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Experimental studies of seed predation in old-fields

Gary G. Mittelbach[1] **and Katherine L. Gross**[2]

[1] Department of Zoology, Ohio State University, Columbus, OH 43210, USA
[2] Department of Botany and Graduate Program in Environmental Biology, Ohio State University, Columbus, OH 43210, USA

Summary. In a pair of experiments conducted in old-field habitats in southwestern Michigan (USA), we examined rates of seed loss to post-dispersal predators (ants and rodents). Seeds from 4–6 species of "biennial" plants were tested over a range of seed densities and habitat types. We found that seed removal was significantly higher in vegetated habitats than in areas of disturbed soil (both simulated small-animal diggings and a plowed field). In the undisturbed vegetation, seed losses ranged from 1–20% of seeds removed/day.

An exclosure experiment demonstrated that ants and rodents foraged selectively for seeds of the six plant species tested. Rodents (*Peromyscus maniculatus*) fed preferentially on species producing large seeds (predominantly *Tragopogon dubius*). Ants (*Myrmica lobicornus*) foraged on smaller seeds, although their foraging preferences were not based strictly on seed size.

Seed density had only a minor effect on predation rate over the range of densities tested. Predators, instead, appeared to treat each experimental group of seeds as a single prey patch. Consequently, predation intensity was quite variable over distances of <20 m within a relatively homogeneous section of habitat.

These field experiments provide initial estimates of seed losses to post-dispersal predators in old-field habitats. Rates of seed loss were generally less than those reported from desert or semi-arid habitats. However, for some old-field species, seed losses averaged an appreciable 10–20% day. The selective nature of the seed predators, plus the relative patchiness of predation intensity in space, suggest that post-dispersal seed predation can play a role in determining the distribution and/or abundance of old-field herbs.

Old-fields and pastures have served as model systems for studying the factors that determine the spatial and temporal distribution and abundance of plants (e.g. Werner 1976, 1979; Harper 1977; Grime 1979). While considerable attention has been focused on how interspecific competition, seed dispersal, seed germination and other factors influence the distribution and abundance of old-fields plants, virtually nothing is known about the impact of post-dispersal seed predators. By seed predators we mean animals which eat and kill seeds (Janzen 1970). This lack of information on seed predation in temperate successional systems stands in stark contrast to a number of studies from tropical and arid environments, where seed predators have been shown to remove large numbers of seeds and to affect the distribution and abundance of plants (Janzen 1971; Brown et al. 1979; Inouye et al. 1980).

This study presents the results of two field experiments designed to answer the following initial questions concerning seed predation in temperate old-fields: 1) Do seeds dispersed to different microhabitats (i.e. large scale disturbances, small animal disturbances, and natural vegetation) differ in their probabilities of being eaten? 2) Are there differences in the vulnerabilities of plant species to post-dispersal predation and are these differences related to seed size? 3) Do the major groups of potential seed predators in old-fields (particularly, ants and rodents) forage selectively among the seeds available and is this selection related to seed size? 4) How do rates of seed loss in old-fields compare with those in other communities?

We examined post-dispersal seed predation among a group of six "biennial" (or more correctly, monocarpic perennial) herbs commonly found in Michigan old-fields (Table 1). Within this group of plants, mean seed size (=seed weight) varies across three orders of magnitude (Table 1). (The term "seed" is used here for simplicity; botanically, the structure is a diaspore.) Gross and Werner (1982) and Gross (1984) have shown that seed size is the principal factor determining the type of microhabitat colonizable by these plants. Small-seeded species are only able to colonize areas of bare ground, whereas large-seeded species can successfully colonize both bare soil and vegetated areas. Seed size has also been implicated to play an important role in the selective predation of seeds by ants and rodents (Da-

Table 1. Plant species used in the seed predation experiments and their average seed weights (±1 SE). 20–25 seeds were weighed for each species

Species	Average seed weight (mg)
Tragopogon dubius Scop.	6.94±0.23
Dipsacus sylvestris Huds.	2.39±0.08
Centaurea maculosa Lam.	2.19±0.09
Daucus carota L.	0.90±0.05
Oenothera biennis L.	0.41±0.08
Verbascum thapsus L.	0.05±0.002

Offprint requests to: G.G. Mittelbach

vidson 1977; Bernstein 1979; Brown et al. 1979; Inouye et al. 1980; Menlhop and Scott 1983). Therefore, we chose to contrast the relative rates of seed loss among these species, examining whether the rate of seed loss varied between microhabitats and whether species with differing seed sizes were differentially susceptible to post-dispersal predation. Like most old-fields herbs, none of the six biennial species we studied produce seeds specifically adapted for ant or rodent dispersal (i.e. structures such as elaiosomes are absent).

