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Biological Soil Crusts: Ecological Roles and Effects of Disturbance in Desert Systems

Biological soil crusts are composed of an assemblage of species of cyanobacteria, lichens, mosses, and fungi. In many desert ecosystems, they fulfill several critical ecological functions in areas where vascular plant growth is limited due to low moisture or harsh temperatures (Belnap et al, 2001). Carbon (C) and nitrogen (N) fixation are two such functions. Photosynthesizing crust organisms facilitate the addition of both organic matter and inorganic carbonates to soils and can increase total soil C by as much as 300 percent (Pointing and Belnap, 2012). Cyanobacteria and lichens fix substantial amounts of N within crusts, increasing soil N levels and providing the nutrient to other microbes and plants that colonize the area. Soils crusts are also critical in promoting soil stabilization and limiting wind and water erosion. Reduced erosion can be important in terms of reducing dust deposition on snowpack within the Colorado River watershed, a process that is decreasing snow albedo and changing the timing of snowmelt. However, crust disturbance by grazing, trampling by hikers, vehicle traffic can reduce functionality of crusts and often cause even more severe erosion. Therefore, better management and regulation of traffic in areas with biological soil crusts is key to preserving their crucial roles in desert ecosystems. Increased monitoring and designation of high- and low-resiliency areas, considering factors such as species composition, soil stability, and water availability, may be key to improving management of crusts in sensitive areas.

General Information

In regions where growth of vegetation may be limited by lack of water, limited soil development, or harsh temperatures, biological soil crusts (BSC) often cover the soil surface, performing similar ecological functions to plants in areas where they are absent (Belnap et al., 2001). These crusts, which are also referred to as cryptogamic or cryptobiotic, can comprise as much as 70% of the living ground cover, and are found in many different ecosystem types, ranging in temperature and degree of aridity (Belnap et al., 2001; Rosentreter et al., 2007). It should be noted that lichens and mosses coating the limbs and leaves of trees and shrubs are also referred to cryptogamic covers, though often distinguished from soil crusts by referring to cryptogamic ground cover versus plant cover (Elbert et al., 2012). This paper will focus on biological soil crusts found in cool, semi-arid regions, and specifically those in the desert of the Colorado Plateau.

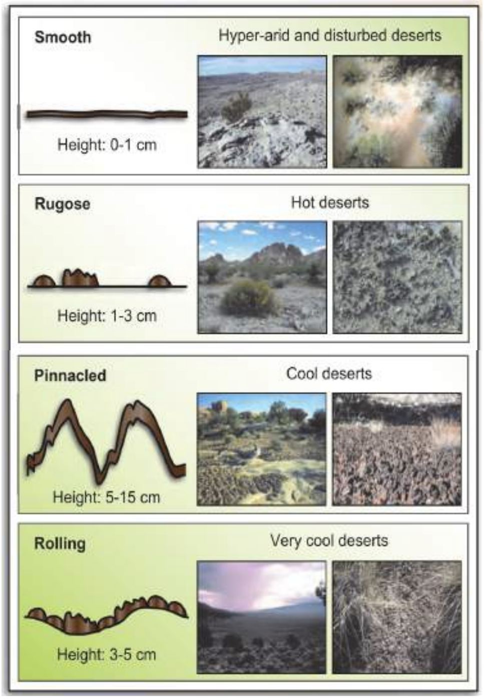

Figure 1. The four general types of biological soil crusts found in different desert types (Figure from Rosentreter et al., 2007)

