



## Soil resource heterogeneity in the Mojave Desert

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Heterogeneity of soil resources was investigated in the Mojave Desert to better understand spatial variability of soil attributes in a *Larrea tridentata*–*Ambrosia dumosa* community. Six soil samples were collected at each of eight microsites, with this sampling scheme replicated for three sites that were 0.7 km apart on a 10-km long bajada. The eight microsites were: five different shrub types (individual shrubs of *L. tridentata*, individual shrubs of *Lycium pallidum*, individual shrubs of *A. dumosa*, mixtures of shrub species with small mammal burrows, and mixtures of shrubs without small mammal burrows), a grass microsite (around individual plants of the tussock grass *Pleuraphis rigida*), and two microsites without perennial vegetation (one within small washes and the other within the interspace between perennial plants). Fifteen soil parameters were assessed, and all were found to differ among microsites. Nutrients were assessed as the pools extractable by vegetation. Mineral nutrients except for Ca, organic matter, and litter were higher in soils collected from shrub microsites compared to the others. Shrub microsites with small mammal burrows had significantly more N and P than those without burrows. Non-vegetated microsites in washes and plant interspaces contained very low N and P levels. Mg, Na, pH and cation exchange capacity were highest in soils under *Lycium* shrubs, while Ca levels were highest in wash soils. Arbuscular mycorrhizal spore densities were generally low (0–0.2 spores g<sup>-1</sup> soil) except for *Lycium* soils, which contained 1.8 spores g<sup>-1</sup> soil. Wash and interspace soils lacked spores but had mycorrhizal inoculum potential values similar to the other microsites, indicating that mycorrhizal propagules were present. Thus, the presence of perennial shrubs strongly influenced microsite soil characteristics and resulted in higher nutrient levels. Small mammal burrows further enhanced the mineral nutrient content of soils. In addition, all soil characteristics except for spore density differed among the three sites across the bajada, and interactions between microsite and site were common. Clearly, soil resources for plants are spatially heterogeneous in this desert ecosystem and differ greatly between adjacent micro- and macrosites in this *L. tridentata*–*A. dumosa* community.

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## Introduction

Considerable spatial heterogeneity in soil resources occurs in arid regions. An island of fertility, or resource island, that forms under shrub canopies in arid regions is a well-documented example of this heterogeneity (e.g. West & Klemmedson, 1978; Wright & Honea, 1986; Herman *et al.*, 1995; Wezel *et al.*, 2000). Fertile islands represent microsite locations where nutrients tied up in on-site primary productivity and trapped organic matter are made available by mineralization. Shrub fertile islands are not only points of high concentrations of nitrogen and other nutrients, but they also contain the largest amounts of mycorrhizal inoculum (Bethlenfalvay *et al.*, 1984; Carrillo-Garcia *et al.*, 1999; Dhillion, 1999), reduced solar radiation and lower soil temperatures (Tiedemann & Klemmedson, 1977; McAuliffe, 1988; Franco & Nobel, 1989; Valiente-Banuet & Ezcurra, 1991).

The particle-size distribution of fertile island soils differs from that of soils between shrubs (interspace soils). Typically, fine-grained soils occur in shrub islands because wind-blown materials are captured by the shrub canopy (Elkins *et al.*, 1986; Coppinger *et al.*, 1991; Whitford *et al.*, 1997). Differential rainsplash, as a result of the dissipation of raindrop energy in the shrub canopy, also results in the directional transport of soil materials toward shrub islands (Parsons *et al.*, 1992). However, coarser soils in shrub islands have been observed (Dunkerly, 2000).

Shrub fertile islands are sites where the biological community modifies the water status of desert soils (Elkins *et al.*, 1986; Nulsen *et al.*, 1986; Caldwell & Richards, 1989). Arid zone fertile islands are the site of high moisture concentrations and rapid infiltration (Pressland, 1976; Rostagno *et al.*, 1991; Dunkerly, 2000). Both physical and biological transport mechanisms are accelerated by moisture (Garner & Steinberger, 1989), and thus fertile islands are predicted to have relatively greater mineralization rates.

In arid environments, water and/or nitrogen are the most common abiotic factors that limit plant growth (Smith *et al.*, 1997). The spatial distribution of these resources appears to be important in determining the vegetation pattern in arid environments (Whitford, 1986; Fisher *et al.*, 1988; Moorhead *et al.*, 1988; Aguiar & Sala, 1999). Any mechanism or activity that increases the availability of nutrients to plants can have profound effects on community dynamics (Dhillion, 1999). Under their canopies, shrubs may improve physical conditions for other species by protecting them from direct insolation and over-heating (Valiente-Banuet & Ezcurra, 1991). Also, by accumulating animal-dispersed seeds and trapping seeds swept across bare soils by wind or sheet water flow, soils under shrubs may be an important foci for plant establishment. These features yield the well-known arid zone nurse plant effects (e.g. Shmida & Whittaker, 1981; Valiente-Banuet & Ezcurra, 1991; Pugnaire *et al.*, 1996; Tielborger & Kadmon, 1997). However, the relationship between shrubs and plants establishing below their canopies may be positive, negative or neutral depending upon environmental conditions (Holzapfel & Mahall, 1999; Tielborger & Kadmon, 2000; Walker *et al.*, 2000).

The accumulation of nutrients in the surface soils under arid region shrubs results from complex interactions between the plant (e.g. nutrient uptake, litter fall), soil (e.g. erosion, deposition), soil biota (microbes, micro-organisms), atmosphere (e.g. deposition of fine dust), and biogeochemical cycling processes (e.g. mineralization, decomposition) (Schlesinger *et al.*, 1996). Plants change the spatial pattern of nutrients, organic matter, and other properties of an ecosystem by virtue of their

physical presence and related influences (Tiedemann & Klemmedson, 1973 $a,b$ ; Charley & West, 1975). Shrub-focused zootransport mechanisms contribute to fertile island formation and maintenance. These zootransport mechanisms gather nitrogen from the area surrounding the island and retain in the island the nitrogen that is already present (Moorhead *et al.*, 1988; Mun & Whitford, 1989; Chew & Whitford, 1992; Wagner, 1997). The fertile island is the major source of food for most herbivores and the animals that prey on them (Garner & Steinberger, 1989; Dhillion, 1999).

Shrub species differ in their contributions to fertile islands by absorbing various minerals in different quantities and from different soil-horizons (Barth & Klemmedson, 1978; Binet, 1981; Quideau *et al.*, 1999; Wezel *et al.*, 2000). Species differences may also be due to differences in leaf litter nutrient concentration and mineralization (Charley & West, 1975; El-Ghonemy *et al.*, 1978; Romney *et al.*, 1980). The ability to fix nitrogen may alter fertile island characteristics (Virginia & Jarrell, 1983; Lajtha & Schlesinger, 1986; Moorhead *et al.*, 1988), although N levels have been found to be lower under N-fixing shrubs than under non-N-fixing shrubs (Garcia-Moya & McKell, 1970). Also, different plant architectures create differences in stemflow volumes, causing fertile islands of species to differ in moisture throughfall and infiltration (Elkins *et al.*, 1986; Navar & Bryan, 1990; Martinez-Meza & Whitford, 1996). Shrub species may also differ in their ability to attract animals, thus contributing to differences in their fertile islands.

Fertile islands are a critical part of the structure and functioning of desert systems and therefore, it is important to understand the characteristics of desert islands when attempting to understand how global change will affect arid environments. Thus, this study was conducted in order to characterize soils and their heterogeneity at the Mojave Global Change Experiment site (MGCE) located on the Nevada Test Site (NTS). The MGCE is a large-scale experiment to measure desert ecosystem responses to increases in summer rain and nitrogen deposition and removal of the biological soil crust. Our null hypotheses were that no differences exist between microsites in soil nutrients, pH, cation exchange capacity, organic matter, particle-size distributions, infiltration rates, and arbuscular mycorrhizal spore density and inoculum potential.

## Materials and methods

### *Study site*

The MGCE site is located in the northern Mojave Desert in Nye County, Nevada, U.S.A. (36°49'<sup>1</sup>N, 115°55'<sup>W</sup>), 90 km north-west of Las Vegas at an elevation of 960–975 m. The NTS, a Department of Energy facility, experiences minimal disturbance and has a pristine environment and security. Unlike much of the Mojave desert, the NTS has not been grazed by cattle or utilized by off-road vehicles for at least 50 years.