Methods

Experiments were conducted in 1982 and 1983 in a 7-ha old-field abandoned from cultivation in 1973 at the W.K. Kellogg Biological Station in southwestern Michigan, USA. Prior to 1973 the field had been under annual cultivation with cereal crops. In 1982 and 1983, the dominant plant species were perennial herbs and grasses and included: *Silene alba* (Mill.) Krause, *Rumex crispus* L., *R. obtusifolius* L., *Medicago sativa* L., *Potentilla recta* L., *Agropyron repens* L. Beauv., *Phleum pratense* L., and *Poa* spp..

In an initial experiment, conducted in August 1982, we examined seed predation in four species: *Tragopogon dubius* Scop., *Daucus carota* L., *Oenothera biennis* L. and *Verbascum thapsus* L. in three microhabitats. The three microhabitats were: 1) a large (~1 ha) area which had been plowed and disked in the fall of the previous year, 2) small soil disturbances in undisturbed vegetation which were designed to mimic animal digging, and 3) undisturbed vegetation. In the newly plowed area, a 16 × 8 m grid with 15 stations at 4 m intervals was established approximately 25 m from the edge of the vegetation. A second grid, 12 × 28 m with 30 stations at 4 m intervals, was established in a section of undisturbed field located approximately 10 m south-east of the plowed area. At 15 randomly selected stations in this grid, small disturbances (1 m dia) were dug by hand with a spade to simulate animal digging (such as a woodchuck, *Marmota monax*, borrow). The vegetation at the other 15 stations was left undisturbed. All reproductive plants of the four species studied that were growing within and adjacent to the experimetal grids were removed prior to the start of the experiment to prevent errant seeds from dispersing into the treatments.

Three seed densities of each species were set up in each habitat type and each density was replicated five times. Species and seed densities used were as follows: *Tragopogon* = 1, 10, and 50 seeds/station, *Daucus* = 2, 50, and 100 seeds/station, *Oenothera* = 5, 50, and 250 seeds/station, and *Verbascum* = 5, 50, and 250 seeds/station. These seed densities encompass the normal range of localized seed fall for each species (Gross 1980 and unpublished data). To facilitate recovery, seeds were placed in plastic petri plates (15 cm dia., 1.5 cm deep), filled with 0.5 cm of a sand-soil mixture which approximated the texture of the soil found in the field. The petri plates were placed level with the soil surface in the plowed field and animal disturbance treatments. In the undisturbed vegetation, the petri plates were carefully nestled into the litter. Four petri plates, one for each species, were placed in the center of a station in a square arrangement that separated each plate by about 30 cm. Within each of the three habitat types, species and seed densities were assigned to stations at random.

The experiment was begun August 25, 1982 and was terminated on August 31, 1982. During this time no rain or high wind occurred, reducing the possibility that seeds were lost through non-biological factors. The experiment was initiated by filling the plates with the soil mixture, placing them at the stations, and then adding the seeds. At the end of the experiment, the entire soil and seed mixture from a petri plate was placed into a zip-lock bag and taken to the laboratory for counting. Seeds of *Tragopogon* and *Daucus* were large enough to be separated from the soil and counted with the naked eye. Seeds of *Verbascum* and *Oenothera* were counted under a dissecting microscope at 10 ×. A check on the processing method for *Verbascum*, the smallest-seeded species, was conducted to determine whether seeds were being missed in counting. One hundred *Verbascum* seeds were placed in a petri plate containing the same soil mixture used in the field experiment and gently agitated. The contents of the petri plate were then dumped into a zip-lock bag and processed in the same manner as all field samples. This procedure was replicated three times. In each case, there was 100% recovery of the seeds.

