

Feeding Preferences of Weed Seed Predators and Effect on Weed Emergence

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We determined feeding preferences of invertebrate seed predators and the effect of seed predation on weed emergence. Feeding choice studies were completed with three species of common ground beetles: (*Amara aenea* DeGeer, *Anisodactylus sanctaecrucis* F., and *Harpalus pensylvanicus* DeGeer) (Coleoptera: Carabidae) and the northern field cricket (*Gryllus pennsylvanicus* DeGeer) (Orthoptera: Gryllidae). *Anisodactylus sanctaecrucis*, *H. pensylvanicus*, and the female and male *G. pennsylvanicus* consumed more redroot pigweed seeds compared with giant foxtail seeds; *A. aenea* seed consumption did not differ between these two weed species. All invertebrates consumed fewer velvetleaf seeds compared with redroot pigweed and giant foxtail seeds; however, when seed biomass was compared, *A. aenea* consumed similar biomass of velvetleaf, giant foxtail, and redroot pigweed, whereas *A. sanctaecrucis* and *H. pensylvanicus* consumed greater biomass of velvetleaf compared with giant foxtail seed. Seed burial depths of 0.5 or 1.0 cm reduced redroot pigweed and giant foxtail seed consumption by *A. aenea* and *A. sanctaecrucis* but not by the larger carabid beetle, *H. pensylvanicus*. In a greenhouse study, *A. sanctaecrucis* decreased total weed emergence by 15%, and *G. pennsylvanicus* females and males decreased weed emergence by 16 and 5%, respectively. Emergence of redroot pigweed, but not velvetleaf or giant foxtail, decreased when *A. sanctaecrucis* and the male *G. pennsylvanicus* were present, whereas the emergence of all three weed species decreased in the presence of the female *G. pennsylvanicus*. In field experiments, vertebrate access to velvetleaf seeds reduced emergence from 4 to 9% across field sites; invertebrate access reduced emergence 4 to 6%. Vertebrate access to giant foxtail seeds reduced emergence 3 to 7%, and invertebrate access reduced emergence 4 to 13%. These results suggest that predation of weed seeds by both vertebrates and invertebrates may reduce weed emergence and influence the weed community.

Nomenclature: Giant foxtail, *Setaria faberi* Herrm. SETFA; redroot pigweed, *Amaranthus retroflexus* L. AMARE; velvetleaf, *Abutilon theophrasti* Medic. ABUTH.

Key words: Biological control, Carabidae, granivory, Gryllidae, integrated weed management, seed consumption, small mammals, weed population dynamics.

Weeds are the primary pest problem in North American agricultural cropping systems. It is estimated that in the United States, the total costs associated with losses, damage, and control of weeds in crops each year reaches \$27 billion (Pimentel et al. 2005). The integration of additional weed management methods, such as biological and cultural control, could reduce weed management costs and mitigate crop yield and quality losses due to weeds (Buhler et al. 1997; Hall et al. 2000).

Seed predation (i.e., the consumption and destruction of weed seeds by granivorous insects and mammals) is one biological control tactic that may contribute to reducing our reliance on mechanical and chemical weed control tactics (Menalled et al. 2006; Tooley and Brust 2002). Seed predation can occur both on the plant (predispersal) and after the seeds have dispersed and fallen from the mother plant (postdispersal). Birds, rodents, and insects are important postdispersal weed seed predators in natural as well as agricultural habitats (Heggenstaller et al. 2006; Inouye et al. 1980; Louda 1989; Menalled et al. 2007). For example, rodents were significant seed feeders in no-tillage, but not in conventional tillage, systems (Brust and House 1988). In Ontario, mice consumed 10 to 22% of the available barnyardgrass [*Echinochloa crus-galli* (L.) Beauv.] and common lambsquarters (*Chenopodium album* L.) seeds in no-till corn (*Zea mays* L.) and soybean [*Glycine max* (L.) Merr.] fields (Cromar et al. 1999). In Oregon, 99.8% of barnyardgrass, redroot pigweed (*Amaranthus retroflexus* L.), and common lambsquarters seed rain in alfalfa (*Medicago sativa* L.) fields

was consumed by the field mouse (*Peromyscus* spp.; Radosovich et al. 1997).

Many insects from the families Coleoptera and Hymenoptera eat weed seeds once they have fallen to the ground (Menalled et al. 2006). Several genera of carabid beetles have been identified as seed predators in North America, including *Harpalus caliginosus*, *Harpalus erraticus*, *Harpalus pensylvanicus*, *Harpalus rufipes* + spp., *Amara cupreolata* + spp., and *Anisodactylus mercula* + spp. (Tooley and Brust 2002). The omnivorous field cricket, *Gryllus pennsylvanicus* Burmeister, is another invertebrate that consumes weed seeds in North American farmlands including common ragweed, velvetleaf, redroot pigweed, large crabgrass [*Digitaria sanguinalis* (L.) Scop.], and giant foxtail seeds (Brust and House 1988; Carmona et al. 1999).

