

# What Makes the Desert Bloom? Contribution of Dust and Crusts to Soil Fertility on the Colorado Plateau

Jayne Belnap  
Richard Reynolds  
Marith Reheis  
Susan L. Phillips

**Abstract**—Eolian dust (windblown silt and clay) and biological soil crusts are both important to ecosystem functioning of arid lands. Dust furnishes essential nutrients, influences hydrology, contributes to soil formation, and renders surfaces vulnerable to erosion. Biological soil crusts contribute directly to soil fertility by fixing carbon and nitrogen, and indirectly by trapping newly-deposited dust and stabilizing already-present soil. Results from crust-stabilized, unconsolidated sandy sediments on prominent rock exposures and grasslands show dust inputs have significantly increased all bio-essential nutrients in soils of SE Utah, including P, K, Mg, Na, and Ca. As plants can be P and K-limited in these soils, dust may be essential for plant growth. Evidence for eolian dust comes from magnetic, chemical, and mineralogic properties of the soils that contrast greatly with those of local bedrock. For example, magnetite, which formed originally in igneous rocks, is common in soils but absent in the local sedimentary bedrock. In view of the regional geology, particle-size distribution of soils, and patterns of properties, the magnetite represents long-distance transport of eolian dust. Dust in the biological soil crusts, when compared to underlying sediment, shows higher magnetite, Zr, and Zr/Ti, suggesting that dust sources have changed over the past few decades. It is suggested that recent human disturbance in areas surrounding the Colorado Plateau may be responsible for this change in dust source. Because most of the fertility in these soils is due to dust input, it is of concern to land managers when soil loss via wind and water erosion exceeds this input. Ever-increasing use of these desert landscapes by recreation, military and agricultural activities generally destroys the biological soil crusts that are critical for nitrogen, carbon, and soil stability. Thus, increased erosion, and reduced dust retention, may be a result of these activities.

## Introduction

The source of desert soil fertility has long been a question for many scientists. Weathering of soils from parent material in this region is generally very slow, taking 5,000–

10,000 years (Dregne 1983). Rainfall is low, and thus nutrient input via wet deposition is limited. Few nitrogen-fixing plants are found in these regions (Wullstein 1989), and sparse vascular vegetation limits carbon inputs. Eolian dust has recently been demonstrated to be an important source of nutrients for a wide range of ecosystems (Chadwick and others 1999). Eolian dust has been identified, primarily on the basis of chemical, mineralogic, and textural properties, in several types of surficial deposits in arid environments (McFadden and McAuliffe 1997; Reheis and others 1995). However, because such dust is wind-transported, it also renders the soils and sediment in which it resides vulnerable to subsequent wind erosion.

Biological soil crusts can contribute to soil fertility in deserts in many ways. They have high C fixation rates, and significant amounts of C can be fixed during seasons when soils remain wet for extended periods (Beymer and Klopatek 1991; Belnap and Lange 2001). Much of the C fixed by crust organisms is used for extracellular polysaccharide production or leaked into surrounding soils. Because desert microbial populations are generally C-limited (Follett 2001), soil crusts may be critical in sustaining decomposition in these soils. Biological soil crusts influence soil temperature, moisture levels, aeration and porosity (Harper and Marble 1988; Belnap 1995; George and others, unpublished data). Soil crusts influence vascular plant productivity by being a dominant source of N (Evans and Ehleringer 1993), mostly due to N fixation by the soil lichen *Collema* (Belnap 1996). Cyanobacteria secrete powerful metal chelators and other substances that maintain nutrients in plant-available forms despite the high pH of desert soils (Belnap and Lange 2001). Crusts are also critical for soil stability and aggregate formation (Belnap and Gardner 1993; Williams and others 1995a; Belnap and Gillette 1997, 1998).

Most lands in the Western United States, once isolated and seldom visited, have undergone escalating use since the late 1800s. Historically, most of the land use was limited to livestock grazing in areas where free surface water was available; more recently, substantial increases in recreation, military activities, and agriculture have expanded human use (both spatially and temporally) of arid and semiarid regions. The current combination of land use is leading to unprecedented levels of surface disturbance on many of these lands. Generally, soil surface disturbance and/or the invasion of annual grasses results in the loss of lichens and mosses, leaving cyanobacterial-dominated crusts (Belnap 1995; Harper and Marble 1988), which is expected

---

In: McArthur, E. Durant; Fairbanks, Daniel J., comps. 2001. Shrubland ecosystem genetics and biodiversity: proceedings; 2000 June 13–15; Provo, UT. Proc. RMRS-P-21. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Jayne Belnap is an Ecologist and Susan L. Phillips a Biologist, Biological Research Division, United States Geological Service, 2290 Resource Blvd., Moab, UT 84532. Richard Reynolds and Marith Reheis are Geologists, United States Geological Service, MS 980, Denver, CO 80225. jayne\_belnap@usgs.gov

to alter many aspects of nutrient cycling and soil stabilization (Belnap and Gillette 1998).

This study documents the presence of eolian silt in surficial sediment on part of the Colorado Plateau. We show how the biological soil crusts in this region enhance and maintain soil fertility through C and N fixation, dust trapping, and soil stabilization. We then discuss how soil surface disturbance alters this situation.

