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LONG-TERM CONSEQUENCES OF DISTURBANCE ON NITROGEN DYNAMICS IN AN ARID ECOSYSTEM

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Abstract. Anthropogenic activity is causing dramatic changes in the nitrogen (N) cycle in many ecosystems. Most research has focused on the increase in N input caused by atmospheric deposition and invasion of N-fixing species, and on their effects on resource availability and species composition. However, in contrast to many ecosystems experiencing large increases in N input, many arid ecosystems are experiencing loss of nutrients due to land-use change. An important component of many arid ecosystems on a worldwide basis is the microbiotic crust, a biological soil crust composed of lichens, cyanobacteria, mosses, and algae. Nitrogen fixation by lichens and cyanobacteria comprising the crust is the primary source of N input in many of these ecosystems. We quantified the long-term consequences of surface disturbance in an arid ecosystem on the Colorado Plateau by comparing pristine sites with those of known disturbance history. Disturbance caused an increase in the abundance of cyanobacteria and a decrease in lichens within the microbiotic crust. Carbon isotope composition ($\delta^{13}\text{C}$) of the crust reflects this shift in species composition; values for disturbed sites were 4.5‰ higher than undisturbed sites. Nitrogen isotope composition ($\delta^{15}\text{N}$) of the microbiotic crust was 1.5–2.2‰ higher for disturbed sites, probably resulting from relatively greater gaseous N loss from the crust. Historic disturbance has caused a long-term decrease in rates of N fixation by the microbiotic crust; nitrogenase activity in pristine sites was 250% greater than sites intermittently disturbed 30 yr ago. The decrease in N input from fixation and continued gaseous N loss has caused a 25–75% decrease in soil N content. Altering relative rates of N input and loss, coupled with input of N from microbiotic crusts with relatively higher $\delta^{15}\text{N}$, has caused an increase in soil and plant $\delta^{15}\text{N}$ at disturbed sites. This decrease in soil N caused by disturbance will likely cause changes in species composition similar to those observed in ecosystems that have been disrupted by excess N input from atmospheric deposition.

Key words: Canyonlands National Park, Utah, USA; cryptogamic crusts; land-use change; microbiotic crusts; microphytic crusts; mineralization; nitrification; nitrogen; stable isotopes.

INTRODUCTION

Ecosystem structure and function are controlled by interactions between climate, resource availability, species composition, and disturbance regime (Chapin et al. 1996). Anthropogenic activity is causing global changes in each of these factors through global warming, alteration of atmospheric chemistry, species invasions and extinction, and land-use change (Vitousek 1994, Chapin et al. 1996). One of the most significant changes in resource dynamics caused by anthropogenic activity is alteration of the nitrogen cycle (Aber et al. 1989, Schulze 1989, Kinzig and Socolow 1994, Vitousek 1994). The increase in atmospheric deposition resulting from anthropogenic N fixation has caused widespread changes in the N dynamics of ecosystems of the northeastern United States and northern Europe (Aber et al. 1989, Schulze 1989, Galloway et al. 1995), and has the potential to alter species composition in for-

merly N-limited ecosystems (Tilman 1987, Inouye and Tilman 1995). However, anthropogenic activity can also decrease N availability within ecosystems. In contrast to many ecosystems experiencing large increases in N input, many arid ecosystems are experiencing loss or redistribution of nutrients due to land-use change (Schlesinger et al. 1990, 1996, Evans and Ehleringer 1993, 1994, Hulme and Kelly 1993, Milton et al. 1994). The extreme environments and low species diversity of arid ecosystems make them especially susceptible to changes caused by land-use change, especially grazing (Verstraete and Schwartz 1991).

Central to resource dynamics in many arid ecosystems are microbiotic (cryptogamic) crusts, consolidated matrices of cyanobacteria, lichens, moss, green algae, and microfungi that cover the soil surface. The natural absence of both fire and grazing by large mammals has allowed the microbiotic crusts of the Intermountain West of North America to become especially well developed (Mack and Thompson 1982); crusts may be up to 10 cm deep and may approach 100% coverage in plant interspaces (Kleiner and Harper 1972,

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Harper and Marble 1988). The cyanobacteria, bacteria, and lichens comprising microbiotic crusts are often capable of N fixation, and this has been shown to be the primary source of N input into some arid ecosystems (Evans and Ehleringer 1993). Surface disturbance caused by land-use change can disrupt the microbiotic crust, and this may directly affect plant and soil N dynamics. The greatest impact of disturbance may be to eliminate or greatly reduce N fixation by altering the species composition of the microbiotic crust. The lichen and moss components of the crust are especially susceptible to disturbance and have the longest rates of recovery (Johansen and St. Clair 1986, Beymer and Klopatek 1992, Eldridge and Greene 1994, Belnap 1995), so disturbance may cause a shift in dominance toward cyanobacteria. This is significant because rates of N fixation for lichens can be an order of magnitude greater (on a surface-area basis) than cyanobacteria (Belnap 1991). Therefore, the greatest impact of disturbance may be to eliminate or greatly reduce N fixation by altering the species composition of the microbiotic crust.

The short-term changes in species composition and N fixation following disturbance may have long-term consequences for N dynamics in arid ecosystems. Mineralization, as well as subsequent N loss from volatilization, nitrification, and denitrification, can be rapid following precipitation (Burke 1989, Matson et al. 1991, Peterjohn and Schlesinger 1991, Schlesinger and Peterjohn 1991). Evans and Ehleringer (1993) hypothesized that the short-term loss of N fixation following disturbance, coupled with rapid N loss, may result in net loss of N from the soil. Rates of N mineralization and nitrification depend on substrate availability and microenvironment, so a decrease in soil N could impact soil N transformations (Virginia et al. 1982, Binkley and Hart 1989, Matson et al. 1991, Peterjohn and Schlesinger 1991), causing a decrease in plant-available N and net primary productivity.