Relatively few studies have been completed on the influence of seed predation on weed communities in agricultural fields, and these do not indicate a simple, direct relationship between seed predators and plant populations (Brust 1994; Tooley and Brust 2002). Some authors suggest that when seed densities are high, postdispersal seed predation rates do not affect weed populations because intense competition for suitable recruitment microsites limits weed emergence (Anderson 1998). However, others suggest that competition for suitable microsites for seedling recruitment in farm fields is minimal (Crawley 1992), and an increase in total seed predation, or selective seed predation, may alter the weed community. Empirical studies and modeling have shown postdispersal seed mortality to be one of the most sensitive parameters in predicting velvetleaf and green foxtail densities the following year (Cardina et al. 1996; Jordan et al. 1995; Westerman et al. 2005). Therefore, the objectives of our research were to determine the feeding preferences of common invertebrate seed predators in feeding-choice studies, determine whether these insects would feed on buried weed seeds, and assess

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whether weed seed predation could alter weed community composition.

Materials and Methods

Insect Collection. The spring-active granivore carabid beetles (*Amare aenea* and *Anisodactylus sanctaecrucis*) were collected using pitfall traps in fallow corn and soybean fields in May and June 1998, and the fall-active carabid beetle (*Harpalus pensylvanicus*) was collected in a soybean field in September 1998 and 1999. Male and female field crickets (*Gryllus pennsylvanicus*) were captured by hand in August and September 1999 from their diurnal resting places (beneath boards, under debris, etc.). Both male and female crickets were included in these tests because females consume larger numbers of weed seeds than males do in the same time period (Carmona et al. 1999). All invertebrates were collected in both years at the Michigan State University Agronomy Farm located in East Lansing, MI. Carabid beetles and field crickets were allowed to acclimate for 48 h in the laboratory in 7.5-L plastic containers containing moist soil before study initiation. At the conclusion of each study, carabid beetles in each study were sent to a specialist¹ for positive identification.

Feeding-Choice Study. Feeding-choice studies for the three carabid beetle species collected and the field cricket were conducted in a growth chamber (22 C, 60% humidity) with a 16 h photoperiod. All insects were starved for 24 h before testing. Individual carabid beetles were then placed in feeding dishes (18 cm diam and 8 cm high) containing 300 g of moist steam-sterilized sandy loam soil (84% sand, 10% silt, and 6% clay, 2% organic matter). Before the study, the soil was sifted using a 1.2-mm opening screen sieve to remove organic materials that could otherwise provide an alternate food source for the insects. Seeds of three common summer annual weeds, giant foxtail, redroot pigweed, and velvetleaf were scattered over the soil surface in each dish and one carabid beetle was added. Predation of these weed species, but not feeding preferences, has been reported by other researchers (Cardina et al. 1996; Lund and Turpin 1977; Tooley and Brust 2002). Seeds were collected in the fall from fields at the Agronomy Farm in the year before study initiation and stored in a cooler at 4 C. *Anisodactylus sanctaecrucis* were given a mixture of 100 velvetleaf, 100 giant foxtail, and 100 redroot pigweed seeds, whereas *A. aenea* and *H. pensylvanicus* were given a mixture of 50 velvetleaf, 100 giant foxtail, and 100 redroot pigweed seeds. Seed density was based on preliminary studies where seed consumption of a single species was measured over 24 h. Carabid beetles remained in the dishes for 48 h before they were removed. Carabid beetles were then sent to an appropriate specialist¹ for confirmation of species identification.

Field crickets were acclimated and handled as above before testing. A mixture of 100 giant foxtail, 400 redroot pigweed, and 100 velvetleaf seeds was placed on the soil surface of the feeding dishes described above. A higher number of redroot pigweed seeds were necessary due to documentation of higher consumption rates of this species by field crickets, especially females (Carmona et al. 1999). When a feeding trial was terminated, soil was sifted using a 1.2-mm opening screen sieve to recover remaining intact seeds. There were 10 replications of each insect species and two control dishes to

measure seed recovery from the soil in the absence of insects, and the study was repeated twice.

