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DISPERSAL OF SAGEBRUSH-STEPPE SEEDS BY THE WESTERN HARVESTER ANT (*POGONOMYRMEX OCCIDENTALIS*)

John F. Mull

**ABSTRACT.**—Like many seed-harvesting ants, the western harvester ant (*Pogonomyrmex occidentalis*) can act as both a seed predator and a seed disperser. Dispersal results when seeds are dropped en route to the nest, are left in nest granaries when colonies die or are abandoned, or are removed from granaries and discarded in nest middens. This study examined the density and species identity of seeds discarded in harvester ant nest middens and compared them with those found in nearby soils. Nineteen species of seeds were recovered from middens, compared with 13 species in 5-m reference areas and 9 species in adjacent disk areas. Total density of sound seeds was nearly 3 times higher in middens than at 5 m from the nest and nearly 50 times higher than in disk soils. Moreover, 4 of the 6 most common species overall were significantly more abundant in middens. One species, *Munro globemallow* (*Sphaeralcea munroana*), was recovered from nearly 50% of middens but was not found in the other 2 areas. These findings suggest that the western harvester ant is a potentially important disperser of some sagebrush-steppe plant species.

**Key words:** seed dispersal, harvester ants, *Pogonomyrmex*, ant-plant interaction, shrub-steppe, granivory.

By definition granivores are predators that consume seeds and cause the death of individual plants (Brown and Ojeda 1987); however, they commonly lose or reject seeds that they have collected and cache others that are never recovered. Thus, granivores may be both predators and dispersers of a particular plant species (Janzen 1971, Archer and Pyke 1991, Byrne and Levey 1993). Even when granivores are primarily seed predators, their rare dispersal services may be highly significant from a plant’s perspective (Levey and Byrne 1993).

Harvester ants (*Pogonomyrmex* spp.) are specialist seed predators that can also disperse seeds in several ways (MacMahon et al. 2000). Seeds that foragers collect (at distances ranging from <1 m to >20 m) and return to the nest may eventually germinate and grow if the colony dies or emigrates. More typically, dispersal occurs when foragers drop seeds en route to the nest or when nest workers discard seeds from nest stores into middens (refuse piles) outside the nest (Rissing 1981, Kelrick et al. 1986, Wolff and Debussche 1999, Detrain and Tasse 2000). A variety of seed attributes may influence the probability that a seed, once harvested, will be discarded. For example, Knoch et al. (1993) found that tall fescue (*Festuca arundinacea*) seeds infected with an endophytic fungus were more likely to be discarded than uninfected seeds. Intrinsic seed attributes, such as nutritional quality (Kelrick et al. 1986) and seed coat thickness (Rissing and Wheeler 1976), may also influence a seed’s chances of being discarded. Ultimately, individuals of some species dispersed in this manner may be more abundant near nests and have increased reproductive output relative to individuals growing in surrounding areas (Janzen 1971, Rissing 1986).

This study quantified the extent to which the western harvester ant (*Pogonomyrmex occidentalis*) discards intact the seeds of shrub-steppe plants upon which it forages. Specifically, the study was concerned with determining density, species identity, and physical attributes of seeds found in colony nest middens that are maintained near nest entrances of *P. occidentalis* colonies.

**STUDY SITE**

The study site is located in the sagebrush-steppe 8 km southwest of Kemmerer in Lincoln County, Wyoming, on lands of the Pittsburg and Midway Coal Mining Company. Climate is cold and arid, with mean monthly temperatures ranging from 8°C (January) to 17°C (July). Mean annual precipitation of 22.6 cm is

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highly variable and falls mainly as snow (Parmenter and MacMahon 1983). Vegetation at the site is dominated by big sagebrush (Artemisia tridentata) and rabbitbrush (Chrysothamnus viscidiflorus). Other shrub species include winterfat (Ceratoides lanata), bitterbrush (Purshia tridentata), gray horsebrush (Tetradymiaeanseens), and Gardner’s saltbush (Atriplex gardneri). Dominant understory plants are 3 perennial grasses, needle-and-thread grass (Stipa comata), Indian ricegrass (Oryzopsis hymenoides), and bluegrass (Poa spp.), and one annual grass, cheatgrass (Bromus tectorum). Density of harvester ant colonies at the site is >30 ha⁻¹ (Parmenter and MacMahon 1983).

METHODS

Soil samples were collected at 30 harvester ant colonies in July 1994. To determine whether density and species composition of seeds in colony middens differed from those in adjacent soils and in the colony foraging area, I took samples from 3 locations at each colony: a midden located near the nest mound entrance, a point on the disk (= denuded area surrounding the mound) located 1 m from the entrance, and a point well beyond the disk located 5 m from the mound center. Thus, I collected a total of 90 samples. Disk and 5-m samples were taken in randomly chosen directions. Though seed densities in littered, undershrub locations at this site are much higher on average than those in open, intershrub spaces (Mull and MacMahon 1996), I made no attempt to stratify the 5-m samples to account for this difference. Thus, reported seed densities for the 5-m samples are a composite of undershrub and interspace samples.

