Role of biological soil crusts in desert hydrology and geomorphology: Implications for military training operations

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ABSTRACT

Biological soil crusts, composed of soil surfaces stabilized by a consortium of cyanobacteria, algae, fungi, lichens, and/or bryophytes, are common in most deserts and perform functions of primary productivity, nitrogen fixation, nutrient cycling, water redistribution, and soil stabilization. The crusts are highly susceptible to disturbance. The degree of perturbation is governed, at least in part, by the nature, intensity, and spatial and temporal distribution of the disturbance, as well as the soil type and soil moisture content at the time of disturbance. When disturbed, biological soil crusts lose their capacity to perform their ecological functions. Natural recovery of disturbed crusts can range from several years to millennia. Several strategies have been attempted to accelerate recovery of crusts. At present, artificial recovery is not economically feasible on large tracts of disturbed desert landscape. Management options available to the military on arid landscapes include: (1) eliminating or minimizing training in desert ecosystems, (2) avoiding critical seasons, (3) avoiding critical areas, (4) artificially restoring damaged crusts, and (5) considering desert training lands as "sacrifice areas." Given the need to train in environments representative of the locations of many current and projected world conflicts, the first option is untenable. At this time, the most plausible alternative is to consider desert training lands as "sacrifice areas." However, it is recommended that attempts be made to avoid critical seasons and areas inasmuch as logistically feasible, and that the military continue to support research into the development of cost-effective technologies for biological soil crust restoration.

INTRODUCTION

Biological soil crusts are characteristic of most arid and semiarid landscapes. Alternatively referred to as cryptobiotic, cryptogamic, microbiotic, microfloral, microphytic, and organogenic soil crusts, they are formed when cyanobacteria, algae, fungi, lichens, and/or bryophytes colonize and inhabit the surface layer of arid soils. Filamentous cyanobacteria, algae, and fungi,

as well as rooting structures of lichens and bryophytes physically entwine soil particles, creating a stable matrix. The crust is further consolidated by glue-like polysaccharide secretions of cyanobacteria, algae, and fungi. Biological soil crusts generally range from 2 mm to 2 cm in thickness, and perform a variety of essential ecological functions.

Biological soil crusts have been reported from virtually every desert in the world (Belnap and Lange, 2001). At least

16 species of cyanobacteria are known to occur in the soils of Death Valley National Monument in the Mojave Desert, USA, where surface temperatures can reach 88 °C (Durrell, 1962). At the opposite end of the temperature spectrum, biological soil crusts have been reported from interior Antarctica, the world's largest desert, where temperatures seldom, if ever, surpass 0 °C (Green and Broady, 2001). Some crust organisms, particularly cyanobacteria, have been found in the driest desert in the world, the Atacama Desert of northern Chile (Forest and Weston, 1966), where precipitation is as low as 1 mm yr^{-1} (Rauh, 1985).

The presence of biological soil crusts is negatively correlated with the percent cover of vascular plants, and hence their abundance, in the desert regions of the world. The crusts generally occupy the interspaces between the scattered vascular plants of most deserts. Biological soil crusts occur on soils of almost any texture and can colonize soils with very low nutrient and high salt contents, although the species composition of the crusts may vary by local conditions.

The appearance of biological soil crusts can vary widely (Belnap et al., 2001). In hotter, drier deserts, the crusts are usually thin, have a smooth appearance, are dominated by cyanobacteria and algae, and are virtually invisible unless lifted, thus exposing the cyanobacterial filaments dangling from the bottom (Fig. 1A). On fine-textured soils, biological soil crusts may take on a rugose appearance due to differential shrinking and swelling (Fig. 1B). On coarse-textured soils that are subject to freezing and thawing, a distinct pinnacled morphology is often evident (Fig. 1C). In more mesic areas, a combination of frost heaving and dominance by lichens and mosses frequently creates a rolling appearance (Fig. 1D).

