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ORIGINAL PAPER

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Soil surface disturbances in cold deserts: effects on nitrogenase activity in cyanobacterial-lichen soil crusts

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Abstract Cyanobacterial-lichen soil crusts can be a dominant source of nitrogen for cold-desert ecosystems. Effects of surface disturbance from footprints, bike and vehicle tracks on the nitrogenase activity in these crusts was investigated. Surface disturbances reduced nitrogenase activity by 30–100%. Crusts dominated by the cyanobacterium *Microcoleus vaginatus* on sandy soils were the most susceptible to disruption; crusts on gypsiferous soils were the least susceptible. Crusts where the soil lichen *Collema tenax* was present showed less immediate effects; however, nitrogenase activity still declined over time. Levels of nitrogenase activity reduction were affected by the degree of soil disruption and whether sites were dominated by cyanobacteria with or without heterocysts. Consequently, anthropogenic surface disturbances may have serious implications for nitrogen budgets in these ecosystems.

Key words Cryptobiotic · Cryptogamic · Microphytic · Microbiotic · Deserts · Nitrogen fixation · Nutrient cycling · Lichens · *Microcoleus vaginatus* · *Collema tenax* · Heterocysts · Acetylene reduction assay · ARA

Introduction

Nitrogen concentrations are known to be low in desert ecosystems relative to other systems. Total atmospheric input over the past 10000 years has been conservatively estimated at ca. 3 kg N m^{-2} (ignoring cyanobacteria inputs), with 77% lost through wind erosion, ammonia volatilization, nitrification, and denitrification (Peterjohn and Schlesinger 1990). Extensive surveys in cold deserts have revealed only a few nitrogen-fixing plants (Farnsworth et al. 1976; Wullstein 1989). Since nitrogen can limit net primary productivity in many desert ecosystems (Ettershank et al. 1978; James and Jurinak 1978; Romney et al. 1978; Fisher et al. 1988; Nobel et al. 1988), any biological input is critical to the fertility of cold-desert regions.

Most cold deserts are dominated by cyanobacterial-lichen (cryptobiotic, microphytic or microbiotic) soil crusts. These crusts cover interspaces between and under vascular plants, often constituting 70% or more of the living ground cover (Belnap 1995). They are capable of atmospheric nitrogen fixation; this activity has been demonstrated to increase nitrogen levels of nearby vascular plants (Mayland et al. 1966; Mayland and MacIntosh 1966; Harper and Pendleton 1993; Belnap 1994, 1995; Belnap and Harper 1995). Since rainfall events in desert areas are often too small to promote plant growth, but do stimulate microbial community activity, soil crusts may contribute greater nitrogen than nitrogen-fixing plant species. Evans and Ehlringer (1993) showed that soil crusts were the dominant contributor of fixed nitrogen in a cold-desert juniper woodland community. In addition, the presence of crusts helps maintain fertility of plant interspaces, counteracting the tendency of nutrients to concentrate around perennial plants.

Nitrogen fixation in soil crusts has been examined on several occasions, with input estimates ranging from 0.02 to 365 kg ha^{-1} annually (Mayland et al. 1966; MacGregor and Johnson 1971; Rychert and Skujins 1974; Eskew and Ting 1978; Jeffries et al. 1992); the lowest estimates are almost 10 times atmospheric input estimates by Peterjohn and Schlesinger (1990). Nitrogen fixation is highly dependent on past and present water and light regimes, as well as species composition (Rychert et al. 1978; Belnap 1994). Timing, extent and type of past disturbance may also be a critical factor in determining fixation rates.

