Journal of Arid Environments (2002) 52: 155–165
doi:10.1006/jare.2002.0991, available online at http://www.idealibrary.com on IDEAL®

Impacts of off-road vehicles on nitrogen cycles in biological soil crusts: resistance in different U.S. deserts

Jayne Belnap

*U.S. Geological Survey, Forest and Rangeland Ecosystem Science Center,
Canyonlands Field Station, 2290 S. West Resource Blvd., Moab, UT 84532,
U.S.A.*

(Received 8 October 2001, accepted 17 January 2002)

Biological soil crusts are an important component of desert ecosystems, as they influence soil stability and fertility. This study examined and compared the short-term vehicular impacts on lichen cover and nitrogenase activity (NA) of biological soil crusts. Experimental disturbance was applied to different types of soil in regions throughout the western U.S. (Great Basin, Colorado Plateau, Sonoran, Chihuahuan, and Mojave deserts). Results show that pre-disturbance cover of soil lichens is significantly correlated with the silt content of soils, and negatively correlated with sand and clay. While disturbance appeared to reduce NA at all sites, differences were statistically significant at only 12 of the 26 sites. Cool desert sites showed a greater decline than hot desert sites, which may indicate non-heterocystic cyanobacterial species are more susceptible to disturbance than non-heterocystic species. Sandy soils showed greater reduction of NA as sand content increased, while fine-textured soils showed a greater decline as sand content increased. At all sites, higher NA before the disturbance resulted in less impact to NA post-disturbance. These results may be useful in predicting the impacts of off-road vehicles in different regions and different soils.

Keywords: soil surface disturbance; microbiotic soil crust; arid land; nitrogen cycles; biological soil crust

Introduction

Thirty per cent of the United States consists of semi-arid or arid landscapes (UNEP, 1992). Human use has increased exponentially in most arid and semi-arid lands of the United States since the late 1800s. Historically, most of this use has been livestock grazing in areas where water was accessible; more recently, substantial increases in off-road vehicle and hiking activity have greatly expanded direct human use both spatially and temporally. Although these uses do not directly remove surface material, they still can have profound impacts on soil resources and nutrient cycles. As recovery times in

E-mail: jayne_belnap@usgs.gov

0140-1963/02/020155 + 11 $35.00/0

these ecosystems can be extremely slow, effective management of this vast resource generally means preserving, to the greatest extent feasible, existing ecosystem structure and function.

Recent ecological discussion has addressed the hypothesis that natural disturbance is a major factor in the structuring of communities, or in the words of Reich (1994), 'the normal state of communities and ecosystems is to be recovering from the last disturbance.' Ecosystems are likely to vary in both their resistance and resilience to disturbance. Deserts are generally considered to have both low resistance and resilience to disturbance (Mack & Thompson, 1982). However, it is expected that resistance and resilience to disturbance will vary among deserts as among ecosystems in general. There are many variables that may control an ecosystem's response to disturbance, among them being the soils, flora and fauna, climate, and the type and levels of disturbance that have been present in these systems over evolutionary time. Comparing the response of different desert systems may provide us with the ability to predict what areas will be less able to withstand anthropogenic activity.

Biological soil crusts play an integral part in the functioning of desert ecosystems (see Belnap & Lange, 2001, for review). They are often the dominant source of nitrogen (N) for these ecosystems, therefore we chose to look at the response of nitrogen fixation in crusts as an indicator of resistance to disturbance. Nitrogen in deserts is of concern because N, after water, is generally considered the element most limiting primary productivity in semi-arid and arid ecosystems (Romney *et al.*, 1978). Input rates of N from atmospheric and parent material sources are extremely low in arid regions, and these systems can be dependent on N fixed by biological soil crusts (Evans & Ehleringer, 1993). Previous studies show that soil surface disturbance can greatly reduce or eliminate N fixation in biological soil crusts (Belnap *et al.*, 1994; Belnap, 1995, 1996; Evans & Belnap, 1999). This lack of input from the biological soil crusts is reflected in plant tissue N levels (Harper & Pendleton, 1993; Belnap & Harper, 1995). Since N loss is a continuous process, understanding factors that decrease N availability is of critical importance to maintaining the sustainability of arid systems (Peterjohn & Schlesinger, 1990).

