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Aerobiology and passive restoration of biological soil crusts

Running head: Biological soil crust restoration

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Abstract: Biological soil crusts (BSCs) commonly occupy the surface of many arid and semiarid soils, and disturbed soils in more mesic environments. BSCs perform many essential ecological services. Substantial resources have been invested trying to restore BSCs that have been damaged by anthropogenic disturbances, largely to no avail. The nexus of science related to crust restoration and to aerobiology strongly suggests that crusts can become reestablished via naturally occurring processes. Propagules of BSC organisms are found naturally in the atmosphere, and are transported long distances. Whether restoration occurs naturally in this way, or by costly attempts to produce and disseminate artificial inoculants, success is ultimately moderated and governed by the timing and frequency of adequate precipitation relative to the arrival of viable propagules on suitable substrate at an appropriate time of the year. For greatest ecological benefit, efforts should focus primarily on minimizing the scope and scale of anthropogenic disturbance of BSCs in arid ecosystems.

Key words: cyanobacteria, algae, lichens, bryophytes, airborne, reclamation, arid lands

Implications:

Biological soil crusts (BSCs) develop when various combinations of diminutive cyanobacteria, algae, nonlichenized fungi, lichens, and/or bryophytes occupy the surface and upper few millimeters of the soil. Historically, they 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. However, they are most prevalent in arid and semiarid ecosystems where vascular plant cover and diversity are characteristically low, leaving large areas available for colonization by some combination of the organismal groups mentioned above. The diversity and distribution of components of BSCs in extreme environments is striking. For example, at least 18 species of cyanobacteria have been documented in the soils of Death Valley National Monument in the Mojave Desert, USA, where surface temperatures can reach 88° C (Durrell 1962), and, at the opposite end of the temperature spectrum, BSC communities are common in interior Antarctica, where soil temperature seldom exceeds 0° C (Green & Broady 2001). BSCs are also present in the hyperarid Atacama Desert of northern Chile (Patzelt et al. 2014), where average annual precipitation, depending on latitude, elevation, and distance from the Pacific coast, can be less than 1 mm.

The ecological roles of BSCs are many and varied, and include the collection, accumulation, and cycling of essential airborne and soil nutrients, redistribution of precipitated water, and soil stabilization (Warren 1995; Belnap & Lange 2001; Weber et al. 2016). BSCs, and their ecological functions, can be disturbed by a variety of factors, including, but not limited to, livestock trampling (Warren & Eldridge 2001), off-road vehicular traffic (Wilshire 1983; Webb et al. 1988), military training (Warren 2014), and fire (Johansen 2001). In spite of 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.

Artificial Restoration

It may seem intuitive to attempt to restore BSCs by inoculating disturbed sites with crust organisms, but such applications have been relatively rare. St. Clair et al. (1986) inoculated small plots with a soil slurry made by stripping BSCs from intact areas, mixing them with water, and applying them on a site damaged by wildfire. Belnap (1993) stripped crusts from an intact area, and used them as a dry inoculant on small plots where the original crust had been removed. The inoculation of soil in petri dishes with dry and slurried inocula, plus additions of water up to 5 times per week and sewage sludge, produced a modicum of establishment (Maestre et al. 2006). Bu et al. (2014) inoculated soil in a greenhouse study with BSCs that had been stripped from intact areas in the field in an attempt to accelerate crust restoration. They found that frequent watering of the crusts in that setting enhanced growth, but field trials were not conducted. In the Mojave Desert, USA, a somewhat similar approach was attempted using crusts composed of cyanobacteria, lichens and bryophytes that had been salvaged from a road construction site and subsequently stored for two years (Chiquoine et al. 2016). Cole et al. (2010) transplanted soil cores with intact bryophyte crusts in the Mojave Desert, USA. The cover and density of the bryophytes declined after transplantation, but at rates similar to the parent population, suggesting that annual declines are natural even in intact populations. In most of the aforementioned cases, inoculation hastened recovery of BSC organisms, particularly in controlled laboratory settings, with some recovery also in field trials. However, 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 (Chiquione et al. 2016). It is unlikely that providing sufficient supplemental water for successful large-scale reclamation in arid environments will be feasible.

