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Prevalence of *Oryzopsis hymenoides* near harvester ant mounds: indirect facilitation by ants

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The distribution of plants in relation to harvester ant mounds was investigated at two study areas to examine associations between ants and plants in semiarid, sagebrush steppe vegetation. The bunchgrass *Oryzopsis hymenoides* usually was the closest plant to the center of *Pogonomyrmex owyheei* ant mounds and often was the only plant found within the disk-shaped areas around mounds that is cleared of vegetation by the ants. Although absolute numbers of *O. hymenoides* seeds were greatest on mounds, proportions of its seeds in the total seedbank were not significantly different among the mound, cleared disk, and the native plant community. Mean size and density of *O. hymenoides* plants near mounds were significantly greater than those of plants 15–20 m from mounds at an undisturbed study area. At the other study area, which three years before the study was burned, mean density and size of *O. hymenoides* plants were not significantly different among plots located at 0, 1, 2, 3, 7, 15, and 20 m from the center of ant mounds.

These measurements of the seedbank and plant density and size were used to differentiate among four mechanisms by which ants may influence plant distribution. The prevalence of *O. hymenoides* near ant mounds was most likely an indirect effect of reduced plant competition caused by the severe defoliation of potential competitors by the ants. A second indirect mechanism, the abundance of *O. hymenoides* near mounds resulted from reduced insect herbivory on *O. hymenoides* because of ant predation on the herbivores, was specious. Two other mechanisms, a direct effect of seed harvesting activity by ants or an indirect effect of microsite modification were at best of minor importance.

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Introduction

Ants are a relatively inconspicuous component of ecosystems, but they can play a significant role in the distribution of plant species. For example, density and diversity of annuals in the Sonoran Desert (Inouye et al. 1980, Davidson et al. 1984) and the distributions of plants in central Australia (Davidson and Morton 1981) and in sand dunes along the shore of Lake Michigan (Beattie and Culver 1977) were influenced by ants. In the semiarid Intermountain Region of the western United States, the harvester ant genus *Pogonomyrmex*

(Hymenoptera: Formicidae) is widespread in sagebrush steppe vegetation (Cole 1968). Harvester ants can have a severe impact on plant communities because they clear vegetation from a disk-shaped area around their nests. The denuded disk areas around mounds may have diameters up to 13 m and the total area cleared by harvester ants can be a significant portion of the landscape (see Sharp and Barr 1960, Willard and Crowell 1965). Despite the potential of harvester ants to modify vegetation, effects of harvester ants on the distribution of plants in the Intermountain West are unclear.

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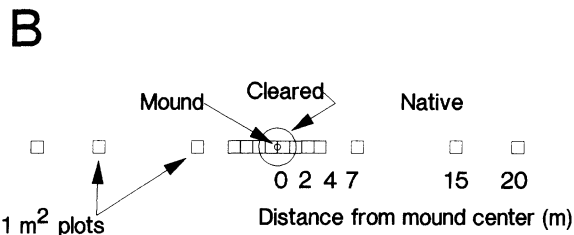
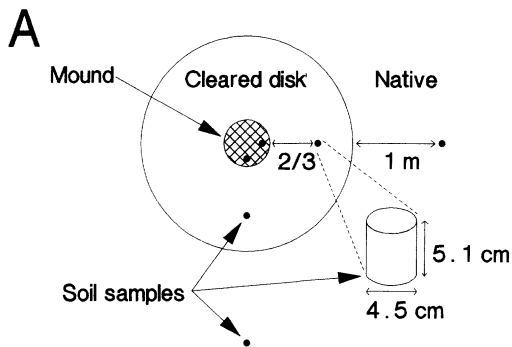


Fig. 1. Location of: A) intact soil cores collected near ant mounds for the seedbank studies at the Burn study area; B) 1 m² plots along the transect through the center of an ant mound that were used for plant density and size measurements at both the Burn and EBR study areas.