The three-dimensional character of the microbiotic crusts makes it difficult to assess changes in species composition simply by quantifying spatial coverage (Belnap 1993). However, changes in species dominance should be apparent in the carbon isotope composition ($\delta^{13}\text{C}$) of the crust. Species comprising the microbiotic crust have very different $\delta^{13}\text{C}$. The $\delta^{13}\text{C}$ of lichens can vary with the photobiont associated with the symbiosis, but values are generally lower than -23‰ (Lange 1988, Máguas et al. 1993, 1995). The $\delta^{13}\text{C}$ of mosses is similar to that of higher plants that possess the C_3 photosynthetic pathway, and values are lower than -26‰ (Rundel et al. 1979, Teeri 1981, Proctor et al. 1992). In contrast to lichens and mosses, $\delta^{13}\text{C}$ of cyanobacteria is similar to that of plants with the C_4 photosynthetic pathway (-12‰) because they possess a CO_2 -concentrating mechanism (Palmqvist 1993, Máguas et al. 1995) and photosynthesis is limited by diffusion (Raven 1991, Máguas et al. 1995).

Long-term changes in soil N dynamics resulting from disturbance should be apparent in the isotopic composition ($\delta^{15}\text{N}$) of soil N (Nadelhoffer and Fry 1988, 1994, Evans and Ehleringer 1993, 1994). The $\delta^{15}\text{N}$ of soil N depends on the $\delta^{15}\text{N}$ of N input into the soil from the crust and plant litter, and on subsequent fractionation that occurs during decomposition (Nadelhoffer and Fry 1988, 1994). Nitrogen input from crust and plant litter can increase the soil N content. This input has a relatively low $\delta^{15}\text{N}$, causing a corresponding decrease in soil $\delta^{15}\text{N}$. Fractionation during decomposition produces inorganic N that has a lower $\delta^{15}\text{N}$ than the bulk soil, causing the remaining soil N to become progressively enriched in ^{15}N (higher $\delta^{15}\text{N}$). Altering the balance between N input and loss by eliminating N input should therefore decrease soil N concentration and increase the $\delta^{15}\text{N}$ of the remaining soil N (Evans and Ehleringer 1993).

We examined the long-term consequences of land-use change on N dynamics at two sites of known disturbance history on the Colorado Plateau. Previous studies on these sites provide a baseline to assess long-term changes following disturbance. We hypothesized that disturbance will (1) cause long-term changes in species composition and rates of N fixation by the microbiotic crust; (2) disrupt the balance between N input and N loss, resulting in net loss of N from the ecosystem; and (3) decrease rates of soil N transformations.

STUDY AREAS

Field studies were conducted at two locations representing 8 and 32 yr post-disturbance. The first (32 yr post-disturbance) was a grassland located in the Needles District of Canyonlands National Park, Utah, USA. Previous studies of this grassland (Kleiner and Harper 1972, 1977, Kleiner 1983) provide a baseline to assess long-term changes following disturbance. The grassland is split into two areas by a narrow rock wall (Kleiner and Harper 1972). Grazing has never occurred in the undisturbed area (Virginia Park) because access is physically restricted. Due to lack of water, the disturbed area (Chesler Park) was grazed by cattle only during winters when snow was present. Grazing has not occurred since formation of the park in 1962. Kleiner and Harper (1972) characterized plant cover and soil properties 5 yr following cessation of disturbance. The primary differences between the two areas were coverage of microbiotic crusts and soil organic matter. Coverage of lichens and mosses in the undisturbed area was 38%, compared to 5% in the disturbed area. Organic matter was higher in the undisturbed area (1.33%) compared to the disturbed area (0.88%), but there was no difference in soil N content (0–0.05 m depth) between the undisturbed (0.43 mg N/g soil) and disturbed (0.46 mg N/g soil) areas. Kleiner and Harper (1972) concluded that 5 yr following disturbance, the primary effect of grazing was a decrease in the coverage of the micro-

biotic crust, and that this caused the decrease in soil organic matter, but no change in soil N. Kleiner (1983) repeated their vegetation sampling 15 yr following cessation of disturbance, and found that coverage of the lichen and moss component of the microbiotic crusts in the disturbed area had increased in 10 yr from 5 to 11%. Soil properties were not measured.

The second study location (8 yr post-disturbance) was established in 1985 (Belnap 1993) and was located in the Behind-the-Rocks regions adjacent to Canyonlands National Park. Eighteen plots, which varied in size from 0.25 to 0.75 m², were assigned to disturbance or control treatments in a completely randomized experimental design. This distance between adjacent plots was <1 m. The plots were resampled 5 yr after disturbance (Belnap 1993). Although adjacent undisturbed plots had 30–40% lichen and moss cover, no lichens or mosses were observed in the disturbed plots. Chlorophyll *a* levels (a measure of algal abundance) in disturbed plots were only 12% of those in undisturbed plots (Belnap 1993).

METHODS

32 yr post-disturbance

Two sites were selected within the disturbed area based on preliminary observations of crust composition. Mosses were dominant at the first location ("disturbed-moss") and a minor component at the second location ("disturbed-cyanobacteria"). A single site was sampled in the undisturbed area. Five parallel transects were established at each site. Transects were 5 m apart and 20 m long. Samples of microbiotic crust were collected for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ analysis along each transect at the 0- and 2-m points, then at 3 m intervals (40 samples/site). Soil samples (0–0.10 m depth) for N content and $\delta^{15}\text{N}$ analysis were collected from beneath the crust at each point with a soil probe. Each sample was placed in a glass vial and sealed with parafilm. Leaf samples from five randomly selected individuals of each of the dominant plant species were also collected at each site.

