



Fine gravel controls hydrologic and erodibility responses to trampling disturbance for coarse-textured soils with weak cyanobacterial crusts

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ABSTRACT

We compared short-term effects of lug-soled boot trampling disturbance on water infiltration and soil erodibility on coarse-textured soils covered by a mixture of fine gravel and coarse sand over weak cyanobacterially-dominated biological soil crusts. Trampling significantly reduced final infiltration rate and total infiltration and increased sediment generation from small (0.5 m²) rainfall simulation plots ($p < 0.01$). Trampling had no effect on time to runoff or time to peak runoff. Trampling had similar effects at sites with both low and very low levels of cyanobacterial biomass, as indicated by chlorophyll *a* concentrations. We concluded that trampling effects are relatively independent of differences in the relatively low levels of cyanobacterial biomass in this environment. Instead, trampling appears to reduce infiltration by significantly reducing the cover of gravel and coarse sand on the soil surface, facilitating the development of a physical crust during rainfall events. The results of this study underscore the importance of carefully characterizing both soil physical and biological properties to understand how disturbance affects ecosystem processes.

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1. Introduction

The effects of soil surface disturbance on water infiltration into arid and semi-arid soils have been widely debated in both the popular and scientific literature. Disturbance nearly always increases soil erodibility. Soil surface disturbance can affect several site factors that influence infiltration, including soil surface cover and structure. Infiltration is generally increased and soil erosion is reduced by greater cover, which protects the soil from raindrop impact and increases flowpath tortuosity. Rock cover, however, can increase or decrease infiltration (Poesen et al. 1990; Valentin 1994; Cerda 2001; Descroix et al. 2001). Several studies have shown that embedded gravel reduces infiltration, while free gravel can increase it relative to soils without gravel cover (Valentin and Casenave 1992; Cerda 2001).

Good soil structure, as reflected in high aggregate stability and macroporosity, generally increases infiltration capacity. However, several studies demonstrate that disturbance to soils with biological crusts (biocrusts), which generally have higher surface aggregate stability than soils without biocrusts, may either increase, decrease or have no effect on infiltration rates (Warren, 2003). Biocrusts are

ubiquitous on arid and semi-arid soils (Belnap and Lange, 2003) and are often particularly well-developed in undisturbed plant inter-spaces. Warren (2003) proposed that biological crusts should increase infiltration for soils with a sand content of less than 80% and reduce infiltration into soils with a sand content above 80%; in the absence of organic matter, fine-textured soils often disperse when wetted, filling water-conducting pores with silt and clay. Cyanobacteria, lichens and mosses bind soil particles together, limiting dispersion and maintaining higher pore volume and continuity. Conversely, soils with a high sand content tend to be relatively porous, even when the particles are not aggregated and soil organisms fill the textural pores, effectively reducing infiltration (Eldridge and Greene, 1994a; Kidron et al., 1999).

Eldridge (1993) and Eldridge et al. (1997) concluded that variability in crust cover had a negligible effect on infiltration rates, except where lichen and moss cover have been reduced below 20% by historic disturbance. On structurally degraded soils, microbiota should increase infiltration by binding soil particles and preventing dispersion. On historically undegraded soils, their contribution is inconsequential because structural macropores that are independent of the crusts dominate the infiltration process (Eldridge, 1993). Given these arguments, effects of microbiotic crust on infiltration should be more accurately predicted where both soil texture and recent and historic regimes are known.

Biological crusts nearly always reduce soil erosion (Eldridge and Greene, 1994a,b; Williams et al., 1995; Eldridge, 1998; Warren, 2003). One exception has been described for sandy soils, where upslope high

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crust cover can increase downslope erosion by increasing runoff (Talbot and Williams, 1978).

We investigated the effects of short-term, soil-surface disturbance on infiltration characteristics and soil erodibility of cyanobacterially-crusted, coarse-textured soils in the Mojave Desert. The cyanobacterial crusts were generally covered with a thin (1–5 mm) layer of coarse sand and fine gravel, a pattern we have observed on granitic soils in arid and semi-arid regions throughout the world. We subjected these soils to simulated, high-intensity rainstorms, as high-intensity storms are the only events that generate significant runoff and sediment, and thus these storms, while rare, are of considerable concern to land managers.

Most studies of disturbance effects on infiltration and erodibility for biologically-crusted soils suffer from two limitations. The first is that they include only soils with well-developed biological crusts, and often conclude that disturbance effects can be attributed solely to crust removal or destruction. This design fails to account for the possibility that short-term disturbance effects on infiltration and erodibility are independent of the presence of a biocrust. The second limitation is that many studies are completed at only one location. This results in pseudo-replication at the landscape level. We addressed both limitations by replicating our study at three sites where cyanobacterial biomass was relatively high compared to our other sites, where cyanobacterial biomass was very low.

2. Materials and methods

2.1. Overview

Two studies are reported here. Both studies were initiated and completed in May 2000. A preliminary study (“site characterization”) was used to confirm the assignment of each of the six sites to high (H1–H3) and low (L1–L3) chlorophyll *a* site types, and to ensure that comparisons are not confounded by textural or bulk density differences among the two types of sites. The main study (“disturbance”) was designed to test the hypotheses that soil surface disturbance (trampling) would increase infiltration at the high chlorophyll *a* sites and have no effect at the low chlorophyll *a* sites. Trampling was expected to increase sediment production at the high chlorophyll *a* sites and have a negligible effect at the low chlorophyll *a* sites.