Related research has investigated the potential for *ex situ* 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. The cyanobacteria were unable to escape intact pellets; however, crushing the pellets, and applying them 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 & Warren 1998). Kubečková 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, there was no significant crust recovery. The general lack of success was attributed, at least in part, to the placement of the inoculants on the soil surface where some species can be negatively affected by incident UV radiation (Garcia-Pichel & Castenholz 1991). If sensitive species occur at a depth off 1-2 mm, UV radiation is attenuated (Dor and Danin 2001). When cyanobacterial inoculants have been applied to the soil surface, rather than incorporated into the surface layer of the soil, mortality has been high. Bowker and Antoninka (2016) sucessfully grew mixed cultures of the lichen *Collema* and the moss *Syntrichia* in the laboratory, but field applications of the BSC organism mix have not been attempted. Moss protonema transplanted into the sands of the Gurbantunggut Desert of China from laboratory-grown mosses has seen some success when supplemented with liquid growth media (Xu et al. 2008). Mosses have been successfully propagated in the laboratory with frequent watering and fertilization (Antoninka et al. 2016) although field trials have not been conducted. The addition of laboratory grown cyanobacteria to polyvinyl alcohol and a liquid soil tackifier appeared to accelerate the formation of a BSC in a laboratory setting (Park et al. 2017).

Although some degree of success has been noted, large-scale field trials have not been attempted, and successful *ex situ* growth is not ubiquitous across BSC components. 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.

Passive Restoration

The fact that BSCs are found in almost all environments, ranging from mesic to hyperarid, and from temperate to extremely hot or cold, justifies the question as to how crust organisms became so spatially and climatically dispersed in the first place, and if the same processes are still operating. In general, as the post-disturbance succession takes place, the initial colonizers tend to be large filamentous cyanobacteria (Belnap & Eldridge 2001). As the surface becomes stabilized, the next to appear are smaller cyanobacteria and green algae. They are often followed 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).

Estimates of the time required 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. Dohani et al. (2011) reported significant recovery to a level beyond the pre-disturbance condition within one year (one moist season) on the Succulent Karoo semi-desert of South Africa where the upper 10 mm of the soil surface was removed. Five years following one-time human trampling, Cole (1990) noted a nearly complete recovery of visible BSC cover, although the complex pinnacled surface microtopography attributable to many crusts had not recovered to pre-disturbance levels. Read et al. (2011) labeled as 'surprisingly fast' the recovery of biological soil crusts following livestock removal from an area that had been previously heavily disturbed by livestock grazing in Australia. Anderson et al. (1982) estimated that 14–18 years were adequate for recovery of a BSC following exclusion of livestock grazing in the cool Great Basin Desert, USA. Johansen and St. Clair (1986) recorded significant, albeit incomplete, recovery of BSC diversity and abundance, in the Great Basin, USA, 7 years following the cessation of grazing on an areas with a long history of heavy grazing. In contrast, there was little evidence of recovery during the first 10 years following cessation of grazing at another Great Basin Desert location (Jeffries & 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, USA (Callison et al. 1985). Belnap (1993) estimated that full recovery of BSCs in the Great Basin

Desert, USA, including visual as well as functional characteristics, could require as long as 30-40 years for the cyanobacterial component, 45-85 years for lichens, and 250 years for mosses. Fifty-six years following abandonment of a military training camp in the Sonoran Desert, USA, a cyanobacterial crust had not recovered to levels typical of adjacent undisturbed areas (Kade & Warren 2002). In the Mojave Desert, USA, according to measurements taken inside and outside of tank tracks created during training for World War II, and assuming a worst-case linear trajectory scenario, full recovery of the cyanobacterial component of the BSC was estimated to require up to 85–120 years (Belnap & Warren 2002).

Similar temporal patterns of BSC recovery following disturbance have been recorded in other regions. In Australia, near complete recovery was documented after 20 years on pastures that had been grazed moderately, while heavily grazed pastures recovered at a much slower rate (Read et al. 2011). Eldridge & Ferris (199) suggested that at least 60 years would be required for full recovery of lichens at a nuclear test site in the Great Victoria Desert of Australia. In an extreme case, Lalley & Viles (2008) estimated that full recovery of lichens in badly disturbed truck ruts in the hyper-arid Namib Desert could take up to 530 years without climatic or anthropogenic intervention. It is important to note, however, that the rate of recovery is likely dependent on the arrival of viable propagules onto suitable substrates at times consistent with adequate moisture. Such conditions may be episodic and infrequent, particularly in the drier and hotter arid zones. We have personally witnessed significant recovery of crust organisms within 2 years following wildfire in the Great Basin Desert, USA, when suitable conditions prevailed.

Regardless of the timeframe required, recovery is dependent on several factors: (1) arrival of suitable propagules, (2) existence of an appropriate substrate on which to establish, including soil texture and chemistry, and (3) timing of the arrival of propagules in relation to cyclical soil moisture conditions necessary for establishment. The failure of any one of the necessary components may substantially delay successful reestablishment.

Aerobiology

As early as 1846, Charles Darwin collected dust from surfaces of HMS Beagle during one of his voyages of exploration, and discovered 17 different organisms (Darwin 1846). Meier & Lindbergh (1935) collected airborne organisms from a fixed-wing aircraft on a flight over the Arctic from Maine to Denmark. Shortly thereafter, but not necessarily correlated with that event, the field of aerobiology was established, originally emphasizing studies of airborne fungi, bacteria, and viruses associated with respiratory illnesses from indoor environments (Benninghoff 1991). Subsequently, the field began to evaluate other potential airborne allergens including protozoans, minute arthropods, algae, and cyanobacteria in the atmosphere, and began to evaluate the seasonality and other factors affecting their presence.