The objectives of this paper are to briefly describe the ecological functions of biological soils crusts, document the effects of military training and other common disturbances on the crusts and on their ability to perform their ecological roles, examine the ability of crusts to regenerate naturally following disturbance, and summarize methodologies that have been explored to accelerate crust recovery. Finally, management strategies are discussed as
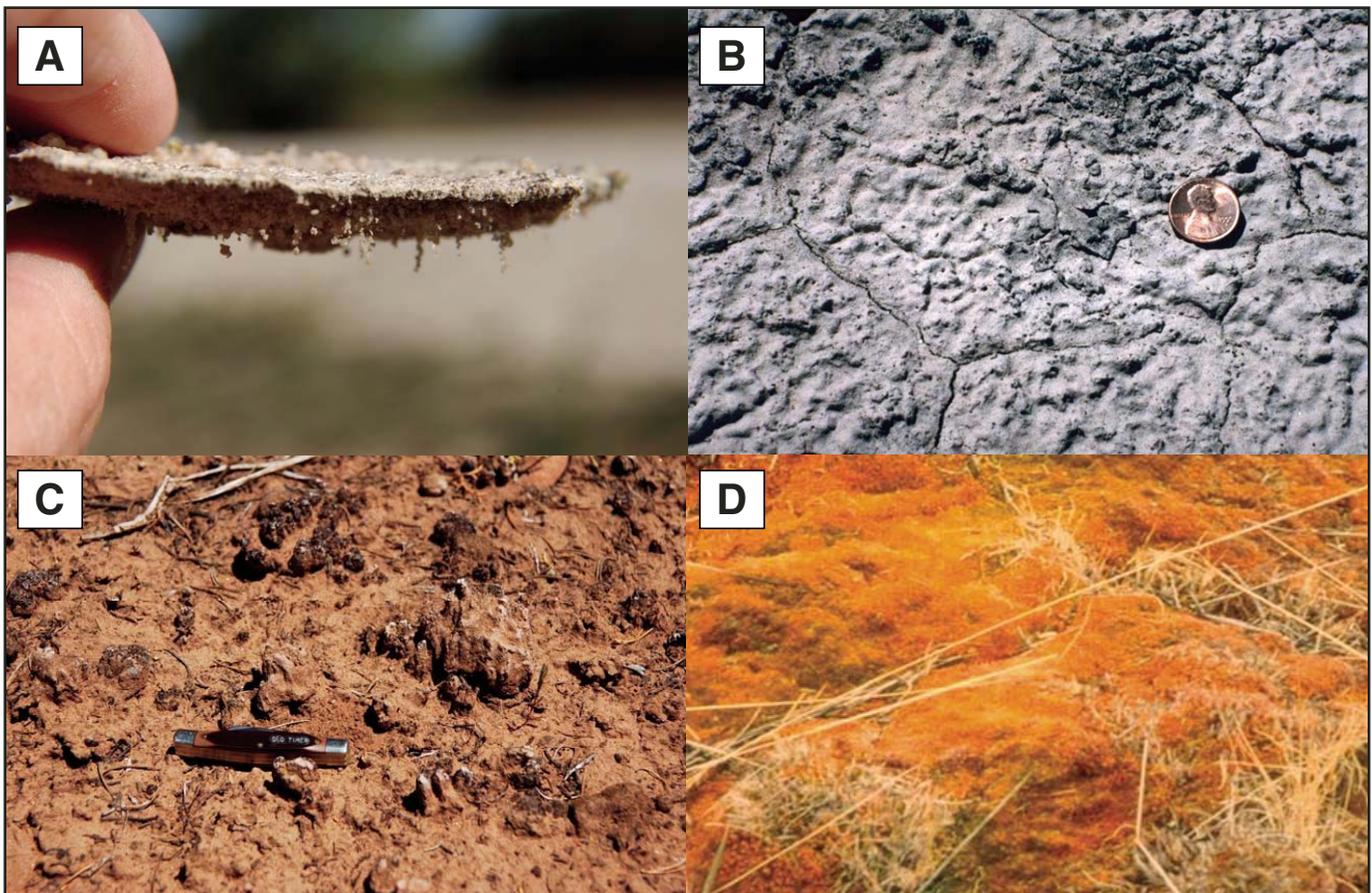

Figure 1. Biological soil crusts occur in four general morphologies: (A) Smooth crusts, typical of hot deserts, are virtually undetectable from the surface, but their presence is often evident by cyanobacterial filaments dangling from the crust when it is removed; (B) rugose crusts are characteristic of fine-textured soils that undergo shrinking and swelling; (C) pinnacled crusts are common on coarse-textured soils that experience freezing and thawing; (D) in more mesic areas, where lichens and mosses dominate, the crusts may have a rolling appearance, as in this crust which was scorched by fire.

they relate to maintaining and/or restoring healthy biological soil crusts on landscapes subjected to intense military training.