2.2. Site selection

The two studies were completed at six sites on and adjacent to Fort Irwin U.S. Army National Training Center, San Bernardino County, California. These sites were previously characterized by Johansen et al. (2001) and additional information is included in Belnap et al. (2007a, b). Site designations used in Johansen et al. (2001) and GPS locations recorded during the study reported here are listed in Table 1. Average annual precipitation in the area was 101 mm and is bimodally distributed. Total precipitation for May, 1999–April 2000 was 46 mm. The area received 23 mm of precipitation during the four months

immediately preceding the experiments. The six sites were located on coarse-textured alluvial soils formed from primarily granitic parent material (Johansen et al., 2001). Perennial plant canopy cover was less than 10% at all sites. It was dominated by the shrubs *Larrea tridentata* and *Ambrosia dumosa* (Johansen et al., 2001).

The chlorophyll *a* data reported in Johansen et al. (2001) were used to stratify the six sites into two site types. Chlorophyll *a* concentrations are often used to estimate cyanobacterial biomass (Karsten and Garcia-Pichel, 1996) and therefore reflect the level of biocrust development in this ecosystem. The three low chlorophyll *a* sites (L1–L3) were located in areas regularly used for military training activities involving tanks, wheeled vehicles and ground troops (R. Sparks, Fort Irwin, Barstow, CA., pers. comm.). The three high chlorophyll *a* sites (H1–H3) were located in areas protected from training activities. These three sites had moderately high cover of cyanobacterial crusts, although the cyanobacterial biodiversity was poor. *Microcoelus vaginatus*, *M. steenstrupii*, and *Schizothrix calcicola* were common, but heterocystous taxa were rare (Johansen et al., 2001). These sites also had a trace (<1%) of lichen (predominantly *Collema tenax*, *Placidium squamulosum*, and *Petula obscurans* var. *hassei*) and moss (mostly *Bryum* spp.) cover. The low chlorophyll *a* sites completely lacked lichens and mosses, and had greatly decreased abundance of cyanobacteria (Johansen et al., 2001). All measurements for both studies were made in plant interspaces where the sum of grass, forb and litter cover was visually estimated to be less than 3%.

2.3. General soil and site characterization

Slope was measured using a clinometer. Soil series for four of the sites were identified using a recently published soil survey (Fahnestock and Novak-Echenique, 2002) together with soil profile descriptions for a single pit located at the center of each site. These data were supplemented by data from the site characterization study (below). No soil or geomorphic maps or soil surveys were available for the other two sites (R. Sparks, Fort Irwin, Barstow, CA, pers. comm.). Additional soil surface observations were made to assist with data interpretation.

2.4. Site characterization study

The objective of the site characterization study was to test the assumptions that (1) soil texture and bulk density were similar at the two site types (H and L), and (2) that the two site types had significantly different levels of cyanobacterial biomass. Prior to trampling, we measured soil particle size distribution, bulk density, chlorophyll *a* content and soil aggregate stability at each of the four to six pairs of plots at each site.

Particle size distributions, including sand size fractions, were determined for 0–0.5, 0.5–2 and 2–10 cm depths based on a composite of four subsamples at each pair of plots. Soil texture was determined using the hydrometer method after dispersal with sodium hexametaphosphate (Gee and Bauder, 1986). The sand fraction was further divided into the following fractions by sonic sieving for five min: 0.053–0.106 mm, 0.106–0.25 mm, 0.25–0.5 mm, 0.5–1 mm and 1–2 mm. Gravel content was measured gravimetrically.

Bulk density was quantified using four composited 45 mm diameter, 100 mm deep soil cores per pair of plots. Samples were oven dried to constant weight at 105 °C in order to determine pre-simulation gravimetric moisture and calculate dry bulk density.

Chlorophyll *a* content was measured on a composite of eight 0–5 mm samples collected from random locations around the edges of each pair of plots. Samples were extracted with dimethylsulfoxide (DMSO) in the dark for 45 min at 65 °C (Ronen and Galun, 1984). Samples were then shaken and centrifuged. The supernatant was immediately placed in a Turner Designs Inc. Fluorometer and fluorescence was measured. Fluorescence values were compared to a calibration curve obtained

Table 1

Corresponding site codes from Johansen et al. (2001), soil series definitions from Fahnestock and Novak-Echenique (2002), and GPS locations (NAD 83) for the center of each site for the current study.

	Study sites					
	H1	H2	H3	L1	L2	L3
	n = 4	n = 6	n = 4	n = 4	n = 4	n = 4
Johansen et al. (2001)	PR2	PR3	FISS	LIZ3	RPL3	RPL4
Northing	3891200	3891050	3886928	3892596	3907988	3906474
Easting	512250	511800	546083	541107	559361	558505

using commercially purchased standards of various concentrations of purified chlorophyll *a* dissolved in DMSO.

An index of soil aggregate stability was obtained using a field soil stability kit (Herrick et al., 2001). Nine 6–8 mm diameter by 2–3 mm thick samples were removed from depths of 0–3 and 20–25 mm at each pair of plots after carefully brushing away any loose gravel. Each sample was placed in a separate 1.5 mm mesh wire basket, immersed in distilled water, observed for 5 min then lifted out of the water five times at a rate of one cycle every 2 s. A value of zero meant that the structure was so weak that a sample could not be removed for testing. A value of one indicated the sample slaked within 5 s following immersion. A maximum value of six was assigned when 75% or more of the sample remained after sieving.

F tests (ANOVA, GLM) were performed to test the hypothesis that those variables that might confound our comparisons of trampling effects were relatively similar across the two site types (high and low chlorophyll *a*). These variables included texture, sand size fractions and bulk density. F tests were also used to test the hypothesis that the two variables (soil aggregate stability and chlorophyll *a*) that were used to define the two site types did differ significantly between the two site types.