## Sampling and Methods

### Dust Inputs

Sediment was collected from potholes on slickrock, mesa tops, and grassland settings. Bedrock consisted of either red sandstone, brown to gray sandstone, or limestone. We analyzed sediment both within the biological soil crust and below to depths of 5 cm. We used a combination of reflected-light petrographic and magnetic techniques to determine the amounts, types, and origins of magnetic minerals. Magnetic property measurements included: (1) magnetic susceptibility (MS), a measure of the amount of all magnetic material but mainly ferromagnetic minerals (such as magnetite) when present; (2) frequency-dependent MS (FDMS; from measurements at 600 Hz and 6000 Hz), a measure of the amount of ultrafine grained magnetite, or magnetite-like maghemite, commonly attributed to pedogenic origins; (3) "hard" isothermal remanent magnetization (HIRM), a measure of the amount of hematite; and (4) the S parameter [the ratio of backfield isothermal remanent magnetization (IRM) at 0.3 Tesla (T) and IRM at 1.2 T], in this setting an indication of relative amounts of magnetite and hematite.

Trace and minor-element chemistry was determined using energy-dispersive X-ray fluorescence (XRF). Changes in Fe (commonly mobilized via primary mineral alteration), Ti (chemically immobile and associated with certain magnetic Fe oxide minerals), and Zr (also chemically immobile) are especially useful in evaluating potential post-depositional alteration of magnetite and possible shifts in sediment sources.

### Biological Crust Inputs and Soil Retention

The site of this study was the Needles District of Canyonlands National Park, located 125 km south of Moab, UT. Annual rainfall averages 215 mm, with approximately 35 percent falling as summer monsoons. To estimate N inputs, we used data from a datalogger that has continuously recorded amount and time of rainfall, and air and soil temperatures, since April 1998. Using this data, we grouped precipitation events into six temperature categories (−4 to 4 °C, 5–8 °C, 9–17 °C, 18–23 °C, 24–27 °C, and 28–35 °C). We used a combination of manual dry-down curves and TDR results (that measured soil moisture in the top 1 cm of soil) to determine how long 1 mm of precipitation at different seasons and different air temperatures lasted in study soils for each temperature category. We then multiplied the precipitation received at a given temperature by the time soils took to dry at that temperature to estimate the number of hours soils are wet. We used a combination of laboratory and field-obtained N fixation values for each of the temperatures and multiplied this by the number of hours soils were

wet at each temperature (Belnap 2001a). Because crusts are able to fix 4–6 hours during the dark, 50 percent of the nighttime hours were considered available for N fixation.

Studies of N fixation utilized the acetylene reduction technique, which requires conversion to absolute N values using  $^{15}\text{N}_2$  calibration. This was done for soil *Nostoc* from the Moab, UT area by Phillips and Belnap (unpublished data); a conversion ratio of 0.31 was obtained, and is used for estimates of N inputs. A similar value for the same organism was measured by Liengen (1999) from arctic soils. It should be noted that this low conversion ratio gives much higher values for N inputs than is commonly reported in the literature. Most of these studies did not do the necessary experiments to find the appropriate conversion ratio, and so relied on the theoretical ratio of  $3\text{C}_2\text{H}_4:1\text{N}$ . However Liengen showed that this value is only accurate for cultured cyanobacteria and that for field-collected organisms, a much lower conversion ratio should be used.

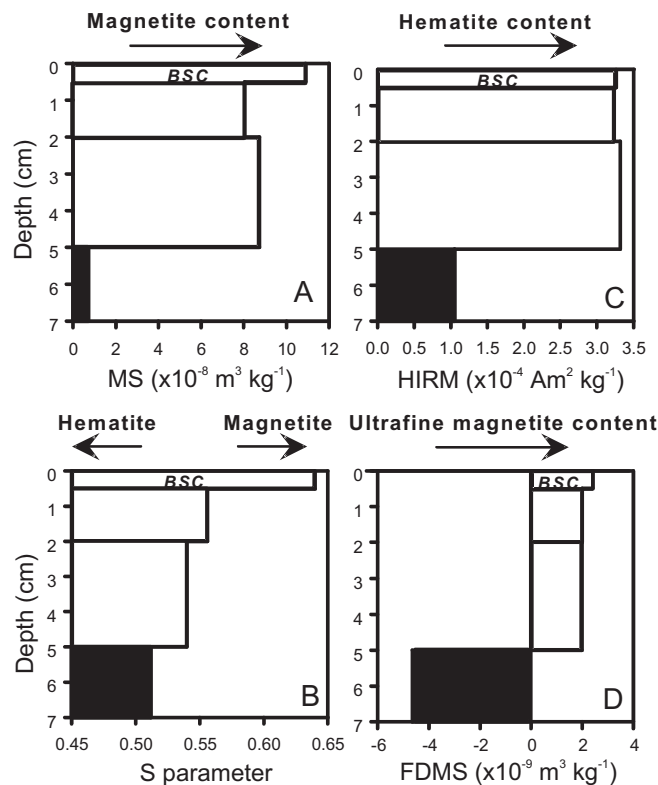
Data from studies previously published (Belnap and Gillette 1997, 1998) and unpublished (Belnap and others) were used to estimate accelerated soil losses due to conversion of lichen crusts to cyanobacterial crusts. This data was also used to estimate losses from wind and water immediately following surface disturbance on sandy soils.

