

SURFACE DISTURBANCES: THEIR ROLE IN ACCELERATING DESERTIFICATION

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Abstract. Maintaining soil stability and normal water and nutrient cycles in desert systems is critical to avoiding desertification. These particular ecosystem processes are threatened by trampling of livestock and people, and by off-road vehicle use. Soil compaction and disruption of cryptobiotic soil surfaces (composed of cyanobacteria, lichens, and mosses) can result in decreased water availability to vascular plants through decreased water infiltration and increased albedo with possible decreased precipitation. Surface disturbance may also cause accelerated soil loss through wind and water erosion and decreased diversity and abundance of soil biota. In addition, nutrient cycles can be altered through lowered nitrogen and carbon inputs and slowed decomposition of soil organic matter, resulting in lower nutrient levels in associated vascular plants. Some cold desert systems may be especially susceptible to these disruptions due to the paucity of surface-rooting vascular plants for soil stabilization, fewer nitrogen-fixing higher plants, and lower soil temperatures, which slow nutrient cycles. Desert soils may recover slowly from surface disturbances, resulting in increased vulnerability to desertification. Recovery from compaction and decreased soil stability is estimated to take several hundred years. Re-establishment rates for soil bacterial and fungal populations are not known. The nitrogen fixation capability of soil requires at least 50 years to recover. Recovery of crusts can be hampered by large amounts of moving sediment, and re-establishment can be extremely difficult in some areas. Given the sensitivity of these resources and slow recovery times, desertification threatens million of hectares of semiarid lands in the United States.

1. Introduction

Most arid and semiarid lands of the United States have been heavily affected by human use since the late 1800s. Historically, most of this impact has been from livestock grazing near areas with forage and water. More recently, substantial increases in off-road vehicle use and hiking have greatly expanded direct and indirect human impacts both spatially and temporally. The combination of recreational use and livestock grazing is resulting in unprecedented levels of local and regional disturbances, accelerating desertification processes.

Many resources in arid ecosystems are sensitive to compressional and shear forces associated with current uses. Soils in arid regions are often highly erodible, and soil formation extremely slow, taking 5,000 to 10,000 years or more (Dregne, 1983a). Low levels of organic matter, large particle size ranges, and shallow soil freezing depths generally found in these soils result in compactible soils with slow dilation rates. Compaction of soils results in less water infiltration and less locally available water (Webb, 1983; Wilshire, 1983), which in turn influence soil biota activity, N cycle dynamics (Torbert and Wood, 1992), vascular plant vigor and reproduction (Crawford, 1979; Skujins, 1984), and decomposition rates of soil

organic matter (West, 1981). Compaction reduces soil aggregates and pore space, which are important for soil stability and infiltration and as microenvironments for soil biota (Dregne, 1983a; Stolzy and Norman, 1961).

Surface disturbance also affects surface cyanobacterial-lichen soil crusts. In the western United States these crusts are important for increased soil stability, water infiltration, and fertility of soils (Harper and Marble, 1988; Johansen, 1993; Metting, 1991; Belnap and Gardner, 1993). Absence of these crusts can lead to increased erosion, resulting in loss of organic matter, fine soil particles, nutrients, and microbial populations in soils (Harper and Marble, 1988; Schimel *et al.*, 1985).

Normal nutrient cycles in these semiarid regions can also be disrupted by soil surface disturbance. Nitrogen is often limiting in desert systems (Zak and Whitford, 1988). Cyanobacterial-lichen soil crusts have been shown to be the dominant source of nitrogen in a cold-desert pinyon-juniper and a grassland ecosystem in southern Utah (Evans and Ehringer, 1993; Evans and Belnap, unpublished data). Experiments have demonstrated that all types of surface disturbance tested dramatically decreased nitrogenase activity in these crusts (Belnap *et al.*, 1994). Plants growing on undisturbed sites consistently show higher N content when compared to adjacent disturbed sites (Belnap and Harper, in press; Harper and Pendleton, 1993).

Cyanobacterial-lichen soil crusts are an important source of fixed carbon for these sparsely vegetated areas (Beymer and Klopatek, 1991). In addition, soil disturbance can alter soil food webs and thereby affect nutrient availability in these systems (Ingham *et al.*, 1989). Disruptions of soil food webs can reverberate throughout the ecosystem, affecting macro-floral and faunal components (Hendrix *et al.*, 1992; Coleman *et al.*, 1992). Soil surface disturbance can also affect plant community composition and architecture. Changes in these critical habitat components have been shown to affect invertebrate and vertebrate populations (MacMahon, 1987). Since preventing desertification depends on maintaining stability and fertility of soils, as well as diversity of processes and species in ecosystems, impacts to sensitive soil surfaces can accelerate the desertification process.

2. Materials and Methods

2.1. STUDY SITES

Arches National Park: Arches is located 16 km north of Moab, Utah, at 1370 m elevation. Annual rainfall is approximately 200 mm. A heavily trampled area was compared with an adjacent, relatively undisturbed area. Both sites are on Arches loamy fine sand with similar depth, slope, inclination, and exposure. The dominant vegetation is *Coleogyne ramosissima* (blackbrush). Plant interspaces in the untrampled area are covered with well-developed cyanobacterial-lichen crust.

Behind-the-Rocks: Situated on Rizo fine sandy loam at 1400 m elevation, this site lies 15 km south of Moab, Utah. Annual rainfall is approximately 200 mm. This site is dominated by *C. ramosissima*. Undisturbed soils are covered by a cyanobacterial crust similar to that at the Arches untrampled site.

Natural Bridges National Monument: Located 73 miles southwest of Moab at 1980 m elevation, these two sites have annual rainfall of approximately 300 mm. Both sites are on Rizo fine sandy loam of similar depth, slope, inclination, and exposure, dominated by *Pinus edulis* and *Juniperus utahensis*. A trampled site was compared to an area 200 m away that had received little trampling.

Canyonlands National Park: Located 31 miles south of Moab at 1513 m elevation, these study sites are in adjacent grasslands. Both have sandy loam soils (Mido and Begay) with similar soil depth, slope, and exposure. Both sites are dominated by the grasses *Stipa hymenoides* and *S. comata* (Kleiner and Harper, 1977). Annual rainfall averages 180 mm.

2.2. ANALYSES

Five randomly located transect lines were placed in each area at the Arches study site. Ground and vegetation cover were estimated with twenty 0.25 m² quadrats per transect using a nested frequency quadrat frame, Daubenmire cover classes, and density counts. All perennial plants were mapped. For shrubs intersecting the transect line, distance from nearest neighbor and hummock height were estimated. Hummock height was estimated as the height at which a rod held parallel to the surface from the base of the shrub intersected a rod held vertically at the lowest point in the interspace between the considered shrub and its nearest neighbor.