2.5. Disturbance study

At each site, we established six (H2) or four (H1, H3, L1–L3) paired rainfall simulation plots (“Non-trampled” and “Trampled”). One plot from each pair was randomly selected and trampled by two people (ca. 68 kg each) wearing lug-soled boots. Each person jogged 50 times through each 90 cm wide plot. A third observer counted the number of passes and inspected the plots to make sure that 100% of the area inside each plot was disturbed. Immediately after trampling the rainfall simulation plot, soil surface cover measurements were completed, borders were placed in the ground and simulation was started.

A 2 m-high single VeeJet nozzle (Spraying Systems Co., H ½ U SS 80 100)¹ was manually moved across each pair of plots (70.7 cm × 70.7 cm, or 5000 cm² each) on a 3 m track for 30 min using a pulley system, generating approximately 200 mm h⁻¹ of rainfall at 0.32 kg/cm² pressure (Fig. 1). Eighty percent of the raindrops emitted by the nozzle are 1–4 mm in diameter. It took 4.0 s for the nozzle to complete one pass across the plots. Actual intensity was calculated using five rain gauges per plot for every simulation. The high rainfall intensity was selected to ensure runoff, as average infiltration rate after 30 min was as high as 145 mm/h. Water flow patterns (as described in Pellant et al. (2000)) observed on the landscape at four of the six sites (H3 and L1–L3) indicated that runoff does occur during natural rainstorms. The five- and 15-minute peak intensities for 100 year storms in this area are 128 and 81 mm/h respectively. The intensities jump to 185 and 136 mm/h for 500 year storms (data extracted from <http://www.hdsc.nws.noaa.gov/hdsc/pfds/> accessed on 21 November 2003). While small, more frequent storms are important for plant growth, large storms are often far more important for runoff and soil erosion (Edwards and Owens, 1991).

All runoff water and sediment were collected and measured. Water was allowed to fill five 1-liter bottles at the beginning of each run; 2-liter bottles were used for the remainder of the run. Elapsed time to fill each bottle was recorded. Volume was determined by weight, then sediment was flocculated using alum (AlKSO₄), oven-dried and weighed. Final infiltration rate was calculated based on the difference between simulated rainfall intensity and water collected for the last three bottles collected from each plot during each run. Intensity was measured based on the average depth of water collected in five 4.8 cm-diameter rain gauges in each plot.



Fig. 1. Rainfall simulator used for all treatments. Nozzle is moved across plots using a metronome-timed hand-operated pulley system.

A small plot rainfall simulator was selected over natural rainfall runoff plots. This approach met the experimental objective of studying potential responses to high-intensity storms. Military training requirements prevented the installation and maintenance of runoff plots at L1–L3. Small plot rainfall simulators are limited in that they do not address the role of rills in runoff and erosion, and because they cannot precisely simulate natural storm characteristics (Kidron and Yair, 1997). However, rainfall simulators do allow runoff and erosion processes to be more easily observed directly and they allow large, infrequent storms to be simulated.

Gravel (>2 mm) and very coarse sand (1–2 mm) cover were measured before simulation on each plot using a 100-point frame. Measurements were repeated following trampling on the trampled plots. The point of a pin was used to define cover at each point and percent cover was calculated as the total number of intercepts in each plot.

The effects of short-term disturbance on infiltration, sediment production and gravel cover were analyzed using the MIXED procedure of SAS® (SAS Institute Inc., 1999). Because sites were not selected at random, it was necessary to model the data with Site and Trampling as fixed effects and Plot (Site) as random effects. The model was

$$y = S_i + P_{ji} + T_k + ST_{ik} + e_{ijkl}$$

where S_i is the Site effect (fixed effect, $i = 1, 2, 3, 4, 5, 6$), $P_{j(i)}$ is plot, nested within Site (random effect), T is Trampling Treatment (fixed effect, $k = 1, 2$), ST_{ik} is the Treatment/Site interaction and e_{ijkl} is the residual error ($l = 1$ through number of pairs at each site). Fixed effect tests involving Site were constructed with contrasts. Some test statistics produced using a mixed model approach are approximate F-tests and thus Satterthwaite's approximate denominator degrees of freedom were used to obtain the best approximations. When the test statistics are exact F-tests, the Satterthwaite option in SAS will produce the usual denominator degrees of freedom. These approximate degrees of freedom are weighted sums of the degrees of freedom of the random effects and often result in fractional degrees of freedom. The weights are functions of the restricted maximum likelihood estimates of the variance components, resulting in different degrees of freedom for different variables (Fai and Cornelius, 1996).

We tested for interaction between site type and Trampling on sediment, infiltration characteristics and gravel cover, and used planned comparisons to test treatment effects within each site type.

¹ Reference to a particular product or manufacturer does not imply endorsement by the USDA or any of the authors.

The site characterization comparisons reported in the Soil Properties section above were based on the same model except that there was no Trampling variable. Based on a comparison of our results with data from the literature, we identified gravel cover as a potentially important explanatory variable (Valentin and Bresson, 1992; Valentin, 1994; de Figuereido and Poesen, 1998). Our observations further suggested that coarse sand might be important. We used simple linear regression to quantify the amount of final infiltration variance explained by gravel alone, and the sum of coarse sand and gravel cover. Only tests of the fixed effects addressed in the experimental objectives are presented in results. Site was included in the analysis only because it was necessary to generate the correct model structure. Results for Site are not reported in order to simplify data presentation.