## Results and Discussion

### Dust Inputs

The MS of the host sedimentary rock was very low at all sites tested (11 sites,  $2.4 \times 10^{-10}$  to  $1.1 \times 10^{-8}$  m<sup>3</sup>/kg). In contrast, MS values of the surficial sediment were between one and three orders of magnitude greater than the corresponding site bedrock (site averages,  $3.5 \times 10^{-8}$  to  $1.5 \times 10^{-7}$  m<sup>3</sup>/kg), with MS at most sites highest in the biological soil crust (fig. 1a). The S parameter values indicate that there is a much greater concentration of magnetite relative to hematite in the soil crusts than below the surface (fig. 1b). While such patterns in MS and S parameters suggest the presence of eolian dust, they are not sufficient proof, as enhanced MS in upland soils and sediments (away from alluvial input) may result from other factors such as pedogenic production of ultrafine grained iron oxide minerals, concentration of residual minerals, and bacterially mediated reactions (Dearing and others 1996). Moreover, diagenetic or pedogenic alteration of magnetite at depth may produce a pattern of highest MS and S values at the surface.

However, the eolian origin of the observed MS enhancement is supported by other magnetic properties and geochemical results seen in these soils. Hematite content was much greater in surficial sediment than in the underlying bedrock, even including hematite-bearing redbeds (fig. 1c), as would be expected for eolian addition of hematite with magnetite. Moreover, FDMS values were small, implying pedogenic iron oxide contributed only a small amount (fig. 1d). Large differences in elemental content were seen between the surficial sediment and bedrock (fig. 2). For example, surficial sediment had higher average contents of Fe (≈1 wt. percent), Ti (≈0.15 wt. percent), and Zr (≥200 ppm) than local bedrock (Fe, 0.7 wt. percent; Ti, 0.08 wt. percent; Zr < 100 ppm). Nearly constant Fe/Ti values (fig. 2), along with textural evidence, indicate a lack of magnetite destruction below the

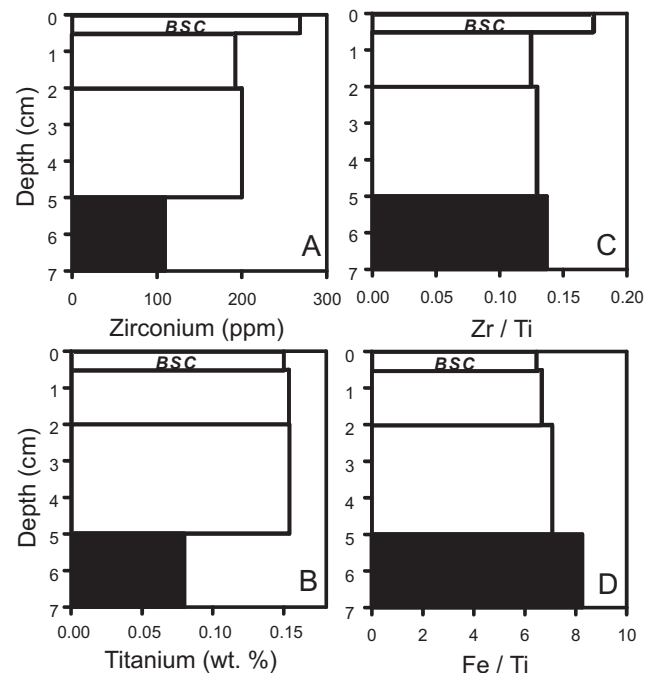


**Figure 1**—Plots of depth versus magnetic properties, as averages from sandstone sites. (A) magnetic susceptibility; (B) S parameter; (C) “hard” isothermal remanent magnetization; (D) frequency-dependent magnetic susceptibility. Uppermost sample represent biologic soil crust values. Solid pattern represents bedrock values.

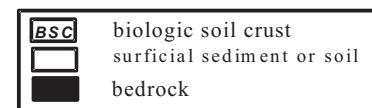
biological soil crust. The overall thinness of layers, magnetic mineralogy, and resistant underlying bedrock preclude magnetic and elemental enrichment of the surficial layers by chemical weathering and residual accumulation.

The definitive test for the origin of magnetite and hematite in this setting is petrographic comparison of grains extracted from the sediment and bedrock. In these sediments, magnetic minerals include mainly silt-sized (5–60  $\mu\text{m}$ ) magnetite and associated oxides, such as ilmenite, hematite, and varieties of other Fe-Ti oxides that result from high-temperature oxidation of magnetite and ilmenite. These associated minerals, and the internal textures of magnetite with ilmenite lamellae, indicate that the magnetic Fe-Ti oxide minerals originated in igneous rocks. Such magnetite and associated minerals are absent in sandstone at the sampling sites, although limestone may contain only very rare magnetite or maghemite formed via oxidation of pyrite.

Combined, this evidence suggests that a major component of the surficial deposits must be eolian to account for their high content of strongly magnetic minerals, which are absent or sparse in the underlying bedrock. Moreover, fly-ash magnetite, produced via coal combustion in power plants, is observed in the biological soil crust, but has not been found in the underlying surficial sediment. Silt plus clay content typically ranges between 20 and 50 percent, implying a similar range in eolian dust content.



