olivine in contact with BSCs (Organ Pipe and Moab).



**Figure 4.** Secondary electron image of olivine, showing no evidence of dissolution (0.00% measured porosity) surrounded by BSC mixed with some inorganic soil particles, collected from the Moab site after 25 years. Secondary electrons were used to collect this image, to provide a better view of BSC. Being organic in nature, BSCs would be dark gray/black if imaged by BSE.

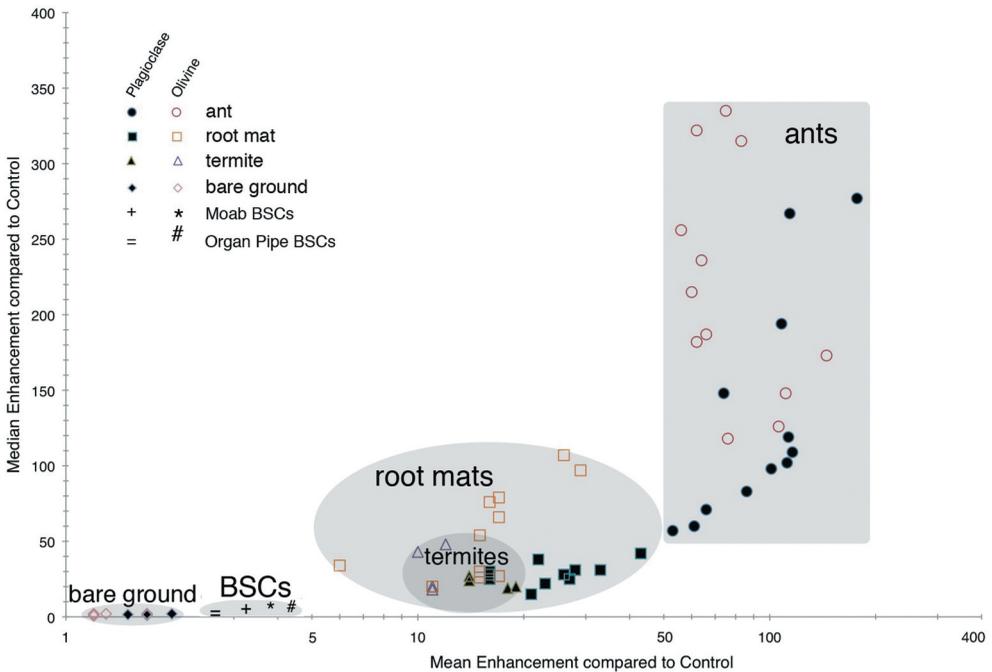
For each of the five separate sampling sites, the ratio of BSC dissolution to the control dissolution produced five mean and five median biological enhancement of weathering (BEW) metrics.

## Results

BSCs at the Organ Pipe and Moab study sites displayed a small BEW effect for both Ca-rich plagioclase and Mg-rich olivine after 25 years of monitoring (Tables 1 and 2). The five data points presented in each cell of Table 1 represents the mean of the five different sampling locations collected after 25 years of BSC interaction, where each data point summarizes 30 separate mineral grain dissolution measurements. Table 2 presents the same information for median BEWs. A data repository presents raw measurements of dissolution for each mineral.

Figures 3 and 4 illustrate the typical electron microscope imagery of BSC-emplaced Hawaiian basalt. Figure 3 contains both plagioclase and olivine, where the plagioclase grain displays one of the larger dissolution “holes” observed in this study. Figure 4 displays an olivine grain without evidence of dissolution.

Figure 5 summarizes results of 25 years of BSC-generated dissolution, comparing the BEW of BSCs to ant colonies, termite colonies, and roots mats studied previously (Dorn, 2014). The mean BEW of BSCs is less than 5×, when compared to the minerals in plastic pipe controls exposed to only precipitation (Table 1). The values for abiotic mineral decay rates in the control setting of plastic pipes experiencing only infiltrating water are similar to other abiotic *in situ* rates of mineral decay (e.g., P. v. Brady et al., 1999).



**Figure 5.** Mineral dissolution BSC enhancements of olivine and plagioclase for 25 years at BSC sites near moab, Utah and near organ pipe national monument, Arizona. The BSC enhancements are plotted along with BEW associated with ant colonies, termite colonies, root mats of trees, and bare ground reported previously (Dorn, 2014). The log-linear nature of the mean BEW versus median BEW is because observations are not normally distributed.