All data were tested to ensure they met required assumptions. A \log_{10} transformation was used to increase the normality of the sediment data prior to analysis, and back-transformed means and standard errors are reported. Using the GROUP option in the MIXED procedure of SAS (SAS Institute Inc., 1999) unequal variances were fit to treatment groups as appropriate. Data that did not meet assumptions even after standard transformations were ranked prior to analysis and the ranks were used in place of the actual values.

3. Results

3.1. General soil and site characterization

Slope at all sites was <2%. Soil series are listed in Table 2. H1–H3 had 2–5 mm thick accumulations of organic material within 1 cm of the surface. Much of this appeared to be cyanobacterial sheaths, but some also appeared to be plant-derived fine litter fragments. No near-surface organic matter accumulations were observed at L1–L3. H3 appeared to have been disturbed at some point by off-road vehicle traffic, but at a much lower level than the three low chlorophyll *a* sites. None of the sites appeared to have a vesicular horizon. Soil texture and degree of crust development varied both within and among sites, although the patchiness typical of many arid areas was less apparent at these sites.

3.2. Site characterization study

Pre-disturbance soil properties at the six sites were largely similar within and among the high and low chlorophyll *a* site types with a few notable exceptions. Soil texture was similar, except for gravel, which varied by a factor of two among all six sites within each of the three depths (Table 2). Sand content was significantly higher ($p < 0.05$) at the low (L1–L3) than at the high (H1–H3) chlorophyll *a* sites in the top 2 cm (Table 2). However, the sand was significantly finer at the L1–L3 than at the H1–H3 throughout the top 10 cm (Table 3). Soil moisture was less than 2% at all sites.

Chlorophyll *a* concentrations were much higher at the H1–H3 (Table 2) compared to L1–L3, as expected based on Johansen et al. (2001). Allowing for variability due to sampling time and depth, the range of values for both H1–H3 and L1–L3 are comparable to those reported by Johansen et al. (2001) (1753–1934 and 54–111 $\mu\text{g/g}$, respectively). However, the values for all sites are very low compared to other sites in the Mojave and other U.S. deserts (see Discussion).

Soil surface stability values were significantly higher at H1–H3 than at L1–L3, consistent with higher chlorophyll *a* values and observations of cyanobacterial sheaths in H1–H3 samples.

3.3. Disturbance study

Trampling significantly reduced final infiltration rate ($p < 0.01$). The reduction averaged 36% across both site types (Table 4; $p < 0.05$ and $p < 0.01$, respectively). Total infiltration during the 30 min simulation was also significantly reduced by trampling ($p < 0.01$) although the difference was only significant at the high chlorophyll *a* site type (H1–H3). Neither Time to Runoff nor Time to Peak Runoff was affected by trampling. There was no significant interaction between site type and trampling for any of the infiltration parameters. Hydrographs (e.g. Fig. 2) showed that the general shape of the infiltration curve was also similar for the two site types.

Trampling significantly increased the amount of sediment collected in runoff during rainfall simulations (Table 4; $p < 0.01$). Sediment generation from trampled plots was more than eight times greater than from non-trampled plots for the high chlorophyll *a* and nearly three times as great

Table 2
Site characterization and average values for high (H) vs. low (L) chlorophyll *a* sites for non-trampled soils. F tests for site type based on GLM. Subscript “r” indicates values replaced by ranks prior to analysis. Sand, silt and clay are percent of total <2 mm by weight; gravel is percent of total soil mass by weight.

	Study sites						Site type		
	H1	H2	H3	L1	L2	L3	High	Low	F _(1,4)
	n=4	n=6	n=4	n=4	n=4	n=4			
Soil Series	n/a	n/a	Cajon	Grave-Summit	Cronese	Arizo			
Chlorophyll <i>a</i> ($\mu\text{g/g}$)	3503	3476	2719	294	363	501	Average (SE)		117**
Bulk density: 0–5 cm (mg/m^3)	1.60	1.58	1.62	1.54	1.57	1.60	3232 (183)	360 (194)	2.5
Stability: surface	3.8	5.7	4.9	1.6	1.0	0.2	1.60 (0.02)	1.57 (0.02)	29**
Stability: 2 cm	3.5	2.8	1.5	1.4	1.3	1.1	4.8 (0.5)	1.0 (0.5)	5 ⁺
Gravel %							2.6 (0.4)	1.3 (0.4)	
0–0.5 cm	40.9	32.8	16.2	26.6	33.8	29.8	30.0 (5.0)	30.1 (5.4)	0.0
0.5–2 cm	30.6	38.1	16.2	24.7	22.2	37.6	28.3 (5.6)	28.2 (5.9)	0.0
2–10 cm	22.9	31.2	12.6	14.6	14.7	24.5	22.2 (4.5)	18.0 (4.8)	0.4
Sand %									
0–0.5 cm	84.7	80.1	84.9	86.5	92.3	89.7	83.2 (1.6)	89.4 (1.7)	7.7 _r
0.5–2 cm	80.2	78.6	83.2	86.5	86.8	85.4	80.7 (1.0)	86.2 (1.0)	14.2*
2–10 cm	79.0	81.9	83.7	82.3	80.9	83.2	81.4 (1.0)	82.2 (1.1)	2.7 _r
Silt %									
0–0.5 cm	7.5	1.4	7.7	6.9	1.6	6.0	8.9 (1.4)	4.8 (1.5)	3.6 _r
0.5–2 cm	11.2	12.8	7.8	6.8	6.7	7.9	10.6 (1.1)	6.9 (1.2)	5.1 ⁺
2–10 cm	10.5	10.5	7.6	8.8	9.8	8.1	9.5 (0.9)	9.4 (1.0)	0.8 _r
Clay %									
0–0.5 cm	7.8	8.4	7.4	6.6	6.1	4.4	7.9 (0.2)	5.8 (0.2)	7.1 ⁺
0.5–2 cm	8.5	8.6	9.0	6.8	6.5	6.6	8.7 (0.6)	6.9 (0.6)	55.9**
2–10 cm	10.5	7.6	9.1	8.3	9.4	8.7	9.1 (0.6)	8.4 (0.7)	0.4 _r

⁺ $p < 0.1$; * $p < 0.05$; ** $p < 0.01$.