Feeding-Depth Study. A 1.5-cm layer of moist steam-sterilized sandy loam soil was placed in the bottom of each feeding dish (as described above). In each feeding dish, seeds of velvetleaf, giant foxtail, or redroot pigweed were scattered on the soil surface and 0.5 or 1.0 cm below the soil surface. If seeds were placed on the soil surface, insects were allowed to acclimate in the dishes for 24 h before adding the seeds and then allowed to forage for 48 h. If seeds were buried, the insects were placed in the dish and allowed a total of 72 h in which to acclimate and forage for the seeds. The dishes were placed in a growth chamber (22 C, 60% humidity) with a 16 h photoperiod and remained there for the duration of the experiment. Seed numbers were selected based on the feeding-preference study results. In the case of *A. aenea* and *A. sanctaecrucis*, 50 giant foxtail, redroot pigweed, or velvetleaf seeds were placed in a dish, either on the soil surface or at one of the seeding depths. For *H. pensylvanicus*, 50 giant foxtail, 100 redroot pigweed, or 50 velvetleaf seeds were placed in a dish. Soil was sifted soil using a 1.2-mm-opening screen sieve to recover remaining intact seeds. There were six replications of each insect–weed species–depth combination and two control dishes to measure seed recovery from the soil in the absence of insects, and the study was repeated twice.

Greenhouse Study. This study was conducted from April to June and August to October in a greenhouse at Michigan State University. The timing of the experiment was based on the time of optimal activity of the seed predators tested in this study (Rivard 1966; Tooley and Brust 2002). *Amare aenea* and *A. sanctaecrucis* were studied in the spring, and *H. pensylvanicus* and male and female common field crickets were studied in the fall. Collected insects were stored and acclimated as described previously.

Plastic boxes (40 by 60 by 25 cm) were placed side by side on greenhouse benches. Twenty drainage holes were drilled in the bottom of each box using a 2-mm drill bit to preclude insects from escaping the boxes through the holes. The bottom 14 cm of each box was painted black to eliminate the effect of light on root growth near the perimeter of the box, and 14 cm of moist, sterilized, sandy loam soil was placed in each box, acting as the base layer. The first watering in each box was 1.3 cm; thereafter, 0.6 cm of water was applied daily. A 38 by 68-cm hole was cut out of the plastic lid, and a screen was hot-glued on the inside of the lid to eliminate any space that would allow insects to escape from the box. Daily watering took place through the screened lid until the lids were removed 1 wk after experiment initiation.

The experimental design was a three factor factorial arranged in a randomized complete-block design with six replications and was repeated in time. The first factor was the presence or absence of an insect, the second factor was the weed species (giant foxtail, velvetleaf, or redroot pigweed), and the third factor was the weed seeding depth (surface or 0.5 cm). Four *A. sanctaecrucis*, six *A. aenea*, four *H. pensylvanicus*, or one male or one female *G. pennsylvanicus* were added to each box. Only one cricket could be placed in each box because male crickets are territorial (Carmona et al. 1999). Seed mixtures for the carabid beetle boxes consisted of 150 redroot pigweed, 150 giant foxtail, and 60 velvetleaf

seeds. Because of the high consumption rate of redroot pigweed by field crickets, 500 redroot pigweed seeds were sown in the cricket boxes. In preliminary germination tests, velvetleaf, giant foxtail, and redroot pigweed seed germination was 54, 40, and 55% respectively (data not shown). When seeds were placed on the soil surface, insects were placed in the box for a 24 h acclimation period before sowing the seed mixture, and remained in the box for 48 h after sowing the seeds. When weed seeds were buried, the seed mixture was sown on the base layer, 0.5 cm of soil was added and leveled, and 1.3 cm of water was applied. The insects were then placed immediately in the box to minimize the effect of imbibed seeds on seed predation (Cardina et al. 1996). Insects remained in the boxes for 72 h to allow for the 24 h acclimation period and a 48 h feeding period, and insects were then killed by the addition of 0.17 g of terbufos, a soil insecticide, to the soil surface of each box. The insecticide was leached into the soil with 1.3 cm of water. Cumulative weed emergence was measured weekly from 1 to 5 wk after planting. Seedlings were marked by placing a dot on the leaf surface using a fine-point permanent marker to ensure that new emergence and death of seedlings could be accounted for.

Field Studies. Field studies were conducted in no-till corn fields from fall 1997 to fall 1998 and from fall 1998 to fall 1999. The first year field study was conducted at the Michigan State University Crop and Soil Science farm. The field was 2 ha and the soil type was a Capac silty clay loam (Aeric Ochraqualf, fine-loamy, mixed mesic) with 3.7% organic matter and pH 7.2. The second year research was conducted at three sites in no-till corn fields. The sites were site 1, the Michigan State University Crop and Soil Science Farm, East Lansing; site 2, a field site near Sunfield, MI; and site 3, the Saginaw Valley Dry Bean and Sugar Beet Research Farm, Saginaw, MI. Site 1 was 2 ha, and the soil type at East Lansing was the same as the previous year. At site 2, the field site was 10 ha, and the soil type was a Lapeer Loam (Mollic Haplaquept, coarse-loamy, mixed mesic) with 2.6% organic matter, and pH 6.1. At site 3, the field was 2 ha, and the soil type was a Misteguay silty clay loam (Aeric Endoaquept, fine-loamy, mixed mesic) with 3.0% organic matter, and pH 7.9. The experiment each year was a two factor factorial arranged in a randomized complete-block design with nine replications during the first year, and 12, 12, and 9 replications at sites 1, 2, and 3, respectively, during the second year. The factors were enclosure type and weed seed species.