Most soil crusts in the cold-desert regions of the Colorado Plateau (southern Utah, northern Arizona, and western Colorado) are dominated by the cyanobacterium *Microcoleus vaginatus*. Well developed, undisturbed crusts also contain the cyanobacterium *Scytonema myochrous* and the soil lichen *Collema tenax* (with the cyanobacterium *Nostoc* as a phycobiont). *M. vaginatus* is a filamentous species that occurs as multiple filaments contained within a single, extracellular polysaccharide sheath. This species

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lacks heterocysts, the structurally differentiated, oxygen-excluding cells where cyanobacterial nitrogen fixation generally takes place. In contrast, *S. myochrous* and *Nostoc* are both heterocystic species. All three species are capable of both light and dark nitrogen fixation (Pearson et al. 1981; Paerl 1990; Belnap 1994).

Response to, and recovery from, disturbance has been investigated in cryptobiotic crusts (Anderson et al. 1982; Jeffries and Klopatek 1987; Callison et al. 1985; Harper and Marble 1990; Cole 1991; Belnap 1993). Recovery has traditionally been measured as visual recovery or by estimates of biomass or numbers of organisms present. Effects on physiology have not been addressed. However, a recent study at Dugway Proving Grounds, Utah, demonstrated that disturbance does affect the physiological functioning of crusts dominated by *Nostoc* sp. (Belnap et al. 1994). Plots receiving surface disturbances including raking, scalping, and compression by a tracked vehicle showed a 77–90% decrease in nitrogenase activity 9 months after the disturbance.

Many of the surface soils in the western United States receive compressional and shear disturbances in the form of human trampling and off-road vehicle use. This study examines the effects of these types of activities on nitrogenase activity in crusts on sandy and gypsiferous soils dominated by *M. vaginatus*.

Materials and methods

Three study sites were used. The first was located in Arches National Park, approximately 16 km north of Moab, Utah, on sandstone-derived soils. *Coleogyne ramosissima* (blackbrush) was the dominant vascular plant at this site. Two types of crusts were present. One was dominated by *M. vaginatus* with no lichens present (referred to as cyanobacterial crusts) and the other contained *M. vaginatus*, the cyanobacterium *S. myochrous* and approximately 5% cover of the nitrogen-fixing soil lichen *C. tenax* (referred to as lichen crust). At Arches, two replicates of all treatments were applied in April 1992. These included one or three passes with a free-rolling Toyota Landcruiser, a knobby-tired mountain bike, or a Vibram-soled boot. These treatments were then resampled in June and October 1992.

The second site, also on sandstone-derived soils, was located in the Behind-the-Rock (BTR) area, 15 km south of Moab, Utah. This site was dominated by *C. ramosissima* as well. Lichen crusts were treated at this site. Two replicates of different treatments were applied at four dates between June and December 1992. Because no significant differences were seen between one and three passes in previous trials, all treatments at this site were one-pass treatments. Treatments included a Toyota Landcruiser; a knobby-tired mountain bike; a deeply knobbed Vibram-soled boot; a medium-deep, knobbed tennis shoe; a smooth-soled sandal; and a small wooden block (15×30 cm) that was stepped on one time to compress the soil with the least possible shear force.

The third site was located 1.5 km west of Moab, Utah, on soils derived from Paradox gypsum. The dominant vascular plant was *Atriplex confertifolia*. The soil lichen *C. tenax* represented approximately 25% of the ground cover, with *M. vaginatus* and *S. myochrous* both present. At this site, two replicates of all treatments were applied in October 1992, and included three passes with a Toyota Landcruiser, one pass with a deeply knobbed vibram-soled boot, or one pass with a smooth-soled sandal.

Difficulty in protecting treatments from vandalism and space constraints resulted in two replicates of all treatments. Each replicate was in a plot approximately 35×70 m. Treatments were applied at the beginning of the study; plots were then sampled through time. Compressional force for the Landcruiser was calculated at 13680 kg m^{-2}, the mountain bike at 15240 kg m^{-2}, and all foot treatments at 29 kg m^{-2}. Shear forces were not calculated. Soil surface disruption resulting from treatments was visually assessed as minor, moderate, or severe.

