

Biological soil crusts in deserts: a short review of their role in soil fertility, stabilization, and water relations

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With 2 figures in the text

Abstract: Cyanobacteria and cyanolichens dominate most desert soil surfaces as the major component of biological soil crusts (BSC). BSCs contribute to soil fertility in many ways. BSC can increase weathering of parent materials by up to 100 times. Soil surface biota are often sticky, and help retain dust falling on the soil surface; this dust provides many plant-essential nutrients including N, P, K, Mg, Na, Mn, Cu, and Fe. BSCs also provide roughened soil surfaces that slow water runoff and aid in retaining seeds and organic matter. They provide inputs of newly-fixed carbon and nitrogen to soils. They are essential in stabilizing soil surfaces by linking soil particles together with filamentous sheaths, enabling soils to resist both water and wind erosion. These same sheaths are important in keeping soil nutrients from becoming bound into plant-unavailable forms. Experimental disturbances applied in US deserts show soil surface impacts decrease N and C inputs from soil biota by up to 100%. The ability to hold aeolian deposits in place is compromised, and underlying soils are exposed to erosion. While most undisturbed sites show little sediment production, disturbance by vehicles or livestock produces up to 36 times more sediment production, with soil movement initiated at wind velocities well below commonly-occurring wind speeds. Winds across disturbed areas can quickly remove this material from the soil surface, thereby potentially removing much of current and future soil fertility. Thus, reduction in the cover of cyanophytes in desert soils can both reduce fertility inputs and accelerate fertility losses.

Key words: Cyanobacteria, biological soil crusts, disturbance, erosion, soil fertility, carbon and nitrogen fixation, nitrogen availability.

Introduction

In arid and semi-arid environments, vegetation cover is sparse. However, the open spaces are not bare but generally covered by biological soil crusts (BSC: also referred to as cryptogamic, cryptobiotic, or microbiotic soil crusts) that are dominated by cyanobacteria, lichens, and/or mosses. Green algae, microfungi, and

other bacteria are also important components of this community. Cyanobacterial and microfungal filaments weave throughout the top few millimeters of soil, gluing loose soil particles together and forming a coherent crust that stabilizes and protects soil surfaces from erosive forces, while providing soil fertility. These crusts occur in all hot, cool, and cold arid and semi-arid regions of the world, but have only recently been recognized as having a major influence on terrestrial ecosystems (HARPER & MARBLE 1988, BELNAP & LANGE 2001).

Species composition and growth forms

Globally, BSCs have many similarities in species composition, in spite of occurring in seemingly dissimilar environments. Many of the dominant cyanobacteria, lichens, and moss species and genera found in soil crusts have a cosmopolitan distribution. The relative proportion of different species, however, varies with climate and soils. The cyanobacterial flora in cool deserts is often dominated by non-heterocystic filamentous species such as *Microcoleus* (Fig. 1). Hot deserts, especially those with summer rainfall, are often dominated by smaller, heterocystic genera such as *Scytonema* and *Nostoc*. Common lichens include *Fulgensia*, *Diploschistes*, *Psora*, *Placidium*, and *Collema*. Common mosses include *Tortula*, *Syntrichia*, *Bryum*, and *Grimmia*.

There are four general morphologies in undisturbed BSCs: **smooth crusts** are found in hyperarid regions that lack frost-heaving and are too dry to support lichens or mosses; **rugose crusts** are found in hot deserts where there is no frost-heaving, but that support a limited moss-lichen cover; **pinnacled crusts**, a result of soils frost-heaving upwards and being differentially eroded downwards, are found in cool deserts where lichen cover is low and soils freeze; **rolling crusts** are found in cool and cold deserts where soils freeze, but high lichen-moss cover prevents extensive pinnacled.