BSC are generally made up of photosynthesizing, nitrogen-fixing, and decomposing organisms, including cyanobacteria, mosses, lichens, green algae, as well as other fungi and bacteria (Belnap et al., 2001). However, the specific organisms within the assemblage, as well as the morphology of the crusts, vary greatly based on the type of desert system. There are four general crust types named based on the varying morphology—smooth, rugose, pinnacled, and rolling—that are found in hyper-arid, hot, cool, and very cool deserts, respectively (Figure 1; Rosentreter et al., 2007). Hyper-arid deserts are often too dry to support lichens and mosses that are found in crusts of other deserts and are therefore dominated by smooth, 1 cm-thick crusts made of up cyanobacteria, algae, and fungi (Rosentreter et al., 2007). The rugose crusts of hot desert environments are caused by patchy moss and lichen clumps while the pinnacled and rolling crusts are a result of frost heaving in colder desert systems. The deserts of the Colorado Plateau are considered cool and semi-arid and are dominated by pinnacled crusts that are largely composed of cyanobacteria and lichen-mosses. *Microcoleus spp.* is a genus of cyanobacteria common in pinnacled crusts; particularly abundant are *M. vaginatus*, a filamentous, non-heterocystic cyanobacterium that brings carbon (C) into the soil system through photosynthesis (Belnap et al., 2001). The filamentous nature of this organism is very important to binding of soil particles, a key mechanism in the stabilization of surfaces by biological soil crusts. Though this species lacks heterocysts, the specialized cells that exclude oxygen to allow for N-fixation, *M. vaginatus* can still fix N under anaerobic soil conditions that may occur immediately following a rain event. Nitrogen is also brought into the system by N-fixing lichens, such as *Collema* (Belnap et al., 2001).

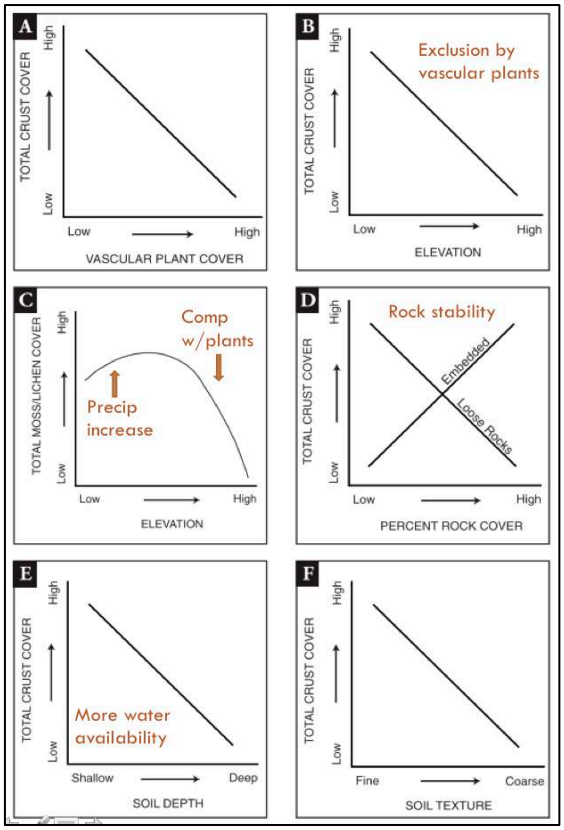

Figure 2. Ecological relationships for biological soil crusts concerning general environmental factors. (Figure from Belnap et al., 2001 with annotations added)

There are general ecological relationships that can be used to predict the location and abundance of soil crusts (Figure 2; Belnap et al., 2001). Crusts predominate where vascular plants are sparse due to the fact that they are filling a similar niche and competing for water and nutrient resources. Therefore, crusts are more common in plant interspaces and at lower elevation where harsh conditions may reduce competition from plants. Crusts establish more easily on stable surfaces, such as those with few loose rocks at the surface. Water is also a main limiting factor for crust establishment and proliferation. Therefore, they tend to prefer shallow, fine-textured soils that hold more water in the top several centimeters of the soil.

Crusts not only prefer establishment on fine-textured soils, but they also tend to have finer materials within their biomass, catching silt and clay particles within the crust matrix (Belnap et al., 2003). Verrechia et al. (1995) measured the particle size distribution within a soil crust, directly underneath the crust, and on top of an active sand dune. Their measurements showed that there was a higher percentage of small particles (on the orders of 10^{-1} to 10^{1} µm) compared to the particle size distribution underneath the crust and on the sand dune summit, which both had a predominance of particles on the order of 10^{2} µm. The rough, biotic matrix of the BSC allows for trapping of fine aeolian and water-transported material, a mechanism that turns out to be a key ecological function performed by crusts in desert ecosystems (Belnap et al., 2003).