Plant tissue elemental content was determined from composite samples comprising at least five individuals of each species. Analysis was conducted by the Brigham Young University Soil Laboratory. Nitrogenase activity in cyanobacterial crusts was determined by methods outlined in Belnap (1992, 1994). Soil biota were sampled at 0–10 cm, the depth at which maximum bacterial, fungal, and nematode biomass was found. Nematodes, total and active bacteria, microarthropods, and total and active fungal biomass were evaluated following methods outlined in Ingham *et al.* (1989).

Physical soil characteristics were determined for cores 0–10 cm deep. Soils were analyzed by the Brigham Young University Soils Laboratory. Soil depth was determined with a metal probe. Compaction was measured with a recording penetrometer and bulk density measurements. Soil temperatures were taken mid-day on five occasions during June and July 1994. Measurements were taken with a 1 mm wide probe inserted just under the soil surface. Results were analyzed using analysis of variance (ANOVA), Duncan's multiple range test, and unpaired t-tests.

TABLE I

Soil physical characteristics of disturbed and undisturbed areas at Arches National Park

	Undisturbed		Disturbed		Significant differences
	Mean	Std. Dev.	Mean	Std. Dev.	
pH	8.30	0.00	8.20	0.00	p < 0.03
% Sand	82.23	0.80	85.76	0.70	p < 0.05
% Clay	8.83	0.50	7.24	0.80	
% Silt	8.96	0.02	7.00	1.50	
% OM	0.55	0.14	0.40	0.30	
ppm P	34.04	0.14	44.38	0.08	p < 0.01
ppm Zn	0.40	0.10	0.50	0.14	
ppm Fe	19.90	0.26	26.50	0.13	
ppmMn	3.20	0.17	4.30	0.08	
ppm Cu	0.20	0.00	0.20	0.00	
ppm N	591.70	47.10	558.30	23.60	
ppm K	90.00	0.71	110.00	14.10	
ppm Ca	4390.00	99.00	3445.00	7.10	p < 0.02
ppm Mg	70.00	0.00	70.00	0.00	
ppm Na	90.00	7.10	110.00	14.14	
0-3 cm BD	104.9	4.4	114.9	10.0	p < 0.007
3-6 cm BD	99.5	4.9	108.1	5.6	p < 0.001

3. Results and Discussion

3.1. SOIL PHYSICAL CHARACTERISTICS

Soils at the trampled and untrampled sites in Arches were very similar (Table I). Percent clay, silt, and organic matter were low at both sites and did not differ significantly. No statistically significant differences were found in zinc, iron, manganese, copper, total nitrogen, potassium, magnesium, or sodium levels. At the two sites pH and percent sand differed slightly but significantly, and differences in phosphorus and calcium were greater and significant.

Bulk density and soil porosity were compared in the two areas. Bulk density was found to be significantly higher at 0-3 and 3-6 cm depths in the trampled area than in the untrampled area. Soil porosity did not significantly differ at 0-3 cm depth between the two areas but was significantly lower at 3-6 cm depth in the trampled area than in the untrampled area. Increasing bulk density often results in lower microbial populations and lower activity levels (Torbert and Wood, 1992). In addition, increased bulk density generally results in less water infiltration and increased runoff (Webb and Wilshire, 1980; Loope and Gifford, 1972). Decreased

TABLE II

Biological characteristics at Arches National Park in disturbed and undisturbed areas. All differences are statistically significant at $p < 0.05$, except for frequency of litter, which did not significantly differ

	Undisturbed		Disturbed	
	Mean	Std. Dev.	Mean	Std. Dev.
<i>Percent cover</i>				
Cyano	45.50	7.20	78.20	14.10
Lichen	2.00	1.20	0.20	0.30
Collema	4.40	2.40	0.60	0.70
Moss	32.70	5.50	4.40	4.00
Litter	31.80	5.00	8.60	3.20
Bare Ground	0.06	0.13	8.36	12.20
Exotics	0.06	0.13	1.40	1.30
Grass	3.56	1.48	2.38	0.95
Shrub	29.81	16.48	29.53	9.99
<i>Frequency</i>				
Lichen	0.36	0.15	0.02	0.02
Collema	0.76	0.05	0.14	0.15
Moss	0.95	0.04	0.31	0.24
Bare Ground	0.03	0.05	0.88	0.06
Gravel	0.08	0.15	0.50	0.40
Grass	0.64	0.17	0.39	0.13
Shrubs	0.81	0.25	0.49	0.21
<i>Community</i>				
# of Shrubs	7.20	1.24	3.20	0.58
Festuca Weight, g	0.80	0.16	1.68	0.33
# of Shrub Species	2.30	0.50	1.40	0.55
Interspace, cm	43.00	4.95	41.31	5.09
Hummock Height, cm	11.11	1.26	25.19	1.97
# of Exotics	0.30	0.50	1.40	0.55
# of Plant Species	8.00	1.20	10.00	1.40

water availability locally can lead to increased water stress for plants, thereby accelerating desertification processes (Dregne, 1983b).

3.2. SOIL SURFACE COVER AND CYANOBACTERIAL-LICHEN SOIL CRUSTS

At the Arches site, soil surfaces of the trampled and untrampled sites were compared (Table II). Cover of plant litter, lichens, mosses, and cyanobacteria was significantly

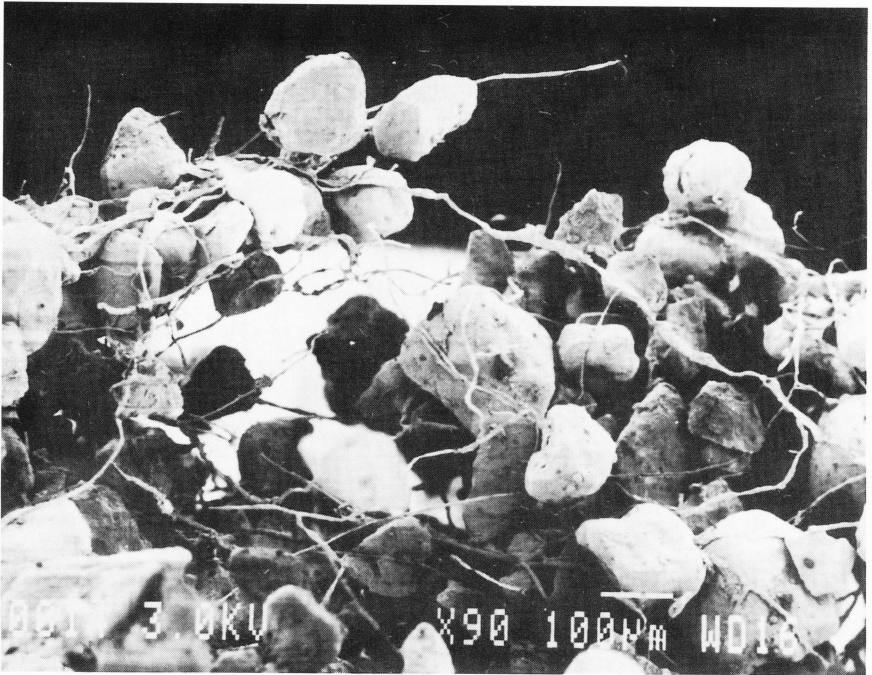


Fig. 1. Scanning electron micrograph of dry cyanobacterial sheaths winding through sandy soils from Moab, Utah. Note firm attachment of sheath material to the individual sand grains, even though sheath material is dry (magnification $\times 90$).