Four mechanisms can account for the influence of ants on plant distribution:

- 1) *The dispersal of plant propagules* by ants is one way ants may affect plant distribution (Hobbs 1985). This dispersal may occur because of myrmecochory or because of accidental loss of seed during foraging or nest cleaning activities. Ants show clear preferences for seeds of certain species (Inouye et al. 1980, Mehlhop and Scott 1983, Carroll and Risch 1984, Davidson et al. 1984), and they quickly and efficiently locate and remove seeds from their foraging area (Bond and Slingsby 1984, Carroll and Risch 1984). *P. occidentalis* (Cresson) and *P. owyheeii* (Cole), the 2 dominant ant species in sagebrush steppe vegetation, have seed preferences (Willard and Crowell 1965, Lavigne 1969), which could differentially affect the distribution of plants.
- 2) Ants may also affect plant distribution through *modification of soil characteristics*. Seeds, detritus, and other organic materials that are collected and deposited by ants enriches the nutrient status of the soil in and around the mound (Rogers and Lavigne 1974, Mandel and Sorenson 1982, Culver and Beattie 1983, Levan and Stone 1983). These changes in soil properties may contribute towards nutrient-enriched microsites for plant establishment and greater production of plants near the disk edge. These altered soil conditions, coupled with the seed harvesting ac-

tivity of ants, may also provide "safe" sites for less competitive plant species to establish and grow.

- 3) A third mechanism is the protection of plants by *ant predation on insect herbivores* (Barton 1986, Heads 1986, Schupp 1986). The localized reduction in insects that feed upon a particular plant may allow enhanced plant growth and establishment near the mounds.
- 4) The fourth mechanism is analogous to *allelopathy* (Janzen 1969). Harvester ants clear vegetation around their mound. If the ants selectively defoliate and remove potential competitors, then undamaged species would have an advantage.

Alternatively, the association of certain plant species with ant mounds may be an artifact caused by the ants' selection of nest sites based upon specific vegetative characteristics. Thus, the prevalence of particular plant species near mounds may be the cause of the mound location, and the distribution of plants influences the ants rather than ants influencing the distribution of plants.

The purpose of our study was to investigate associations between ants and plants in semiarid, sagebrush steppe vegetation. Preliminary observations suggested that a particular plant species, *Oryzopsis hymenoides*, was the closest plant to *P. owyheeii* ant mounds. Thus, we conducted a series of studies: first, to determine if the distribution of *O. hymenoides* was indeed associated with ant mounds, and second, to determine which of the potential mechanisms most likely affected plant distribution.

Study areas

Two study areas were located on the Idaho National Engineering Laboratory in southeastern Idaho, U.S.A. The first study area, called the "Burn", was burned in the autumn, 1981. The Burn study area received moderate grazing from sheep and cattle before 1981, but the area had been closed to grazing since the burn. The second study area, called "EBR", was approximately 21 km south of the Burn. EBR had not been grazed or burned since at least the mid-1950's. The Burn study area (43°42' N, 113° W) was located between 1490 and 1550 m elevation and the EBR study area (43°31' N, 112°30' W) was at approximately 1515 m elevation. Climatic information for the Idaho National Engineering Laboratory is found in Anderson et al. (1987).

The vegetation of both areas is a mixture of shrubs, grasses, and forbs that is typical of sagebrush steppe in the northern Intermountain West. Shrubs, such as *Artemisia tridentata* and *Chrysothamnus viscidiflorus*, dominate the landscape. Total grass cover is approximately an order of magnitude less than total shrub cover (Floyd 1982). Most grass species, including *O. hymenoides* and *Agropyron spicatum*, are tussock or bunchgrasses, but some rhizomatous grasses, primarily *Agropyron dasy-*

stachyum, are present. Total forb cover is approximately 45% greater than total grass cover, but there are many more forb species than both grass and shrub species combined. Consequently, cover of any particular forb species is very low. Further information about the vegetation is also found in Floyd and Anderson (1986).

Methods

Seedbank and initial vegetation studies were conducted in September, 1984 at the Burn. A total of 16 ant mounds was sampled: four mounds along four permanently-marked vegetation transects (Floyd 1982). At each ant mound, the three plants closest to the center of the mound were identified. All plants in the cleared disk around the mound were also identified and counted. In addition, two transects were established that radiated from the center of the mound and were perpendicular to each other (Fig. 1A). Along each transect, 80 ml of soil was collected at each of three locations by pushing a 4.5 cm diameter, aluminum tube into the ground. Locations of the soil samples were: on the mound at $\frac{2}{3}$ of the distance from the center of the mound to the edge of the mound; in the cleared disk at $\frac{2}{3}$ of the distance from the edge of the mound to the edge of the disk; and in the native community at 1 m from the edge of the cleared disk (Fig. 1A). These soil samples were used for seedbank analyses. Finally, whenever we found ants on the mound, we collected specimens for identification. All specimens were *P. owyheeii*.