Biological soil crusts in different U.S. deserts generally have similar cyanobacterial and cyanolichen species, but these species occur in different proportions in different regions. This is likely to influence the resistance of a given biological soil crust to disturbance. Crusts in cool deserts (e.g. Colorado Plateau, northern Great Basin) receive most precipitation during winter; cyanobacteria in these crusts are dominated by *Microcoleus vaginatus* (Vauch.) Gom., a cyanobacterial species with only limited N-fixing capability, and contain lesser amounts of *Scytonema myochrous* (Dillwyn) Agardh ex Bornet et Flahault em. Jaag, and *Nostoc* sp., both of which are active N fixers. In these cool desert ecosystems, most of the N input comes from the very active N fixing soil lichen *Collema tenax* (Sw.) Ach. Hot U.S. deserts with mostly summer rainfall (e.g. Chihuahuan, Sonoran, and parts of the Mojave) generally have a much more mixed cyanobacterial flora and are dominated by active N fixers such as *Scytonema* sp., several *Nostoc* species, *Calothrix parietina* (Naeg.) Thur., and *Schizothrix calcicola* (Ag.) Gom. In contrast to the cooler deserts, these deserts have only small amounts of *Microcoleus* and much less *Collema tenax* cover (Rosentreter & Belnap, 2001).

Management of off-road vehicles is a major challenge for most land managers in deserts, yet only a handful of studies have addressed their impacts. The few studies done show that off-road vehicles compact soils, crush vegetation and crusts, and increase soil erosion (reviewed in Webb & Wilshire, 1983). As off-road use is increasing throughout the world, it is a relevant agent to use for disturbance treatments. Thus, this project was intended to establish if, and how, off-road vehicle activity affects N inputs in deserts with different climates, crust floras, and disturbance regimes over evolutionary time. Accordingly, experimental off-road disturbance was applied to biological soil crusts in five U.S. desert regions (Chihuahuan, Sonoran, Mojave, Great Basin, and Colorado Plateau) and the short-term impact of this disturbance to nitrogenase activity (as an indicator of nitrogen fixation) in the crusts was measured.

Methods

Plots were established in spring 1993 on the southern Colorado Plateau 15 miles south of Moab, UT (cool desert, summer rains), during spring 1995 in the Sonoran Desert (Organ Pipe National Monument near Ajo, AZ; hot desert, summer rains), the Mojave Desert (Joshua Tree National Monument near Joshua Tree, CA; hot desert, winter rains), the Chihuahuan Desert (Jornada Experimental Range near Las Cruces, NM; hot desert, summer rain), the northern Colorado Plateau (Dinosaur National Monument near Vernal, UT; cool desert, summer rains) and the Great Basin Desert (Dugway Proving Grounds, Dugway, UT; cool desert, winter rains). Additional plots were established in the Mojave Desert (Nevada Test Site near Mercury, NV) in spring 1996.

Biological soil crust cover and composition was determined over a 0·5 ha area before the disturbance was applied using a 25 cm^2 quadrat frame, with a minimum of 20 plots per site. Two composite soil samples consisting of 30 subsamples each were collected for textural and nutrient analyses. These were sifted through a 2 mm sieve and then sent to the Brigham Young University Soil and Plant Analysis Lab in Provo, UT for analysis of cation exchange capacity, organic matter, K, Na, Ca, Mg, Cu, Fe, Mn, Zn, and N.