Enclosures. The three enclosure types were based on previous work by Marino et al. (1997). The enclosures were invertebrate access only, invertebrate and vertebrate access (no enclosure), and no predator access (total exclusion) as a control treatment. Cages measuring 38 by 69 by 25 cm were constructed of 1.3-cm hardware cloth. An opening measuring 20 by 15 by 20 cm was cut in the top of each cage to allow for removal of weed seedlings. These openings were held shut with cable ties. Cages that excluded both vertebrates and invertebrates included a 20-cm strip of thick plastic treated with a no-stick spray placed around the bottom of the cage; 10 cm of plastic was located on the inside and 10 cm on the outside of the cage. Cage edges were placed 2.5 cm into the soil to minimize burrowing of predators into the feeding area. Cages were placed in a grid pattern at each field site,

beginning 12 rows from a field edge and 20 m from the headland. Each replication consisted of a row of cages placed between two corn rows. There was a minimum of four corn rows between each replication of enclosures; the number of corn rows was dependent on tire spacing on the combines to prevent cage disturbance during corn harvest. To ease placement of cages into the soil, a 15 by 27-cm metal L was constructed, which enabled us to make an indentation into the soil at the desired depth. Soil displaced by removal of the L was pressed back into place, holding soil disturbance to a minimum, and helping to set the cage in the soil. Feeding sites without cages (no enclosure) were marked with flags. Enclosures remained in the field for 12 mo.

Weed Seeding and Emergence. Two hundred giant foxtail, velvetleaf, or redroot pigweed seeds were sown into the enclosures in late August of each year at the beginning of seed rain. Giant foxtail, velvetleaf, and redroot pigweed seeds were sown in separate enclosures. A fourth treatment was included to allow us to estimate weed emergence from the seed bank with and without predator access. Seeding rates were increased to 400 velvetleaf, 400 redroot pigweed, and 400 giant foxtail seeds in the second year of this study. Weed seedlings were counted every 2 wk from September to November and again from April to August. Emerged seedlings were accessed through the openings cut in the top of the cage and were removed from the cage area by pulling (in moist soil) or cutting off the weeds at the soil surface (dry soil). Care was taken to minimize soil disturbance. Seedling counts were then combined to determine total emergence.

Pitfall Traps. To monitor the activity-density of invertebrate seed predators, pitfall traps (11 mm diam by 14 mm deep) were set 1 cm below the soil surface at each field site in the second year only because of budget limitations. Cups contained no killing agents, and beetles were released close to their capture location to avoid depletion of seed predators. Twenty pitfall traps were placed at each site and monitored daily for 5 consecutive d mo^{-1} from August to November and again from March to August for a total of 50 trap-days (5 d mo^{-1}) at each site.

Rodent Trapping. To monitor the activity-density of rodents, 36 Sherman traps were placed in a grid pattern at each of the three field sites in the spring of 1999 only. The traps were opened once for 5 consecutive d each month from March to August 1999 for a total of 30 trap-days. The traps, baited with old-fashioned oats, were opened in the evening and checked early in the morning. Rodents were released in the same area daily.

Statistical Analysis. All analyses were conducted using SAS.² In the field studies, weed emergence from the nonseeded control for each enclosure treatment was subtracted from weed emergence for the seeded treatments in each enclosure before analysis. Data were transformed using ARCSINE, and an ANOVA was conducted on the transformed data in each study. Differences among treatments were separated by Fischer's Protected LSD test ($P = 0.05$); nontransformed data are reported in this article. In the field studies, data were not combined over year and location because of the existence

Table 1. Mean number of seeds and estimated biomass of velvetleaf (ABUTH), redroot pigweed (AMARE), and giant foxtail (SETFA) seeds consumed by adult carabid beetles, *Amara aenea*, *Anisodactylus sanctaerucis*, and *Harpalus pensylvanicus*, and adult female (♀) and male (♂) field cricket *Gryllus pensylvanicus* in a 48-h feeding-choice study.^{a-d}