Two techniques were used for seedbank analyses. First, the set of soil samples from one transect was floated for seed retrieval. Floated material was dried, then whole, intact seeds were handpicked from the floated material and identified using a seed reference collection housed at the Desert Research Institute, Reno, Nevada, U.S.A. The other set of soil cores was left intact in the aluminum tubes, and the bottoms of the tubes were sealed with aluminum foil. Cores were placed in a freezer (-10°C) for 3 wk to vernalize seeds, then moved to a greenhouse and watered. One month later, seedlings were counted and identified to the extent possible. Unidentified seedlings were transplanted into pots and many of these were later identified. Unfortunately, we were unable to positively identify some forb and grass seedlings.

In summer 1986, 15 ant mounds were randomly selected at each study area. Mound diameter, diameter of the cleared disk around the mound, and the three plants closest to the center of the mound were recorded. For each mound, transects were established through the center of the mound in a randomly-selected compass direction (Fig. 1B). If another ant mound was within 50 m of any point along the transect, either a new compass direction was randomly selected or another ant mound was located. Along each transect, seven $1\text{ m} \times 1\text{ m}$ plots were located on each side of the mound at 0, 1, 2, 3, 7, 15, and 20 m from the center of the mound. These plot

locations were chosen because they encompass the mound and cleared disk (0 m), the transition from cleared disk to vegetated area (1, 2, and 3 m), the middle of the foraging area (7 m), the edge of the foraging area (15 m), and beyond the foraging area (20 m) of a typical ant colony (Willard and Crowell 1965).

Size and density of plants within each 1 m^2 plot were measured for each taxon. Density was the number of individuals in the 1 m^2 plot. Canopy dimensions were used to estimate plant size. For taxa that had leaves down to ground level (for example, bunchgrasses such as *O. hymenoides*), the maximum basal diameter, the basal diameter perpendicular to the maximum, and the mean plant height were measured. For taxa that had a basal stem without foliage (for example, shrubs such as *Artemisia tridentata*), the maximum canopy diameter, the canopy diameter perpendicular to the maximum, and mean canopy height were measured. Plant size was the volume calculated from the area of an ellipse, which was formed by the 2 diameter measurements, multiplied by the height dimension. For rhizomatous or single-stalked taxa (for example, *Bromus tectorum*), plant height was used as the estimate of plant size.

Because we thought that the sampling date in 1986 at EBR preceded the annual clearing of the disk area by ants, some additional measurements were taken in mid-summer 1987 at EBR. The three plants closest to the center of 21 mounds were measured. Eight of these mounds were the same ones measured in 1986 (the remaining seven mounds that were measured in 1986 could not be relocated). Additional measurements of plant size were also made to increase the sample size for *O. hymenoides*. The size of five randomly-selected *O. hymenoides* plants located between 0 and 4 m from the center of the mound and five plants located between 15 and 20 m from the center of the mound were measured for 15 mounds.

Three statistical tests were used in data analysis. Two-sample t-tests were used to compare diameters of mounds and of cleared areas between the two study areas. A G goodness-of-fit test with the appropriate correction was used to determine if *O. hymenoides* was the closest plant to mounds more frequently than expected (Sokal and Rohlf 1981). Expected values for the G test were based on the mean plant densities within 4 m of the center of the mound for *O. hymenoides* and for all plants, determined for each study area from our 1986 transect measurements. To determine if plant density or size differed among plots located at the various distances from the center of the mound, a Kruskal-Wallis nonparametric analysis of variance (K-W AOV) was used. Each mound was considered a replicate, and the data from pairs of plots that were located at the same distance from the center of each mound were averaged together. If the K-W AOV was significant, nonparametric mean comparisons were made according to the procedures of Sokal and Rohlf (1981). A K-W AOV was

Tab. 1. Percentages of plants closest to the center of ant mounds and of plants in the cleared disks around mounds at the Burn study area, given as percentages of the total number of plants observed.