Disturbance consisted of driving a GM Suburban four-wheel drive vehicle with fully inflated tires over a dry soil surface four times (driving back and forth two times). Variability in the treatment effect was reduced by driving slowly so that the soil surface was crushed but not churned. This was considered a conservative disturbance, as most off-road vehicles accelerate while driving over the soil surface and soil is both crushed and turned over, burying biological soil crust organisms. At least two parallel tracks were established at each site.

Nitrogenase activity (NA: used to estimate nitrogen fixation rates) was measured immediately after the disturbance. Ten samples were collected from within each track, and ten samples from outside each of the two tracks, resulting in a minimum of 20 samples in and 20 samples outside tracks for each site; sites with multiple tracks had higher numbers of samples. Samples were placed in clear, gas-tight tubes, the entire crustal surface wetted equally with distilled water, and then injected with enough acetylene to create a 10% acetylene atmosphere (Belnap, 1996). After injection, samples were incubated for 4 h at 26°C in a chamber lighted with Chromo50 (5000 K) and cool white fluorescent bulbs. Subsamples (0·25 ml) of the head space within the tubes were then analysed for acetylene and ethylene content on a Schimadzu FID gas chromatograph equipped with an 8-foot, 8% NaCl on alumina column, using helium as the carrier gas (30 ml min^{-1}).

All statistical analysis was done using a SPSS statistical package (SPSS, 1999). Data at individual sites were analysed for normality. The disturbed tracked area and undisturbed untracked area were compared using a *t*-test when data had a normal distribution or the Kolmogorov–Smirnov *Z* test (using log-transformed data) when data did not have a normal distribution. Pearson's correlation coefficients were also calculated for the following combinations of sites: all sites, non-gypsum sites (gypsum crusts are much more resistant to crushing than the other substrates tested), cool deserts, hot deserts, hot deserts without gypsum soils, sandy soils (>60% sand), and fine-textured (>40% clay and silt) soils. Results are reported as significant when $p < 0{\cdot}05$ unless otherwise noted.

Results and discussion

Crust cover

Table 1 summarizes the crust cover, soil texture, and the percent decline of NA of the sampled sites. This experiment covered a wide range of crust and soils types: total lichen cover ranged from 0% to 66%, the N-fixing lichen *Collema* cover ranged from 0% to 48%, and cyanobacterial cover ranged from 29% to 100%. Soils ranged from coarse to fine-textured.

In this study, cover of *Collema* and other lichens was highly correlated with soil texture in most of the site groupings (Table 2). Both *Collema* and other lichen cover decreased with increasing sand. *Collema* cover increased with increases in silt, while other lichens increased with increases in clay. Both *Collema* and other lichen cover was positively correlated with soil Ca content, while cyanobacterial cover was negatively correlated with soil Ca.

Gypsum soils consistently had the highest *Collema* and total lichen cover of all soil types. This is a pattern that has been observed globally (Belnap *et al.*, 2001). It is not known why gypsiferous soils provide such a favorable environment for lichens, but it has been speculated that gypsum provides high levels of stability, P, Ca, and/or high water availability.

While overall lichen cover, in general, is lower in desert regions with summer rainfall around the world (Eldridge, 2001; Rosentreter & Belnap, 2001), only a few published studies have addressed the environmental controls on specific species. A study of 70 sites in the Mojave Desert showed a similar result for *Collema* cover as this study, with cover positively correlated with silt ($r = 0{\cdot}78$). Higher silt likely corresponds with greater water-holding capacity of soils. Because biological soil crust organisms are only active when wet, and water is limited in deserts, greater soil moisture retention times mean longer periods of metabolic activity for *Collema*. While results from this study showed no correlation between *Collema* cover and soil P, data from the Mojave Desert showed soil P was also very important in predicting *Collema* cover.