In 1983, a second field experiment was conducted to identify the major seed predators in the old-field and to determine whether these predators foraged differentially on the seeds of a group of six plants which differed in their average seed weights (Table 1). Four experimental treatments were created to allow access to seeds either by: 1) ants only, 2) rodents only, 3) both ants and rodents, and 4) neither ants nor rodents (control). Seeds of each species were again placed in shallow petri plates filled with a sand-soil mixture similar to that used in the 1982 experiment. In the "rodents only" treatment, ants were excluded by mounting the petri plates on a large nail (~10 cm long) which held the plate 3–4 cm above the soil surface. The outer surface of the petri plate and the nail were painted with Fluon®, which made the surface too slick for ants to climb. Care was taken to make sure no vegetation touched or overhung the plates that would have allowed ants access to the seeds. In the "ants only" treatment, rodents were excluded by placing a petri plate under a 20 × 20 × 5 cm wire cage (6 mm sq mesh). The bottom of each cage was placed flush with the ground surface and anchored securely with large stones. Ants were allowed access to the seeds within the cage by placing the petri plate directly on the ground and placing a piece of vegetation over the lip of the plate. In the "control" treatment, both ants and rodents were excluded from petri plates which were painted with Fluon®, mounted on nails, and covered with wire cages. The "ants plus rodents" treatment allowed both groups of predators access to seeds by placing petri plates directly on the soil surface as in the 1982 experiments. Treatments which allowed rodents access to the seeds also potentially permitted access to birds. However, we found no evidence of seed predation by birds in these experiments. In the treatments where seeds were exposed to vertebrate predators, foraging occurred at night and most seeds were found chewed open, indicating that rodents were the primary predators.

Prior to initiating the experiment, the effectiveness of these treatments at excluding ants and rodents was checked. Peanut butter-baited crackers were placed in petri plates in three replicates of each of the above treatments. The plates were checked twice daily for evidence of ants or rodents foraging on the bait. Over a four day period, there was no evidence of ants or rodents in the treatments designed to exclude them, and neither group was excluded from the reciprocal treatment (i.e. ants were present in the rodent exclosure petri plates and vice-versa).

Two 10 × 22 m grids were established in undisturbed vegetation in the same old-field used in the 1982 experiment. Each grid contained 72 stations set up at 2 m intervals. The vegetation at each station was clipped to ground level in a 30 cm circle. This clipping was necessary to prevent ants from entering the ant exclusion treatments, but it did not prevent their access to other treatments. Within each grid, species and treatments were assigned randomly to stations. Only one species was present at each station. Because the results of the 1982 experiment had indicated that percent seed removal was independent of seed density, a single density of 50 seeds per plate was used in this experiment. Each treatment was replicated three times in each grid, making a total of six replicates of each treatment/species combination. The experiment was initiated on July 12, 1983 and terminated on July 21, 1983. During this period the petri plates were checked daily to make sure no vegetation fell across the plates designed to exclude ants and to make a check of seed removal rates for those species with seeds large enough to be counted in the field. The weather throughout the experiment was hot and dry with no high winds or heavy rain. At the end of the experiment seeds were collected and counted as in 1982.

Because the 1982 and 1983 experiments were of unequal duration (six and nine days respectively) and because we wished to compare our results to other studies, rates of seed loss from each experiment are reported as the percentage of seeds removed/petri plate/day. We assumed an exponential decline and calculated daily removal as: $P = 100\,(1-(R)^{1/t})$, where P = the percentage of seeds removed/petri plate/day, R = the mean proportion of seeds remaining at the end of the experiment, and t = the duration of the experiment in days. All data analyses were performed using nonparametric procedures, as the data were generally not normally distributed.

Results

1982 Experiment. The experiment conducted in 1982 examined the effects of seed density, habitat type, and plant species on the loss of seeds to post-dispersal predators. Seed density had only a very minor effect on the percentage of seeds removed. Of the four species studied, only *Daucus* showed a significant density effect (Kruskal-Wallis test, $P<0.01$, all habitats combined). For this species, the percentage of seeds removed from the two seeds/plate treatment was significantly less than that for the 50 and 100 seeds/plate treatments (K-W test, $P<0.05$). The 50 and 100 seeds/plate treatments did not differ (K-W test, $P>0.05$). Density had no significant effect on seed removal for any other species ($P>0.05$). Thus, only two of the 12 possible density comparisons (four species, three densities/species) showed significant differences. This is only about one more significant difference than would be expected by chance at the 0.05 level. Therefore, we concluded that density effects were minor and in all further analyses we combined the three density treatments for each species to increase statistical power.