## Discussion

### *Implications for modern carbon sequestration*

Schwartzman (2017) analyzed available data on BEW and concluded that the “likely magnitude of BEW factor at present is at the very minimum 10 (more likely closer to 50) to 100” for agents like lichens, mosses and vascular plants. Ants (Dorn, 2014) exemplify the potential for animals to also influence BEW at the higher end of Schwartzman’s (2017) range. By comparison, the impact of BSCs on BEW is much lower, in the range of 2–4× (Table 1).

It is possible that the comparatively low BEWs of the Sonoran Desert and Colorado Plateau, western USA, BSC sites (Figure 5) might not be representative of BSCs elsewhere. Tremendous complexity exists in BSCs, for example, in chemical processes (Marusenko et al., 2013) and fungal diversity (Bates et al., 2012). This is certainly true for the Moab sampling site in terms of bacterial populations (Garcia-Pichel et al., 2003) and also true for the Organ Pipe area site with tremendous prokaryotic diversity (Nagy et al., 2005). Thus, it is probably unwise to generalize too much from these research findings based on only two sites – albeit monitored for a quarter century. However, if the findings observed here are truly representative of BSCs elsewhere, then BSCs would offer little help as a carbon sequestration tool, especially compared to

potential geoengineering such as spreading crushed basalt on croplands (Beerling et al., 2020).

### *Implications for Archean carbon sequestration*

Dramatic declines in atmospheric CO<sub>2</sub> began in the Devonian and may have been linked to the spread of deeply rooted trees and their symbiotic fungal mycorrhizal partners (Taylor et al., 2009). Well before the Devonian CO<sub>2</sub> decline, the Archean's absence of an ozone layer resulted in more short-wave radiation than today, even though the sun was likely ~30% dimmer (Kasting et al., 1989). At the same time, sulfur vapor and hydrocarbon smog could have reduced some of the ultraviolet (UV) radiation (Kasting et al., 1989). This meant that subaerial Archean land surfaces, theoretically, might have hosted early photosynthesizers (Garcia-Pichel, 1998), even before the Great Oxidation Event (Havig & Hamilton, 2019; Thomazo et al., 2018). The presence of Archean land surface BCS is supported by 3.0–3.2 Ga paleosol evidence (Retallack et al., 2016) and also 3.22 Ga microfossils of microbial mats preserved in silicic-clastic sediments (Homann et al., 2015). Support for the existence of fossil BCSs also occurs in the 1.2 Ga Dripping Springs Formation of Arizona (Beraldi-Campesi et al., 2014).

Again theoretically, BCSs might have been a dominant life form on these subaerial Archaean landscapes since BCSs are primarily driven by cyanobacteria performing oxygenic photosynthesis (Garcia-Pichel, 2002). Even today, BCSs represent the Earth's largest biofilm, covering 12% of continental surfaces (Rodriguez-Caballero et al., 2018) and dominating areas where plant growth is limited. Molecular clock analyses of cyanobacterial diversification suggest that land might have been colonized between 2.78 and 3.05 Ga (Garcia-Pichel et al., 2019; Uyeda et al., 2016).

The possible existence and perhaps widespread distribution of BCSs in the Archaean would pose a paradox for the current understanding of early Earth's CO<sub>2</sub> composition, that is, if BCSs were major BEW agents. If BCSs were widespread in the Archean and if BCSs are major agents of BEW, then there should have been a more substantial draw-down of CO<sub>2</sub> – a drawdown that has not been observed.

The solution to such a paradox may rest in the findings of this study. If the modern BEW or BCSs observed in this study reflects Archaean BEW of Archaean BCSs, then the aforementioned possible paradox is solved. That the observed modern BCSs are not major agents of BEW would be consistent with both the existence of widespread Archaean BCSs and with our current understanding of Archaean CO<sub>2</sub> levels.

### **Conclusion**

BSCs, formerly known as cryptobiotic soils crusts, are best known as geomorphic agents of soil stability, reducing soil erosion rates for desert surfaces not protected by vascular plants. A claim exists in the BSC literature that these living crusts enhance mineral decay and hence act as an agent of biological enhancement of weathering (BEW). No known prior research, however, assessed the quantitative BEW of BSCs.