Vegetation and ground cover were evaluated at 1-m intervals along each transect using 0.25-m² quadrats (100 samples/site). Frequency and coverage of the dominant plant species, plant litter, rocks, gravel, mosses, lichens, cyanobacteria, and bare ground were estimated using the coverage classes of Daubenmire (1959).

Relative rates of N fixation were estimated by measuring nitrogenase activity. Rates of acetylene reduction are accurate indicators of the relative rates of N fixation; actual rates may be higher (Jeffries et al. 1992). Twenty 5.1-cm² samples of microbiotic crusts were randomly collected from each site. Samples were placed in clear, gas-tight tubes. The surface of the sample was wetted equally with distilled water, and then injected with acetylene to create a 10% acetylene at-

mosphere. 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 analyzed for acetylene and ethylene content using a Carle FID gas chromatograph (Spectra-Physics, San Jose, California, USA) equipped with a 2.4-m, 8% NaCl on alumina column, with helium as the carrier gas (30 mL/min). Calibrations with ethylene standards were done at the time of observations. Results are reported as nanomoles of C₂H₂ per square meter per hour.

Soil N concentration was determined for four randomly selected samples from each transect line ($n = 20$ samples/site). Total N in soil samples was determined on an auto-analyzer (WESTCO Scientific Instruments, Danbury, Connecticut, USA) following micro-Kjeldahl digestion. Two grams of soil from each sample were combined with 4 mL H₂SO₄, 1.5 g K₂SO₄, and 50 mg CuSO₄–5H₂O, and heated at 350°C for 6 h on the block digester (Lachat Instruments, Milwaukee, Wisconsin, USA). The NH₄⁺ of the solution was then measured on the autoanalyzer.

The level of $\delta^{15}\text{N}$ was determined for all soil samples used for total N analysis ($n = 20$ samples/site) and for five individuals of each of the dominant plant species at each site. The levels of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were determined for five randomly chosen crust samples from each site. Preparation of samples for isotopic analysis followed Evans and Ehleringer (1993, 1994). Nitrogen and carbon within the samples were converted to N₂ and CO₂, respectively, by combusting the samples with CuO and Cu in evacuated Pyrex tubes at 580°C for at least 8 h. CaO was also added to samples for $\delta^{15}\text{N}$ analysis to eliminate excess CO₂. The tubes were then allowed to cool slowly within the furnace until they reached room temperature. The gas within the sample was purified cryogenically, then analyzed at the Stable Isotope Ratio Facility for Environmental Research at the University of Utah. Isotope ratios are expressed in δ notation as

$$\delta X = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1000\text{‰}$$

where δX represents either $\delta^{15}\text{N}$ or $\delta^{13}\text{C}$, and R is the molar ratio of the heavier to the lighter isotope for the standard or sample. Standards for N and carbon are atmospheric air ($R = 0.0036765$) and PeeDee Belemnite ($R = 0.011237$), respectively (Ehleringer and Rundel 1988).

The impact of disturbance on soil processes was evaluated using anaerobic and aerobic incubations. For anaerobic incubations, 10-g subsamples of each sample were weighed into three glass vials. The first was dried at 70°C for at least 48 h for determination of soil moisture. Enough deionized, distilled water was added to the remaining two samples to completely fill the volume of the vial. One was randomly chosen for initial determination of NH₄⁺. The second vial was placed in an incubator at 30°C for 10 d. The amount of NH₄⁺

released was calculated by subtracting the initial NH_4^+ from the NH_4^+ concentration of the incubated sample. NH_4^+ from both vials was extracted using 30 mL of a 2 mol/L solution of KCl. NH_4^+ concentrations were determined using the autoanalyzer.

Aerobic incubations were also done on the same samples used for anaerobic incubations. Subsamples of each sample were weighed into three vials, as described for anaerobic incubations. One vial was randomly chosen for determination of soil moisture. Deionized, distilled water was added to the second and third vials, bringing the soil to field capacity. One of these vials was chosen for determination of initial NH_4^+ and NO_3^- concentrations. The second was placed in an incubator at 30°C for 30 d. Water was added as needed to maintain the soils at field capacity. NH_4^+ and NO_3^- in the soils used for both the initial and incubated samples were extracted with a 2 mol/L solution of KCl. Net mineralization was calculated as the net change in ($\text{NH}_4^+ + \text{NO}_3^-$) concentration over the 30-d incubation (Binkley and Hart 1989). Net ammonification and nitrification were calculated as the net changes in the NH_4^+ and NO_3^- pools, respectively (Binkley and Hart 1989).

8 yr post-disturbance

Soil samples were collected from five randomly selected plots in each treatment (a total of 10 samples) during fall 1993. Five subsamples were collected from each plot at 0–10 cm depth below the microbiotic crust using a soil probe. The subsamples were composited in a soil tin, placed on ice, and transported back to the laboratory. Soil N and $\delta^{15}\text{N}$ were measured for each sample as described above. Mineralization potential was also measured for each sample using anaerobic incubation as described above.

Statistical analysis

All data were analyzed as a completely randomized design using the General Linear Models Procedure of the SAS statistical package for the Macintosh (Littell et al. 1991). Mean values were compared using a Waller-Duncan multiple-range test. A significance level of 0.05 was used for all analyses.

