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By

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ABSTRACT

WEED SEED PREDATION IN AGROECOSYSTEMS

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The fate of weed seeds in the soil includes germination, dormancy, degradation by soil microbes, and consumption by seed predators. Seed predators include invertebrates such as carabid beetles and crickets, as well as vertebrates including birds and rodents. This research involved growth chamber, greenhouse, and field experiments that determined weed seed consumption by chosen predators and the effect of seed predation on the resulting weed seedling communities. Feeding choice studies with seeds of three summer annual weed species 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). The female *Gryllus pennsylvanicus*, *Anisodactylus sanctaecrucis*, and *Harpalus pensylvanicus*, consumed more redroot pigweed (*Amaranthus retroflexus* L.) seed compared with giant foxtail (*Setaria faberi* Herrm.) seed while *Amara aenea* did not show a preference between the two weed species. All insect species consumed less velvetleaf (*Abutilon theophrasti* Medic.) seed when compared to redroot pigweed and giant foxtail seed consumption. We also determined how shallow weed seed burial in soil affects seed consumption by three of these predators. *Amara*

aenea consumed more redroot pigweed seeds placed on the soil surface than seeds buried at a 0.5 or 1.0 cm depth, while *Anisodactylus sanctaecrucis* only consumed velvetleaf, giant foxtail, and redroot pigweed seed on the soil surface. *Harpalus pensylvanicus* consumed large numbers of giant foxtail and redroot pigweed seeds placed at a one-cm soil depth. In the greenhouse, we determined the impact of post-dispersal seed predation by three carabid beetle species and the northern field cricket on annual weed seedling establishment. *Anisodactylus sanctaecrucis* decreased redroot pigweed emergence by 18% when compared to emergence of redroot pigweed in the absence of this carabid beetle species. Field experiments identified the change in seedling emergence between sites where vertebrates or invertebrates were allowed access to weed seed compared to sites where no seed consumers were allowed seed access. In the first field study (1997-98), vertebrate predation decreased emergence of velvetleaf seed placed in the field the previous August by 9%. Giant foxtail emergence in the spring from fall seed placement was decreased by 15% in the presence of vertebrates and invertebrates when compared to the exclusion of all predators. In the second series of field studies in 1998-99 giant foxtail emergence decreased at one of three sites and velvetleaf emergence decreased at two of three sites when invertebrates were allowed access the seed. Giant foxtail emergence in 1999 decreased at two of three sites and velvetleaf emergence decreased at three of three sites and further decreased at another site when all predators could access the seed.

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CHAPTER 1

REVIEW OF LITERATURE

Introduction

Weeds are the primary pest problem in North American agricultural cropping systems. In 1982, 400 million pounds of active ingredient of herbicides was applied to corn and soybeans in the United States to control annual weeds (Osteen and Szmedra 1989). In 1997, over 2,400 tons and 700 tons of herbicides were applied in Michigan to control weeds in corn and soybean fields, respectively. Mechanical weed control, including rotary hoeing and cultivation, is used in combination with herbicides to control weeds but in spite of these efforts, it is estimated that $4 billion (Bridges and Anderson 1992) in revenue is lost each year due to weed competition in row crops. The integration of additional weed management methods, including biological control, can reduce herbicide usage and yield losses due to weed competition in row crops. Seed consumers that prey on the seed of multiple weed species may play an important role in weed management in agricultural systems.

SEED PREDATION

Existing plant populations depend on seed for the initiation of new populations. Thus, seed must be both produced and dispersed for a weed species to be successful. The relative importance of seed recruitment, especially from seed banks, varies among plant species and communities (Harper 1977; Louda 1989). Soil seed banks are influenced by seed loss as well as seed input. Seed predation is one cause of seed loss that occurs both on the plant and in the soil seed bank. Seed predators include insects and rodents as well as many other invertebrates and vertebrates.