Table 3
Sand size fractions (% of total sand by weight) for top 10 cm. F tests for site type based on GLM. Subscript “r” indicates ranks used for tests.

	Site						Site type		
	H1	H2	H3	L1	L2	L3	High	Low	F _(1,4)
Very coarse sand (1–2 mm)							Average (SE)		
0–0.5 cm	38.3	31.4	29.1	14.4	17.5	13.0	32.9 (2.5)	16.2 (2.7)	20.3*
0.5–2 cm	25.1	27.1	21.3	12.2	5.4	8.7	24.5 (1.7)	9.0 (1.8)	39.2**
2–10 cm	20.3	24.8	18.4	13.8	7.3	12.7	21.1 (1.9)	11.4 (2.0)	25.5 _r *
Coarse sand (0.5–1 mm)									
0–0.5 cm	28.8	30.3	25.7	27.9	16.7	14.8	28.3 (3.1)	19.1 (3.3)	6.1 _r ⁺
0.5–2 cm	31.6	28.2	25.4	22.2	9.1	12.8	28.4 (2.8)	14.8 (3.0)	17.0 _r
2–10 cm	31.0	31.8	22.2	22.5	12.0	15.9	28.3 (2.9)	17.0 (3.1)	7.3*
Medium sand (0.25–0.5 mm)									
0–0.5 cm	17.1	19.1	19.8	26.5	25.0	37.8	18.6 (3.2)	28.7 (3.4)	4.6 ⁺
0.5–2 cm	21.6	19.9	24.4	27.8	28.2	23.0	21.9 (1.5)	26.6 (1.6)	4.3
2–10 cm	24.8	21.3	24.9	25.9	33.7	26.0	23.7 (3.0)	30.3 (3.2)	2.3
Fine sand (0.106–0.25 mm)									
0–0.5 cm	10.0	12.9	10.2	22.2	30.9	27.0	11.1 (1.9)	26.9 (2.0)	21.1 _r *
0.5–2 cm	13.1	15.5	12.9	26.9	45.5	40.8	13.8 (3.6)	37.4 (3.9)	19.8*
2–10 cm	16.1	14.4	22.1	26.6	37.0	35.6	17.5 (2.4)	31.5 (2.6)	16.0*
Very fine sand (0.053–0.106 mm)									
0–0.5 cm	5.8	6.4	15.2	9.0	9.9	7.4	9.1 (2.2)	9.1 (2.3)	0.0 _r
0.5–2 cm	8.7	9.4	16.0	10.9	11.8	14.6	11.3 (1.8)	12.1 (1.9)	0.1
2–10 cm	7.7	7.8	12.4	11.2	10.1	9.8	9.3 (1.2)	9.8 (1.2)	0.1

⁺p<0.1; *p<0.05; **p<0.01.

from trampled plots at the low chlorophyll *a* site type (Table 4; p<0.05 and p<0.01, respectively). There was a trend towards a proportionally larger increase in sediment production after trampling at high vs. low chlorophyll *a* sites, but this was not statistically distinct (Table 4; p<0.11).

Trampling significantly reduced gravel cover by more than 60% (p<0.001; F_(1,23) = 75.0). Reductions were similar for the two site types (67% and 60% for the H1–H3 and L1–L3 respectively; Fig. 3) and there was no interaction between trampling and site type (p>0.1; F_(1,23) = 1.9). Trampling reduced very coarse sand cover (p<0.001; F_(1,20) = 25.7), though the reduction was less at H1–H3 (44 vs. 40%; p = 0.11) than at the L1–L3 (36 vs. 21%; p<0.001). A simple linear regression showed that final infiltration was much more highly correlated with combined total coarse sand and gravel (r² = 0.45; p<0.001; F_(1,50) = 42.3) than with gravel cover alone (r² = 0.25; p<0.001; F_(1,50) = 18.0) measured prior to simulation. This analysis showed that the final infiltration rate increased 1.6 mm/h for every 1% increase in combined coarse sand and gravel cover. Although we did not measure gravel cover following rainfall simulation, we observed that post-simulation gravel cover appeared to be more similar to pre-simulation cover in the non-trampled plots (Fig. 4b vs. Fig. 4a) than in the trampled plots (Fig. 4d vs. Fig. 4c).

4. Discussion

4.1. Infiltration

The hypothesis that trampling would increase infiltration into cyanobacterially-crusts soils at the High chlorophyll *a* sites (H1–H3)

was rejected. The alternative hypothesis, that trampling reduces infiltration on these soils, was strongly supported by the analyses. We also rejected the hypothesis that trampling has no effect on infiltration at the sites where chlorophyll *a* content was negligible. Soil surface disturbance reduced infiltration capacity independent of the level of cyanobacterial biomass present. Thus, trampling negatively affected infiltration at both site types through its effect on one or more other soil properties.