Foreign mineral material consisting of ground-up fresh (undecayed) Hawaiian basalt was emplaced in BSCs in the Sonoran Desert, Arizona and Colorado Plateau, Utah. The

lower Sonoran Desert setting on the northern border of Organ Pipe National Monument hosts rugose crusts with abundant cyanobacteria and fungi with patches of moss and lichen, while the Moab site in Utah includes light pinnacled BSCs with abundant lichen and moss cover. The basalt grains were extracted every 5 years in a 25-year study monitoring the dissolution of the Ca-silicate plagioclase and the Mg-silicate olivine. Compared to control samples resting in plastic pipes exposed only to precipitation, the mean BEW of these BSCs ranged from 2.3× to 4.9×, while the median BEW ranged from 3.3× to 7.5×.

One component of the significance of these findings relates to Earth's habitability over geological time scales. As solar irradiance increased over the lifetime of Earth, atmospheric CO<sub>2</sub> has been gradually drawdown by the formation of calcium and magnesium carbonates that stores atmospheric CO<sub>2</sub>. The source of the Ca and Mg came from dissolution of Ca–Mg silicates. The magnitude of BEW for agents like lichens, mosses, vascular plants, termites and especially ants is an order of magnitude higher than these measurements for BSCs. These comparatively low BEWs offer a solution to the possible paradox of having BSCs covering an Archean Earth surface and yet not drawing down significant levels of atmospheric CO<sub>2</sub> from the Archean atmosphere; the BEWs of BSCs are too low to have resulted in atmospheric CO<sub>2</sub> drawdown in Earth's early.

These findings are also significant in that they indicate that BSCs will not be of value as a potential solution to the modern crisis of increasing atmospheric concentrations of CO<sub>2</sub>. Although this study reports on only two sites monitored over a quarter century, if these measurements reflect modern BSCs as a whole, that cover some 12% of the planet's surface, then modern BSCs would not offer a means to reduce the anthropogenic loading of tropospheric CO<sub>2</sub>.

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## Disclosure statement

No potential conflict of interest was reported by the author.

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## References

- Aghamiri, R., & Schwartzman, D. W. (2002). Weathering rates of bedrock by lichens: A mini watershed study. *Chemical Geology*, 188(3–4), 249–259. [https://doi.org/10.1016/S0009-2541\(02\)00105-5](https://doi.org/10.1016/S0009-2541(02)00105-5)
- Angel, R., & Conrad, R. (2013). Elucidating the microbial resuscitation cascade in biological soil crusts following a simulated rain event. *Environmental Microbiology*, 15(10), 2799–2815. <https://doi.org/10.1111/1462-2920.12140>