The Role of Crusts in Desert Ecosystems

Nutrient Dynamics

In non-desert systems, we discuss the importance of soil cover in reducing erosion, promoting aggregation, increasing soil water storage, and enhancing nutrient retention and availability of important elements like C and N. Biological soil crusts provide these functions in many desert ecosystems. However, unlike plant cover, all of these processes occur within just a few centimeters on the soil surface (Figure 3). Therefore, these functions can be particularly sensitive to disturbance and damage.

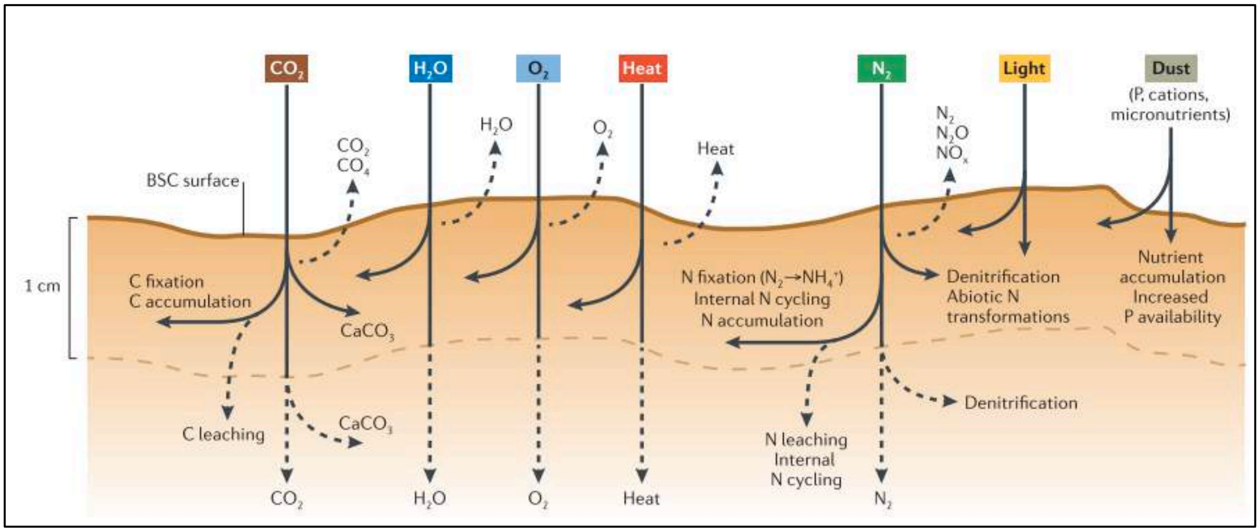

Figure 3. Nutrient dynamics facilitated by biological soil crusts within the soil surface of desert ecosystems. (Figure from Pointing and Belnap, 2012)

BSCs are able to fix C at a rate comparable to vascular plants, though their productivity is highly dependent on climatic conditions, particularly the availability of water (Pointing and Belnap, 2012; Belnap et al., 2003). Crusts that are able to get enough water to be dominant in mosses and lichens can fix >10 µmol CO_2 m^{-2} s^{-1}, while those made up mostly of *Microcoleus* often have lower photosynthetic rates of ~1 µmol CO_2 m^{-2} s^{-1} (Housman et al., 2006). Crusts are often dry for long periods of time due to the variability of rain in the desert, so photosynthetic activity is generally dormant until a precipitation event occurs. Belnap et al. (2001) report that crustal organisms generally begin to respire 3 minutes after a wetting event and that the rates of C fixation will usually peak approximately 30 minutes following wetting. Housman et al. (2006) point out that for maximum photosynthetic potential, it is important that temperatures are not too extreme, even while crusts are hydrated. They compared early and late successional crusts in Canyonlands National Park on the Colorado Plateau and found that photosynthetic rates were highest during the spring compared to the summer when hotter temperatures would cause crusts to dry more quickly (Housman et al., 2006). The study also found that late successional crusts of the Colorado Plateau had 1.2-1.3 times greater C fixation capacity compared to early successional crusts in the area. Overall, they report that, though photosynthetic rates may appear low, the fact that crusts can cover such a large percentage of desert surface area (up to ~70%) means that C inputs can be substantial. Annual inputs range from 0.4-2.3 g C m^{-2} $year^{-1}$ for early successional crusts and 12-37 g C m^{-2} $year^{-1}$ (Housman et al., 2006).

