Impacts of biological soil crust disturbance and composition on C and N loss from water erosion

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Abstract. In this study, we conducted rainfall simulation experiments in a cool desert ecosystem to examine the role of biological soil crust disturbance and composition on dissolved and sediment C and N losses. We compared runoff and sediment C and N losses from intact late-successional dark cyanolichen crusts (intact) to both trampled dark crusts (trampled) and dark crusts where the top 1 cm of the soil surface was removed (scraped). In a second experiment, we compared C and N losses in runoff and sediments in early-successional light cyanobacterial crusts (light) to that of intact late-successional dark cyanolichen crusts (dark). A relatively high rainfall intensity of approximately 38 mm per 10-min period was used to ensure that at least some runoff was generated from all plots. Losses of dissolved organic carbon (DOC), dissolved organic nitrogen (DON), and ammonium (NH_4^+) were significantly higher from trampled plots as compared to scraped and intact plots. Sediment C and N losses, which made up more than 98% of total nutrient losses in all treatments, were more than 4-fold higher from trampled plots relative to intact plots (sediment C g/m^2, intact = 0.74, trampled = 3.47; sediment N g/m^2, intact = 0.06, trampled = 0.28). In light crusts, DOC loss was higher relative to dark crusts, but no differences were observed in dissolved N. Higher sediment loss in light crusts relative to dark crusts resulted in 5-fold higher loss of sediment-bound C and N. Total C flux (sediment + dissolved) was on the order of 0.9 and 7.9 g/m^2 for dark and light crusts, respectively. Sediment N concentration in the first minutes after runoff from light crusts was 3-fold higher than the percent N of the top 1 cm of soil, suggesting that even short-term runoff events may have a high potential for N loss due to the movement of sediments highly enriched in N. Total N loss from dark crusts was an order of magnitude lower than light crusts (dark = 0.06 g N/m^2, light = 0.63 g/m^2). Overall, our results from the small plot scale (0.5 m^2) suggest that C and N losses are much lower from intact late-successional cyanolichen crusts as compared to recently disturbed or early-successional light cyanobacterial crusts.

Introduction

In aridland ecosystems that are characterized by sparse vegetation and exposed soils, surface runoff is a dominant pathway of nutrient transfer (Ludwig et al. 1997). Biological soil crusts (i.e. cryptogamic, cryptobiotic,

microphytic, microbiotic) are assemblages of lichens, fungi, cyanobacteria, and mosses that colonize soil surfaces in aridland soils. Biological soil crusts represent up to or more than 70% of the living ground cover in many aridland environments (Belnap et al. 2001). Thus, runoff and sediment loss dynamics from biological soil crusts may have a large impact on nutrient redistribution or loss from aridland watersheds. Numerous studies have been conducted on the role of biological soil crusts on surface hydrology and erosional dynamics, but associated nutrient losses from biological soil crusts are poorly understood.

Nutrients may be lost during water erosion as dissolved constituents in runoff and as associated elements in mobilized sediments. Runoff amount is determined by soil infiltration capacity, which is affected by soil porosity and residence time of water on the soil surface. In plant interspaces where biological soil crusts occur, Schlesinger et al. (1999) showed that more than 60% of added water in rainfall simulation may be lost in runoff. Biological soil crusts in particular do not have a uniform impact on soil infiltration capacity. In a recent review, biological soil crusts were shown to negatively impact infiltration in coarse textured soils ($> 80\%$ sand content) (Warren 2001). Organisms associated with biological soil crusts expand when wet, which may result in 'clogging' water flow through matrix pores resulting in reduced hydraulic conductivity at the soil surface, which, in some cases, may even become slightly hydrophobic (Bond and Harris 1964; Roberts and Carbon 1972; Kidron et al. 1999). Several of the studies reviewed by Warren (2001) were conducted in hot desert ecosystems, where soils often display little or no microtopography or surface roughness. In cool desert ecosystems, frost-heaving results in rolling or pinnacled surfaces of up to 15 cm (Belnap et al. 2001). Infiltration capacity increases with surface roughness due to changes in ponding dynamics and overland flow paths that promote water retention (Warren 2001; Belnap et al. 2005). Disturbance of a biological soil crust, however, may decrease infiltration capacity, resulting in increased runoff and sediment loss. Rainfall simulations conducted in a coastal California scrubland showed that simulated livestock trampling of plots containing biological soil crusts resulted in a 42% decrease in infiltration capacity (Fierer and Gabet 2002).

Nutrient concentrations in runoff are affected by available nutrients at and near the soil surface, which depends on both the quantity of nutrients and soil exchange characteristics. Biological soil crusts fix atmospheric N_2, which leaks to the surrounding environment in the form of NH_4^+ or simple amino acids (Mayland 1966) and may be easily leached away in surface runoff. Later successional cyanolichen crusts have higher N fixation rates and subsequently higher nutrient content in the surface 2 cm than early successional cyanobacterial crusts (Barger 2003; Belnap et al. 2003). Consequently, nutrient concentrations in runoff from later successional cyanolichen crusts should be higher than early successional cyanobacterial crusts.