Because the dominant components of biological soil crusts are photosynthetic organisms, they are found near or at the soil surface. When soils are dry, the bulk of the crustal biomass is about 0.5 mm below the soil surface, with some individuals found down to 4 mm (GARCIA-PICHEL & BELNAP 1996). Mosses, lichens, and some cyanobacteria (e.g., *Scytonema*, *Nostoc*) have pigments to protect them from UV and are found on the soil surface. These species provide shade for the large filamentous species that lack UV-protective pigments (e.g., *Microcoleus*, *Phoridium*, and *Oscillatoria*), which are found slightly below the soil surface. On cloudy days and/or when soils are moist, these larger species glide to the surface, retreating as soils dry.

Ecological Roles

Weathering: Worldwide, cyanobacteria have been shown to increase the pH of the soils and rock in which they occur under lighted conditions. This has been

reported from soils in the western US (GARCIA-PICHEL & BELNAP 1996), Venezuela, and South Africa (BÜDEL 2000). Studies have shown that such an increase of pH in siliceous materials can accelerate weathering. In addition, stabilization of soils, organic secretions, and increasing water retention may enhance weathering up to 100 times (SCHWARTZMAN & VOLK 1989). In addition, the presence of BSCs enables soils to retain moisture longer, increasing the probability of mineral dissolution and freeze-thaw weathering of the underlying parent material.

Dust Trapping: Dust can provide many of the soil fine particles found in desert soils, thus significantly increasing soil fertility and water-holding capacity. In southeastern Utah, USA, dust has increased bioessential nutrients (e.g., N, P, K, Mg, Cu, Fe, Mn) 1.3–4.6 times over bedrock values. Soil fines are concentrated in the BSC relative to underlying soils (DANIN et al. 1989, VERRECCHIA et al. 1995, REYNOLDS et al. 2001).

Carbon and Nitrogen Fixation: BSCs are an important source of fixed carbon (C) in deserts (BEYMER & KLOPATEK 1991). While vascular plants provide C via organic matter to soils directly underneath them, the large interspaces between plants in deserts do not receive such input. However, where BSCs are present, they fix C. This C becomes available to surrounding organisms both through C leakage associated with wetting and drying, and by the death of crust organisms. Thus, BSCs help keep plant interspaces fertile and aid in providing other microbial populations with C. This contribution is most important in areas where plant cover is limited and/or soils are less fertile.

Nitrogen (N) levels are low in desert ecosystems relative to other ecosystems, yet surveys in cold deserts have revealed only a few N-fixing plants and natural atmospheric inputs are low (PETERJOHN & SCHLESINGER 1990, WULLSTEIN 1989). Since N can limit plant productivity (ETTERSHANK et al. 1978, NOBEL et al. 1988), maintaining normal N cycles is critical to maintaining the fertility of desert soils. Most soil crusts in deserts are dominated by complexes of organisms capable of fixing N, including *Microcoleus*, *Scytonema*, *Nostoc*, and the soil lichen *Collema*. These organisms can be the dominant source of N for desert communities (EVANS & EHLERINGER 1993, EVANS & BELNAP 1999). Past input estimates ranged from 1–100 kg ha⁻¹ annually, with a more recent estimate being 1–10 kg ha⁻¹ yr⁻¹ (reviewed in BELNAP 2001b, BELNAP 2002). N inputs are highly dependent on temperature, moisture, and crustal species composition (BELNAP 2001b), thus timing, extent and type of climatic regimes and past disturbance is critical in determining fixation rates. Five to 88% of N fixed by crusts leaks into the surrounding medium and is utilized by nearby vascular plants and microbial communities, including fungi, actinomycetes, and bacteria (reviewed in BELNAP 2001b). Vascular plants growing in crusted areas show higher leaf concentrations of N when compared to plants in uncrusted soils.