Pre-dispersal seed predation. Pre-dispersal seed predation is the consumption of ripening seed on the plant prior to dispersal. In many plant species, pre-dispersal seed predation accounts for massive losses in reproductive potential while the seed of other species is protected so well that pre-dispersal seed predation is minimal (Radosevich *et al.* 1997). Pre-dispersal seed consumption often leads to reduced seed size (Crawley and Nachapong 1986; Hendrix 1988; Thompson 1985), which has potential effects on seedling competitiveness. Pre-dispersal predation may also influence the evolution of seed size, by exhibiting feeding preferences for seeds of particular sizes (Mazer 1988; Nelson and Johnson 1983) and by inflicting higher death rates on some sizes of seeds compared to others. Insects are important in pre-dispersal seed predation. Most of the insect species involved in pre-dispersal seed predation are small, sedentary specialist feeders belonging to the orders Diptera, Lepidoptera, Coleoptera, and Hymenoptera (Crawley 1992).

Post-dispersal seed predation. Post-dispersal seed predation occurs after the seed has been dispersed from the parent plant and enters the soil seed bank. It is a potentially important source of seed loss that reduces seed supply and seedling emergence in old fields, pastures, forests, and deserts (Crawley 1989; Louda 1989). Weed seed losses up to 60% day^{-1} have been reported in prairies (Platt 1976) while losses in undisturbed fields, attributed to ants and rodents, ranged from 1 to 20% day^{-1} (Mittelbach and Gross 1984). In soybean fields, Brust and House (1988) reported weed seed predation rates of 1 to 5% day^{-1} for a five-week period in autumn with twice as much activity in no-tillage compared to moldboard plow fields. Seed density had little effect on predation rate in old fields (Mittelbach and Gross 1984) or in plowed and no-tillage crop fields (Brust and House 1988).

PREDATORS

The suite of potential seed predators in agricultural fields include birds, rodents, large and small carabid beetles, crickets, and ants.

Birds. Granivorous birds are among the known pre- and post-dispersal seed predators. Birds also disperse seed as they carry the seed to their hoard and/or consume the seed and fly to another area. As an example, young acorns of the oak *Quercus robur* are prey to the jay *Garrulus garrulus glandarius* as the bird removes the ripe acorns from the tree in late summer. The jay is believed to have a positive impact on oak fitness through long-distance dispersal of the acorns (Bossema 1979; Chettleburgh 1952).

However, in a study in continuous no-tillage and moldboard plow corn fields, Cardina *et al.* (1996) found no evidence of bird predation. This is consistent with the results of House and Brust (1989) in their study of low-input, no-tillage agroecosystems.

Rodents. Many species of small mammals are important post-dispersal seed predators. In addition to eating the seeds, rodents also husk, move and bury seed, affecting seed spatial distributions and establishment as well as seed numbers. Brown *et al.* (1975) found rodents were much more efficient at harvesting large clumps of seeds than ants. Reichman (1981) found rodents were able to exploit seeds below the soil surface.

In no-tillage systems, Rodents were significant seed feeders in no-tillage but not conventional tillage systems (Brust and House 1988). Mice were the only consistent feeders of the hard-coated jimsonweed seeds. In a study by Hulme (1990) in two Berkshire grasslands, small mammals removed an average of 43% of the seeds placed in the dry grassland site and 37% from the meadow site.

The caching of harvested seeds by rodents is an expensive activity as seeds are transported, stored, and reharvested. Therefore, rodents tend to select larger seeds that tend to have higher nutritional values (Brown *et al.* 1975).

Ants. Due to their size, ants typically harvest fruits and seeds one at a time. By selecting seeds relative to the ants' size, they are able to optimize harvest and maximize the nutritive value of food brought to the nest. Small seeds are easily transported but low in energy while large seeds are high in energy but difficult to transport (Brown *et al.* 1975).

Ants are ectothermic and are typically unable to be active at extreme environmental temperatures (Bernstein 1971). In desert environments, high insolation and substrate temperatures in the summer months may inhibit diurnal foraging in open areas away from shrubs. During the cold months, all activity is drastically curtailed and the impact of ants as seed predators is greatly reduced (Brown *et al.* 1975).

In agricultural sites, ants have been observed feeding on smaller weed seed species in both no-till and conventional-tillage (Brust and House 1988). Although ants were more abundant in no-till compared to conventional-tillage fields, they were still important seed feeders in the conventional-tillage systems. Reichman (1981) noted that ants were unable to find and exploit seeds covered with soil and were less efficient in locating and harvesting large quantities of seeds in comparison to rodents.