Habitat had a pronounced effect on the rate of seed removal (K-W test, $P<0.001$). The percentage of seeds lost for all species combined was greatest in the undisturbed vegetation ($P<0.01$) compared to small disturbances and the plowed field. Seed loss in the latter two habitats did not differ significantly ($P>0.05$). Each species individually showed the same general pattern of highest seed loss in the undisturbed vegetation and lowest seed loss in the plowed field (Table 2). However, among individual species, we were only able to detect a statistically significant habitat effect for *Verbascum* (K-W test, $P<0.01$) due to small sample sizes and fairly high variability within habitats.

Table 2. Average percent of seeds removed/petri plate/day from each of 3 habitats in 1982. Sample size for each species in each habitat is 15. Within a habitat, species' means followed by the same letter are not significantly different ($P>0.05$ by K-W test)

Habitat	*Tragopogon*	*Daucus*	*Oenothera*	*Verbascum*
Plowed field	3.1^{a}	1.1^{a}	5.9^{a}	2.3^{a}
Small disturbances	5.5^{ab}	0.8^{a}	8.0^{bc}	7.2^{c}
Undisturbed vegetation	8.4^{ab}	2.9^{a}	11.9^{b}	15.3^{b}

Within the natural vegetation and small disturbances, there were significant differences among the four species in the percentage of seeds lost over the course of the experiment (K-W test, $P<0.01$). In general, the small-seeded species (*Verbascum* and *Oenothera*) had higher rates of seed loss than did the large-seeded species *Tragopogon* and *Daucus* (Table 2). In the plowed field, which had the lowest overall rate of seed removal, there was no significant species effect ($P>0.05$).

Thus, the 1982 experiment demonstrated that there was appreciable post-dispersal predation on seeds, that seeds were removed most rapidly in undisturbed vegetation, that the four plant species differed in percentage of seeds removed, and that seed density had little or no detectable effect on seed predation levels over the range of densities tested.

1983 Experiment. The primary intent of the 1983 experiment was to determine whether ants or rodents were the major post-dispersal seed predators in old-fields and whether these predators foraged selectively among the plant species tested. Table 3 lists the mean percentage of seeds removed/petri plate/day for each treatment and species. In three of the six plant species tested (*Tragopogon*, *Daucus* and *Centaurea*), we found significant treatment effects ($P<0.01$, K-W test), demonstrating that there was differential removal of seeds by either ants or rodents.

Tragopogon seeds, which were by far the largest tested (Table 1), were eaten only by rodents and were not removed by ants (Table 3). When feeding on *Tragopogon*, rodents chewed the fruit open in a characteristic manner and left husks in and around the petri plates (both in 1982 and 1983). Live and snap traps set in the field in 1982 caught predominantly *Peromyscus maniculatus*. When *Peromyscus* were offered *Tragopogon* seeds in the laboratory they readily ate the seeds and the husks that were left looked identical to those found in the field, indicating that these mice were the likely vertebrate predators on *Tragopogon* seeds. *Daucus* seeds were also taken only from the treatments which allowed access to rodents (Table 3), and were not consumed by ants. The number of *Daucus* seeds removed, however, was much lower than that for *Tragopogon*.

Table 3. Average percent of seeds removed/petri plate/day in 1983. Sample size is 6 petri plates/species/treatment. Within a species, means followed by the same letter are not significantly different ($P > 0.05$ by K-W test)

Treatment	*Tragopogon*	*Dipsacus*	*Centaurea*	*Daucus*	*Oenothera*	*Verbascum*
Control	0^{a}	0.04^{a}	0.8^{a}	0.04^{a}	0.3^{a}	2.9^{a}
Ants only	0.04^{a}	0.2^{a}	45.8^{b}	0.2^{a}	2.4^{a}	4.3^{a}
Rodents only	6.3^{b}	0.5^{a}	0.3^{a}	1.1^{b}	1.1^{a}	1.4^{a}
Ants plus rodents	1.8^{b}	2.6^{a}	13.3^{c}	2.0^{b}	5.3^{a}	4.9^{a}