Effects on Vascular Plants: There are many ways in which BSCs can influence vascular plant community structure. In hot deserts, cyanobacteria can smooth soil surfaces, increasing the tendency of seeds to skid off these surfaces to the next obstacle (e.g., rocks, plants; BELNAP et al. 2001). Slightly-roughened rugose

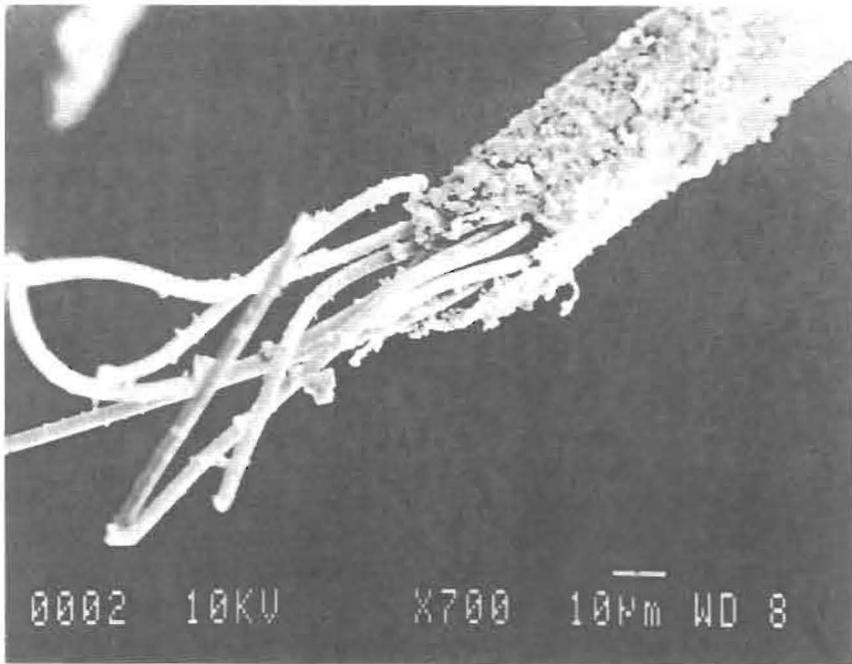


Fig. 1. *Microcoleus vaginatus*: note the large extracellular sheath surrounding the filaments. [Bar = 10 μm .]

crusts provide for some seed retention. In contrast, frost-heaved crusts (pinnacled and rolling) in cool and cold deserts vastly increase retention of seeds in plant interspaces (BELNAP in prep). While BSCs have not been shown to affect native plant germination, BSCs can reduce the germination of the exotic grass *Bromus tectorum* by limiting loose sediment available for seed burial (HOWELL & BELNAP, in prep.). Although it has been claimed that BSCs reduce field germination of plants (SAVORY 1988) this has not been shown in any published study. In addition, seedling germination *per se* has not been shown to limit species density in desert plant communities. Rather, vascular plant cover in arid lands appears controlled by water and nutrient availability (DUNKERLEY & BROWN 1995, MABBUTT & FANNING 1987).

Once seeds germinate, no studies have shown BSCs constitute a barrier to root penetration. Instead, electron micrographs show that soil crusts do not make an impenetrable "skin" on the soil surface, but instead are single filaments with large spaces between each other (Fig. 2). Survival of vascular plants is either much higher or unaffected when biologically crusted areas are compared with uncrusted areas (HARPER & MARBLE 1988, LESICA & SHELLEY 1992, BELNAP 1994; reviewed in BELNAP et al. 2001). No controlled studies have shown crusts to decrease vascular plant survival.

Many studies have examined the relationship of BSCs with total vascular plant cover and found negative, positive, or no relationship between the two factors (HARPER & MARBLE 1988, LADYMAN & MULDAVIN 1996). When considering all these studies, a few general patterns can be seen: at more arid sites, correlations between vascular plant cover and cover of crustal components is generally positive, suggesting plants aid survival of crustal components, especially mosses and lichens, perhaps due to microclimate conditions associated with perennial vegetation (such as decreased soil surface temperatures and increased surface moisture). At higher elevations and/or plant cover, it appears that plant cover inhibits crust cover by restricting the amount of light reaching the soil surface. No study has demonstrated a negative effect of crust cover on plant cover.