Taxa	Closest plant		Disk plants
	Sep '84	Aug '86	Sep '84
<i>Oryzopsis hymenoides</i> (R. & S.) Ricker	55.1	57.8	71.3
<i>Agropyron dasystachyum</i> (Hook.) Scribn.	4.1	0.0	4.3
<i>Agropyron spicatum</i> (Pursh) Scribn.	2.0	0.0	0.0
<i>Artemisia tridentata</i> Nutt.	12.2	0.0	0.0
<i>Astragalus</i> sp.	0.0	0.0	3.2
<i>Chrysothamnus viscidiflorus</i> (Hook.) Nutt.	0.0	4.4	0.0
<i>Cordylanthus ramosus</i> Nutt.	0.0	13.3	0.0
<i>Descurainia pinnata</i> (Walt.) Brit.	0.0	13.3	0.0
<i>Erigeron divergens</i> T. & G.	0.0	2.2	0.0
<i>Gilia congesta</i> Hook.	2.0	0.0	9.6
<i>Lactuca</i> sp.	4.1	0.0	1.1
<i>Leptodactylon pungens</i> (Torr.) Nutt.	2.0	0.0	0.0
<i>Machaeranthera canescens</i> Greene	2.0	0.0	0.0
<i>Opuntia polyacantha</i> Haw.	0.0	0.0	1.1
<i>Orobanche fasciculata</i> Nutt.	4.1	0.0	2.1
<i>Phlox hoodii</i> Rich.	0.0	0.0	1.1
<i>Poa</i> sp.	2.0	0.0	1.1
<i>Salsola kali</i> L.	2.0	0.0	1.1
<i>Sitanion hystrix</i> (Nutt.) J. G. Smith	8.2	2.2	2.1
Unknown plants	0.0	6.7	0.0
Lichen	0.0	0.0	2.1

also used in analyses of the seed data. Nonparametric AOV's were more appropriate for our data than parametric tests because Bartlett's test of equal variance (Snedecor and Cochran 1980) was always significant. For all statistical tests, $P < 0.05$ was considered significant.

Results

The diameters of mounds and of cleared disks around mounds were not significantly different between study areas (for mound diameter: $t = -0.34$, 28 d.f., $P = 0.74$; for cleared disks: $t = 1.58$, 28 d.f., $P = 0.12$). Average mound diameters were 0.51 m for the Burn study area and 0.53 m for EBR. Mean diameters of the cleared disks were 2.6 m for the Burn area and 2.1 m for EBR.

Oryzopsis hymenoides frequently was the closest taxon to the center of ant mounds at the Burn study area and was also the predominant taxon found in the cleared disks around ant mounds (Tab. 1). The prevalence of *O. hymenoides* near mounds was significantly greater than expected (for 1986 data: $G = 76.5$, 1 d.f., $P < 0.005$), given the mean plant density within 4 m of the center of a mound for *O. hymenoides* (1.29 plants m^{-2}) and for all plants (17.54 plants m^{-2}). In fact, density of *O. hymenoides* would have had to have been almost 6 times greater in order for the observed frequency of *O. hymenoides* as closest plant to mounds to be not-significantly different from expected. We also calculated expected frequencies based upon mean plant densities within 2 m of the center of the mound and based upon mean plant densities from all points along

the transects. In both cases, the G test was highly significant ($P < 0.005$), again indicating that *O. hymenoides* occurs as the closest plant at a frequency greater than expected. The "Unknown" plants in the 1986 field measurements were probably *Agropyron dasystachyum* and *Descurainia pinnata*, but the plants were difficult to identify positively because they were severely defoliated.

The observed occurrence of *O. hymenoides* as a closest plant to the center of ant mounds at EBR (Tab. 2) was also greater than expected (for 1986 data: $G = 16.43$, 1 d.f., $P < 0.005$), based upon plant densities at

Tab. 2. Percentages of plants closest to the center of ant mounds at the EBR study area, given as a percent of the total number of plants observed.

Taxa	Closest plants	
	Jun '86	Jul '87
<i>Oryzopsis hymenoides</i>	11.1	54.0
<i>Agropyron spicatum</i>	0.0	4.8
<i>Agropyron dasystachyum</i>	6.7	15.9
<i>Arabis holboellii</i> Hornem.	0.0	1.6
<i>Artemisia tridentata</i>	2.2	4.8
<i>Bromus tectorum</i> L.	4.4	1.6
<i>Ceratoides lanata</i> (Pursh) J. T. Howell	2.2	4.8
<i>Chrysothamnus viscidiflorus</i>	0.0	3.2
<i>Cordylanthus ramosus</i>	4.4	0.0
<i>Descurainia pinnata</i>	26.7	0.0
<i>Lappula redowskii</i> (Hornem.) Greene	6.7	0.0
<i>Opuntia polyacantha</i>	0.0	3.2
<i>Phlox hoodii</i>	4.4	3.2
<i>Sitanion hystrix</i>	2.2	3.2
Unknown plants	28.9	0.0

Tab. 3. Seedbank samples from soil cores collected at the Burn study area. Results for seeds are mean number per litre of soil, and those for seedlings are mean number per m² of soil surface. For some taxa, more than one species of seeds or seedlings were identified; lists of all taxa are in brackets. For total of all plants, the standard error (SE) is given in addition to the mean.

