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4.2 Disturbance Effects

Disturbance can directly and indirectly affect many aspects of the structure and function of biological crust communities, including cover, species composition, and carbon and nitrogen fixation. The impact of a given disturbance depends on its severity, frequency, timing, and type, as well as the climatic conditions during and after it.

Methods of assessing impacts of, and recovery from, disturbance have been highly variable. Generally, measurements have been limited to visual estimates of crust cover. However, Belnap (1993) showed visual assessment can only accurately assess moss and lichen cover, and cannot be used to measure the degree of recovery of cyanobacterial biomass, soil stability, and/or physiological functioning of crustal organisms. In addition, some studies have only considered total crust cover but have not delimited the relative cover of cyanobacteria, mosses, and lichens. The relationship between total crust cover and disturbance impacts can be weak, as cyanobacterial cover generally increases, while moss and lichen cover decreases, after disturbance. This often makes total crust cover a poor measure of the dynamics of soil crust recovery. Differentiating between crustal components is also important because alteration of species composition can heavily influence the crust's ecological functioning (Eldridge 1998). Comparing recovery rates from different studies can be problematic, as factors known to control recovery rates (such as site stability and precipitation following disturbance) are often not reported. More importantly, disturbance severity is seldom quantified. Studies generally report disturbance levels as "light," "moderate," or "heavy" without any definition of these categories; thus, what is "moderate" in one study may be considered "heavy" in another. As studies cover a large range of climatic zones, soil types, and levels of disturbance, and as there has been no standard for measuring crust recovery, it is not surprising that in the literature recovery rates have ranged widely (2 to more than 3,800 years), and either appear to show no pattern or often appear contradictory (Anderson et al.1982a; Callison et al. 1985; Jeffries and Klopatek 1987; Cole 1990; Belnap 1995, 1996; Belnap and Warren 1998).

4.2.1 Disturbance Severity, Size, Frequency, and Timing

The impact of a disturbance is affected by its severity, size, frequency, and timing. While most compressional disturbances (such as from vehicles and trampling by people or animals) result in similar types of impacts, severity can vary widely depending on disturbance source. For instance, vehicles and trampling exert compressional and shear forces; however, these forces are much greater for vehicles than trampling. In addition, vehicles often turn soils over and bury crustal organisms, while trampling tends to only compress the surface. Vehicle tracks often channel water off-site and thus slow or prevent recovery (Webb and Wilshire 1983). Intensifying physical impacts (such as high-intensity, short-duration grazing) is deleterious to biological soil crust cover and its species richness (Johansen 1993). Disturbance that removes or kills crustal organisms results in greater impact and slower recovery than disturbance that leaves crushed crust material in place. As lichens and mosses are less tolerant of disturbance than cyanobacteria, frequent disturbance can maintain the biological soil crust at a low-successional stage (e.g., dominated by cyanobacteria; Fig. 4.3, Harper and Marble 1988).

Disturbance timing can affect the degree to which the cover and species richness of a biological crust is reduced. Soils have different intrinsic soil strengths that vary with moisture content (see Fig. 2.5). Soils with little tendency to form aggregates, such as sands, are more susceptible to compressional stresses when dry. Fine-textured soils or those with inorganic crusts are more vulnerable to compressional disturbance when wet (Webb and Wilshire 1983). Crust components are brittle when dry, and the connections they make between soil particles are easily crushed. Thus, compressional disturbances can severely affect the crust's ability to stabilize soils, especially in dry sandy and silty soils. On silty soils of the Great Basin, early wet season (winter) use by livestock has been shown to have less impact on crust cover and species composition than late winter or spring use. As crustal species are only metabolically active when wet and are brittle when dry, disturbance in dry seasons is generally more destructive, and organisms are less able to recover, than when disturbed in wet seasons (Harper and Marble 1988; Marble and Harper 1989). Crusts on clay soils can be an exception, as they are often more vulnerable when wet (Fig. 2.5).