- Arens, S., & Kleidon, A. (2011). Eco-hydrological versus supply-limited weathering regimes and the potential for biotic enhancement of weathering at the global scale. *Applied Geochemistry*, 26, 5274–5278. <https://doi.org/10.1016/j.apgeochem.2011.03.079>
- Arthur, M. A., & Fahey, T. J. (1993). Controls on soil solution chemistry in a subalpine forest in north-central Colorado. *Soil Science Society of America Journal*, 57(4), 1123–1130. <https://doi.org/10.2136/sssaj1993.03615995005700040040x>
- Azam, M. M., Chaudhary, A., Kumar, P., & Tripathi, J. K. (2019). Manifestations of weathering on granitic rocks in the himalaya and bundelkhand regions: A field-based observation. *Proceedings of the Indian National Science Academy*, 85(3), 659–665.
- Bates, S. T., Nash, T. H., & Garcia-Pichel, F. (2012). Patterns of diversity for fungal assemblages of biological soil crusts from the southwestern United States. *Mycologia*, 104(2), 353–361. <https://doi.org/10.3852/11-232>
- Beerling, D. J., Kantzas, E. P., Lomas, M. R., Wade, P., Eufrazio, R. M., Renforth, P., Sarkar, B., Andrews, M. G., James, R. H., Pearce, C. R., Mercure, J. F., Pollitt, H., Holden, P. B., Edwards, N. R., Khanna, M., Koh, L., Quegan, S., Pidgeon, N. F., Janssens, I. A., Hansen, J., & Banwart, S. A. (2020). Potential for large-scale CO<sub>2</sub> removal via enhanced rock weathering with croplands. *Nature*, 583(7815), 242–248. <https://doi.org/10.1038/s41586-020-2448-9>
- Belnap, J. (2003). The world at your feet: Desert biological soil crusts. *Frontiers in Ecology and the Environment*, 1(4), 81–189. [https://doi.org/10.1890/1540-9295\(2003\)001\[0181:TWAYFD\]2.0.CO;2](https://doi.org/10.1890/1540-9295(2003)001[0181:TWAYFD]2.0.CO;2)
- Belnap, J. (2006). The potential roles of biological soil crusts in dryland hydrologic cycles. *Hydrological Processes: An International Journal*, 20(15), 3159–3178. <https://doi.org/10.1002/hyp.6325>
- Belnap, J., Büdel, B., & Lange, O. L. (2001). Biological soil crusts: Characteristics and distribution. *Ecological Studies*, 150, 3–31.
- Beraldi-Campesi, H., Farmer, J. D., & Garcia-Pichel, F. (2014). Modern terrestrial sedimentary biostructures and their fossil analogs in mesoproterozoic subaerial deposits. *Palaios*, 29(2), 45–54. <https://doi.org/10.2110/palo.2013.084>
- Bowker, M. A., Belnap, J., Chaudhary, V. B., & Johnson, N. C. (2008). Revisiting classic water erosion models in drylands: The strong impact of biological soil crusts. *Soil Biology & Biochemistry*, 40(9), 2309–2316. <https://doi.org/10.1016/j.soilbio.2008.05.008>
- Brady, P. V., Dorn, R. I., Brazel, A. J., Clark, J., Moore, R. B., & Glidewell, T. (1999). Direct measurement of the combined effects of lichen, rainfall, and temperature on silicate weathering. *Geochimica et Cosmochimica Acta*, 63(19–20), 3293–3300. [https://doi.org/10.1016/S0016-7037\(99\)00251-3](https://doi.org/10.1016/S0016-7037(99)00251-3)
- Brantley, S. L. (2005). Reaction kinetics of primary rock-forming minerals under ambient conditions. In J. I. Drever (Ed.), *Surface and ground water, weathering, and soils. treatise on geochemistry* (Vol. 5, pp. 73–117). Elsevier.
- Brantley, S. L., & Velbel, M. A. Eds. (1993). Geochemical kinetics of mineral-water reactions in the field and the laboratory. Special issue volume. *Chemical geology*, 105.
- Cochran, M. F., & Berner, R. A. (1992). Quantitative role of plants in weathering. In Y. K. Kharaka & A. S. Maest (Eds.), *Water-rock interaction. Volume 1. Low temperature environments* (pp. 473–476). A.A. Balkema.
- Dontsova, K., Balogh-Brunstad, Z., & Chorover, J. (2020). Plants as drivers of rock weathering. In K. Dontsova, Z. Balogh-Brunstad, G. Le Roux, & M.-C. Pierret (Eds.), *Biogeochemical cycles: ecological drivers and environmental impact* (pp. 33–58). American Geophysical Union.
- Dorn, R. I. (1995). Digital processing of back-scatter electron imagery: A microscopic approach to quantifying chemical weathering. *Geological Society of America Bulletin*, 107(6), 725–741. [https://doi.org/10.1130/0016-7606\(1995\)107<0725:DPOBSE>2.3.CO;2](https://doi.org/10.1130/0016-7606(1995)107<0725:DPOBSE>2.3.CO;2)
- Dorn, R. I. (2014). Ants as a powerful biotic agent of olivine and plagioclase dissolution. *Geology*, 42(9), 771–774. <https://doi.org/10.1130/G35825.1>
- Drever, J. I. (1994). The effect of land plants on weathering rates of silicate minerals. *Geochimica et Cosmochimica Acta*, 58(10), 2325–2332. [https://doi.org/10.1016/0016-7037\(94\)90013-2](https://doi.org/10.1016/0016-7037(94)90013-2)