The Mojave Desert experiences sporadic, low precipitation with an annual rainfall of <200 mm. Winter rains are widespread and may last up to several days. Summer storms generally occur in July and August and are usually local, intense and unpredictable. Relative humidity is low (<20% is common), resulting in very high potential evaporation. Moisture is the primary limitation to plant growth in the Mojave Desert (Turner & Randall, 1989; Smith *et al.*, 1997). Temperatures are extreme, with a minimum winter temperature of –10°C and maximum summer temperature >47°C. A large diurnal temperature fluctuation occurs throughout the year (Bowers, 1987).

The vegetation is a *Larrea tridentata*–*Ambrosia dumosa* plant community (Ostler *et al.*, 1999; taxonomy based on Hickman, 1993). Common shrubs include *L. tridentata*, *A. dumosa*, *Lycium pallidum*, *L. andersonii*, *Krascheninnikovia lanata*, *Acamptopappus shockleyi*, *Ephedra nevadensis*, *Grayia spinosa* and *Krameria erecta*. Common subshrubs include *Polygala subspinoso* and *Mirabilis pudica*. Dominant native grasses are *Pleuraphis rigida* (C<sub>4</sub>), *Achnatherum hymenoides* (C<sub>3</sub>), and the short-lived *Erionueron pulchellum* (C<sub>4</sub>). The non-native annual grass *Bromus madritensis* ssp. *rubens* is common in shrub understories. To the north of the study area, there is an *Atriplex*–*Lycium* dominated playa. Vegetation is further described in Beatley (1967, 1976) and Jordan *et al.* (1999). The area has a largely intact biological soil crust which covers ~20% of the soil surface (J. Titus, unpubl. data).

Soils are aridisols derived from calcareous alluvium with textures ranging from loamy sands in the shallow A1 horizon (0–16 cm) to coarse sands in subsoil horizons. Caliche layers do not appear to occur in the subsoils resulting in well-drained soils. Soils are characterized by spatial heterogeneity in nutrients, infiltration, and texture (Romney *et al.*, 1973, 1980). Mounds and burrows created by the activities of small mammals, particularly kangaroo rats (*Dipodomys* spp.) and desert tortoises (*Gopherus agassizii*), are common and frequently located at the base of shrubs.

### Soil Samples

Soil samples were collected on 30–31 May 1999 from three sites ~700 m from each other on the east, north and south of the MGCE. At each site, six soil samples were collected from each of eight microsite types. The eight microsites were: (1–2) base of a mixed *L. tridentata*–deciduous shrub clump with and without small mammal burrows; (3–6) beneath *L. tridentata*, *A. dumosa*, *L. pallidum*, and *P. rigida*; (7) interspaces; and (8) washes. This yielded 48 samples per site and a total of 144 soil samples. Soils were excavated under the north-east side of shrubs because on this side prevailing winds accumulate litter (Parker *et al.*, 1982, J. Titus, pers. obs.). Interspace and wash samples were collected >1 m from the nearest plant which is generally greater than the shrub zone of influence (Brisson & Reynolds, 1994; Gile *et al.*, 1998; Dunkerly, 2000). Before each soil sample was collected, litter was collected from a 10 cm diameter circular area and placed in a paper bag. Litter was air dried at 60°C for 48 h and then weighed. Soil samples of ~1.5 kg were excavated from small pits 10 cm in diameter and 20 cm deep. Soil was sieved in the field through a 2 mm sieve to separate out the gravel component. Soil samples were transported to the University of Nevada, Las Vegas and stored at 2°C until analysed.

Height and two perpendicular width measurements were made for each shrub. If the shrub was a mixed shrub clump, these measurements were made for total clump size and for each individual shrub.

Soil samples were analysed for phosphorus, potassium, magnesium, calcium, sodium, nitrate and ammonium by A & L Western Laboratories, Inc., Modesto, California. Soil pH, cation exchange capacity (CEC), and soil organic matter (SOM) were also determined. Available phosphorus levels were determined by Olsen's procedure (Miller *et al.*, 1998, p. 55). Ammonium acetate was used to measure extractable cations (Simard, 1993; Miller *et al.*, 1998, p. 73). Exchangeable nitrate levels were determined by cadmium reduction in 2.0 N KCl extract (Maynard & Kalra, 1993; Miller *et al.*, 1998, p. 47) and ammonium levels were determined by 2.0 N KCl extraction (Maynard & Kalra, 1993, Miller *et al.*, 1998, p. 53). SOM levels were determined by loss on ignition (Miller *et al.*, 1998, p. 86), pH by saturated paste (Miller *et al.*, 1998, p. 15), and CEC by ammonium replacement (Miller *et al.*, 1998, p. 90).

*Particle-size analysis*

In September and October 1999, samples were analysed for particle size distributions. The >2 and <2 mm particle-size components of each sample were weighed in order to determine percent gravel. The litter component was dried at 60°C for 48 h and weighed. For the sand, silt and clay components particle-size analysis was conducted using the hydrometer method (Gee & Bauder, 1986). Soils were initially treated with a dispersant.

*Infiltration rates*

Soil infiltration rates were determined using a double ring of pvc pipes 10 and 20 cm in diameter plunged 3 cm into the soil. Water was maintained in the area between the two pipes at a height of 13 cm. One liter of water was then poured into the central pipe yielding a column of water 13 cm high. In the inner pipe, the water level was never allowed to go below a height of 10 cm and was usually refilled before the water level had dropped to 11 cm. The quantity of water needed to refill the inner pipe to 13 cm and the time of refilling were recorded. If after 1 h water levels had not stabilised, water was added for a minimum of another 30 min. Infiltration tests were conducted at four of each of the mixed shrub assemblages with and without burrows, interspace, and wash microsites at the north and south sites only. Infiltration rates were calculated by averaging the last 20 min of each test.

*Mycorrhizal inoculum potential*

For each soil sample, 600 g of soil was amended with 20% sterile perlite to increase porosity, split into half and each placed into 10 cm × 10 cm freely draining plastic pots. Bioassays were conducted with non-fungicide treated *Zea mays* seeds. All pots were watered daily with tap water. Fertilizer was applied in 50 ml aliquots per pot as 10% Hoagland's solution minus phosphorus at planting, and at weekly intervals throughout the experiment. The control consisted of ten pots of sterile greenhouse soil placed randomly among the treatment pots and planted with corn to determine if contamination by greenhouse arbuscular mycorrhizae (AM) propagules occurred. Previous work showed that AM propagules, if present, rapidly colonize corn in the greenhouse (Titus *et al.*, 1998). Pots were randomized and maintained at the University of Nevada-Las Vegas glasshouse facility at 23–28°C, and rotated every 15 days. Bioassay plants were grown for 42 days from August 20 to September 30, 1999. Plants were harvested, roots washed, and frozen at –5°C until October 1999, at which time roots were assayed for AM colonization.

Corn roots were washed, cleared and stained with trypan blue (Brundrett *et al.*, 1994). Percent colonization was estimated by placing a grid of 1 cm squares below a Petri plate that contained the root sample under a dissecting microscope. One hundred locations where a root crossed a line on the grid were scored for AM fungi. Many samples were examined under higher power to ascertain that the fungus was indeed AM. Root segments containing vesicles, arbuscules or intercellular hyphal coils or hyphae were recorded as being colonized. The number of mycorrhizal 'hits' is an estimate of the percent of the root colonized (Brundrett *et al.*, 1994). The quantity of inoculum in the soil, mycorrhizal inoculum potential (MIP), was estimated by the percent AM fungal colonization of the corn roots (Moorman & Reeves, 1979; Johnson & McGraw, 1988; Titus *et al.*, 2002). Thus, only total AM colonization is reported here. For each soil sample, the percent colonization of the two corn plants were averaged together to achieve MIP.

*Spore isolation*

Spores were extracted from two 10 g subsamples of each soil sample by using the Vilarino & Arines (1990) modification of the Gerdemann & Nicolson (1963) wet sieving and decanting method. Sieves with mesh sizes of 500, 125 and 60  $\mu\text{m}$  were used to capture the spores. The material in the three sieves was examined under a dissecting microscope at  $40\times$  power for AM spores. The number of spores isolated in ten samples was compared between the Gerdemann & Nicolson (1963) wet sieving and decanting method and the Vilarino & Arines (1990) modification of this method. In these very low organic matter desert soils, the number of spores isolated was found to be similar between the two techniques; however, since the Vilarino & Arines (1990) method was found to require less time, it was used. Spores were preserved on slides in both polyvinyl alcohol glycerol and Melzer's solution. However, spore types could not be determined because most of the spores were unidentifiable due to natural decay processes (J. Morton, U. West Virginia). For each sample, spore densities from the two subsamples were averaged to achieve the density of spores per 10 g of soil.