Preliminary nitrogenase activity and chlorophyll *a* analyses were done to assure that the sites were equal with respect to those variables. No significant differences were seen within sites. All soils had less than 1% soil moisture (gravimetrically determined) when the treatments were applied. Nitrogenase activity and chlorophyll *a* concentrations were analyzed in disturbed areas and directly adjacent controls immediately after treatments were applied; selected treatments were then sampled over time. Since nitrogenase levels naturally fluctuate throughout the year, controls and treatments were sampled simultaneously throughout the experiment.

For nitrogenase activity analyses, twenty 5.1-cm^2 samples were randomly collected dry from each replicate of each treatment and adjacent controls. Samples were placed in clear, gas-tight tubes; the entire crustal surface was wetted equally with distilled water, and then injected with enough acetylene to create a 10% acetylene atmosphere. After injection, samples were incubated for 4 h at 26°C in a chamber lit with Chromo50 (5000 K) and cool white fluorescent bulbs. Subsamples (0.25 ml) of the head space within the tubes were then analyzed for acetylene and ethylene content on a Carle FID gas chromatograph equipped with a 2.4-m, 8% NaCl on alumina column, using helium as the carrier gas (30 ml min^{-1}). Calibrations with ethylene standards were done at the time of observations. Results are reported in nmol C_2H_2 m^{-2} h^{-1}.

Chlorophyll *a* concentrations have long been used to estimate cyanobacterial and green algal biomass (Pearl 1990), and were used to estimate cyanobacterial biomass in this study. Fifteen samples of dry soil were collected from type of treatment and adjacent controls. Samples were extracted immediately with dimethylsulfoxide (DMSO) in the dark for 45 min at 65°C (Ronen and Galun 1984). Samples were then shaken and centrifuged. Absorption spectra were measured in a Hewlett-Packard diode array spectrophotometer, after calibration with a DMSO blank. Optical densities used for measurements were at OD 398 (chlorophyll *a*) and OD 665 (both chlorophyll *a* and phaeophytin).

Results were analyzed using analysis of variance (ANOVA), Duncan's multiple range test, and, where only two treatments were applied, an unpaired *t*-test. Results were deemed significant when $P<0.05$.

Results

Surface disturbance significantly reduced nitrogenase activity in crusts with almost all types and levels of treatments. Cyanobacterial biomass, as estimated by chlorophyll *a* concentrations, was not significantly different from controls in any of the treatments (Table 1), indicating nitrogenase activity reductions were not a result of decreased cyanobacterial or lichen biomass.

Four-wheel drive vehicle and mountain bike

All sites showed significantly lowered nitrogenase activity when impacted by a four-wheel drive vehicle or mountain bike. Between all sites and treatment dates, one pass of a four-wheel drive vehicle reduced nitrogenase activity 40–92% (Fig. 1). At Arches, activity in the cyanobacterial crusts was reduced 86–88%, and in the lichen crusts, 49–52%. At BTR, vehicular tracks reduced activity by 40–92% in the lichen crusts. These results suggest that, in the

Table 1 Biomass estimates of treatments and adjacent controls at Arches (cyanobacterial crusts) and BTR (cyanobacterial and lichen crusts), using chlorophyll *a* concentrations (μg mg^{-1}). No significant differences were found between controls and treatment type

	Arches Vehicle Cyano,	BTR				
		Bike Cyano.	Deep boot Cyano.	Vehicle Cyano.	Vehicle Lichen	Medium boot Lichen
Treated	0.26±0.32	0.18±0.06	0.21±0.10	0.57±0.19	1.21±0.49	1.00±0.36
Control	0.32±0.32	0.22±0.14	0.39±0.14	0.70±0.31	0.96±0.48	0.96±0.48
P value	<0.36	<0.32	<0.19	<0.09	<0.42	<0.10