higher in the untrampled area. The untrampled area had 32% litter cover, contrasted with only 8% litter cover in the trampled area. Six species of lichens and four species of cyanobacteria were found in the untrampled area, whereas only one species of cyanobacteria was found in the trampled area. Lichens and mosses combined covered 39% of the surface in the untrampled area but only 4% in trampled area. Lichen and moss species had a combined frequency four times greater in the untrampled than the trampled area. Trampled interspace surfaces were generally flat, whereas untrampled interspace surfaces supported cyanobacterial pedicels up to 7 cm high.

Litter and cryptobiotic crust cover and roughened microtopography play important roles in protecting soil surfaces from wind and water erosion and in enhancing water infiltration. Combining litter, vascular plant, lichens, and moss cover, the untrampled area had virtually no surfaces exposed to wind or water erosion, whereas most of the interspaces in the trampled area had little if any protection. Surfaces trampled flat promote sheet erosion. Untrampled, pedicelled surfaces create microcatchments for water and reduce the velocity of surface water flows, thus encouraging suspended sediments to settle out (Harper and Marble, 1988).

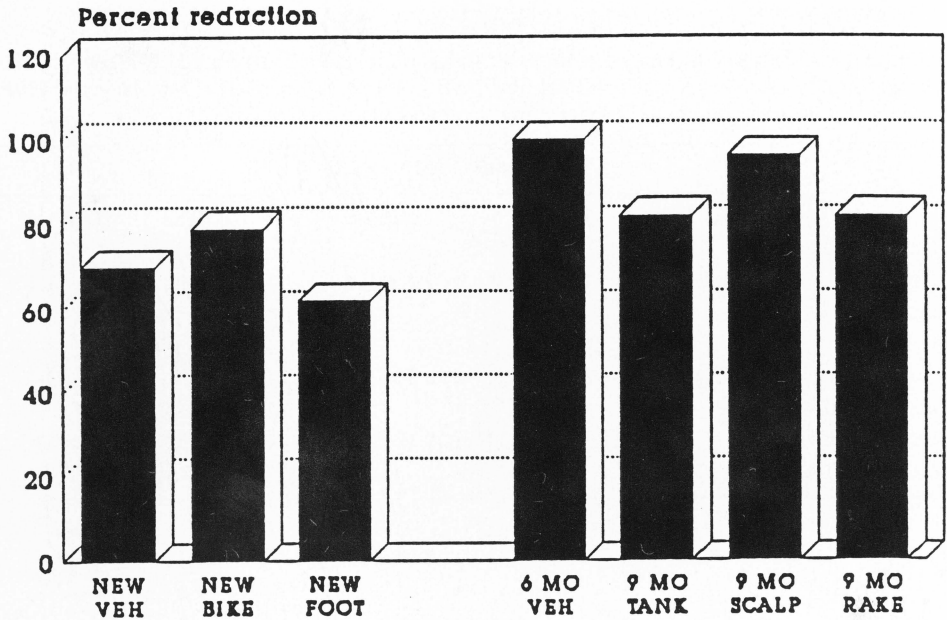


Fig. 2. Percent reduction of nitrogenase activity after soil surface disturbances were experimentally applied. All differences from the control were significant. Bicycle, motor vehicle, and footprint treatments were applied near Moab, Utah. Tank, rake, and scalped treatments were applied at Dugway Proving Ground, Utah (Belnap *et al.*, 1994).

Consequently, trampling can greatly accelerate desertification processes through increased soil loss and water runoff (Dregne, 1983b).

As cyanobacteria move through the soil, they leave behind polysaccharide material that firmly adheres to soil particles, even when dry or no longer associated with a living cyanobacterium (Figure 1). Sheath material can absorb up to eight times its weight in water, increasing the water-holding capacity of the soil (Brock, 1975; Campbell, 1979; Campbell *et al.*, 1989). In addition, nutrient-rich clay particles adhere to sheath material, thus increasing the fertility of soils (Belnap and Gardner, 1993; Belnap and Harper, in press). Soil crusts can also affect higher plant seedling establishment and survival. Experiments with fine and coarsely textured soils demonstrated that seedling establishment was higher for forbs and grasses in crusted areas than uncrusted areas. Survival over a 3-year period was enhanced in two species and unaffected in one species. Overall plant survival was three times higher in the crusted plots (Belnap, 1994). Other studies have reported similar enhancement of seedling germination and establishment in crusted areas when compared to uncrusted surfaces (Harper and Marble, 1988; St. Clair *et al.*, 1986; Lesica and Shelley, 1992).

Surface disturbance has been shown to negatively affect the cohesion and coverage of cyanobacterial crusts, since crustal components are brittle when dry and

TABLE III

Active and total bacterial and fungal biomass at Arches National Park and Natural Bridges National Monument. AF = Active fungi; TF = Total fungi; AB = Active bacteria; TB = Total bacteria; TF/B = Total fungi/bacteria. Asterisk (*) denotes statistical differences at $p < 0.05$

	AF	TF	AB	TB	TF/B
Arches undisturbed	0.3 ± 0.2	14.5 ± 5.5	$2.3 \pm 1.0^*$	$3.78 \pm 0.82^*$	$4.0 \pm 1.4^*$
Arches disturbed	0.4 ± 0.5	11.6 ± 4.9	$1.2 \pm 0.7^*$	$5.35 \pm 1.6^*$	$2.5 \pm 1.7^*$
Natural Bridges undisturbed	$0.59 \pm 0.67^*$	25.2 ± 7.7	$0.8 \pm 0.35^*$	$3.4 \pm 0.6^*$	$7.5 \pm 2.4^*$
Natural Bridges disturbed	0	31.5 ± 24.5	$0.12 \pm 0.14^*$	$14.2 \pm 4.8^*$	$3.1 \pm 3.6^*$

easily crushed (Belnap, 1993; Campbell *et al.*, 1989; Harper and Marble, 1988). Surface disturbance also reduces the depth to which abandoned cyanobacterial sheath accumulates, thereby reducing resistance to water erosion. At many disturbed sites, sheath material is often not observed below 1 mm depth, in contrast to 7 cm thick crusts in untrampled areas. Consequently, impacts to surface crusts can reduce soil stability, soil fertility, and soil moisture retention, thus accelerating desertification in impacted areas (Dregne, 1983b).

