Soil Fertility in Deserts: A Review on the Influence of Biological Soil Crusts and the Effect of Soil Surface Disturbance on Nutrient Inputs and Losses

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ABSTRACT: Sources of desert soil fertility include parent material weathering, aeolian deposition, and on-site C and N biotic fixation. While parent materials provide many soil nutrients, aeolian deposition can provide up to 75% of plant-essential nutrients including N, P, K, Mg, Na, Mn, Cu, and Fe. Soil surface biota are often sticky, and help retain wind-deposited nutrients, as well as providing much of the N inputs. Carbon inputs are from both plants and soil surface biota. Most desert soils are protected by cyanobacterial-lichen-moss soil crusts, chemical crusts and/or desert pavement. Experimental disturbances applied in US deserts show disruption of soil surfaces result in decreased N and C inputs from soil biota by up to 100%. The ability to glue aeolian deposits in place is compromised, and underlying soils are exposed to erosion. The ability to withstand wind increases with biological and physical soil crust development. While most undisturbed sites show little sediment production, disturbance by vehicles or livestock produce up to 36 times more sediment production, with soil movement initiated at wind velocities well below commonly-occurring wind speeds. Soil fines and flora are often concentrated in the top 3 mm of the soil surface. Winds across disturbed areas can quickly remove this material from the soil surface, thereby potentially removing much of current and future soil fertility. Thus, disturbance of desert soil surfaces can both reduce fertility inputs and accelerate fertility losses.

INTRODUCTION

In arid and semi-arid environments, vegetation cover is generally sparse. The open spaces between higher plants are usually covered by biological soil crusts (also referred to as cryptogamic, cryptobiotic, microbiotic or microphytic soil crusts), an interwoven community of cyanobacteria, green algae, microfungi, bacteria, lichens, and/or mosses. Cyanobacterial and microfungal filaments weave throughout the top few millimeters of soil, gluing loose soil particles together, forming a coherent crust that stabilizes and protects soil surfaces from erosive forces, as will be discussed below. 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 and Marble, 1988).

SPECIES COMPOSITION AND GROWTH FORMS

Globally, biological soil crusts have many similarities in species composition, in spite of occurring in unconnected and seemingly dissimilar environments. Many of the dominant cyanobacteria, lichens, and moss species and genera found in soil crusts have a cosmopolitan distribution. The relative dominance of the different species, however, varies with climate. The cyanobacterial flora in deserts where most rain falls during cool seasons are dominated by filamentous species such as *Microcoleus*. Hot deserts, especially those with summer rainfall, are often dominated by smaller genera such as *Scytonema*, *Nostoc* and *Schizothrix*. Common lichens found include *Fulgensia*, *Diploschistes*, *Psora*, *Placidium*, and *Collema*. Common mosses include *Tortula*, *Bryum*, and *Grimmia*.

Four general growth forms are found in different deserts. Hot deserts that lack frost heaving are generally characterized by smooth cyanobacterial crusts or rugose lichen-moss crusts. In cool deserts where frost-heaving is present, soil crusts with low lichen cover are often pinnacled, due to frost-heaving upwards and differential erosion downwards. Crusts in cool deserts with a heavy lichen-moss cover are generally rolling, as frost-heaving and erosion are mitigated by the extensive lichen-moss cover.

Because the dominant components of biological soils crusts are photosynthetic organisms, they require sunlight. When soils are dry, the bulk of the crustal biomass is up to 0.5 mm below the soil surface, with some individuals found down to 4 mm (Garcia-Pichel and Belnap, 1996). While mosses and lichens have UV pigments or heavy coloration to protect them from UV, only some cyanobacteria have such protection. Large filamentous species, such as *Microcoleus*, *Lyngbya*,

Desertification in the Third Millennium. Edited by A.S. Alsharhan, W.W. Wood, A.S. Goudie, A. Fowler and E.M. Abdellatif.
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Phoridium, and *Oscillatoria* do not have UV-protective pigments, and so are seldom found on the soil surface except on cloudy days when soils are moistened. Cyanobacteria such as *Scytonema* and *Nostoc* do manufacture UV-screening pigments, and can be found on the soil surface.