Biological soil crusts reduce soil erosion by water (Booth 1941; McCalla 1946; Fletcher and Martin 1948; Osborn 1952; Faust 1970; Tchoupopnou 1989; Eldridge and Greene 1994; Eldridge and Kinnell 1997; Eldridge 1998). Once biological soils crusts are disturbed, sediment loss increases dramatically (e.g. Loope and Gifford 1972; Warren et al. 1986; Eldridge 1993, 1998). Most soil erosion by water occurs when raindrop impact detaches soil particles from the surface, which may then be moved downslope via sheet flow. Networks of fungal hyphae, cyanobacterial sheaths, and lichen and moss attachment structures in biological soil crusts bind soil particles together (Belnap and Gardner 1993) and increase aggregate stability (Schulten 1985; Eldridge 1993; de Cano et al. 1997). Thus sediment-bound nutrient loss should be lower from biological soil crusts as compared to bare soils. The higher biomass found in cyanolichen crusts protects the soils more effectively than the lesser biomass of cyanobacterial crusts (McKenna-Neuman et al. 1996).

Functional group composition of the biological soil crust also impacts surface erosion. Lichens and mosses are more effective than cyanobacteria in reducing splash erosion and sediment production (Tchoupopnou 1989), as their tissue occurs above the soil surface, dissipating the energy of incoming raindrops. Later-successional cyanobacteria (e.g., *Nostoc* spp., *Scytonema* spp.) reside right at the soil surface, and thus are more effective at protecting soil surfaces than early-successional *Microcoleus vaginatus*, which resides 1 mm or more below the surface (Garcia-Pichel and Belnap 2001).

Disturbances such as livestock grazing and recent increases in recreational uses of public lands dramatically alter soil surfaces in arid and semiarid regions of the western US by converting late successional cyanolichen crusts (containing lichens, mosses, *Nostoc*, and *Scytonema*) to cyanobacterial crusts dominated by *Microcoleus* (Belnap 1996). Climate change is also likely to alter species composition in biological crusts, as increased temperature and/or summer precipitation reduces cover of the later successional species (Bowker et al. 2002; Belnap et al. 2004; Belnap et al., in press). In this study, we conducted rainfall simulation experiments in a cool desert ecosystem to examine the role of biological soil crust composition and soil surface disturbance on dissolved and sediment C and N loss in water erosion. We addressed the first question: What effect does disturbance of a late-successional cyanolichen soil crust have on dissolved and sediment-bound C and N loss? In this experiment, we hypothesized that surface disturbance would result in increased C and N losses due to increased runoff and sediment loss. In a second experiment, we addressed the question: Are C and N losses higher in early-successional cyanobacterial crusts as compared to the late-successional cyanolichen crusts? In this experiment, we hypothesized that C and N losses would be higher from early-successional cyanobacterial crusts relative to late-successional cyanolichen crusts, due to lower soil surface stability and increased erosional losses from early-successional cyanobacterial crusts.

Methods

Site description

This study was conducted near the Island-in-the-Sky District of Canyonlands National Park, near southeast Utah on land managed by the United States Bureau of Land Management. The site was located at 1813 m elevation and the 50 yr mean annual precipitation was 215 mm. Dominant plant species at the site were *Coleogyne ramosissima* (blackbrush), *Pinus edulis* (pinyon pine), *Juniperus osteosperma* (Utah juniper) and *Yucca harrimaniae* (Harriman's yucca). We selected 2×3 m plots with biological soil crusts located in vascular plant interspaces. Since soils in this area have not been mapped, soil identification was based on soil profile comparisons with soil series descriptions included in a soil survey located approximately 3 km south of the study sites (Lammers 1991). The survey includes areas on the same geomorphic surface with similar soil features. Soils were coarse-textured (Table 1) and all subplots were classified as Arches loamy fine sands (mixed, mesic Lithic Torripsamments). Soil texture was uniform throughout the profile and depth to Navajo sandstone bedrock ranged from 20 to 53 cm. Average slope of the plots was $3.6\% \pm 1.7$ S.D.

In the first experiment, we examined the impact of disturbance of late-successional cyanolichen crusts on dissolved and sediment-bound C and N loss. Plots within this experiment were located on biological soil crusts containing both lichens and free-living cyanobacteria. Coloration is a good indicator of development and successional stage of a biological soil crust since darker-pigmented cyanobacteria such as *Nostoc* and *Scytonema* colonize biological soil crusts at later stages in biological soil crust development. In the field, we used ocular observation of crust color and the presence/absence of lichens to determine successional stage of the biological soil crusts and subsequent plot locations. We conducted the disturbance experiment on dark cyanolichen soil crusts in October 2001. These late-successional or dark biological soil crusts

Table 1. Pre-rainfall simulation soil measurements.