Cyanobacteria and cyanobacterial components of soil lichens fix atmospheric nitrogen (Belnap, 1992; Skujins and Klubek, 1978; West and Skujins, 1977; Terry and Burns, 1987). Studies have shown that nitrogen fixed by soil cyanobacteria is available to neighboring vascular plants under laboratory conditions (Mayland *et al.*, 1966; Mayland and McIntosh, 1966). In some desert systems, these crusts have been found to be the dominant source of this often-limiting element (Evans and Ehrlinger, 1993).

Nitrogenase activity was dramatically reduced in soil crusts regardless of the type of experimentally applied disturbance (Figure 2; Belnap *et al.*, 1994; Belnap, unpublished data). Disturbance by human feet, mountain bikes, four-wheel drive trucks, tracked vehicles (tanks), and shallow and deep raking all resulted in an immediate 40–80% reduction in nitrogenase activity. Measurements taken 6–9 months after treatment showed that nitrogenase activity had dropped still lower in the disturbed areas, with treatments showing an 80–100% reduction (Belnap, *et al.*, 1994). At the Arches trampled site, no nitrogenase activity could be detected, while the undisturbed site showed normal nitrogenase activity. Because disturbance generally increases nitrogen losses through enhanced denitrification and accelerated soil erosion (Peterjohn and Schlesinger, 1990), less nitrogen input often results in

TABLE IV-A

Nematode populations at Arches National Park and Natural Bridges National Monument. Total numbers, bacterial feeders, and fungal feeders were significantly higher in the undisturbed area ($p < 0.05$). Numbers of root feeders did not significantly differ

	Bacterial feeders	Fungal feeders	Root feeders	Total individuals
<i>Nematode functional groups</i>				
Arches undisturbed	505.0 ± 287.0*	97.0 ± 142.0*	35.0 ± 38.0	651.0 ± 646.0*
Arches disturbed	370.0 ± 287.0*	54.0 ± 127.0*	67.0 ± 54.0	493.0 ± 360.0*
Natural Bridges undisturbed	36.12 ± 33.56*	30.09 ± 44.0*	4.08 ± 9.5	70.44 ± 82.56*
Natural Bridges disturbed	5.02 ± 2.85*	2.81 ± 2.71*	0.07 ± 2.52	8.56 ± 4.9*

TABLE IV-B

Microarthropods: Numbers of microarthropods in a never grazed and a previously grazed site in Canyonlands National Park. These samples were not statistically analyzed

	Shrub total species	Grass total species	Shrub canopy	Shrub interspace	Grass canopy	Grass interspace	Total individuals
<i>Microarthropods</i>							
Undisturbed	15	11	44	7	14	10	72
Disturbed	11	7	18	1	5	7	34

less total nitrogen for the ecosystem. Reduced fertility of systems is one of the most definitive and problematic aspects of desertification (Dregne, 1983b).

3.3. SOIL FOOD WEBS

Biomass of active bacteria, total bacteria, active fungi, and total fungi, as well as nematode numbers, were measured in paired trampled and untrampled areas in Arches National Park and Natural Bridges National Monument. Results obtained from the two areas were similar. At Arches the biomass of active bacteria in the untrampled area exceeded by more than three times that in the trampled area (Table III). Total bacterial biomass was higher in the trampled area, whereas active

and total fungal biomass were not significantly affected by disturbance. The ratio of total fungi to bacteria had significantly shifted in the trampled area by a factor of two, with relatively more bacteria present. Nematode populations were also significantly affected (Table IVa). The number of bacterial and fungal feeding nematodes in the untrampled area was twice that found in the trampled area. Numbers of plant root feeders in the trampled and untrampled area did not significantly differ. Twice as many nematodes were found in the untrampled area as in the trampled area.

Soil biota were also analyzed at Natural Bridges National Monument (Tables III and IVa) with results similar to those from Arches. Biomass of active bacteria and fungi was six to seven times higher in the untrampled area than in the trampled area. Total bacterial biomass was three times higher in the trampled area, while total fungal biomass did not significantly differ. The ratio of fungi to bacteria was found to have significantly shifted in the trampled area by a factor of three, with relatively more bacteria in the trampled area. Nematode numbers were significantly affected as well, with numbers of bacterial and fungal feeders 7–10 times higher in the untrampled area. Plant root feeders were not significantly affected. Total nematode numbers were almost seven times greater in the untrampled area than in the trampled area.

Microarthropod populations were compared between trampled and untrampled areas in Canyonlands National Park. Although the trampled site had not been grazed for 30 years, numbers of individuals of each species were still higher in the untrampled area, both under plants and in plant interspaces, than in the disturbed area (Table IVb). Total individuals were more than twice as abundant (44 vs. 18) under shrubs of the untrampled than the trampled area. In shrub interspaces, individuals were seven times more abundant (1 vs. 7) in the untrampled area than in the trampled area. In the grass community, the same pattern was observed. Individuals were almost three times as abundant in the untrampled area under grass plants (14 vs. 5) than the trampled area. Microarthropod individuals were 1.4 times more abundant (10 vs. 7) in the untrampled interspace between grasses than in trampled interspaces. Total numbers of individuals found in the untrampled area were more than double those observed in the trampled area (72 vs. 34). Fewer species were found in trampled than untrampled areas in both shrub (11 vs. 15 species) and grass (7 vs. 11 species) communities. The results represent a decline in species richness of 26% and 36% respectively. Four species found in the trampled area were not found in the untrampled area, and six species from the untrampled area were not found in the trampled area.

