Chapter 3.4. Biological Soil Crusts

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Introduction

Biological soil crusts (BSCs) develop when various combinations of a vast array of bacteria, cyanobacteria, fungi, lichens, terrestrial algae, and mosses occupy the surface and upper few millimeters of the soil (Warren et al. 2019b). Historically, BSCs have been referred to as cryptobiotic, cryptogamic, microbiotic, microfloral, microphytic, and organogenic crusts. They can be present in a wide range of ecological, successional, and climatic conditions when and where disturbance and/or aridity have resulted in opportunities for colonization of exposed bare soil surfaces. BSCs are most prevalent, however, in arid and semiarid ecosystems, such as those of Northeastern California, where vascular plant cover and diversity are perennially low, leaving large areas available for colonization by some combination of the organismal groups mentioned above.

Ecological Roles of, and Threats to, BSCs

The ecological roles of BSCs are many and varied and include: (1) the redistribution of precipitated rainwater; (2) the capture, collection, and use of airborne and soil nutrients; (3) interaction with vascular plants; and (4) soil stabilization (Belnap and Lange 2001; Warren 1995; Weber et al. 2016).

Hydrology

The scientific literature is replete with apparent contradictions regarding role of BSCs relative to their effects on soil hydrology. Many authors have concluded that BSCs enhance infiltration, while others have concluded that the presence of a crust diminishes it. An extensive review by Warren (2001) revealed that much of the variation can be attributed to soil texture. Where the sand content of the soil exceeds about 80 percent, and the soil is not frost-heaved, BSCs generally reduce water infiltration compared to soil without crust. This seems to be attributable to soil porosity. Porosity of sandy soil may be reduced as BSCs accumulate finer soil particles or when polysaccharide exudates, rooting structures, or cyanobacterial filaments clog the soil pores, thus impeding the free passage of water. Where sand content is less than about 80 percent, BSC organisms contribute to soil aggregation, and, thus, higher effective porosity and higher rates of infiltration than in similar soil without biological crusts.

Research has shown BSCs impede evaporation and help retain moisture in the soil (Booth 1941). This may be accomplished as the BSCs create a surface seal or mulch layer (Booth 1941; Fritsch 1922), increase organic matter content of the soil (Metting 1981), or the polysaccharide exudates of cyanobacteria absorb moisture (Belnap and Gardner 1993).

Despite the overall importance of BSCs, and the well-documented effects of disturbance on these communities, restoring degraded habitats has received proportionately little attention (Bowker 2007). Reflection on the broader scope of BSC restoration can improve our perspective of how to effectively manage important dryland regions, in addition to directing future research.

Nutrient Cycling

The presence of BSCs is positively correlated to the presence and abundance of many micro- and macro-nutrients in the soil. Numerous studies documented the fixation of atmospheric nitrogen by BSCs dominated by cyanobacteria or lichens possessing cyanobacterial symbionts. Vascular plants in the Great Basin take up 9 to 11 pounds of nitrogen per ac (10 to 12 kg per ha) (West and Skujiņš 1977). Of this nitrogen requirement, precipitation provides 0.9 to 5.4 pounds per ac (1 to 6 kg per ha) per year (Schlesinger 1991; West 1978). Heterogeneous nitrogen fixers contribute a fraction of that need (Reichert et al. 1978; Steyn and Delwiche 1970). The balance is attributable to BSCs.

Much of the nitrogen fixed by BSCs is retained in the surface few centimeters of the soil (Fletcher and Martin 1948) where it is available to vascular plants. The nitrogen content of soils with BSCs may be up to 7 times higher than in similar soils without BSCs (Shields 1957). Other essential elements are also accumulated in surface soils with BSCs (Harper and Pendleton 1993; Loope and Gifford 1972; Kleiner and Harper 1972). While this can be attributed, in part, to the accumulation of fine soil

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particles by the rough surface of crusted soil (Kleiner and Harper 1972), other factors also play a role. BSC organisms accelerate weathering of rocks, thus speeding the genesis of soil and adding important minerals (Metting 1991). It has also been demonstrated that cyanobacteria exude polysaccharides that contain chelating agents that concentrate essential nutrients (Lange 1974, 1976). In addition, negatively charged clay particles may be bound to, or incorporated into, the polysaccharide exudates of some cyanobacteria, thus attracting and binding with positively charged essential elements (Belnap and Gardner 1993).