Carabid beetles. In a lab experiment (Brust and House 1988), the carabid beetle *Harpalus pensylvanicus* consumed 60% of the common ragweed seeds, less than 40% of the wheat seeds, and only small amounts of sicklepod and jimsonweed seeds. Another species of carabid beetle, *Harpalus caliginosus,* preferred sicklepod and wheat seeds to common ragweed and redroot pigweed seeds and consumed only a few jimsonweed seeds. The carabid beetles were also noted to remove the larger seeds from the resource area and transport them to covered areas (under straw, corn stalks, etc) within their lab containers to consume them. In soybean fields, carabid beetles had the greatest impact and importance in removing seed species in both no-till and conventional tillage systems (Brust and House 1988). *Harpalus pensylvanicus* DeGeer and *H. caliginosus* F. were the most abundant carabid beetle species at this site. *Harpalus caliginosus* was unable to penetrate the pericarp of wheat or sicklepod until the seed coat had been softened after exposure to environmental conditions (~2 weeks). However, after softening, they could readily crush either wheat or sicklepod seed and consume the endosperm. In contrast to *H. caliginosus, H.*

pensylvanicus penetrated the pericarp in 2 to 3 minutes and consumed the seed of wheat or sicklepod. This carabid beetle species also readily consumed common ragweed and redroot pigweed seeds (Brust and House 1988).

In laboratory studies, Cardina *et al.* (1996) found the carabid beetle, *Amara cupreolata* was a more effective velvetleaf predator while *H. pensylvanicus* was a significant predator of imbibed wheat seeds. Only the carabid beetle, *A. cupreolata*, and a slug (*Arion subfuscus*) damaged unimbibed velvetleaf seeds.

In alfalfa fields, *Harpalus pensylvanicus* fed on small grass weed seeds whereas *Amara cupreolata*, fed on common chickweed (*Stellaria media* (L.) Vill.) and grass seeds (Barney and Pass 1986) as well as consuming imbibed velvetleaf (*Abutilon theophrasti* Medicus) seeds (Cardina *et al.* 1996).

Selenophorus species, a small carabid beetle, preferentially removed small seed species, such as common ragweed and redroot pigweed in the no-till system. These carabid beetles removed relatively few weed seed species in the conventional-tillage system (Brust and House 1988).

SYSTEMS

Desert. Studies by Brown *et al.* (1975), Inouye *et al.* (1980), and Reichman (1979) have identified rodents and ants as major seed predators in the desert ecosystems. Brown *et al.* (1975) found that rodents and ants are important and efficient seed predators in desert systems and overlap in spatial distribution of foraging activity and in sizes and species of seeds taken. Ant predation generally occurred during the daytime while rodents were more active predators at night and were also more efficient in locating available bait compared to ants.

Inouye *et al.* (1980) found seed predation greatly reduced plant densities but granivorous ants and rodents had qualitatively different effects on the plant community. Rodents preyed selectively on larger seeded species while the ants often harvested the smaller seeds of certain abundant species.

In the desert habitat studies by Brown *et al.* (1975), nocturnal rodent predation (70 to 80%) of known quantities of seeds was much higher than diurnal ant predation (20%). In Reichman's (1979) study, ants found 85% of the experimental seed distributions on the surface and retrieved 45% of these seeds. Rodents however, found 100% of all distributions and gathered 96% of seeds on the surface in caches and 75% of seeds that were scattered or below ground.

Old field, pastures, and grasslands. Dense ground cover in old fields, pastures, and grasslands can often restrict seedling emergence as demonstrated by Sagar and Harper (1961), Putwain and Harper (1970), Gross and Werner (1982), and Reader and Buck (1986). In these studies, higher seedling emergence occurred in plots cleared of ground cover compared with plots with ground cover intact.

Four mechanisms have been suggested to explain why ground cover restricts seedling emergence. These include: 1) inhibition of seed germination by changing microclimatic conditions (Rice 1985; Keizer *et al.* 1985; VanTooren 1988); 2) inhibition of seed germination by changing soil chemistry (McPherson and Thompson 1972; Werner 1975); 3) the ground cover acts as a physical barrier to shoot extension by germinated seeds (McPherson and Thompson

1972; Sydes and Grime 1981); and 4) the ground cover provides a habitat for seed predators who decrease seedling emergence by removing seeds (Reader 1991).