Taxa	Seeds (number/litre)			Seedlings (number/m ²)		
	Mound	Disk	Native	Mound	Disk	Native
<i>Oryzopsis hymenoides</i>	38.3	3.9	9.4	*	*	*
<i>Agropyron</i> {sp., <i>spicatum</i> }	15.6	0.8	0.8	*	*	199
<i>Allium textile</i> Nels. & Macbr.	3.9	*	0.8	*	*	*
<i>Arabis holboellii</i>	*	*	*	40	*	*
<i>Arenaria</i> sp.	2.3	*	0.8	*	*	*
<i>Artemisia</i> {sp., <i>tridentata</i> }	2.3	2.3	0.8	*	*	40
<i>Astragalus</i> sp.	1.6	*	*	199	*	*
<i>Bromus tectorum</i>	*	*	*	159	*	*
<i>Castilleja angustifolia</i> G. Don	1.6	0.8	*	*	*	*
<i>Centaurea repens</i> L.	0.8	*	*	*	*	*
<i>Chaenactis douglasii</i> (Hook.) H. & A.	*	*	0.8	*	*	*
<i>Chenopodium</i> sp.	41.4	3.9	0.8	40	*	*
<i>Chrysothamnus viscidiflorus</i>	3.1	0.8	9.4	*	*	*
<i>Cordylanthus ramosus</i>	*	*	2.3	*	*	*
<i>Crepis</i> sp.	0.8	*	*	*	*	*
<i>Cryptantha</i> sp.	8.6	1.6	*	40	*	*
<i>Descurainia</i> sp.	1.6	*	0.8	478	*	40
<i>Eriogonum</i> sp.	*	*	*	80	40	*
<i>Lappula redowskii</i>	18.8	1.6	0.8	199	*	*
<i>Melilotus officinalis</i> (L.) Lam.	*	*	*	80	*	*
<i>Monolepis nuttalliana</i> (R. & S.) Wats.	0.8	*	*	*	*	*
<i>Oenothera</i> sp.	*	*	1.6	*	*	*
<i>Phacelia</i> sp.	12.5	*	*	*	*	*
<i>Poa</i> sp.	101.6	*	3.1	*	*	*
<i>Scrophulariaceae</i>	5.5	*	*	*	*	*
<i>Sisymbrium altissimum</i> L.	*	*	*	319	40	80
<i>Sitanion hystrix</i>	4.7	0.8	0.8	797	*	*
<i>Taraxacum officinale</i> Weber.	0.8	*	0.8	*	*	*
Unknown forb species	*	*	*	120	40	*
Unknown grass species	*	*	*	917	*	*
Total of all plants: Mean	266.4	16.4	33.6	3,468	120	359
SE	105.8	5.8	7.8	705	64	199

* No seeds or seedlings of this taxon found in the soil cores at this location.

EBR of 0.39 plants m⁻² for *O. hymenoides* and 44.17 plants m⁻² for all plants. As with data from the Burn study area, the results were significant even if we used expected frequencies based on plant densities either within 2 m of the mound's center or for all points along the transects. In 1986, the highest percentage of plants closest to the mound were *D. pinnata* and "Unknown". As at the Burn, the unknown plants were severely defoliated and were probably *A. dasystachyum* and *D. pinnata*. In 1987, mounds were sampled later in the summer to allow ants more time to clear vegetation from the disks around their mounds. The ants are active outside the mound only when surface temperature exceeds 20°C, and thus the clearing activity is not initiated until late-May or early-June (Willard and Crowell 1965). If ants were given time to clear the disks, *O. hymenoides* became the taxon with the highest percentage of plants closest to the center of ant mounds (Tab. 2).

For many plant taxa, the greatest number of seeds and seedlings in soil cores was from samples collected on the ant mound itself (Tab. 3). The number of seeds from the mound samples was 84% of the total number

of seeds, and approximately 90% of the seedlings that emerged from intact soil cores were from mound samples. Although the absolute number of *O. hymenoides* seeds in the seedbank was greatest on the mound, the proportion of *O. hymenoides* seeds of the total number of seeds was not significantly different among samples from the mound, the cleared area, and the native area (K-W statistic = 4.83, P = 0.09). Despite the large number of *O. hymenoides* seeds, none of the intact soil cores produced any *O. hymenoides* seedlings. Because *O. hymenoides* leaf blades are distinctly rolled, none of the unknown grass seedlings were *O. hymenoides*.