- Drever, J. I., & Zobrist, J. (1992). Chemical weathering of silicate rocks as a function of elevation in the southern swiss alps. *Geochimica Cosmochimica Acta*, 56(8), 3209–3216. [https://doi.org/10.1016/0016-7037\(92\)90298-W](https://doi.org/10.1016/0016-7037(92)90298-W)
- Faist, A. M., Herrick, J. E., Belnap, J., Van Zee, J. W., & Barger, N. N. (2017). Biological soil crust and disturbance controls on surface hydrology in a semi-arid ecosystem. *Ecosphere*, 8(3), e01691. <https://doi.org/10.1002/ecs2.1691>
- Finlay, R. D., Mahmood, S., Rosenstock, N., Bolou-Bi, E. B., Kohler, S. J., Fahad, Z., Rosling, A., Wallander, H., Belyazid, S., Bishop, K., & Lian, B. (2020). Reviews and syntheses: Biological weathering and its consequences at different spatial levels—from nanoscale to global scale. *Biogeosciences*, 17(6), 1507–1533. <https://doi.org/10.5194/bg-17-1507-2020>
- Garcia-Pichel, F. (1998). Solar ultraviolet and the evolutionary history of cyanobacteria. *Origins of Life and Evolution of the Biosphere*, 28(3), 321–347. <https://doi.org/10.1023/A:1006545303412>
- Garcia-Pichel, F. (2002). Desert environments: Biological soil crusts. In G. Bitton (Ed.), *Encyclopedia of environmental microbiology* (pp. 1019–2023). Wiley.
- Garcia-Pichel, F., & Belnap, J. (2003). Small-scale environments and distribution of biological soil crusts. In J. Belnap & O. Lange (Eds.), *Biological soil crusts: Structure, function, and management* (pp. 193–201). Springer.
- Garcia-Pichel, F., Johnson, S. L., Youngkin, D., & Belnap, J. (2003). Small-scale vertical distribution of bacterial biomass and diversity in biological soil crusts from arid lands in the Colorado Plateau. *Microbial Ecology*, 46(3), 312–321. <https://doi.org/10.1007/s00248-003-1004-0>
- Garcia-Pichel, F., Lombard, J., Soule, T., Dunaj, S., Wu, S. H., Wojciechowski, M. F., & Giovannoni, S. J. (2019). Timing the evolutionary advent of cyanobacteria and the later great oxidation event using gene phylogenies of a sunscreen. *MBio*, 10(3), e00561–00519. <https://doi.org/10.1128/mBio.00561-19>
- Havig, J. R., & Hamilton, T. L. (2019). Hypolithic photosynthesis in hydrothermal areas and implications for cryptic oxygen oases on archean continental surfaces. *Frontiers in Earth Science*, 7. <https://doi.org/10.3389/feart.2019.00015>
- Homann, M., Heubeck, C., Airo, A., & Tice, M. M. (2015). Morphological adaptations of 3.22 Ga-old tufted microbial mats to archean coastal habitats (moodies group, barberton greenstone belt, South Africa). *Precambrian Research*, 266, 47–64. <https://doi.org/10.1016/j.precamres.2015.04.018>
- Kasting, J. F., Zahnle, K. J., Pinto, J. P., & Young, A. T. (1989). Sulfur, ultraviolet radiation, and the early evolution of life. *Origins of Life and Evolution of the Biosphere*, 19(2), 95–108. <https://doi.org/10.1007/BF01808144>
- Marusenko, Y., Bates, S. T., Anderson, I., Johnson, S. L., Soule, T., & Garcia-Pichel, F. (2013). Ammonia-oxidizing archaea and bacteria are structured by geography in biological soil crusts across North American arid lands. *Ecological Processes*, 2(1), 1–10. <https://doi.org/10.1186/2192-1709-2-9>
- Metting, B. (1991). Biological soil features of semiarid lands and deserts. In J. Skujing (Ed.), *Semiarid lands and deserts* (pp. 257–293). Marcel Dekker.
- Moulton, K. L. (2000). Solute flux and mineral mass balance approaches to the quantification of plant effects on silica weathering. *American Journal of Science*, 300(7), 539–570. <https://doi.org/10.2475/ajs.300.7.539>
- Nagy, M. L., Perez, A., & Garcia-Pichel, F. (2005). The prokaryotic diversity of biological soil crusts in the Sonoran desert (organ pipe cactus national monument, AZ). *FEMS Microbial Ecology*, 54(2), 233–245. <https://doi.org/10.1016/j.femsec.2005.03.011>
- Navarre-Sitchler, A., & Brantley, S. (2007). Basalt weathering across scales. *Earth and Planetary Science Letters*, 261(1–2), 321–334. <https://doi.org/10.1016/j.epsl.2007.07.010>
- Pacheco, F. A. L., & Alencao, A. M. P. (2006). Role of fractures in weathering of solid rocks: Narrowing the gap between laboratory and field weathering rates. *Journal of Hydrology*, 316(1–4), 248–265. <https://doi.org/10.1016/j.jhydrol.2005.05.003>
- Porada, P., Lenton, T. M., Pohl, A., Weber, B., Mander, L., Donnadieu, Y., Beer, C., Pöschl, U., & Kleidon, A. (2016). High potential for weathering and climate effects of non-vascular vegetation