Invertebrate	Seed			Biomass		
	ABUTH	AMARE	SETFA	ABUTH	AMARE	SETFA
	no.			mg		
<i>A. aenea</i>	2 b	32 a	33 a	17 a	12 a	13 a
<i>A. sanctaerucis</i>	4 c	78 a	40 b	34 a	29 a	16 ab
<i>H. pensylvanicus</i>	7 c	89 a	60 b	60 a	33 ab	24 b
<i>G. pensylvanicus</i> ♀	4 c	322 a	63 b	34 b	119 a	25 b
<i>G. pensylvanicus</i> ♂	1 c	262 a	55 b	8 b	97 a	22 b

^a Means followed by the same letter are not significantly different at P = 0.05. Comparisons of weed seed consumption are valid only within each insect species.

^b Mean seed biomass (mg) of 100 seeds: SETFA, 40 mg/100 seeds; ABUTH, 850 mg/100 seeds; AMARE, 37 mg/100 seeds.

^c *Amara aenea* and *H. pensylvanicus* were given 50 ABUTH and 100 SETFA and AMARE seeds. *Anisodactylus sanctaerucis* were each given 100 ABUTH, 100 SETFA, and 100 AMARE seeds. *Gryllus pensylvanicus* were each given 100 ABUTH, 100 SETFA, and 400 AMARE seeds.

^d WSSA-approved letter code for weed names.

of significant interactions between year and location and treatment.

Results and Discussion

Feeding Choice Study. The number of weed seeds consumed and the estimated biomass of weed seed consumed by the adult carabid beetles and the male and female field cricket are presented in Table 1. *Amara aenea* consumed more giant foxtail and redroot pigweed seeds compared with velvetleaf seeds, which could have been due to density-dependent consumption because the number of velvetleaf seeds presented were half that of giant foxtail and redroot pigweed seeds. *Anisodactylus sanctaerucis* consumed more redroot pigweed compared with giant foxtail seeds (Table 1), and this was not due to density-dependent availability because 100 seeds of each species were presented. These two carabid species have been reported to consume redroot pigweed and common ragweed seeds (Brust and House 1988), but feeding preferences have not been reported previously. *Harpalus pensylvanicus* consumed more redroot pigweed seeds than giant foxtail seeds (Table 1). All carabid beetle species consumed fewer velvetleaf seeds compared with the other two weed species; however, when seed biomass is compared, *Amara aenea* consumed similar biomass of velvetleaf, giant foxtail, and redroot pigweed, whereas *A. sanctaerucis* and *H. pensylvanicus* consumed greater biomass of velvetleaf compared with giant foxtail seed. Most feeding preference trials are based on the number of seeds consumed (Lund and Turpin 1977; Tooley and Brust 2002); however, this should not be the only measurement determining feeding preference. Seed predators may prefer larger seeds or seeds with a high protein or caloric content because these seeds provide a high-energy return for the time spent in handling (Brust and House 1988).

Female and male *G. pensylvanicus* preferred redroot pigweed seeds to that of velvetleaf or giant foxtail (Table 2). *G. pensylvanicus* consumed more redroot pigweed seeds and greater redroot pigweed seed biomass compared with giant foxtail and velvetleaf seeds (Table 1). Density-dependent feeding may have occurred because redroot pigweed seed numbers were four times that of giant foxtail or velvetleaf seeds, although seeds of all species remained in the dishes after the feeding period. Field crickets have been reported to remove a substantial portion of weed seeds, especially common ragweed and redroot pigweed seeds (Brust and

House 1988); female crickets consumed 223 redroot pigweed seeds in a 24 h period in the laboratory (Carmona et al. 1999). The time of maximum feeding for the northern field cricket would be in the fall, coinciding with seed rain of these summer annual weed species in agroecosystems.

Brown et al. (1975) and Brust and House (1988) hypothesized that differences in weed seed consumption among soil arthropod groups was a function of both the arthropod and the seed size. Small seeds, such as giant foxtail (~0.4 mg seed⁻¹) and redroot pigweed (~0.37 mg seed⁻¹) are easily transported but low in energy, whereas large seeds are high in energy but difficult to transport (Brown et al. 1975). Furthermore, weed seeds, such as velvetleaf, may be more difficult for small predators because of the relatively large seed size and the hard seed coat, which makes it difficult for the predator to reach the endosperm (Brust and House 1988; Carmona et al. 1999; Kremer and Spencer 1989; Tooley and Brust 2002). Other factors may influence seed preference including proportion of endosperm to seed coat, as well as toxicity of seeds (Tooley and Brust 2002).