RESULTS

32 yr post-disturbance

The composition of the microbiotic crust was different at disturbed and undisturbed sites. Lichens were a dominant component of the crust in the undisturbed area, but were virtually absent from the disturbed area (Fig. 1). Coverage of *Collema tenax* and *C. coccophorum*, the dominant lichens capable of N fixation, was 5.5% in the undisturbed site and <1% at the disturbed sites. Lichens with a green algal symbiont were absent at disturbed sites, while coverage at the undisturbed site was 11.8%. The two sites in the disturbed area were classified according to the relative coverage of

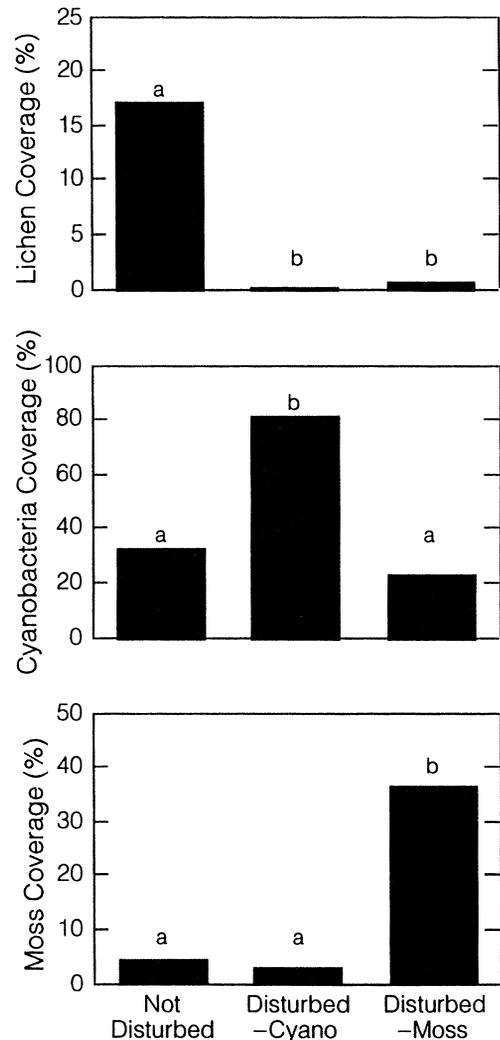


FIG. 1. Mean coverage of the major components of the microbiotic crust in undisturbed and 32-yr post-disturbance grassland sites at Canyonlands National Park. Disturbance has not occurred in the disturbed grasslands in 32 yr. Differences in lichen, cyanobacteria, and moss coverage are significant ($P < 0.05$) among the three sites. Error bars (± 1 SE) are too small to be visible. Means with the same letter are not significantly different.

cyanobacteria and mosses. Coverage of soil surfaces containing cyanobacteria in the disturbed–cyanobacteria site was 81.7%, while coverage of lichens and mosses was <3%. Mosses were the dominant component at the disturbed–moss site with a coverage of 36.7%, while soil with cyanobacteria coverage was 24.2%.

Nitrogenase activity and soil N content were both significantly greater in the undisturbed site. Nitrogenase activity did not differ significantly for the two disturbed sites, with a mean value of 19.7 ± 4.4 nmol $\text{C}_2\text{H}_2\text{m}^{-2}\text{h}^{-1}$ (Fig. 2). Nitrogenase activity by microbiotic crusts in the undisturbed area was over 250%

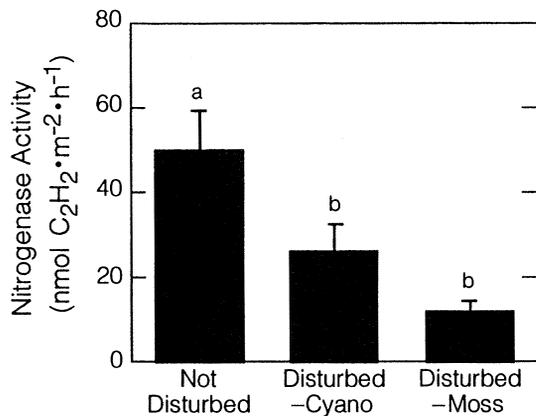


FIG. 2. Mean (+1 SE) nitrogenase activity in the undisturbed and 32-yr post-disturbance sites at Canyonlands. Differences are significant ($P < 0.05$) among the three sites. Means with the same letter are not significantly different.

greater than disturbed sites, with a mean value of 50.5 ± 9.2 nmol C₂H₂ · m⁻² · h⁻¹. Soil N contents at the disturbed-moss and disturbed-cyanobacteria sites were only 74 and 39% of the undisturbed site, respectively (Fig. 3).

Plant $\delta^{15}\text{N}$ values were not different between the two disturbed sites, and both disturbed sites had significantly higher plant $\delta^{15}\text{N}$ than the undisturbed site (Fig. 4). At the undisturbed site, *Stipa hymenoides* R.&S. had significantly higher $\delta^{15}\text{N}$ ($1.7 \pm 0.4\text{‰}$) than *Sporobolus cryptandrus* (Torr.) Gray ($-0.8 \pm 0.4\text{‰}$), while $\delta^{15}\text{N}$ values for *Stipa comata* Trin. & Rupr. ($0.7 \pm 0.7\text{‰}$) were not significantly different than either of the other species. At the disturbed-moss site, *S. hymenoides* ($2.4 \pm 0.3\text{‰}$) and *S. comata* ($2.4 \pm 0.1\text{‰}$) both had significantly higher $\delta^{15}\text{N}$ than *Sporobolus cryptandrus* ($1.1 \pm 0.3\text{‰}$). Differences among species (*S. cryptandrus*, *S. comata*, *S. hymenoides*) at the disturbed-cyanobacteria site were not significant.