Nitrogenase activity

Twelve of the 26 tested sites showed significantly lower NA in disturbed areas relative to controls immediately following application of the disturbance treatment (Table 1). Two additional sites were significantly different at $p < 0{\cdot}10$. Decline in NA at these 14 sites ranged from 27% to 100%, and included both hot and cool desert sites. Of the 13 sites that did not show significant decline, 11 did have lower values in the disturbed area relative to the control, indicating most sites tend to be impacted by off-road vehicle activity. This result is similar to previous studies on the Colorado Plateau and the Great Basin which found that soil surface disturbance greatly reduces or eliminates nitrogenase activity in biological soil crusts (Belnap *et al.*, 1994; Belnap, 1995, 1996). Three study sites in Joshua Tree (sand 2), Organ Pipe (sand 1), and Jornada Experimental Range (sand 2) had a high rock cover. After disturbance was applied, the tracks could not be visually identified, and no decline in nitrogenase activity was detected. This indicates that sufficient rock cover can prevent vehicular traffic from reducing NA in biological soil crusts.

Cool desert sites showed significantly greater decline in NA after disturbance than hot desert sites ($p < 0{\cdot}05$). Cool desert sites were most susceptible to disturbance when pre-disturbance NA was low and soils were coarse-textured. While coarse-textured soils in hot deserts were also more susceptible to disturbance, this effect was less pronounced than at cool desert sites. These results are best explained by considering the different features of the dominant cyanobacteria in these two types of

Table 1. *Study site characteristics, including desert type, year study site established, pre-disturbance crust cover, soil texture, and percent decline in nitrogenase activity following disturbance*

					%Cover			Soil%			% decline nitrogenase activity
Desert	Desert type	Site	Year established	Track ID	*Collema* sp.	Cyanobacterial Crust	Other Lichens	Sand	Clay	Silt	
Mojave	Hot	Nevada Test Site	1996	Sand	13	29	0	70	12	18	70***
		Joshua Tree NP	1995	Sand 1	nd	nd	nd	80	9	12	100***
				Sand 2	nd	nd	nd	77	7	16	−1
Sonoran	Hot	Organ Pipe NM	1995	Silt 1	7	88	0	60	11	29	14
				Silt 2	13	80	0	65	9	25	42***
				Silt 3	24	64	7	49	15	37	32**
				Silt 4	nd	nd	nd	55	12	32	27**
Chihuahuan	Hot	Jornada Experimental Range	1995	Sand 1	nd	nd	nd	80	7	12	3
				Sand 1	6	81	13	61	20	19	18
				Sand 2	3	94	3	61	21	18	−73
				Sand 3	4	77	19	61	21	18	13
				Silt 1	3	90	7	55	27	18	50**
				Silt 2	3	70	27	45	35	21	42**
				Silt 3	8	75	18	50	31	19	57
		Holloman AFB	1995	Gypsum 1	28	61	7	42	g	g	27
				Gypsum 2	29	58	11	38	g	g	27
				Gypsum 3	48	33	18	43	g	g	36
		Whitesands NM	1995	Gypsum 1	29	57	10	54	g	g	16
				Gypsum 2	32	39	21	47	g	g	44
				Gypsum 3	22	63	7	50	g	g	44*
Colorado Plateau	Cool	Arches NP[a]	1992	Sand 1	5	95	0	78	11	11	51**
				Sand 2	0	100	0				87**
		Dinosaur NM	1996	Silt	10	61	10	nd	nd	nd	86***
Great Basin	Cool	Dugway Proving Grounds	1995	Sand 1	2	nd	nd	83	9	8	65***
				Sand 2	1	nd	nd	74	13	13	37**
				Silt 1	1	nd	nd	44	28	28	25*
				Silt 2	0	nd	nd	66	14	20	31

[a] Arches sites were directly adjacent so soil characterization was done once for the entire site.