Soil food webs can profoundly influence nutrient availability in ecosystems, and changes in soil biota populations can result in slower decomposition rates and fewer nutrients available to plants, thereby hastening the desertification process. Nutrient uptake rates can be affected by the ability of bacteria to solubilize or chelate elements (Lange, 1974). Symbiotic fungi can increase a plant's ability to exploit more soil volume and increase the spatial distribution of carbon in soils. Carbon- and nitrogen-fixing soil microbiota contribute to site fertility. Larger

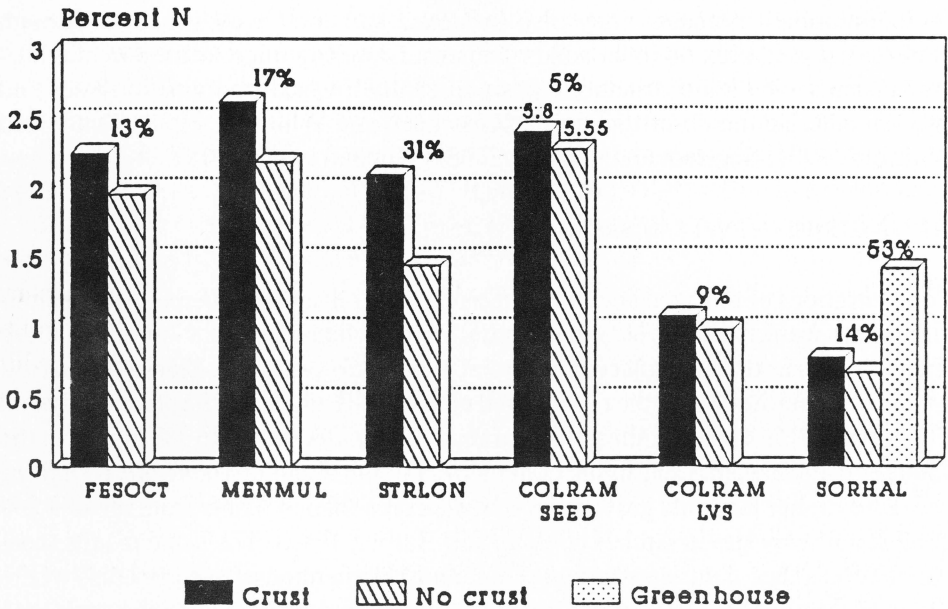


Fig. 3. Nitrogen levels in vascular plant tissue from sites around the state of Utah, USA. Plants were collected from adjacent crusted and uncrusted soils. All differences were statistically significant at $p < 0.05$. FESOCT = *Festuca octoflora* (annual grass); MENMUL = *Mentzelia multiflora* (annual forb); STRLON = *Streptanthella longirostris* (perennial forb); COLRAM = *Coleogyne ramosissima* seedlings and leaves (perennial shrub); SORHAL = *Sorghum halepense* (annual grass).

microbial populations mean greater retention of N, P, and other nutrients bound up in microbial biomass (Skujins, 1984). Bacteria are known to secrete IAA and other plant growth regulators. Both bacteria and fungi secrete polysaccharide material that acts to aggregate soil particles (Lange, 1974). The presence of bacteria and fungi can also affect vascular plant root morphology (Skujins, 1984).

Ratios of microbes vary in different systems. Shrub-dominated systems generally have relatively higher fungal numbers to decompose more recalcitrant woody litter. Grass systems have relatively more bacteria. Disturbance often shifts these ratios. Both the blackbrush community at Arches and the pinyon-juniper community at Natural Bridges resulted in stimulation of bacterial activity and a depression in fungal activity. Because different soil biota process litter differently, such a shift in soil food web structure or relative activity levels can significantly lower litter decomposition rates and nutrient availability to systems and thus increase desertification rates.

Predators, such as nematodes and microarthropods, are also an essential part of the soil food web. These organisms play important roles in decomposition cycles by shredding litter, mixing soil layers, and carrying litter underground. They act as dispersers of other soil microorganisms. They can modify soil pH and contribute N, P, and other nutrients to soils through fecal material and release of nutrients bound

up in microbial biomass. They also influence soil food web structure through preferential predation on other soil organisms. Lowering microarthropod numbers and altering population structure can significantly lower decomposition rates and again accelerate the desertification process (Zak and Whitford, 1988; Santos and Whitford, 1981; Seastedt and Crossley, 1984; Kitchell *et al.*, 1979).

3.4. NUTRIENT LEVELS IN VASCULAR PLANTS

Concentrations of nitrogen and other macronutrients in annual, biennial, and perennial plants were found to be significantly higher when they grew on undisturbed crusted surfaces than on adjacent trampled areas at all study sites tested (Figure 3). At Arches, leaf tissue N in the untrampled area was 9% higher in the perennial shrub *Coleogyne*, 31% higher in the perennial forb *Streptanthella*, and 13% higher in the annual grass *Festuca*. Leaf tissue content of N in the biennial *Mentzelia multiflora* was 17% higher in plants growing in a crusted area than in plants from an adjacent dune at a nearby site in Arches (Belnap and Harper, 1995). The same results were obtained at other field sites around Utah and in greenhouse experiments, where levels of nitrogen in sorghum and rape were higher in pots with cyanobacteria than in pots without cyanobacteria. Dry weight of plants in pots with cyanobacteria were up to four times greater than in pots without cyanobacteria (Harper and Pendleton, 1993). Dry weight of *Festuca* plants in the untrampled area was twice the *Festuca* dry weight of the trampled area (Belnap and Harper, 1995).

Maintaining normal nitrogen cycles is critical to maintaining the fertility of semiarid soils and preventing desertification (Dregne, 1983b). After water, nitrogen is generally considered the element most likely to limit primary productivity in semiarid and arid ecosystems (Ettershank *et al.*, 1978; Romney *et al.*, 1978).

3.5. VASCULAR PLANT COMMUNITY STRUCTURE

Plant community composition and structure were examined at the Arches trampled site and compared to a nearby untrampled area (Table II). Many significant differences were observed. Fewer, larger individuals of the dominant shrub *Coleogyne ramosissima* were found in the trampled area than in the untrampled area. Shrubs dominated the interspace of the untrampled area, whereas annuals or perennial bulbs (with above-ground parts only in the spring) dominated the interspace in the trampled area. Exotic grasses contributed significantly to grass cover in the trampled area, whereas the untrampled area had only a few exotic plant individuals.

Interspaces between *Coleogyne* plants were significantly larger and hummocks under the shrubs four times higher in the trampled area than in the untrampled area. Consequently more soil is exposed to erosion in the trampled area. In addition, small animals face crossing an average of 4.8 m between *Coleogyne* plants in the trampled area, compared to 2.0 m in the untrampled area, resulting in higher exposure to predation. The trampled area also had only small annual plants in the