Table 4. Average percent seeds removed/petri plate/day for the 6 plant species studied in 1983. For those species whose predators could be identified, only treatments to which their predators had access were considered (i.e. "rodents only" and "ants plus rodents" for *Tragopogon* and *Daucus*, "ants only" and "ants plus rodents" for *Centaurea* and *Oenothera*). For *Verbascum* and *Dipsacus*, data from all treatments except the "control" were combined. Means followed by the same letter are not significantly different ($P > 0.05$ by K-W test)

Species	% seeds lost/day	n
Centaurea	19.5^{a}	12
Tragopogon	3.8^{b}	12
Oenothera	3.7^{b}	12
Verbascum	3.4^{b}	18
Daucus	1.5^{b}	12
Dipsacus	1.0^{c}	18

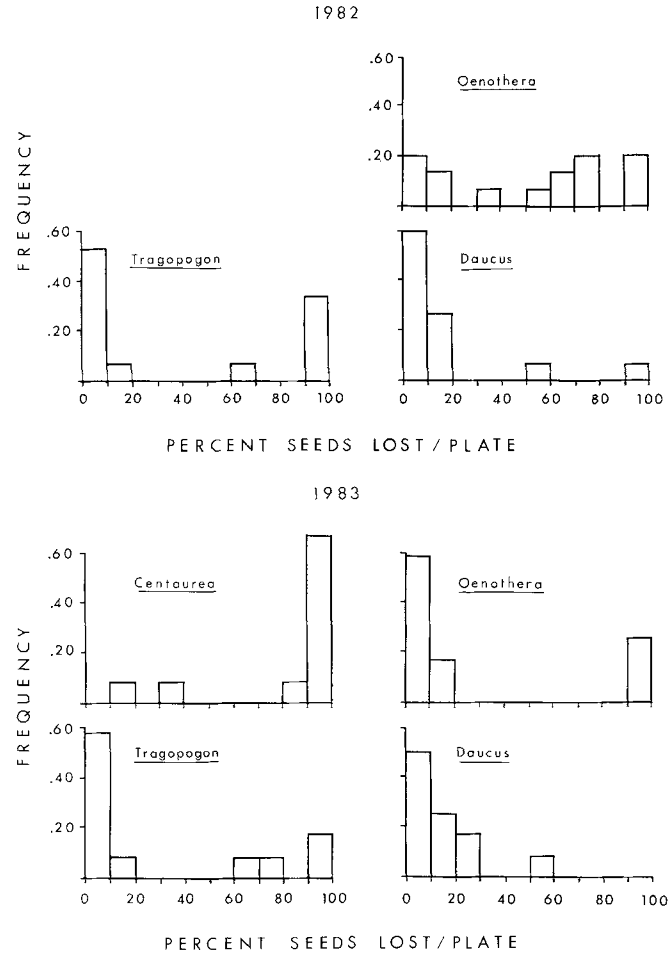

Fig. 1. Frequency distributions of the percentage of seeds removed from petri plates in 1982 and 1983 for species whose seed predators could be identified. The 1982 distributions were calculated using data from the undisturbed habitat, all seed densities combined (n = 15/species). *Centaurea* and *Oenothera* distributions in 1983 are from those treatments which allowed ants access to seeds; *Tragopogon* and *Daucus* distributions in 1983 are from treatments which allowed rodents access to seeds (n = 12/species)

Centaurea seeds were removed exclusively by ants and showed only minimal losses from the control and the rodents only treatments (Table 3). Ants observed removing *Centaurea* seeds from the petri plates were identified as *Myrmica lobicornus*. Other ant species present in the field included: *Formica lasioides*, *F. neogagates*, *Lasius umbiatus*, and *Monomorium minimum*, however it is not known whether these species also harvested seeds. Seed loss for *Centaurea* was the highest for any species tested (Table 4). *Centaurea* seeds are large enough to be counted in the field, so we were able to record seed predation on a daily basis for this species. After two days, 33% of all *Centaurea* seeds exposed to ants were missing. After three days, ants had removed 75% of the seeds.

The other three plant species (*Oenothera*, *Verbascum*, and *Dipsacus*) showed no significant treatment effects ($P >$ 0.05, K-W test, Table 3). This does not mean, however, that their seeds were not preyed upon. In three of the 12 *Oenothera* plates where seeds were exposed to either ants only or ants plus rodents, there were no seeds left at the end of the experiment. All other plates of *Oenotthera* seeds in the experiment contained between 41–50 seeds (mean = 47, 50 seeds present originally). Thus, ants appear to be the major agents removing *Oenothera* seeds. However, the extreme variance between replicates prevented us from detecting a statistically significant treatment effect of ants.