*Data analysis*

Data were tested for normality and homoscedascity of variances and transformed accordingly (Table 1) (Zar, 1984). For the data that could be tested parametrically, ANOVAs were conducted to compare soil parameters across microsites and sites and for interactions. *Post hoc* tests were conducted by Tukey's honestly significant difference test. Data that could not be normalized and/or the variances equalized were tested by the non-parametric Kruskal-Wallis test with a chi-square correction for ties (Zar, 1984). Post-hoc tests were conducted with the non-parametric variant of Tukey's honestly significant difference test (Zar, 1984, p. 199).

Spearman's rank correlation tests (Zar, 1984) were conducted between soil parameters and plant size in order to assess if soil factors are correlated with plant size. Plants were considered to be elliptical cylinders for the purpose of this analysis. In addition, MIP and spore density were tested for correlation with the measured soil factors and plant size. Due to zero values, wash and interspace microsites were not included in the plant size and spore density correlation tests.

Data were interpreted by principle components analysis (PCA) using the program CANOCO (ter Braak, 1990) and graphics by CANOPOST (Smilauer, 1993). PCA is analogous to multiple regression when the response variable is multivariate. Plots (i.e. microsites) were the independent variables and soil factors (i.e., environmental variables) the dependent response variable. PCA is the recommended multivariate analysis technique when vegetation gradients are short, i.e. the vegetation is relatively homogeneous (Jongman *et al.*, 1987).

**Results***Plant size*

Mixed shrubs with small mammal burrows were larger than mixed shrubs without burrows (Table 1, Fig. 1(a)). Mixed shrubs without burrows did not differ in size from lone *Larrea* shrubs. ANOVA analysis detected a significant site effect, but the *post hoc* test did not detect a significant site effect (Table 2). All of the measured soil factors were positively correlated with plant size, except for pH, which was negatively correlated, and spore density and clay content, which were not correlated (Table 3).

*Soil variables*

All soil variables measured had significant differences across microsites (Table 1, Fig. 1(b-s)).  $\text{NO}_3$ ,  $\text{NH}_4$ , P and K levels were highest in soils under mixed shrubs with small mammal burrows and lowest in interspaces, washes and under the smallest plants, *Ambrosia* and *Pleuraphis* (Fig. 1(b-e)). Soil under *Lycium* shrubs had high P and K levels. Ca levels were highest in wash soils and soils from mixed shrubs with mammal burrows (Fig. 1(f)). Mg and Na levels were the highest in soils under *Lycium*, and these were the only nutrients that were not present at high levels in soils under mixed shrubs with small mammal burrows (Fig. 1(g,h)). Wash and interspace soils had low levels of all the nutrients except Ca and Na. Many soil factors were significantly correlated with each other (Table 3). Soil organic matter (SOM) and litter were positively correlated with plant size and with most of the nutrients (Table 3). The highest levels of SOM and litter were found under the mixed shrubs and *Larrea* (Fig. 1(i,j)). Significantly, less SOM and litter were found in wash and

**Table 1.** Univariate two-way ANOVA *F*'s and *P*'s for measured soil parameters at eight different Mojave Desert microsites at three different sites ( $n = 18$  for microsite,  $n = 48$  for site;  $P \leq 0.05$  for significance)

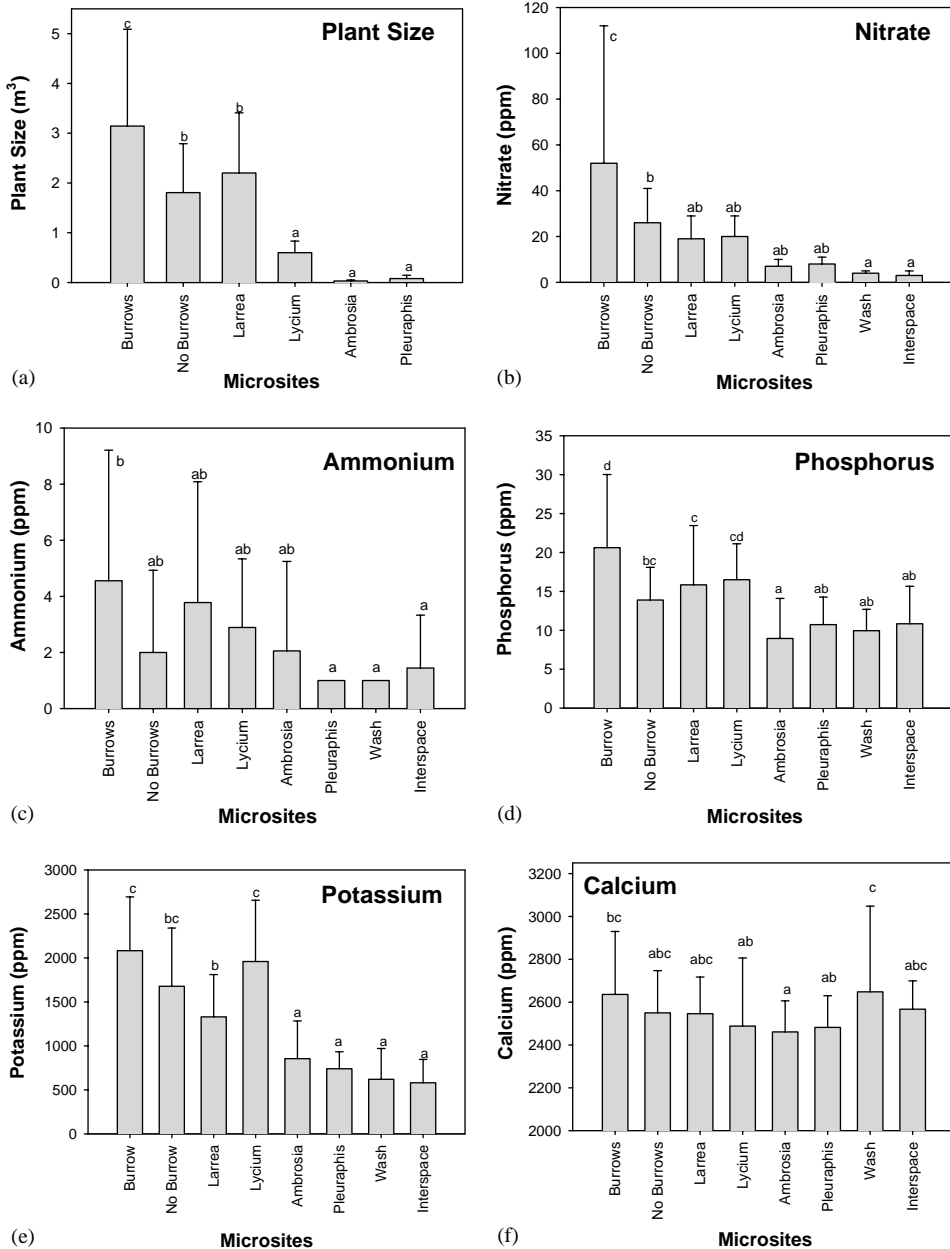
Soil Parameter	Transformation	Microsite		Site		Interaction	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Plant size ( $\text{m}^3$ )	None	<b>3.252</b>	<b>0.034</b>	<b>34.229</b>	<b>&lt;0.001</b>	1.782	0.075
Nitrate (p.p.m.)	Natural log	<b>10.404</b>	<b>&lt;0.001</b>	<b>5.521</b>	<b>0.005</b>	1.706	0.063
Ammonium (p.p.m.)	Non-parametric*	<b>4.123</b>	<b>&lt;0.001</b>	0.519	0.597	<b>2.595</b>	<b>0.003</b>
Olsen's phosphorus (p.p.m.)	Natural log	<b>17.617</b>	<b>&lt;0.001</b>	<b>19.551</b>	<b>&lt;0.001</b>	<b>7.374</b>	<b>&lt;0.001</b>
Calcium (p.p.m.)	None	<b>3.729</b>	<b>0.001</b>	<b>13.047</b>	<b>&lt;0.001</b>	<b>14.432</b>	<b>&lt;0.001</b>
Magnesium (p.p.m.)	Natural log	<b>46.173</b>	<b>&lt;0.001</b>	<b>10.916</b>	<b>&lt;0.001</b>	1.193	0.290
Potassium (p.p.m.)	Natural log	<b>36.268</b>	<b>&lt;0.001</b>	<b>18.939</b>	<b>&lt;0.001</b>	1.316	0.208
Sodium (p.p.m.)	Natural log	<b>9.936</b>	<b>&lt;0.001</b>	<b>6.213</b>	<b>0.003</b>	1.720	0.060
pH	None	<b>13.210</b>	<b>&lt;0.001</b>	1.973	0.144	<b>2.821</b>	<b>0.001</b>
Cation exchange capacity	None	<b>37.534</b>	<b>&lt;0.001</b>	<b>31.465</b>	<b>&lt;0.001</b>	<b>4.684</b>	<b>&lt;0.001</b>
% soil organic matter	Arcsine	<b>24.880</b>	<b>&lt;0.001</b>	0.237	0.790	1.216	0.273
Litter ( $\text{g m}^{-2}$ )	None	<b>21.011</b>	<b>&lt;0.001</b>	<b>7.262</b>	<b>0.001</b>	1.342	0.193
Gravel (%)	Arcsine	<b>9.531</b>	<b>&lt;0.001</b>	<b>14.518</b>	<b>&lt;0.001</b>	1.575	0.096
Sand (%)	Arcsine	<b>3.622</b>	<b>0.001</b>	<b>19.821</b>	<b>&lt;0.001</b>	1.141	0.330
Silt (%)	Arcsine	<b>8.358</b>	<b>&lt;0.001</b>	<b>7.606</b>	<b>0.001</b>	0.831	0.634
Clay (%)	Arcsine	<b>3.843</b>	<b>0.001</b>	<b>17.364</b>	<b>&lt;0.001</b>	1.196	0.288
Infiltration ( $\text{ml min}^{-1}$ )†	None	<b>10.636</b>	<b>&lt;0.001</b>	<b>4.904</b>	<b>0.042</b>	0.627	0.608
AM spores ( $\text{spores g}^{-1}$ soil)	Non-parametric*	<b>7.458</b>	<b>&lt;0.001</b>	1.492	0.231	1.008	0.450
% Mycorrhizal inoculum potential	Arcsine	<b>12.009</b>	<b>&lt;0.001</b>	<b>3.055</b>	<b>0.005</b>	<b>2.083</b>	0.017