Note: nd = no data; g = gypsum soils; * = $p<0{\cdot}10$, ** = $p<0{\cdot}05$, *** = $p<0{\cdot}01$

Table 2. *Correlations of Collema cover, other lichen cover, and cyanobacterial biomass with soil characteristics for different combinations of sites*

	% Stand		% Silt		% Clay		Ca, ppm	
	r	Site grouping	*r*	Site grouping	*r*	Site grouping	*r*	Site grouping
Collema sp. cover	−0·65**	All	+0·77**	All	−0·60*	Hot, NG	+0·84**	All
	−0·60**	Hot	+0·77**	NG	−0·56*	Hot	+0·92*	Sand
			+0·85**	Silt				
			+0·76**	Hot, NG				
			+0·75**	Hot				
Other lichen cover	−0·63**	All			+0·86**	All	+0·63*	NG
	−0·67**	NG			+0·84**	NG	+0·80*	Silt
	−0·84**	Silt			+0·90**	Silt		
	−0·75*	Sand			+0·78*	Sand		
	−0·63*	Hot, NG			+0·81**	Hot, NG		
Cyanobacteria biomass	+0·52**	All					−0·60**	All
							+0·96**	Sand

All = all data pooled; NG = no gypsum soils included; Fine = sites with fine-textured soils (<60% sand); Sand = sandy sites (>60% sand); Cool = cool desert sites; Hot = hot desert sites. Only values with significant correlations were listed, with * = $p<0{\cdot}05$, ** = $p<0{\cdot}01$

desert. The cyanobacterial flora of cool deserts is dominated by the large, highly mobile, non-heterocystic *Microcoleus vaginatus* that fixes very low amounts of N (Belnap & Gardner, 1993; Steppe *et al.*, 1996). Lack of heterocysts means this species must employ other means of excluding oxygen such as creating micro-anaerobic zones in the soil through packing together of multiple organisms or within the extra-cellular polysaccharide sheath surrounding the cyanobacteria (Belnap, 1996; Steppe *et al.*, 1996). Such micro-anaerobic zones could be easily disrupted with soil surface disturbance. In addition, the low N-fixing capability of *Microcoleus* means N inputs from N-fixing lichens such as *Collema* are very important for cool desert ecosystems.

In contrast, the cyanobacterial flora of hot deserts is dominated by small, relatively non-mobile, heterocystic species such as *Schizothrix*, *Calothrix*, and *Nostoc* that fix high amounts of N (Cameron, 1969), while cover by *Collema* is limited and patchy. Because these cyanobacteria have heterocysts, they do not rely on external conditions for oxygen exclusion. Consequently, disruption of NA with disturbance appears less likely when communities are dominated by heterocystic cyanobacteria rather than the non-heterocystic *Microcoleus*.

These data also show that in hot deserts, NA declines were lower at sites with higher cyanobacterial and lower *Collema* cover. This result was opposite that found in a previous study at cool desert sites, where cyanobacteria-only sites were more sensitive to off-road vehicle impacts than sites with high *Collema* cover (Belnap, 1996). In *Collema*, the nitrogen-fixing cyanobacterial partner is embedded in fungal tissue and thus is likely to be well-protected from exposure to oxygen even when lichen pieces are broken off. However, if the pieces are buried, they will die. Thus, susceptibility of *Collema* in different deserts is probably dependent on soil characteristics (e.g. soils that are easily churned will probably result in higher mortality). In contrast, the increased sensitivity of cyanobacteria in cool deserts over hot deserts may be explained by the hypothesis that heterocystic species are less susceptible to disturbance than non-heterocystic species (as discussed above), especially if oxygen exclusion is attained by clumping of the organisms. If this is true, understanding the factors that control the composition of cyanobacterial communities may be important in predicting the effects of soil surface disturbance in different regions.

Most of the data in this study show NA rates in both disturbed and undisturbed sites decline as sand content increases, while increasing with an increase in clay content (Table 3). Sandy soils, having lower aggregate stability than finer-textured soils, are less stable and more likely to be disrupted with the same type and intensity of disturbance than finer-textured soils. Stability is needed both for the formation of micro-anaerobic zones as well as for colonization of N-fixing lichens. Thus, it is expected that sandy soils would have lower NA before and after disturbance than fine-textured soils, and that this pattern would be most pronounced where NA requires more stability: that is, in cool deserts dominated by *Microcoleus*. Other studies from cool deserts show similar results when disturbed by vehicles: NA in sandy soils declined 76–89% while NA in finer-textured soils declined 25–40% (Belnap *et al.*, 1994; Belnap, 1995, 1996).