Very few *Dipsacus* seeds were lost from any of the treatments (Table 3), although there were husked seeds in one of the petri plates exposed to both ants and rodents. *Peromyscus* have been observed to feed on *Dipsacus* seeds in the laboratory and to leave husks similar to those found in the field (Mittelbach, personal observation).

Verbascum seeds were lost from the control as well as the predator treatments (Table 3). As a result, no significant treatment effects were found in this species ($P > 0.05$). The loss of *Verbascum* seeds from the control plates is perplexing. These seeds are by far the smallest tested (Table 1), and thus it is possible they were inadvertently washed or blown out of the petri plates over the course of the experiment. However, this seems unlikely as the weather throughout the experimental period was dry and moderately calm. Also, wind velocities near ground level are always quite low, so it is not likely that the seeds were blown out of the petri plates. It is also unlikely that large numbers of seeds were missed in counting since a previous check on counting methods showed 100% recovery of this species (see Methods). A more plausible explanation is that some other type of seed predator (e.g. mites?) was not excluded from the control treatments and may have removed *Verbascum* seeds from all of the treatments. The fact that in 1982 *Verbascum* seed losses were significantly higher in the natural vegetation than in small disturbances or the plowed field (Table 2) strongly suggests that a biological agent was responsible for the losses of *Verbascum* seeds we observed in both 1982 and 1983.

Among the four species whose seed predators could be identified (rodents for *Tragopogon* and *Daucus*, ants for *Centaurea* and *Oenothera*), the impact of predation was very patchy. Predators either removed most of the seeds from a petri plate, or very few of them, resulting in bimodal distributions of the percentage of seeds removed at a station (Fig. 1). Evidently, once a petri plate was discoved, the predators continued to forage from that plate until most of the seeds were removed. Our daily field observations clearly showed this to be the case for *Centaurea* and *Tragopogon* (whose seeds could be counted in the field). On average, >90% of the seeds of these species were removed from a petri plate within one day of when predation activity was first noticed at that plate. Thus, ants and rodents were treating each petri plate as a single prey clump. This pattern of predation may account for the general lack of seed density effects observed in 1982 (see O'Dowd and Hay (1980) for a similar result).

Discussion

The seed predation rates we observed in these experiments in old-field habitats are in general lower than those reported from studies in other systems. Among the species tested in this study, rates of seed loss (% removed/day) ranged from 1–6% in the plowed field, 1–8% in the small disturbances and 3–45% in the undisturbed vegetation. By comparison, Platt (1976) found that seed losses for *Mirabilis hirsuta* in a native lowa prairie ranged from 5–60% per day. Ants (*Formica fossaceps*) and rodents (possibly *Zapus hudsonicus*) were the major seed predators in Platt's study. Most other quantitive measures of seed predation rates are for desert or semi-arid habitats. Reported rates of seed loss in deserts range from 70–100% of seeds removed per day by rodents and 10–70% of seeds removed per day by ants (Brown et al. 1975; Reichman 1979; Abramsky 1983). Although these studies from arid environments have all been conducted with non-native seeds, other observations suggest that losses of native seeds in these habitats would also be high (Tevis 1958; Whitford 1978; Reichman 1981). Andersen (1982) measured seed removal rates by ants of 14 native plant species in arid regions of Australia and found that ants removed 30–45% of the seeds he presented in a day.

The fact that predation rates are higher for seeds in the desert than in old-fields is not surprising. In arid habitats, seeds provide one of the few food resources consistently available to ants and rodents. Consequently, desert faunas generally contain animals specifically adapted to finding and consuming seeds (e.g. heteromyid rodents and harvester ants in the American southwest). The seed predators observed in our study (*P. maniculatus* and *M. lobicornus*) are not seed specialists and instead have quite generalized and opportunistic diets (Howard and Evans 1961; Whitaker 1966; Kritzman 1974). Therefore, we might expect their impact on dispersed seeds to be less than that found in desert communities. Still, seed losses for some of the old-field biennials averaged an appreciable 10–20% day.

