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Ant Mound Influence on Vegetation and Soils in a Semiarid Mountain Ecosystem

STAN R. CARLSON AND WALTER G. WHITFORD
Department of Biology, New Mexico State University, Las Cruces 88003

ABSTRACT.—We examined vegetation patterns and soil properties associated with western harvester (*Pogonomyrmex occidentalis*) mounds in a pinyon-juniper community and a ponderosa pine community near Los Alamos, New Mexico. Plant-clearing habits of the ants exerted a minor influence on total plant cover. Denuded zones (discs) around the mounds in the pinyon-juniper and ponderosa pine sites represented 1.2% and 1.0% of the total surface area and reduced plant cover 0.35% and 0.49%, respectively. Vegetation near the perimeter of the cleared discs had decreased species richness and lowered percent cover compared with adjacent reference areas (sampled 3.0 m from discs). Comparisons of plant species occurrences around the discs revealed that (1) most species, including dominant understory plants, were evenly dispersed in relation to nest discs; (2) two species—one in each site—were significantly associated with areas near discs; and (3) six species—four in the pinyon-juniper site and two in the ponderosa pine site—were significantly associated with reference areas. Analysis of vegetation on abandoned mounds suggested that seed predation by the ants influences patterns of plant species occurrence adjacent to nests.

Active mounds in the pinyon-juniper and ponderosa pine sites occurred at densities of 17/ha and 14/ha and had an average mass of 38 kg and 48 kg, respectively. Particle size analysis indicated that the ants construct mounds primarily of gravel and sand fractions. Mound soils at both sites had elevated concentrations of NO_3, P and K, increased conductivity and lower water content compared with disc and reference soils. Disc soils in both sites had lower organic matter content but were otherwise similar to reference soils. Activities of *P. occidentalis* cause localized accumulations of nutrients that are unavailable to plants until mound abandonment. Colony influences on vegetation patterns beyond the denuded discs and lingering effects of abandoned mounds contribute to plant community heterogeneity.

INTRODUCTION

Several studies have documented the role of mound-building ants in soil modification. For example, Baxter and Hole (1967) found that *Formica cinerea* mounds in a southwestern Wisconsin prairie occupied 1.7% of the surface area and had elevated clay contents, lower bulk density and increased concentrations of available P and K compared with nonnest soils. They attributed the observed differences to upward transport of subsoil, excavation of channels and chambers and deposition of organic materials in the mound. Lockaby and Adams (1985) reported that *Solenopsis invicta* excavated 1594 kg soil/ha in a northern Louisiana forest and that mounds had reduced bulk density, increased organic matter content and higher concentrations of P, K, Ca and Mg compared with adjacent undisturbed soils. Similarly, studies in other ecosystems (Salem and Hole, 1968; Wiken *et al.,* 1976; Mandel and Sorenson, 1982; Levan and Stone, 1983) have shown that, in general, ant activity impedes formation of soil horizons, alters soil texture, reduces soil bulk density and causes localized accumulations of organic and inorganic nutrients. Ants may also affect soil pH, moisture content and microorganism populations (Czerwinski *et al.,* 1971; Rogers and Lavigne, 1974; Briese, 1982; Beattie and Culver, 1983).

Some studies have linked ant activity to changes in vegetation patterns. King (1977a) reported that plant species occurrences on *Lasius flavus* mounds in southern England differed from associated nonmound areas. Culver and Beattie (1983) found distinct vegetation composition on *Formica canadensis* mounds compared with surrounding areas in a Colorado montane meadow. Other studies have reported changes in plant diversity (Beattie and Culver, 1977) and vegetation production (Rogers and Lavigne, 1974) associated with ant nests. Ants may alter vegetation by soil modification (Gentry and Stiritz, 1972), destruction of plants (Clark and Comanor, 1975), seed dispersal (Davidson and Morton, 1981) and/or seed predation (Hobbs, 1985).

Pogonomyrmex occidentalis (western harvester ant) occurs commonly in arid and semiarid plant associations throughout much of the western United States (Cole, 1932a, 1968) where it forages primarily on seeds (Cole, 1932a; Rogers, 1974). Nests of *P. occidentalis* consist, surficially, of large cone-shaped gravel mounds surrounded by conspicuous clearings (discs) from which the ants have removed the vegetation (Cole, 1932a, 1968; Lavigne and Rogers, 1974). We designed a study to assess the influence of *P. occidentalis* on vegetation patterns and soil properties in a semiarid mountain environment by comparing nest-associated areas with surrounding nonnest (reference) areas to address the following questions:

1. Do vegetation patterns around ant nests differ from areas away from nest sites?
2. Do various physical and chemical properties of nest soils differ from nonnest areas?
3. What are the spatial characteristics (*i.e.*, mound size, area denuded and dispersion patterns) of nests?
4. Do vegetation and soil responses and spatial patterns of the nests differ among the major vegetation communities—pinyon-juniper woodland and ponderosa pine forest—in the study area?

METHODS AND MATERIALS

Study area.—The study was conducted on Frijoles Mesa, Bandelier National Monument, Los Alamos County, New Mexico (35°48′N, 106°18′W). Foxx (1981) and Foxx and Tierney (1984) previously described the area. Soils on Frijoles Mesa are derived from volcanic tuff and range from sandy loam to sandy in texture. The mesa slopes gently from north to south (2200–1900 m) and is dominated by pinyon-juniper woodlands and ponderosa pine forests. The area has a semiarid continental mountain climate with cool winters and moderately warm summers. The average rainfall is 380 mm, 75% of which occurs in July and August. Two sites were selected for the study: a 2.1-ha site in a pinyon-juniper/blue grama grass (*Pinus edulis–Juniperus monosperma/Bouteloua gracilis*) association at an elevation of 2075 m and a 2.5 ha site in a ponderosa pine/mountain muhly (*Pinus ponderosa/Muhlenbergia montana*) association at an elevation of 2150 m. The study was conducted from June-August 1987.