Significant values are in bold. Transformations were conducted to improve normality and homoscedasticity.

\*Non-parametric Kruskal-Wallis test with a chi-square correction for ties.

† $n = 8$  for microsite,  $n = 16$  for site.

interspace soils. pH values were highest from *Lycium* soils and lowest from the mixed shrubs and *Larrea* soils (Fig. 1(k)). pH values were negatively correlated with plant size, litter, SOM and several of the nutrients. Cation exchange capacity (CEC) was



**Figure 1.** (a–s) Mean levels of soil parameters at eight microsites at the Nevada Test Site in the Mojave Desert ( $n = 18$ ; infiltration  $n = 8$ ). Vertical bars are one standard deviation. Burrows and no burrows refer to mixed shrubs with and without small mammal burrows. Soil parameter columns with different letters are significantly different at  $p \leq 0.05$  based on Tukey’s post hoc test. See Table 2 for ANOVA results and data transformations.

highest in *Lycium* soils, followed by mixed shrubs with small mammal burrows (Fig. 1(l)). CEC values were low in wash and interspace soils and by the smallest plants. CEC values showed a pattern similar to that of Na.

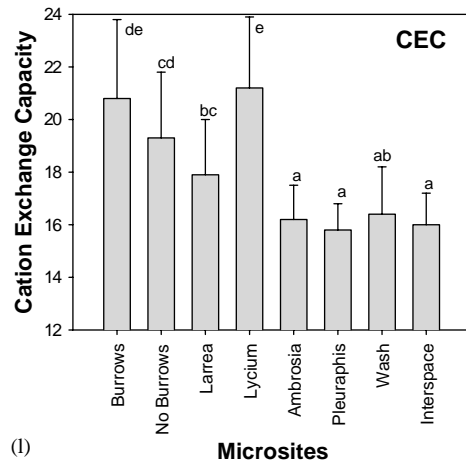
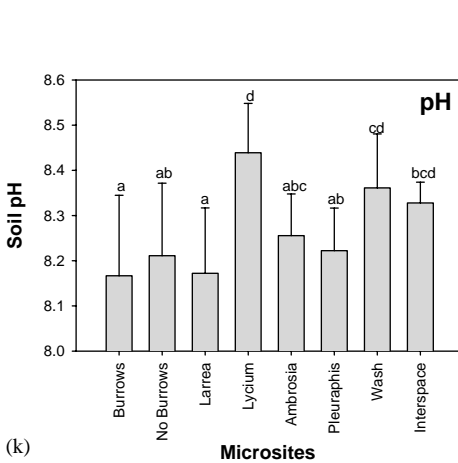
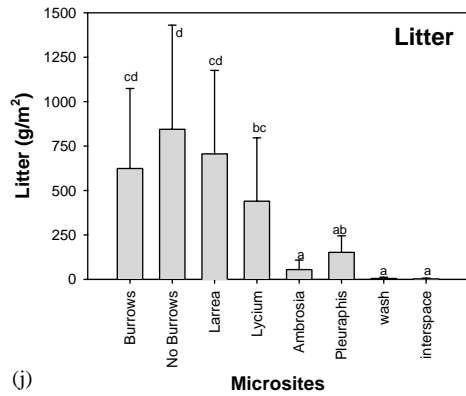
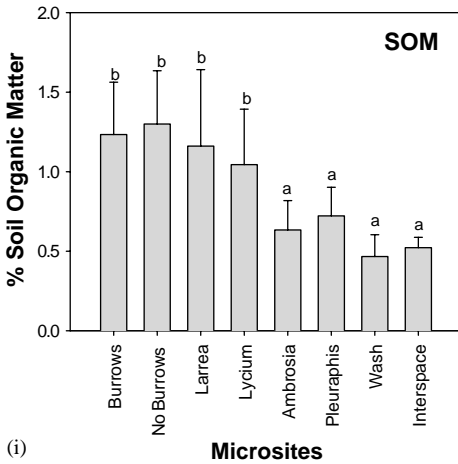
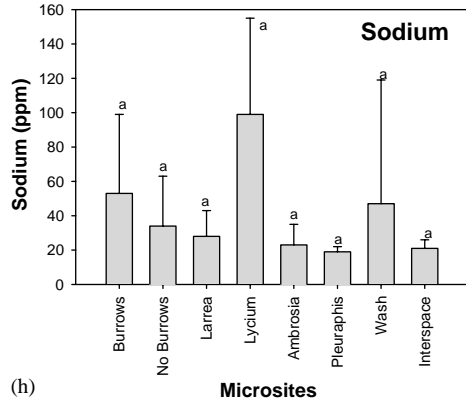
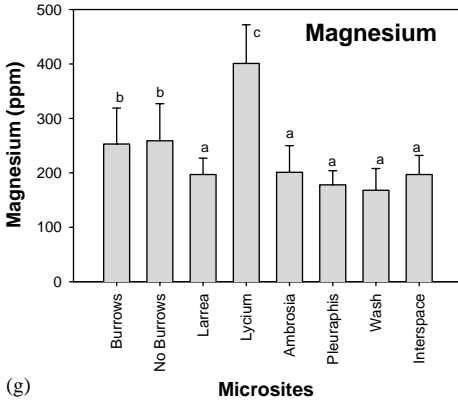
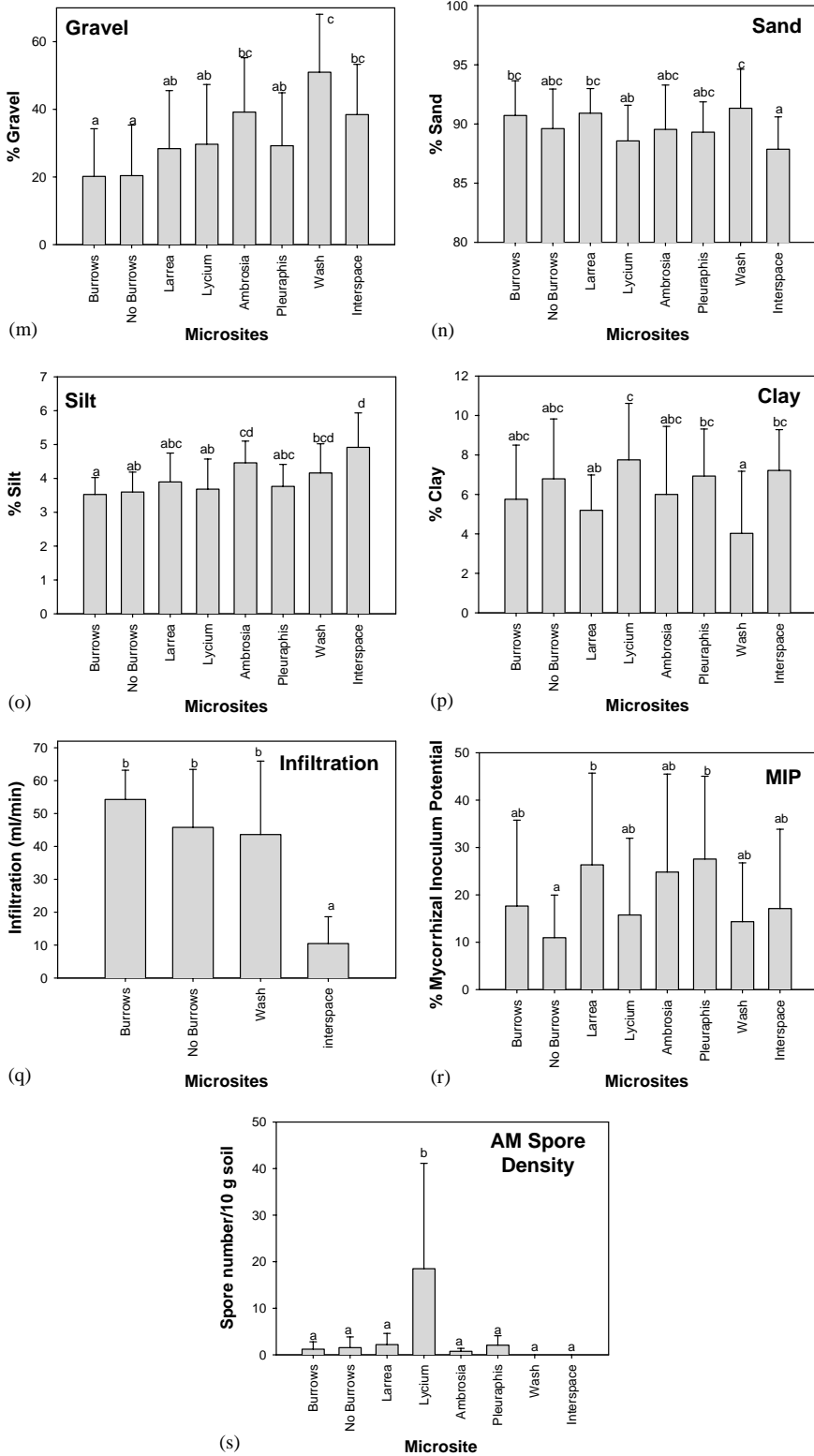