Feeding Depth Study. Seed placement influenced weed seed consumption by the carabid beetles (Table 2). *Amara aenea* consumed 23% of the redroot pigweed seeds sown on the soil surface but consumed 1% or less of seeds placed below the soil surface. The consumption of giant foxtail seeds by *A. aenea* was greater on the soil surface compared with predation of seed 1.0 cm below the soil surface. Velvetleaf seed was consumed when placed on the soil surface or at a 0.5-cm burial depth. Consumption of redroot pigweed and velvetleaf seeds by *A. sanctaerucis* occurred only on the soil surface, and giant foxtail seed consumption was greater at the surface than at the 1.0 cm depth (Table 2). *Anisodactylus sanctaerucis* and *A. aenea* consumed fewer seeds in this study compared with seeds placed on the surface in the feeding preference study (Table 1). These studies were completed in the same year, and the carabid beetles were collected from the same environment. Insect starvation and feeding periods, growth chamber and settings, as well as dimensions of the foraging and seed placement area were identical in both studies. It is possible that a feeding difference between male and female *A. aenea* and *A. sanctaerucis* exists and is yet undocumented. Another possibility is that the insects were at a different maturity level in each study. Carabids may consume fewer seeds as they approach diapause compared with seed consumption during

Table 2. Mean number of weed seeds consumed by three carabid beetle species, *Amara aenea*, *Anisodactylus sanctaerucis*, and *Harpalus pensylvanicus* at burial depths of 0, 0.5, and 1.0 cm.^{a-d}

Invertebrate	ABUTH			AMARE			SETFA		
	0.0	0.5	1.0	0.0	0.5	1.0	0.0	0.5	1.0
	% consumed								
<i>A. aenea</i>	2 a	1 a	0 a	23 a	1 b	0 b	12 a	4 ab	0 b
<i>A. sanctaerucis</i>	4 a	0 b	0 b	22 a	0 b	0 b	17 a	3 ab	0 b
<i>H. pensylvanicus</i>	2 a	8 a	11 a	57 a	33 b	40 ab	72 a	78 a	76 a

^a Means followed by the same letter are not significantly different at P = 0.05. Comparisons of weed seed consumption are valid only within each insect and weed species.

^b Insects were allowed to acclimate in the dishes for 24 h before adding weed seeds to the soil surface and then allowed to forage for 48 h. If the weed seeds were buried below the soil surface, the insects were allowed a total of 72 h in which to acclimate and forage for the seeds.

^c *Amara aenea* and *A. sanctaerucis* were given 50 ABUTH and 50 SETFA and 50 AMARE seeds. *H. pensylvanicus* were each given 50 ABUTH, 50 SETFA, and 100 AMARE seeds.

^d WSSA-approved letter code for weed names.

the breeding and egg-laying season (Holland 2002; Tooley and Brust 2002).

Seed consumption by *H. pensylvanicus* in the feeding-depth study was similar to consumption in the feeding-preference study. *Harpalus pensylvanicus* consumed seed of all weed species from all depths. Giant foxtail consumption was greater from the soil surface compared with seed buried at 0.5 cm (Table 2). Burrowing of this beetle species to a 45 cm depth has been reported (Holland 2002), and seed predation by this carabid species could reduce weed seeds in the upper portion of the soil profile.

Greenhouse Study. There was a significant weed emergence by burial depth interaction for all three weed species when averaged over the presence-absence of insects for each experiment (data not presented). Emergence of velvetleaf was 21% greater from a seeding depth of 0.5 cm compared with emergence from the soil surface, when averaged over all insect experiments. These results support those of Buhler et al. (1997), where germination of velvetleaf seeds decreased when placed on the soil surface. Giant foxtail and redroot pigweed emergence was similar when seeds were sown on the surface or at a 0.5-cm depth (data not shown). Wiese and Davis (1987) and Siriwardana and Zimdahl (1983) concluded that 1 cm was optimal for redroot pigweed emergence, whereas in previous research, emergence of giant foxtail was greatest at a 1 cm depth (Fausey and Renner 1997).

Anisodactylus sanctaerucis decreased total weed emergence by 15%, and *G. pennsylvanicus* females and males decreased weed emergence by 16% and 5%, respectively (Table 3). Emergence of redroot pigweed, but not of velvetleaf or giant foxtail, decreased when *A. sanctaerucis* and the male *G. pennsylvanicus* were present, whereas the emergence of all three weed species decreased in the presence of the female *G. pennsylvanicus* (data not shown). As expected from the low weed seed consumption rates detected for *A. aenea*, this carabid species did not affect weed seedling emergence (Table 3). Based on the results of the feeding trials, we hypothesized that *H. pensylvanicus* would reduce emergence of all three weed species; however, this did not occur (Table 3). A possible explanation for the lack of impact of *H. pensylvanicus* on weed seedling emergence could be because, during this study, this carabid species was closer to diapause, which may have led to lower seed consumption. Alternatively, low soil moisture or high temperatures in the greenhouse may

have reduced seed consumption by this hydrophilic beetle (Holland 2002).