**Figure 2**—Plots of depth versus zirconium. (A) Titanium; (B) Zr/Ti; (C) Fe/Ti; (D) Patterns as in figure 1.



The biological soil crust, which stabilizes the surficial material, is a natural dust trap and appears to have documented a change in dust source over the past several decades. Relative to underlying sediment, this crust layer has higher magnetite (both absolute and relative to hematite), higher Zr/Ti, and nearly constant Fe/Ti (fig. 2). These shifts in magnetic and chemical properties are consistent with increased eolian input from desert regions (much underlain by granitic and rhyolitic rocks) west and southwest of the Colorado Plateau. The shifts may also represent more input from the mildly alkaline intrusive rocks that form the Henry, Abajo, and La Sal Mountains of the central Colorado Plateau. Either way, the magnetic and chemical shifts recorded in the biological soil crusts may reflect recent, intensive human disturbance of arid lands.

In light of the above evidence, the contribution of dust to soil fertility in this region is striking. As can be seen in figure 2, the deposition of dust has enhanced most plant-essential nutrients in these soils. Enriched nutrients include phosphorus (2x), potassium (1.2x), magnesium (4.4x), sodium (3.8x), calcium (10.5x, except in calcite-cemented sandstone sites), iron (1.6x), copper (1.4x), manganese (2.1x) and molybdenum (13x). Amounts and distribution patterns of enrichment are similar between sites, and magnesium, sodium, calcium, copper and zinc are consistently higher in the biological soil crust relative to underlying sediment.

## Biological Soil Crust Inputs and Soil Retention

Biological soil crusts have long been known to fix carbon and nitrogen, and estimates of their annual contributions have been made by multiple authors (Jeffries and others 1993; Belnap 2001a; Evans and Lange 2001). Beymer and Klopatek (1991) estimated potential annual C contribution of lichen soil crusts to be 12–37 gC m<sup>-2</sup> year<sup>-1</sup>. Lange and others (1994) estimated lichen crusts in Namibia to contribute 32 gC m<sup>-2</sup> year<sup>-1</sup> lower range. Lower rates have been reported for cyanobacteria-dominated crusts (0.4–2.3 gC m<sup>-2</sup> year<sup>-1</sup>; Garcia-Pichel and Belnap 1996). Because short wet-dry cycles in summer lead to C deficits due to drying of soils before net photosynthesis can be reached (Jeffries and others 1993), most C inputs occur during the cooler seasons.

Less is known about N fixation in this region. Our recording datalogger showed that rainfall events were surprisingly common in SE Utah during the measurement period. Between June 15, 1998, and September 15, 2000, 129 soil-wetting events were recorded (intermittent rains during consecutive days were considered one event if the soils did not dry between rain showers), an average of 4.8 events each month. The number of rain events in any given season, and the amount of rainfall, was highly variable, and within the 2-year measurement period, showed no obvious pattern among seasons (table 1). The number of rain events at night relative to those occurring during the day was also highly variable. Combining these results with average N fixation rates at a given temperature, we were able to estimate seasonal and annual N inputs for 2 measured years: 41 kgN/ha/yr for lichen crusts, and up to 13 kgN/ha/yr for cyanobacterial crusts (depending on biomass of a given crust). This represents a major input of N to soils of these ecosystems.

All crust components secrete extracellular C within minutes to a few days of C acquisition, and the presence of soil-crust organisms can increase soil polysaccharides and total carbon by up to 300 percent (Rao and Burns 1990; Rogers and Burns 1994), benefitting surrounding heterotrophic microbes which are often carbon limited. In addition, this input of carbon can lower soil C:N ratios, thus increasing decomposition rates (Kleiner and Harper 1972).

**Table 1**—Amount of precipitation (mm) by time of day and season for 1998–2000. Spring = March 16–June 15; Summer = June 16–September 15; Fall = September 16–December 15; Winter = December 16–March 15.

	Day	Night	Total
Spring 1999	129	318	447
Spring 2000	162	19	181
Summer 1998	40	49	89
Summer 1999	121	61	183
Summer 2000	8	10	18
Fall 1998	308	271	579
Fall 1999	128	70	199
Winter 1998	183	56	239
Winter 1999	206	146	352

Up to 70 percent of the nitrogen fixed by cyanobacteria and cyanolichens is released immediately into the surrounding soil environment, and is available to associated organisms including vascular plants, mosses, fungi, and other microbes (Belnap 2001a). Multiple studies have reported that the presence of soil crusts increases surrounding soil N by up to 200 percent (Shields and Durrell 1964; Rogers and Burns 1994; DeFalco 1995; Harper and Belnap 2001), and stable isotopes show soil crusts can be the dominant source of N for desert soils and plants (Evans and Ehleringer 1993; Evans and Belnap 1999).