For the analyses of plant density and size data, taxa were first divided into three groups based upon the number of plots in which the particular taxon was present. A total of 210 plots were examined at each study area. If a taxon occurred in less than 30 plots at each of the two study areas, then the taxon was classified as "rare". If a taxon occurred in 30 or more plots at only one of the two study areas, then the taxon was classified as "restricted". Finally, if the taxon occurred in more than 30 plots at both study areas, then the taxon was

Tab. 4. Mean plant density (no. m⁻²) of abundant taxa for plots located at various distances from the center of ant mounds. For rows without letters, the K-W AOV's of plant density were not significant for those taxa at those study areas. For all other rows, the K-W AOV's were significant, and within each row, means followed by different letters belong to different statistical groups.

Taxon	Study area	Distance of plot from center of ant mound						
		0	1	2	3	7	15	20
<i>Oryzopsis hymenoides</i>	Burn	0.83	1.57	1.43	1.33	0.93	1.33	1.23
	EBR	0.30ab	0.63b	0.20ab	0.43b	0.67ab	0.03a	0.03a
<i>Agropyron spicatum</i>	Burn	0.00a	0.47b	0.50ab	0.53ab	1.03b	0.57b	0.60b
	EBR	0.03	0.37	0.50	0.33	0.67	0.63	0.53
<i>Artemisia tridentata</i>	Burn	0.00a	0.63ab	0.63b	1.30b	2.40b	3.30b	1.50b
	EBR	0.00a	0.30b	1.03bc	1.27bc	1.20c	0.93c	1.30c
<i>Chrysothamnus viscidiflorus</i>	Burn	0.03a	0.77ab	1.30ab	0.83b	0.87ab	1.07b	1.27b
	EBR	0.03a	1.00b	1.80bc	2.13bc	2.30bc	1.77bc	2.33c
<i>Cordylanthus ramosus</i>	Burn	0.10a	2.50b	6.67c	9.07c	9.73c	10.00c	7.40c
	EBR	0.07a	5.40b	13.37b	16.97b	15.17b	11.70b	14.10b
<i>Descurainia pinnata</i>	Burn	0.07	0.60	0.13	0.50	0.40	0.90	2.07
	EBR	1.70a	6.93ab	12.10b	13.53ab	7.67ab	7.43ab	16.87ab
<i>Phlox hoodii</i>	Burn	0.07a	0.13ab	0.27ab	0.27ab	0.53ab	0.80b	0.47ab
	EBR	0.23a	1.30ab	1.97b	1.33ab	2.43b	2.03b	2.53b
<i>Sitanion hystrix</i>	Burn	0.03a	0.40ab	1.33b	1.17b	0.83b	1.43b	1.20b
	EBR	0.00a	2.37b	3.43b	4.10b	3.77b	3.77b	3.13b

classified as "abundant". The rare taxa, which were excluded from further data analyses, were: *Agropyron cristatum* (L.) Gaerta., *Arenaria* sp., *Artemisia tripartita* Rydb., *Astragalus* sp., *Balsamorhiza sagittata* (Pursh) Nutt., *Bromus tectorum*, *Castilleja* sp., *Chaenactis douglasii*, *Crepis acuminata* Nutt., *Erigeron divergens*, *Eriogonum microthecum* Nutt., *Gayophytum ramosissimum* T. & G., *Gilia congesta*, *Lepidium densiflorum* Schrad., *Opuntia polyacantha*, *Phacelia hastata* Dougl., *Stipa comata* Trin. & Rupr., *Tetradymia canescens* DC., and *Tragopogon dubius* Scop.

The restricted taxa were: *Agropyron dasystachyum*,

Arabis holboellii, *Chenopodium leptophyllum* Wats., *Cryptantha* sp., *Lappula redowskii*, and *Poa* sp.

The density and size of each restricted taxon were examined only at the study area where they occurred in 30 or more plots. For all the restricted taxa, neither plant density nor size was significantly different among plots located at various distances from the center of the ant mounds. Results for the abundant taxa, which are listed in Tabs 4 and 5, are presented in the next two paragraphs.

Plant density of *O. hymenoides* near the center of ant mounds at the EBR study area was significantly greater

Tab. 5. Mean plant size of abundant taxa for plots located at various distances from the center of ant mounds. For all taxa, the K-W AOV was not significant at both study areas.