4.2.2 Disturbance Effects on Species Composition

Disturbance generally results in loss of species diversity, biomass, and surface cover of biological crust components. The more severe the disturbance, the greater the loss. Thus, after severe disturbance, the resulting crust community is generally greatly simplified from multiple species of cyanobacteria, lichens, and mosses to a community often dominated by one or a few species of cyanobacteria.

4.2.2.1 Air Pollution: A few studies have addressed the impact of air pollutants on soil lichens in desert environments. No differences have been found in species composition near pollution sources when compared to control sites. It is reasoned that lichens with thalli closely appressed to the soil surface, a condition common

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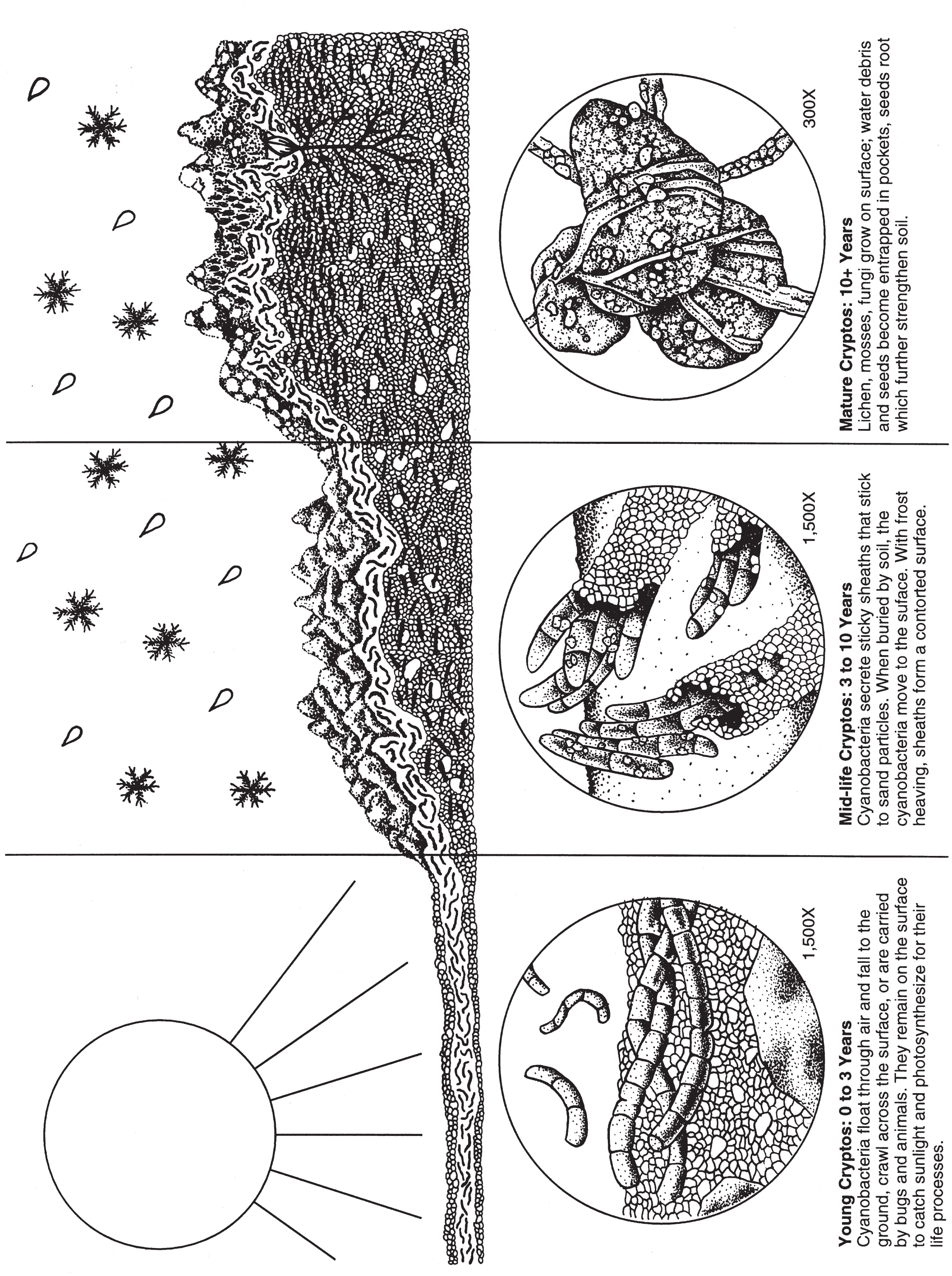
Figure 4.3 *Successional sequence for biological soil crusts. This example is for* Microcoleus vaginatus*-dominated crusts on the Colorado Plateau. Sequences in other ecoregions are similar but may involve different taxa. (Illustration by Gloria Brown)*