Samples were extracted with a cylindrical sampling core having a cross-sectional area of 40 cm². Samples were returned to the laboratory and placed in a freezer until processing. Each sample was sieved to remove the fine mineral portion (<0.25 mm). Seeds were then recovered from the remainder of the sample while it was viewed under a dissecting microscope. Recovered seeds were classified as either sound or unsound. Sound seeds were firm under the pressure of forceps and were not discolored or otherwise visibly degraded; unsound seeds were not firm under pressure and were either discolored or degraded. As used here, “sound seed” is comparable to Roberts’ (1981) “apparently viable” and to Young et al.’s (1983) “potentially germinable” seed. I used only sound seeds in the analyses. Seeds were identified to species using a reference collection previously established for the site. The term “seeds” is used broadly here to refer to the dispersal units, or diaspores, of each species, most of which are actually fruits.

Differences in total seed densities among the 3 sampling locations were analyzed with a 1-way ANOVA. A Tukey-Kramer test was used to test for pairwise differences (Wilkinson et al. 1992). All other statistical tests involved comparisons of individual species in the midden and 5-m samples because disk samples contained too few seeds of most species to be included in the analyses of individual species. Densities of the 4 most abundant species were compared using t tests. Chi-square goodness-of-fit tests were used to compare total number of midden and 5-m samples containing the 6 most common species of seeds.

RESULTS

I recovered 19 species of seeds from midden samples, 13 species from 5-m samples and 9 from disk samples. Soil seed densities were nearly 3 times higher in middens than in the 5-m reference areas and nearly 50 times higher than in disk samples (Fig. 1).
Four of the 6 most abundant species in soil samples occurred more frequently in middens than in the 5-m reference areas (Table 1). Most notably, seeds of Munro globemallow (Sphaeralcea munroana) were found in nearly half of the midden samples but were not present in any of the 5-m samples.

Three of the 4 most abundant species were present in significantly higher densities in middens (Table 2). Midden densities of the 4th species, B. tectorum, were not significantly different from those in 5-m reference areas but were still much higher than those in adjacent disk areas (mean = 32.5, $s_x = 19.6$ seeds $\cdot m^{-2}$; $t = 4.27$, df = 58, $P < 0.001$), indicating that harvester ants discarded large numbers of intact B. tectorum seeds. In addition, 87% of all midden samples contained at least 1 (mean no./sample = 2.5, $s_x = 0.49$) discarded B. tectorum caryopsis from which ants had clipped the embryo. Middens at all colonies contained various quantities of partially chewed and fragmented B. tectorum caryopses as well.

**Discussion**

Seed banks of arid and semiarid ecosystems show considerable spatial heterogeneity across the soil surface, with both biotic and abiotic factors contributing to this heterogeneity (Price and Reichman 1987, Crist and MacMahon 1992, Mull and MacMahon 1996). This study found that the collection and subsequent discarding of seeds by harvester ants is an additional source of spatial variability in seed density. Ants create small, high-density seed patches associated with middens that have higher seed densities than either adjacent disk areas or areas beyond the nest within the colony foraging range (Fig. 1). Densities recorded at 5 m from the nest in this study are comparable to those reported for various parts of colony foraging areas sampled in previous studies at the site (Crist and MacMahon 1992, Mull and MacMahon 1996). This indicates that midden seed densities, though greatly limited in their spatial extent, exceed those in most of the background seed pool.

As is true of aridland seed bank composition in general, most of the 19 species found in middens were rare, occurring in 15% or fewer of all samples. Those species that occurred in at least 30% of all midden samples or that were present in midden samples at high densities (Tables 1, 2) are either common in the seed pool at the site (B. tectorum, A. desertorum, O. hymenoides, and C. parciflora) or may be difficult for harvester ants to process and consume once they have been collected (S. munroana and L. redowskii). Rejection of previously collected seeds is a behavior that has been frequently observed in harvester ants. Explanations proposed to account for the rejection of viable seeds by harvester ants, though varied and sometimes speculative, include the addition of more preferred species to nest stores, differential rates of infection with fungal endophytes, seed novelty, and “mistakes” made by nest workers (Rissing 1981, Kelrick et al. 1986, Knoch et al. 1993, Wolff and Debusche 1999, MacMahon et al. 2000).