Taxa	Study area	Distance of plot from center of ant mound						
		0	1	2	3	7	15	20
<i>Oryzopsis hymenoides</i>	Burn	2.59	0.74	1.66	0.75	0.86	1.16	1.11
	EBR	4.04	4.74	3.28	2.67	2.78	6.16	0.38
<i>Agropyron spicatum</i>	Burn	*	19.80	1.37	2.25	5.61	5.80	0.92
	EBR	10.76	4.95	3.22	6.06	2.69	5.07	22.98
<i>Artemisia tridentata</i>	Burn	*	307.6	135.3	160.5	73.6	51.6	88.5
	EBR	*	121.7	128.6	97.4	40.0	116.8	42.3
<i>Chrysothamnus viscidiflorus</i>	Burn	413.7	36.1	51.7	25.4	19.6	36.0	15.6
	EBR	3.4	38.2	15.5	16.0	10.8	12.2	12.3
<i>Cordylanthus ramosus</i> [†]	Burn	212	191	179	191	189	186	190
	EBR	53	63	83	77	75	72	72
<i>Descurainia pinnata</i> [†]	Burn	205	308	380	328	341	349	485
	EBR	162	191	202	188	176	188	201
<i>Phlox hoodii</i>	Burn	0.11	0.48	0.12	0.14	0.14	0.16	0.35
	EBR	0.14	0.22	0.33	0.25	0.20	0.21	0.28
<i>Sitanion hystrix</i>	Burn	0.01	0.08	0.15	0.26	0.31	0.70	0.10
	EBR	*	0.47	0.55	0.41	0.44	0.50	0.31

* No plants were found in the plots located at this distance.

† Mean plant size represents a height measurement and is reported in mm; for all other taxa, plant size was calculated from the dimensional analysis described in the Methods and is given in litre.

than that at 15 or 20 m from the center of mounds (Tab. 4). At the Burn study area, however, plant density of *O. hymenoides* was not significantly different among plots located at various distances from the center of mounds. In contrast, plant densities of *Artemisia tridentata*, *Chrysothamnus viscidiflorus*, and *Cordylanthus ramosus* were greater for plots located farther from the center of ant mounds. For the remaining four species that were abundant, mean plant density of the first plot along the transects, plot 0, tended to be significantly less than that of most of the other plots along the transects. Among these other plot locations, however, mean plant densities were not significantly different.

The mean size of *O. hymenoides* plants that were located near mounds at the EBR study area was greater than that of plants located far from mounds. Although the K-W AOV was not significant for the 1986 measurements (Tab. 5), the mean sizes for plots located at 15 and 20 m from the center of mounds at the EBR study area represent measurements from only one plant each. In 1987, we sampled 15 mounds located at the EBR study area and measured an equal number of randomly-selected plants near and far from the mound. Mean size of plants located between 0 and 4 m from the center of mounds (1.77 litre) was significantly greater (K-W statistic = 5.3, $P = 0.02$) than that of plants between 15 and 21 m (1.03 litre). For *O. hymenoides* at the Burn study area, as well as all other species at both areas, plant size was not significantly different among plots at different distances from mounds (Tab. 5).

Discussion

At both study areas, *Oryzopsis hymenoides* occurred as the plant closest to ant mounds and in the cleared disks more frequently than expected. These patterns were consistent for both years at each study area. Although we only measured plant density in 1986, there was no evidence for large changes in plant densities over the 3-yr study period. We observed very few seedlings and, with the exception of plants killed by the fire or defoliated by ants, very few dead plants. Furthermore, density of *Chrysothamnus viscidiflorus* before the fire, 1.92 plants m^{-2} (Floyd 1982), was very similar to our measurements taken 5 yr later along the same transects, even though this species vigorously resprouts and reseeds after fire (Young 1983, Young and Evans 1978). Thus, G tests for the prevalence of *O. hymenoides* near mounds in 1984 and 1987 probably also would be significant.

What mechanism(s) may account for the prevalence of *O. hymenoides* near ant mounds? Results from the seedbank studies suggest that dispersal of plant propagules by ants is not responsible for the prevalence of *O. hymenoides* near ant mounds. Marlette and Anderson (1986) found good correlations between abundance in the seedbank and composition of the vegetation for sagebrush steppe communities. However, at the Burn

study area, *O. hymenoides* was over 70% of the plants in the cleared disks, but its proportion of the seedbank was less than 25% in the cleared disk and did not vary significantly among the mound, cleared disk, and native area. The most striking aspect of these seedbank studies was that the size of the seedbank was greatest on the ant mounds, but only two plants were found growing on one mound among all the mounds studied. Both of these plants were *Orobanche fasciculata*, an achlorophyllous species that is generally considered to be parasitic.