The pattern of microbiotic crust and soil $\delta^{15}\text{N}$ was

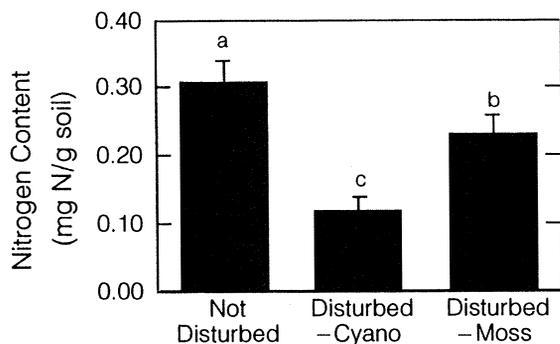


FIG. 3. Mean (+1 SE) soil nitrogen content at 0–10 cm depth in the undisturbed and 32-yr post-disturbance sites at Canyonlands. Differences are significant ($P < 0.05$) among the three sites. Means with the same letter are not significantly different.

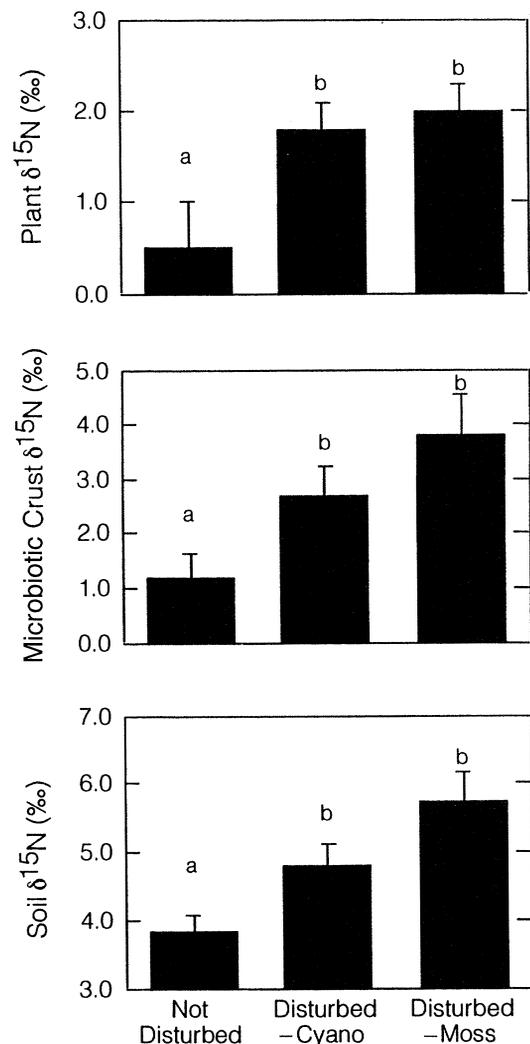


FIG. 4. Mean (+1 SE) $\delta^{15}\text{N}$ of plants, microbiotic crusts, and soils (0–10 cm depth) in the undisturbed and 32-yr post-disturbance sites at Canyonlands. Differences are significant ($P < 0.05$) among the three sites for all variables. Means with the same letter are not significantly different.

similar to that seen for plants. Values for crust and soil $\delta^{15}\text{N}$ were not significantly different between disturbed sites, and both were significantly higher when compared to the undisturbed site (Fig. 4). Microbiotic crust and soil $\delta^{15}\text{N}$ were 1.5 and 2.2‰ higher, respectively, for disturbed sites compared to the undisturbed site. Mean $\delta^{13}\text{C}$ values were significantly higher for disturbed ($-19.1 \pm 0.5\text{‰}$) compared to undisturbed ($-23.9 \pm 0.4\text{‰}$) areas. The $\delta^{15}\text{N}$ of the microbiotic crust was positively correlated ($R > 0.99$) with $\delta^{13}\text{C}$ (Fig. 5).

The rate of NH_4^+ mineralization under anaerobic conditions was over 450% greater for soil from the undisturbed site compared to soil from the disturbed site (Fig. 6). Greater rates of mineralization were not solely due to differences in soil N content; rates of

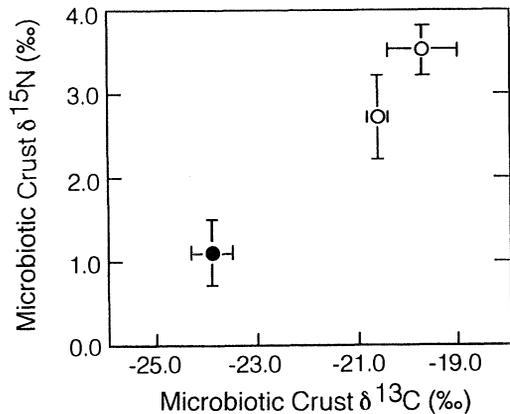


FIG. 5. The $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of microbiotic crusts at the disturbed (open symbols) and 32-yr post-disturbance (closed symbol) sites at Canyonlands. Each point represents the mean (± 1 SE) of five observations. The correlation between $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ is significant ($R > 0.99$).

NH_4^+ mineralization for undisturbed and disturbed sites were 35.8 and 10.4 $\text{mg NH}_4^+\text{-N}\cdot(\text{g soil N})^{-1}\cdot\text{d}^{-1}$, respectively. In contrast, net mineralization, nitrification, and ammonification in soils from both disturbed and undisturbed sites were not significantly different under aerobic conditions, and values were approximately two orders of magnitude less than those observed under anaerobic conditions. Mean net mineralization and net nitrification for the three sites were $0.12 \pm 0.03 \mu\text{g} (\text{NH}_4^+ + \text{NO}_3^-\text{-N})\cdot\text{g}^{-1}\cdot\text{d}^{-1}$ and $0.12 \pm 0.03 \mu\text{g NO}_3^-\text{-N}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$, respectively. Net ammonification was negative for each of the sites, and the mean value was $-0.06 \mu\text{g NH}_4^+\text{-N}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$.