ECOLOGICAL ROLES

***Carbon fixation*:** Biological soil crusts are an important source of fixed carbon on sparsely vegetated areas common throughout the West (Beymer and Klopatek, 1991). While vascular plants provide organic matter to soils directly underneath them, large interspaces between plants have little opportunity to receive such input. Where biological soil crusts are present, carbon contributed by these organisms help keep plant interspaces fertile, and aid in supporting other microbial populations. This is probably less important in areas with high productivity, and more important as soils get shallower and/or less fertile.

***Nitrogen fixation*:** Nitrogen levels are low in desert ecosystems relative to other ecosystems. Surveys in cold deserts have revealed only a few nitrogen-fixing plants (Wullstein, 1989). Since nitrogen can limit plant productivity (Ettershank et al., 1978; Nobel et al., 1988), maintaining normal nitrogen cycles is critical to maintaining the fertility of semi-arid soils. Most soil crusts in deserts are dominated by complexes of organisms capable of fixing nitrogen, including *Microcoleus, Scytonema, Nostoc* and the soil lichen *Collema*. Rainfall events in desert areas too small to promote plant growth often do stimulate crustal activity; thus, time of soil crust activity can be high. As with carbon, crusts contribute nitrogen to soils both underneath plants, and in plant interspaces, counteracting the tendency of nutrients to concentrate around plants. Five to 88% of N fixed by crusts has been shown to leak into the surrounding soils. N leaked from these organisms is available to nearby vascular plants and microbial communities. Vascular plants growing in crusted areas show higher leaf concentrations of N when compared to plants in uncrusted soils. Leaked N has also been found in associated fungi, actinomycetes, and bacteria.

Soil crusts can be the dominant source of nitrogen for desert shrub and grassland communities (Evans and Ehleringer, 1993; Evans and Belnap, 1999), where nitrogen-fixing plants are generally locally scarce. Input estimates range from 1 to 365 kg ha-1 annually (reviewed in Harper and Marble, 1988). Nitrogen inputs are highly dependent on temperature, moisture, and crustal species composition, thus timing, extent and type of climatic regimes and past disturbance is critical in determining fixation rates (Belnap, 1995, 1996).

***Dust trapping*:** Dust can be an essential component of desert soil fertility, and soil crusts are effective in capturing eolian dust deposits (Fig. 1). Recent work in SE Utah shows dust input significantly increase levels of all major and minor soil nutrients in the tested soils. The bioessential macronutrients N, P, K, and Mg, and micronutrients Cu, Fe, Mn were enriched up to 3 times that of surrounding bedrock (Table 1; Reynolds et al., unpubl. data).

***Effects on vascular plants*:** Germination and Establishment: Soil crusts can influence the location of safe sites for seeds, and the germination and establishment of vascular plants. In hot deserts with smooth cyanobacterial crusts, seeds can skid off the smoothed surfaces. Rugose crusts in these areas can provide limited safe sites. In contrast, seeds in cool and cold deserts find many safe sites where frost-heaved crusts occur.

Crusts can influence the germination of seeds. While soil cracks can provide favorable conditions for small seeds to germinate, most large-seeded plants need soil or litter cover (or an increase in humidity similar to that litter and soil cover can provide) to germinate. Native seeds often have self-burial mechanisms (such as hygroscopic awns) or are cached by rodents. However, germination of seeds that lack such adaptations can be inhibited by crusts. Once seeds germinate, crusts have never been shown to constitute a barrier to root penetration. However, it should be kept in mind that seedling germination per se has not been shown to limit species density in desert plant communities. Rather, studies suggest vascular plant cover in arid lands world-wide is controlled by water and nutrient availability rather than other site factors.

Survival of vascular plants is generally much higher, or unaffected, when crusted areas are compared with uncrusted areas (Lesica and Shelley, 1992; Harper and Marble, 1988). No studies have shown crusts to decrease vascular plant survival.