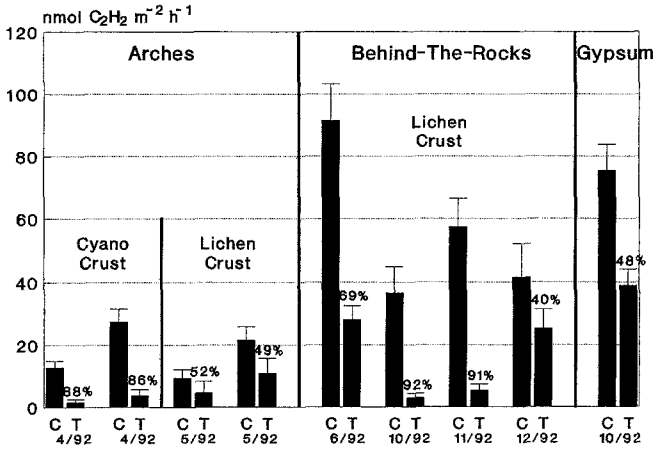

Fig. 1 Nitrogenase activity levels immediately after one pass with a four-wheel drive vehicle at Arches (cyanobacterial and lichen crust), Behind-the-Rocks (lichen crust) and Gypsum (lichen crust) sites. All treatments (*T*) were compared with an adjacent control (*C*) Percentages represent the percent declines in nitrogenase activity when compared to adjacent controls. all treatment values were significantly different from controls ($P<0.05$). *Error bars* indicate 1 SD. Dtes indicate time of treatment and analysis

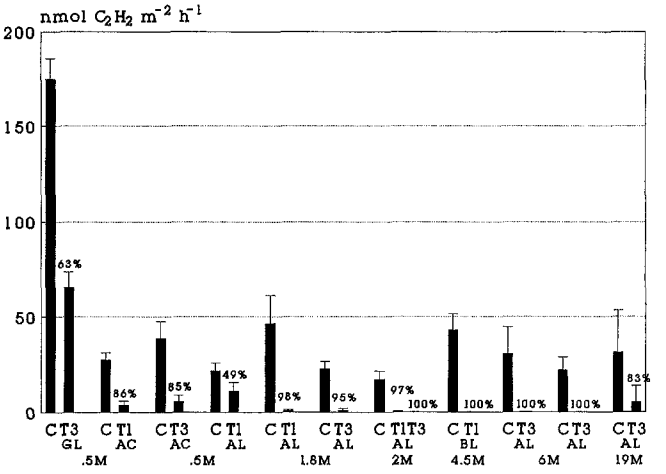

Fig. 2 Nitrogenase activity levels, over time, after one and three passes with a four-wheel drive vehicle. All treatments (*T*) were compared with an adjacent control (*C*). *T1* one pass, *T3* three passes, *GL* Gypsum lichen crust, *AC* Arches cyanobacterial crust, *AL* Arches lichen crust, *BL* Behind-the-Rocks lichen crust, *M* months after initial treatments. Percentages represent the percent declines in nitrogenase activity when compared to adjacent controls. All treatment values were significantly different from controls ($P<0.05$). One- and three-pass values on the same date in the same crust types were not significantly different from each other. *Error bars* indicate 1 SD

spring, lichen crusts have less initial reduction of nitrogenase activity than cyanobacterial crusts in response to the four-wheel drive vehicle. In the fall, the response of lichen crusts was similar to that of spring cyanobacterial crusts. In addition, vehicle tracks at BTR placed in the fall tended to be more disruptive than those placed in the spring or winter. Comparisons between one pass and three vehicular passes on the same day (14 April 1992) in cyanobacterial and lichen crusts showed no significant differences either immediately or over time (Fig. 2).

The pattern in gypsiferous soils was similar to that in sandy sites, although overall activity differences tended to be less. No visible damage was seen with one pass or two passes. Three passes with a vehicle resulted in nitrogenase activity reductions of 48% (Fig. 1).