Nest dimensions and spatial patterns.—Density of active nests at each site was determined by counting mounds and dividing by the total area of the site. Mound locations were mapped at each site by measuring the distance to grid markers placed at 10-m intervals. Spatial dispersion of active mounds was determined using Morisita's (1971) Index across sample unit areas of 100 m^2, 400 m^2, 900 m^2 and 1600 m^2. The significance of dispersion patterns was tested against an F distribution. The area cleared of vegetation around each mound (the nest disc) was determined by assuming a circular disc shape. The percent of area denuded at each site was calculated based on nest density. Mound volume was calculated from diameter and height measurements, assuming a conical mound shape. Mound weight was determined by multiplying average bulk density of mound material by mound volume. The relationship between mound volume and disc area was investigated by linear regression analysis. Abandoned mounds were also surveyed.

Vegetation influence.—Thirty active nests were selected at each site for the vegetation study. In addition to quantification of the denuded areas vegetation around the perimeter of the cleared discs was compared with surrounding (reference) areas. Plant species abundance (number of individuals) and percent cover estimates were obtained in each of three 25-cm by 100-cm quadrats (0.25 m^2) at each of the thirty nests: one immediately adjacent to the disc (edge), another 0.5 m from the disc (a moderate distance away) and the third 3.0 m beyond the disc (reference area). Quadrat placement was in a random direction from each mound. Means of plant species-richness (number of species/quadrat), total abundance (number of plants/quadrat), and total percent cover were compared by protected least-significant-difference (lsd) tests for randomized complete block designs. Cover data were rank-transformed before the analysis to achieve residual normality. Species abundance and cover data were also compared by protected lsd tests on rank-transformed data.

An assessment of vegetation on eight abandoned mounds was also made. Five of these were located within the pinyon-juniper site and the other three were located nearby (within the pinyon-juniper association). The ponderosa pine site had only one abandoned mound and therefore was not included in this part of the study. Vegetation associated with the unoccupied mounds was compared with reference areas as follows. Species abundance and cover data were obtained in 0.25 m^2 quadrats placed directly over the mound, adjacent to the mound (within the old disc), and 3.0 m beyond the mound, in a randomly selected direction. The data were analyzed as described previously for the active nests.

Soil influence.—Fifteen active nests were selected at each site for the soil study. Soils were sampled to a depth of 15 cm with a 5-cm-diameter stainless steel hand-corer. Mound, disc and reference soils were sampled in a randomly selected direction from each mound. Mounds were cored perpendicular to the surface approximately halfway between the base and apex. Any ants collected inadvertently in these soils were rapidly removed in order not to bias the chemical analyses. Disc samples were obtained 30 cm from the base of the mound (approximately midway between the disc edge and the mound). Reference soils were sampled 3.0 m beyond the disc edge. Two adjacent sets of soil cores were obtained—one for physical analyses and one for chemical analyses. Samples for physical analyses were immediately placed in tared plastic soil bags, sealed, then carried to the Los Alamos Environmental Science Group Soils Laboratory where they were weighed and oven-dried at 105 C. The soils were then analyzed for water content by the gravimetric method (Gardner, 1986) and gravel (<75–2.0 mm) and sand (<2.0–0.05 mm) fractions using a Ro-Tap testing sieve shaker. Silt and clay fractions were determined by laser analysis at the New Mexico State University Soil, Plant and Water Testing Laboratory. Soils for chemical analyses were air-dried, sealed and transported to the NMSU Laboratory where six soil properties were measured: pH (saturated paste procedure), conductivity (saturated extract), organic matter content (Walkley-Black method), extractable nitrate (1:5 H_2O, Cd reduction), extractable phosphorous (Olsen method) and extractable potassium (1:5 H_2O, flame emission). Means of the soil variables were compared by protected lsd tests for randomized complete block designs.

RESULTS

Nest dimensions and spatial patterns.—Active mounds were uniformly dispersed within both sites, a trend that was slightly more pronounced in the pinyon-juniper community (Table 1). The ponderosa pine site had two mounds within 10 m of each other and a slightly contagious pattern in one area. In general, the ponderosa pine site had fewer and larger active nests than the pinyon-juniper site (Table 1). However, the total mass of mounds (about 650 kg) and the total denuded (disc) area (about 1%) were similar at the two sites (Table 1).

TABLE 1.—Spatial patterns and nest dimensions of active ant colonies in the pinyon-juniper and ponderosa pine study sites. Numbers in parentheses are SE. Dispersion probabilities (F-test): ** = 0.01, * = 0.05

	Study site	
Characteristic	Pinyon-juniper	Ponderosa pine
Dispersion	Even**	Even*
Density (nests·ha^{-1})	17	14
Mound vol. (mean L)	32 (4.0)	61 (7.0)
(L·ha^{-1})	543	826
Mound mass (mean kg)	38 (4.8)	48 (5.5)
(kg·ha^{-1})	651	652
Disc area (mean ms^2)	6.9 (0.6)	7.6 (0.7)
(m^2·ha^{-1})	118	103
(%)	1.18	1.03

Abandoned nests occurred at low densities in both study sites. There were five abandoned mounds (2–3/ha) in the pinyon-juniper site and only one abandoned mound on the 2.5 ha ponderosa pine site.

Mound size explained 69% and 68% of the variation in disc area, respectively, at the pinyon-juniper and ponderosa pine sites (Fig. 1).

Vegetation influence.—At both sites plant species richness of the disc perimeter was lower, on average, than reference areas (Table 2). Plant cover was also lower near the disc edge in both sites but significantly so ($P < 0.05$) only in the pinyon-juniper site. Quadrats located 0.5 m beyond the discs had intermediate richness and cover values. Plant abundance did not vary significantly in relation to nest discs at either site (Table 2).