8 yr post-disturbance

Nitrogen content, mineralization potential, and soil $\delta^{15}\text{N}$ were all significantly different between disturbed and undisturbed plots 8 yr after initial disturbance (Fig. 7). Soil N content and $\text{NH}_4^+\text{-N}$ mineralized were over 250 and 400% greater, respectively, for the undisturbed compared to the disturbed plots. Soil $\delta^{15}\text{N}$ was 1.5‰ greater for the disturbed plot.

DISCUSSION

Surface disturbance has had long-term consequences for N dynamics in the arid ecosystems examined in this study. Five years following cessation of disturbance, Kleiner and Harper (1972) observed lower soil organic matter and less moss and lichen cover in the disturbed site, but no difference in soil N content between the disturbed and undisturbed sites. Twenty-five years later we observed large differences in soil N content, even though the sites had not been disturbed in the preceding 30 yr. Similar differences were observed for sites that had not been disturbed in 8 yr. The large decreases in soil N content following disturbance observed in this and other studies (Evans and Ehleringer 1993) suggests

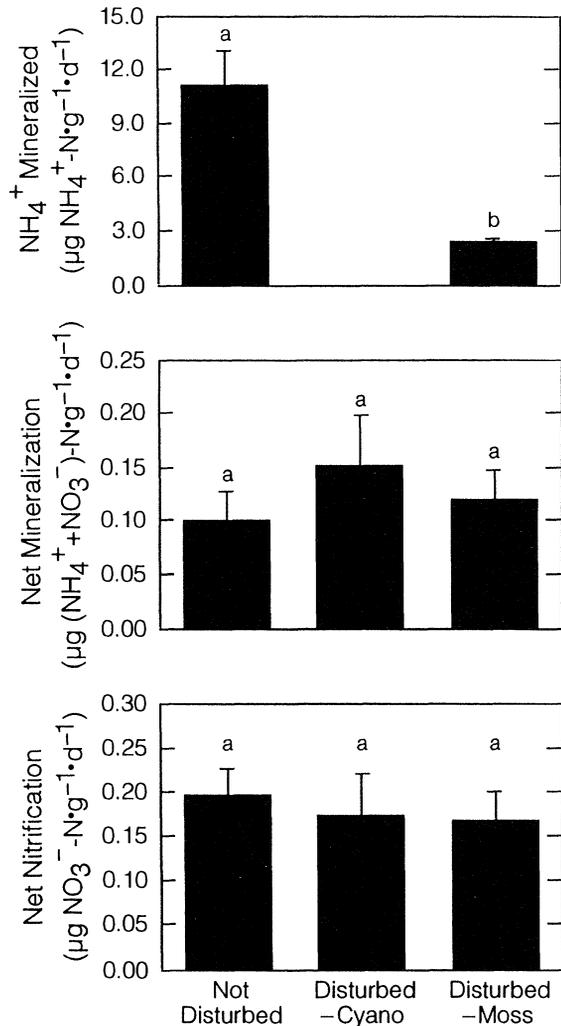


FIG. 6. Mean (± 1 SE) $\text{NH}_4^+\text{-N}$ mineralized in anaerobic incubations, and net mineralization and nitrification from aerobic incubation for soils from the undisturbed and 32-yr post-disturbance sites at Canyonlands. Note the difference in scale for the y-axis in each of the figures. Mineralization potential was significantly different ($P < 0.05$) among sites. Differences in net mineralization and net nitrification were not significant ($P > 0.05$). Means with the same letter are not significantly different.

that disturbance can alter the balance between N input and loss, causing a decrease in N storage within the soil.

The primary source of N input into these arid ecosystems is N fixation by the microbiotic crust (West and Skujins 1977, Evans and Ehleringer 1993). Free-living and symbiotic bacteria capable of N fixation besides those comprising the microbiotic crust are rare, both at this site (Kleiner and Harper 1972) and elsewhere in the Great Basin and Colorado Plateau (West and Skujins 1977, Callison and Brotherson 1985), and atmospheric deposition of N is low (Young et al. 1988, Peterjohn and Schlesinger 1990). Disturbance often

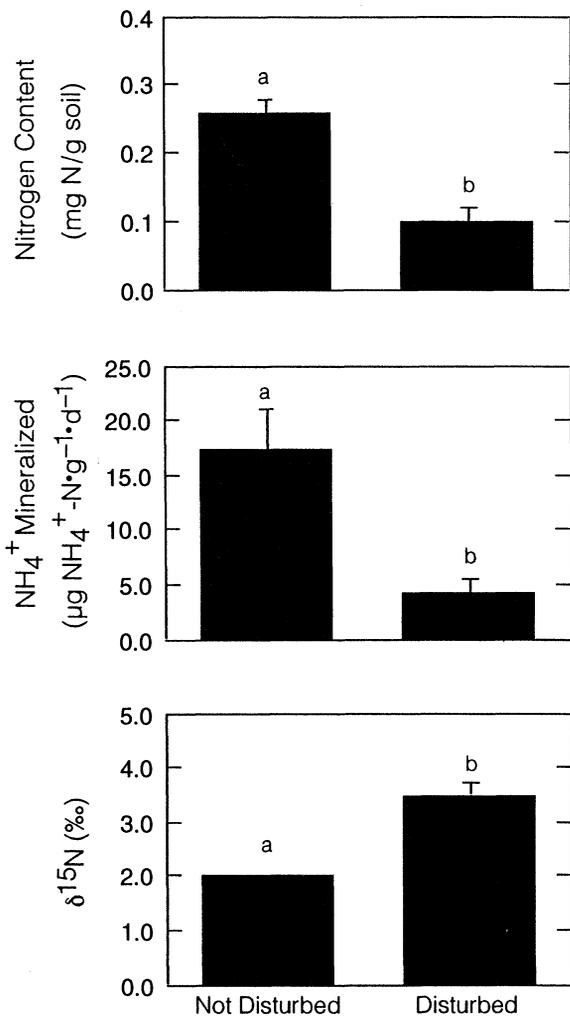


FIG. 7. Mean (+1 SE) nitrogen content, NH_4^+ -N mineralized in anaerobic incubations, and $\delta^{15}\text{N}$ for soils collected at 0–10 cm depth in undisturbed and 8-yr post-disturbance sites at Behind-the-Rocks. Mineralization potential was measured using an anaerobic incubation. Differences were significant ($P < 0.05$) between disturbance treatments for all variables.

