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ECOLOGICAL IMPACTS OF SEED HARVESTER ANTS ON SOIL ATTRIBUTES IN A *LARREA*-DOMINATED SHRUBLAND

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ABSTRACT.—The influence of seed harvester ant (*Pogonomyrmex rugosus*) colonies on soil properties and soil surface and moisture characteristics was investigated through comparison of adjacent, nonnest (reference, 4 m beyond ant colony) areas in Las Vegas, Nevada. Effects of ant colonies on both terrace and slope sites were investigated. Soil moisture content and soil bulk density in a creosote bush (*Larrea tridentata*)–dominated shrubland were significantly lower, while soil temperature, soil organic matter, and percent pore space were significantly higher in soils with ant nests relative to adjacent reference soils. Soil pH and texture did not differ significantly between nest and reference soils. Among soil surface characteristics, percent bare soil and rock (gravel, cobble, and boulder) cover were not significantly different between nest and reference soils. In evaluating soil moisture characteristics, soils with ant nests had a significantly higher water infiltrability and greater depth of water penetration, but a significantly lower area of water spread (surface-water runoff) at both terrace and slope sites. Between the 2 geomorphic surfaces, water infiltrability and depth of water penetration were significantly greater at the terrace than at the slope. Water-borne soil movement (fluvial erosion) was significantly greater at the slope than terrace but did not differ significantly between nest and reference soils. The presence of active *P. rugosus* colonies in the *L. tridentata*–dominated shrubland altered certain soil properties and appeared to have a protective influence on the soil by fostering more infiltration and less runoff of surface water in southern Nevada.

Key words: Pogonomyrmex rugosus, *nests, colonies, soil properties, soil surface, soil moisture, geomorphic surfaces, terrace, slope,* Larrea tridentata, *Las Vegas, southern Nevada.*

The seed harvester ant (*Pogonomyrmex rugosus* Emery) occurs in arid and semiarid plant communities throughout much of the southwestern United States (Carlson and Whitford 1991). *Pogonomyrmex rugosus* nests are often surrounded by conspicuous clearings from which the ants have removed vegetation. Soils of subterranean *Pogonomyrmex rugosus* have lower bulk density, higher water infiltrability, and higher organic matter content than surrounding soils in New Mexico (Whitford 1988). The western harvester ant (*P. occidentalis*), a closely related species, also affects soil properties in New Mexico by reducing soil pH, bulk density, and moisture content and by increasing soil salinity and organic matter (Carlson and Whitford 1991). Subterranean ants may also alter soil texture, affect soil pore size, and cause localized accumulations of organic and inorganic nutrients in ponderosa pine (*Pinus ponderosa*) and pinyon pine–Utah juniper (*Pinus monophylla–Juniperus osteosperma*) woodlands in New Mexico (Carlson and Whitford 1991).

The xerophytic creosote bush–white bursage (*Larrea tridentata–Ambrosia dumosa*) shrubland is a common vegetation type in southern Nevada, and yet the extent of ant nest influence on soil properties, as well as on soil surface and moisture characteristics, remains poorly understood. The presence of 217 ant colonies located in a 10-ha site appears to have localized influences on soil surface variables and soil moisture status in southern Nevada. The objectives of this study were to determine if subterranean *P. rugosus* activity significantly alters soil attributes in a *Larrea tridentata*–dominated shrubland in southern Nevada. Two questions were addressed: (1) Do various properties and surface (bare soil and rock) characteristics of nest soils differ from adjacent reference (nonnest) soils? (2) Do ant activities alter the moisture status of nest soils compared to adjacent reference soils on 2 distinct geomorphic surfaces (terrace and slope)?

METHODS

Study Site

The study site is in Henderson, Clark County, Nevada (roughly 36°00′N, 115°00′W; elevation 750 m). This site is dominated by

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xerophytic *L. tridentata* shrubs. Other woody taxa are sparsely distributed, including white bursage (*Ambrosia dumosa*), ratany (*Krameria parvifolia*), winterfat (*Eurotia lantata*), goldenhead (*Acamptopappus shockleyi*), Mojave yucca (*Yucca schidigera*), indigo bush (*Psorothamnus fremontii*), and brittle bush (*Encelia virginensis*). Several species of cacti (*Opuntia* spp.) are also present in low abundance in this vegetation zone. Soils are sandy in texture and calcareous with abundant loose rocks on the surface. Soils are derived from nearby limestone-dolomite mountains and hills (Rowlands et al. 1977).