Crusts affect soil nutrients in many other ways as well. Microbial exopolymers both add carbon to soils as well as create a mosaic of polyfunctional metal binding sites that bind both cations and anions (Greene and Darnall 1990), thus preventing them from leaching from sandy soils. Most of these polymers also concentrate plant-essential nutrients such as Na, K, Mg, Ca, Mn, Fe, Ni, Cu, and Zn (Lange 1976; Geesey and Jang 1990). As they are adsorbed to the extracellular sheath, and are not absorbed by the cells, they remain available to plants (Geesey and Jang 1990). Cyanobacteria, green algae, fungi, lichens, and bacteria also secrete powerful metal chelators such as siderochromes (Lange 1974; McLean and Beveridge 1990; Schelske 1962) that can maintain metals in bio-available forms, and can concentrate essential trace metals found at exceedingly low ambient concentrations (Paerl 1988). Cyanobacteria secrete peptide nitrogen and riboflavin which, together with siderochromes, keep P, Cu, Zn, Ni, and Fe plant-available. These secreted chelators are water soluble, and capable of being translocated in soil and water. Consequently, chelated compounds are made available to associated plants or microbes (Bose and others 1971; Lange 1974; Geesey and Jang 1990; Gadd 1990a). Cyanobacteria also secrete glycollate, which stimulates the uptake of P in cyanobacteria (Fogg 1966), as well as various vitamins such as B<sub>12</sub>, auxin-like substances, and other substances that promote growth and cell division in plant and animal tissue (Fogg 1966; Venkataraman and Neelakantan 1967). Biological crusts are also important in trapping dust and stabilizing soils. Studies have shown that the top few mm of soil contain a much higher percentage of soil fine particles than underlying soils, indicating that crusts trap and entrain falling dust particles (Danin and Ganor 1991; Verrecchia and others 1995). Because dust can be a critical component of soil fertility, as discussed above, this capture and retention is an essential part of soil building in deserts.

Over 30 studies worldwide have shown that biological soil crusts reduce soil loss by wind and water (Belnap 2001b; Warren 2001a,b). Cyanobacterial and microfungi polysaccharides entrap and bind soil particles together, creating soil aggregates, which are then further linked together into larger aggregates (Belnap and Gardner 1993). These larger, linked aggregates require greater wind and water velocity to move than single soil particles (Gillette and others 1980; Marticorena and others 1997). Resistance to erosion increases with biological crust development (Belnap and Gillette 1998), with cyanobacterial crusts showing the least, and lichen crusts showing the greatest, resistance to erosive forces. In most cases, lichen crusts can withstand winds well above those recorded at field sites, and so offer complete protection from wind erosion, even in coarse soils (Leys

1990; Williams and others 1995a; Belnap and Gillette 1997, 1998; Leys and Eldridge 1998). Exhaustive field and lab studies show that increasing crust cover and/or development also significantly reduces sediment loss via water erosion (Booth 1941; Loope and Gifford 1972; Rushforth and Brotherson 1982; Brotherson and Rushforth 1983; Harper and St. Clair 1985; Williams and others 1995b).

## Effects of Soil Surface Disturbance on Soil Fertility

Overall, disturbance generally results in loss of species diversity, biomass, and surface cover of cyanobacteria, lichens, and mosses. The more severe the disturbance, the greater the loss. Thus, after severe disturbance, the resulting crust community is greatly simplified from a community with multiple species of cyanobacteria, lichens, and mosses to a community often dominated by one or a few species of cyanobacteria. A shift from a lichen to a cyanobacterial-dominated crust will reduce C inputs, as cyanobacteria fix less C than lichens and mosses per unit soil surface area (Phillips and Belnap 1998). As discussed above, much of this C is released into the surrounding soils (Lewin 1956); thus, reduced C fixation is expected to reduce soil C available for microbial populations, decomposition rates and soil nutrient levels (Paul and Clark 1996).

Soil surface disturbance and/or a shift from a lichen to a cyanobacterial-dominated crust also decreases N inputs. Our annual input estimates are four times higher for lichen crusts than cyanobacterial crusts. Laboratory and field studies have consistently shown that lichen crusts have higher N fixation rates than cyanobacterial crusts (Jeffries and others 1993 a,b; Belnap and others 1994; Belnap 1995, 1996; Belnap 2001a). Multiple studies have shown less N input from crusts following disturbance. Vehicles, human foot traffic, mountain bikes, and raking reduced N input from crusts 25-89 percent, with a drop of 80-100 percent over time due to subsequent death of buried material (Belnap and others 1994; Belnap 1995, 1996). Grazing reduces N inputs by 50-95 percent (Brotherson and others 1983; Johansen and St. Clair 1986; Jeffries and others 1992; Terry and Burns 1987). Burning can reduce N inputs by 64 percent and tilling by 99 percent (Terry and Burns 1987). Evans and Belnap (1999) showed N fixation was still 2.5 times less than an adjacent, never-grazed area 30 years after grazing had ceased. Decreased N inputs from crusts can have long-term impacts on soil N levels. On the Colorado Plateau, Jeffries (1989) found 50 percent less N in non-crusts compared to adjacent crusted soils. Evans and Belnap (1999) found a 42 percent decrease in soil N and a 34 percent decrease in plant tissue N when comparing a cyanobacterial-moss dominated crust (previously grazed) to an adjacent lichen-dominated (ungrazed) area. In the same area, stable N isotopes showed that both soil and plants in the lichen-dominated area contained less newly fixed N than the cyanobacteria-moss dominated area. This has large implications for ecosystems that are dependent on soil crusts for N inputs, such as found on the Colorado Plateau (Evans and Ehleringer 1993).

As noted above, disturbance also results in increased soil loss (and thus reduced fertility) via wind and water erosion, as compressional disturbance breaks apart soil aggregates

formed by the polysaccharide connections. Recent studies have shown that disturbance of crusted soils increases sediment loss by up to 300 percent (Belnap and Gillette 1997, 1998; Belnap, unpublished data). After disturbance and once a soil is stabilized by cyanobacteria, less erosion is expected compared to the bare soils; however, cyanobacteria are less able to protect soils from erosion than lichens or mosses, and thus accelerated losses are expected until the moss and lichen components recolonize the site. In addition, burial of nearby biological soil crusts from wind-blown sediments generally means death for the photosynthetic components of the soil crusts, further reducing fertility and stability of these soils. Most of the soil photosynthetic productivity and nitrogen fixation in desert soils is concentrated within 3 mm of the surface (Garcia-Pichel and Belnap 1996).