ECOLOGICAL FUNCTIONS

Primary Production

Most crust organisms are photoautotrophic and, therefore, contribute to primary production or carbon cycling in the ecosystems where they occur. Estimates of annual carbon contributions by biological soil crusts in undisturbed deserts range from 6.4 (Jeffries et al., 1993) to 370 kg C ha^{-1} yr^{-1} (Klopatek, 1992), with lower values occurring in crusts dominated by cyanobacteria and higher contributions reported where lichens and/or mosses predominate. While these values may appear small when compared to carbon fixation rates of vascular plants, they represent a significant contribution to many desert ecosystems where vascular plant cover is naturally limited. Indeed, it has been reported that the biomass produced by cyanobacterial/algal crusts in some deserts exceeds that of vascular plants (Rodin and Bazilevich, 1967).

Nitrogen Fixation

Cyanobacteria and cyanolichens (i.e., those with a cyanobacterial photobiont) are capable of fixing atmospheric nitrogen and making it available to vascular plants. However, the net nitrogen contribution from biological soil crusts has been a source of considerable debate given the variety of methods used for estimation (Evans and Lange, 2001). Estimates of nitrogen input by biological soil crusts have ranged as high as 100 kg ha^{-1} yr^{-1} (Rychert and Skujins, 1974). However, controlled experimentation under representative conditions indicates that more realistic values probably seldom exceed 10 kg ha^{-1} yr^{-1} (Warren, 1995). Nitrogen fixation by biological soil crusts is the dominant form of nitrogen input into many arid ecosystems (Evans and Ehleringer, 1993). Much of the nitrogen fixed by biological soil crusts is retained in the upper few centimeters of the soil (Skujiņš, 1984), where it is available to vascular plants. The nitrogen content of soils with biological crusts may be up to seven times that of similar soils lacking crusts (Shields et al., 1957). Plants grown in soils with biological crusts respond to the increased levels of nitrogen by producing more biomass (Belnap and Harper, 1995; Pendleton et al., 2003).

Cycling of Other Nutrients

Numerous other essential elements have also been shown to accumulate in the surface layer of soil occupied by biological crusts (Reynaud, 1987; Harper and Pendleton, 1993). Although this has been attributed to the accumulation of fine soil particles by the roughness of the crusts (Kleiner and Harper, 1972), other mechanisms may also play a significant role. Biological soil crust organisms accelerate the weathering of rocks, thus speeding the genesis of soil and adding important minerals (Metting et al.,

1988). Polysaccharide secretions of cyanobacteria contain chelating agents that concentrate essential nutrients (Lange, 1974). In addition, negatively charged clay particles may be bound by the polysaccharide secretions, thus attracting positively charged essential elements (Belnap and Gardner, 1993). Vascular plants grown in soils with biological crusts accumulate significantly greater quantities of many essential elements than plants grown in the same soil without a crust (Harper and Pendleton, 1993; DeFalco et al., 2001).

Water Redistribution

The effect of biological soil crusts on infiltration has been a source of controversy, with some researchers claiming that biological soil crusts reduce infiltration and others suggesting that they enhance infiltration. A comprehensive literature review by Warren (2001b) revealed that the differential effects can be largely attributed to soil texture. As a general rule, where the sand content of the soil exceeds ~80%, the presence of a biological soil crust results in a decline in infiltration rate. Sandy soils are typically characterized by large pores and rapid infiltration. Biological soil crusts, when present, tend to facilitate the accumulation of fine soil particles (Danin and Ganor, 1997; Verrecchia et al., 1995). The accumulation of as little as 10%–20% fine soil particles in a sandy soil can reduce its hydraulic conductivity by as much as three orders of magnitude (Rawls et al., 1983). In addition, fungal hyphae, cyanobacterial filaments, and rooting structures of lichens and bryophytes may occupy soil pores and limit the transmission of water. Upon wetting, the sheaths of some cyanobacteria absorb up to eight times their weight in water (Belnap and Gardner, 1993) and swell to several times their original volume (Campbell, 1979), further blocking available pore space near the soil surface and reducing infiltration rates (Kidron et al., 1999). When infiltration is reduced, runoff increases. In sandy soils, the reduction of infiltration in some areas contributes runoff to others. The accumulation of runoff at the base of shrubs allows them to persist in desert areas that would otherwise to be too dry to support them (Kidron, 1999; Yair, 2001) and contributes to the patchy nature of many desert landscapes (Zaady, 2005).