causes an immediate decrease in N fixation by the microbiotic crust; nitrogenase activity can decrease by 75–90% immediately following disturbance (Belnap 1995), and activity may still be absent for over 2 yr without further disturbance (Belnap 1996). Results from this study suggest that disturbance may cause a long-term decrease in N input into the ecosystem from N fixation; nitrogenase activity in disturbed sites was less than 40% of that observed in undisturbed sites, even after 30 yr of recovery.

The lack of recovery of N fixation following disturbance corresponds to the loss of the lichen component of the crust and an increase in abundance of cyanobacteria. It is difficult to assess recovery of the crust using spatial coverage (Belnap 1993); however, the

$\delta^{13}\text{C}$ of crusts from undisturbed and disturbed sites reflects this shift in species composition. The $\delta^{13}\text{C}$ of microbiotic crusts from undisturbed sites were “ C_3 -like,” indicating dominance by lichens and mosses, while disturbance shifted $\delta^{13}\text{C}$ values toward those characteristic of cyanobacteria. The dominant cyanobacteria at these sites is the nonheterocystic species *Microcoleus vaginatus*. *Microcoleus vaginatus* is not capable of N fixation and cannot grow in a nitrogen-free medium. Instead, this species relies on a symbiotic relationship with an epiphytic bacterium that is responsible for N fixation (Steppe et al. 1996). *Microcoleus vaginatus* exudes a gelatinous sheath that creates anaerobic zones that are favorable for N fixation by the symbiont (Steppe et al. 1996). The sheath is brittle when dry, and disturbance can disrupt the structure of the sheath, eliminating anaerobic zones within the crust and causing the large decrease in N fixation (Belnap 1996).

Microbiotic crusts at disturbed sites also had significantly higher $\delta^{15}\text{N}$ values than those at the undisturbed site. The $\delta^{15}\text{N}$ of an organism depends on the $\delta^{15}\text{N}$ of its N source and on subsequent enrichment caused by fractionation during N loss. The potential sources of N for these surface-dwelling organisms are N fixation and atmospheric deposition. The increase in $\delta^{15}\text{N}$ values following disturbance did not result from increased reliance on atmospheric deposition. Nitrogenase activity was present at disturbed sites, and a shift to atmospheric deposition should cause a decrease in $\delta^{15}\text{N}$ values, not an increase, as the $\delta^{15}\text{N}$ of atmospheric deposition is often lower than -3‰ (Heaton 1986). We measured $\delta^{15}\text{N}$ of mosses growing on rocks at the study sites. The only source of N for these organisms is atmospheric deposition, and values are less than -2‰ .

The more positive $\delta^{15}\text{N}$ values for cyanobacteria-dominated crusts are probably due to relatively greater gaseous N loss compared to lichen-dominated crusts. It is often assumed that gaseous N loss is not significant in most living organisms (but see Farquhar et al. 1983), so the $\delta^{15}\text{N}$ value of an organism reflects that of the N source. However, leakage of inorganic N can be significant for cyanobacteria and cyanobacteria-containing lichens. As much as 20% of N recently fixed by N fixation can leak to the extracellular ammonium pool (Klubek et al. 1978), and 1–2% of the total N in the crust can be found as extracellular ammonium. Gaseous loss from volatilization and denitrification that result from this leakage are significant (Klubek et al. 1978). West and Skujins (1977) estimate that 70% of N assimilated by N fixation is subsequently lost through volatilization and denitrification. Denitrification can be especially high because the crust provides an important source of carbon for the denitrifying organisms (West and Skujins 1977). Both volatilization and denitrification are accompanied by significant fractionation (Handley and Raven 1992), causing the remaining N to become enriched in ^{15}N and to have higher $\delta^{15}\text{N}$

values. This suggests that the more positive $\delta^{15}\text{N}$ values for cyanobacteria-dominated crusts are due to relatively greater gaseous N loss compared to lichen-dominated crusts. Therefore, microbiotic crusts on disturbed sites not only have lower rates of N fixation, but relatively more of this assimilated N is subsequently lost back to the atmosphere.

It appears that the long-term decrease in N input from the microbiotic crust, coupled with rapid rates of N loss, comprise the mechanisms responsible for the decrease in soil N content following disturbance (Evans and Ehleringer 1993). Nitrogen loss via volatilization, nitrification, and denitrification can be rapid in desert ecosystems (Virginia et al. 1982, Peterjohn and Schlesinger 1991, Zaady et al. 1996). Rates of denitrification following precipitation can approach those of more mesic ecosystems (Peterjohn 1991), and West and Skujins (1977) estimate that over 70% of new N input in undisturbed sites are subsequently lost to the atmosphere via volatilization and denitrification.