Many studies have correlated crust cover with vascular plant cover, and results have been variable, with negative, positive, and no relationship found between crust and vascular plant cover (Harper and Marble, 1988; Ladyman and Muldavin, 1996). 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 plants inhibit crust cover by restricting the amount of light reaching the soil surface. No study has demonstrated a negative influence of crusts on overall plant cover.

***Nutrient levels in vascular plants*:** Plants growing on crusted soil generally show higher concentrations

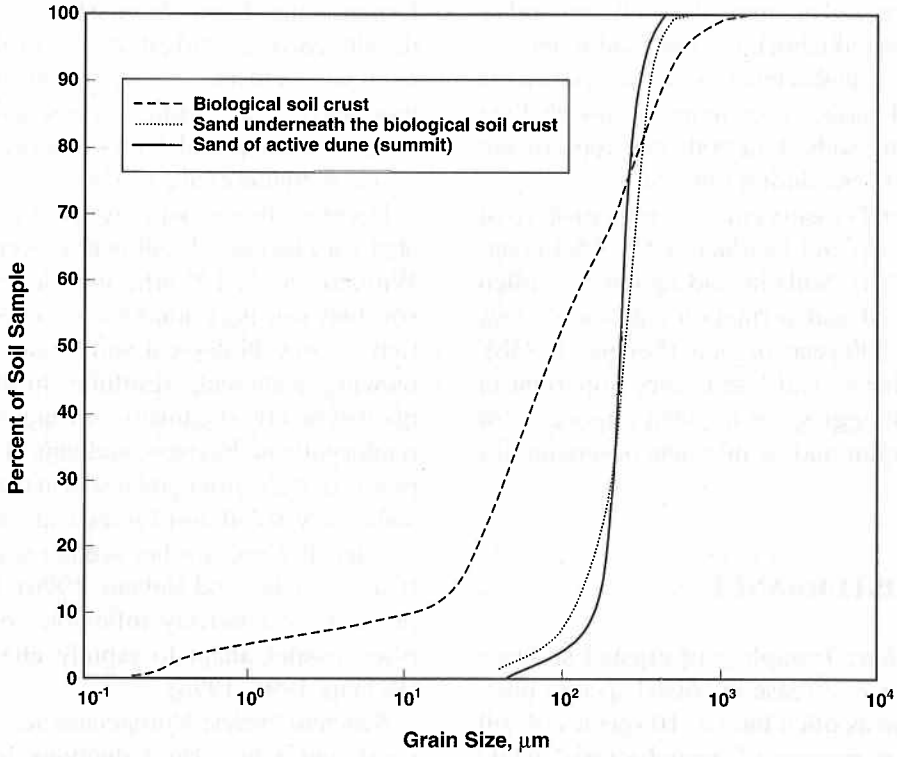

Figure 1 Grain size distribution curves for three dune samples. The biological soil crust contains a much higher percentage of silt and clay particles. Adapted from Verrecchia et al., 1995.

Table 1 Nutrient enrichments of soils above parent materials by Aeolian dust (Reynolds et al., unpubl.).

Bioessential elements	P	K	Mg	Na	Ca	Mn	Zn	Cu	Fe
Soil	271	1.49	0.37	0.17	2.7	196	21.4	13.8	1.04
Parent material	104	1.27	0.08	0.04	2.1	94	7.8	10.2	0.66
Enrichment (x)	2.6	1.2	4.6	4.3	1.3	2.1	2.7	1.4	1.6

and/or greater total accumulation of various bioessential nutrients when compared to plants growing in adjacent, uncrusted soils, including N, K, Na, Ca, Fe and Mg. Dry weight of plants in pots with cyanobacteria are up to four times greater than in pots without cyanobacteria (Harper and Pendleton, 1993). Dry weight of plants in untrampled areas can be two times greater than in trampled areas (Belnap, 1995; Brotherson and Rushforth, 1983; Shields and Durrell, 1964; Belnap and Harper, 1995).