BSCs can affect the nutritional status of vascular plants. Plants growing on crusted soil in the lab and the field generally show higher concentrations and/or greater total accumulation of various bioessential nutrients (e.g., N, K, Na, Ca, Fe and Mg) when compared to plants growing in adjacent, uncrusted soils (HARPER & PENDLETON 1993, BELNAP & HARPER 1995, HARPER & BELNAP 2001). Dry weights of plants in pots with cyanobacteria are up to four times greater than in pots without cyanobacteria (HARPER & PENDLETON 1993), while dry weights of plants in untrampled areas can be two times greater than in trampled areas (BELNAP 1995, BROTHERTON & RUSHFORTH 1983, SHIELDS & DURRELL 1964, BELNAP & HARPER 1995). Several mechanisms have been postulated to explain how crusts may increase the nutritional status of plants: 1) cyanobacterial sheath material is negatively charged and thus can bind positively-charged nutrients, preventing leaching losses (BELNAP & GARDNER 1993, BLACK 1968); 2) cyanobacteria secrete chelators that keep iron, copper, molybdenum, zinc, cobalt, and manganese plant-available in high pH soils (LANGE 1974); 3) BSCs decrease soil albedo and thus increase soil temperature that increases nutrient uptake rates in plants; 4) BSCs contribute newly fixed C and N to soils, increasing soil fertility; 5) enhanced dust capture by BSCs significantly increases levels of many plant nutrients and water-holding capacity of soils and 6) BSCs stabilize soils, thus aiding in maintaining soil fertility and water-holding capacity.

Soil Physical Structure: Polysaccharides extruded by mosses, cyanobacteria, lichens, and microfungi entrap and bind soil particles together to form soil aggregates (Fig. 2). Soil aggregates are important as microhabitats for soil biota, as sites for chemical reactions, in maintaining soil aeration, and for increasing water infiltration (HERRICK & WANDER 1998). Formation of soil aggregates is especially important in the coarse soils that characterize many deserts, as there are limited fine particles to help bind soil particles together.

Soil Stabilization: BSCs have been shown to reduce wind and water erosion in all deserts and all soils around the world (reviewed in BELNAP 2001c, WARREN 2001). Soil aggregates formed by polysaccharides extruded by crust organisms are heavier and have a greater surface area than individual soil particles and are more difficult for wind and/or water to move (BELNAP & GARDNER 1993, MCKENNA-NEUMAN et al. 1996). In addition, wetted cyanobacterial sheath mate-

rial swells and covers soil surfaces even more extensively than when dry, protecting soils from both raindrop erosion and overland water flow during rainstorms (BELNAP & GARDNER 1993). This is in contrast to physical soil crusts that dissolve when wet and thus offer little or no protection from water erosion (BELNAP 2001a). The resistance of a soil to wind erosion parallels BSC development, as an increase in biomass results in more extruded polysaccharides and more and larger soil aggregates (MCKENNA-NEUMAN et al. 1996, BELNAP & GILLETTE 1998). Soils in arid regions are highly erodible, and take 5,000–10,000 years to form (DREGNE 1983b), making soil loss a great concern.

Soil Water Relations: The effect of BSCs on water infiltration and soil moisture is variable from site to site and region to region, as it is heavily influenced by climate, soil texture, soil structure, and the growth form of the crusts. In hyperarid deserts, the presence of mucilaginous cyanobacteria increases the smoothness of soil surfaces and partially fills the pore spaces between sand grains. Combined, this often decreases water infiltration on all soil types. With the minimal rainfall experienced in these regions, this decreased infiltration between plants is often necessary for plant growth, as the often-clumped plants depend on water runoff from the interspaces for sufficient water (TONGWAY et al. 2001). Experimental disruption of BSCs in these interspaces can result in the death of downslope plants (ZAADY & SHACHAK 1994). In hot deserts with rugose crusts, BSCs appear to have a variable effect, sometimes increasing and sometimes decreasing infiltration (HERRICK unpub. data, WARREN 2001). In contrast, the greatly roughened surface of BSCs in cool and cold deserts increases surface roughness, thus increasing water pooling and residence time. As a result, in cool and cold deserts the presence of soil crusts increases the amount and depth of rainfall infiltration (HARPER & MARBLE 1988, JOHANSEN 1993). Soil moisture retention under crusts has been examined in three studies. One found BSCs decreased soil moisture retention, while another found that they increased soil moisture retention. A third study showed that retention time was dependent on BSC type: in the same soils, less-developed cyanobacterial BSCs showed no effect on the time soils were moist, while well-developed lichen-cyanobacterial BSCs showed a significant increase in soil moisture retention time (GEORGE 2000).