Reader (1991) hypothesized that the presence of ground cover could restrict seedling emergence by providing a habitat for seed predators. In a field experiment, using three old field forbs (*Daucus carota* L., *Centaurea nigra* L., *Taraxacum officinale* Weber), the ground cover was either removed or left in place and the seeds of the three forbs were either protected from predators or left unprotected. Seedling emergence was greatest in the absence of ground cover and in the absence of predators. If seeds were not protected from predators, seedling emergence improved significantly for all three species when ground cover was removed, indicating that seed predators remove more unprotected seeds if ground cover is present versus absent. These results support the idea that groundcover can restrict seedling emergence by providing a habitat for seed predators.

In 1993, Reader conducted studies to determine if environmental factors may control seedling emergence in old fields, pastures and grasslands. He determined that control of seedling emergence by seed predation and groundcover depends on seed size. Protecting the seed with a caged exclosure increased seedling emergence significantly for some species, probably by reducing seed predation. Removing groundcover increased seedling emergence significantly for some species, probably by reducing the inhibition of seed germination and (or) restriction of shoot extension. When ground cover was removed, seedling emergence increased more for species with small seeds (<1.4 mg) compared to emergence of larger seeds. Presumably, more small seeds were shaded or covered where ground cover was left intact.

Non-crop habitats. Non-crop habitats are often assumed to be a major source of weeds into adjacent crop fields (Cavers and Benoit 1989). However, long distance seed dispersal by weeds into crop fields may be infrequent (Hume and Archibold 1986; Marshall 1988 a, b; Marshall and Hopkins 1990). There is some evidence that seed rain from these habitats can significantly add to the seed bank in the crop fields (Archibold and Hume 1983). However, these non-crop habitats also provide food and shelter for potential seed predators such as mammals (Pollard and Relton 1970), birds (Lewis 1969; Best 1983), and insects (Thomas *et al.* 1991, 1992). The abundance and diversity of birds (Best 1983; Castrale 1987) and small mammals (Castrale 1987) was higher in non-crop habitats compared to the crop field. Carabid beetles, which are important seed consumers in temperate agroecosystems (Best and Beegle 1977; Brust and House 1988; Johnson and Cameron 1969; Kjellsson 1985; Lund and Turpin 1977; Manley 1992), also use these habitats as over-wintering sites (Descender 1982; Southerton 1984, 1985; Thomas *et al.* 1991, 1992; Wallin 1985, 1986).

Marino *et al.* (1997) conducted a field experiment to determine if adjacent non-crop habitats enhanced biological control of weeds in corn fields. Because hedgerows are being removed from farming systems to increase field size, this research focused on whether the distance between fields and hedgerows had an effect on seed predation. Although seed predation rates were high at this site, the results did not support the expectation that seed loss in crop fields would be higher nearer the hedgerows than in the field interior. The inability to detect this difference may have occurred due to low rates of seedling emergence, the experimental design, the presence of crop residue in the fields, and the small size of the fields when looking at the diverse landscape surrounding the fields. They concluded that the impact of post-dispersal predators is patchy and not consistently related to field location relative to hedgerows.

Menalled *et al.* (1997) conducted a field experiment looking at the effect of the agricultural landscape structure on post-dispersal weed seed removal. Known weed seed numbers of four common agricultural weeds were placed in complex and simple landscape fields. The mean seed removal rate was 52.1% in a complex landscape compared to 31.8% in a simple landscape suggesting that landscape complexity influences the effectiveness of natural enemies of weed seeds in agroecosystems.

Agricultural systems. The potential impacts of conservation tillage, conventional tillage, and adjacent habitats have been studied to determine if populations of predators can be enhanced in cropping systems. Low input, no-tillage agroecosystems possess characteristics similar to those in natural or less disturbed systems, such as old fields and prairies (House *et al.* 1984). In no-tillage systems, most of the seeds that germinate are within the top 2 cm of soil or on the surface, thus exposing many seeds to seed consumption by predators (Brust and House 1988). No-tillage systems generally generate different weed species than those of conventional tillage systems (Triplett and Worsham 1986).