Several mechanisms have been postulated to explain this effect. Cyanobacterial sheath material is negatively charged, binding positively-charged macro-nutrients and thus preventing their leaching (Belnap and Gardner, 1993; Black, 1968). Cyanobacteria secrete chelators that keep iron, copper, molybdenum, zinc, cobalt, and manganese more available in high pH soils (Lange, 1974). Nutrient differences may also result from a thermal effect. Dark-colored crusts warm soils, thus increasing nutrient uptake rates.

SOIL HYDROLOGY AND STABILIZATION

The effect of biological soil crusts on soil water relations is heavily influenced by soil texture, soil structure, and the growth form of the crusts. In hot deserts, the presence of the mucilaginous cyanobacteria and surface smoothness can decrease water infiltration. In cold deserts where frost-heaving is common, increased surface roughness can increase water pooling and residence time. As a result, here the presence of soil crusts generally increases the amount and depth of rainfall infiltration (Brotherson and Rushforth, 1983; Harper and Marble, 1988; Johansen, 1993; Loope and Gifford, 1972).

Crusts have been shown to reduce soil loss by wind and water erosion in all types of deserts (Williams et al., 1995a, b). Polysaccharides extruaded by the cyanobacteria and green algae, in combination with lichen and moss rhizines entrap and bind soil particles together. As soil aggregates get larger, they are heavier, have a

greater surface area, and are more difficult for wind or water to move, thus reducing both wind and water erosion. When wetted, cyanobacterial sheath material swells and covers the soil surface even more extensively than when dry, protecting soils from both raindrop erosion and overland water flow during rainstorms.

Resistance to wind erosion parallels biological crust development (Belnap and Gardner, 1993; McKenna-Neuman et al., 1996). Soils in arid regions are often highly erodible, and soil formation extremely slow, taking 5,000 to 10,000 years or more (Dregne, 1983b). Consequently, reducing soil loss is very important in these regions. Soil aggregates are also important for increasing infiltration and as microenvironments for soil biota.

EFFECTS OF DISTURBANCE

Species composition: Trampling of crusted surfaces generally results in a decrease in crustal species present. Untrampled areas often have 2–10 species of soil lichens and/or 4–6 species of cyanobacteria, while adjacent, trampled areas will have no lichens and only one species of cyanobacteria (Belnap, 1995).

Water erosion: As crustal components are brittle when dry and easily crushed (Belnap and Gardner, 1993; Campbell et al., 1989; Harper and Marble, 1988) the soil aggregates formed by the presence of soil crusts are disrupted when trampled (Dregne, 1983a; Stolzy and Norman, 1961). When the roughened microtopography of undisturbed cool desert crusts are flattened, velocity of surface water flows is increased. Thus, suspended sediments do not settle out and surfaces are subjected to sheet erosion (Harper and Marble, 1988). Surface disturbance also reduces the depth to which abandoned cyanobacterial sheath 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 and Calvo, 1990; Beymer and Klopatek, 1992; Eldridge, 1993a, b; Eldridge and Greene, 1994; Foth 1978; Harper and Marble, 1988; Ladyman and 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, any compressional disturbance to these crusts leave surfaces vulnerable to wind erosion (Fig. 2; Belnap and Gillette, 1997 and 1998; Leys, 1990; Williams et al., 1995a).

Decrease in soil wind resistance is directly associated with increased sediment movement (Leys, 1990; Williams et al., 1995a). 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 organisms. 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 further reduce soil surface stability (Garcia-Pichel and Belnap, 1996). In addition, many plants have relatively inflexible rooting depths, and often cannot adapt to rapidly changing soil depths (Belnap, 1995, 1996).

Nutrient cycles: Nitrogenase activity in crusts show short and long-term reductions in response to all types of experimentally-applied disturbance, including human feet, mountain bikes, four-wheel drive trucks, tracked vehicles (tanks), and shallow and deep raking. 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 and soil loss. Short-term reduction (2 years) in nitrogen inputs range up to 100% (Belnap, 1996), while long-term studies in SE Utah have demonstrated a 42% decrease in soil nitrogen in the 25 years following disturbance. The greatest long-term impact of disturbance may be on the soil microbial pool: production of plant-available nitrogen by soil microbes has been found to decrease almost 80% following disturbance (Evans and Ehleringer, 1993; Evans and Belnap, 1999).