to most desert soil crust lichens, are less susceptible to damage by air pollutants than lichens whose tissues are more exposed to air. In addition, most desert soils are very alkaline, and thus thought to buffer acidity from pollutants (Sheridan 1979; Nash and Sommerfeld 1981).

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4.2.2.2 Oil Spills, Insecticides, and Herbicides: No known studies have directly addressed the effects of oil, oil dispersants, or insecticides on species composition of intact soil crusts. However, there has been a great deal of work on individual cyanobacteria, green algae, and mosses isolated from soil crusts. These experiments have shown that crustal species are differentially affected, depending on the compound and the species tested. Thus, exposure to these agents could potentially alter species composition of crusts (Metting 1981).

One study addressed herbicide effects on intact biological soil crusts. Direct application of two glyphosate herbicides (Roundup® and Accord®) on moss-dominated biological soil crusts had no short-term negative impact on bryophyte cover (Youtie et al. 1999). In fact, bryophyte cover decreased significantly in control plots due to litter buildup from exotic annual grasses that had invaded the site (see 4.2.2.3 below), while cover stayed the same or increased slightly in treated plots. However, repeated treatments are often required to effectively control weedy species. There is little information on the effects of repeated application or long-term effects of glyphosate and other herbicides. Therefore, caution should be used when applying these chemicals to remnant native areas supporting biological soil crusts (Youtie et al. 1989).

4.2.2.3 Annual Plant Invasion: Invasion of exotic annual plants into perennial plant communities can pose a long-term threat to biological soil crusts, as the crust-dominated interspace between perennial plants is often heavily invaded. Surveys in invaded communities show rich perennial moss/lichen communities are quickly replaced with only a few species of annual mosses and cyanobacteria (Kaltenecker 1997; Belnap and Phillips in press). The mechanism by which this shift occurs is not known, but probably results from a decrease in available soil surfaces (via increased cover of live plants and litter; Fig. 4.2, 4.4), higher cover of plant material shading the soil surface, and/or increased fire frequency (Kaltenecker 1997; Kaltenecker et al. 1999a; Youtie et al. 1999).

4.2.2.4 Fire: Biological crusts are generally killed by hot ground fires, resulting in loss of biomass and visible cover (Johansen et al. 1993). Frequent fires prevent recovery of lichens and

Figure 4.4 *Changes in the vascular plant community structure due to cheatgrass invasion.*