	Dark crust scraped	Dark crust trampled	Dark crust intact	Light crust
Texture				
% Sand	81.21 (0.86)	79.54 (1.49)	79.02 (0.67)	79.94 (2.09)
% Silt	10.91 (0.62)	13.22 (1.34)	13.76 (1.70)	13.39 (2.35)
% Clay	7.82 (0.53)	7.24 (0.45)	7.22 (1.03)	6.67 (0.57)
Bulk density (g/cm^3)	1.70 (0.03)	1.95 (0.03)	1.69 (0.03)	1.68 (0.04)
Soil stability class	1.16 (0.11)	1.00 (0.00)	5.09 (0.24)	3.38 (0.34)
Chlorophyll *a* (μg/g soil)	0.72 (0.14)	2.67 (0.16)	11.40 (1.82)	1.48 (0.16)
% Soil moisture	0.7 (0.1)	0.7 (0.1)	0.6 (0.1)	2.1 (0.3)
Roughness class	0.984 (0.002)	0.973 (0.001)	0.853 (0.012)	Not measured

Values are means ± 1 SE ($n = 7$).

were dominated by the cyanobacteria *Microcoleus vaginatus*, but also contained large amounts of the darker pigmented cyanobacteria *Scytonema myochrous* and *Nostoc commune* and up to 10% cover of the soil lichens, *Collema tenax*, *C. coccophorum*, and *Placidium lachneum*. We selected seven plots that were then divided into three 71×71 cm subplots, all of which received the rainfall treatment at the same time. The following treatments were randomly assigned to the subplots: (1) dark trampled, (2) dark scraped, and (3) dark intact. In the trampled treatment, 100 passes were made over the plot by foot (jogging in hard-soled hiking boots), moving from the downslope to the upslope side of the plot on each pass. We also implemented a scraped treatment to remove biological soil crusts while keeping subsurface soils intact. In this treatment, we identified the lowest point in the plot and removed the top 1 cm of soil in addition to all crust pinnacles above the soil surface with a straight edged flat trowel. Soils were dry at the time the treatments were applied. Simulations were completed within 6 h of treatment application to prevent interactions with eolian processes.

In a later experiment in November 2001, we conducted rainfall simulations on seven cyanobacterial or 'light' crust plots. Light crusts were dominated by the cyanobacteria *Microcoleus vaginatus*, with no lichens, mosses, or darker-pigmented cyanobacteria present. Percent soil moisture in the top 5 cm ranged from 0.5 to 3% in light crust plots compared to 0.4–1% in dark crust plots. Differences in soil moisture were due to a small (< 5 mm) rain event that occurred before rainfall simulation was completed on 6 of the 7 light crust plots.

Pre-simulation soil measurements

Soil sampling was completed following treatment application and prior to simulation. Bulk density and antecedent soil moisture content were measured on one 0–5 cm deep sample per treatment plot, composited from four 5 cm-diameter cores. Bulk density was measured by the core method and soil moisture was determined by gravimetric water content. Soil texture was determined using the hydrometer method (Gee and Bauder 1979) on one 0–2 cm deep sample per plot. Each of these samples was also a composite of four subsamples for each treatment. We generated an index of soil aggregate stability for the top 5 mm for eight samples per plot using a field soil stability test (Herrick et al. 2001). Each 6–8 mm diameter crust fragment was immersed in deionized water on a 1.5 mm sieve for 5 min, then pulled completely out of the 2.5 cm deep water five times at a rate of one cycle every 2 s and rated on a scale from one to six. We measured surface roughness with a 696 mm flexible chain. The chain was placed on the soil surface at four different locations perpendicular to the downward slope within each plot. Chain length at the surface was divided by total chain length to get an index of surface roughness, where 1 was equal to a completely flat surface and values near 0 displayed a

large amount of microtopography. We measured soil chlorophyll *a* content, which we used as an indicator of cyanobacterial biomass, on one sample per plot composited from 12, 5-mm deep soil cores. In the lab, soil samples were ground to a fine powder with a mortar and pestle. Quantitative and qualitative HPLC analysis was performed according to the method of Karsten and Garcia-Pichel (1996).

Rainfall simulation

The presence of rills and waterflow patterns (Pyke et al. 2002) throughout the study area indicated that runoff had occurred at these sites within the past several years. Based on preliminary experiments, we estimated that average infiltration rates after 10 min could be as high as 17 mm per 10-min period, which is equivalent to a 50 year storm in the Moab area (http://hdsc.nws.noaa.gov/hdsc/pfds/). Because this is an average value, some plots would be expected to generate runoff more frequently, while other plots would generate runoff only during extreme events. In order to ensure that we generated runoff from all plots, we approximately doubled this value to 38 mm per 10-min period, which would occur during a 500–1000 year storm (http://hdsc.nws.noaa.gov/hdsc/pfds/).