Although the Las Vegas valley is an area of primarily winter and summer rainfalls, total amount of annual precipitation varies considerably from year to year. Rainfall can last from several hours to several days (Rowlands et al. 1977). Mean annual precipitation ranges from 118 to 183 mm in the *L. tridentata–Ambrosia dumosa* shrublands (Beatley 1974). Summer monsoonal rainfalls and storms can sometimes be locally intense. Spring 1997 was extremely arid, with total precipitation of <10.0 mm, falling well below the annual average of 25.4 mm (Climatological Data, Las Vegas). Maximum summer and minimum winter air temperatures range from above 40°C to below 0°C, respectively (Lei and Walker 1997a, 1997b). Relative humidity of 20% or less is common due to a combination of low precipitation, low cloud cover, high evaporation rate, and high air temperature during summer seasons (Lei and Walker 1997a).

Field Surveys and Soil Collections

Field surveys were conducted during spring 1997 in southern Nevada. At the time of soil collection, the weather was hot and the soil appeared extremely dry. All 217 *P. rugosus* nests at a 10-ha site were identified. Each ant colony had multiple nest entrances, subterranean chambers (cavities), and tunnels (runways). Diameters of the exposed soil surface (disc) at each ant colony were measured to the nearest centimeter by computing average length and width of the nest. A reference (adjacent, nonnest areas) was established 4 m from the edge in a random direction from each nest.

Soil samples from the 217 nest discs of *P. rugosus* and from adjacent reference points were excavated approximately 10 cm in diameter to depths of 15 cm. Soil samples were sieved through a 2-mm mesh to remove plant roots and rocks >2 mm in diameter. Soil was defined as <2 mm in diameter, while large particles were not considered soil. Nest soils were collected approximately midway between the disc edge and center of each ant nest. All tests were performed on sieved soils dried at 105°C for 72 h. Soil samples were measured for pH, percent moisture, bulk density, compaction, percent pore space, organic matter, and texture.

Laboratory and Statistical Analyses

Soil moisture was determined gravimetrically by calculating the difference between fresh and oven-dried mass. Soil temperature readings were taken in the field at the soil surface (0 cm) and at 15 cm below the soil surface on ant colonies and reference points. To measure bulk density, a core of soil of known volume was carefully removed from the field. Fresh soil cores were oven-dried at 105°C until they reached a constant mass. Soil cores were then weighed, dividing dry mass by volume to determine soil bulk density. Soil compaction was estimated using a penetrometer inserted into the soil. Average pore space was determined using the equation:

$$\text{pore space (\%)} = 100 - (D_b/D_p * 100),$$

where D_b is bulk density of the soil and D_p is average particle density, usually about 2.65 g cc^{-1} (Hausenbuiller 1972, Davidson and Fox 1974). Soil organic matter was obtained by mass loss on ignition at 550°C for 4 h. Soil pH was measured by preparing a paste consisting of a ratio of 1:1 soil:distilled water mixture and by measuring with an electrode pH meter. Soil salinity (total soluble salts) was determined by a Beckman electrical conductivity bridge. A slurry consisting of equal parts of soil and distilled water paste was used to determine total soluble salts. Soil particle size distribution was determined by the hydrometer method as described by Bouycoucos (1951).

For each ant nest and reference area, soil surface characteristics of bare ground, gravel (2–64 mm in diameter), cobble (65–256 mm), and boulder (>256 mm) were visually quantified using 10% increments.

Water infiltration rates were measured by using PVC pipe, 5.5 cm in diameter and 9.5 cm tall. This pipe was open at both ends and was gently tamped into the disc and reference soils to a depth of 2 cm to prevent leakage, and then 50 mL of water was poured into the pipe. Time taken for the water to disappear completely into the soil surface was recorded with a stop-watch.