The high, non-embedded gravel (>2 mm) cover in the non-trampled plots protected finer soil particles from raindrop impact, reducing the formation of a sieving structural crust, a type of physical crust. The lower surface cover of more extensively embedded gravel in the trampled plots was less effective in protecting the soil surface and may have even reduced infiltration capacity. This conclusion is supported by our experimental data and observations as well as previous literature reports (Valentin and Bresson, 1992). Physical crusts, which reduce infiltration, have been reported to form within 5–15 min of rainfall initiation on soils with similar texture to those at our sites (Zhang and Miller, 1993). In addition, physical crust formation can increase following trampling of soils that lack significant rock cover (Eldridge, 1998; Hiernaux et al., 1999).

Rock cover can increase infiltration where the rocks are relatively small and not embedded. de Figueiredo and Poesen (1998) attributed a positive correlation between rock cover and infiltration depth to a reduction in surface sealing. They also found that at 30% rock fragment cover, smaller rocks were more effective than larger rocks at maintaining high infiltration rates. Descroix et al. (2001) and Poesen et al. (1990) found that surfaces with embedded gravel tended to have

Table 4
Mean (SE (upper and lower for transformed variables)) of final infiltration rate and ANOVA results. Means within a single site type (high or low chlorophyll *a*) differ significantly at p<0.05 (bold) or p<0.1 (non-bold). Upper and lower standard errors are included for total sediment based on log transformed data (Littell et al., 2002).

	High chlorophyll <i>a</i> sites		Low chlorophyll <i>a</i> sites		F _(degrees of freedom)		
	Non-trampled	Trampled	Non-trampled	Trampled	Trampling	Site type	Site type × trampling
	Average (SE)						
Final infiltration (mm/h)	132 (14) a	84 (5) b	82 (15)a	52 (5)b	13.1 _(1,25) **	14.2 _(1,25) **	0.7 _(1,25)
Total infiltration (mm)	78 (7) a	58 (4) b	70 (7)	58 (4)	8.0 _(1,33) **	0.7 _(1,33)	0.5 _(1,33)
Time to runoff (min)	2.3 (0.5)	2.8 (0.5)	4.8 (0.6)	3.7 (0.6)	0.2 _(1,40)	8.8 _(1,40) **	2.0 _(1,40)
Time to peak runoff (min)	17.8 (2.3)	14.5 (1.3)	17.4 (2.4)	15.4 (1.4)	1.9 _(1,32)	0.0 _(1,32)	0.1 _(1,32)
Total sediment (g/m ²)	10 (6,4) a	84 (20,16) b	25 (16,10)a	70 (16,13)b	20.5 _(1,27) **	0.8 _(1,27)	2.7 _(1,27)

*p<0.05; **p<0.01.

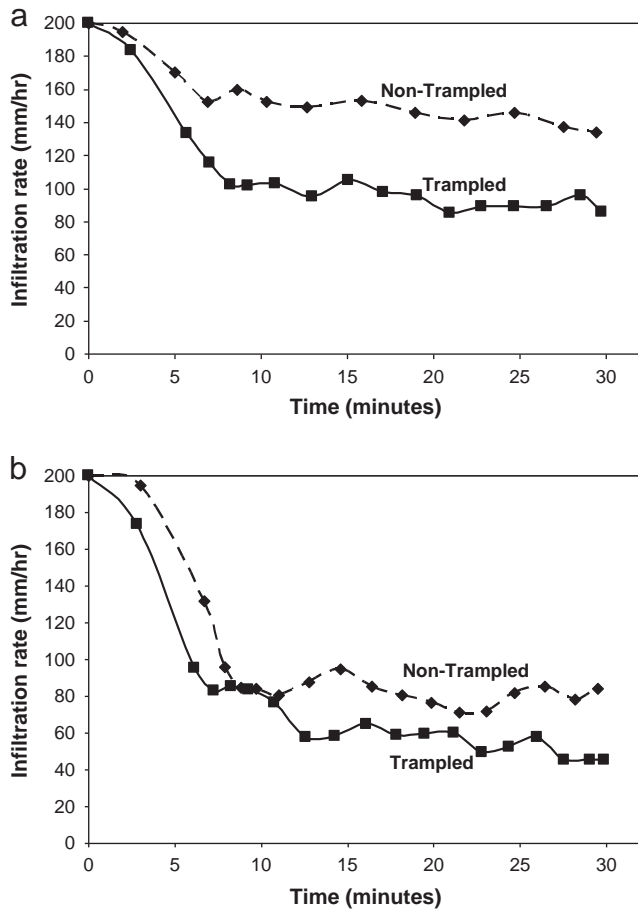


Fig. 2. Typical infiltration curves for high (a) and low (b) chlorophyll *a* sites. Results from sites H2 and L2, respectively.

higher runoff rates than surfaces with “free” pebbles. These three studies are consistent with Valentin's (1994) field study, where infiltration was positively correlated with non-embedded fine and medium gravel and negatively correlated with embedded coarse gravel.

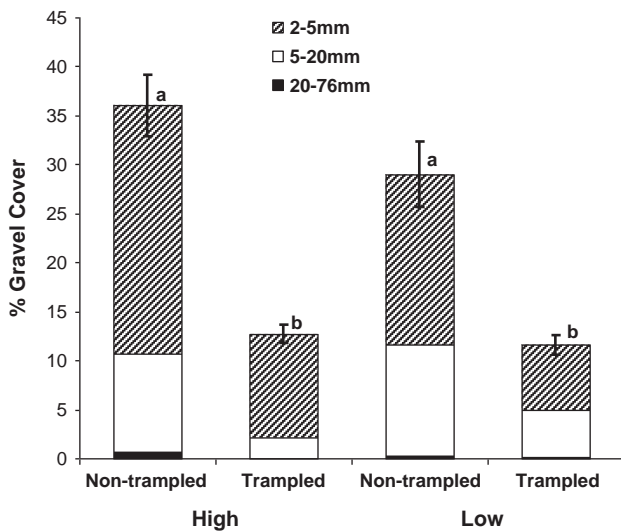


Fig. 3. Average gravel cover by size class in trampled and non-trampled plots (SE for total gravel content). Different letters within each site type reflect significant differences in total gravel content ($p < 0.01$).