Water was applied simultaneously to all three 71×71 cm treatment plots for 30 min at an average rate of 227 mm/h with a VeeJet 80/100 nozzle located 2.0 m above the soil surface. Water pressure was controlled at 31.0 kPa and the nozzle was moved once across the plots every 4 s using a hand-pulley system, generating a uniform spatial distribution: the coefficient of variation of the 15 precipitation gauges located in the plots was generally less than 5%. A collection tray was installed at the downslope end of each plot which diverted water and sediments to collection bottles.

The N composition of natural rainfall that occurs within Island-In-The-Sky District of Canyonlands National Park was simulated using water purified by reverse osmosis supplemented with NH_4OH and HNO_3. Ammonium and NO_3^- concentrations in rainfall simulation water ranged from 0.05 to 0.079 and 0.09 to 0.13 mg/l, respectively. Runoff samples were collected for chemical analysis every minute for the first 5 min of runoff and every 5 min thereafter.

Analysis of C and N in sediment and water samples

Once all the samples were collected in the field, they were immediately transported to the laboratory where they were kept frozen. In the laboratory, subsets of the runoff waters were thawed and sediments were separated from the water. Each sample was centrifuged and the water was filtered through a 0.75 μm Millipore glass fiber filter. Remaining sediments were dried in a 70 °C oven. Once all the waters were filtered, samples were

analyzed for dissolved organic carbon (DOC), total dissolved nitrogen, NO_3^-, and NH_4^+. Nitrate and NH_4^+ were measured colorimetrically on an Alpkem autoanalyzer. Total dissolved nitrogen and TOC were measured on a Shimadzu TOC analyzer coupled with a total nitrogen analyzer. Dissolved organic nitrogen was calculated as total dissolved nitrogen–inorganic nitrogen. Pre-simulation background values of dissolved constituents in rainfall simulation water were subtracted from those in runoff waters. Total C and N in sediments were measured on a LECO CHN analyzer. Total organic C in sediments was calculated as total C − inorganic C. Inorganic C was measured by modified pressure-calcimeter as described by Sherrod et al. (2002).

Statistical analysis

Carbon and N loss data presented in this paper were cumulative over the first 10 min of the rainfall simulation. Concentrations of C and N were linearly interpolated for time periods that were not sampled since samples were not collected every minute during the simulation. Carbon and N losses in runoff and associated sediments were analyzed with a one-way ANOVA within the disturbance experiment on the dark crust plots (dark intact, dark scraped, and dark trampled) and a Student's *t*-test in the crust composition experiment (dark vs. light crust). Intact plots in the disturbance experiment and dark crusts in the soil crust experiment were the same plots. A Newman–Keuls post-hoc test to evaluate differences among treatments was used in the disturbance experiment. Correlation coefficients were calculated to examine the relationship between runoff and C and N concentrations as related to total dissolved and sediment-bound C and N loss. Significance levels of $p < 0.10$ are discussed.