Once water has entered the soil, biological soil crusts control, to some degree, the loss of soil moisture via evaporation. In a shrubland community near the southern edge of the Chihuahuan Desert, in the state of San Luis Potosí, Mexico, Meyer and García-Moya (1989) detected greater soil moisture in an intact soil than where livestock trampling had destroyed the biological crust. The authors suggested that the difference was due to greater evaporative loss where the crust was destroyed. During a very dry period in the southern Great Plains, Booth (1941) was unable to detect differences in soil moisture in the first 2.5 cm below biologically crusted versus physically crusted soils. Two days following a light rain, moisture beneath the biological crust averaged 8.9% compared to 1.3% beneath the physical crust. Rushforth and Brotherson (1982) reported 75% more moisture

under a biological crust than below a disturbed surface in the Colorado Plateau region of the Great Basin Desert. Also in the Great Basin, George et al. (2003) determined that soils with biological crusts retained moisture longer than bare soils. Cyanobacterial crusts were more effective than lichen crusts.

Soil Stability

One of the more important ecological roles of biological soil crusts, certainly in the context of this volume, is soil stability. Soil erosion occurs as a result of a three-part process, including detachment, transport, and deposition of soil particles and aggregates. Well-developed biological soil crusts generally protect the soil surface from the erosive forces of wind and water.

Water Erosion

The energy of falling raindrops or water moving across the soil surface may cause detachment and movement of soil particles, i.e., erosion. Coarse-textured soils and soils with large, water-stable aggregates are less susceptible to detachment and transport than finer and/or less-aggregated soils. Where larger organisms such as bryophytes and lichens cover the soil, raindrops are unable to directly impact the soil surface and detach soil particles. Fungal hyphae, cyanobacterial filaments, and rooting structures of lichens and mosses create a complex mesh throughout the surface layer of the soil, physically entwining soil particles and aggregates (Fletcher and Martin, 1948; Belnap and Gardner, 1993). Various fungi and cyanobacteria secrete extracellular polysaccharide compounds that glue soil particles together (Tisdall and Oades, 1982; de Cano et al., 1997). Soil aggregates formed in association with biological soil crusts are more resistant to disintegration by falling raindrops than aggregates formed without the benefit of crust organisms (McCalla, 1947). Soils stabilized by biological soil crusts may experience up to two orders of magnitude less splash erosion than unprotected soils of the same texture (Hill et al., 2002). Biological soil crusts also minimize detachment and transport of soil particles by runoff (Booth, 1941; Fletcher and Martin, 1948). In addition to surface aggregation, many biological soil crusts contribute to a rough surface microtopography (Belnap, 2001b) that serves to diminish the energy of surface runoff, thus reducing soil erosion.

Wind Erosion

Biological soil crusts, particularly those with a large component of filamentous cyanobacteria, are also effective at stabilizing soil against the erosive forces of wind. The wind velocity required to detach and move soil particles from the soil surface is known as the threshold friction velocity. The threshold friction velocity of soils with intact biological crusts generally far exceeds naturally occurring maximum wind speeds, thus affording near-complete protection of the soil surface against wind erosion (McKenna Neuman et al., 1996; Hu et al., 2002).

EFFECTS OF DISTURBANCE

Military Maneuvers

Studies examining the effects of military activity on biological soil crusts are limited in number. Marston (1986) evaluated the impacts of armored military maneuvers on the biological crusts associated with desert grasslands at the Fort Bliss Military Reservation in the Chihuahuan Desert. The study was of limited scope, and the only conclusion related to the grassland areas was that they did not generate windblown sediments. Unfortunately, the nature of the military maneuver disturbance was not characterized, and the extent of the disturbance was not quantified.

Barringer (1997) evaluated the impacts of the M1 Abrams main battle tank and the M2 Bradley Fighting Vehicle on various soil and vegetation parameters at the Yakima Training Center located in the Columbia Basin of Washington. Biological crust cover was low (1%–19%) prior to treatment. Tracking with up to 16 passes of the vehicles caused relatively large declines in percent cover of crusts immediately following treatment. However, the limited sample size and methodologies were inadequate to assign statistical significance to the differences.

At Dugway Proving Ground, Utah, in the Great Basin Desert, soil chlorophyll content, used as an index for the biomass of biological crust organisms, was measured 9 months following tracking by a self-propelled howitzer (Belnap et al., 1994). Chlorophyll contents from plots representing 1 and 10 passes of the howitzer were statistically similar to the undisturbed control, while the chlorophyll content of plots treated by four passes of the howitzer was significantly lower than the control. The inconsistency of statistically significant differences in chlorophyll content was attributed to the dominance of the cyanobacterium *Microcoleus vaginatus*. While the integrity of the crusts was largely destroyed by the passage of the vehicles, the cyanobacteria were not killed and quickly recovered their ability to photosynthesize.