Some of the sites chosen for this study were dominated by gypsiferous soils. The surface of the gypsum soils was much more difficult to disrupt with the vehicle than any of the other soil types tested (except where high gravel soils prevented formation of any identifiable tracks). For this reason, we tested correlations of the different variables and NA with and without the gypsiferous sites. Exclusion of the gypsum sites did not alter whether or not there was a significant correlation with any variable, but exclusion of the gypsum sites did result in higher correlation coefficients. The small number of gypsum sites precluded analysis of those sites alone.

Sandy soils (>60% sand) were also analysed separately from finer-textured (<60% sand) soils. NA on finer-textured soils in both disturbed and undisturbed sites was

Table 3. *Correlation coefficients for different combinations of sites*

	Nitrogenase activity, undisturbed		Soil texture						Cyano-bacteria cover		Other lichen cover	
			% Sand		% Silt		% Clay					
	r	Site grouping	*r*	Site grouping	*r*	Site grouping	*r*	Site grouping	*r*	Site grouping	*r*	Site grouping
% Decline in nitrogenase activity	−0·67*	Cool	−0·54*	Fine	−0·73**	Cool	+0·65**	Fine	−0·61**	Hot, NG		
			+0·57**	Sand			−0·58**	Sand	−0·49**	Hot		
			+0·72**	Cool			−0·68*	Cool				
Nitrogenase activity, disturbed	+0·90***	All	−0·38**	All	+0·78**	Cool, NG	+0·59***	All			+0·59***	All
	+0·91***	NG	−0·55***	NG			+0·67***	NG			+0·67***	NG
	+0·95***	Fine	−0·87**	Cool			+0·71***	Sand			+0·82***	Fine
	+0·74***	Sand	−0·48**	Hot, NG			+0·93***	Cool			+0·72***	Hot, NG
	+0·96***	Cool	−0·35*	Hot			+0·63***	Hot, NG			+0·59***	Hot
	+0·90***	Hot, NG					+0·56***	Hot				
	+0·90***	Hot										
Nitrogenase activity, undisturbed			−0·34**	All			+0·63***	All			+0·71***	All
			−0·47**	NG			+0·65***	NG			+0·74***	NG
			−0·59***	Fine			+0·68***	Fine			+0·92***	Fine
			−0·70*	Cool			+0·81***	Cool			+0·79***	Hot, NG
			−0·58***	Hot, NG			+0·71***	Hot, NG			+0·73***	Hot
			−0·48***	Hot			+0·71***	Hot				

Note: All = all data pooled; NG = no gypsum soils included; Fine = sites with fine textured soils (<60% sand); Sand = sandy sites (>60% sand), Cool = cool desert sites; Hot = hot desert sites. Only values with significant correlations were listed, with * = $p<0·10$, ** = $p<0·05$, *** = $p<0·01$.

more often significantly correlated with soil variables than NA on sandy soils, indicating that NA on finer-textured soils may be more predictable than on sandy soils. The relationship between soil texture and response to disturbance NA was also of interest. When the sandy sites were analysed alone, both increasing sand content and a decline in clay resulted in greater NA decline after disturbance. Within the finer-textured sites, the response was the opposite: more sand and less clay resulted in less damage. This may indicate a threshold response: while some clay or sand confers resistance to disturbance, too much of either may increase susceptibility to disturbance.

All data showed a very high correlation between NA in disturbed and undisturbed soils, indicating that the susceptibility to disturbance can be predicted from pre-disturbance conditions. Interestingly, at most sites other than cool deserts, the total cover of all lichens other than *Collema* was highly correlated with both pre- and post-disturbance NA levels, while the cover of *Collema* was not correlated with either NA level. This may be explained by the presence of N-fixing *Heppia* and *Peltula* at hot desert sites, which were not distinguished by species.