Plots of cumulative numbers of species against number of quadrats sampled (Fig. 2) also show that species richness decreased near the perimeter of discs and give a more complete picture of species occurrences in relation to the nests. Of the 21 plant species encountered in the pinyon-juniper site, 13 occurred in edge quadrats, 15 occurred in the 0.5 m quadrats, and 20 occurred in reference quadrats. Of the 30 plant species encountered in the ponderosa pine site, 18 occurred in edge quadrats, 22 occurred in the 0.5 m quadrats, and 29 occurred in reference quadrats. The cumulative species graphs also gauge the completeness of the floral census. In the pinyon-juniper site, curves of edge and 0.5 m quadrats appear asymptotic at a sample size of around 15 (Fig. 2). This indicates that these areas were completely censused. However, the reference quadrat (3.0 m) curves do not level off. In the ponderosa pine site the edge and 0.5 m quadrats level off slightly while the reference quadrats do not level off (Fig. 2). At both sites, therefore, the floral census of reference areas was apparently incomplete. To help alleviate this problem and minimize the effect of "rare" plants, only species that occurred in more than three quadrats were statistically compared. This left a total of 14 species in the pinyon-juniper site and 16 species in the ponderosa pine site. Of the 7 remaining (rare) species in the pinyon-juniper site, 5 occurred exclusively in reference areas, one occurred in both 0.5 m quadrats and reference quadrats and one occurred in all three sample areas. Of the 14 rare species in the ponderosa pine site, 6 occurred exclusively in reference areas, 4 occurred in 0.5 m quadrats and reference quadrats, one occurred in 0.5 m quadrats only and 3 occurred in all three sample locations.

Means of both species abundance and percent cover data gave similar results (Table 3). At both sites some species were unequally dispersed in relation to nest discs. In the pinyon-

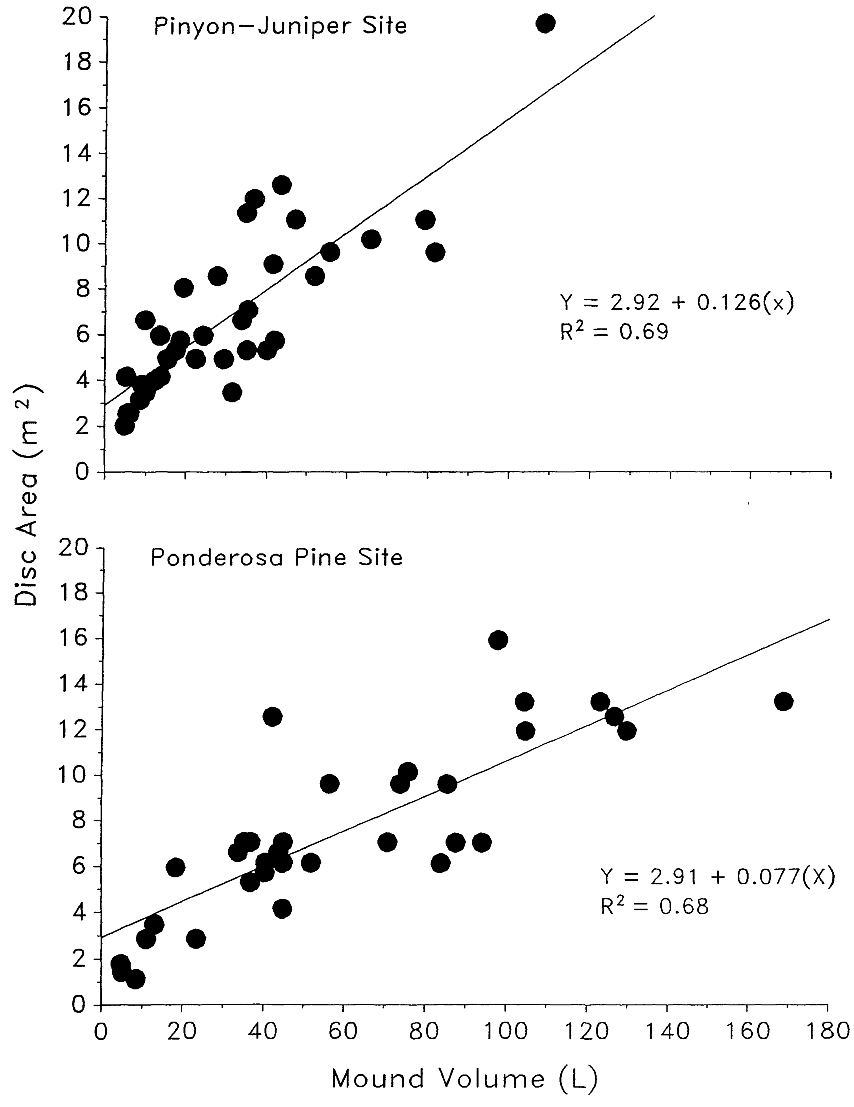

FIG. 1.—Relationship between mound volume and area denuded by ants in the two study sites

juniper site *Opuntia polyacantha* characterized areas near the perimeter of discs while *Epilobium ciliatum, Erigeron philadelphicus, Gutierrezia sarothrae* and *Lotus wrightii* characterized reference areas. In the ponderosa pine site *Andropogon gerardii* characterized areas 0.5 m beyond the disc edge while *Chrysopsis villosa* and *Vicia americana* characterized reference areas. A few species were weakly associated with nest or nonnest areas, based on an observed significance level of $P < 0.1$ (*see* Table 3). Most species, including most of the dominant understory plants, were not significantly associated with one of the three sample locations and thus appeared evenly dispersed in relation to ant nests.