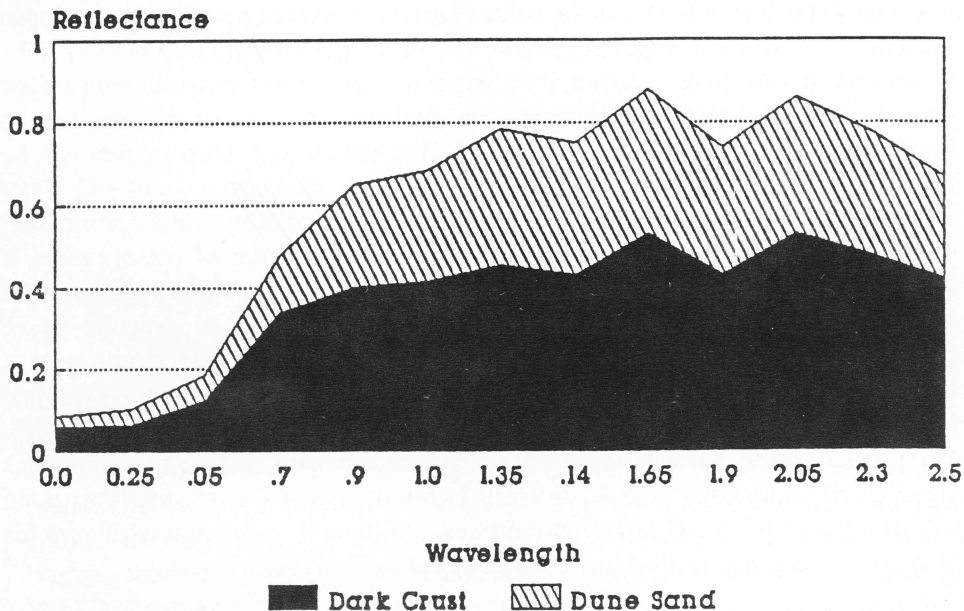


Fig. 4. Reflectance of bare sand and *Microcoleus*-dominated soil surfaces. Measurements were taken using a laboratory spectrophotometer. (From Gregg Swayze and Roger Clark (U.S. Geological Survey, Denver).

interspaces, instead of perennials such as *Opuntia polyacantha*, which might offer more protective cover.

Changes in plant community architecture have been shown to affect populations of invertebrates and vertebrates living in these communities (MacMahon, 1987). As a result, on semiarid and arid landscapes trampling may have many as yet undocumented effects that increase susceptibility to desertification.

3.6. SURFACE ALBEDO AND TEMPERATURE

Albedo is also of concern in semiarid and arid systems. When trampled surfaces were compared to untrampled surfaces, there was up to a 50% increase in reflectance from 0.25 to 2.5 μ (Figure 4). This represents a change in the surface energy flux of approximately 40 watts/m² (R. Clark, U.S. Geological Survey, Denver, personal communication). Extensive trampled areas, combined with lack of urban areas to offset this energy loss, could lead to changes in regional climate patterns in many semiarid regions (Sagan *et al.*, 1979).

Concomitant with albedo changes, trampled and untrampled surfaces significantly differed in surface temperatures. Mid-day temperatures were taken in June and July 1994. Air temperatures were found to average 39 °C (S.D. 0.25 °C), bare sand 52 °C (S.D. 0.5 °C), and dark crusted surfaces 62 °C (S.D. 1.0 °C). These dif-

ferences were all significant. In the winter, surface temperatures of well-developed crusts were up to 14 °C higher than ambient air temperature.

Surface temperatures can be very important in desert systems. Nitrogenase activity is heavily temperature dependent, with lower temperatures resulting in lowered activity levels (Rychert *et al.*, 1978). Altered soil temperatures can be expected to affect microbial activity, plant nutrient uptake rates, and soil water evaporation rates. Soil temperatures have been shown to 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.

3.7. RECOVERY FROM SURFACE DISTURBANCE

Some research has been conducted to estimate recovery rates of soil disturbances in arid systems. Recovery of soils from compaction has been estimated to require 100–130 years in the Great Basin Desert (Knapp, 1992) and 80–140 years in the Mojave Desert (Webb and Wilshire, 1980). Recovery rates of soil biota are expected to be slow, given the slow recovery of soil porosity, moisture-dependent microbial activity in a dry environment, limited dispersal ability, naturally low microbial populations, and large disturbance areas.

Much more is known about the recovery rates of cyanobacterial-lichen soil crusts. Recovery rates have been found to depend on the type and extent of disturbance, the availability of nearby inoculation material, and the temperature and moisture regimes that follow disturbance. Estimates of time for visually assessed recovery have varied from 5 to 100 years (Anderson *et al.*, 1982; Jeffries and Klopatek, 1987; Callison *et al.*, 1985; Cole, 1990). However, Belnap (1993) showed that many components of recovery cannot be assessed visually. Assuming linear recovery rates, recovery was estimated to be 35–65 years for cyanobacterial biomass, 45–85 years for lichen cover, and 250 years for moss cover in scalped 0.25 m² plots surrounded by well-developed crusts. Since recovery time depends on the presence of a nearby inoculant, larger disturbed areas will take longer to recover. Several studies have shown that inoculation can hasten the biological recovery of disturbed crusts (Tidemann *et al.*, 1980; Ashley and Rushforth, 1984; Belnap, 1993).

Nitrogenase activity recovery appears to be quite slow. In scalped areas, 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 by four-wheel drive vehicles, no recovery could be documented after 2 years (Belnap, unpublished data). With the use of isotopic ratios of N, soil and plant N and nitrogenase activity levels were found to be significantly lower in an area that livestock had not grazed for 30 years than in an area that livestock had never grazed. These data suggest that negative effects on nitrogen dynamics may persist in systems for extended periods after disturbance ceases. This slow recovery from disturbance indicates that this system is vulnerable to desertification.

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 (Belnap, 1993). Consequently, recovery of surface albedo characteristics in severely disturbed areas could take up to 250 years for even very small areas.

Different deserts may show very different resistance and resilience to surface disturbances. Some characteristics of deserts suggest that these ecosystems probably evolved with low levels of soil surface disturbance by ungulates. These characteristics include the presence of cryptobiotic soil crust, the morphology and phenology of perennial bunch grasses found in these deserts, and the dominance of C₃ grasses (Mack and Thompson, 1982). Some deserts, such as those in the Colorado Plateau biogeographic province, may have also evolved with low levels of microdisturbance such as those created by soil and surface invertebrates, and thus depend more heavily on soil surface integrity for natural ecosystem functioning. As a result, these deserts may be harmed more by soil surface disturbances than deserts that evolved under higher levels of surface disturbance.

4. Conclusion

Thirty percent of the United States consists of semiarid or arid landscapes. Preventing desertification of these areas requires maintaining the sustainability and productivity of the ecosystems within these areas. Because most current land use practices involve extensive impacts to soil surfaces, we must understand the short- and long-term effects of such impacts on nutrient cycles and soil food webs in these ecosystems and how these processes accelerate desertification.

The data presented here show that nutrient cycles in deserts can be extremely sensitive to soil surface disturbances. Nitrogen cycles may be at the greatest risk from current land use practices. Input of available nitrogen from atmospheric and parent material sources is extremely low in arid regions, and these systems generally depend on biologically fixed nitrogen and nitrogen released from the decomposition of organic matter. The above data show that both of these input pathways are threatened by soil surface disturbances. Because nitrogen loss is a continuous process, understanding factors that decrease the input or availability of

nitrogen is of critical importance to maintaining the sustainability of arid systems (Peterjohn and Schlesinger, 1990) and preventing desertification.