## Conclusion

Accelerated soil loss is of great concern to land managers worldwide. Based on this study, soil fertility on the Colorado Plateau is dependent on the retention of atmospherically deposited dust and N inputs from lichen-dominated biological soil crusts. Well-developed biological soil crusts reduce erosional losses. In addition, the crusts contribute substantial amounts of C and N. Current dust deposition rates in the Colorado Plateau region are low, and when soils are disturbed, loss rates may exceed deposition (Gillette and others 1980; Offer and others 1992; Belnap and Gillette 1997, 1998; Reynolds and others 1998). Biological soil crusts are easily disturbed by soil surface disturbances, and recovery is very slow in this region (Belnap 1993). Thus, it is recommended that soil surface disturbance be kept to a minimum to maintain long-term soil fertility and productivity.

## References

- Belnap, J. 1993. Recovery rates of cryptobiotic crusts: inoculant use and assessment methods. *Great Basin Naturalist*. 53(1): 89-95.
- Belnap, J. 1995. Surface disturbances: their role in accelerating desertification. *Environmental Monitoring and Assessment*. 37:39-57.
- Belnap, J. 1996. Soil surface disturbances in cold deserts: effects on nitrogenase activity in cyanobacterial-lichen soil crusts. *Biology and Fertility of Soils*. 23:362-367.
- Belnap, J. 2001a. Factors influencing nitrogen fixation and nitrogen release in biological soil crusts. In: Belnap, J. and O.L. Lange, eds. *Biological soil crusts: structure, function, and management*. Ecological Studies Series 150. Berlin: Springer-Verlag. In press.
- Belnap, J. 2001b. Biological soil crusts and wind erosion. In: Belnap, J. and O.L. Lange, eds. *Biological soil crusts: structure, function, and management*. Ecological Studies Series 150. Berlin: Springer-Verlag. In press.
- Belnap, J.; Gardner, J.S. 1993. Soil microstructure in soils of the Colorado Plateau: the role of the cyanobacterium *Microcoleus vaginatus*. *Great Basin Naturalist*. 53(1):40-47.
- Belnap, J.; Gillette, D.A. 1997. Disturbance of biological soil crusts: impacts on potential wind erodibility of sandy desert soils in southeastern Utah. *Land Degradation and Development*. 8:355-362.
- Belnap, J.; Gillette, D.A. 1998. Vulnerability of desert biological soil crusts to wind erosion: the influences of crust development, soil texture, and disturbance. *Journal of Arid Environments*. 39:133-142.
- Belnap, J.; Harper, K.T.; Warren, S.D. 1994. Surface disturbance of cryptobiotic soil crusts: nitrogenase activity, chlorophyll content