House and Parmelee (1985) found that no-tillage provided a more favorable microhabitat for seed feeders through increased residue, decrease or lack of insecticide usage, decreased herbicide rates, and less soil disturbance. The exposed dry microhabitats in conventional-tillage are believed to be less conducive to extended periods of seed-feeding (Barney *et al.* 1982; Brust *et al.* 1986). In the southeastern United States, conventional-tillage systems generally supported fewer arthropods than no-tillage systems (Blumburg and Crossley 1983; House and All 1981; House and Parmelee 1985).

In soybean agroecosystems, House and All (1981) found greater carabid beetle populations in conservation tillage systems compared with conventional tillage. Greater predation occurred throughout most of the growth and maturation phases of the crop in the conservation tillage systems. In further seed predation research, Brust and House (1988) looked at the removal of weed seed over a 5-week period in low-input (no insecticide, low herbicide usage) conventional- and no-tillage soybean agroecosystems. Seeds of four broadleaf weed species (common ragweed, redroot pigweed, sicklepod [*Cassia obtusifolia* L., and jimsonweed), and one crop species (wheat) were used in the different cropping systems. Significantly less weed seed consumption by arthropods and rodents occurred in the conventional-till treatment compared with the no-till treatments. They also found that weed-seed resource partitioning among soil arthropod groups and mice was evident. Large carabid beetles and mice preferred large seeds such as wheat (*Triticum aestivum* L.) and sicklepod (*Cassia obtusifolia* L.). The smaller carabid beetles, ants, and field crickets removed two of the smaller weed seed species, common ragweed (*Ambrosia artemisiifolia* L.) and redroot pigweed (*Amaranthus retroflexus* L.), with common ragweed being the preferred species.

Cardina *et al.* (1996) conducted a four year study in continuous no-tillage and moldboard plow corn fields in Ohio to describe patterns of velvetleaf seed predation and found daily predation rate for all sample periods over four years was 11%. Predation was generally low in the winter months, increased in mid-summer and declined in late summer. In the field, exclosures were set up excluding mice, large carabid beetles, and slugs. These exclosures reduced predation 48 to 69%, suggesting that these animals were responsible for about half of the seed predation.

In the Cardina *et al.* (1996) trap study, field mice (*Peromyscus maniculatus*) were caught occasionally in velvetleaf seed-baited traps but not in unbaited traps. Arthropods collected in pitfall traps included large and small carabid beetles, spiders, millipedes, and crickets. There was not a difference in species composition or numbers between the two tillage systems or in plots with and without velvetleaf seeds. Cardina *et al.* (1996) found no evidence of bird predation, which is consistent with the results of House and Brust (1989).

Cromar *et al.* (1999) examined the influence of tillage and ground cover on postdispersal seed predation of common lambsquarters (*Chenopodium album* L.)and barnyardgrass (*Echinochloa crus-galli* (L.) Beauv.) in southern Ontario. They found that predation was highest in no-till and moldboard-plowed environments (32%) and lowest in chisel-plowed environments (24%). In no-till, the type of crop residue also influenced the level of predation with higher rates (31%) occurring in corn residue than in soybean and wheat residues (24% and 21% respectively). Ground dwelling invertebrates were found to have consumed 25% of the available seed while the mice and small animals consumed 10 to 22% of the available seed.

WEEDS

In agroecosystems, a weed can be defined as a plant growing where it is not desired, any plant other than the crop sown, or a plant that grows spontaneously in a habitat greatly modified by human action (Terminology Committee of the Weed Science Society of America 1956; Brenchley 1920; Harper 1944). Velvetleaf, giant foxtail, and redroot pigweed are three weeds that fit these definitions in agroecosystems.

Velvetleaf

History. Velvetleaf, *Abutilon theophrasti* Medic) [Malvaceae], also known as Indian mallow, butterprint, or buttonweed, is an annual forb and is considered to be an important and serious row crop weed. Velvetleaf was introduced from China to North America during European colonization for use as a fiber crop. It was unsuccessful as a fiber crop (Spencer 1984) and escaped cultivation, quickly spreading throughout the United States. It is found between 32° and 45° N in North America, although other members of its genus are all tropical or subtropical (Mitich 1991; Stegink and Spencer 1988; Spencer 1984). It is a major weed in 35% of corn and soybean-producing areas of the north-central

United States (Andersen *et al.* 1985; Ritter 1986; Spencer 1987) and is also found in waste places, pastures, roadsides and fencerows.