Nitrogenase activity in a subset of vehicle tracks was measured over time (Fig. 2). No further reduction of nitrogenase activity was observed in cyanobacterial crusts over time (88% vs 86%). However, a further reduction in nitrogenase activity in all lichen crusts was seen. In sandy soils, reduction in nitrogenase activity went from 52–62% to 97–100% 1.8 months later. When measured 24 months later, activity was still reduced by 97–100% (data not presented). At 32 months, no activity was detected (100% reduction; data not presented). In gypsiferous soils, reduction in activity went from 48% to 63% over a 2-week period.

Mountain bike tracks had a similar impact to the four-wheel drive vehicle. Immediate reductions in nitrogenase activity ranged from 44% to 92% (Fig. 3). There were no significant differences between one-pass and three-pass tracks. At Behind-the-Rocks, one pass with a mountain bike reduced activity in lichen crusts by an average of 79%.

Footprints

Three types of shoes were used for footprints. These included boots with deep tread (D) tennis shoes with medium-deep tread (M), and sandals with no, or smooth tread (S). One and three passes with a deep-tread boot showed a 32–92% decline in nitrogenase activity, with no significant difference between one and three passes. Combining one

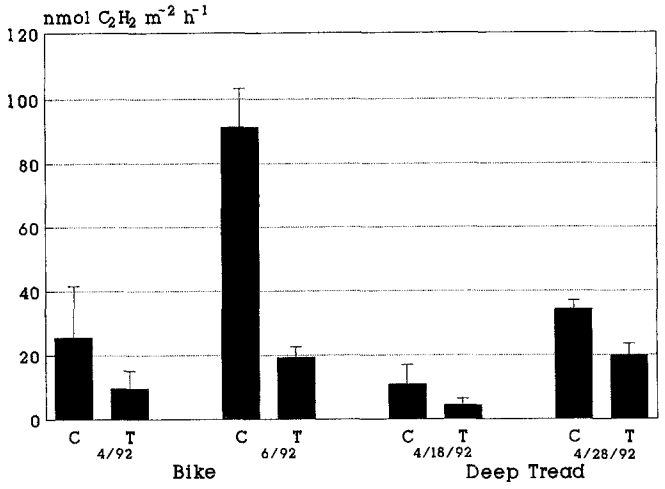

Fig. 3 Average nitrogenase activity levels immediately after one or three passes with a mountain bike and deep-tread boot in cyanobacterial crusts on sandy soils at Arches. All treatments (*T*) were compared with an adjacent control (*C*). Percentages represent the percent declines in nitrogenase activity when compared to adjacent controls. All treatment values were significantly different from controls ($P<0.05$). *Error bars* indicate 1 SD

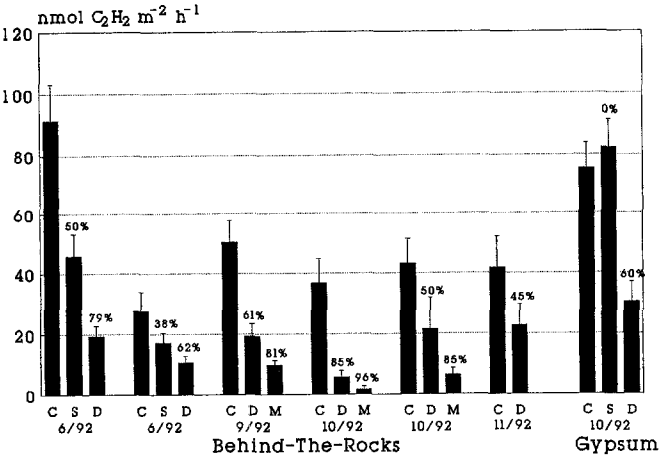

Fig. 4 Nitrogenase activity levels after one pass with shoes having deep (*D*), medium (*M*), or smooth (*S*) tread at Behind-the-Rocks and Gypsum sites. All treatments (*D, M,* or *S*) were compared with an adjacent control (*C*). Footprints were placed in lichen crusts. Percentages represent the percent declines in nitrogenase activity when compared to adjacent controls. No differences were seen among treatment types

and three passes, deep-tread boots showed a statistically significant average decline of 76% on 18 April 1992 and 40% on 28 April 1992 (Fig. 3). When compared with vehicle and mountain bike treatments applied at the same site on the same day, deep-tread boot treatments were not statistically different.