Earlier studies showed that short-term declines in NA are often followed by even greater declines in NA over time (Belnap, 2001). This is presumably due to subsequent death of buried material, as the dominant N fixers are all photosynthetic organisms. Similarly, a further decline at these study sites is expected over time. Decreased N inputs from crusts can have long-term impacts on soil and plant N. Jeffries (1989) found 50% less N in grazed soils compared to adjacent ungrazed soils where *Collema* cover had declined as well. Evans & Belnap (1999) found that grazed soils had a 42% decrease in soil N and a 34% decrease in plant tissue N when compared to nearby ungrazed soil. Plants growing in crusted soils have higher tissue concentrations of N than those growing in uncrusted soils (Harper & Pendleton, 1993; Belnap & Harper, 1995; Harper & Belnap, 2001). Other studies have documented that N fixed by crusts is utilized by nearby plants and other surrounding organisms including fungi, actinomycetes, and bacteria (Stewart, 1967; Jones & Stewart, 1969*a*, *b*; Rogers & Burns, 1994). Disturbance of biological soil crusts also decreases soil stability and albedo, both of which can influence N inputs and N cycles (Williams *et al.*, 1995*a*, *b*; Belnap, 1995, 1996; Belnap & Gillette, 1997, 1998). Thus, reductions in N inputs from crusts can have large implications for N cycles in places dominated by biological soil crusts, and should be considered in land management decisions.

Many thanks to Gary Gurtler, Danielle Barr, Cindy Furman, Lynda Sperry, Sue Rutman, Jane Rogers, and Jeff Herrick for field assistance. Special thanks to Sue Phillips for editorial and graphics assistance. Funding from the National Park Service is gratefully acknowledged.

References

Belnap, J. (1995). Soil 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. (2001). Factors influencing nitrogen fixation and nitrogen release in biological soil crusts. In: Belnap, J. & Lange, O.L. (Eds), *Biological Soil Crusts: Structure, Function, and Management*, pp. 241–261. *Ecological Studies*, Vol. 150. Berlin: Springer-Verlag. 503 pp.

Belnap, J. & Gardner, J. (1993). Soil microstructure in soils of the Colorado Plateau: the role of the cyanobacterium *Microcoleus vaginatus. Great Basin Naturalist*, **53**: 40–47.

Belnap, J. & Gillette, D.A. (1997). Disturbance of biological soil crusts: impacts on potential wind erodibility of sandy desert soils in SE Utah. *Land Degradation and Development*, **8**: 355–362.

Belnap, J. & Gillette, D.A. (1998). Vulnerability of desert soil surfaces to wind erosion: impacts of soil texture and disturbance. *Journal of Arid Environments*, **39**: 133–142.

Belnap, J. & Harper, K.T. (1995). 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. & Lange, O.L. (Eds) (2001). Biological Soil Crusts: Structure, Function, and Management. *Ecological Studies*, Vol. 150. Berlin: Springer-Verlag. 503 pp.

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., Büdel, B. & Lange, O.L. (2001). Biological soil crusts: characteristics and distribution. In: Belnap, J. & Lange, O.L. (Eds), *Biological Soil Crusts: Structure, Function and Management*, pp. 3–30. *Ecological Studies*, Vol. 150. Berlin: Springer-Verlag. 503 pp.

Cameron, R.E. (1969). Abundance of microflora in soils of desert regions. National Aeronautics and Space Administration, Jet Propulsion Laboratory, Technical Report 32–1378. Pasadena, CA: California Institute of Technology. 16 pp.

Eldridge, D. (2001). Biological soil crusts and water relations in Australian deserts. In: Belnap, J. & Lange, O.L. (Eds), *Biological Soil Crusts: Structure, Function and Management*, pp. 31–50. *Ecological Studies*, Vol. 150. Berlin: Springer-Verlag. 503 pp.