Most of the gravel in our experimental plots was fine (less than 5 mm in diameter), and nearly all of it was less than 20 mm diameter (Fig. 3). Furthermore, much of the gravel in non-trampled plots was not embedded, while most of the gravel in trampled plots appeared to be at least partially embedded in the soil below. Non-embedded gravel frequently moves laterally when struck by raindrops, further reducing the energy that is available for physical crust formation, while all energy is absorbed by embedded gravel, which can increase crust density. Both embedded and non-embedded gravel break the raindrops into smaller, lighter droplets before they strike the finer-textured surface. Both of these phenomena were observed during our simulations.

In addition to lower gravel content, the trampled plots had significantly lower cover of loose coarse sand on the soil surface (Table 3). The gravel and coarse sand particles that remained on the surface in the trampled plots were more often embedded in the soil than in the non-trampled plots. Soil surface sand fractions are rarely reported and coarse sand cover is almost never reported in infiltration and soil erosion studies. Consequently, there is little basis for an interpretation of their role. Our observations during the rainfall simulations suggest that the coarse sand is functioning similarly to the smaller gravel fractions. It protects the potentially crust-forming particles from direct impact. Coarse sand particles also transfer at least some of the vertical energy of the raindrops into lateral movement. This mechanism is supported by our data, as the final infiltration rate was positively correlated with combined coarse sand and gravel cover.

4.2. Sediment production

Our data supported the hypothesis that trampling would increase sediment production. This is consistent with most other soil surface disturbance studies (e.g. Eldridge and Robson, 1997). Both higher runoff and the reduction of protective gravel cover likely contributed to increased sediment loss from the plots. Poesen et al. (1994) and Valentin and Casenave (1992) concluded that rock fragments usually reduce interrill erosion provided that the rocks are not deeply embedded in the soil. Based on a rainfall simulation study of rocks 3.0–22.3 cm in average diameter, Poesen and Lavee (1991) found that smaller rocks are more effective at reducing sediment loss and that only the smallest (3.0 cm diameter) rock fragments reduced sediment loss at all levels, from 30% to 90% cover. Embedded rock fragments are less likely to reduce sediment loss because of their potentially negative effects on infiltration (Poesen and Lavee, 1991).

Due to small plot size, the sediment data should be treated as relative results and should not be extrapolated to the landscape (Mutchler et al., 1994). Subsequent storms would be expected to remove less sediment, as the most highly erodible, newly exposed material was removed early in the simulated storm.

4.3. Alternative mechanisms

Three other explanatory mechanisms were considered. While none can be completely rejected, none appear to be as strongly supported as the gravel mechanism described above. Trampling may have caused an increase in bulk density. While possible, this seems unlikely given the fact that pre-treatment densities were similar at both site types (Table 2), despite the fact that the low chlorophyll *a* sites were subjected to much more intensive disturbances during the years prior to the study.

A second possible mechanism is that disturbance of the soil surface may have facilitated development of a more impermeable crust by reducing resistance of soil particles to re-arrangement by raindrop impact. This mechanism is consistent with the gravel cover mechanism.

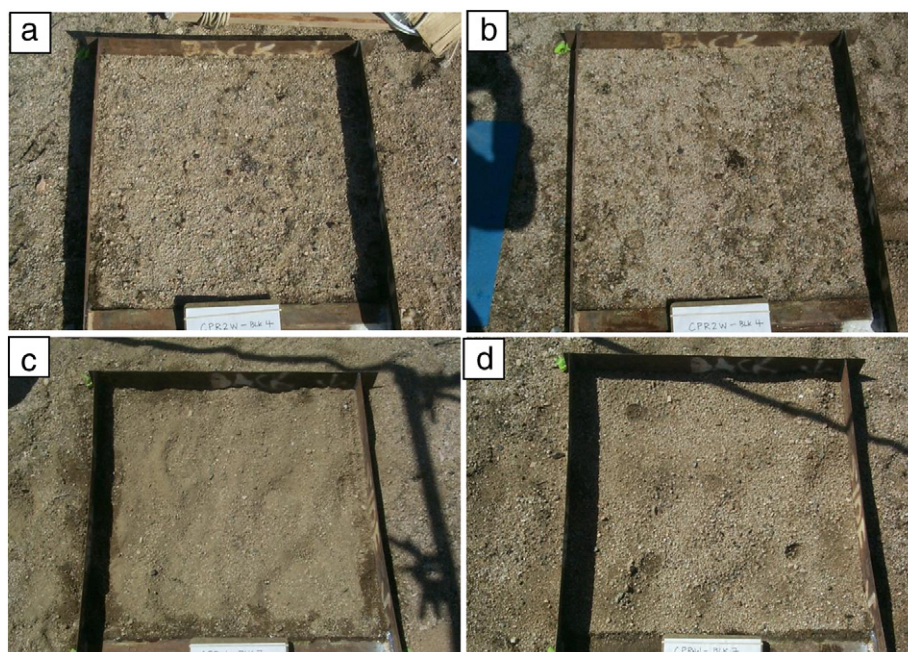


Fig. 4. Typical soil surface at a high chlorophyll *a* site in a non-trampled plot pre- (a) and post- (b) rainfall simulation and in a trampled plot pre- (c) and post- (d) rainfall simulation.