Results

Disturbance experiment

Dissolved organic carbon (DOC) losses from trampled plots were higher relative to scraped and intact plots (Figure 1a). Dissolved organic nitrogen (DON) losses were similar to patterns observed in DOC, where losses were higher from trampled plots relative to scraped and intact plots (Figure 1b). Differences in organic C and N losses were due to a trend toward higher runoff in the trampled plots relative to the scraped and intact plots ($F_{2,18} = 2.45$, $p = 0.11$, Table 2), and not differences in concentration. Ammonium loss from trampled plots was higher than scraped and intact plots (Figure 1b). Differences in NH_4^+ losses were due to both a trend in higher runoff and significantly higher volume-weighted mean (total constituent loss/total runoff)
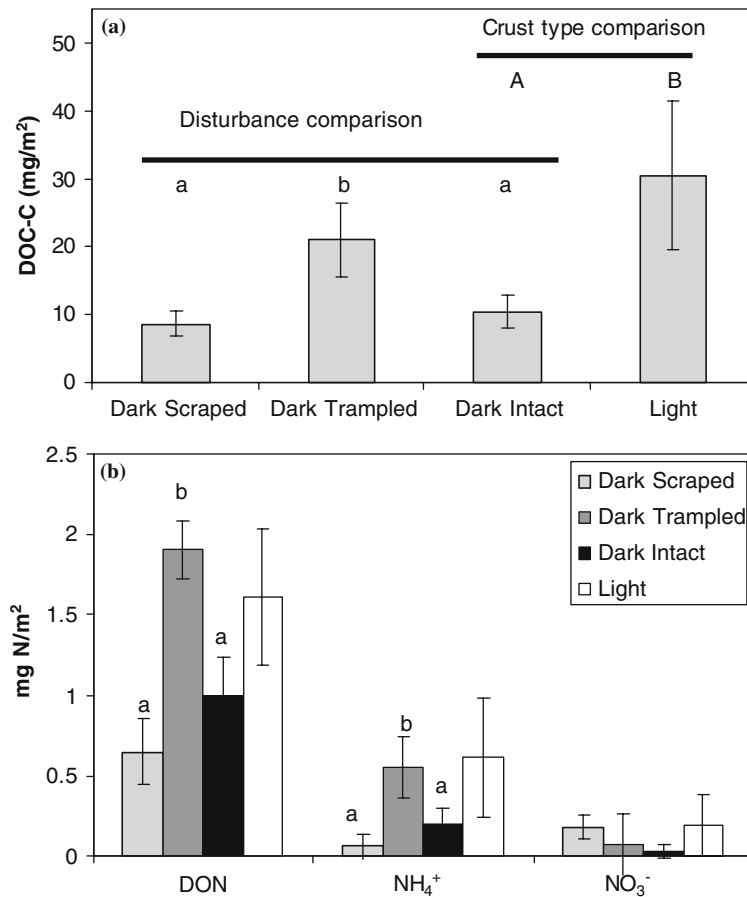
Figure 1. Dissolved C and N losses as (a) DOC and (b) DON, NH_4^+, and NO_3^-. Above each bar, lower case letters denote differences within the disturbance experiment, whereas lower case letters signify treatment differences by crust type. If a different letter appears above a treatment, means are significantly different at $p < 0.10$.

NH_4^+ concentrations in trampled plots as compared to scraped and intact plots (Table 2). No differences were observed in NO_3^- loss with trampling or scraping. DON was the dominant form of dissolved N loss within all treatments; average DON loss ranged from 72 to 85% of the total dissolved N losses (Figure 1b).

Sediment-bound C and N losses in trampled plots were higher relative to scraped and intact plots (Figure 2a and b). Mean sediment-bound C loss from trampled plots was 3.47 g C/m^2 as compared to 0.74 g C/m^2 from intact plots. Sediment-bound N followed a similar pattern where mean sediment N loss from intact plots was 0.06 g N/m^2, which increased to 0.28 g N/m^2 with trampling.

Table 2. Runoff and volume-weighted mean C and N concentrations (total dissolved C and N loss/total runoff) after 10 min of rainfall simulation.

	Dark scraped	Dark trampled	Dark intact	Light
Runoff l/m^2	4.02 (1.40) a	8.69 (1.77) a	5.12 (1.48) aA	24.30 (0.77) B
mg DOC-C/l	3.28 (0.80) a	2.47 (0.31) a	2.76 (0.57) aA	1.29 (0.49) B
μg DON-N/l	206 (44) a	260 (43) a	245 (56) aA	67 (19) B
μg NH_4^+-N/l	25 (12) a	95 (32) b	34 (16) aA	7 (8) A
μg NO_3^--N/l	48 (7) b	2 (8) a	9 (7) aA	25 (15) A

Values are means within each treatment ± 1 SE. Within each row, lower case letters represent difference within the disturbance treatment and capital letter signify treatment differences by crust type. If a different letter appears by a treatment within a row, means are significantly different at $p < 0.10$.
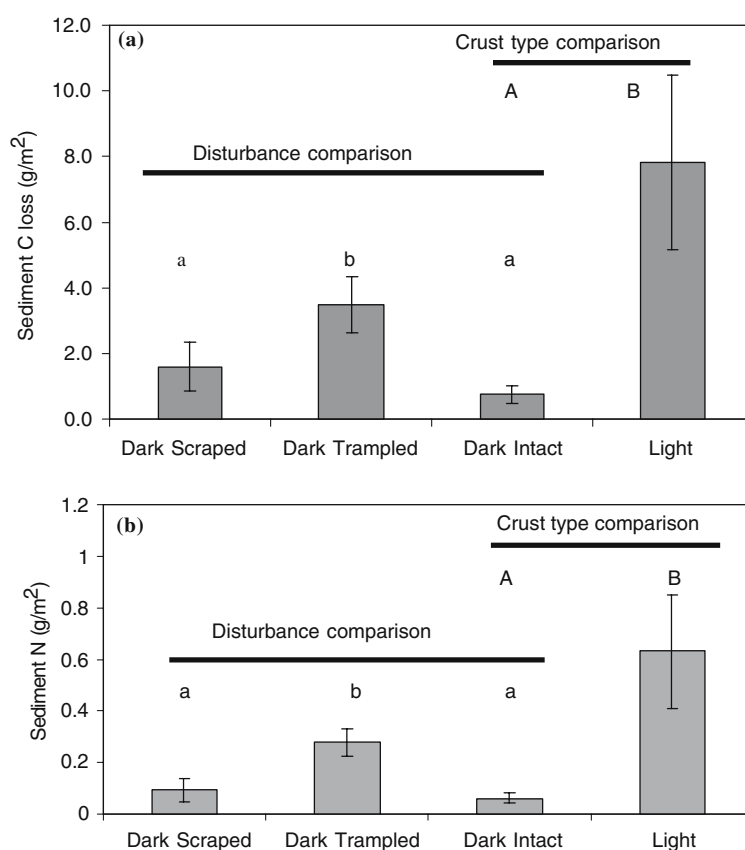