- in the Late Ordovician. *Nature Communications*, 7(1), 1–13. <https://doi.org/10.1038/ncomms12113>
- Rajeev, L., Da Rocha, U. N., Klitgord, N., Luning, E. G., Fortney, J., Axen, S. D., Shih, P. M., Bouskill, N. J., Bowen, B. P., Kerfeld, C. A., Garcia-Pichel, F., Brodie, E. L., Northen, T. R., & Mukhopadhyay, A. (2013). Dynamic cyanobacterial response to hydration and dehydration in a desert biological soil crust. *The ISME Journal*, 7(11), 2178–2191. <https://doi.org/10.1038/ismej.2013.83>
- Retallack, G.J., Krinsley, D.H., Fischer, R., Razink, J.J., & Langworthy, K.A. (2016). Archean coastal-plain paleosols and life on land. *Gondwana Resesearch*, 40, 1–20.
- Rodriguez-Caballero, E., Belnap, J., Büdel, B., Crutzen, P. J., Andreae, M. O., Pöschl, U., & Weber, B. (2018). Dryland photoautotrophic soil surface communities endangered by global change. *Nature Geoscience*, 11(3), 185–189. <https://doi.org/10.1038/s41561-018-0072-1>
- Rosenstock, N. P., Van Hees, P. A., Fransson, P., Finlay, R. D., & Rosling, A. (2019). Biological enhancement of mineral weathering by *Pinus sylvestris* seedlings – Effects of plants, ectomycorrhizal fungi, and elevated CO<sub>2</sub>. *Biogeosciences*, 16(18), 3637–3649. <https://doi.org/10.5194/bg-16-3637-2019>
- Schwartzman, D. W. (2002). *Life, temperature and the earth*. Columbia University Press.
- Schwartzman, D. W. (2017). Life's critical role in the long-term carbon cycle: The biotic enhancement of weathering. *AIMS Geosciences*, 3(2), 216–238. <https://doi.org/10.3934/geosci.2017.2.216>
- Schwartzman, D. W., & Volk, T. (1989). Biotic enhancement of weathering and the habitability of earth. *Nature*, 340(6233), 457–460. <https://doi.org/10.1038/340457a0>
- Schwartzman, D. W., & Volk, T. (1991). Biotic enhancement of weathering and surface temperatures on earth since the origin of life. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 90(4), 357–371. [https://doi.org/10.1016/S0031-0182\(12\)80035-6](https://doi.org/10.1016/S0031-0182(12)80035-6)
- Schwartzman, D. W., & Volk, T. (1992). Biotic enhancement of earth habitability. *Encyclopedia of Earth Science*, 1, 387–394.
- Swoboda-Colberg, N. G., & Drever, J. I. (1993). Mineral dissolution rates in plot-scale field and laboratory experiments. *Chemical Geology*, 105(1–3), 51–69. [https://doi.org/10.1016/0009-2541\(93\)90118-3](https://doi.org/10.1016/0009-2541(93)90118-3)
- Taylor, L. L., Leake, J. R., Quirk, J., Hardy, K., Banwart, S. A., & Beerling, D. J. (2009). Biological weathering and the long-term carbon cycle: Integrating mycorrhizal evolution and function into the current paradigm. *Geobiology*, 7(2), 171–191. <https://doi.org/10.1111/j.1472-4669.2009.00194.x>
- Thomazo, C., Couradeau, E., & Garcia-Pichel, F. (2018). Possible nitrogen fertilization of the early earth ocean by microbial continental ecosystems. *Nature Communications*, 9(1), 1–8. <https://doi.org/10.1038/s41467-018-04995-y>
- Urey, H. C. (1952). *The planets, their origin and development*. Yale University Press.
- Uyeda, J. C., Harmon, L. J., & Blank, C. E. (2016). A comprehensive study of cyanobacterial morphological and ecological evolutionary dynamics through deep geologic time. *PloS One*, 42(9), e0162539. <https://doi.org/10.1371/journal.pone.0162539>
- White, A. F., & Brantley, S. L. (2003). The effect of time on the weathering of silicate minerals: Why do weathering rates differ in the laboratory and field? *Chemical Geology*, 202(3–4), 479–506. <https://doi.org/10.1016/j.chemgeo.2003.03.001>