Growth and Development. Velvetleaf is self-fertilizing and the average number of seeds produced ranges from 35 to 45 per capsule, with 70 to 199 mature capsules per plant. Seed production ranges from 700 to 17,000 seeds per plant (Winter 1960; Chandler and Dale 1974; Shaw *et al.* 1974; Hartgerink and Bazzaz 1984; Andersen *et al.* 1985; Brown 1985; Warwick and Black 1986).

The medium-sized seed of velvetleaf is kidney-shaped in outline. It is thickest along the outer margin and usually has a rounded concave area on each face. A distinct notch along the edge divides the seed into two unequal lobes. One lobe is usually thinner and more angular than the other lobe. The surface is covered with lighter colored fungus-like growth making it rough and dull. Scattered hairs are usually present and are more abundant in the notch region. The seed is grayish-brown and is 2.9 to 3.4 mm in length, 2.6 to 2.9 mm wide and 1.4 to 1.6 mm thick (Davis 1993; Delorit 1970).

Velvetleaf has the ability to outgrow the crop if both crop and weed emerge at the same time. Velvetleaf grows most rapidly in the six to eight weeks after emergence. It is very competitive during this vegetative stage as height and leaf area increase rapidly, producing a major part of the biomass at this time (Sattin *et al.* 1992). Velvetleaf inhibits crop growth by interfering with light interception (Kremer and Spencer 1989; Zanin *et al.* 1989) and by competing for moisture and nutrients (Kremer and Spencer 1989). Velvetleaf is efficient under conditions of low sunlight. It grows well when partially shaded and will produce seed under a crop canopy. Velvetleaf root growth exceeds that of redroot pigweed, green foxtail (*Setaria viridis* (L.) Beauv.), and many other weeds (Roeth 1987). Because of these abilities, and because velvetleaf can grow taller than corn, velvetleaf can infest a corn field even after the crop forms a dense canopy. Velvetleaf germinates throughout the summer with even the small end-of-season plants successfully flowering and producing viable seed.

The seeds mature quickly (within 20 days of pollination) and have high viability and longevity (Burnside *et al.* 1981; Lueschen and Andersen 1980; Toole and Brown 1946; Winter 1960). Velvetleaf dormancy mechanisms (hard seed coat and anti-microbial compounds) result in large persistent seed banks as the seeds can survive for 40 to 50 years in the soil (Kremer *et al.* 1984; Kremer 1986; Warwick and Black 1988). Normally only 5 to 15% of the velvetleaf seeds in the soil will germinate in a year creating a long-term problem with velvetleaf (Roeth 1987). In controlled-environment experiments by Mester and Buhler (1991), velvetleaf seed on the soil surface without adequate seed/soil contact did not germinate or failed to become established. However, emergence from the soil surface increased when mulch was applied. Velvetleaf seedling emergence occurred from a two to six cm soil depth.

Predation. Results of field studies and simulations have shown that seed production by velvetleaf at subthreshold densities would allow populations to increase unless post-dispersal seed losses were high (Bauer and Mortensen 1992; Cardina *et al.* 1995). Because seeds of velvetleaf and other annual weeds are an important food source for many ground-feeding birds and small animals, predation that results in consistent and significant seed losses could be an important constraint on the growth of velvetleaf populations (Martin *et al.* 1951). A lab study by Lund and Turpin (1977) found four species of carabid beetles that damaged seeds of 12 grass and small-seeded broad-leaved weeds but none of these species consumed velvetleaf. Only the carabid beetle, *A. cupreolata*, and a slug (*Arion subfuscus*) damaged unimbibed velvetleaf seeds in laboratory research (Cardina et al. 1996).