A final possible mechanism is that trampling exposed more highly dispersible subsurface soil. This explanation is not consistent with the data from L1–L3, where soils were too unstable to be either sampled or slaked within 30 s of immersion in water (stability kit values of 0–2).

4.4. Potential interaction with wind erosion

The relatively high gravel cover in the non-trampled plots at L1–L3 was surprising because all three sites have been repeatedly used in the past for military training exercises that involve extremely high levels of soil surface disturbance (R. Sparks, Fort Irwin, Barstow, CA, pers. comm.). These disturbances should have had a similar effect on gravel cover as our trampling treatments. It is likely that wind erosion had already removed fine sediment exposed at the soil surface during the most recent military training disturbance. This would have regenerated the high coarse sand and gravel cover encountered on the non-trampled plots at both site types (Fig. 3). This mechanism is consistent with longer-term patterns reflected in the relatively higher coarse sand fraction encountered at L1–L3 (Table 3), and with other studies showing that areas with high disturbance frequency, such as those near grazing waterholes, tend to have higher coarse sand content at and near the soil surface (Valentin, 1985).

Wind erosion following soil surface disturbance may limit runoff and water erosion during high intensity rainstorms by removing silt and medium, fine and very fine sand. This winnowing process leaves gravel and coarse sand to protect the soil against crust formation during extreme precipitation events. Wind velocities exceeding the threshold required to move unprotected disturbed soil are extremely common in the Mojave Desert, while rainfall events of sufficient duration and intensity to exceed the soil infiltration capacity are quite rare. Consequently, there is a high probability that wind erosion will restore high gravel and coarse sand cover prior to a runoff event simply by removing the fine particles exposed at the surface. Individual soil surface disturbances are unlikely to affect runoff and erosion by water.

Over longer time periods, wind erosion associated with repeated soil disturbance may, in fact, affect runoff by modifying soil texture (Hennessy et al., 1986). Soil texture is strongly correlated with infiltration characteristics. Existing vertical stratification suggests that

cyanobacteria themselves may have been modifying near-surface soil texture, as reported by Williams et al. (1995).

4.5. Future research needs on interactions between biological and physical factors

The results for H1–H3 would appear to contradict Warren's (2003) conclusion that biocrusts limit infiltration on soils with over 80% sand. Most previous studies he reviewed were based on biocrust disturbance or removal at just one site with much higher crust biomass (see summary in Warren (2003)). Based on the results of the disturbance comparisons on H1–H3 alone, we would have concluded that cyanobacterial crust disturbance reduces infiltration on sandy soils, and therefore that intact biocrusts can generate higher runoff. A crust removal experiment would likely have yielded similar results, as the loose gravel would have been removed, generating the same incorrect conclusion. By taking a more mechanistic approach and including two levels of biocrust development, our results suggest that physical processes (fine gravel redistribution) rather than biological processes control disturbance effects in coarse-textured soils with weak biocrusts.

More work is required to clearly define the role of cyanobacterial crusts on different desert soils. The biomass and morphology of cyanobacterial biomass at relatively undisturbed sites reflect climatic factors. In hot deserts with very low precipitation (e.g., Mojave, Sonoran, Negev), soil surfaces support a low biomass of cyanobacteria (up to ~0.06 mg chlorophyll *a*/g soil; Belnap et al., 2007a) and because of the lack of frost heaving, most soil surfaces are relatively flat. This contrasts with colder deserts, where cyanobacteria biomass is high (up to ~0.18 mg chlorophyll *a*/g soil) and frost heaving creates pinnacles up to 15 cm high (Belnap 2003). In the study reported here, the maximum value at the high chlorophyll sites was only 0.006 mg chlorophyll *a*/g soil, far less than other sites in the Mojave or other deserts. Given this very low level of cyanobacterial biomass at these sites, it is not surprising that they had little or no influence on infiltration or sediment production in this study. Wind tunnel runs at these same sites also found no influence of cyanobacterial biomass on sediment production (Belnap et al., 2007b). Therefore, it appears that there is a minimum threshold of cyanobacterial biomass required

before this variable becomes a dominant factor in determining sediment movement by wind or water.

In order to gain a full understanding of the interactions between biological crusts and local hydrology, a much broader, more mechanistic approach is required. The role of disturbance in modifying soil structural characteristics that affect infiltration must be addressed. The resistance of the soil to further structural modifications (e.g. physical crust formation) needs to be evaluated. Both pre- and post-disturbance measurements of as many soil structure-related variables as possible must be included. Some of these, such as fine-scale vertical stratification of soil particles at the soil surface, are difficult to quantify and should be carefully described. Future studies should also include contextual information (e.g. historic disturbance regime) that may shed light on possible processes and properties that could help to explain seemingly contradictory results, even where this information is incomplete. Studies should also include more than one treatment (e.g. Williams et al., 1995), such as a combination of crust removal and trampling. Lastly, it is crucial that investigators report data on soil texture, climate, surface morphology, soil aggregate stability and cyanobacterial biomass at a given site.

5. Summary and conclusions

Trampling reduced infiltration and increased sediment production at sites with both low and very low chlorophyll *a* content. Reduced infiltration appears to be due to the formation of a physical crust at the initiation of rainfall simulation, which is facilitated by the vertical redistribution of gravel by trampling. Controlled experiments, like those previously completed by Poesen and colleagues for larger rock fragments, are required to define the dynamics of surface gravel and coarse sand and their potential role in limiting soil physical crust formation. Experiments replicated at the landscape scale on carefully paired plots are also required to define the long-term effects of repeated disturbance on soil structure and hydrology.

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