Figure 2. Sediment C and N losses. Above each bar, a lower case letter represents differences within the disturbance experiment, whereas capital letters signify treatment differences by crust type. If a different letter appears above a bar, means are significantly different at $p < 0.10$.

Impacts of biological soil crust community on C and N loss

Mean DOC loss was 3-fold higher in light crusts relative to dark crusts (Figure 1a), with no significant differences in DON loss (Figure 1b). Although volume-weighted mean DOC concentrations were higher from dark crusts (Table 2), the nearly 5-fold increase in runoff from light crusts resulted in the higher DOC loss from light crusts relative to dark crusts (Figure 1a). No differences in NH_4^+ or NO_3^- losses were observed by crust type (Figure 1b). Sediment-bound C and N losses were 9- and 10-fold higher in light as compared to dark crusts (Figure 2a and b). Sediment loss was the dominant pathway of C and N loss within all treatments in the two experiments. Sediment-bound C and N made up 98% or higher of the C and N loss from all treatments. Mean sediment C loss from light crusts was 7.82 g C/m^2, nearly 11-fold higher compared to dark crusts with mean sediment C loss of 0.74 g C/m^2. Even though sediment concentrations of C and N were higher in dark crusts relative to light crusts (Table 3), total C and N loss was higher in light crusts due to higher sediment loss. Sediment loss was 8-fold higher per unit runoff in light crusts relative to dark crusts (Table 3).

Sediments were more highly enriched in N in the first few minutes of the simulation than they were after 10 min. In a typical light crust plot, sediment percent N in the first minute of runoff was nearly 3-fold higher than sediment percent N after 10 min of rainfall (Figure 3). Changes in sediment percent N in a typical dark crust plot declined after 10 min, but to a lesser extent than the typical light crust plot. Across all treatments (light, dark intact, dark scraped, and dark trampled) dissolved C and N losses were positively correlated with runoff (carbon, r = 0.50; nitrogen, r = 0.41) (Table 4). Sediment N loss was positively correlated with total sediment loss ($r = 0.96$), but negatively correlated with sediment N concentrations ($r = 0.44$) (Table 4).

Discussion

Light (*Microcoleus*-dominated) soil crusts are representative of a post-disturbance soil surface in the western US, where surface disturbance often results in

Table 3. Sediment concentration and mass-weighted sediment-bound C and N concentrations (total C and N in sediment/total sediment loss) after 10 min of rainfall simulation.

	Dark scraped	Dark trampled	Dark intact	Light
Sediment concentration g/l runoff	7.7 (2.9) a	15.1 (6.7) a	3.5 (1.0) aA	29.7 (8.1) B
Sediment C mg C/g sediment	36.8 (10.7) a	33.3 (12.7) a	36.0 (10.5) aA	16.7 (10.3) B
Sediment N mg N/g sediment	4.5 (0.9) a	4.5 (1.0) a	4.5 (0.9) aA	1.4 (0.1) B

Values are means within each treatment $\pm$ 1 SE. Within each row, lower case letters represent differences within the disturbance experiment and capital letters signify treatment differences by crust type. If a different letter appears by a treatment, means are significantly different at $p < 0.10$.
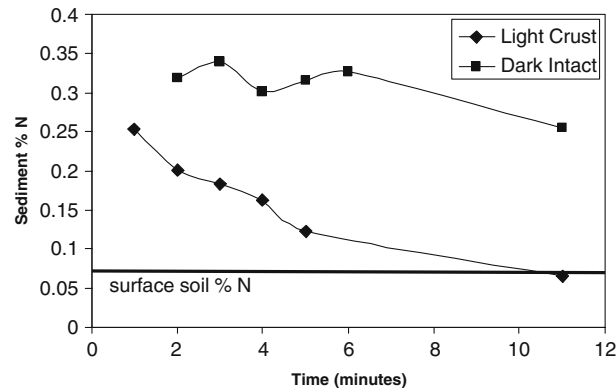
Figure 3. Nitrogen content in sediment throughout the duration of the rainfall simulation for a typical light and dark crust plot. The horizontal line represents the upper bound of soil % N in the top 1 cm in similar soils at a nearby site.