Over a period of several years, this crustal photosynthetic activity can increase total soil carbon storage in these soils by up to 300% (Pointing and Belnap, 2012). This C is likely largely in the form of organic molecules; however, inorganic C in the form of calcite ($CaCO_3$) is also very commonly formed in these higher pH desert soils. CO_2 produced by microbial and plant respiration reacts with water to form carbonic acid (H_2CO_3), which at more alkaline soil pH will shed its protons and exist primarily as carbonate (CO_3^{2-}) in soil solution (Schlesinger and Bernhardt, 2013). This carbonate can then react with Ca^{2+}, which is present at fairly high concentrations in desert soils due to low leaching capacity. Calcite formation in calcic soil horizons is a very important pool of inorganic carbon in desert soils, and their development is certainly promoted by BSCs.

BSCs also facilitate additions of N to desert systems. Housman et al. (2006) report that early successional crusts in the southwestern US can fix roughly 1.4 kg N ha^{-1} $year^{-1}$ while late successional crusts in the same region fix approximately 9.0 kg N ha^{-1} $year^{-1}$. Their study found that, similarly to photosynthesis rates, activity of the nitrogenase enzyme involved in N fixation was 1.3-7.5 times higher in late successional crusts of the Colorado Plateau compared to early successional crusts in the same area. The authors attribute the higher rates of both C and N fixation in late successional crusts partially to increases in percentages of *Nostoc* and *Scytonema spp.*, C and N-fixing cyanobacteria within the crusts (Housman et al., 2006). This is important to consider when thinking about management of crust disturbance as destruction of more developed crusts will result in greater reduction in C and N inputs.

Crusts not only contribute to greater C and N inputs in desert soils, they also facilitate greater availability of other macro- and micronutrients, including phosphorus (P), molybdenum (Mo), zinc (Zn), copper (Cu), magnesium (Mg), and iron (Fe) (Belnap et al., 2003). One mechanism for enhancement of these elements is the exudation of organic acids by organisms within the crust (Pointing and Belnap, 2012). These organic acids act as chelating agents that release anions including phosphate (PO_4^{3-}) and molybdate (MoO_4^{2-}) that are often bound to Ca^{2+} at high pH soils. Organic acids also bind with metal cations, such as Cu, Zn, Mg, and Fe, creating complexes that are plant available. Exudation of organic acids can also contribute to increased mineral weathering, which would also enhance the release of ions, particularly Ca, Mg, and Fe (Pointer and Belnap, 2012). Harper and Belnap (2001) reviewed the availability of nutrients to vascular plants when they were grown on crusted soils, and they found that >70% of the studies reported higher plant tissue concentrations of Cu, K, Zn, Mg. These nutrient increases are most often found in short-lived herbaceous plants that have shallow root systems that explore only the top few centimeters of the soil profile (Harper and Belnap, 2001). In addition to the chelating mechanism, many micronutrients may be more available due to collection of fine dust particles within the soil crust, as was described earlier. This process is, of course, also tied to another important ecosystem function performed by BSCs.

Effects on Erosion

BSCs are known to stabilize the soil surface by aggregating soil particles through filamentous networks and extra-polymeric compounds exuded by the microorganisms (Belnap et al., 2001). This stabilization has the potential to reduce both wind and water erosion, trapping dust particles and, in many cases, slowing water movement, increasing water infiltration and reducing surface runoff. The latter is particularly true in areas with rough, pinnacled crusts, such as the Colorado Plateau. However, when crusts are thick with mucilaginous organisms, they can also cause the soil surface to be more impervious to water. This is more common in hot deserts where the crust morphology is smoother and the matrix is dominated by cyanobacteria.