On sites in Colorado and Utah, BSCs were found to increase plant uptake of many nutrients, especially for herbaceous plants, results similar to other field and greenhouse studies under a variety of different soil conditions (Harper and Belnap 2001). This improved nutrient availability may occur because BSCs typically accumulate finer soil particles important for holding and exchanging nutrients, many accumulate or fix nitrogen from the atmosphere, and release it to the soil environment for use by vascular plants and other organisms, and BSCs might modify the soil carbon-to-nitrogen ratio that promotes decomposition and release of nutrients. Research also indicates that later-successional BSCs have rates of photosynthesis 3 to 4 times higher than early-successional BSCs (Grote et al. 2010); this carbon accumulation may have implications on polymer secretion.

Enhancement of Vascular Plant Germination and Survival

BSCs frequently improve infiltration of rainwater into the soil. Dark-colored BSCs absorb more solar radiation than soil without a crust, raising the temperature near the surface by as much as 9 °F (5 °C) (Harper and Marble 1988). Elevated soil temperatures, when coupled with adequate soil moisture, may accelerate the germination and initial growth of vascular plants (Harper and Pendleton 1993). The effects of BSCs on seed germination are mixed. Greenhouse studies either show no difference in germination (Godínez-Alvarez et al. 2012; Pando-Moreno et al. 2014; Serpe et al. 2006) or reduced germination (Song et al. 2017) on BSC-covered soil. Mendoza-Aguilar et al. (2014) found no germination effect on field sites. Some of these effects may be attributable to the type of crust tested; Serpe et al. (2006) in a laboratory setting, found that germination of native Western United States grasses, as well as cheatgrass (*Bromus tectorum*), was about the same on bare soil or one with a tall-moss crust, but significantly reduced when the BSC was dominated by short mosses.

Soil Stabilization

BSCs contribute to soil stability in at least three ways. First, the presence of vegetative structures such as larger lichens and mosses tends to dissipate the kinetic energy of wind, raindrops, and overland flow of water, thus reducing the susceptibility of soil erosion. Second, even where larger structures are absent, many BSCs are characterized by an uneven micro-topography that decreases the velocity of both wind and water. Third, BSCs contribute to mechanical and chemical aggregation of soil particles. Moss rhizoids, fungal hyphae, and filamentous cyanobacteria and algae often form a dense fibrous mesh that holds soil particles in place (Belnap and Gardner 1993; Fletcher and Martin 1948; Schulten 1985; Tisdall and Oades 1982). The extracellular polysaccharide exudates of some BSC organisms, particularly cyanobacteria, form glue-like bonds that prevent detachment.

McCalla (1946) first showed that soil aggregates formed by association with mosses, algae, and fungi were more resistant to disintegration by falling raindrops than aggregates formed without the benefit of BSC organisms. Osborn (1952) subsequently determined that the presence of a cyanobacteria-dominated crust on a deteriorated rangeland significantly reduced detachment and splash erosion by raindrops. Greater rainfall intensity was required to initiate splash erosion on moss- and lichen-dominated crusts than cyanobacterial crusts or bare ground.

Effects of Disturbance

BSCs can be disturbed and often killed by a variety of disturbances. These may include livestock trampling (Warren and Eldridge 2001), human trampling (Cole 1990), off-road vehicular traffic (Webb et al. 1988; Wilshire 1983), fire (Johansen 2001), military training (Warren 2014), competition for resources from invasive species (Dettweiler-Robinson et al. 2013), and several other disturbance vectors.

Most physical disturbance leads to increased soil erosion (Booth 1941; Brotherson and Rushforth 1983; Loope and Gifford 1972), and loss of ecological function when compared to intact crusts. Belnap (2002) found that four passes of a vehicle reduced the ability of BSCs to fix nitrogen from the atmosphere, especially on coarse-textured soils. This reduction affects other organisms, too, because BSC-fixed nitrogen is readily used by other plants and microorganisms (Belnap 2002). Grazing can reduce soil nitrogen levels by up to 50 percent (Jeffries 1989) and plants growing on grazed land have lower nitrogen concentrations (Evans and Belnap 1999), reflecting the reduced nitrogen fixation and sharing by the BSC. Fire can also degrade or destroy BSCs, thus having an immediate effect on nitrogen fixation (Johansen 2001); fire disturbance is greater under burned woody plants and less so under herbaceous material, a reflection of differing fire intensities. Manipulating fire intensity through prescribed burning can reduce impacts to BSCs (Warren et al. 2015). Johansen (2001) noted, however, that if a BSC is damaged and cheatgrass invades, BSCs may never regain their pre-disturbance levels. Recent work by Dettweiler-Robinson et al. (2013) reveals that lichen cover, in both early and late-successional stages, is negatively affected by cheatgrass. Rosentreter et al. (2001) discuss monitoring and management of BSCs to reduce degradation.