Giant foxtail

History. Giant foxtail, *Setaria faberi* Herrm., is a member of the Poaceae family. It is native to Asia (Evers 1949; Fernald 1944; Wood 1946) and was introduced to the United States by importing millet from China during the drought in the early 1930's (Fairbrothers 1959; Knake 1977). Also known as giant bristlegrass, Chinese foxtail, Chinese millet, and nodding foxtail, it is one of the most troublesome species of *Setaria* in the United States today (Whitson 1991). It is a serious weed in row crops and is also found in waste places, disturbed sites, and cultivated fields, occurring when soil is frequently disturbed. Foxtails are quite competitive with crops under moist conditions (Blackman and Templeman 1938; Staniforth 1957, 1958) and also interfere with harvesting operations in row crops (Santelmann *et al.*1963). Giant foxtail is often confused with other smaller foxtails such as green foxtail (*S. viridis* (L.) Beauv.) and yellow foxtail (*S. glauca* (L.) Beauv. [=*S. lutescens* (Wieg.) Stuntz].).

Growth and development. Giant foxtail is an annual monocot that only reproduces by seed (Anonymous 1981). Each plant can have up to eight individual inflorescence (panicles) where seed is produced (Defelice *et al.* 1989; Santelmann *et al.* 1963). Each inflorescence can produce 30 to 1400 seeds (Defelice *et al.* 1989; Schreiber 1965) varying with the length of the inflorescence (Barbour and Forcella 1993; Schreiber 1965). Individual giant foxtail plants can produce more than 10,000 viable seeds (Schreiber 1965). In Michigan, giant foxtail seed production ranged from 518 to 2,544 seeds per plant (Fausey and Renner 1997). The fertile floret consists of a hull (tightly joined lemma and palea) that encloses the caryopsis (Narayanaswami 1956; Rost 1973, 1975). The lemma and the palea are both hard and shiny. Depending on maturity, the floret may be yellowish-green, brown or black. The length of the floret is 2.5 to 2.8 mm, width is 1.4 to 1.5 mm and the thickness is 1.0 to 1.2 mm (Davis 1993; Delorit 1970).

Giant foxtail emergence is greatest from seeds at or near the soil surface with emergence decreasing as depth of seed increases (Dawson and Bruns 1962). In Michigan, it was found that the greatest emergence of giant foxtail was from one cm with less than 5% of the giant foxtail emerging from 7.5 cm (Fausey and Renner 1997). Mester and Buhler (1986), found 50% of emerged seedlings originated from the depth of one cm or less in a no-till system. In a controlled-environment, Mester and Buhler (1991) proposed a seedling survival rate of 100% if weeds germinated on the soil surface. Field studies conducted by (Mester and Buhler 1986; Santelmann *et al.* 1963; Taylorson 1972) conclude that the maximum depth for giant foxtail emergence is 10 cm.

Predation. Lund and Turpin (1977) included giant foxtail seeds in their study of carabid damage to 16 weed seed species found in Indiana corn fields. They found that *Harpalus pensylvanicus* damaged and consumed giant foxtail seeds although there were six weed seeds that sustained greater damage, including yellow and green foxtail.

Redroot pigweed

History. Redroot pigweed, *Amaranthus retroflexus* L., is a member of the Amaranthaceae family and is one of the most widely distributed weed species of arable crops in the world, occurring in 60 crops in 70 countries (Holm *et al.* 1997). It is a native of tropical America (Gates 1941; Muenscher 1955) and is believed to have been introduced to other countries through seedstock and grain. The Native Americans cultivated it in North America and the seeds were ground into flour or popped like popcorn. In times of emergency, the seeds provided a food of great importance (Harrington and Matsumura 1967). The young shoots and stems were also considered a favorite green by Native Americans and early white settlers. Today, it is very common in cultivated and fallow fields, gardens, waste places, and roadsides and prefers open, sunny areas and appears quickly when soil is disturbed (Holm *et al.* 1997).