Preventing soil loss is another major challenge in preventing desertification of these areas. Many semiarid and arid areas rely on soil surface cyanobacteria for stability, and current land uses are affecting large areas of this resource (Belnap, personal observation). In addition, loss of diversity of processes and species results from current types of soil surface disturbance. The sensitivity of the semiarid and arid lands of the western United States to these impacts, combined with the low resiliency of these systems, indicate that they are at risk from desertification. These areas must be managed to conserve the fertility and stability of soil resources.

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References

- Anderson, D.C., K.T. Harper, and S.R. Rushforth. 1982. Recovery of cryptogamic soil crusts from grazing on Utah winter ranges. *Journal of Range Management* **35**: 355–359.
- Ashley, J. and S.R. Rushforth. 1984. Growth of soil algae on topsoil and processed oil shale from the Uintah Basin, Utah, USA. *Reclamation and Revegetation Research* **3**: 49–63.
- Belnap, J. 1992. *Effects of wet and dry pollutants on the physiology and elemental accumulation of cryptobiotic crusts and selected rock lichens on the Colorado Plateau*. Final Report, National Park Service, Washington Air Quality Division, December 1991. NPS/AQ-91, on file at Washington Office of Air Quality, National Park Service, Denver, Colorado.
- Belnap, J. 1993. Recovery rates of cryptobiotic crusts: Inoculant use and assessment methods. *Great Basin Naturalist* **53**(1): 89–95.
- Belnap, J. 1994. Potential value of cyanobacterial inoculation in revegetation efforts. In *Proceedings, ecology and management of annual rangelands*, edited by S.B. Monsen and S.G. Kitchen, General Technical Report INT-GTR-313, USDA Forest Service, Intermountain Research Station, Ogden, Utah, pp. 179–185.
- Belnap, J. and J.S. Gardner. 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. and K.T. Harper. 1995. The influence of cryptobiotic soil crusts on elemental content of tissue in two desert seed plants. *Arid Soil Research and Rehabilitation* **9**: 107–115.
- Belnap, J., K.T. Harper and S.D. Warren. 1994. Surface disturbance of cryptobiotic soil crusts: Nitrogenase activity, chlorophyll content, and chlorophyll degradation. *Arid Soil Research and Rehabilitation* **8**: 1–8.

- Beymer, R.J. and J.M. Klopatek. 1991. Potential contribution of carbon by microphytic crusts in pinyon-juniper woodlands. *Arid Soil Research and Rehabilitation* **5**: 187–198.
- Brock, T.D. 1975. Effect of water potential on a *Microcoleus* from a desert crust. *Journal of Phycology* **11**: 316–320.
- Bush, J.K. and O.W. Van Auken. 1991. Importance of time of germination and soil depth on growth of *Prosopis glandulosa* seedling in the presence of a C₄ grass. *American Journal of Botany* **78**: 1732–1739.
- Callison, J., J.D. Brotherson, and J.E. Bowns. 1985. The effects of fire on the blackbrush (*Coleogyne ramosissima*) community of southwest Utah. *Journal of Range Management* **38**: 535–538.
- Campbell, S.E. 1979. Soil stabilization by a prokaryotic desert crust: Implications for Precambrian land biota. *Origins of Life* **9**: 335–348.
- Campbell, S.E., J.S. Seeler, and S. Golubic. 1989. Desert crust formation and soil stabilization. *Arid Soil Research and Rehabilitation* **3**: 217–228.
- Cole, D.N. 1990. Trampling disturbance and recovery of cryptogamic soil crusts in Grand Canyon National Park. *Great Basin Naturalist* **50**: 321–325.
- Coleman, D.C., E.P. Odum, and D.A. Crossley Jr. 1992. Soil biology, soil ecology, and global change. *Biology and Fertility of Soils* **14**: 104–111.
- Crawford, C.S. 1979. Desert detritivores: A review of life history patterns and trophic roles. *Journal of Arid Environments* **2**: 31–42.
- Crawford, C.S. 1991. The community ecology of macroarthropod detritivores. In *Ecology of Desert Communities*, edited by G. Polis, University of Arizona Press, Tucson, Arizona, pp. 89–112.
- Doyen, J.T. and W.F. Tschinkel. 1974. Population size, microgeographic distribution and habitat separation in some tenebrionid beetles. *Annals of the Entomological Society of America* **67**: 617–626.
- Dregne, H.E. 1983a. Physical effects of off-road vehicle use. In *Environmental effects of off-road vehicles: impacts and management in arid regions*, edited by R.H. Webb and H.G. Wilshire, Springer-Verlag, New York, pp. 15–30.
- Dregne, H.E. 1983b. *Desertification of arid lands*, Harwood Academic Publishers, New York, pp. 1–15.
- Ettershank, G., J. Ettershank, M. Bryant, and W.G. Whitford. 1978. Effects of nitrogen fertilization on primary production in a Chihuahuan Desert ecosystem. *Journal of Arid Environments* **1**: 135–139.
- Evans, D. and J.R. Ehrlinger. 1993. Broken nitrogen cycles in arid lands: Evidence from ¹⁵N of soils. *Oecologia* **94**: 314–317.
- Harper, K.T. and J.R. Marble. 1988. A role for nonvascular plants in management of arid and semiarid rangeland. In *Vegetation science applications for rangeland analysis and management*, edited by P.T. Tueller, Kluwer Academic Publishers, Dordrecht, pp. 135–169.
- Harper, K.T. and R.L. Pendleton. 1993. Cyanobacteria and cyanolichens: Can they enhance availability of essential minerals for higher plants? *Great Basin Naturalist* **53**(1): 59–72.
- Hendrix, P.F., D.C. Coleman, and D.A. Crossley Jr. 1992. Using knowledge of soil nutrient cycling processes to design sustainable agriculture. *Journal of Sustainable Agriculture* **2**: 63–82.
- Ingham, E.R., D.C. Coleman, and J.C. Moore. 1989. An analysis of food-web structure and function in a shortgrass prairie, a mountain meadow, and a lodgepole pine forest. *Biology and Fertility of Soils* **8**: 29–37.
- Jeffries, D.L. and J.M. Klopatek. 1987. Effects of grazing on the vegetation of the blackbrush association. *Journal of Range Management* **40**: 390–392.
- Johansen, J.R. 1993. Cryptogamic crusts of semiarid and arid lands of North America. *Journal of Phycology* **29**: 140–147.
- Kitchell, J.F., R.V. O'Neill, D. Webb, G.W. Gallepp, S.M. Bartell, J.F. Koonce, and B.S. Ausmus. 1979. Consumer regulation of nutrient cycling. *BioScience* **29**: 28–34.
- Kleiner, E.F. and K.T. Harper. 1977. Soil properties in relation to cryptogamic ground cover in Canyonlands National Park. *Journal of Range Management* **30**: 202–205.
- Knapp, P. 1992. Soil loosening processes following the abandonment of two arid western Nevada townsites. *Great Basin Naturalist* **52**: 149–154.