Several studies have found that while most intact crusts reduce erosion, crusts that have been disturbed often lead to even more severe erosion than would have otherwise occurred due to greater exposure of soil surfaces (Draut, 2012; Belnap et al., 2001; Sankey and Draut, 2014). Some researchers have also looked at potentially negative effects of crusts on sediment stabilization. Sankey and Draut (2014) performed a recent study along the Colorado River corridor investigating the role of aeolian deposited sediment in annealing gullies formed by water erosion. Gully erosion has destroyed precious archaeological sites belonging to native Havasupai and Hualapai tribes surrounding the Grand Canyon, and their formation has been magnified since the dams were built due to reduced sediment deposition further downstream. One of the goals of the controlled flooding that has taken place periodically over the last few years has actually been to increase sand bar formation to boost aeolian sediment supply. Sankey and Draut (2014) hypothesized that potential gullies are

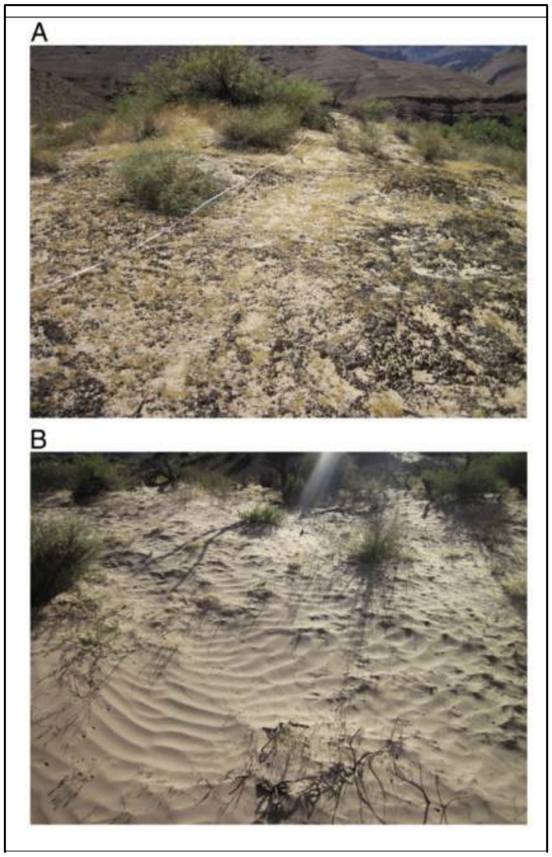

Figure 4. Examples of (A) inactive aeolian transport areas covered by biological soil crusts, and (B) an active aeolian transport area. (Figure from Sankey and Draut, 2014)

more common in areas with inactive aeolian transport because the wind-blown sediments can fill in eroded areas, preventing them from getting larger. Of course, biological soil crusts will trap loose sediment and prevent movement of sediment by the wind. Therefore, areas that are heavily crusted could contribute to greater gully erosion (Figure 4).

The study used remote sensing and GIS methods to create maps of potential gully areas based on topographic data and the direction of concavity in relation to slope (Sankey and Draut, 2014). They then mapped areas as either active or inactive in terms of aeolian transport and determined whether potential gullies were more likely to terminate in inactive areas, as they hypothesized. The authors found that there were fewer potential gullies terminating in active aeolian transport areas and that there was greater evidence of gully erosion in areas with biological soil crusts present. They reported that crusts that had been disturbed showed higher potential for gully formation, and that once incised, gullies in these crusted areas are more likely to expand because of low aeolian sediment supply.

These results do not indicate that reduced wind erosion by biological soil crusts is not important, however. Increased aeolian erosion caused by destruction of crusts has caused increased dust deposition on snowpack in the Colorado River watershed, which has actually decreased albedo and changed the timing of snowmelt (Painter et al., 2010; Deems et al., 2013). The Colorado River receives the majority of its annual flow from snowmelt, and the timing of snowpack melt is very important for the Upper Basin regions along the river above Lake Powell as people in these areas do not have reservoirs to hold water until it is needed (Deems et al., 2013). The snowpack acts as their water storage mechanism, and it is therefore critical for melt to occur at a time that provides runoff during the drier spring and summer months. Dust can decrease snow albedo from ~0.7 to ~0.3, and greater dust deposition in the watershed has shortened snow cover by 1 month, a fact which will affect the entire Colorado River system. Researchers studying this phenomenon believe that the increased dust is due at least in part to crust destruction (Deems et al., 2013; Painter et al., 2010). Dust accumulation in 2009-2010 was 5 times higher than in previous years, which may be due to greater human and livestock pressure in the area (Painter et al., 2010).