Abandoned mounds and remnant discs in the pinyon-juniper site had lower mean species

TABLE 2.—Species richness, total abundance and percent cover of vegetation sampled in 0.25 m^2 quadrats at various distances from nest discs in the two study sites (means, $n = 30$). Values with the same letter (read horizontally) are not significantly different at the $P = 0.05$ level. Numbers in parentheses are SE. Cover data were rank transformed before the analyses

	Distance from disc		
Property	Edge	0.5 m	3.0 m
Pinyon-juniper site			
Richness	3.4 (0.22)^{a}	3.9 (0.23)^{ab}	4.3 (0.19)^{b}
Abundance	15.3 (1.2)^{a}	15.4 (1.3)^{a}	16.8 (1.5)^{a}
Cover (%)	22.8 (3.7)^{a}	23.8 (3.7)^{a}	29.3 (3.6)^{b}
Ponderosa pine site			
Richness	3.2 (0.26)^{a}	3.9 (0.25)^{b}	4.2 (0.20)^{b}
Abundance	11.6 (1.5)^{a}	12.7 (1.3)^{a}	13.8 (1.9)^{a}
Cover (%)	40.5 (2.9)^{a}	45.3 (3.3)^{a}	47.2 (4.0)^{a}

richness and lower mean percent cover than adjacent reference areas (Table 4). Number of species encountered was also higher in reference quadrats compared to disc or mound quadrats (14 versus 9 and 8, respectively). However, plant abundance did not vary in relation to the unoccupied mounds (Table 4). *Blepharoneuron tricholepsis, Bouteloua gracilis* and *Gutierrezia sarothrae* were significantly associated with reference areas (Table 5). The remaining species were evenly dispersed relative to abandoned mounds.

Soil influence.—Mound soils in both sites had significantly higher concentrations of NO_3, P and K and higher conductivity than disc or reference soils (Table 6). Soil pH values varied among the three sample locations but were all slightly acidic and ranged from 6.1 to 6.8. In the pinyon-juniper site, organic matter content was highest in mound soils, followed by reference, then disc soils (Table 6). In the ponderosa pine site, organic matter content was higher in reference soils than either mound or disc soils (Table 6). At both sites mound soils were drier than nonmound soils. Disc soils in the ponderosa pine site had significantly higher water content than reference soils (and mound soils). Bulk density of soils did not vary among the sample locations at either site. At both sites mounds had higher gravel content than nonmound soils. Soil of mounds in the pinyon-juniper site had significantly higher sand content and lower silt and clay contents than disc or reference soils, although all soils were classified as loamy sands. Soil textures did not vary significantly among mound, disc and reference soils in the ponderosa pine site and were also loamy sands.

DISCUSSION

Nest dimensions and spatial patterns.—Spatial dispersion analysis showed that mounds were significant uniformly (evenly) dispersed in both study sites. In general nests were more widely spaced in the ponderosa pine community, as evidenced by the lower density of mounds (14/ha) compared to the pinyon-juniper community (17/ha). Several investigators (*e.g.*, Bernstein, 1975; Holldobbler, 1976) have suggested that uniform dispersion of nests indicates intercolony defense and territoriality. Clark and Comanor (1973) noted aggressive interactions between two *Pogonomyrmex occidentalis* colonies separated by 7 m that resulted in several dead ants. Intraspecific and interspecific aggression commonly occurs among colonies of seed-harvesting ants in more arid regions and appears to play an important role in spatial dispersion characteristics of nests (Buckley, 1982).