At Behind-the-Rocks, deep, medium, and smooth tread was compared in lichen crusts (Fig. 4). When different treads were compared with the undisturbed control, deep and medium tread were always significantly less than the control ($P<0.05$), as seen at Arches. Smooth tread was significantly different from the control on the first June sampling date ($P<0.01$), and not significantly different on the second sampling date. There was no difference among any of the treads on any treatment date. When comparing deep or medium tread treatments with wheeled vehicle treatments, there was no significant differences on any treatment date. Smooth tread was always significantly less than vehicle treatments on the same date.

Gypsiferous soils showed a significant nitrogenase activity reduction of 60% when deep-tread boots were compared to the control (Fig. 4). No disruption was seen with the smooth-tread sandals. As seen for sandy soils, values for deep tread and vehicles were not significantly different from each other, but were significantly lower than smooth tread.

Wooden block

To reduce surface disruption even further, but to still apply a compressional force, a wooden block was placed on the soil and then stepped on. This was used in sandy soil lichen crust at the Behind-the-Rocks site. This treatment resulted in the least disruption for any treatment on sandy soils, and values were not statistically different from the control (data not presented).

Discussion

This study used the acetylene-reduction technique to measure nitrogenase activity. There are limitations to this method that should be recognized. Without calibration with ^{15}N, it is impossible to accurately convert ethylene values to fixed N values. Consequently, this technique should be limited to comparative studies such as this one. Nitrogenase activity is also highly variable, with rates depending on previous and current environmental conditions such as temperature, light, and moisture levels. Under the experimental conditions used in this study, rates reported are probably less than 2% of potential nitrogenase activity in these crusts (Jeffries et al. 1992; Belnap, unpublished data). For these reason, yearly budgets cannot be extrapolated from the spot measurements reported here.

There are four important findings of this study. First, most soil surface disturbances resulted in a reduction of nitrogenase activity in the tested cyanobacterial and lichen soil crusts. Second, the more the disrupted the surface, the greater was the reduction of nitrogenase activity. Third, cyanobacterial crusts showed more immediate disruption than lichen crusts. And fourth, nitrogenase activity rates in lichen crusts decreased over time to the same level as the cyanobacterial crusts. Explaining these observations requires understanding the morphology and physiological constraints of the nitrogen-fixing species in these crusts, as well as soil characteristics of the study sites.

Since nitrogen fixation is an anaerobic process, non-heterocystic cyanobacterial species must utilize other methods to exclude oxygen. Nitrogenase activity has been de-

monstrated repeatedly in aquatic non-heterocystous species. Separation of the nitrogenase enzyme from oxygen in these species is accomplished spatially, temporally, or through a combination of both (Paerl and Bland 1982; Paerl and Prufert 1987; Paerl 1990). *Trichodesmium, aphanizomenon flos-aquae,* and *Microcoleus chthonoplastes* (morphologically almost identical to *M. vaginatus*) have been shown to create anaerobic microzones spatially through aggregation both between and within sheaths. These species all showed reduced nitrogenase activity when shaken or when aggregates were disrupted (Paerl 1985, 1990). Bacteria associated with these species may be partially responsible for anaerobic microzone formation through the scavenging of oxygen or may contribute N through their own fixation (Paerl et al. 1989). Given the structure of these soils crusts and *M. vaginatus*, along with the documented bacterial associations of *M. vaginatus*, any of these strategies could be employed by these crusts (Belnap and Garnder 1993).

Previous studies have shown that many types of disturbances negatively affect the cohesion and coverage of soil cyanobacterial-lichen crusts (Belnap and Gardner 1993; Cole 1991; Wilshire 1983). The most common disturbance to these crusts is compressional and shear force created by livestock, human feet, or off-road vehicles. Cyanobacterial filaments and lichens are brittle when dry and easily crushed by compressional force (Webb and Wilshire 1983; Harper and Marble 1990; Belnap 1993). These types of disturbance would have the potential of disrupting cyanobacterial aggregations.