Approximately 1.5 L of water, acting as an artificial rain, was manually poured through a perforated 13-cm disk, with perforations being evenly spaced on a 0.1-cm grid. The disk was placed 1.0 m aboveground. Total delivery time was 1 min for the water to be dispensed on the nest or soil surface and to create precipitation at a cloudburst level (Brotherson and Rushford 1983). A sudden heavy precipitation is significant due to its impact on surface-water runoff and fluvial erosion. Depth of water penetration was measured once the water had soaked into the soil.

Surface-water runoff was measured by recording the downslope and across-slope spread of water that was artificially rained onto study sites (Brotherson and Rushforth 1983). The area of water spread from these 2 slope measurements was computed using the formula for the area of an ellipse.

Soil movement was assessed by estimating the amount of soil moved through fluvial erosion during a measured rain. The following index was used: 1 = no appreciable movement; 2 = moderate movement, up to 10% of soil being displaced; and 3 = heavy movement, between 10% and 20% of soil being displaced (Brotherson and Rushforth 1983).

Paired *t* tests (Analytical Software 1994) were performed to compare differences between properties, surface characteristics, and moisture status of disc (nest) and adjacent reference soils. Student's *t* tests (Analytical Software 1994) were conducted to compare differences between terrace and slope habitats (geomorphic surfaces). Mean values are presented with standard errors, and statistical significance was determined at the 5% level.

RESULTS

Mean distance between ant nests and nearest shrubs was 164.0 ± 15.6 cm. Mean ant nest diameter was 88.9 ± 10.7 cm ($n = 217$). Moisture content, bulk density, and compaction of nest soils decreased ($P \leq 0.05$; Table 1) compared to adjacent reference soils in the *L. tridentata*–dominated shrubland. However, percent pore space, soil organic matter content, and soil temperatures increased ($P \leq 0.05$) in nest soils compared to reference soils. Soil pH, salinity, and texture (percentages of sand, silt, and clay) did not differ between nest and reference soils ($P > 0.05$; Table 1).

Percent bare soil and rock (gravel, cobble, and boulder) cover did not differ ($P > 0.05$; Table 2) between nest and reference soils. A relatively high percent ground cover of bare soil and a low percent cover of rock were observed in both nest and reference soils.

Moreover, nest soils increased ($P \leq 0.01$; Table 3) the water infiltration rate and depth of water penetration during a measured rain compared to reference soils at both terrace and slope habitats. Between the 2 geomorphic surfaces, infiltration rates ($t = -10.38$, df = 216, $P \leq 0.0001$) and depth of water penetration ($t = 7.06$, df = 216, $P = 0.0001$) were greater in terrace than slope habitat. However, nest soils decreased the area of water spread as well as the downslope and across-slope water spread (surface-water runoff) in both geomorphic surfaces during the artificial rain ($P \leq 0.05$; Table 3). Water-borne soil movement (fluvial erosion) was reduced at terrace habitat compared to slope habitat ($t = -4.04$, df = 216, $P = 0.003$). Yet, fluvial erosion did not differ between nest and reference soils despite the occurrence of a minor fluvial erosion in both soils ($P > 0.05$; Table 3).

DISCUSSION

Pogonomyrmex rugosus colonies alter certain soil properties as well as soil surface and moisture characteristics in southern Nevada. Viable *P. rugosus* nests modified a number of edaphic parameters.

Water relations of *P. rugosus* colonies are not well documented. Soil moisture is an important source of colony water, and workers have clear preferences for moist soil (Rissing 1988). *Pogonomyrmex rugosus* conserves soil moisture by removing transpiring plants (Rissing 1988). However, soil moisture content declines significantly in nest soils compared to adjacent reference soils (Table 1). Low moisture content in nest soils is expected if changes in vegetation cover and evapotranspiration rates

TABLE 1. Chemical and physical properties (mean ± $s_{\bar{x}}$, n = 217) of ant nest and adjacent reference (nonnest, 4 m beyond nest) soils in the *L. tridentata*–dominated shrubland. Soil moisture, organic matter, and texture (sand, silt, and clay) are expressed in percentages.