mortality of the later successional crust species, such as lichens, mosses, *Nostoc*, and *Scytonema*. Trampling of late-successional dark cyanolichen crusts will eventually result in the disturbed sites being dominated by an early-successional *Microcoleus* crust, as the mortality of buried later-successional lichens and cyanobacteria will continue after disturbance (Belnap and Eldridge 2001). Interestingly, C and N loss from light cyanobacterial crusts was not intermediate between late-successional dark cyanolichen crusts and those that had been recently disturbed. Carbon and N losses from both recently trampled dark crust and early-successional cyanobacterial crusts were high, which suggests that these soils are especially vulnerable to nutrient loss during the recovery period to a late successional cyanolichen crust, which may take decades to centuries. Surface chlorophyll *a* content in light crusts was lower than trampled dark crusts in this experiment (Table 1), which supports the idea that

Table 4. Correlation coefficients examining runoff and C and N concentrations as related to dissolved and sediment-bound C and N loss.

	Correlation coefficients
Dissolved organic C loss (mg) and:	
Runoff (l)	0.50*
C concentration (mg C/l runoff)	0.07
Dissolved N loss (μg) and:	
Runoff (l)	0.41*
N concentration (μg N/l runoff)	0.26
Sediment N loss (mg N) and:	
Sediment loss (g)	0.96*
N concentration (mg N/g sediment)	-0.44*

*denotes a significance level of $p < 0.10$.

residual cyanobacterial biomass at the surface of the trampled dark crust plots may be conferring some resistance to sediment detachment until those cyanobacteria buried by trampling die due to lack of light. It is also possible that the structure of developing light crusts makes them more erodible than more established crusts. During the rainfall simulation, we observed that soil pinnacles on light crusts readily collapsed under raindrop impact, which may also partially explain the high sediment losses.

Even small runoff events may be an important N loss pathway from biological soil crusts. Soil percent N in the top 1 cm in similar soils at a nearby site ranged from 0.01 to 0.07%, much lower than sediment percent N in the first few minutes of runoff (0.25–0.32%). There are several factors that may explain elevated soil N concentrations in the first few minutes of runoff. Finer soil fractions, which are generally elevated in N content, are mobilized early in a runoff event with coarser fractions being mobilized later (Palis et al. 1997). In addition, microrelief of biological soil crusts traps atmospheric dust on the soil surface (Danin and Ganor 1991; Verrecchia et al. 1995; Reynolds et al. 2001), which may be easily washed off by overland flow. Blank et al. (1999) showed that aqueous soluble NH_4^+ and NO_3^- in dust were much higher than in the top 5 cm of mineral soil, which suggests that dust inputs may elevate N concentrations at the soil surface. Nitrogen-fixing cyanobacteria and lichens within sediment samples may have also been important in elevating the N content of sediments. Runoff disperses soil microorganisms, especially lichens and cyanobacteria living at the soil surface. In a study of microphyte dispersal in surface runoff in Australian woodland, *Collema coccophorum*, a lichen also commonly found on the Colorado Plateau, was the most abundant lichen collected in the early stages of runoff (Eldridge 1996). In this study, there was visible evidence that soil cyanobacteria were detached from the soil surface and transported in runoff waters, with *Microcoleus vaginatus* the most commonly observed cyanobacteria in sediment samples.

Carbon loss (sediment + dissolved organic C) was on the order of 7.9 and 3.5 g C/m^2 for light and trampled crusts and 0.8 g C/m^2 for intact dark crusts, which constitutes <1% of the surface organic C (top 2 cm) at these sites. Carbon loss from intact dark crusts in our study was more than 4-fold higher than estimates of annual sediment C losses reported for a California grassland and scrubland (0.2 g C/m^2/yr) (Fierer and Gabet 2002). These differences may be partially explained by the higher rainfall intensity in our study and smaller plot size (0.5 m^2 vs. 15 m^2) in which more localized redistribution would be detected. In addition, C losses should be especially high from our simulation experiments due to the absence of vascular plant cover. In the study by Fierer and Gabet (2002), model estimates of sediment C losses were 16-fold higher in non-vegetated plots as compared to fully vegetated plots.

Nitrogen loss from dark crust plots (0.06 g N/m^2) was an order of magnitude lower than light crusts (0.63 g N/m^2). Nitrogen export in suspended sediments was 0.05 and 0.19 g N/m^2 for 1 m^2 plots in pinyon–juniper and grassland sites in New Mexico and Arizona (Bolton et al. 1991), values that are

comparable to intact dark crust plots in our study. Nearly 3% of the estimated surface organic N was removed from light crust plots during the rainfall simulation, whereas <1% was removed from intact dark crusts. In a Chihuahuan desert shrubland, average dissolved N losses from intershrub plots was 0.30 g N/m^2 (Schlesinger et al. 2000), two orders of magnitude higher than dissolved N losses we observed in our intact dark crust plots (0.002 g N/m^2). These differences in dissolved N losses may be partially explained by large differences in dissolved N concentrations early in the rainfall simulation. In Schlesinger et al. (2000) dissolved N concentrations were upwards of 20 mg/l in the first minutes of runoff, whereas in our study dissolved N concentrations did not exceed 1 mg/l throughout the experiment.