Artificial Restoration of BSCs

It may seem intuitive to attempt to restore BSCs by inoculating disturbed sites with crust organisms, but such applications have been relatively rare. Several researchers have harvested BSCs from the field in an attempt to use them as inocula for restoration sites (Belnap 1993; Bu et al. 2014; Maestre et al. 2006). This work was generally done under controlled conditions and yielded limited success. In general, the best results, which provided a modicum of success, required very moist substrates. Salvaging BSC from construction sites has also been examined (Chiquoine et al. 2016), as has transplanting soil cores with intact BSCs (Cole et al. 2010). In most of the aforementioned cases, inoculation hastened recovery of BSC organisms, particularly in controlled laboratory settings, with some recovery also in field studies. While the results were promising, the destruction of BSCs in one area to provide inoculants for another area is counterproductive in the context of large-scale arid land reclamation. Use of salvaged crusts from construction sites is promising for limited areas (Chiquoine et al. 2016). It is unlikely that providing sufficient supplemental water for successful large-scale reclamation in arid environments will be feasible.

To avoid destroying BSCs for use as inocula, some research has investigated the potential for laboratory-grown BSC amendments for use in inoculating disturbed areas (Zhao et al. 2016). For example, Buttars et al. (1998) incorporated laboratory-grown cyanobacteria into alginate pellets. These pellets, once crushed to allow release of the organisms and applied to moistened soil in the laboratory, resulted in significant increases in cyanobacterial biomass and frequency and nitrogen fixation. Incorporation of cyanobacteria into starch pellets was not successful due to poor survival during the pelletization process (Howard and Warren 1998). Kubeková et al. (2003) grew cyanobacteria and immobilized it on hemp cloth. Laboratory trials indicated improved growth compared to alginate pellets, but in four of five field trials, no significant crust recovery occurred. When cyanobacterial inoculants have been applied to the soil surface, rather than incorporated into the surface layer of the soil, mortality has been high. Laboratory-grown moss protonema, the earliest stage of growth, transplanted into the sands of the Gurbantunggut Desert of China has seen some success when supplemented with liquid growth media (Xu et al. 2008). The addition of laboratory-grown cyanobacteria to polyvinyl alcohol and a liquid soil tackifier appeared to accelerate the formation of a biocrust in a laboratory setting (Park et al. 2017).

Although some degree of success has been noted, large-scale field trials have yet to be attempted, and successful laboratory production and growth across BSC components is not universal. Given the general lack of success of artificial techniques to restore the BSC component, the levels of water required, and the per-acre costs, it is reasonable to question whether these approaches merit further consideration in arid areas except in critical situations where cost is not a constraint.

Aerobiology and Natural Recovery of BSCs

BSCs are found in almost all environments, justifying the question as to how crust organisms became so spatially and climatically dispersed in the first place and if that same process is still operating. In general, as post-disturbance succession takes place, the initial colonizers that stabilize the surface tend to be large filamentous cyanobacteria (Belnap and Eldridge 2001). They are followed by smaller cyanobacteria and green algae, which are followed, in turn, by small lichens. Where climatic conditions permit, larger lichens and mosses appear in later-successional communities. The distribution and successful establishment of these organisms is governed both by historical and contemporary factors (Leavitt and Lumbsch 2016).