- and chlorophyll degradation. *Arid Soil Research and Rehabilitation*. 8:1–8.
- Belnap, J.; Lange, O.L., eds. 2001. *Biological soil crusts: structure, function, and management*. Ecological Studies Series 150. Berlin: Springer-Verlag. In press.
- Beymer, R.J.; Klopatek, J.M. 1991. Potential contribution of carbon by microphytic crusts in pinyon-juniper woodlands. *Arid Soil Research and Rehabilitation*. 5:187–198.
- Booth, W.E. 1941. Algae as pioneers in plant succession and their importance in erosion control. *Ecology*. 22(1):38–46.
- Bose, P.; Nagpal, U.S.; Venkataraman, G.S.; Goyal, S.K. 1971. Solubilization of tricalcium phosphate by blue-green algae. *Current Science*. 7:165–166.
- Brotherson, J.D.; Rushforth, S.R. 1983. Influence of cryptogamic crusts on moisture relationships of soils in Navajo National Monument, Arizona. *Great Basin Naturalist*. 43(1):73–78.
- Brotherson, J.D.; Rushforth, S.R.; Johansen, J.R. 1983. Effects of long-term grazing on cryptogam crust cover in Navajo National Monument, Arizona. *Journal of Range Management*. 36(5):579–581.
- Chadwick, O.A.; Derry, L.A.; Vitousek, P.M.; Huebert, B.J.; Hedin, L.O. 1999. Changing sources of nutrients during four million years of ecosystem development. *Nature*. 397:491–497.
- Danin, A.; Ganor, E. 1991. Trapping of airborne dust by mosses in the Negev Desert, Israel. *Earth Surface Processes and Landforms*. 16:153–162.
- Dearing, J.A.; Hay, K.L.; Baban, M.J.; Huddleston, A.S.; Wellington, E.M.; Loveland, P.J. 1996. Magnetic susceptibility of soil: an evaluation of conflicting theories using a national data set. *Geophysical Journal International*. 127:728–734.
- DeFalco, L.A. 1995. Influence of cryptobiotic crusts on winter annuals and foraging movements of the desert tortoise. MS Thesis. Fort Collins: Colorado State University: 48 p.
- Dregne, H.E. 1983. Physical effects of off-road vehicle use. In: Webb, R.H. and H.G. Wilshire, eds. *Environmental effects of off-road vehicles: impacts and management in arid regions*. New York: Springer-Verlag: 15–30.
- Evans, R.D.; Belnap, J. 1999. Long-term consequences of disturbance on nitrogen dynamics in an arid ecosystem. *Ecology*. 80:150–160.
- Evans, R.D.; Ehleringer, J.R. 1993. A break in the nitrogen cycle in arid lands? Evidence from  $N^{15}$  of soils. *Oecologia*. 94:314–317.
- Evans, R.D.; Lange, O.L. 2001. Biological soil crusts and ecosystem nitrogen and carbon dynamics. In: Belnap, J. and O.L. Lange, eds. *Biological soil crusts: structure, function, and management*. Ecological Studies Series 150. Berlin: Springer-Verlag. In press.
- Fogg, G.E. 1966. The extracellular products of algae. *Oceanography and Marine Biology Review*. 4:195–212.
- Follett, R.F.; Kimble, J.M.; Lal, R. 2001. The potential of US grazing lands to sequester carbon and mitigate the greenhouse effect. New York: Lewis Publishers.
- Gadd, G.M. 1990. Fungi and yeasts for metal accumulation. In: Ehrlich, H.L. and C.L. Brierley, eds. *Microbial mineral recovery*. New York: McGraw-Hill: 249–275.
- Garcia-Pichel, F.; Belnap, J. 1996. Microenvironments and microscale productivity of cyanobacterial desert crusts. *Journal of Phycology*. 32:774–782.
- Geesey, G.; Jang, L. 1990. Extracellular polymers for metal binding. In: Ehrlich, H.L. and C.L. Brierley, eds. *Microbial mineral recovery*. New York: McGraw-Hill: 223–247.
- Gillette, D.A.; Adams, J.; Endo, A.; Smith, D.; Kihl, R. 1980. Threshold velocities for input of soil particles into the air by desert soils. *Journal of Geophysical Research*. 86(C10):5621–5630.
- Greene, B.; Darnall, D.W. 1990. Microbial oxygenic photoautotrophs (cyanobacteria and algae) for metal-ion binding. In: Ehrlich, H.L. and C.L. Brierley, eds. *Microbial mineral recovery*. New York: McGraw-Hill: 277–302.
- Harper, K.T.; Marble, J.R. 1988. A role for nonvascular plants in management of arid and semiarid rangelands. In: Tueller, P.T., ed. *Vegetation science applications for rangeland analysis and management*. Dordrecht: Kluwer Academic Publishers: 135–169.
- Harper, K.T.; St. Clair, L. 1985. Cryptogamic soil crusts on arid and semiarid rangelands in Utah: effects of seedling establishment and soil stability. Final Report. Salt Lake City: Bureau of Land Management.
- Harper, K.T.; Belnap, J. 2001. The influence of biological soil crusts on mineral uptake by associated vascular plants. *Journal of Arid Environments*. 47:347–357.
- Jeffries, D.L. 1989. The vegetation, soil, and cryptogamic crusts of blackbrush communities in the Kaiparowits Basin. Ph.D. Dissertation. Tempe: Arizona State University: 157 p.
- Jeffries, D.L.; Klopatek, J.M.; Link, S.O.; Bolton Jr., H. 1992. Acetylene reduction by cryptogamic crusts from a blackbrush community as related to resaturation and dehydration. *Soil Biology and Biochemistry*. 24:1101–1105.
- Jeffries, D.L.; Link, S.O.; Klopatek, J.M. 1993a.  $CO_2$  fluxes of cryptogamic crusts. I. Response to saturation. *New Phytologist*. 125:165–173.
- Jeffries, D.L.; Link, S.O.; Klopatek, J.M. 1993b.  $CO_2$  fluxes of cryptogamic crusts. II. Response to dehydration. *New Phytologist*. 125:391–396.
- Johansen, J.R.; St. Clair, L. 1986. Cryptogamic soil crusts: recovery from grazing near Camp Floyd State Park, Utah, USA. *Great Basin Naturalist*. 46(4):632–640.
- Kleiner, E.F.; Harper, K.T. 1972. Environment and community organization in grasslands of Canyonlands National Park. *Ecology*. 53:299–309.
- Lange, O.L. 1974. Chelating agents and blue-green algae. *Canadian Journal of Microbiology*. 20:1311–1321.
- Lange, W. 1976. Speculation on a possible essential function of the gelatinous sheath of blue-green algae. *Canadian Journal of Microbiology*. 22:1181–1185.
- Lange, O.L.; Meyer, A.; Zellner, H.; Heber, U. 1994. Photosynthesis and water relations of lichen soil crusts: field measurements in the coastal fog zone of the Namib Desert. *Functional Ecology*. 8:253–264.
- Lewin, R.A. 1956. Extracellular polysaccharides of green algae. *Canadian Journal of Microbiology*. 2:665–672.
- Leys, J.N. 1990. Soil crusts: their effect on wind erosion. Research Note 1/90. Soil Conservation Service of New South Wales, Australia.
- Leys, J.F.; Eldridge, D.J. 1998. Influence of cryptogamic crust disturbance to wind erosion on sand and loam rangeland soils. *Earth Surface Processes and Landforms*. 23:963–974.
- Liengen, T. 1999. Conversion factor between acetylene reduction and nitrogen fixation in free-living cyanobacteria from high arctic habitats. *Canadian Journal of Microbiology*. 45:223–229.
- Loope, W.L.; Gifford, G.F. 1972. Influence of a soil microfloral crust on select properties of soil under pinyon-juniper in southeastern Utah. *Journal of Soil and Water Conservation*. 27:164–167.
- Martcorena, B.; Bergametti, G.; Gillette, D.; Belnap, J. 1997. Factors controlling threshold friction velocity in semiarid and arid areas of the United States. *Journal of Geophysical Research*. 102(D19):23,277–23,287.
- McFadden, L.; McAuliffe, J.R. 1997. Lithologically influenced geomorphic response to Holocene climatic changes in the southern Colorado Plateau, Arizona: a soil-geomorphic and ecologic perspective. *Geomorphology*. 19:303–332.
- McLean, R.J.C.; Beveridge, T.J. 1990. Metal-binding capacity of bacterial surfaces and their ability to form mineralized aggregates. In: Ehrlich, H.L. and C.L. Brierley, eds. *Microbial mineral recovery*. New York: McGraw-Hill: 185–222.
- Offer, Z.Y.; Goossens, D.; Shachak, M. 1992. Aeolian deposition of nitrogen to sandy and loessial ecosystems in the Negev Desert. *Journal of Arid Environments*. 23:355–363.
- Paerl, H. 1988. Growth and reproductive strategies of freshwater (cyanobacteria) blue-green algae. In: Sandgren, C.D., ed. *Growth and reproductive strategies of freshwater phytoplankton*. Cambridge: Cambridge University Press: 261–315.
- Paul, E.A.; Clark, F.E. 1996. *Soil microbiology and biochemistry*. London: Academic Press.
- Phillips, S.; Belnap, J. 1998. Shifting carbon dynamics due to the effects of *Bromus tectorum* invasion on biological soil crust. Baltimore: Ecological Society of America Annual Proceedings: 205.
- Rao, D.L.N.; Burns, R.G. 1990. Use of blue-green algae and bryophyte biomass as a source of nitrogen for oil-seed rape. *Biology and Fertility of Soils*. 10:61–64.