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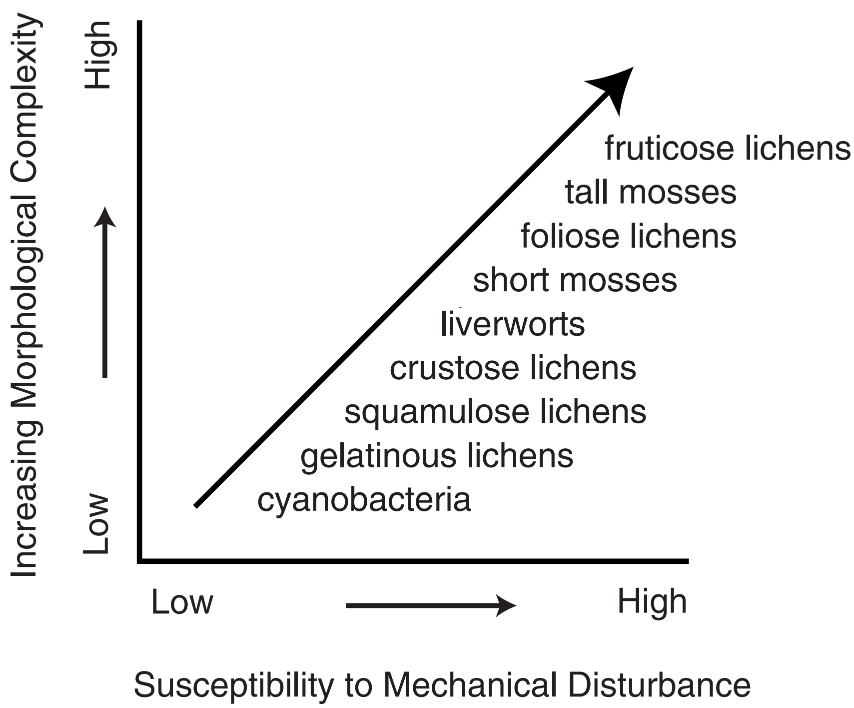
mosses, leaving only a few species of cyanobacteria (Whisenant 1990; Eldridge and Bradstock 1994). Damage to, and recovery of, biological crusts depend on the pre-fire composition and structure of the vascular plant community and on fuel distribution, fire intensity, and fire frequency. Historic fire regimes in semi-arid and arid landscapes generally left small-scale patches of unburned areas between perennial plants, and/or larger-scale patches of unburned shrubs across the landscape (Fig. 4.2). This resulted in a mosaic of successional stages of plants and biological crusts, with propagules readily available to replenish burned sites. Historic fires were also relatively infrequent, leaving time for later-successional crustal organisms to recolonize (Whisenant 1990; Peters and Bunting 1994). Many semi-arid areas are now invaded by annual weeds, and unnaturally frequent, large fires that preclude crustal species' recolonization or succession are common.

Figure 4.5 *Susceptibility of biological crusts to mechanical disturbance based on dominant morphological group.*



4.2.2.5 Mechanical Disturbance: Mechanical disturbance results from activities such as vehicle traffic (military and recreational), trampling by livestock and people, and land-clearing (such as mining). Such uses are increasing exponentially in arid and semi-arid areas of the world. Effects of mechanical disturbance are especially noticeable at sites with highly erodible soils and large topographic relief (Harper and Marble 1988).

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Over 30 studies on four continents document that livestock grazing, vehicle use (both recreational and military), and human trampling dramatically reduce lichen/moss cover and species richness of crusts. Resistance to disturbance generally decreases as the organisms become more morphologically complex (Fig. 4.5; Harper and Marble 1988; West 1990; Johansen 1993; Eldridge and Greene 1994; Ladyman and Muldavin 1996). Cyanobacteria, the most resistant to disturbance, are highly mobile and can recolonize disturbed surfaces rapidly. Lichens use a combination of adaptive thallus structures and pigments (Blum 1973; Galun et al.1982), water storage capacities, tolerance of frequent and/or prolonged inundation, and/or an ability to fix atmospheric nitrogen to increase resistance to disturbance. For example, Rogers and Lange (1971) showed that lichens *Collema coccophorum* and *Heppia lutosa* (*H. despreauxii*) were the least affected by sheep trampling around a watering point compared to other taxa. These lichens are able to fix atmospheric nitrogen and to store greater amounts of water than stratified green lichens (Galun et al. 1982). In a comparison of species inside and outside a grazing exclosure, vagrant foliose lichens *Chondropsis semiviridis* and *Xanthoparmelia convoluta*, crustose lichens *Diploschistes scruposus* and *Caloplaca* spp., and the squamulose lichens *Peltula imbricata* were associated with ungrazed sites (Table 4.1; Crisp 1975; Eldridge and Koen 1998). The gelatinous lichen *Collema coccophorum* was the most tolerant of livestock trampling (Rogers and Lange 1971; Eldridge 1996).