In the sagebrush steppe at the Idaho National Guard's Orchard Training Area in the northern Great Basin Desert near Boise, Idaho, the effects of tracking by an M1 Abrams main battle tank were evaluated 2 yr post-treatment (Watts, 1998). Lichen and moss cover showed no significant difference between disturbed and undisturbed areas after 2 yr where tracking occurred in a straight line. However, where the tanks turned, and thus sheared the soil surface, the loss of biological soil crust cover was highly significant after 2 yr. The same treatments were imposed on a burned site and measured after 1 yr. The reduction in crust cover was significant, but it did not vary significantly between straight-line tracks and turning tracks. Moss cover was affected more than lichen cover.

The short-term effects of military maneuvers on biological soil crusts of the hotter, more arid deserts of North America have not been evaluated. However, the lasting effects of military training in those deserts have been investigated. The Desert Training Center, covering 5 million ha of the Mojave and Sonoran Deserts, was established by General George Patton Jr. in 1942 and

operated until 1944 (Bischoff, 2000). Parts of the area were utilized again in 1964 for a 2 wk training exercise called Operation Desert Strike. Prose and Wilshire (2000) examined tracks from both exercises in 1985 at the former Camp Granite. Significant reductions in biological soil crust cover persisted in both 41-yr-old and 21-yr-old tracks. Ten years later, in 1995, Belnap and Warren (2002) examined World War II–era tracks in the Chemehuevi Valley near Needles, California. After more than 50 yr, chlorophyll content in the tracks was still reduced by half, compared to adjacent untracked areas. In the interspaces between the scattered shrubs, cover of the lichens *Collema tenax* and *Catapyrenium squamulosum* was still lower by 94% and 97%, respectively.

Kade and Warren (2002) examined the long-term effects of a former World War II–era military base camp in the Sonoran Desert 56 yr following abandonment. Cyanobacteria occurred significantly less frequently in the former tent city than in a nearby undisturbed area. However, occurrence in the former motor pool was statistically equivalent to the undisturbed area.

Fire

Military training maneuvers often involve the use of high-explosive munitions, tracer rounds, flares, and other pyrotechnics. While there have been no studies regarding the effects of military-caused fires on biological soil crusts in arid areas, there have been five studies involving the effects of fire not caused by military training. Four of the studies were conducted in the Great Basin Desert and one in the Chihuahuan Desert. Studies involving fire in desert regions are rare because wildfires are generally uncommon in deserts.

Where the Great Basin Desert transitions into the Mojave Desert, fire in a blackbrush shrub community significantly reduced biological soil crust cover (Callison et al., 1985). The reduction persisted for at least 37 yr. Three years following a wildfire in a sagebrush community in Wasatch County, Utah, Johansen et al. (1982) found a significantly lower frequency of algal/cyanobacterial species in the burned area. Likewise, 3 yr following a wildfire in a salt desert shrubland community in Utah County, Utah, the frequency of algal/cyanobacterial species was significantly less than in an adjacent unburned area (Johansen et al., 1984). The visible cover of algae/cyanobacteria was reduced by over half, while lichens were reduced by over 98%, and mosses were eliminated altogether. In a controlled experiment within a salt desert shrubland community at Dugway Proving Ground in Toole County, Utah, a 22% reduction in the chlorophyll content of the crust was recorded in burned plots (Kasper, 1994). A wildfire in a sagebrush-grassland at the Arid Lands Ecology Reserve in the Columbia Basin of eastern Washington completely eliminated lichens and mosses from intensively burned areas; algae and cyanobacteria were significantly reduced but not eliminated (Johansen et al., 1993).

At Fort Bliss, in Texas and New Mexico, a controlled experiment examined the effects of fire on biological soil crusts of the Chihuahuan Desert (Johansen et al., 1998). Intense fire reduced soil chlorophyll content by 75%. Visual cover of a cyanobacterial crust dropped 89%, while lichen cover declined by 97%.

Off-Road Vehicles

Although off-road vehicles are generally different than military vehicles in terms of weight and maneuverability, their impacts on biological soil crusts are likely similar. However, despite the widespread use of desert areas by off-road vehicles, surprisingly few studies have examined the impacts on the biological soil crust communities. Wilshire (1983) concluded, based on observations, that a single pass of an off-road vehicle was sufficient to severely damage biological soil crusts on sandy soils in the Mojave Desert, but that multiple passes were required to destroy the crust. Both Wilshire (1983) and Webb et al. (1988) provided compelling anecdotal and photographic evidence of the destructive nature of off-road traffic on biological soil crusts. In the southern Great Basin Desert near Moab, Utah, one-time off-road vehicle traffic destroyed the physical integrity of biological soil crusts (Belnap, 1996) but had only minimal impact on the biomass of cyanobacteria, thus indicating that a single event did not kill the organisms.