- Reheis, M.C.; Goodmacher, J.C.; Harden, J.; McFadden, L.D.; Rockwell, T.; Shroba, R.; Sowers, J.; Taylor, E. 1995. Quaternary soils and dust deposition in southern Nevada. *Geological Society of America Bulletin*. 107:1003–1022.
- Reynolds, R.; Belnap, J.; Reheis, M.; Mazza, N. 1998. Eolian dust on the Colorado Plateau—magnetic and geochemical evidence from sediment in potholes and biologic soil crust. Seattle: Proceedings of Conference on Dust Aerosols, Loess, Soils, and Global Change: 5.
- Rogers, S.L.; Burns, R.G. 1994. Changes in aggregate stability, nutrient status, indigenous microbial populations, and seedling emergence following inoculation of soil with *Nostoc muscorum*. *Biology and Fertility of Soils*. 18:209–215.
- Rushforth, S.L.; Brotherson, J.D. 1982. Cryptogamic soil crusts in the deserts of North America. *The American Biology Teacher*. 44(8):472–475.
- Schelske, C.L.; Hooper, F.F.; Haertl, E.J. 1962. Responses of a marl lake to chelated iron and fertilizer. *Ecology*. 43:646–653.
- Shields, L.M.; Durrell, L.W. 1964. Algae in relation to soil fertility. *The Botanical Review*. 30:92–128.
- Terry, R.E.; Burns, S.J. 1987. Nitrogen fixation in cryptogamic soil crusts as affected by disturbance. In: Proceedings of the Pinyon-Juniper Conference, Reno: USDA Forest Service, 369–372.
- Venkataraman, G.S.; Neelakantan, S. 1967. Effect of the cellular constituents of the nitrogen-fixing blue-green algae *Cylindrospermum muscicola* on the root growth of rice seedlings. *Journal of General and Applied Microbiology*. 13:53–61.
- Verrecchia, E.; Yair, A.; Kidron, G.; Verrecchia, K. 1995. Physical properties of the psammophile cryptogamic crust and their consequences to the water regime of sandy soils, northwestern Negev Desert, Israel. *Journal of Arid Environments*. 29:427–437.
- Warren, S.D. 2001a. Biological soil crusts and hydrology in North American deserts. In: Belnap, J. and O.L. Lange, eds. *Biological soil crusts: structure, function, and management*. Ecological Series 150. Berlin: Springer-Verlag. In press.
- Warren, S.D. 2001b. Synopsis: influence of biological soil crusts on arid land hydrology and soil stability. In: Belnap, J. and O.L. Lange, eds. *Biological soil crusts: structure, function, and management*. Ecological Series 150. Berlin: Springer-Verlag. In press.
- Williams, J.D.; Dobrowolski, J.P.; West, N.E.; Gillette, D.A. 1995a. Microphytic crust influence on wind erosion. *Transactions of the American Society of Agricultural Engineers*. 38(1):131–137.
- Williams, J.D.; Dobrowolski, J.P.; West, N.E. 1995b. Microphytic crust influence on interrill erosion and infiltration capacity. *Transactions of the American Society of Agricultural Engineers*. 38(1):139–146.
- Wullstein, L.H. 1989. Evaluation and significance of associative dinitrogen fixation for arid soil rehabilitation. *Arid Soil Research and Rehabilitation*. 3:259–265.