BSCs are naturally dispersed by wind (Warren et al. 2019a, b). Aerially dispersed microorganisms were first observed by Darwin (1846). Meier and Lindbergh (1935) collected airborne organisms during a flight over the Arctic. Shortly thereafter, the field of aerobiology was established (Benninghoff 1991) and large numbers of microorganisms, including bacteria, fungi, terrestrial algae, and bryophytes, have been documented throughout the Earth's atmosphere (Després et al. 2012; Genitsaris et al. 2011; Schlichting 1969; Sharma et al. 2007; Tesson et al. 2016). Some of these organisms may have multiple generations while in the atmosphere, such that the atmosphere becomes a truly aerial habitat (Womack et al. 2010). Not surprisingly many of the species documented in the atmosphere are also common in BSC communities and may be deposited almost anywhere, including bare soil (Harding et al. 2011; Kvíderová 2012; Marshall and Chalmers 1997; Takeuchi 2013; Vonnahme et al. 2016), buildings (Samad and Adhikary 2008; Sethi et al. 2012), stone monuments (Macedo et al. 2009; Tomaselli et al. 2000), and plant surfaces (McGorum et al. 2015; Sethi et al. 2012). In addition to algae and cyanobacteria, other BSC components, including asexual reproductive lichen fragments, soredia, and/or lichen-forming fungal spores (Heinken 1999; Leavitt and Lumbsch 2016; Tormo et al. 2001), as well as spores, gametophyte fragments, and specialized asexual diaspores of bryophytes (Laaka-Lindberg et al. 2003; Stark 2003) can also be dispersed by wind.

BSC organisms can achieve airborne status when strong non-convective horizontal winds blowing over unconsolidated soil surfaces pick up large quantities of soil and the associated organisms. Strong dust storms occur in North America (McLeman et al. 2014), Alaska (Nickling 1978), China (Wang et al. 2004), Australia (Ekström et al. 2004), Africa (Prospero and Mayor-Bacero 2013), and the Middle East (Almuhanna 2015). On a smaller, but more common scale, dust may be lifted into the atmosphere by strong vertical vortices or "dust devils" (Horton et al. 2016; Metzger et al. 2011). Once airborne, dust particles and the BSC organisms that often accompany them, are subject to a variety of forces, including trade winds and the jet stream, that carry them, often rapidly, between hemispheres, continents, and climatic zones (Doherty et al. 2008; Griffin et al. 2002; Kellogg and Griffin 2006; Lee et al. 2006; Prospero 1999; Prospero and Lamb 2003; Uno et al. 2009). Many of these windborne BSC propagules can survive long periods of desiccation (Holzinger and Karsten 2013; Rajeev et al. 2013). Thus, given the forces mixing the atmosphere, the likelihood for BSC propagules to be present in it, and BSC resistance to desiccation, little doubt exists that organisms originating from almost any given location have the potential to be deposited anywhere on Earth (Barberán et al. 2014; Herbold et al. 2014; Jungblut et al. 2010), as evidenced by similarity of BSC species in the northern and southern polar regions, Iceland, and extreme southern Chile (Galloway and Aptroot 1995; Jungblut et al. 2012; Piñeiro et al. 2012).

Thus, natural recovery of BSC is expected due to windborne deposition. Time estimates for natural recovery of BSCs following disturbance have varied widely depending on the nature, periodicity, extent, and spatial and temporal distribution of the disturbance, and soil and climatic conditions. Five years following one-time human trampling, Cole (1990) noted a nearly complete recovery of visible BSC cover, although the complex pinnacled surface micro-topography attributable to many crusts had not recovered to pre-disturbance levels. Anderson et al. (1982) estimated that 14 to 18 years were adequate for recovery of a BSC following exclusion of livestock grazing in the cool Great Basin. In contrast, little evidence of recovery was observed during the first 10 years following cessation of grazing at another Great Basin location (Jeffries and Klopatek 1987). Recovery lagged 20 years following burning of a shrub community in the transition zone between the Great Basin and Mojave Deserts in Southwestern Utah (Callison et al. 1985). Belnap (1993) estimated that full recovery of BSCs in the Great Basin, including visual as well as functional characteristics, could require as many as 30 to 40 years for the cyanobacterial component, 45 to 85 years for lichens, and 250 years for mosses. In the Sonoran Desert, after 56 years, a cyanobacterial crust degraded by military exercises had not recovered to levels typical of adjacent undisturbed areas (Kade and Warren 2002). And, in the Mojave Desert full recovery of the cyanobacterial component of the BSC from disturbance caused by military vehicles was estimated to require up to 85 to 120 years (Belnap and Warren 2002). Hilty et al. (2004) found that active restoration of burned sagebrush steppe through direct seeding increased natural recruitment of BSC compared to passive restoration, especially when grazing was temporarily suspended.

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