Dust deposition began to be a problem for the region in the mid-1800s when settlement of the area increased dramatically (Painter et al., 2010). Settlers increased livestock populations and intensified grazing in the area, an activity that certainly would have destroyed soil crusts. Lake sediment analysis revealed that dust accumulation increased 6 times between the mid-1800s and early 1900s. However, dust deposition did successfully decline slightly in the mid-1900s following implementation of the Taylor Grazing Act in 1930. This indicates that changes at the local level to reduce disturbance could have a significant impact on the whole Colorado River system.

Disturbance and Recovery

BSCs are most commonly disturbed and destroyed by increased intensity of erosion, livestock grazing, trampling by hikers and vehicles, and changes in precipitation timing (Belnap et al., 2001). Over the past few decades, many studies have looked at the recovery of crusts following disturbance, both in terms of function and structure. Belnap et al. (2001) report that crusts are less vulnerable and more likely to recover in areas that have good stability and plenty of moisture. Though crusts do compete with vascular plants, they are more likely to recover under shrub canopy than in plant interspaces, mostly likely due to greater soil stability and greater moisture content from reduced evaporation. The authors show a study by Belnap and Gilette (1997) that compared undisturbed crusts to those that had been disturbed by foot and tire trampling. They determined the amount of wind force that each could withstand before soil particles were dislodged, which was reported as threshold friction velocity. Twenty years after disturbance, those crusts that had experienced foot trampling (consisting of one pass with boots) could withstand a threshold friction velocity of approximately 100 compared with ~ 375 for undisturbed crusts (Belnap et al., 2001). Those disturbed by tires showed even less recovery, with threshold friction velocities of approximately 60 and 30 for one-pass and two-pass tire disturbance, respectively. Evidently, even a single disturbance can have significant lasting effects.

Belnap et al. (2003) have found that the nitrogenase activity of the crust is also slow to recover following a disturbance. Colorado Plateau crusts that had been scalped still showed almost no nitrogenase activity nine years after disturbance (Belnap et al., 2003). Even less severe disturbances cause significant decreases in N fixation. New vehicle, bike, and foot disturbances showed 68, 79, and 62 percent reductions in nitrogenase activity, respectively, and after 6 months, the crust disturbed by vehicle actually showed 100% reduction in N fixation (Belnap et al., 2001). This is a critical ecological function performed by crusts that can be severely limited following disturbance.

Conclusions and Recommendations for Management

Biological soil crusts play several important ecological roles within desert systems, including C and N fixation, increases in soil water holding capacity due to accumulation of fine material, and reduction of wind and water erosion. However, these services can be significantly deteriorated when crusts are disturbed, and recovery of the functions may be slow. As desert systems become more trafficked by increasing resident, hiker, and livestock populations, better management and regulations will become even more critical to reduce disturbance of biological soil crusts.

In managing for disturbance of these soil communities, there are many factors to consider, including disturbance type, intensity, frequency, extent, and timing (Belnap et al., 2001). It is also necessary to be aware of which types of species are present as recovery capacity may differ among organism types. Lichens in particular, which are responsible for much of the N fixation, are often slow to recover due to the mechanism with which they recolonize an area. Belnap et al. (2001) recommend that an impact analysis be required for every activity within an area known to have soil crusts. They report that it is important to designate high- and low-resiliency sites based on the species composition, surface stability, water availability, and history of disturbance. Areas with low resilience should have more thorough monitoring of BSC cover and extra measures should be taken to regulate traffic in these areas. For example, hikers should be made more aware of biological crusts and have restricted access in certain areas. In addition, grazing should be confined to early and mid-wet seasons, as crusts are most susceptible when conditions are dry. Livestock should be removed before the end of the wet season so that crusts have time to recover before water is unavailable. Hopefully, with more awareness and better regulation using these types of strategies, we can preserve desert soil crusts and the functions that they provide.

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