Rodents and ants foraging on seeds sometimes act as seed dispersers rather than seed predators. Rodents are known to cache or hoard seeds which may go uneaten (Howard and Evans 1961; Barry 1976; others) and ants have been reported to take seeds and then discard them (Bullock 1974; Culver and Beattie 1978; E.R. Heithaus, personal communication). In our study, there was no evidence that rodents were removing and hoarding seeds. Rather, most of the seeds fed on by *Peromyscus* were husked and eaten on the spot. Most cases of seed dispersal by ants involve seeds which have specialized structures (i.e. elaiosomes) which provide an incentive for ants to disperse them (Culver and Beattie 1978; Heithaus 1981; Buckley 1982; Westoby et al. 1982). The fate of seeds removed by the ants in our experiments is unknown as we did not follow foraging ants to their nest. However, none of the plant species we studied produce seeds specifically adapted for ant dispersal. Thus, it seems likely that seeds collected by ants in these experiments were used as a food source and that their removal should be viewed as seed predation rather than dispersal.

Rodents and ants fed selectively on seeds of the six biennial species tested. *Tragopogon*, which produces the largest seeds of the six plant species tested (Table 1), was preyed upon extensively by rodents in both 1982 and 1983. The exclosure experiments further showed that *Tragopogon* seeds were not removed by ants. The selective predation by rodents on *Tragopogon* is consistent with previous studies which suggest that rodents forage preferentially on large seeds (Soholt 1973; Hallagin 1974; Reichman 1977; Inouye et al. 1980; Abramsky 1983). It is reasonable to assume that *Tragopogon* seeds would provide rodents a higher energtic return/time spent handling than would small seeds such as those produced by *Oenothera* and *Verbascum*. The other species for which there was evidence of rodent predation were *Daucus* and *Dipsacus*. However, seeds of these species were consumed in far lower numbers than *Tragopogon*. *Dipsacus* and *Daucus* are, respectively, the second and fourth largest-seeded species of the six herbs tested. It appears then that old-field herbs producing relatively large seeds may be at greater risk to post-dispersal predation by rodents than are species with small seeds.

Ants foraged preferentially on *Centaurea* seeds, removing 75% of the seeds offered in three days. There was also evidence that ants removed seeds of *Oenothera*. Seeds of both *Centaurea* and *Oenothera* are substantially smaller than those of *Tragopogon* (Table 1), and there is some evidence from desert systems that ants tend to prefer smaller seeds than rodents (Brown et al. 1975; Campbell 1982; Abramsky 1983). However, it is difficult to account for the foraging preference of the ants in the old-field based solely on seed size. For example, *Dipsacus* seeds were not taken by ants, yet they are almost identical in size to the highly preferred *Centaurea* seeds (2.39 and 2.19 mg respectively). Likewise *Daucus* seeds, which are intermediate in size (0.9 mg), were not consumed by ants.

Selection of seeds by ants in desert systems appears to be based on a number of factors in addition to seed size. These factors include: seed distribution and abundance, seed morphology, and possibly nutritional quality (Tevis

1958; Pulliam and Brand 1975; Whitford 1978; Inouye et al. 1980; Rissing 1981; Anderson 1982; Buckley 1982). In those experimental studies where ants have shown pronounced size selection (e.g. Davidson 1978; Abramsky 1983), the ants were only given a choice between different sizes of the same type of seed.

One of the more pronounced features of seed predation observed in this study was the variability in predation intensity between sites. For example, of the 12 petri plates of *Centaurea* seeds exposed to ants in 1983, >95% of the seeds were removed from nine plates in four days. However, the three remaining plates of *Centaurea* seeds still contained 14, 60 and 80% of their seeds at the end of the nine day experiment. Marked patchiness in predation was also observed for *Tragopogon* and *Oenothera* seeds (Fig. 1). This variability in predation intensity occurred over a scale of 10–20 m, in what appeared to be a homogeneous section of field. Thus, seed predators have the potential to generate patchiness in the distribution of seeds within an old-field, and perhaps patchiness in the distribution of seedlings. Such spatial patchiness in seed predation may also allow seeds of species which are highly preferred by predators to escape predation.