Albedo: Trampled surfaces show up to a 50% increase in reflectance of wavelengths from 0.25 to 2.5 um (Belnap, 1995) when compared to untrampled crusted surfaces. This represents a change in the surface energy flux of approximately 40 watts/m2. Large acreages of trampled areas, combined with 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).

Because of albedo changes, trampled surfaces have significantly lower surface temperatures than untrampled surfaces. Mid-day temperatures in SE Utah in June and July show air temperatures averaged 39°C and bare sand 52°C, while dark crusted surfaces averaged 62°C. In the winter, surface temperatures of well-developed crusts are up to 14°C higher than ambient air temperatures (Belnap, 1995).

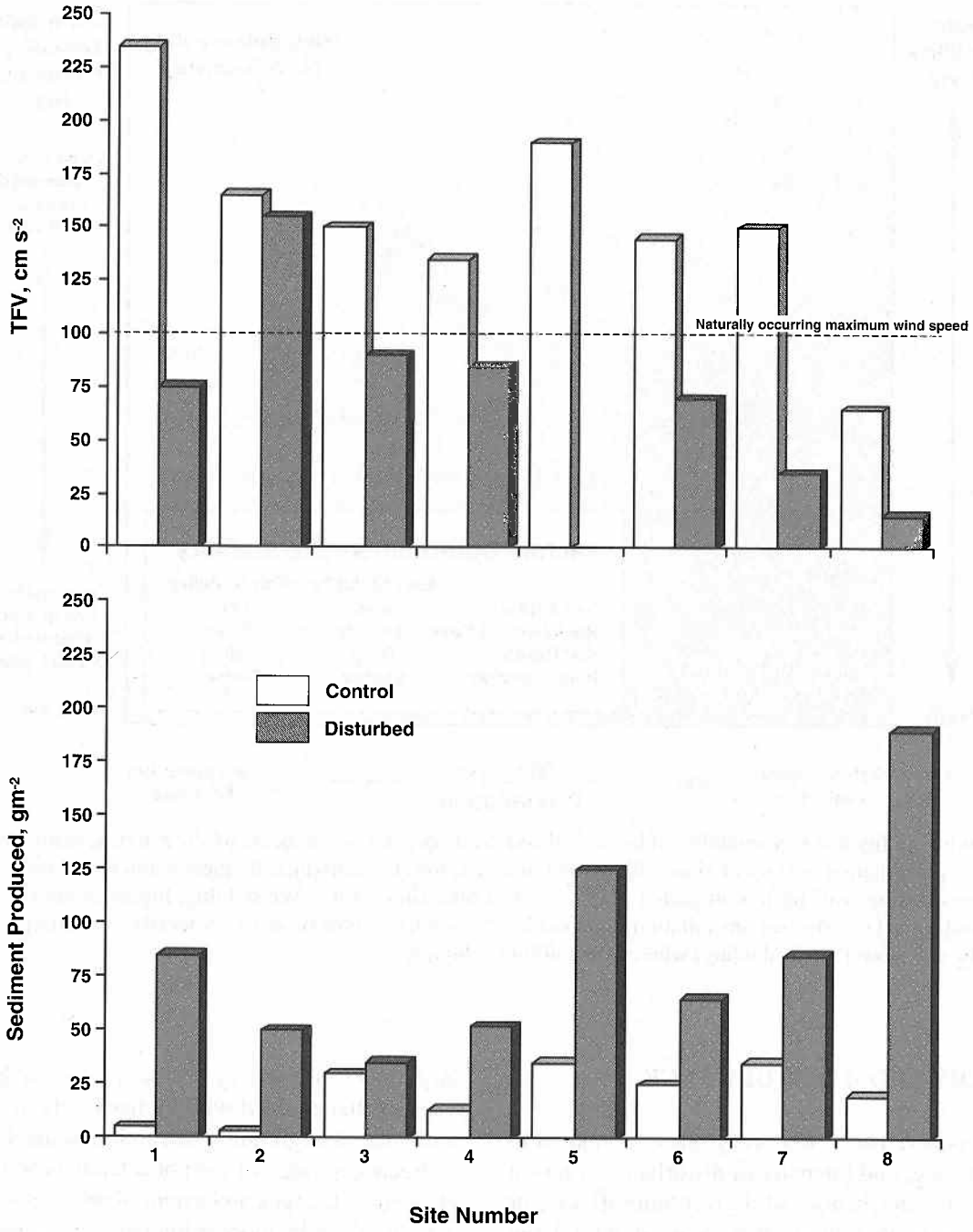

Figure 2 Threshold friction velocity (TFV) and sediment production measured on undisturbed and disturbed surfaces in Joshua Tree National Park, California, USA. Seven of the eight control sites have TFV above the highest recorded wind speeds; seven of the eight disturbed sites have TFV below recorded wind speeds. Sediment production is increased 35× with disturbance (Belnap et al., unpublished).

Surface temperatures can regulate many ecosystem functions. Nitrogen and carbon fixation are heavily temperature dependent, with lower temperatures resulting in lowered activity levels. Altered soil temperatures affect microbial activity, plant nutrient uptake rates and soil water evaporation rates. Soil temperatures affect seed germination time and seedling growth rates for vascular plants. 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 and Van Auken, 1991). Food and other resources are often partitioned among ants, arthropods and small mammals on the basis of surface temperature-controlled foraging times (Doyen and 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.