			Paired *t* test	
Soil property	Ant nest	Reference	*t*-value	*P*-value
Moisture (%)	1.1 ± 0.3	1.8 ± 0.4	–10.82	0.0000
Temperature (°C)				
At soil surface	24.7 ± 1.2	22.9 ± 0.8	3.59	0.0058
At 15 cm below	26.3 ± 0.7	24.4 ± 0.5	3.72	0.0048
Bulk density (g cm^{-3})	1.3 ± 0.1	1.5 ± 0.1	–6.00	0.0002
Compaction (g cm^{-2})	6.0 ± 0.3	6.8 ± 0.3	–3.87	0.004
Pore space (%)	47.2 ± 4.6	43.4 ± 3.1	11.11	0.0000
Organic matter (%)	3.1 ± 0.4	2.4 ± 0.2	8.80	0.0000
pH	7.8 ± 0.1	7.9 ± 0.1	–1.34	0.213
Salinity (mmho cm^{-1})	0.3 ± 0.03	0.3 ± 0.01	–0.50	0.626
Sand (%)	77.6 ± 1.4	78.7 ± 1.5	–2.19	0.056
Silt (%)	19.3 ± 1.2	19.5 ± 1.0	–2.24	0.052
Clay (%)	3.1 ± 0.3	2.8 ± 0.2	2.09	0.066

TABLE 2. Percent ground cover of bare soil, gravel, cobble, and boulder (mean ± $s_{\bar{x}}$, n = 217) in ant nest and adjacent reference (nonnest, 4 m beyond nest) soils in the *L. tridentata*–dominated shrubland.

			Paired *t* test	
Soil surface variable (%)	Ant nest	Reference	*t*-value	*P*-value
Bare soil	35.6 ± 4.2	32.3 ± 3.8	1.57	0.151
Gravel	48.7 ± 4.7	52.1 ± 3.1	–1.81	0.104
Cobble	11.0 ± 1.4	10.2 ± 1.1	2.09	0.066
Boulder	4.7 ± 0.1	5.4 ± 0.1	–2.10	0.065

TABLE 3. Moisture characteristics (mean ± $s_{\bar{x}}$, n = 217) of ant nest and adjacent reference (nonnest, 4 m beyond nest) soils on 2 distinct geomorphic surfaces in the *L. tridentata*–dominated shrubland.

			Paired *t* test	
Moisture parameter	Ant nest	Reference	*t*-value	*P*-value
Infiltration (seconds)				
Terrace	184.7 ± 11.7	212.4 ± 10.3	–5.78	0.0000
Slope	239.1 ± 12.5	263.9 ± 11.8	–5.04	0.0000
Depth of water penetration (cm)				
Terrace	3.7 ± 0.02	3.0 ± 0.01	7.13	0.0001
Slope	3.1 ± 0.01	2.4 ± 0.01	7.36	0.0000
Downslope spread (cm)				
Terrace	71.1 ± 4.2	81.3 ± 4.1	–4.24	0.0022
Slope	83.8 ± 5.2	94.0 ± 4.4	–4.89	0.0002
Across slope spread (cm)				
Terrace	68.6 ± 4.0	77.5 ± 4.0	–2.70	0.025
Slope	76.2 ± 4.2	88.9 ± 5.4	–3.42	0.008
Area of spread (cm^2)				
Terrace	3828.8 ± 435.9	4961.1 ± 442.0	–14.86	0.0000
Slope	5012.7 ± 701.3	6560.0 ± 740.8	–17.23	0.0000
Soil movement				
Terrace	1.2 ± 0.01	1.3 ± 0.01	–1.63	0.137
Slope	1.4 ± 0.01	1.5 ± 0.01	–1.66	0.132

result from constant ant activities. Reduced water content may be due to numerous tiny openings at nest entrances on the soil surface that dry, aerate, and loosen soils more quickly in *Pinus ponderosa* and *P. monophylla–J. osteosperma* stands of New Mexico (Carlson and Whitford 1991).