Non-seed tissues attached to seeds may lower granivore preference because they increase handling time costs and contain a high proportion of indigestible structural carbohydrates and other nonnutritive matter (Kelrick et al. 1986). The 2 species most disproportionately represented in midden samples, S. munroana and L. redowskii, have seed morphologies that would make it costly for nest workers to process them. The nutlet of L. redowskii is hard and armed with stiff marginal prickles (Shaw 1989); the seed coat of S. munroana is thick and very hard. Rissing and Wheeler (1976) suggested that *Chorizanthe rigida*, an annual of the Mojave Desert, is often discarded into refuse piles of *Messor* (= *Veromessor*) pergandei because of its hard seed coat. In 2 other reported cases, *Pogonomyrmex* workers discarded the thick-seeded propagules of *Opuntia* spp. (Gonzalez-Espinoza and Quintana-Ascencio 1986) and *Datura discolor* (O’Dowd and Hay 1980) into their nest middens after removing the associated fleshy pulp and elaiosome (= oil body), respectively, of these 2 species.

In their early review of ant foraging ecology, Carroll and Janzen (1973) speculated that seed-eating ants may be capable of finely portioning collected seeds by eating only the embryo and discarding other portions. Middens of most colonies contained clipped B. tectorum caryopses, indicating that ants preferentially consumed the embryo. Embryo and endosperm portions of B. tectorum seeds differ only slightly in their nutritional content (T.O. Crist personal communication), but it is unclear if such small differences are sufficient
Table 1. Chi-square tests comparing total number of midden and 5-m soil samples (n = 30 for each type of sample) containing seeds of the 6 most common species. For all comparisons df = 1.

<table>
<thead>
<tr>
<th>Species</th>
<th>Midden</th>
<th>5 m</th>
<th>Chi-square</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bromus tectorum</td>
<td>24</td>
<td>19</td>
<td>0.58</td>
<td>&gt; 0.25</td>
</tr>
<tr>
<td>Sphaeralcea munroana</td>
<td>13</td>
<td>0</td>
<td>13.0</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Lappula redowskii</td>
<td>26</td>
<td>8</td>
<td>9.52</td>
<td>&lt; 0.005</td>
</tr>
<tr>
<td>Alyssum desertorum</td>
<td>27</td>
<td>17</td>
<td>2.26</td>
<td>&gt; 0.10</td>
</tr>
<tr>
<td>Collinsia parejiforma</td>
<td>15</td>
<td>6</td>
<td>3.84</td>
<td>= 0.05</td>
</tr>
<tr>
<td>Oryzopsis hymenoides</td>
<td>9</td>
<td>2</td>
<td>4.46</td>
<td>&lt; 0.05</td>
</tr>
</tbody>
</table>

Table 2. Comparison of mean seed densities in soil samples taken in midden and 5-m locations (n = 30 for each type of sample) for the 4 most abundant species. For all comparisons df = 58.

<table>
<thead>
<tr>
<th>Species</th>
<th>Midden</th>
<th>5 m</th>
<th>t-value</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bromus tectorum</td>
<td>1200.3 (269.6)</td>
<td>707.5 (185.1)</td>
<td>1.51</td>
<td>&gt; 0.10</td>
</tr>
<tr>
<td>Sphaeralcea munroana</td>
<td>557.5 (189.2)</td>
<td>0</td>
<td>3.03</td>
<td>&lt; 0.005</td>
</tr>
<tr>
<td>Lappula redowskii</td>
<td>1307.5 (286.1)</td>
<td>250.1 (119.3)</td>
<td>3.41</td>
<td>&lt; 0.005</td>
</tr>
<tr>
<td>Alyssum desertorum</td>
<td>3725.6 (538.2)</td>
<td>1390 (325.7)</td>
<td>2.34</td>
<td>&lt; 0.05</td>
</tr>
</tbody>
</table>

to cause the observed consumption pattern. Alternatively, nest workers may remove the embryo from Bromus seeds to prevent germination and then store or feed to the larvae both portions of the caryopsis. However, this seems unlikely given that no discarded B. tectorum embryos were found in refuse piles. Preferential consumption of grass seed embryos has also been observed in Tetramorium caespitum, Messor structor, and M. capitatus (Brian 1983). Risch and Carroll (1986) reported that Solenopsis geminata removed grass seed embryos before storing the seeds, but they did not specify whether seed embryos were eaten in preference to the non-embryo portions.

This study has demonstrated that P. occidentalis individuals deposit many intact seeds of a variety of species into their middens. Because nest maintenance workers rapidly remove seedlings that emerge on the disk, middens are not reliable safe sites for discarded seeds. Given this feature of ant behavior, the effectiveness (sensu Schupp 1993) of harvester ant seed dispersal will depend upon the extent to which discarded seeds are transported away from the disk and to sites more favorable for germination and establishment. Potential vectors for such transport include seed-caching rodents that may occasionally forage in middens, as well as wind and water. For example, the strong and consistent winds typical of the sagebrush-steppe (Allen et al. 1989) coupled with the periodic surface flow of water (Anderson and Mull 1993) quickly remove most litter, including seeds, from intershrub spaces and deposit it beneath shrubs (Kelrick 1991). Thus, detailed studies of the fate of harvester ant-dispersed seeds would be required to determine if P. occidentalis provides high-quality as well as high-quantity dispersal.

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LITERATURE CITED


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