Fig. 1 — Continued.



**Fig. 1** — *Continued.*

**Table 2.** Levels of soil parameters at three Mojave Desert sites (mean  $\pm$  standard deviation,  $n = 48$ ). Soil parameter values with different superscripts are different at  $p \leq 0.05$  by Tukey's post hoc test

Soil parameter	South site	East site	North site
Plant size (m <sup>3</sup> )*	0.96 $\pm$ 0.99 <sup>a</sup>	1.43 $\pm$ 1.77 <sup>a</sup>	1.54 $\pm$ 1.69 <sup>a</sup>
Nitrate (p.p.m.)	11 $\pm$ 10.5 <sup>a</sup>	25 $\pm$ 41 <sup>b</sup>	16 $\pm$ 17 <sup>ab</sup>
Ammonium (p.p.m.)	2.6 $\pm$ 2.9 <sup>a</sup>	2.4 $\pm$ 3.7 <sup>a</sup>	2.0 $\pm$ 2.7 <sup>a</sup>
Olsen's phosphorus (p.p.m.)	15 $\pm$ 5 <sup>b</sup>	10 $\pm$ 5 <sup>a</sup>	15 $\pm$ 9 <sup>b</sup>
Calcium (p.p.m.)	2458 $\pm$ 150 <sup>a</sup>	2570 $\pm$ 207 <sup>b</sup>	2613 $\pm$ 327 <sup>b</sup>
Magnesium (p.p.m.)	208 $\pm$ 72 <sup>a</sup>	253 $\pm$ 97 <sup>b</sup>	234 $\pm$ 85 <sup>b</sup>
Potassium (p.p.m.)	972 $\pm$ 515 <sup>a</sup>	1514 $\pm$ 876 <sup>c</sup>	1205 $\pm$ 730 <sup>b</sup>
Sodium (p.p.m.)	29 $\pm$ 24 <sup>a</sup>	54 $\pm$ 64 <sup>b</sup>	37 $\pm$ 34 <sup>ab</sup>
pH	8.3 $\pm$ 0.1 <sup>a</sup>	8.2 $\pm$ 0.2 <sup>a</sup>	8.3 $\pm$ 0.1 <sup>a</sup>
Cation exchange capacity	17 $\pm$ 1.8 <sup>a</sup>	19 $\pm$ 3 <sup>c</sup>	18 $\pm$ 3 <sup>b</sup>
Soil organic matter	0.87 $\pm$ 0.38 <sup>a</sup>	0.91 $\pm$ 0.44 <sup>a</sup>	0.88 $\pm$ 0.45 <sup>a</sup>
Litter (g m <sup>-2</sup> )	341 $\pm$ 441 <sup>ab</sup>	237 $\pm$ 233 <sup>a</sup>	483 $\pm$ 601 <sup>b</sup>
Gravel (%)†	34 $\pm$ 22 <sup>b</sup>	39 $\pm$ 15 <sup>b</sup>	24 $\pm$ 13 <sup>a</sup>
Sand (%)‡	89 $\pm$ 3 <sup>a</sup>	88 $\pm$ 3 <sup>a</sup>	92 $\pm$ 13 <sup>b</sup>
Silt (%)§	4.3 $\pm$ 1.0 <sup>b</sup>	4.0 $\pm$ 0.7 <sup>a</sup>	3.7 $\pm$ 0.8 <sup>a</sup>
Clay (%)¶	7.3 $\pm$ 2.6 <sup>b</sup>	6.9 $\pm$ 3.2 <sup>b</sup>	4.5 $\pm$ 2.0 <sup>a</sup>
Infiltration (ml min <sup>-1</sup> )	32 $\pm$ 22 <sup>a</sup>	—	45 $\pm$ 21 <sup>b</sup>
AM spores (spores g <sup>-1</sup> soil)	5.3 $\pm$ 14.3 <sup>a</sup>	5.5 $\pm$ 11.9 <sup>a</sup>	1.6 $\pm$ 4.3 <sup>a</sup>
Mycorrhizal inoculum potential (%)	16 $\pm$ 14 <sup>a</sup>	28 $\pm$ 22 <sup>b</sup>	14 $\pm$ 11 <sup>a</sup>

\*Differences found by ANOVA but not by *post hoc* test.

†% particles > 2 mm in diameter in the total soil sample.

‡% particles 0.05–2.0 mm diameter in the < 2 mm component of the soil sample.

§ % particles 0.002–0.05 mm diameter in the < 2 mm component of the soil sample.

¶% particles < 0.002 mm diameter in the < 2 mm component of the soil sample.

|| $n = 16$ , infiltration not collected from the east site.

Soils were typically sandy and gravelly. Significant soil textural differences occurred in each of the textural classes but differences were only significant between the highest and lowest values (Table 1, Fig. 1(m–p)). Wash soils were the coarsest grained, with the greatest amount of gravel and sand and the least amount of clay. The mixed shrubs, with and without burrows, had the least gravel and were sandy and low in silt. Interspace soils were the finest grained, with the highest clay and silt levels and the lowest sand level. Clay content was highest in *Lycium* soils. Clay was not correlated, gravel and silt were negatively correlated, and sand was positively correlated with plant size (Table 3). Textural classes were correlated with several other soil factors, particularly K.

Infiltration rates were significantly lower in interspace soils than in wash and mixed-shrub soils (Fig. 1(q)). The presence of burrows did not significantly influence infiltration rate.