Evans, R.D. & Belnap, J. (1999). Long-term consequences of disturbance on nitrogen cycling in an arid grassland. *Ecology*, **80**: 150–160.

Evans, D. & Ehleringer, J.R. (1993). Broken nitrogen cycles in aridlands: evidence from ^{15}N of soils. *Oecologia*, **94**: 314–317.

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.

Harper, K.T. & Pendleton, R.L. (1993). Cyanobacteria and cyanolichens: Can they enhance availability of essential minerals for higher plants? *Great Basin Naturalist*, **53**: 59–72.

Jeffries, D.L. (1989). The vegetation, soil, and cryptogamic crusts of blackbrush communities in the Kaiparowits Basin. Ph.D. dissertation, Arizona State University, Tempe, Arizona. 157 pp.

Jones, K. & Stewart, W.D.P. (1969*a*). Nitrogen turnover in marine and brackish habitats. III. The production of extracellular nitrogen by *Calothrix scopulorum*. *Journal of Marine Biology Association U.K.*, **49**: 476–488.

Jones, K. & Stewart, W.D.P. (1969*b*). Nitrogen turnover in marine and brackish habitats. IV. Uptake of the extracellular products of the nitrogen fixing algae *Calothrix scopulorum*. *Journal of Marine Biology Association U.K.*, **49**: 701–716.

Mack, R.N. & Thompson, J.N. (1982). Evolution in steppe with few large, hooved mammals. *The American Naturalist*, **119**: 757–773.

Peterjohn, W.T. & Schlesinger, W.H. (1990). Nitrogen loss from deserts in the southwestern United States. *Biogeochemistry*, **10**: 67–79.

Reich, S.R. (1994). Nonequilibrium determinants of community structure. *American Scientist*, **82**: 424–435.

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.

Romney, E.M., Wallace, A. & Hunter, R.B. (1978). Plant response to nitrogen fertilization in the northern Mojave Desert and its relationship to water manipulation. In: West, N.E. & Skujins, J. (Eds), *Nitrogen in Desert Ecosystems*, pp. 232–243. Stroudsburg, PA: Dowden, Hutchinson, and Ross. 307 pp.

Rosentreter, R. & Belnap, J. (2001). Biological soil crusts of North America. In: Belnap, J. & Lange, O.L. (Eds), *Biological Soil Crusts: Structure, Function and Management*, pp. 31–50. *Ecological Studies*, Vol. 150. Berlin: Springer-Verlag. 503 pp.

SPSS, Inc. 1999. *SPSS Base* 10 *Applications*. Chicago, IL.

Steppe, T. F., Olson, J.B., Paerl, H.W., Litaker, R.W. & Belnap, J. (1996). Consortial N_2 fixation: a strategy for meeting nitrogen requirements of marine and terrestrial cyanobacterial mats. *FEMS Microbiology Ecology*, **21**: 149-156.

Stewart, W.D.P. (1967). Transfer of biologically fixed nitrogen in a sand dune slack region. *Nature*, **214**: 603–604.

UNEP (United Nations Environmental Program) (1992). *World Atlas of Desertification*. London: Edward Arnold Publishers. 69 pp.

Webb, R.H. & Wilshire, H.G. (Eds) (1983). *Environmental Effects of Off-Road Vehicles: Impacts and Management in Arid Regions*. New York: Springer-Verlag. 534 pp.

Williams, J.D., Dobrowolski, J.P., West, N.E. & Gillette, D.A. (1995*a*). Microphytic crust influence on wind erosion. *Transactions of the American Society of Agricultural Engineers*, **38**: 131–137.

Williams, J.D., Dobrowolski, J.P. & West, N.E. (1995*b*). Microphytic crust influence on interrill erosion and infiltration capacity. *Transactions of the American Society of Agricultural Engineers*, **38**: 139–146.