Most soil surface disturbance compacts soils. Compaction influences soil water and nutrient-holding capacity, which can lead to changes in soil crust community species composition. These subtle compositional changes often occur before cover changes are apparent (Eldridge 1996).

4.2.2.6 Burial: Crust disruption often destabilizes underlying soils, leaving adjacent crusts vulnerable to burial by wind- and water-moved sediments. When soils are moist, the large filamentous cyanobacteria can respond to burial by moving up to 5 mm every 24 hours. When dry, these organisms are not able to move. Burial kills non-mobile photosynthetic components of the crust, including mosses, lichens, green algae, and smaller cyano-bacteria (Campbell 1979). Therefore, burial generally results in a greatly simplified crustal community.

4.2.3 Disturbance Effects on Nutrient Inputs and Retention

4.2.3.1 Carbon Fixation: Cyanobacterial crusts near coal-fired power plants have greater chlorophyll *a* per unit soil surface area

Table 4.1 *Percent frequency of biological soil crust organisms on loamy and sandy soils inside and outside the exclosure at Koonamore Vegetation Reserve, South Australia, in May 1972. Adapted from Crisp (1975).*

		LOAMY SOIL		SANDY SOIL		
Species	Morphological Group	Exclosed	Grazed	Exclosed	Grazed	*p*
Lichens						
Acarospora smaragdula	crustose	2.4	0.5	7.6	2.2	n.s.
Aspicilia calcarea	crustose	39.4	20.6	26	26.2	*
Aspicilia calcarea	fruticose	13.6	1.1	18.2	2.4	*
Chondropsis semiviridis	foliose	0.08	0	0.1	0	n.s.
Collema coccophorum	gelatinous	81.4	63.6	21	0	*
Diploschistes scruposus	crustose	0.6	0	2.4	35.6	n.s.
Fulgensia subbracteata	crustose	20	5	25.2	14.2	*
Psora decipiens	squamulose	38.7	15.1	33.8	24.6	*
Psora crystallifera	squamulose	11.4	0.7	13.8	2	*
Toninia sedifolia	squamulose	13.1	3.8	13.8	7.6	*
Xanthoparmelia convulata	foliose	0.04	0	0.1	0	n.s.
Liverworts						
Riccia lamellosa	liverwort	4.2	0.4	8.2	1.2	*

* *Indicates significant effect of exclosure at $p<0.10$; n.s. = effect of excosure was not significant.*

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than crusts away from the plant, implying higher levels of carbon fixation. This is partially a result of fertilization by nitrogen and sulfur compounds from effluents (Sheridan 1979; Belnap 1991). Photosynthesis-inhibiting herbicides show significant impact on *Nostoc* growth and nitrogen fixation (Gadkari 1988). In general, herbicides inhibit growth and reproduction in culture (Metting 1981). However, effects appear to be more pronounced in the laboratory than the field, and may be transitory (Prasad et al. 1984).

Alteration in crust species composition will affect total carbon fixation, as lichens and mosses fix more carbon per unit soil surface area than cyanobacteria (Phillips and Belnap 1998). Because much of the carbon fixed by crustal organisms is released into the surrounding soils (Lewin 1956), crust cover reduction is expected to reduce soil carbon available for microbial populations that are often carbon limited. This, in turn, may affect decomposition rates of plant litter, and thus, levels of nutrients available to vascular plants (Paul and Clark 1996).