#### MIP and spore density

Significant differences in MIP were few (Fig. 1(r)). The MIP was highest from *Pleuraphis* and *Larrea* soils. Interestingly, the lowest MIP occurred in mixed-shrub

**Table 3.** *F-values of Spearman's correlations between soil factors determined at eight Mojave Desert microsites at three different sites (n=144)*

	P	K	Mg	Ca	Na	NO <sub>3</sub>	NH <sub>4</sub>	pH	CEC	SOM	Litter
K	<b>0.346***</b>										
Mg	<b>0.323***</b>	<b>0.535***</b>									
Ca	-0.105	0.038	0.152								
Na	<b>0.229**</b>	<b>0.717***</b>	<b>0.511***</b>	-0.152							
NO <sub>3</sub>	<b>0.413***</b>	<b>0.841***</b>	<b>0.579***</b>	0.017	<b>0.556***</b>						
NH <sub>4</sub>	<b>0.248**</b>	<b>0.302***</b>	<b>0.262**</b>	-0.005	<b>0.190*</b>	<b>0.403***</b>					
pH	-0.039	-0.143	0.054	<b>-0.253**</b>	0.137	<b>-0.413***</b>	<b>-0.192*</b>				
CEC	<b>0.298***</b>	<b>0.817***</b>	<b>0.703***</b>	<b>0.451***</b>	<b>0.571***</b>	<b>0.710***</b>	<b>0.244**</b>	-0.111			
SOM	<b>0.524***</b>	<b>0.674***</b>	<b>0.560***</b>	0.137	<b>0.336***</b>	<b>0.818***</b>	<b>0.361***</b>	<b>-0.376***</b>	<b>0.625***</b>		
Litter	<b>0.430***</b>	<b>0.687***</b>	<b>0.402***</b>	0.014	<b>0.338***</b>	<b>0.784***</b>	<b>0.334***</b>	<b>-0.289***</b>	<b>0.540***</b>	<b>0.761***</b>	
Plant size†	<b>0.417***</b>	<b>0.594***</b>	<b>0.265**</b>	<b>0.227*</b>	<b>0.276**</b>	<b>0.659***</b>	<b>0.223*</b>	<b>-0.202*</b>	<b>0.530***</b>	<b>0.635***</b>	<b>0.673***</b>
MIP	<b>-0.228**</b>	-0.004	0.015	<b>0.248**</b>	-0.043	0.032	0.061	<b>-0.269**</b>	0.045	0.003	-0.002
Spore density†	0.094	0.069	0.07	0.207	-0.106	0.037	0.111	<b>0.248*</b>	0.103	0.094	-0.004
Gravel	<b>-0.304***</b>	<b>-0.364***</b>	<b>-0.201</b>	0.000	-0.140	<b>-0.321***</b>	-0.109	0.003	<b>-0.290***</b>	<b>-0.371***</b>	<b>-0.460***</b>
Sand	-0.104	<b>0.210*</b>	<b>-0.282**</b>	-0.071	0.122	0.100	-0.053	<b>-0.171*</b>	0.037	-0.051	<b>0.169*</b>
Silt	<b>-0.178*</b>	<b>-0.501***</b>	-0.120	-0.009	<b>-0.281**</b>	<b>-0.497***</b>	-0.142	0.159	<b>-0.384***</b>	<b>-0.358***</b>	<b>-0.505***</b>
Clay	0.151	-0.091	<b>0.340***</b>	0.085	-0.055	0.032	0.095	0.137	0.065	0.149	-0.051
	Plant size†	MIP	Spore density†	Gravel	Sand	Silt					
MIP	<b>-0.192*</b>										
Spore density†	-0.089	0.158									
Gravel	<b>-0.315**</b>	0.050	0.096								
Sand	<b>0.246*</b>	-0.138	<b>-0.295**</b>	-0.132							
Silt	<b>-0.357***</b>	0.100	-0.025	<b>0.239**</b>	<b>-0.440***</b>						
Clay	-0.153	0.133	<b>0.290**</b>	0.090	<b>-0.961***</b>	<b>0.208*</b>					

F-values in bold are significant at  $p < 0.05$ .†  $n = 108$ .\* Significant at  $p = 0.05$ .\*\* Significant at  $p = 0.01$ .\*\*\* Significant at  $p = 0.001$ .

soils without mammal holes. This microsite had a MIP significantly lower than did the *Larrea* microsites even though the mixed-shrub soils contain *Larrea*. Spore densities were significantly higher in *Lycium* soils than in soil from the other microsites (Fig. 1(s)). While wash and interspace soils did not contain spores, other microsites ranged from ~1–3 spores per 10 g soil, with *Lycium* soils containing 25 spores per 10 g soil. MIP was positively correlated with Ca and negatively correlated with P, pH and plant size (Table 3). Spore density was positively correlated with pH and clay and negatively correlated with sand. MIP and spore density were not correlated.

### Sites

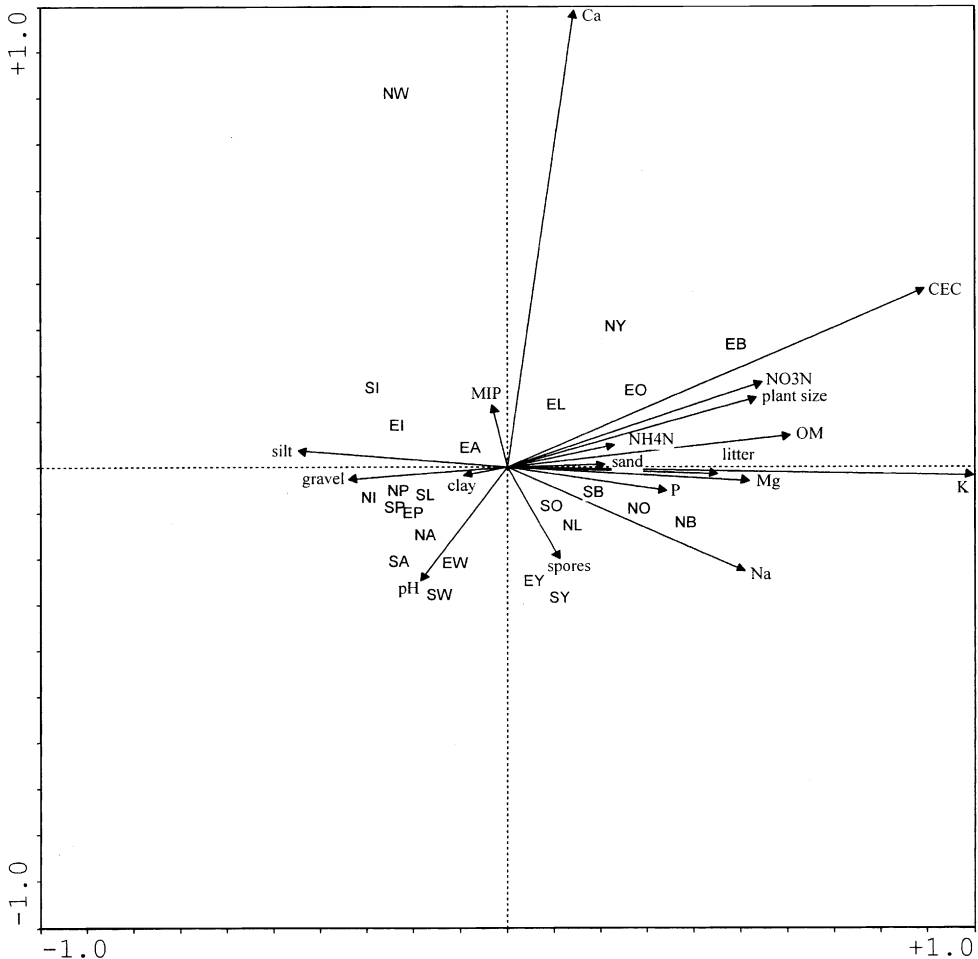
Most of the soil variables measured had significant differences across the three sites (Tables 1 and 2).  $\text{NH}_4$ , pH, SOM, and spore densities did not differ across the three sites. Mg, K, Na, CEC,  $\text{NO}_3$  and MIP showed a similar pattern, with the highest levels of these factors in the east site and lowest levels in the south site. Ca also showed the lowest levels at the south site. P and litter differed from the other soil factors by having their lowest value at the east site. Particle-size distributions were significantly different across sites. North site soils were the sandiest and had the least gravel, silt and clay. North site soils also had higher infiltration rates than south site soils.

### PCA

With the exception of Ca, all of the measured nutrients were correlated in their distribution, that is, they occur at higher levels in similar microsites and sites (the arrows for these nutrients all point to the right side of the bi-plot (Fig. 2). The soils in which the nutrients, as well as SOM, CEC and litter, occurred at the highest overall levels were the mixed shrub with and without burrows, *Lycium* and *Larrea* (with the exception of south site *Larrea*). The correlation with plant size is also clear. Nutrients were at overall lower levels in wash and interspace soils (interspace and wash microsites are on the left side of the bi-plot). Soils with more gravel and silt were more nutrient poor. The PCA illustrates how the distribution of Ca is different than the other nutrients and occurs at high levels in north site wash soils. Increasing pH is negatively correlated with SOM, CEC, litter and higher nutrient levels. Although there were no strong patterns in the mycorrhizal factors (shown by the shortness of the arrows), MIP and spore density were not positively correlated. In addition, mycorrhizal factors were not related to nutrient distributions. Percent variance explained by the successive axes are 87.2, 9.1, 2.5, and 0.8.