Field Studies. First-Year Field Site. Emergence of velvetleaf and giant foxtail was affected by predator exclusion type (Table 4). Allowing only invertebrate access to the seeds did not reduce velvetleaf or giant foxtail emergence compared with the control treatment (complete exclusion). However, velvetleaf emergence decreased when both vertebrates and invertebrates were allowed access to the seeds, implying that vertebrates were consuming velvetleaf seeds. In contrast, giant foxtail emergence decreased from 36% in the total exclusion to 23% in the invertebrate access exclusion. Giant foxtail emergence decreased by an additional 2% when vertebrates were also allowed access to the seeds. These results suggest that invertebrates were largely responsible for the decrease in giant foxtail emergence the following spring and summer. Only one or two redroot pigweed seedlings emerged, so the effect of seed predation on this species could not be evaluated (data not presented).

Second-Year Field Sites. Redroot pigweed emergence was very low at all three sites and no significant differences were detected among treatments (data not presented). Soil beneath all of the complete exclusions at site 1 was removed to a 2.5-cm depth in August and intact seeds extracted and counted. An average of 9 velvetleaf, 25 redroot pigweed, and 1 giant foxtail seed were counted in these soil samples. It is unlikely that seed loss from our sample units occurred through wind or soil dispersal because there was a 7.6-cm band of plastic around the base of each total exclusion treatment to prevent washing and blowing, and the cage edges were set 2.5 cm in the soil. However, weed seeds probably moved during rainfall

Table 3. Invertebrate effect (i.e., present or absent) on weed emergence combined over three weed species: velvetleaf, redroot pigweed, and giant foxtail.

Invertebrate ^a	Present	Absent	P value
	% emergence		
<i>A. aenea</i>	38	41	0.0985
<i>A. sanctaerucis</i>	25	40	0.0235
<i>H. pensylvanicus</i>	34	39	0.2087
<i>G. pennsylvanicus</i> ♀	25	41	0.0001
<i>G. pennsylvanicus</i> ♂	36	41	0.0189

^a ♀, female; ♂, male.

Table 4. Emergence of velvetleaf (ABUTH) and giant foxtail (SETFA) from the fall seeding in the first year field site.^{a,b}

Organism access	% emergence	
	ABUTH	SETFA
None	16 a	36 a
Invertebrate	16 a	23 ab
Invertebrate + vertebrate	7 b	21 b

^a Means in the same column with the same letter are not significantly different at $P = 0.05$.

^b Seeds were sown in August of 1997 and weed emergence measured from August 1997 through July 1998.

and snow melt below 2.5 cm in the soil via macropores and cracks in the soil. Buhler and Hartzler (2001) recovered 38 and 49% of velvetleaf and giant foxtail seeds, respectively, after mixing weed seeds to a 5-cm soil depth and excavating to a 7.5-cm soil depth 1 yr later. Alternatively, redroot pigweed seeds may have decayed on the soil surface or been eaten by earthworms or burrowing insects because our enclosures did not have a bottom.

Velvetleaf emergence decreased by 4 and 6% at two sites when invertebrates were allowed access to the seeds, and emergence declined by another 4% at site 1 when vertebrates were also allowed access to the seeds (Table 5). At site 3, velvetleaf emergence decreased by 8% when both vertebrates and invertebrates were allowed access to seeds compared with the total enclosure treatment. Therefore, vertebrates reduced velvetleaf emergence by 50, 0, and 100% at sites 1, 2, and 3, respectively.

Giant foxtail emergence at site 2 decreased by 4% in the invertebrate access only; emergence did not decline further when vertebrates were allowed access to the seeds. In contrast, giant foxtail emergence at sites 1 and 3 decreased when vertebrates and invertebrates could access the seeds compared with the total enclosure treatment, implying that vertebrates were responsible for predation on giant foxtail seeds at these two sites (Table 5). In desert systems, rodents prey selectively on larger-seeded species, whereas the ants harvest the smaller seeds of certain abundant species (Inouye et al. 1980; Reichman 1979). Our results in the feeding, greenhouse, and no-till field studies suggest that velvetleaf and giant foxtail seeds are eaten by invertebrates and vertebrates, depending on the field site.