Effects of disturbance

Species Composition: Trampling of crusted surfaces generally results in a decrease in the cover and number of crustal species present. Untrampled areas generally have 2–10 species of soil lichens (except in hyperarid deserts) and a minimum of six species of cyanobacteria present, while adjacent disturbed areas will often have no lichens and only one species of cyanobacteria (BELNAP 1995).

Water Erosion: As crustal components are brittle when dry and easily crushed (BELNAP & GARDNER 1993, CAMPBELL et al. 1989), soil aggregates formed by the soil crusts are disrupted when trampled (DREGNE 1983a, STOLZY & NORMAN

1961). In addition, the roughened microtopography is flattened, increasing the velocity of surface water flow. Combined, these factors mean an increase in sheet erosion (HARPER & MARBLE 1988). Surface disturbance also reduces the depth to which abandoned cyanobacterial sheaths can accumulate, thereby reducing resistance to water erosion at depth. At many disturbed sites, sheath material is often not observed below 1 mm depth, in contrast to up to 10 cm thick crusts in untrampled areas (BELNAP 1995). Buried sheath material is still capable of binding soil particles together and still increases nutrient and moisture retention of associated soil. However, damage to such abandoned sheath material is non-repairable, since living cyanobacteria are no longer present at these depths to regenerate filament and sheath materials. Consequently, trampling can greatly accelerate desertification processes through increased soil loss and water runoff (ALEXANDER & CALVO 1990, BEYMER & KLOPATEK 1992, ELDRIDGE 1993a, b, ELDRIDGE & GREEN 1994, FOTH 1978, HARPER & MARBLE 1988, LADYMAN & MULDAVIN 1996).

Wind Erosion: Wind is a major erosive force in deserts, where there is little soil surface protection by organic matter or vegetative cover (GOUDIE 1978). Experiments have demonstrated that while well-developed, undisturbed crusts protect soil surfaces from wind erosion, compressional disturbances to these crusts leave soils vulnerable to wind erosion by decreasing the wind speed required to move soil particles and increasing the amount of sediment produced from a site (BELNAP & GILLETTE 1997, 1998; LEYS 1990, WILLIAMS et al. 1995). Since soil formation is slow, soil loss can have long-term consequences. In addition, nearby biological soil crusts can be buried by blowing sediment, resulting in the death of the photosynthetic components of the soil crusts. Because over 75% of the photosynthetic biomass, and almost all photosynthetic productivity, is from organisms in the top 3 mm of these soils, very small soil losses can dramatically reduce site fertility and soil surface stability (GARCIA-PICHEL & BELNAP 1996).

Nutrient Cycles: Nitrogenase activity in crusts show short and long-term reductions in response to all types of experimentally-applied disturbance, including human foot traffic, mountain bikes, four-wheel drive trucks, tracked vehicles (tanks), and shallow and deep raking. Disturbance also elevates gaseous N loss. Consequently, crust disturbance can result in large decreases in soil nitrogen through a combination of reduced biological nitrogen input and elevated gaseous loss of nitrogen. Short-term reduction (2 years) in nitrogen inputs can be as great as 100% (BELNAP 1996), while long-term studies in southeast Utah have shown a 42% decrease in soil nitrogen 25 years following disturbance (EVANS & BELNAP 1999).

Albedo: Trampled surfaces show up to a 50% increase in reflectance of wavelengths from 0.25 to 2.5 μm when compared to untrampled crusted surfaces (BELNAP 1995). This represents a change in the surface energy flux of approximately 40 $\text{watts} \cdot \text{m}^{-2}$. Large amounts of trampled areas, combined with a lack of urban areas to offset this energy loss, may lead to changes in regional climate patterns in many semi-arid regions (SAGAN et al. 1979).