### Discussion

Soil nutrients were found to be heterogeneously distributed, and N, P and K were positively correlated with shrub size and the associated litter and SOM levels, as clearly seen in the PCA (Fig. 2). The larger mixed shrubs have greater N, P and K levels than do the smaller mixed shrubs, and these have greater levels than the single shrubs. Likewise, the larger lone shrubs have greater N, P and K levels than the smaller shrubs. This pattern is likely due to greater litter fall, more animal habitats (spiders, small mammals), greater age of the island, and a greater ability to capture aeolian particles (Elkins *et al.*, 1986; Coppinger *et al.*, 1991; Whitford *et al.*, 1997). Although mixed shrubs without burrows are not greater in size than lone *Larrea* shrubs, nutrient levels are higher in the mixed shrubs without burrows. Mixed shrubs have more leaves, stems (J. Titus, pers. obs.) and litter than do lone *Larrea*. Due to the difficulty of aging desert shrubs, the actual correlation between shrub size and age



**Figure 2.** Principal components analysis (PCA) of soil parameters at eight microsites in three sites at the Nevada Test Site in the Mojave Desert. Microsites are the independent variables and soil parameters the dependent variables. Soil parameters are represented by arrows and microsites by labels. Sites: N = North, E = East, S = South. Microsites: B = With Burrows, O = No Burrows, L = *Larrea tridentata*, Y = *Lycium pallidum*, A = *Ambrosia dumosa*, P = *Pleuraphis rigida*, W = Wash, I = Interspace. The bi-plot yields information about correlations between microsites and soil factors. Arrows pointing toward an environmental variable point indicate a high positive correlation, arrows pointing in an opposite direction indicate a high negative correlation, and arrows pointing at a right angle from a line connecting the environmental variable point with the center indicate a near-zero correlation. Soil parameters with longer arrows are more important in the analysis. Infiltration is not included because it was not measured at all locations.

is unknown (McAuliffe, 1988). It should also be stated that soil nutrients are labile through time. For example, extractable nitrate and ammonium may have high temporal variability. The nutrient values obtained should, therefore, be viewed as a snap-shot in time. This study builds on previous research where nutrient pools have also been measured to increase our understanding of fertile islands in arid systems.

The presence of animal burrows had a significant influence on nutrient levels, particularly nitrogen. This has been found in a number of other studies (reviewed in Whitford & Kay, 1999). Shrubs with animal burrows occupy locations on the right side of the PCA bi-plot, indicating higher overall nutrient levels.  $\text{NH}_3$  and  $\text{NO}_2$  levels were 2.5 and 2 times higher in mixed shrubs with burrows than in mixed shrubs without burrows, respectively. Also, large mixed-shrub assemblages without burrows are difficult to find at the study site. Kangaroo rats increase nutrient levels because nitrogen and other nutrients originate from their urine and feces (Moorhead *et al.*, 1988; Chew & Whitford, 1992) and from cached or discarded plant material (Reichman & Smith, 1985). Kangaroo rats cache large amounts of seeds and other plant parts—over 5 kg potentially—in their dens (Vorhies & Taylor, 1922; Chew & Whitford, 1992). In addition, modification of soil and its turnover via rodents may enhance bacterial activity so that more N is made available to plants (Brooks *et al.*, 1985). South site animal burrow microsites were markedly lower in nutrients than the other two sites, indicating the importance of landscape position in influencing nutrient levels.

Apart from plant size, species are known to differ in their contributions to fertile islands. For example, *Lycium* soils had high levels of Na and Mg. Why *Lycium* created a fertile island with these characteristics is unknown, but the higher Na and Mg levels and/or other attributes of *Lycium* fertile islands creates an environment with significantly higher AM spore densities. Higher spore densities did not, however, lead to greater MIP.

Nutrient distribution patterns observed here support the idea that vegetation appears to maintain a tight control over the cycles of biologically limiting nutrients (N, P and K) and abiotic forces appear to regulate the cycling of non-limiting elements as they are more or less equally distributed under and between shrubs or more highly concentrated in interspaces (Schlesinger *et al.*, 1996; Cross & Schlesinger, 1999; Wezel *et al.*, 2000). The biologically limiting nutrients, once acquired from the soil solution through root uptake, remain under the plant through recycling via litterfall, microbial litter decomposition, and microbial immobilization (Crawford & Gosz, 1982; Caldwell & Richards, 1989; West, 1991).

Significant differences were found in CEC in this study, with *Lycium* and the mixed shrubs having higher CECs than the smaller plants and the unvegetated microsites. Although CEC is positively correlated with the plant size, the presence of a *Lycium* also appears to affect soil chemistry in such a way as to cause increased CEC. No differences in CEC between soils under *Larrea* shrubs and interspaces were found by Cox *et al.* (1983) and Cross & Schlesinger (1999), or by Wright & Honea (1986) between *Prosopis glandulosa* and interspace soils. However, Romney *et al.* (1980) found CECs to be higher under shrubs than in interspaces and Charley & West (1975) found that soil under *Artemisia tridentata* and *Atriplex confertifolia* had higher CECs than interspace soil, whereas CECs were the same under and between *Coleogyne ramosissima* shrubs. These studies point out the importance of species differences in influencing soil chemistry.

As was found here, past studies have shown desert soils to be strongly alkaline (e.g. Charley & West, 1975). In the Mojave Desert, Romney *et al.* (1980) found soil from below five shrub species and interspaces to not differ in pH values and no difference in pH was found between *P. glandulosa* and interspace soils in the Chihuahuan Desert (Wright & Honea, 1986). Walker *et al.* (2000) found pH levels to be higher under *Ambrosia*, *Larrea*, and *C. ramosissima* than in interspaces, whereas this study (except for *Lycium*) and that of Rostagno *et al.* (1991) in Patagonia, found interspace and wash soils to have a higher pH than under shrubs. We found pH was negatively correlated with plant size and the associated variables of litter and SOM. Negative correlations may result if the litter is acidic in composition.

*Particle size*

Few studies report soil gravel content. Soils in this study contained similar levels of gravel as some Chihuahuan Desert sites (Gile *et al.*, 1998) and several sites in the more mesic Kruger National Park (Thrash, 1997). An Australian desert site had markedly less gravel (Dunkerly, 2000). Wash soils are the most gravelly and sandy and have the least clay due to floodwaters carrying away the finer grained soil particles. Negative correlations between gravel and silt content and SOM, plant size, and litter and positive correlations between sand and litter and plant size show a biotic influence on particle size (Table 3). Clay, however, was not correlated with these variables. Animal burrows did not influence particle size, as there were no differences between mixed shrubs with and without burrows. This may be because animal activity around any shrub complex is considerable whether or not a burrow is visible.

In general, interspace soils contained more silt and less sand than shrub soils (Fig. 1(n,o)). Similar patterns were observed in the Chihuahuan Desert between interspace and *Larrea* soils (Cross & Schlesinger, 1999), in an Australian desert (Dunkerly, 2000), and in the Sahel (Wezel *et al.*, 2000). However, at a Mojave Desert site soil texture distributions were found to be similar between shrub and interspace soils (Romney *et al.*, 1980) and in the Chihuahuan Desert interspace soils were found to be the same as *P. glandulosa* soils (Wright & Honea, 1986). A plant-size-dependent mediated directional movement of soil particles where silt is moved away from the plant by wind or rain may be a powerful force in the Mojave. However, site landscape position on the bajada (McAuliffe, 1994) is also important as shown by the significant site effects. The north site, closest to the playa, had the sandiest soils.

*Infiltration*

The sandier soils of the shrubs and washes are a reason why infiltration may be greater at those microsites (Fig. 1(q)). Other reasons for differences in infiltration rates are more abundant litter and SOM under shrubs (Wood & Blackburn, 1981; Bedunah & Sosebee, 1986; Elkins *et al.*, 1986), presumably more soil compaction from raindrops and trampling in interspaces (Naeth *et al.*, 1990; Thrash, 1997), and more abundant root (Kummerow *et al.*, 1977; Brisson & Reynolds, 1994) and faunal (Elkins *et al.*, 1986; Eldridge & Robson, 1997) macropores under shrub canopies. Several studies have found burrows to increase infiltration (reviewed in Whitford & Kay, 1999); this was the case here but differences were not significant between mixed shrubs with and without burrows. The sandier soils of the north site may be the reason for the higher infiltration rates at this site.