If anaerobic microzone formation is dependent on filament and sheath aggregation for *Microcoleus* in soils as it is in water, surface disturbances may reduce or eliminate the capability of these organisms to fix nitrogen. As there was no difference in chlorophyll *a* concentration among the treatments or in comparison with the control, the large differences seen in nitrogenase activity between treatments cannot be explained by differences in biomass of cyanobacteria present. Aggregations of cyanobacteria, however, would be disrupted by any surface disturbance, with more disruptive disturbances resulting in greater reduction of nitrogenase activity, as was seen in this study.

Increasing the magnitude of compressional forces involved did not result in greater nitrogenase activity reduction in sandy soils: bikes and Vibram soles were just as damaging as a vehicle. Similar results were seen in a study of fine-textured lacustrine soils at Dugway Proving Grounds, Utah (Belnap et al. 1994). Treatments included shallow and deep raking; scalping of the top 1 cm of soil; and one, four, and ten passes of a mobile howitzer (a tracked vehicle). All were highly disruptive of the surface, and resulted in a 77–90% reduction in nitrogenase activity. All were significantly different from the control, and none were significantly different from each other, regardless of the difference in compressional and shear forces applied. However, in soils with greater compressional and shear strength, such as gypsum, there was less overall surface disturbance and less reduction in nitrogenase activity. In addition, there were significant differences in both surface disruption and nitrogenase activity reduction when vehicles and footprints were compared.

Relative to controls, lichen crusts showed less disruption in nitrogenase activity than cyanobacterial crusts. This could be explained by the species present. The cyanobacterial crusts tested were almost exclusively then non-heterocystic *M. vaginatus*, and therefore would be highly sensitive to any surface disturbance that would disrupt aggregations. Lichen crusts, however, contain heterocystic species such as the cyanobacteria *Scytonema myochorus* and *Nostoc* sp., as well as the soil lichen *Collema tenax*, which has *Nostoc* sp. as a phycobiont. This would mean this type of crust may be less dependent on aggregation for nitrogenase activity.

Greater reduction of nitrogenase activity over time was seen in lichen crusts at both Arches and BTR. Disruption of the soil surface would immediately affect nitrogenase activity in the non-heterocystous species such as *M. vaginatus*. Nitrogenase activity in heterocystous species of cyanobacteria and lichens would not necessarily be affected directly by surface disruption since they are not dependent on packing for exclusion of oxygen. However, death by burial or removal of dislodged material by wind or water erosion would result in decreased nitrogen contributions from these sources over time.

This study has many implications for ecosystems which are dependent on cryptobiotic crusts for nitrogen. Because many of the cold-desert systems in which these crusts occur have few, if any, nitrogen-fixing plants, any surface disturbance (such as trampling by livestock, people, and/or recreational vehicles) could result in dramatic decreases in nitrogen input from these crusts and would consequently have ecosystem-wide effects. Results from studies done by Harper and Pendleton (1993) and Belnap and Harper (1995) show that plants growing in uncrusted areas have significantly lower nitrogen content than plants growing in well-developed crusts. Evans and Ehlringer (1993) showed that crusts were the predominant source of nitrogen for the two juniper woodland sites measured. Since North American deserts have been grazed extensively for 100 years, and now are receiving ever-increasing recreational uses, understanding of the relationship between surface disturbances and nitrogen cycles is critical.

This study also forces re-examination of the definition of recovery for these soil crusts. Traditional recovery assessment using visual estimates or using estimations of biomass may not be adequate, as recovery of physiological functioning needs to be included as well. Only one aspect of physiology, nitrogenase activity, has been examined relative to disturbance. There may be other physiological aspects that are disrupted as well.

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