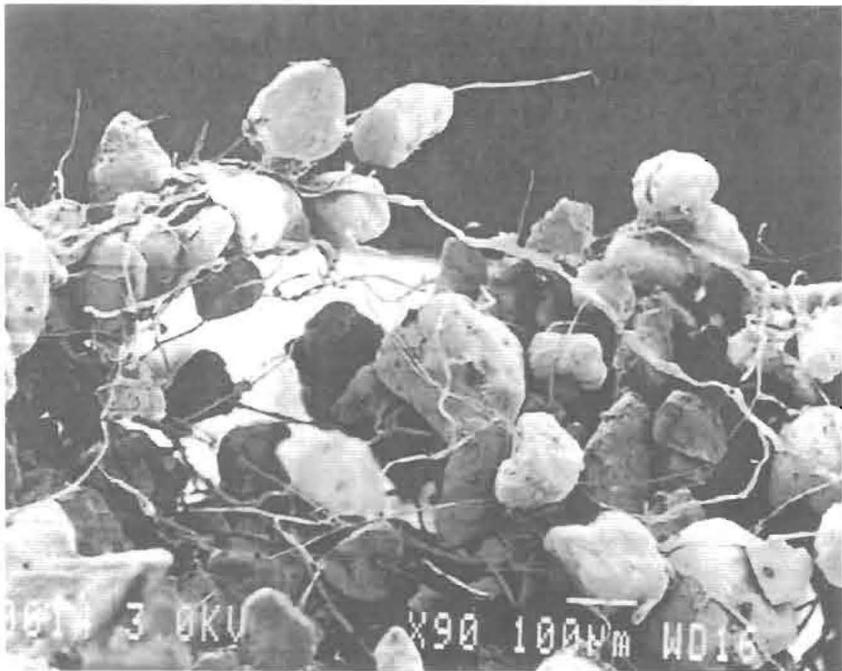


Fig. 2. *Microcoleus vaginatus* sheath material binds sand grains together (note the sheaths are wound around and among the sand grains). [Bar = 100 μ m.]

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Because of albedo changes, trampled surfaces can have significantly lower surface temperatures than untrampled surfaces. While mid-day temperatures in southeast Utah in June and July show air averaging 39°C (S. D. 0.25°C), bare sand averaged 52°C (S.D. 0.5°C) and dark crusted surfaces 62°C (S.D. 1.0°C). In the winter, surface temperatures of well-developed crusts were up to 14°C higher than ambient air temperature (BELNAP 1995).

Surface temperatures can regulate many ecosystem functions. Nitrogen and C fixation are heavily temperature dependent, with lower temperatures resulting in lowered activity levels (BELNAP 2001b, LANGE 2001). Decreased soil temperatures decrease microbial activity, plant nutrient uptake rates, and soil water evaporation rates while increasing vascular plant seed germination time and seedling growth rates. Timing of these events is often critical in deserts, and relatively small delays can reduce species fitness and seedling establishment which may eventually affect community structure (BUSH & VAN AUKEN 1991). Animals are also often dependent on soil surface temperatures: food and other resources are often partitioned among ants, arthropods, and small mammals on the basis of surface temperature-controlled foraging times (DOYEN & TSCHINKEL 1974, CRAWFORD 1991, WALLWORK 1982). Many small desert animals are weak burrowers and soil surface microclimates are of great importance to their survival

(LARMUTH 1978). Consequently, altering surface temperatures can affect nutrient availability and community structure for many desert organisms, thus increasing susceptibility to desertification.

Recovery from disturbance

Natural Recovery Rates: Recovery rates are related to the type, timing, and intensity of disturbances present in the evolutionary history of a given microflora. For instance, crusts in regions that evolved with large ungulate herds (e.g., the US Great Plains, the Serengeti of eastern Africa) have a different flora than crusts in areas that evolved with low disturbance levels and a different response to disturbance. While it has yet to be demonstrated, it may be that surfaces that did not evolve with disturbance may depend more heavily on soil surface integrity for natural ecosystem functioning than other regions. As a result, these deserts may be more negatively affected by soil surface disturbances than regions that evolved with higher levels of surface disturbance.