Directly comparing infiltration rates between studies is difficult due to differences in methods (e.g. Blackburn & Skau, 1974; Tromble *et al.*, 1974). However, rates found here are quite similar to those found in Australian arid lands and Patagonia, with a similar decline from under shrubs to the interspaces (Pressland, 1976; Rostagno, 1989; Dunkerly, 2000). Infiltration rates were also similar to those found in crusted soils in Jordan and in compacted soils in Kruger National Park (Thrash, 1997), but lower than infiltration rates in Chihuahuan Desert (Elkins *et al.*, 1986) and Somalian (Takar *et al.*, 1990) soils.

Site histories are very different between the Nevada Test Site in the Mojave Desert and the Chihuahuan Desert Sevilleta NWR. The Mojave Desert was a shrubland prior to Anglo settlement, whereas the Chihuahuan Desert shrubland was converted from semi-arid grassland over the past 150 years by overgrazing (Schlesinger *et al.*, 1990; 1996; Kieft *et al.*, 1998). Despite differences in site history, patterns in nutrient distribution, soil texture and infiltration are similar, including high Ca values (Schlesinger *et al.*, 1996). Concentrations of N and P under shrubs enhance soil

fertility over the long-term and create favorable microsites for shrub regeneration that, in turn, function as a positive feedback mechanism for continued desertification (Schlesinger *et al.*, 1990). Thus, the development of fertile islands is a relatively rapid process (Wezel *et al.*, 2000).

#### *MIP and spore densities*

Fungal spore densities are low in arid soils, and zero counts are common (McGee, 1989; Cui & Nobel, 1992; Requena *et al.*, 1996; Siguenza *et al.*, 1996; Carrillo-Garcia *et al.*, 1999). AM species richness has also been found to be low in arid areas (Rose, 1981; Stahl & Christensen, 1982; Bethlenfalvai *et al.*, 1984; Pond *et al.*, 1984), although higher richness has been found in semi-arid parts of the Sonoran Desert (Bloss, 1985; Bloss & Walker, 1987). Stutz & Morton (1996) and Stutz *et al.* (1999) postulated that a reason for the low richness may be the low spore density; by using three successive cycles of trap cultures of Sonoran and Chihuahuan soils from mesquite roots, they greatly increased species richness to a level approaching that of mesic environments (7–9 species). Arid zone AM fungal species may only sporulate infrequently in response to a period of favorable temperature and moisture (Zak *et al.*, 1995; Stutz & Morton, 1996; Stutz *et al.*, 1999).

Spore densities have been found to be higher in beneath-shrub soils than in interspaces (Carrillo-Garcia *et al.*, 1999) as they were in this study. Spores have been found to be located <50 cm deep in some arid soils (Schwab & Reeves, 1981; Al-Agely & Reeves, 1995), but much deeper in other arid soils (White *et al.*, 1989). AM colonized mesquite roots have been found 4.5–4.8 m deep in the Sonoran Desert (Virginia *et al.*, 1986). A patchy distribution of spores was found in this study (e.g. higher spore densities in *Lycium* soils, no spores in unvegetated microsites), and large standard deviations occurred within microsites. However, whether or not at least part of this pattern is due to the present or past distribution of fine plant roots, as has been found in mesic environments (Friese & Koske, 1991), is difficult to say.

In mesic environments, SOM has been found to be positively correlated (Anderson *et al.*, 1984; Johnson *et al.*, 1991b), and P (Anderson *et al.*, 1984; Johnson *et al.*, 1991b; Martensson & Carlgren, 1994), N (Hayman, 1970), Mg (Anderson *et al.*, 1984), Na (Ho, 1987) and Ca (Anderson *et al.*, 1984) levels have been found to be negatively correlated with spore densities. pH has been found to be both positively (Wang *et al.*, 1985, 1993; Johnson *et al.*, 1991b) and negatively (Anderson *et al.*, 1984; Johnson *et al.*, 1991a) correlated with spore densities. These differences in response are not surprising because of species-specific seasonal fluctuations in spore densities (Brundrett, 1991; Siguenza *et al.*, 1996; Guadarrama & Alvarez-Sanchez, 1999) and individual responses of AM fungal species to different environmental conditions (Johnson *et al.*, 1992). pH, the only variable with a significant correlation, was positively correlated with spore density. This positive correlation may be directly due to pH, but because pH differences between microsites are slight, the correlation is more likely due to the fact that the highest pH was found under *Lycium* and is another characteristic of *Lycium* that encourages AM fungal sporulation.

Because most perennial arid zone plants in undisturbed environments are mycorrhizal (Rose, 1981; Trappe, 1981; Mejsstrik & Cudlin, 1983; Bloss, 1985; Carrillo-Garcia *et al.*, 1999, Titus *et al.*, 2002) positive MIP values would be expected in arid zones. Although few studies have been performed on arid zone MIP, it appears to vary seasonally and spatially and in relation to the surrounding vegetation and environmental variables (Al-Agely & Reeves, 1995; Requena *et al.*, 1996), as it does in more mesic environments (Johnson *et al.*, 1991b; Brundrett *et al.*, 1996).

Indices of AM, MIP and spore counts are often not correlated (Hetrick & Bloom, 1986; Scheltma *et al.*, 1987; Johnson *et al.*, 1991a), as was the case in this study. Spore counts assess only one type of propagule while MIP indirectly measures all types, i.e., spores, hyphae and AM colonized roots. In addition, different AM species do not sporulate to the same degree, at the same time, or in response to the same environmental variables across a wide range of environments (Siguenza *et al.*, 1996; Allen *et al.*, 1998; Guadarrama & Alvarez-Sanchez, 1999). In mesic zones both soil factors and plant species have been found to influence MIP and spore density (Henkel *et al.*, 1989; Johnson *et al.*, 1992; Sanders and Fitter, 1992; Blaszkowski, 1994). In this study, host species appear to be more important in influencing spore density because of the lack of correlation between spore density and soil parameters, and the powerful effect of *Lycium* on spore density. MIP, however, appears to be more heavily influenced by soil factors. In any case, it is likely that a combination of abiotic and biotic factors combine with competitive interactions between AM species to determine AM sporulation patterns and help maintain a diverse AM fungal flora (Gemma *et al.*, 1989).

### *Lycium*

Soil from below *Lycium* shrubs stand out as having soil characteristics markedly different than the other species. Soils under *Lycium* are particularly high in Na, Mg, and AM spore density and are also high in K. The high levels of these nutrients may cause the high pH and CEC found under *Lycium* and could possibly influence sporulation. Why the high levels of these nutrients occur is difficult to determine from the available data. El-Ghonemy *et al.* (1978) found high levels of N and Na in *Lycium* foliage and they also found high Na levels in the soil beneath the shrub. Thus, soil attributes of the *Lycium* fertile island may be partially due to foliage nutrient levels.

### *Sites*

A playa is located north of the MGCE. Playas contain markedly different nutrient composition and particle-size distribution than bajadas (Vasek & Lund, 1980), with generally finer grained soils with high Na levels. These finer grained soils occur in playas because floodwaters drop coarser particle before they reach the playa and wind-blown sediments may settle in playas. Salt accumulates in playas from the evaporation of water. If the gradient is sufficiently strong, then the part of the bajada closest to the playa would be expected to have the finest particles. The north site, closest to the playa, did contain the least gravel but also contained the least clay. As for nutrients, the north site contained the most Ca but did not contain the highest levels of the highly water soluble Na and K. The east site contained the most washes and also had the most gravel. Why the east site contained the highest levels of most of the nutrients is unknown. It is likely that the proximity of the playa has some influence on the composition of north site soils, however, other historical landscape-level effects have caused the east site soils to contain higher levels of many of the nutrients (McAuliffe, 1994).

### **Conclusion**

This study further expands our knowledge of arid zone fertile islands, which are an integral part of the desert landscape. It points out important differences between species, particularly *Lycium*, in influencing soil characteristics of fertile islands in the Mojave Desert. In addition, differences between microsites in AM levels are also

shown. Differences between fertile islands are due to a complex combination of factors both abiotic and biotic, such as species attributes. Differences between locations on the bajada illustrate the importance of landscape level factors in structuring fertile islands.

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