Soil $\delta^{15}\text{N}$ also increased following disturbance. The $\delta^{15}\text{N}$ of soils depends on the $\delta^{15}\text{N}$ of N input and on subsequent increases in $\delta^{15}\text{N}$ caused by fractionation during decomposition (Nadelhoffer and Fry 1988). An increase in $\delta^{15}\text{N}$ can occur if disturbance alters the balance between N input into the soil and N loss, causing a net decrease in soil N content (Evans and Ehleringer 1993), or can occur from N input from microbiotic crusts with higher $\delta^{15}\text{N}$. The increase in soil $\delta^{15}\text{N}$ observed on sites 8 yr post-disturbance was probably the result of increased N loss relative to input, since crusts were absent on disturbed plots. However, nitrogenase activity was detected at disturbed sites 32 yr post-disturbance, and it is likely that N input was occurring into the soil. The higher $\delta^{15}\text{N}$ values of microbiotic crusts and their lower soil N contents suggest that the higher $\delta^{15}\text{N}$ values observed on these sites are caused both by input of N from the crust with relatively higher $\delta^{15}\text{N}$ and by greater N loss relative to N input.

Large differences were observed between disturbed and undisturbed sites in the amount of NH_4^+ mineralized under anaerobic conditions. In contrast, potential net mineralization and nitrification were not significantly different under aerobic conditions, and rates were two orders of magnitude less than those observed in anaerobic incubations. Higher rates of net mineralization are not uncommon for anaerobic vs. aerobic incubations (Hart and Binkley 1985), and can result from much reduced rates of immobilization (Paul and Clark 1996) and from the release of N from microbial biomass (Myrold 1987, Smith et al. 1989). Low or negative rates of net mineralization and nitrification are often observed for soils with low N because of high rates of immobilization into microbial biomass (Binkley and Hart 1989, Holland et al. 1995, Zaady et al. 1996). Immobilization can be especially important in desert soils (Fisher et al. 1987, Gallardo and Schlesinger 1992, Zaady et al. 1996), and supplemental N

may need to be added to observe the net accumulation of NH_4^+ and NO_3^- (Fisher et al. 1987). The contrasting patterns for mineralization experiments in this study suggest that gross rates of mineralization and microbial biomass may be greatly reduced following disturbance, but that immobilization is great enough under both disturbed and undisturbed conditions to prevent large accumulations of NH_4^+ and NO_3^- in the soil. Other studies have noted that net rates of ammonification and nitrification do not necessarily reflect gross fluxes in the soil (Davidson et al. 1992, Hart et al. 1994).

The $\delta^{15}\text{N}$ of the dominant plant species were strongly correlated with soil $\delta^{15}\text{N}$. Plants often have more negative $\delta^{15}\text{N}$ than soil (Shearer and Kohl 1986, Gebauer and Schulze 1991, Evans and Ehleringer 1994, Frank and Evans 1997), because fractionation occurs during mineralization and nitrification, causing NH_4^+ and NO_3^- to have lower $\delta^{15}\text{N}$ than soil organic N (Shearer and Kohl 1986, Nadelhoffer and Fry 1988). Fractionation with uptake of inorganic N does not occur at concentrations typical of the soil (Evans et al. 1996), so whole-plant $\delta^{15}\text{N}$ values reflect those of the N source. The differences observed between soil and plant $\delta^{15}\text{N}$ values in this study (-3.0 to -3.7‰) are very similar to those observed in other arid ecosystems (-3.0 to -3.1‰) by Evans and Ehleringer (1994). Differences in plant and soil $\delta^{15}\text{N}$ from both locations are similar to earlier estimates of discrimination during net mineralization (-1.8‰) (Evans and Ehleringer 1993). Discrimination during net mineralization apparently controls plant $\delta^{15}\text{N}$ values, suggesting that plants may be using NH_4^+ as their primary N source. The $\delta^{15}\text{N}$ of NO_3^- can be as much as 15‰ lower than NH_4^+ because of fractionation during nitrification (Feigin et al. 1974). However, the $\delta^{15}\text{N}$ of soil NH_4^+ and NO_3^- can exhibit considerable temporal and spatial variation (Feigin et al. 1974, Binkley et al. 1985, Herman and Rundel 1989), so direct measurements of integrated values of soil NH_4^+ and NO_3^- would be needed to support this hypothesis.

Microbiotic crusts are dominant features of many arid and semi-arid ecosystems around the globe (Harper and Marble 1988, West 1990, Metting 1991, Eldridge and Greene 1994). The slow rates of recovery observed for the microbiotic crusts in this and other studies (Eldridge and Greene 1994) indicate that the widespread surface disturbance caused by land-use change can have important consequences for N dynamics. Next to water, N is the resource that most often limits net primary production in arid ecosystems (Etershank et al. 1978, Fisher et al. 1988, Gutierrez et al. 1988, Sharifi et al. 1988, Lajtha and Whitford 1989, Ludwig et al. 1989). Nitrogen limitations are not the result of slow cycling within soils; on the contrary, rates of N transformations and loss are relatively fast (Westerman and Tucker 1978, Peterjohn and Schlesinger 1991), causing low rates of accumulation (Schlesinger et al. 1990). Rapid rates of transformation and loss, coupled with

loss of N input following disturbance, cause the observed decrease in soil N content. This decrease in soil fertility caused by land-use change contrasts with many ecosystems where the N cycle has been disrupted by excess N input from anthropogenic atmospheric deposition (Aber et al. 1989, Schulze 1989). However, in both cases large changes in resource availability have the potential to permanently alter the species composition of these ecosystems (Lauenroth et al. 1978, Tilman 1987, Schlesinger et al. 1990, Inouye and Tilman 1995, Coffin et al. 1996). In arid ecosystems, the large-scale decrease in soil fertility will favor species that can best exploit localized zones of nutrient availability (Jackson and Caldwell 1989, Jackson et al. 1990, Caldwell et al. 1991, Bilbrough and Caldwell 1997), as well as species that are able to acquire N and water at depth in the soil (Evans and Ehleringer 1994) or that are most efficient in their N use (Schlesinger et al. 1990, Ehleringer et al. 1998).

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