There is a general pattern among weeky plants that those species with long-lived seeds that can remain viable in the soil for years, also produce comparatively small seeds (Grime 1979). Within the group of six biennial species tested, the two species with the smallest seeds (*Oenothera* and *Verbascum*) are known to have extremely long-lived seeds (>50 yrs, see Kivilaan and Bandurski 1973). Seeds of the other four species we studied have little or no longevity and generally remain viable in the field for < three yrs (Gross and Werner 1982). Originally, we hypothesized that old-field herbs producing large seeds would be most preferred by post-dispersal predators (based on energetic rewards) and would suffer the highest rates of seed loss. Therefore, one reason we might not see the evolution of seed longevity among these species is that their seeds are rapidly consumed by predators and do not enter the seed bank. However, the observed rates of seed predation among the six biennials tested do not show any clear pattern with seed size or longevity (see Tables 1 and 3). Species producing small seeds are just as likely to be eaten as large-seeded species (perhaps more so), although the animal responsible for the predation may differ.

It is possible that under natural conditions smaller seeds will more rapidly sift into the litter or be washed into soil crevasses (Grime 1979; Hopkins and Graham 1983). If this is true, small seeds could become less vulnerable to predators than larger seeds. Our experimental design necessarily restricted the movement of seeds by non-biological agents because we wanted to recover all seeds not removed by predators. If experiments can be designed which somehow allow seeds to move freely through the soil and litter, a seed-size effect on predation loss may be discovered. The evidence to date, however, suggests that the evolution of seed longevity among small-seeded herbs is not related to their vulnerabilities to post-dispersal predation. Other hypotheses which consider seed size vs. seed number tradeoffs (MacArthur 1972) may better account for the observed pattern between seed size and longevity.

Seed losses in 1982 were significantly less in the disturbed habitats (both large and small scale), than in the natural vegetation. Rodent trapping conducted at the end of the 1982 experiment documented that *Peromyscus* were more abundant in the natural vegetation than in the plowed field. Live and snap traps baited with peanut butter and oatmeal were placed within the grids established in both fields (six traps in the plowed field (4.7 traps/100 m^2) and 12 traps in the larger area of undisturbed vegetation (3.6 traps/100 m^2)). Over six nights of trapping, five *Peromyscus* were captured in the undisturbed vegetation. No mice were captured in the plowed field over the same time period. Similar observations of reduced *Peromyscus* densities in open habitats have been reported by Kaufman and Fleharty (1974); Holbrook (1978); Kaufman and Kaufman (1983); Price and Waser (1984). Ants were also observed to be less numerous in the plowed field. Although we did not take quantitative data on the abundance of ants in these habitats, we did observe that far fewer ants were attracted to peanut-butter baits placed in the plowed field as compared to the vegetation. Thus, the lower rate of seed predation found in the plowed field is likely due to the presence of relatively fewer predators in this habitat.

The reduced seed predation in the small disturbances as compared to the undisturbed vegetation is more surprising. The simulated animal disturbances were only 1 m in diameter and were surrounded by natural vegetation. Therefore, it would seem that rodents and ants could easily venture out into these disturbances from the nearby vegetation. In fact, Platt (1976) found predation on *Mirabilis* seeds by ants was actually higher on badger mounds than in the surrounding native prairie. However, many rodent species have been shown to respond to very small scale differences in microhabitat and some species avoid open areas the size of our disturbances (Rosenzweig 1973; Holbrook 1978; Price 1978; O'Dowd and Hay 1980; Thompson 1982a, b; and others). There is some evidence that rodents may limit their use of open space in response to increased predation risk in these areas; although the primacy of this factor in governing habitat use is debated (see Price and Brown 1983; Price 1984 for reviews). In any case, our data indicate that seeds dispersed to disturbed habitats in old fields are less likely to be consumed by post-dispersal predators than those which fall in undisturbed vegetation.

The results of these experiments demonstrate that the seeds of old-field plants are vulnerable to post-dispersal predation. While the seed removal rates in old fields are generally lower than those observed in more arid environments, some plant species (e.g. *Centaurea*) can lose a large proportion of their seeds to predators in a short time. Thus, while the total biomass of seeds removed by ants and rodents may be small, selective seed harvesting by these predators could potentially be an important factor determining the distribution and/or abundance of some old-field plants. Our data also suggest that the impact of post-dispersal predators on the structure of successional plant communities may increase with time. Seed removal rates in the newly plowed field were significantly lower than those in the undisturbed vegetation. Thus, as the diversity and cover of a successional plant community increases (due to the colonization and establishment of more plants), the intensity of seed predation and its affect on the community may also increase.

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