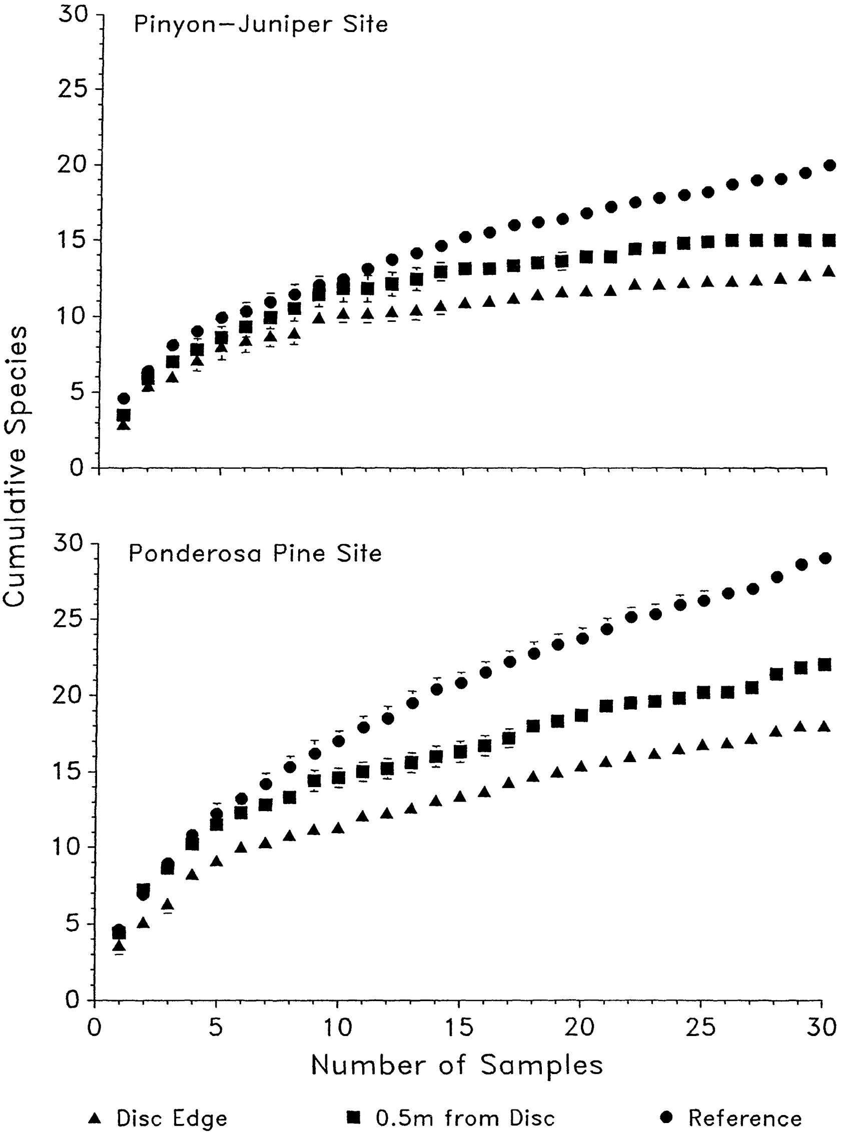

FIG. 2.—Cumulative plant species curves for quadrats sampled at the disc edge, 0.5 m beyond discs and 3.0 m beyond discs (reference areas) in the two study sites. Each curve was generated from 10 random sequences of 30 replicate quadrats. Vertical bars are SE

At both sites nests occupied approximately the same total surface area (1%, including the area denuded), although the ponderosa pine site had fewer larger mounds and discs than the pinyon-juniper site. Studies in other ecosystems have reported a range of size and numbers of *Pogonomyrmex occidentalis* nests. For example, Rogers and Lavigne (1974) found that mound densities in a shortgrass prairie varied from 31/ha on a moderately grazed site to

TABLE 3.—Mean abundance and percent cover of plant species sampled at various distances from nest discs in the two study sites (n = 30). Only species found in 4 or more quadrats are listed. Species marked with a * were significantly unevenly dispersed in relation to nests. Means with the same letter (for each type of data, read horizontally) are not significantly different at the P = 0.05 level. The fifth and ninth columns give observed significance levels for the analysis of variance. Data were rank transformed before the analyses

	Abundance				Cover			
Species	Edge	+0.5 m	+3.0 m	OSL	Edge	+0.5 m	+3.0 m	OSL
Pinyon-juniper site								
Artemisia dracunculus	0	0.23	0.23	<0.1	0	0.43	0.73	<0.1
Blepharoneuron tricholepis	0.33	0.27	0.47	>0.1	1.57	0.55	0.53	>0.1
Bouteloua gracilis	6.17	5.37	5.60	>0.1	6.12	4.68	5.57	>0.1
Cosmos parviflorus	0.67	0.53	0.33	>0.1	0.90	0.70	0.67	>0.1
*Epilobium ciliatum**	0.07^{a}	0.43^{ab}	0.90^{b}	<0.05	0.03^{a}	0.18^{ab}	0.60^{b}	<0.05
*Erigeron philadelphicus**	0^{a}	0.07^{a}	0.53^{b}	<0.05	0^{a}	0.03^{ab}	0.22^{b}	<0.05
*Gutierrezia sarothrae**	0.67^{a}	1.20^{b}	1.30^{b}	<0.05	2.37^{a}	4.97^{b}	3.80^{b}	<0.05
Hymenopappus filifolius	0.27	0	0.07	>0.1	0.30	0	0.07	>0.1
Juniperus monosperma	0.07	0.07	0.10	>0.1	2.67	3.17	3.83	>0.1
Linum neomexicana	0.13	0.13	0	>0.1	0.02	0.05	0	>0.1
*Lotus wrightii**	0.33^{a}	0.37^{a}	0.93^{b}	<0.05	0.79^{a}	0.67^{a}	3.25^{b}	<0.01
Lupinus kingii	5.23	6.03	5.73	>0.1	2.83	3.44	3.20	>0.1
*Opuntia polyacantha**	0.77^{a}	0.37^{ab}	0.07^{b}	<0.05	2.22^{a}	0.88^{b}	0.10^{b}	<0.01
Pinus edulis	0.07	0.13	0.23	>0.1	2.83	3.67	5.87	>0.1
Ponderosa pine site								
*Andropogon gerardii**	0.43^{a}	1.00^{b}	0.40^{a}	<0.05	3.87^{a}	8.77^{b}	3.60^{a}	<0.05
Bouteloua gracilis	0.10	0.13	0.17	>0.1	0.40	0.17	0.53	>0.1
Bromus anomalus	0.23	0.27	0.10	>0.1	0.27	0.27	0.23	>0.1
Bromus tectorum	2.53	2.20	2.53	>0.1	1.45	1.10	1.07	>0.1
*Chrysopsis villosa**	0^{a}	0.07^{a}	0.17^{b}	<0.05	0^{a}	0.07^{a}	0.60^{b}	<0.05
Cirsium undulatum	0.10	0	0.10	>0.1	0.30	0	0.60	>0.1
Erysimum capitatum	0.10	0.10	0.13	>0.1	0.20	0.17	0.20	>0.1
Gaura coccinea	0.03	0.17	0.03	>0.1	0.03	0.23	0.03	>0.1
Koeleria cristata	0.07	0.30	0.23	>0.1	0.27	0.87	0.83	>0.1
Muhlenbergia montana	2.0	2.0	2.13	>0.1	13.6	12.7	12.1	>0.1
Sitanion hystrix	2.57	1.83	2.03	>0.1	6.37	3.97	4.97	>0.1
Taraxacum officinale	0.30	0.10	0.03	<0.1	0.33	0.20	0.03	<0.1
Tragopogon pratensis	0.37	0.30	0.30	>0.1	0.90	0.63	0.70	>0.1
Verbascum thapsus	1.17	1.6	1.37	<0.1	9.17	11.5	8.20	>0.1
*Vicia americana**	1.00^{a}	1.27^{a}	2.10^{b}	<0.05	1.57^{a}	1.80^{a}	2.87^{b}	<0.05
Viguiera multiflora	0.33	0.73	0.93	<0.1	1.13	1.57	1.87	<0.1