- Lange, W. 1974. Chelating agents and blue-green algae. *Canadian Journal of Microbiology* **20**: 1311–1321.
- Larmuth, J. 1978. Temperatures beneath stones used as daytime retreats by desert animals. *Journal of Arid Environments* **1**: 35–40.
- Lesica, P. and J.S. Shelley. 1992. Effects of cryptogamic soil crust on the population dynamics of *Arabis fecunda* (Brassicaceae). *American Midland Naturalist* **128**: 53–60.
- Loope, W.L. and G.F. Gifford. 1972. Influence of a soil microfloral crust on select properties of soils under pinyon-juniper in southeastern Utah. *Journal of Soil and Water Conservation* **27**: 164–167.
- Mack, R.N. and Thompson, J.N. 1982. Evolution in steppe with few large, hooved mammals. *The American Naturalist* **119**: 757–773.
- MacMahon, J.A. 1987. Disturbed lands and ecological theory: An essay about a mutualistic association. In *Restoration ecology*, edited by W.R. Jordan, M. Gilpin, and J.D. Aber, Cambridge University Press, New York, pp. 221–238.
- Mayland, H.F. and T.H. McIntosh. 1966. Availability of biologically fixed atmosphere nitrogen-15 to higher plants. *Nature* **209**: 421–422.
- Mayland, H.F., T.H. McIntosh, and W.H. Fuller. 1966. Fixation of isotopic nitrogen in a semi-arid soil by algal crust organisms. *Soil Science of America Proceedings* **30**: 56–60.
- Metting, B. 1991. Biological surface features of semiarid lands and deserts. In *Semiarid lands and deserts: Soil resource and reclamation*, edited by J. Skujins, Marcel Dekker, Inc., New York, pp. 257–293.
- Peterjohn, W.T. and W.H. Schlesinger. 1990. Nitrogen loss from deserts in the southwestern United States. *Biogeochemistry* **10**: 67–79.
- Romney, E.M., A. Wallace, and R.B. Hunter. 1978. Plant response to nitrogen fertilization in the northern Mohave Desert and its relationship to water manipulation. In *Nitrogen in desert ecosystems*, edited by N.E. West and J.J. Skujins, Dowden, Hutchinson & Ross, Stroudsburg, Pennsylvania, pp. 232–243.
- Rychert, R., J. Skujins, D. Sorensen, and D. Porcella. 1978. Nitrogen fixation by lichens and free-living microorganisms in deserts. In *Nitrogen in desert ecosystems*, edited by N.E. West and J.J. Skujins, Dowden, Hutchinson & Ross, Stroudsburg, Pennsylvania, pp. 20–30.
- Sagan, C., O.B. Toon, and J.B. Pollack. 1979. Anthropogenic albedo changes and the earth's climate. *Science* **206**: 1363–1368.
- St. Clair, L.L., J.R. Johansen, and B.L. Webb. 1986. Rapid stabilization of fire-disturbed sites using a soil crust slurry: Inoculation studies. *Reclamation and Revegetation Research* **4**: 261–269.
- Santos, P.F. and W.G. Whitford. 1981. The effects of microarthropods on litter decomposition in a Chihuahuan Desert ecosystem. *Ecology* **62**: 554–669.
- Schimel, D.S., E.F. Kelly, C. Yonker, R. Aguilar, and R.D. Heil. 1985. Effects of erosional processes on nutrient cycling in semiarid landscapes. In *Planetary ecology*, edited by D.E. Caldwell, J.A. Brierley, and C.L. Brierley, Van Nostrand Reinhold, New York, pp. 571–580.
- Seastedt, T.R. and D.A. Crossley, Jr. 1984. The influence of arthropods on ecosystems. *BioScience* **34**: 157–161.
- Skujins, J. 1984. Microbial ecology of desert soils. *Advances in Microbial Ecology* **7**: 49–91.
- Skujins, J. and B. Klubek. 1978. Nitrogen fixation and denitrification in arid soil cryptogamic crust microenvironments. In *Environmental Biogeochemistry and Geomicrobiology*, vol. 2., edited by W. E. Krumbein, Ann Arbor Publishers, Ann Arbor, Michigan, pp. 543–552.
- Stolzy, G. and A.G. Norman. 1961. Factors limiting microbial activities in soil. *Archiv Mikrobiologie* **40**: 341–350.
- Terry, R.E. and S.J. Burns. 1987. Nitrogen fixation in cryptogamic soils crusts as affected by disturbance. In *Proceedings, Pinyon-Juniper Conference*. Technical Report INT-215, USDA Forest Service, Intermountain Research Station, Ogden, Utah, pp. 369–372.
- Tidemann, A.R., W. Lopushinsky, and H.J. Larsen Jr. 1980. Plant and soil responses to a commercial blue-green algae inoculant. *Soil Biology and Biochemistry* **12**: 471–475.
- Torbert, H.A. and C.W. Wood. 1992. Effects of soil compaction and water-filled pore space on soil microbial activity and nitrogen losses. *Communications in Soil Science Plant Analysis* **23**: 1321–1331.
- Wallwork, J.A. 1982. *Desert soil fauna*, Praeger Scientific Publishers, London.

- Webb, R.H. 1983. Compaction of desert soils by off-road vehicles. In *Environmental effects of off-road vehicles: Impacts and management in arid regions*, edited by R.H. Webb and H.G. Wilshire, Springer-Verlag, New York, pp. 31–80.
- Webb, R.H. and H.G. Wilshire. 1980. Recovery of soils and vegetation in a Mojave Desert ghost town, Nevada, USA. *Journal of Arid Environments* **3**: 291–303.
- West, N.E. 1981. Nutrient cycling in desert ecosystems. In *Arid land ecosystems: Structure, functioning, and management*, vol. 2, edited by D.A. Goodall and R.A. Perry, Cambridge University Press, Cambridge, pp. 301–324.
- West, N.E. and J. Skujins. 1977. The nitrogen cycle in North American cold-winter semi-desert ecosystems. *Oecologia Planta* **12**: 45–53.
- Wilshire, H.G. 1983. The impact of vehicles on desert soil stabilizers. In *Environmental effects of off-road vehicles: Impacts and management in arid regions*, edited by R.H. Webb and H.G. Wilshire, Springer-Verlag, New York, pp. 31–50.
- Zak, J. and W. Whitford. 1988. Interactions among soil biota in desert ecosystems. *Agriculture, Ecosystems, and Environment* **24**: 88–100.