Livestock

While the impacts of livestock differ in nature and intensity from military training, the extensive literature on the subject may lend insight into military impacts. Trampling is the most common form of disturbance caused by grazing animals to biological soil crusts. Warren and Eldridge (2001) conducted an exhaustive review of the literature and found an overwhelming consensus that livestock trampling is detrimental to biological soil crusts in desert regions of the world.

The timing of livestock impacts in relation to the season of year may affect the degree of damage. Marble and Harper (1989) determined that heavy grazing in early winter had no significant effect on crust cover in southwestern Utah compared to an ungrazed control. When grazing was conducted at the same intensity but in both early and late winter, the cover and species richness of the crust were significantly reduced. Because late winter is generally dry in that portion of the Great Basin Desert, the authors concluded that grazing during dry periods is more detrimental to biological soil crusts than grazing during moister periods. Lusby (1979) monitored vegetation and sediment yield from a grazed watershed in the Colorado Plateau region of the southern Great Basin Desert over 20 years. He discovered that sediment yield was reduced by 38% when the period of livestock grazing was reduced from winter through late spring to early and midwinter only, even though the overall forage utilization rate remained approximately equal. Lusby did not specifically monitor biological soil crusts, but because no changes in vascular plant cover were detected, Marble and Harper (1989) concluded that the differences were likely due to greater damage to the crusts in late spring when conditions were drier. Others have suggested

that biological soil crusts are most susceptible to damage when dry (Anderson et al., 1982a; Eldridge and Kinnell, 1997). Among the various crust components, lichens (Pegau, 1970) and cyanobacteria (Campbell et al., 1989; Belnap and Gardner, 1993; Belnap et al., 1994) appear to be particularly susceptible to damage when dry.

Biological soil crusts in grazed areas exhibited less species diversity than in undisturbed areas of Canyonlands National Park, Utah (Kleiner and Harper, 1972), implying that some species are more susceptible than others. Similarly, the species richness of biological crusts decreased along a gradient of increasing disturbance surrounding livestock water sources in Australia (Hodgins and Rogers, 1997). In Great Basin and Colorado Plateau cold-desert shrublands, mosses tend to be most susceptible to physical damage, followed by lichens and then microscopic organisms (Anderson et al., 1982a, 1982b; Brotherson et al., 1983). Crusts dominated by filamentous cyanobacteria and algae are more stable than those dominated by nonfilamentous forms (McKenna Neuman et al., 1996). Among lichens, some species seem more tolerant of trampling than others (Rogers and Lange, 1971). Foliose and fruticose lichens with elevated vegetative structures seem to be more susceptible than crustose or squamulose forms that grow flat against the soil surface; gelatinous forms appear to be least susceptible (Eldridge and Rosentreter, 1999).

FUNCTIONAL CONSEQUENCES OF CRUST DISTURBANCE

When biological soil crusts are damaged or destroyed, their ability to perform the ecological functions previously described is diminished or eliminated. Although chlorophyll content of biological soil crusts is often used as an index to biomass, it also reflects the ability of the crusts to photosynthesize. Studies involving single or short-term disturbances occasionally show little difference in chlorophyll content of disturbed and undisturbed soils (Belnap et al., 1994), reflecting minimal mortality of crust organisms. However, intense and/or repeated disturbance may eliminate crust organisms and diminish carbon inputs into the system (Kasper, 1994; Johansen et al., 1998). In harsh environments, reductions may last half a century or more (Belnap and Warren, 2002).

At Dugway Proving Ground, Utah, in the Great Basin Desert, nitrogenase activity, as an index for nitrogen fixation by biological soil crusts, was measured 9 months following tracking by a self-propelled howitzer (Belnap et al., 1994). Nitrogenase activity was significantly lower than the undisturbed control for all levels of vehicular tracking and was slow to recover. The slow recovery was attributed to the dominance of the cyanobacterium *Microcoleus vaginatus*. Nitrogen fixation is an anaerobic process; *Microcoleus* does not possess the intracellular heterocysts utilized by many other cyanobacteria to produce oxygen-free zones where nitrogen fixation can take place. Instead, they apparently produce anaerobic sites by tightly packing multiple filaments inside a thick extracellular sheath where symbiotic bac-

teria perform nitrogen fixation (Steppe et al., 1996). Disruption of the sheaths by vehicular traffic likely eliminates the anaerobic zones, thus diminishing the potential for nitrogen fixation. Off-road vehicle traffic and livestock grazing have also been shown to significantly diminish nitrogen fixation (Belnap, 2002; Evans and Belnap, 1999; respectively). The effects of disturbance on nitrogen fixation can be particularly long-lasting. After more than 50 yr following military training in the Mojave Desert, nitrogenase activity was still half that of adjacent untracked areas (Belnap and Warren, 2002).