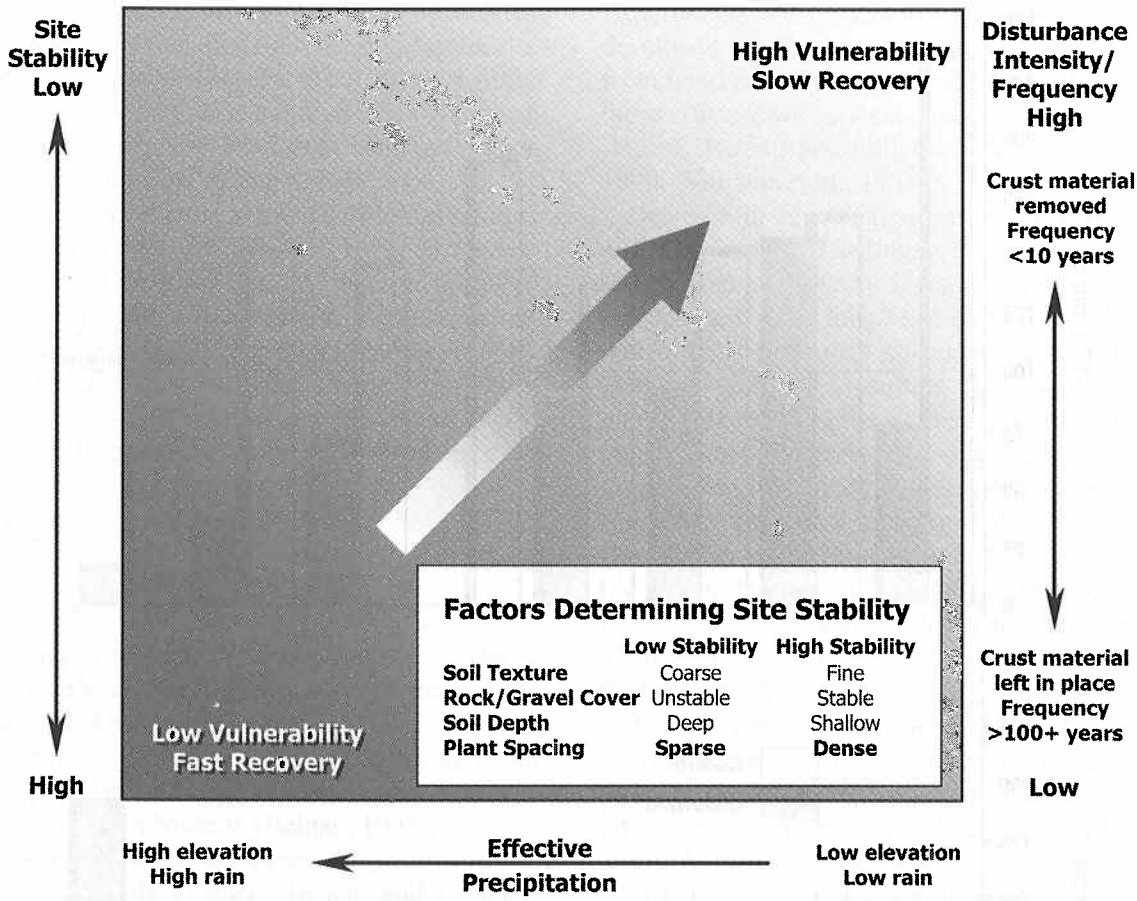

Figure 3 Vulnerability and recoverability of biological soil crusts depend on gradients of site stability, disturbance regimes, and effective precipitation. Crusts at sites with greater stability, lower disturbance frequency and/or intensity, and greater effective precipitation, will be less impacted (dark shading) than sites with lower stability, higher disturbance frequency and/or intensity, and less effective precipitation (light shading). Similarly, recovery time is faster (dark shading) in areas of low vulnerability, and slower (light shading) where vulnerability is higher.

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, eastern Africa) have a different flora than crusts in areas that evolved with low levels of disturbance from hooved animals (e.g., most hot deserts, US Colorado Plateau), and have a different response to disturbance (Mack and Thompson, 1982). Recovery from disturbance appears to parallel levels of evolutionary soil disturbance. For instance, experimentally-applied disturbances in US deserts show the Sonoran and Chihuahuan deserts have much faster recovery than disturbance in the Mojave and Colorado Plateau deserts (Belnap, unpubl. data). 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, though much research remains to be done.

Recovery rates of cyanobacterial-lichen soil crusts depend on the type and extent of disturbance, the availability of nearby inoculation material, as well as on the temperature and moisture regimes that follow disturbance events (Fig. 3). Estimates of time for visually-assessed recovery have varied from 5 to 100 years (Harper and Marble, 1988; Johansen 1993; Ladyman and Muldavin, 1996). However, it has been shown that many components of recovery can not be assessed visually (Belnap, 1993). Assuming linear recovery rates, recovery in SE Utah is estimated