3/ha on a heavily grazed site. The nests they studied were much smaller than those reported here and averaged only 2.8 kg mound mass, 0.4–1.2 m^2 disc area, and ranged from 0.3% (ungrazed site) to 0.02% (heavily grazed site) of total surface area denuded. Mandel and Sorenson (1982) found mound densities in a southern Colorado grass-shrub community of 40/ha on 2% of the land area with an average mound volume of 32 L and an average disc area of 4.5 m^2. Variation in size, number and distributional patterns of nests among communities or habitats appears largely dependent upon the quantity and quality of seeds, the

TABLE 4.—Species richness, abundance and percent cover of vegetation sampled in 0.25 m^2 quadrats on abandoned mounds, remnant discs and reference areas (3.0 m away from old mounds) in the pinyon-juniper study site (means, n = 8). Values with the same letter (read horizontally) are not significantly different at the P = 0.05 level. Numbers in parentheses are SE. Cover data were rank transformed before the analysis. The fourth row gives cumulative numbers of species encountered

Property	Mound	Disc	Reference
Richness	2.8 (0.41)^a	2.3 (0.49)^a	4.5 (0.50)^b
Abundance	11.0 (1.8)^a	13.6 (4.0)^a	13.6 (1.5)^a
Cover (%)	10.5 (2.7)^a	9.5 (2.4)^a	15.5 (2.3)^b
Total species	8	9	14

ants' primary nutritional source (Cole, 1932b; Costello, 1944; Sharp and Barr, 1960; Melendez, 1963).

Vegetation influence.—Mound size may reflect the age or number of ants in the colony (Cole, 1932a; Lavigne, 1969; King, 1977b). Therefore, the significant correlation between mound volume and disc area suggests that colony age or size may be an important factor in determining the amount of vegetation cleared by the ants. Cole (1932a) and Melendez (1963) reported a proportional relationship between the size of *Pogonomyrmex occidentalis* colonies and area denuded but did not discuss how they obtained the data.

Quantification of the area denuded around the mounds, although a useful measurement, may be of limited value in understanding the details of plant-clearing by the ants. Alternatively, total reductions in plant cover attributable to the ant activity can be estimated as the difference between the average percent cover of reference areas and the product of this value and the proportion of area not denuded by ants. This computation does not account for cover changes around the perimeter of discs, which, in the present study, were too small to affect the calculation. Estimated cover reductions of 0.35% in the pinyon-juniper site and 0.49% in the ponderosa pine site indicate that the plant-clearing habits of the ants exerted only a minor influence on plant cover. Effects were slightly more pronounced in the ponderosa pine site due to the higher average percent cover of reference areas.

Comparisons of plant species occurrences around the denuded discs revealed four response patterns of the flora: (1) most plant species, including the dominant understory species, were evenly dispersed in relation to nests; (2) two species, one in each site, characterized areas near the cleared discs; (3) six species, four in the pinyon-juniper site and two in the ponderosa pine site, characterized reference areas; and (4) infrequently encountered ("rare") species were usually found in reference areas. The first three patterns correspond to Malozemovas' (1970) three categories: indifferent, gravitating and avoiding plants. Presumably, favorable interactions occur between ants and gravitating plants. Conversely, unfavorable interactions occur between ants and avoiding species. Indifferent species are apparently unaffected by ant activity. The occurrence of more rare species in reference areas suggests that ant activities lead to localized patches (adjacent to discs) of increased species homogeneity.

Rogers and Lavigne (1974) reported a ring of increased grass production adjacent to *Pogonomyrmex occidentalis* discs in a shortgrass plain in northeastern Colorado. Similarly, Wight and Nichols (1966), who worked with a closely related species *Pogonomyrmex owyheei* in a Wyoming saltbush community, found an increase in shrub biomass around the denuded zones. Both of these studies reported visible as well as quantitative increases in plant productivity. In contrast, plant cover estimates indicated a trend of decreased plant growth adjacent to discs in the pinyon-juniper and ponderosa pine sites. Although data collection

TABLE 5.—Mean abundance and percent cover of plant species sampled on abandoned mounds, remnant discs and reference areas (3.0 m away from mounds) in the pinyon-juniper study site (n = 8). Only species found in two or more quadrats are listed. Species marked with a * were significantly unevenly dispersed in relation to mounds. Means with the same letter (for each type of data, read horizontally) are not significantly different at the P = 0.05 level. The fifth and ninth columns give observed significance levels for the analysis of variance. Data were rank transformed before the analyses

	Abundance				Cover			
Species	Mound	Disc	Ref.	OSL	Mound	Disc	Ref.	OSL
Artemisia dracunculus	0.25	0.50	0.13	>0.1	0.38	0.50	0.63	>0.1
*Blepharoneuron tricholepis**	0^{a}	0^{a}	0.50^{b}	<0.05	0^{a}	0^{a}	0.75^{b}	<0.05
*Bouteloua gracilis**	0^{a}	0^{a}	3.38^{b}	<0.01	0^{a}	0^{a}	3.18^{b}	<0.01
Cosmos parviflorus	0.25	0.50	0.63	>0.1	0.75	0.88	0.50	>0.1
Cryptantha jamesii	0.38	0	0	>0.1	0.75	0	0	>0.1
Erigeron philadelphicus	0.25	0.13	1.50	>0.1	0.25	0.01	0.44	>0.1
*Gutierrezia sarothrae**	0^{a}	0.38^{a}	0.75^{b}	<0.05	0^{a}	0.25^{a}	2.13^{b}	<0.05
Koeleria cristata	0	0.25	0.38	>0.1	0	0.13	0.75	>0.1
Linum neomexicana	1.25	0.75	0.25	>0.1	0.20	0.19	0.01	>0.1
Lotus wrightii	2.00	0.38	0.38	>0.1	3.19	0.26	1.13	>0.1
Lupinus kingii	6.38	10.6	3.63	>0.1	4.56	7.13	2.94	>0.1
Opuntia polyacantha	0.50	0	0.75	>0.1	0.75	0	1.13	>0.1

occurred within a short time, we observed no increased plant growth adjacent to discs from July–August 1987.