In sandy soils, where the presence of a biological soil crust tends to limit infiltration, disturbance to the crusts often results in an increase in infiltration (Graetz and Tongway, 1986; Dulieu et al., 1977). In such systems, the increase in infiltration and concomitant reduction in runoff can have negative consequences for patchy vegetation that depends on supplemental moisture from the crusted areas (Tongway and Ludwig, 1995). In contrast, in soils with less sand, biological soil crusts generally enhance water infiltration, and disturbance usually results in a decline in infiltration rate (Warren, 2001b). Infiltration rate and soil erosion by water are inversely related; as infiltration declines, more water runs off the surface, increasing the potential for soil erosion. Hence, disturbance to crusts on finer soils results in an increase in soil erosion (see reviews by Eldridge, 2001; Warren, 2001a).

The threshold friction velocity of the soil surface is reduced when biological crusts are damaged or removed (Williams et al., 1995; Belnap and Gillette, 1997, 1998; Belnap, 2001a); the greater the disturbance, the greater is the reduction (Leys and Eldridge, 1998). As the threshold friction velocity declines, more soil is mobilized, and wind erosion increases. Two- to 35-fold increases in the amount of soil erosion by wind have been reported where biological soil crusts have been disturbed (Williams et al., 1995; Belnap and Gillette, 1997; Leys and Eldridge, 1998; Belnap, 2001a). Accelerated wind erosion is not limited to the immediate location of the disturbance. Soil particles dislodged and subsequently blown from the point of disturbance often saltate across the soil surface, impacting and dislodging additional soil particles downwind of the initial disturbance (McKenna Neuman et al., 2005). The process may be perpetuated over long distances until a change in soil characteristics, topography, or vegetative cover limits the ability of the wind to move additional soil particles.

NATURAL RECOVERY

In general, where disturbance has been severe, filamentous cyanobacteria are the first colonizers of the soil surface (Belnap and Eldridge, 2001). As the surface is stabilized, smaller cyanobacteria and green algae appear, followed by small lichens. Where climatic conditions permit, larger lichens and mosses will culminate the successional process. Estimates of the time required for natural recovery of biological soil crusts following disturbance have varied widely depending on the nature, periodicity, extent, and spatial and temporal distribution of the disturbance, as well as soil type, and climatic conditions during and

after the disturbance (Warren, 1995; Belnap and Eldridge, 2001). Five years following one-time human trampling of a biological crust in the Great Basin Desert, Cole (1990) noted a nearly complete recovery of visible cover. The pinnacled surface microtopography attributable to the crusts, however, had not recovered to predisturbance levels. Anderson et al. (1982b) estimated that 14–18 yr were adequate for recovery of a biological soil crust following exclusion of livestock grazing in the Great Basin Desert. However, there was little evidence of recovery 10 yr following the cessation of grazing at another Great Basin Desert location (Jeffries and Klopatek, 1987) and almost 20 yr after 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 biological soil crusts at a Great Basin Desert site, including visual as well as functional characteristics, could take as long as 30–40 yr for cyanobacteria, 45–85 yr for lichens, and 250 yr for mosses. Eldridge and Ferris (1999) suggested that at least 60 yr would be required for the recovery of lichens at a nuclear test site in the Great Victoria Desert of Australia. Fifty-six years following abandonment of a military camp in the Sonoran Desert, the cyanobacterial crust had not recovered to levels in an adjacent undisturbed area (Kade and Warren, 2002). Based on measurements inside and outside of tank tracks created during training for World War II in the Mojave Desert, Belnap and Warren (2002) estimated that recovery of the cyanobacterial component of the biological soil crust would require 85–120 yr. Full recovery of the lichen component was estimated to require 2000 yr.