The results of small plot experiments, such as the one reported here, reflect the relative amount of sediment-bound C and N that is likely to be displaced during a storm from different types of soil surfaces (Meyer 1994). However watershed level C and N loss dynamics may be very different from those reported at the small plot scale. For example, in both Chihuahuan and Sonoran desert runoff studies, net N accumulation (N inputs exceed outputs) was estimated at the plot (4 m^2) and watershed scale (Fisher and Grimm 1985; Schlesinger et al. 2000), whereas we observed net N release (outputs exceed inputs) at the 0.5 m^2 scale in our study. Wilcox et al. (2003) examined runoff and erosional dynamics at several spatial scales in a semi-arid woodland and showed that runoff decreased by 50-fold from the microplot (1–3 m^2) to the hillslope (2000 m^2) scale. Patterns in erosional losses in that same study were similar to runoff dynamics. Sediment losses from the microplot scale ranged from 1000 to 4000 kg/ha, but decreased to <100 kg/ha at the hillslope scale. In our study, sediment N loss was strongly and linearly related to total sediment loss (Table 4). Assuming that sediment loss decreases with increasing spatial scale, we expect N should also decline with increasing spatial scale. Therefore N losses we observed at the small plot scale more likely reflect local redistribution of nutrients and not N losses at the watershed level.

Nutrient redistribution via physical processes such as wind and water erosion is recognized as an important feature in nutrient cycling in arid ecosystems (Parsons et al. 1992; Abrahams et al. 1994; Schlesinger et al. 1996; Schlesinger and Pilmanis 1998; Ludwig et al. 1997). Ludwig et al. (1997) proposed that transfer of resources between source areas (plant interspaces) to sink areas (vegetated patches) is a critical process in maintaining plant productivity. Disturbance of these source/sink relationships may alter nutrient delivery downslope and impact plant communities. Over the last century, many late-successional biological soil crust communities in the western US have been disturbed by intensive land use practices such as livestock grazing and recreational use of public lands, resulting in the large scale conversion of late-successional dark cyanolichen crusts to early-successional cyanobacterial crusts. Before the introduction of domestic livestock and changes in recreational use of public lands, much of the area covered by biological soil crusts was thought to be dominated by dark cyanolichen crusts. Of the 100 million ha

of grazing lands in the western US, approximately 40% of this area is covered by biological soil crusts (Garcia-Pichel et al. 2003). Current estimates of light cyanobacterial crust coverage are upwards of 70%, with only 30% remaining in dark cyanolichen crusts (M. Miller, pers. com.). Runoff and sediment loss increased with disturbance and the presence of early-successional vs. late-successional soil crusts, which suggests that downslope plant communities may receive a higher flux of nutrients in water and sediments in a post-disturbance environment. Alternatively, higher runoff and sediment transport from plant interspaces may also result in higher nutrient losses from the watershed. In a post-disturbance environment and subsequent recovery to early-successional cyanobacterial crust, soil nutrients should be heterogeneously distributed, with plant interspaces being highly depleted in nutrients relative to tree and shrub canopies due to higher losses of water and sediments in runoff. Schlesinger et al. (1990) hypothesized that increasing spatial heterogeneity of soil water and nutrients promotes invasion by desert shrubs and declines in soil fertility in plant interspaces. In a community dominated by late-successional cyanolichen crusts, nutrient distribution should be more homogeneous relative to disturbed and early successional biological soil crust communities; as runoff and sediment production decreases nutrients will be retained in the plant interspaces. Spatial redistribution of nutrients during runoff events in disturbed biological soil crusts should lead to changes in soil C and N cycling, location of plant available nutrients, and composition of soil food webs in these ecosystems.

Long-term monitoring studies of nutrient loss in water erosion are costly and the analytical equipment needed for elemental analysis of runoff waters and sediments are often unavailable for low budget monitoring programs. As a result, there are few sites in the western US that monitor nutrient loss in water erosion. However, there are a great number of sites that monitor sediment loss dynamics in watersheds throughout the West. In our study, 98% and higher of total C and N losses were from sediment sources which was highly correlated with total sediment loss (Table 4). Thus, with little additional effort, results from current monitoring programs of sediment loss dynamics in conjunction with surveys of biological soil crust development and successional stage within western watersheds, may further inform us of sites that are potentially vulnerable to high nutrient loss that may lead to subsequent declines in soil fertility in aridland soils.

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