Of the possible explanations for the vegetation changes around the cleared discs it seems unlikely that the ants have selectively removed plants. The boundary at the disc edge is very abrupt and the ants appear to clear vegetation nonselectively within the disc (Clark and Comanor, 1975). Wight and Nichols (1966) and Rogers and Lavigne (1974) suggested that increased moisture content of disc soils caused the higher vegetative productivity that they observed around the denuded zones. However, disc soils in the ponderosa pine site had increased water content but decreased vegetation cover around the disc perimeter. Soil moisture may have been a limiting factor in their study sites but not in our ponderosa pine or pinyon-juniper sites, thus explaining the incongruous results. Gentry and Stiritz (1972) attributed increased vegetative growth around *Pogonomyrmex badius* mounds to nutrient enrichment of the mounds. However, this species does not clear vegetation around the mounds and the zone of influence was only within a few centimeters of the mounds. The possibility of detrimental soil effects around or within discs, such as elevated concentrations of toxic heavy metals, has not been investigated.

Whitford (1978) suggested that granivory by *Pogonomyrmex* spp., while it does not significantly reduce the seed production of most species, may affect relative abundances of plant species. Hobbs (1985) presented a convincing case for effects of granivory on plant composition by the harvester ant *Veromessor andrei.* He found increases in plant species with preferred seeds inside exclosures placed adjacent to colonies. He also suggested that inadvertent dispersal of seeds may affect vegetation patterns around the nest. Rissing (1986) also discussed the possibility of dispersal of preferred seeds (nonelaiosome) by harvester ants *Veromessor pergandei* and *Pogonomyrmex rugosus.* He reported increased density and reproductive output of preferred species in refuse piles around the nests. This explanation may not be plausible for *Pogonomyrmex occidentalis* because refuse piles are usually located

TABLE 6.—Chemical and physical properties of mound, disc, and reference soils in the two study sites (means, n = 15). Values with the same letter (read horizontally) are not significantly different at the P = 0.05 level. Numbers in parentheses are SE

Property	Mound	Disc	Reference
Pinyon-juniper site			
pH	6.4 (0.08)^a	6.1 (0.07)^b	6.2 (0.06)^{ab}
Conductivity	0.61 (0.06)^a	0.27 (0.02)^b	0.22 (0.02)^b
% organic matter	1.9 (0.16)^a	0.7 (0.07)^b	1.2 (0.12)^c
NO_3 (ppm)	6.6 (0.81)^a	2.6 (0.11)^b	3.2 (0.19)^b
P (ppm)	19.3 (3.3)^a	2.6 (0.46)^b	1.5 (0.15)^b
K (ppm)	40.3 (4.7)^a	5.4 (1.2)^b	6.3 (1.5)^b
H_2O (%)	2.0 (0.10)^a	7.9 (0.25)^b	7.6 (0.20)^b
Bulk density	1.20 (0.02)^a	1.21 (0.01)^a	1.19 (0.02)^a
Gravel (%)	22.4 (3.4)^a	4.1 (0.63)^b	3.1 (0.30)^b
Sand (%)	82.0 (0.70)^a	74.2 (1.3)^b	74.0 (1.2)^b
Silt (%)	16.2 (0.61)^a	23.3 (1.2)^b	22.8 (1.1)^b
Clay (%)	1.2 (0.06)^a	2.3 (0.14)^b	2.7 (0.10)^c
Ponderosa pine site			
pH	6.4 (0.11)^a	6.5 (0.07)^a	6.8 (0.08)^b
Conductivity	0.77 (0.13)^a	0.42 (0.08)^b	0.29 (0.02)^b
% organic matter	2.4 (0.21)^a	2.4 (0.19)^a	3.5 (0.34)^b
NO_3 (ppm)	24.4 (5.7)^a	13.0 (3.2)^b	5.0 (0.38)^b
P (ppm)	25.4 (6.4)^a	4.9 (1.3)^b	5.2 (1.2)^b
K (ppm)	33.0 (4.3)^a	11.6 (1.6)^b	13.5 (2.6)^b
H_2O (%)	4.8 (0.52)^a	25.0 (1.4)^b	20.6 (0.63)^c
Bulk density	0.81 (0.04)^a	0.80 (0.02)^a	0.76 (0.02)^a
Gravel (%)	47.5 (3.1)^a	27.5 (1.6)^b	28.5 (1.9)^b
Sand (%)	83.5 (1.0)^a	85.1 (0.79)^a	83.2 (0.89)^a
Silt (%)	14.2 (0.86)^a	12.8 (0.73)^a	14.5 (0.79)^a
Clay (%)	1.1 (0.07)^a	1.0 (0.06)^a	1.2 (0.11)^a

within the denuded discs (Lavigne, 1969; S. R. Carlson, pers. observ.). However, inadvertent seed dispersal around the perimeter of discs is possible.

If granivory influences vegetation patterns around the colonies, decreased densities of some (seed-harvested) annual or biennial plants should occur near the ant colony, given that foraging activity decreases with distance from the nest and that the ants have removed enough seeds to affect relative species abundances. Also, a flush of growth of these species may occur on abandoned mounds from viable seed stores in the shallow granaries (essentially a primitive form of dispersal). In the pinyon-juniper site, two species, *Erigeron philadelphicus* (a biennial) and *Lotus wrightii* (an annual), that occurred at low densities near active colonies also occurred at high densities on abandoned mounds. Therefore, we suggest that granivory plays a role in patterns of species occurrences around the colonies, although other factors may be operating.