ARTIFICIAL RESTORATION

Given the long recovery periods apparently required for natural restoration of biological soil crusts, it seems logical that attempts should be made to accelerate their recovery by inoculating disturbed sites with crust organisms. While agricultural applications of algae and cyanobacteria via irrigation water to improve soil aggregation, moisture relations, nutrient content, and tilth are not uncommon in mesic areas (Metting et al., 1988), applications in deserts are comparatively rare. On a site subjected to wildfire in the Great Basin Desert, St. Clair et al. (1986) treated small plots with a soil slurry made by stripping intact areas of their crusts and mixing them with water. Also in the Great Basin Desert, Belnap (1993) used stripped crusts as a dry inoculant for small plots where the original crust had been removed. In both cases, inoculation significantly hastened recovery of the biological crust. While the results are promising, the destruction of crusts in one area to provide inoculants for other areas is counterproductive for large-scale desert reclamation.

Recent research has involved the development of cyanobacterial amendments for use in inoculation of disturbed areas. Buttars et al. (1998) incorporated live, laboratory-grown cyanobacteria into alginate pellets. Application of crushed pellets 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 of the organisms during the pelletization process (Howard and Warren, 1998). Kubečková et al. (2003) subsequently immobilized cyanobacteria on hemp cloth. Laboratory trials indicated improved growth compared to alginate pellets. However, in four of five field trials, there was no significant crust recovery. The lack of success was attributed, at least in part, to ultraviolet (UV) radiation sensitivity of the species used. Some cyanobacterial species contain pigments that protect them from UV radiation (Garcia-Pichel and Castenholz, 1991) and are thus able to survive at the soil surface. Species that do not contain protective pigments often occur at a depth of 1–2 mm below the surface, where UV radiation is attenuated (Dor and Danin, 2001). When cyanobacterial inoculants are placed on the soil surface rather than incorporated into the surface layer of the soil, mortality can be unacceptably high.

IMPLICATIONS FOR MILITARY TRAINING

Based on the information presented herein, it is apparent that biological soil crusts are highly susceptible to damage by physical disturbances and wildfires caused by military training. As the crusts are damaged, they lose their capacity to perform their ecological functions of primary production, nutrient cycling, soil hydrology, and soil stability. Natural recovery of crusts following damage in desert areas is generally very slow. Hence, the options available to the military for limiting or mitigating damage to biological soil crusts in desert terrain are limited. They include: (1) eliminating or minimizing training in desert ecosystems, (2) avoiding critical seasons, (3) avoiding critical areas, (4) artificially restoring damaged crusts, and (5) considering desert training lands as "sacrifice areas."

The unofficial U.S. Army training motto is "train as you fight, fight as you train." Given the geographic locations of many of the current world conflicts, and those that are likely to occur in the foreseeable future, the need for desert training areas will probably increase. Indeed, there will likely be an increased demand for variety in desert training lands in order to replicate the various desert terrains on which the military may be called to do battle. From a military perspective, the option to eliminate or minimize training in desert terrains is currently untenable.

It may be possible in some instances to minimize intensive training during those seasons when the crusts are most susceptible to physical damage and are less able to recover from that damage. As a general rule, crusts are most susceptible to disturbance during the dry part of the year (Marble and Harper, 1989). Unfortunately, most deserts, by definition, are characterized by long, dry periods, thus minimizing the potential to limit training in the "dry season."

Biological soil crusts can have a significant impact on soil hydrology, generally enhancing infiltration in finer textured soils and limiting infiltration in soils with a sand content ≥80% (Warren, 2001b). They may also control evaporation of water from the soil surface. The amount of water infiltrating into the

soil and percolating to various depths has a significant effect on soil development (McDonald et al., 1996) and plant responses (Hamerlynck et al., 2002) in desert ecosystems. To the degree to which the military could identify those desert land surfaces where biological crusts have the greatest influence, there exists limited potential to adapt training scenarios to avoid the most critical areas.

Although restoration of crusts is likely possible in some locations, the technology is not yet at a point where such restoration can be considered economically feasible. To date, application of liquid slurries seems to have been the most successful technique (St. Clair et al., 1986). Mass culture of cyanobacteria is possible (Tredici, 2004), but the logistics and cost of growing and applying liquid cultures to large areas typical of military training lands are currently prohibitive.

The final option available to the military is to simply do nothing with regard to biological soil crusts. Given the need for training in desert areas and the inherently destructive nature of war and training for war, the most plausible scenario is to consider desert training areas as "sacrifice areas" in the interest of national security. Even under this scenario, however, there exists potential to identify the most sensitive areas and the most sensitive seasons and attempt to create realistic training scenarios that exclude the most sensitive areas when they are most vulnerable. When, in the interest of national and international security, sensitive areas must be disturbed, it is recommended that the military explore the potential for postmaneuver inoculation of the disturbed areas with cyanobacteria in an attempt to restore ecosystem functioning to the degree that logistics and funding allow.

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