In this study tiny openings on the soil surface caused by ant activities were also likely to lower soil compaction and bulk density and to raise soil temperature at 15 cm beneath ant colonies. A lack of dense vegetation also increased soil temperatures. Percent pore space increased significantly in nest soils relative to adjacent reference soils (Table 1). Soil excavation by *P. barbatus* (harvester ant) may have increased average soil pore size (Wagner et al. 1997). Sandy soils normally show a range of 35%–50% pore space (Brady 1974), which concurs with this study. Pore space of soils generally contains air and water, and this space consists of macropores that allow ready movement of air and water (Davidson and Fox 1974). The decrease in soil compaction and bulk density, along with the increase in macropore space and soil temperature, may result in greater evaporative losses of soil moisture and less potential storage of soil water at depth.

Soil organic matter was higher in nests than surrounding reference soils (Table 1). In numerous excavations of *P. rugosus* colonies, decomposing plant materials in shallow nest chambers were observed; these would increase organic content of nest soils (Wagner et al. 1997). Elevated organic matter content may relate to accumulation and retention of waste plant materials and, to a lesser extent, turnovers and metabolic wastes of the ants (Carlson and Whitford 1991). However, soil pH and salinity did not vary significantly between nest and adjacent reference soils (Table 1). Mandel and Sorenson (1982) found no pH difference for *P. occidentalis* mounds that occurred in alkaline soils compared to adjacent reference soils.

Soil texture (percent sand, silt, and clay) also did not vary significantly between nest and reference soils (Table 1), which corresponds with Carlson and Whitford's (1991) study. Despite significant publications and contributions in the past regarding the presence of ants that alter certain soil properties, no comparative data are available because a number of soil physical and chemical properties have not been measured in the *L. tridentata*–dominated shrublands in southwestern deserts.

A high percentage of bare soil cover and a low percentage of rock cover were observed on the surface of nest and reference soils throughout much of my study site (Table 2). Previous studies of *P. rugosus* in the *L. tridentata*–dominated shrublands did not report rock size and abundance, which are 2 major components of soil surface characteristics in this study. In New Mexico rock content may affect a variety of other soil attributes including infiltration, porosity, water-holding capacity, and erodibility (Carlson and Whitford 1991).

In this study significantly lower compaction and bulk density of nest soils, partially due to subterranean cavities and runways around the nest entrances, improved aeration and water infiltration without regard to geomorphic surfaces (Table 3). Dean and Yeaton's (1993) study in South Africa demonstrated that infiltrability of soils is influenced by many factors: organic matter, pore size, texture, and slope. Higher water infiltrability is expected on ant nests where soils contain significantly more organic matter and are less compacted than reference soils (Dean and Yeaton 1993).

Significantly lower surface-water runoff was detected in nest than surrounding reference soils because nest soils absorbed more water during and shortly after a measured cloudburst in this study (Table 3). Similarly, water disappeared significantly faster into the surface of nest soils than reference soils irrespective of geomorphic surface. Fluvial erosion was significantly greater for the slope than terrace site. A small movement of soil occurred when water traveled rapidly downslope during a cloudburst, perhaps due to a lack of abundant rocks on the soil surfaces. A minor fluvial erosion led to partial destruction of upper portions of vertical subterranean tunnels beneath nest entrances in this study. More surface-water runoff and fluvial erosion would be expected if this cloudburst had a much longer duration, higher frequency, and greater intensity.

The terrace site had significantly greater depth of water penetration compared to the slope site in this study (Table 3). With increased infiltration and reduced surface-water movement, deeper penetration of water into the soil occurs (Brotherson and Rushforth 1983). Viable ant nests appeared to have a protective influence on the soil in terms of significantly reducing surface-water runoff, enhancing water infiltrability, and increasing depth of water penetration, presumably due to multiple subterranean cavities and runways.

Although the total area covered by active *P. rugosus* colonies is relatively small, localized influences of subterranean *P. rugosus* on soil properties and on soil surface and moisture characteristics are evident. *Pogonomyrmex rugosus* significantly modifies a number of edaphic attributes including soil properties, water infiltration, water storage, and surface-water runoff in the *L. tridentata*–dominated shrubland in southern Nevada.

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