at 15 years for cyanobacterial biomass, 45–85 years for lichen cover, and 200 years for moss cover in scalped 0.25 m^2 plots surrounded by well-developed crusts. Lichen recovery in some plots in the Mojave Desert, assessed after 50 years, show recovery times of over 1000 years. Since recovery time is dependent on presence of nearby inoculant, larger disturbed areas will take longer to recover.

Nitrogenase activity recovery appears to be quite slow. In scalped areas on the Colorado Plateau, no nitrogenase activity was detectable after 9 years and N content of soils was still much lower when compared to adjacent control plots. In areas disturbed with 4-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 and Belnap, 1999). These data suggest that negative effects on nitrogen dynamics may persist in systems for extended, but variable, periods of time after disturbance cease.

Restoration of normal surface albedos and temperatures will depend on the restoration 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 SE Utah (Belnap, 1993). Consequently, recovery of surface albedo characteristics in severely disturbed areas could take up to 250 years for even very small areas.

***Assisted recovery*:** The use of inoculants to speed up recovery of these crusts has been reported by several authors (St. Clair et al., 1986; Tiedmann et al., 1980; Ashley and Rushforth, 1984; Belnap, 1993). Inoculation has been shown to significantly hasten crustal recovery.

CONCLUSION

Unfortunately, the increasing activities of man in desert areas are often incompatible with the well-being of biological soil crusts. 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. Unfortunately, disturbed crusts now cover vast areas as a result of ever-increasing recreational and commercial uses of these semi-arid and arid areas.

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