As a consequence, the presence of large numbers of cyanobacteria and algae have been documented as being present in indoor and outdoor airborne environments ranging from low to high altitudes above the Earth (Schlichting 1969; Sharma et al. 2007; Genitsaris et al. 2011; Després et al. 2012; Tesson et al. 2016). Recent studies have revealed the presence of hundreds of BSC taxa and thousands of individuals in dust samples collected from the external surfaces of homes around the United States (Barberán et al. 2015). It has been recently suggested that some organisms may go through multiple generations while in the atmosphere, such that the atmosphere becomes a truly aerial habitat (Womack et al. 2010). Unsurprisingly, many of the species documented in the atmosphere are also common in BSC communities.

Airborne BSC organisms may be deposited almost anywhere. For example, algae and cyanobacteria have been reported to occur on high latitude and high elevation glaciers from the Arctic to the Antarctic (Marshall & Chalmers 1997; Harding et al. 2011; Kvíderová 2012; Takeuchi 2013; Vonnahme 2016). They have been collected from building facades (Samad & Adhikary 2008; Sethi et al. 2012), stone monuments (Tomaselli et al. 2000; Macedo et al. 2009), exposed rocks (Danin 1999) and plant surfaces (Sethi et al. 2012; McGorum et al. 2015). In addition to algae and cyanobacteria, other BSC components can also be dispersed by wind. These include non-lichenized fungi (Miller & McDaniel 2004; Golan and Pringle 2017), asexual reproductive lichen fragments, soredia, and/or lichen-forming fungal spores (Marshall 1996; Heinken 1999; Tormo et al. 2001; Bailey 1966; Leavitt and Lumbsch 2016), as well as spores, gametophyte fragments, and specialized asexual diaspores of bryophytes (Stark 2003; Laaka-Lindberg et al. 2003; Pohjamo et al. 2006; Lönnell et al. 2012). This pattern of airborne dispersal of BSC propagules has resulted in many species occurring in both the northern and southern polar regions, Iceland, and extreme southern Chile (Piñeiro et al. 2012).

Atmospheric mixing and dispersion

A logical question may arise as to how BSC organisms are able to achieve airborne status. Many people living in arid and hyperarid regions of the world have, at one time or another, heard stories of, or personally witnessed, dust storms that develop when strong non-convective horizontal winds blowing over unconsolidated soil surfaces pick up large quantities of soil. Although not at all limited to the Dust Bowl era, such conditions prevailed in the 1930's in the North America (McLeman et al. 2014). Similarly, strong dust storms have been recorded in Alaska (Nickling 1978), China (Wang et al. 2004), Australia (Ekström et al. 2004), Africa (Prospero & Mayor-Bacero 2013), and the Middle East (Almuhanna 2015). On a smaller, but much more common scale, dust may be lifted into the atmosphere by strong vertical vortices or 'dust devils' (Metzger et al. 2011; Horton et al. 2016).

Once airborne, dust particles and the BSC organisms that often accompany them, are subject to a variety of forces that carry them between hemispheres, continents, and climatic zones (Griffin et al. 2002; Prospero & Lamb 2003; Kellogg & Griffin 2006; Uno et al. 2009). Near the Earth's surface, airborne particles are carried predominantly by trade winds, which were given their name because of the effect they had on global oceanic trade prior to the advent of powered locomotion. Trade winds exist in six major belts which circle the globe. Between the equator and 30 north or south latitude, the trade winds generally blow from east to west; between 30 and 60 latitude, the winds shift to from west to east; between 60 north or south latitude and the respective poles, easterly winds again prevail. The major jet streams exist at about 9 – 15 km above the Earth's surface and blow from west to east (Lewis 2003). They meander north or south, and may cross between the northern and southern hemispheres (Rangarajan & Eapen 2012). Other than the trade winds and jet streams, a primary force mixing the atmosphere within the southern and northern hemispheres are the global Hadley, Ferrel and polar cells (Kjellsson & Döös 2012; Huang and McElroy 2014) which correspond latitudinally with the trade wind belts. Hadley cells begin where warm air rises near the equator, generally resulting in heavy rainfall. After reaching the upper atmosphere the Hadley cells carry the flow of air poleward. At approximately 30˚ north and south latitude, the Hadley cells diverge earthward, converging with the downward flow of the Ferrel cells bringing air masses from higher latitudes. The result in both hemispheres is a very large body of descending dry air and high pressure. As descending air masses typically offer little precipitation, the zones of convergence correspond with some of the world's most recognized arid zones. The dry air moves poleward after reaching the Earth's surface. As the Ferrel cells pass over the Earth's surface, they collect moisture until they reach approximately 60˚ north and south latitude where the air masses ascend after converging with the polar cells. In order to continue the ascent, the air masses lose moisture, and precipitation increases. The polar cells descend earthward near the poles, a region also widely known for aridity.