Soil influence.—The ants excavated a considerable amount of soil (approximately 650 kg/ha) at each site. The ponderosa pine site had fewer mounds of greater volume but lower bulk density than the pinyon-juniper site. Rogers and Lavigne (1974) reported a maximum of only 87 kg/ha of soil excavated by *Pogonomyrmex occidentalis* in a semiarid shortgrass prairie. Petal (1978) estimated the rate of soil excavation and found that *P. occidentalis* moved from 80–280 kg/ha in one growing season in a Colorado pasture. Briese (1982) reported that the ant community turns over 350–420 kg soil/ha/yr in a semiarid shrub steppe in Australia. Whitford *et al.* (1986) reported that ants in a semiarid area in eastern New Mexico seasonally moved to the surface an average 840 kg/ha of soil, a rate comparable to that in more mesic regions.

The high nutrient content of mounds suggests that *Pogonomyrmex occidentalis* deposits and incorporates organic materials and metabolic wastes in the nest. This is supported by observations of plant fragments, debris and humified material in mound soils. High soluble NO_3 content of mounds suggests deposition of excreta by the ants followed by rapid mineralization. These findings are similar to those of Rogers and Lavigne (1974) and Mandel and Sorenson (1982) who also reported nutrient enrichment of mounds and evidence of organic matter deposition. Briese (1982), who worked with the harvester ants *Chelaner* spp. and *Pheidole* spp. in a semiarid shrub steppe in Australia, also suggested that nutrient enrichment of nests was due to the presence of waste plant material and, to a lesser extent, metabolic wastes of the ants. Nutrient enrichment of mounds also occurs in more mesic regions (reviewed by Buckley, 1982; Culver and Beattie, 1983) and thus appears ubiquitous among mound-building ants.

Comparisons of the soil analyses revealed that the nutrient status of reference soils varied between the two study sites, with higher organic matter content and higher concentrations of extractable NO_3, P and K in the ponderosa pine site. The relative nutrient enrichment of mounds also differed between the two sites. Nutrient increases of mound soils compared to reference soils in the pinyon-juniper site were 1.6 times for organic matter content, 2.1 times for nitrate concentration, 12.9 times for phosphorous concentration and 6.4 times for potassium concentration. In the ponderosa pine site organic matter content of mounds was 0.7 that of reference soils but nutrient content increased 4.9 times for nitrate concentration, 4.9 times for phosphorous concentration and 2.4 times for potassium concentration. Although the nutrient status of mounds was higher in the ponderosa pine site, relative nutrient enrichment of mounds was generally greater in the pinyon-juniper site.

Some studies in areas with acidic soils (Czerwinski *et al.*, 1971; Wiken *et al.*, 1976; Levan and Stone, 1983) have reported that ants increase mound pH, presumably due to accumulation and retention of basic materials by the ants. However, most studies (*e.g.*, Baxter and Hole, 1967; Culver and Beattie, 1983; Lockaby and Adams, 1985) reported no effects of ant activity on pH in either slightly acidic or near-neutral soils. Mandel and Sorenson (1982) found no pH differences for *Pogonomyrmex occidentalis* mounds that occurred in alkaline soils. Mound pH reported here was the same at both sites (6.4) but lower than reference soils in the ponderosa pine site and not significantly different than reference soils in the pinyon-juniper site. In all cases, however, soils were only slightly acidic (pH 6.1 to 6.8), an expected result in sandy soils where base leaching should occur.

Results of particle size analyses of mounds indicate that ants preferentially transport particles in the order gravel > sand > silt > clay. Studies in other ecosystems (Rogers and Lavigne, 1974; Mandel and Sorenson, 1982) did not report gravel content, a major component of mounds in the two study sites reported here. Materials used to construct mounds serve several functions. At higher elevations large gravel mounds should be advantageous because they heat up quickly, due to the lower thermal capacity of coarse fragments, and provide insulation (Ettershank, 1971). Gravel content also affects a variety of other soil characteristics, including infiltration, porosity, water holding capacity and erodability.

The low water content of mounds may be due, in part, to the presence of crusts observed on the mound surfaces that shed rain during the brief thundershowers common in the study area. Mandel and Sorenson (1982) described the crusts as a mulch of plant fragments and sand-sized grains. We also observed that ants made numerous openings on mounds after heavy rains, perhaps to aerate and thus dry the mounds quickly.

One surprising result was that bulk densities of mounds were not lower than disc or reference soils at either site. This contrasts with Rogers and Lavigne (1974) who reported lower bulk densities of *Pogonomyrmex occidentalis* mounds in northeastern Colorado. A possible explanation for this is that particle densities of materials used by the ants to construct the mounds were higher than particle densities of reference soils. This would offset channeling and mixing activities that generally reduce bulk density of mounds.

Environmental role.—Localized influences of *Pogonomyrmex occidentalis* on vegetation patterns and soil properties represent a source of spatial heterogeneity within the semiarid mountain ecosystem. Although ant activities enhance soil nutrient status, plant-clearing habits of the ants prevent exploitation of nest sites by vegetation until mound abandonment, which appears to be rare. *Pogonomyrmex occidentalis* also influences floristic patterns beyond the denuded areas as evidenced by decreased species richness, reduced cover and altered composition of vegetation adjacent to discs.

Total area affected by *Pogonomyrmex occidentalis* colonies is obviously not great. Plant-clearing, for example, exerts only a minor influence on the total cover of understory vegetation. Abandoned mounds may have a lingering impact on pedologic processes and vegetation patterns, but occur only at low densities in the study area. However, patterns of colony abandonment and re-establishment may affect a large percentage of the area over time and therefore influence patterns of soil development and community succession.

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