Further evidence that a direct influence of ants on *O. hymenoides* distribution was unlikely came from the plant density measurements. If the distribution of *O. hymenoides* was directly affected by harvester ants, then plant density of *O. hymenoides* should have been greatest near the mound and decreased with distance from the center of the mound. Plant density of *O. hymenoides* at the EBR study area was significantly greater for plots located near mounds than for plots located at 15 and 20 m from the center of the mound, but not at the Burn study area. These differences between study areas are not consistent with a hypothesis that ants directly influence *O. hymenoides* distribution.

Distribution of *O. hymenoides* also does not appear to be indirectly influenced by ants through a modification of soil characteristics. If ants modify the local soil environment such that growth of *O. hymenoides* is enhanced, then the size of plants near the mound should be significantly greater than that far from the mound at both study areas. However, measurements of *O. hymenoides* plant size were not significantly different among plot locations at the Burn study area. Furthermore, soil in the cleared disks did not enhance *O. hymenoides* seed germination; *O. hymenoides* seedlings were not found in any of the intact soil cores. Finally, we would expect larger plants near mounds for other taxa, unless ants are able to modify the soil such that only *O. hymenoides* is affected. None of the other abundant taxa and none of the restricted taxa had significantly larger plants near ant mounds at either study area. Although soil chemical data would be needed to completely eliminate this hypothesis, other researchers have also rejected a nutrient-enriched microsite hypothesis (Rice and Westoby 1986).

The third mechanism, the indirect effects on *O. hymenoides* distribution by ant predation on insect herbivores, cannot be completely ruled out by our data but is unlikely. For this mechanism to operate, two criteria need to be met: the insect herbivore must feed selectively upon *O. hymenoides*, and second, some mechanism must exist to exclude other plant species. Otherwise, all species would benefit from the removal of insect herbivores. We have observed the second criterion: ants selectively defoliate and remove all plants except *O. hymenoides*. However, we know of no evidence for the first criterion. None-the-less, the even distribution of *O. hymenoides* at the Burn is difficult to

explain with this mechanism unless the fire also selectively removed the damaging insect herbivores for several years after the fire. A long-term loss of insect herbivores is unlikely because phytophagous insects rapidly become more abundant after fire in sagebrush steppe vegetation than in unburned areas (Hansen 1986). Finally, predictions of plant size in relation to distance from the mound are more difficult to make for this third mechanism. If the herbivores reduced plant size, then plant size should have been greatest near mounds only at EBR, which are the same results predicted by the indirect mechanism of reduced competition. If the herbivores cause plant mortality but do not affect plant growth, then plant size should be the same at all distances from the mound at both study areas, which is not consistent with data from EBR.

The most plausible mechanism by which ants could influence *O. hymenoides* distribution is the fourth mechanism, which is analogous to allelopathy: ants defoliate and remove potential competitors. The harvester ants do not defoliate *O. hymenoides* in the disk area (pers. obs.). The selective defoliation by ants kills all potential competitors of *O. hymenoides*, which reduces interspecific competition. Thus, the abundance of *O. hymenoides* within the plant community would be increased in areas near ant mounds. The controlled burn at the Burn study area also removed competitors, especially shrubs. Thus, *O. hymenoides* would not be necessarily restricted to areas near ant mounds at the Burn, and the even distribution of *O. hymenoides* at the Burn is expected. If ants remove potential competitors, then the size of *O. hymenoides* plants near the mound should be significantly greater than that far from the mound only at EBR. At the Burn, where fire removed competitors, the size of *O. hymenoides* plants should not change with distance from the center of an ant mound. Our data are consistent with these predictions.

The alternative hypothesis that ants select their nest sites based upon the abundance of *O. hymenoides*, and thus ants do not affect *O. hymenoides* distribution, is unlikely for two principal reasons. First, the longevity of mounds is at least 14–30 yr and at least 25% of abandoned mounds are reoccupied (Porter and Jorgensen 1988). Also, the size of the disk area increases over time (Sneva 1979). Thus, mound and disk areas persist for several generations of plants, and ample time exists for localized plant distributions to change from the time that the nest site was established. Second, abandoned mounds are invaded by many species, including *Artemisia tridentata* and other perennial species (Porter and Jorgensen 1988, pers. obs.). Thus, without continued ant activity, the prevalence of *O. hymenoides* would be lost.

In summary, the abundance of *O. hymenoides* near ant mounds is most probably due to the indirect mechanism analogous to allelopathy: ants completely defoliate all plants near the mound except for *O. hymenoides*. Ant predation on insect herbivores that in turn reduces

O. hymenoides growth could also account for the distribution of *O. hymenoides* near mounds, but this mechanism is very unlikely. To categorically reject this predation mechanism, manipulative studies would have to be conducted.

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