Table 4.2 *Reduction of nitrogenase activity for new and older disturbances on silty soils of the Dugway Proving Ground, Utah. All disturbance types resulted in material left on site except "Scalp," which removed the top 1 cm of crust.*

Age of Disturbance	Type of Disturbance	Percent Reduction in Nitrogenase Activity
New	Vehicle	68
New	Bike	79
New	Foot	62
6 months	Vehicle	100
9 months	Tank	83
9 months	Scalp	95
9 months	Rake	81

4.2.3.2 Nitrogen Inputs: Power plant effluents have been shown to decrease nitrogen fixation in *Collema* and *Microcoleus*/*Nostoc*/*Scytonema*-dominated crusts (Sheridan 1979; Belnap 1991). Atmospheric nitrogen deposition may offset reduced nitrogen inputs from crusts; alternatively, anthropogenic nitrogen deposition may aggravate nitrogen loss through increased ammonia volatilization and denitrification. In addition, biological soil crusts release ammonia in the soils, while anthropogenic nitrogen deposition contains large amounts of nitrate (Garcia-Pichel, unpublished data). Microbial and vascular plant species differentially use ammonia and nitrate; thus, deposition of additional nitrates may alter the dynamics of both soil and plant communities (Binkley et al. 1997).

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Free-living or lichenized *Nostoc* show stimulation of nitrogen fixation at low concentrations of, or short exposure to, arsenic, nickel, lead, palladium, and zinc. However, longer-term exposure to cadmium, lead, and zinc inhibits fixation (Henriksson and DaSilva 1978). Exposure to crude oil and oil dispersants decreases nitrogen fixation in *Nostoc* (Marowitch et al. 1988). Nitrogen fixation is significantly inhibited in *Nostoc* by many insecticides, herbicides, and phenolic compounds tested (Bhunia et al. 1991; Megharaj et al. 1988).

Mechanical disturbance can result in large decreases in soil nitrogen through a combination of reduced input and elevated losses (Peterjohn and Schlesinger 1990; Evans and Belnap 1999). In all soils tested, disturbance by vehicles, human foot traffic, mountain bikes, and raking immediately reduces nitrogen input from crusts (25 to 40% on silty soils; 76 to 89% on sandy soils). Over time, nitrogenase activity can drop by 80 to 100% relative to controls, due to subsequent death of buried material (Table 4.2; Belnap et al. 1994; Belnap 1995,1996).

Species composition changes also affect nitrogen inputs, as cyanolichens (such as *Collema*) fix an order of magnitude more nitrogen than the equivalent soil surface area of cyanobacteria. Thus, the shift from a lichen crust to a cyanobacterial crust can result in less nitrogen entering the ecosystem, as has been shown in multiple studies. Jeffries et al. (1992) showed that heavy grazing reduced nitrogen fixation in sandy soils by 95%. In silty loam soil, Terry and Burns (1987) showed a 64% reduction of nitrogen fixation in burned areas, 85 to 94% reduction in grazed areas, and 99% reduction in a tilled area. *Collema* cover was reduced 50 to 80% in grazed areas relative to adjacent ungrazed areas (Brotherson et al. 1983; Johansen and St. Clair 1986). Expected nitrogen inputs would be reduced accordingly. Evans and Belnap (1999) showed nitrogen fixation in an area released from grazing 25 years was still 2.5 times less than an adjacent, never-grazed area due to reduction in *Collema* cover.

Decreased nitrogen inputs from crusts can have long-term impacts on soil nitrogen levels. Jeffries (1989) found 50% less nitrogen in grazed soils compared to adjacent ungrazed soils. Evans and Belnap (1999) found a 42% decrease in soil nitrogen and 34% decrease in plant tissue nitrogen when comparing a previously grazed (released 30 years previous to the study) site to an adjacent ungrazed area. In the same area, stable nitrogen isotopes showed that both soil and plants in the grazed area contained less newly fixed nitrogen than the ungrazed area, and nitrogen mineralization potential decreased almost 80% (Rimer and Evans 1997). This has large implications for ecosystems that are dependent on biological crusts for nitrogen inputs, such as those on the Colorado Plateau (Evans and Ehleringer 1993).