The activity–density of the carabid beetle seed predators (*A. aenea*, *A. sanctaecrucis*, and *H. pensylvanicus*) measured at our three field sites was very low and did not capture field crickets (Table 6). Three factors could explain the low number of these carabid beetle species trapped in this study. First, the

5-d trapping period each month may not have been coincident with peak seasonal activity–density (Gallandt et al. 2005). Second, pitfall trap numbers can be misleading because carabid movement is strongly affected by hunger levels (Holland 2002). Finally, few of these three carabid beetle species may have been present within these field sites, as field borders may have provided food sources (Holland 2002; Menalled et al. 2006). Site 1 was bordered by two mown grassy borders and two field sides planted to no-till soybeans, whereas site 3 had three mown grassy borders with the fourth border plowed and planted to soybeans and corn. Site 2 has been farmed as a no-till field for 7 yr and had a grassy–weedy border along one edge, a road on one edge, and the remaining edges planted to soybeans.

Only one rodent species, the white-footed mouse (*Peromyscus leucopus* Fischer: Cricetidae), was captured and released at each field site (Table 6). This rodent is common in agricultural fields (Burt and Grossenheider 1980). Rodent capture was greater at site 3 than at the other two sites in the second year, and allowing vertebrate access to our seeds reduced velvetleaf and giant foxtail emergence compared with the total enclosure treatment at this site (Table 5).

Overall, our laboratory, greenhouse, and field studies indicate that invertebrates consume seed of all three weed species from the soil surface and some seed from shallow burial depths. It would be of interest to know whether *G. pennsylvanicus* consume buried weed seed because seed consumption by the larger carabid beetle *H. pensylvanicus* did not differ between seed scattered on the soil surface or buried at a 1 cm depth. Should feeding preferences for these seed predators be based on seed number or seed biomass consumption? One seed produces one weed, and thus a farmer may prefer a seed predator to consume many small seeds instead of one single large seed, unless of course the large-seeded species is more difficult to control than the small-seeded species. Seed predation may be one reason why weed pressure declines over time in no-till agroecosystems, because most weed seeds are disseminated on the soil surface where they are available to seed predators (Radosevich et al. 1997). Consumption of weed seeds by these three carabid beetle genera and field crickets, as well as consumption of seeds by the white-footed mouse had some influence on the composition of the weed community at these field sites. Further field studies are needed to confirm the fate of weed seeds following seed rain, and the role of weed seed predation in seed mortality and the composition of weed communities in agricultural cropping systems.

Table 5. Emergence of velvetleaf (ABUTH) and giant foxtail (SETFA) in three fallow no-till corn fields^a from the fall seeding in the second year field sites.^{b–d}

Organism access	ABUTH			SETFA		
	Site 1	Site 2	Site 3	Site 1	Site 2	Site 3
	% emergence					
None	9 a	8 a	8 a	10 a	7 a	9 a
Invertebrate	5 b	2 b	8 a	9 a	3 b	8 a
Invertebrate + vertebrate	1 c	2 b	0 c	2 c	2 b	5 b

^a Site 1 = MSU, East Lansing, MI; site 2 = Sunfield, MI; site 3 = Saginaw Valley Dry Bean and Sugar Beet Research Farm

^b Seeds were sown in August of 1998 and weed emergence measured from August 1998 through July 1999.

^c ABUTH, *Abutilon theophrasti* (velvetleaf) $n = 400$ seeds; SETFA, *Setaria faberi* (giant foxtail) $n = 400$ seeds; AMARE, *Amaranthus retroflexus* (redroot pigweed) $n = 400$ seeds.

^d Means with the same letter are not significantly different at $P = 0.05$. Comparisons are not valid between sites.

Table 6. Total number of two spring common ground beetle species (*A. aenea* and *A. sanctaecrucis*), one fall common ground beetle species (*H. pennsylvanicus*), and white footed-mice (*Peromyscus leucopus*) captured and released from the sites in the second year studies.^a

Predator	Site 1	Site 2	Site 3
Common ground beetles	no.		
Spring ^b	2	13	1
Fall ^c	5	14	3
White footed-mice ^d	39	30	69

^a Only the carabid beetle species studied in the growth chamber and greenhouse studies were recorded. These numbers are not an accurate reflection of all insect seed predators in the field (e.g., the northern field cricket was not trapped or counted at these field sites). Only one rodent species, the white-footed mouse (*Peromyscus leucopus* Fischer), was captured and released in the Sherman traps at all three field sites.

^b Twenty pitfall traps were placed at each site and monitored daily for 5 consecutive d per month from August to November 1999 for a total of 20 trap-days at each site.

^c Twenty pitfall traps were placed at each site and monitored daily for 5 consecutive d per month days from March to August 1999 for a total of 30 trap-days at each site.

^d Thirty-six Sherman traps were placed in a six by six over each of the three field sites. Traps were opened for 5 consecutive d each month from March to August 1999 for a total of 30 trap-days.

Sources of Materials

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