Given the forces mixing the atmosphere, and the likelihood for BSC propagules to be present in it, there can be little doubt that organisms originating from almost any given location have the potential to be deposited anywhere on Earth (Jungblut et al. 2010; Barberán et al. 2014; Herbold et al. 2014). Carson and Brown (1976) found little correlation between the diversity of airborne algae, and soil algae at corresponding altitudes on the Island of Hawaii, suggesting atmospheric mixing of airborne organisms. Evidence of mixing can also be seen on a global scale by the similarity of BSC species in the Arctic and Antarctic (Jungblut et al. 2012; Galloway & Aptroot 1995). Dust deposited in Antarctica originates in Patagonia, Australia, and the Northern Hemisphere (Li et al. 2008). Dust originating during dust storms in China and the Middle East has been documented as arriving in Japan within just a few days (Lee et al. 2006). Dust from the Middle East has been recorded in the Caribbean (Doherty et al. 2008) and the southeastern USA (Prospero 1999). Many BSC propagules carried with dust can survive long periods of desiccation (Holzinger & Karsten 2013; Rajeev et al. 2013), thus becoming immigrants to BSC communities globally (Rosselli et al. 2015; Rahav et al. 2016). For example, lichen species of South African origin are now present in Australia and South America (Amo de Paz et al. 2012). Similarity of BSC communities is better predicted by the so-called 'dust highways' than by the proximity of source species (Muñoz et al. 2004). Dust and microbial deposition are both seasonal (Sharma et al. 2006; Sahu & Tangutur 2015) and cyclical over time (Rousseau et al. 2007).

The apparent airborne and global distribution of BSC propagules should not be construed to imply that BSC species composition will be the same worldwide, nor that natural recovery of BSC's will be necessarily rapid. The distribution of BSC propagules is shaped by the dynamic interplay of a range of factors operating across multiple temporal scales. That many propagules are distributed globally is apparently true. However, whether they will develop and thrive is still dependent on being deposited on appropriate substrate, with appropriate being defined as suitable in terms of chemistry, fertility, particle and pore size analysis, moisture content and seasonality, and temperature. For example, it is hardly realistic to expect most BSC species adapted to the frigid conditions of polar regions to survive and persist in hot deserts, and vice versa.

The nexus of aerobiology and land reclamation

The use of corn stalk fences and wheat straw checkboard sand barriers to stabilize moving sands of sand dunes have been successfully used for years to stabilize moving sand dunes in China (Qiu et al. 2004; Zhang et al. 2004; Li et al. 2006). These barriers create turbulence in the flow of wind across the dune surfaces, and cause the deposition of sand particles and associated BSC organisms. Researchers have discovered that biological soil crust organisms precipitated in this fashion can successfully colonize stabilized dunes (Li et al. 2003; Guo et al. 2008; Zhang 2014).

One must bear in mind that while airborne BSC propagules may provide an answer to the restoration of BSCs in many situations, their presence and composition depends on climatic conditions in locations very far away. As discussed, BSC propagules may originate from distant continents. BSC organisms from a specific soil type, chemistry, and alkalinity may not always be suitable for other situations. The arrival of appropriate propagules is likely episodic, seasonal, and less common than desired. There can be little doubt that airborne propagules are found in the atmosphere circling the globe. That they will be deposited in sufficient quantities, and in the right species composition, and at the right season for any specific area remains unknown.

Conclusions

Over the years, many hundreds of thousands of dollars have been expended on various approaches of crust restoration, often culminating in the production and application of large quantities of inoculants. Most approaches have failed to one degree or another. Those that did not fail, have been so dependent on large quantities of water for production and application, that they are not practical for broad-scale arid and semiarid environments. Several approaches to restoration depended on the destruction of one area to restore another. A review of the field of aerobiology seems to indicate that we may have been 'barking up the wrong tree'. Many propagules of many, if not most BSC organisms are already present and circulating the globe in the atmosphere. Perhaps, now we need to shift to a more natural approach of crust restoration. Whether we artificially produce and apply inoculants, or rely on natural, passive dispersal, the overall success depends on coordination of inoculation with appropriate environmental conditions. At any given location, regardless of the mode of inoculation, success depends on receiving adequate moisture at the right time of year, appropriate substrate, other environmental factors, and some measure of better controlling anthropogenic disturbance to BSC communities. We anticipate that incorporating principles of aerobiology and passive dispersal into the BSC restoration paradigm will facilitate more effective and less costly management of BSCs.

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