Recovery rates of BSCs depend on soil stability and fertility; the type, intensity, and extent of disturbance; the availability of inoculation material; and the temperature and moisture regimes that follow disturbance events. Estimates of time for visually-assessed recovery have varied from 5 to 100 years (HARPER & MARBLE 1988, JOHANSEN 1993, LADYMAN & MULDAVIN 1996). However, it has been shown that many components of recovery can not be assessed visually (Belnap 1993). Coarse soils show the slowest recovery rates, which is probably related to their inherent instability, low fertility, and low water-holding capacity. Fine-textured soils show a quicker recovery, probably a result of high water-holding capacity and greater fertility. Gypsiferous soils appear to recover fastest; it is not known if this is because of their great stability or unique chemistry.

Disturbance that is severe or frequent enough to remove crust material results in much slower recovery than when organisms are crushed but left in place. Disturbances with large internal areas relative to borders recover more slowly, as much of the colonization by lichens and mosses are by pieces breaking off and rolling or being washed into the disturbed area. Cyanobacteria, on the other hand, are often blown in and thus recover more quickly. Because crust organisms are only metabolically active when wet, climatic regimes after disturbances are very important in determining recovery rates. Accordingly, regions with greater effective rainfall recover much more quickly than those with lower rainfall (BELNAP & ELDRIDGE 2001). For example, assuming linear recovery rates, full re-establishment of a lichen soil crust in southeast Utah, USA, with 215 mm of rain, is estimated at 200+ years. Recovery time of a similar disturbance in an area with 350 mm of rain and cooler annual temperatures is estimated at 50 years.

Nitrogenase activity recovery appears to be quite slow, as it is dependent on recovery of the N_2 -fixing components of the crusts. In areas on the Colorado Plateau where BSCs were removed, no nitrogenase activity was detectable after nine years and N content of soils was still much lower when compared to adjacent control plots. In areas disturbed with four-wheel drive vehicles, no recovery

could be documented after 2 years (Belnap 1996). Using isotopic ratios of N, soil and plant N and nitrogenase activity levels were found to be significantly lower in an area that had been released from livestock grazing for 30 years when compared to an area that was never grazed (Evans & Belnap 1999). These data suggest that negative effects on nitrogen dynamics may persist in systems for extended, but variable, periods of time after disturbance ceases.

Restoration of normal surface albedos and temperatures depends on the recovery of cover of cyanobacteria, lichens and mosses. While cyanobacteria form a dark matrix in which other components are embedded, dark mosses and lichens contribute up to 40% of the cover in an undisturbed crust in southeast Utah (BELNAP 1993). Consequently, recovery of surface albedo characteristics in severely disturbed areas could take 200+ years for even very small areas.

Assisted Recovery: Inoculants can be used to speed up recovery of BSCs, as has been reported by several authors (ST. CLAIR et al. 1986, TIEDEMANN et al. 1980, ASHLEY & RUSHFORTH 1984, BELNAP 1993, BUTTARS et al. 1998). However, the lack of commercially-available inoculant requires that intact crusts be destroyed to provide the inoculating material. Therefore, the use of this method is currently fairly limited.

Conclusion

Unfortunately, the increasing activities of man in desert areas are often incompatible with the well-being of BSCs. The cyanobacterial fibers that confer such tensile strength to these crusts are no match for the compressional stresses placed on them by vehicles or trampling. Crushed crusts contribute less nitrogen and organic matter to the ecosystem. Impacted soils are left highly susceptible to both wind and water erosion. Raindrop erosion is increased, and overland water flows carry detached material away.

Relatively undisturbed biological soil crusts can contribute a great deal of stability to otherwise highly erodible soils. Unlike vascular plant cover, crustal cover is not reduced in drought, and unlike rain crusts, these organic crusts are present year-round. Consequently, they offer stability over time and in adverse conditions that is often lacking in other soil surface protectors. Thus, the condition and cover of BSCs should be considered in management of these regions.

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