Growth and Development. Redroot pigweed has a long, fleshy, reddish to pink taproot and pink or white rootlets. The erect stems are light green to reddish, stout, branched, rough and angular. The plants can reach two m in height. Leaves are alternate, pedicillate, dull green, oval, and rough and typically 8 - 10 cm long with prominent veins on the underside (Gates 1941;

Georgia 1942; Pammel and King 1926; Weaver and McWilliams 1980). Redroot pigweed is monoecious with numerous small, green flowers crowded into dense finger-like spikes in axils of the leaves and in a large terminal spike or panicle. They are predominantly wind-pollinated, although insects may pollinate under certain circumstances (Frankton and Mulligan 1970; Montgomery 1964). Each flower produces a single smooth and shiny seed that is oval, flattened, and dark brown or jet-black (Georgia 1942). The seeds have a water-permeable seed coat, are notched at the narrow end and 0.8 - 1.2 mm in diameter. Seed quantities of 230,000 and 500,000 by single large plants of redroot pigweed have been reported by Stevens (1957). Depending upon the environment, plants usually produce between 13,860 to 34,600 seeds per plant. Seed is dispersed by wind, water, and birds with manure, movement of farm machines, and as a contaminant in crop seed. Redroot pigweed also resprouts easily from the taproot (Holm *et al.* 1997).

In general, the optimum seeding depth for giant foxtail emergence is one cm (Wiese and Davis 1967; Siriwardana and Zimdahl 1983). Koch (1970) concluded, after a literature survey of seed germination for many major weeds, the optimum temperature for redroot pigweed germination was 35 to 40° C. Freshly harvested seed reacted strongly to temperature changes, while older seeds exhibited little or no response. In the United States, redroot pigweed emergence peaks in late spring and early summer and then continues steadily into August (Ogg and Dawson 1984; Roberts 1986).

The duration of seed viability varies with site, soil, conditions of the storage place, seed fitness at the outset, and other factors (Barton 1962). Some researchers have reported a lack of dormancy in freshly harvested seed of redroot pigweed while others have reported populations with considerable dormancy at harvest (Egley and Chandler 1978; Weaver and McWilliams 1980). Egley and Chandler (1978) found a 90% decrease in seed viability after 18 months of burial but almost no decrease after 30 months in dry storage. Burnside *et al.* (1981) in the central United States buried pigweed seeds and found little loss of viability in 10 years. In the 100-year Beal buried seed experiment, some redroot pigweed seeds were still viable after 40 years (Darlington and Steinbauer 1961).

Predation. In a laboratory study, Lund and Turpin (1977) included redroot pigweed seeds in their study of carabid damage to weed seed species found in Indiana corn fields. In a study to determine if carabid beetles would attack seeds in a laboratory setting, *Harpalus pensylvanicus* damaged and/or consumed a high number of redroot pigweed seeds. In ranking seed damage by *H. pensylvanicus*, redroot pigweed was in a group of six seeds that sustained significant damage. In a field choice study by Brust and House (1988), seed predators were given a choice of four weed seeds and one crop seed. Redroot pigweed was consumed in the field by large and small carabids, ants, field mice, and crickets but was never the seed of choice.

SURVIVAL OF SEEDS IN THE SOIL

Longevity of velvetleaf seeds in the soil has received considerable attention, including the famous studies of Beal established in 1879 and Duvel in 1902. However, both of these studies were conducted under artificial means, making it difficult to determine the longevity of seeds in agricultural fields (Lueschen and Andersen 1980).

Several studies have looked at natural populations of weed seeds in field environments with standard cultural practices. Brenchley and Warington (1936) fallowed field plots for four years and greatly reduced the seed bank. However, their fallowing operations occasionally allowed weeds to produce seeds during this study. Chepil (1946a) studied the longevity of seeds of numerous weed species over a six year period in shallowly cultivated soil. He also conducted short-term studies with five weed species subjected to various tillage operations (1946b). From these studies he concluded the number of viable seeds remaining at the end of the fallow period was lower in fallow fields that had been cultivated periodically than those left undisturbed. He attributed the decrease in the seed bank to cultivation bringing the seeds closer to the surface rather than any direct effect on germination itself. Roberts (1962) studied the effect of three vegetable crop rotations on weed seed populations for six years. The plots were kept relatively weed free but in year five, "extensive seeding occurred." Before this occurred, the weed seed bank had declined about 50% per year. Roberts and Dawkins (1967) conducted another field study where they used a contact herbicide to control weed seedlings. This study did not involve cropping systems, but rather tilled versus undisturbed soil. In this study, the population (average over species) declined exponentially at a rate of 22% per year in undisturbed soil, 30% per year in soil "dug" two times a year, and 36% per year in soil "dug" four times a year. ("Dug" refers to a tillage operation, but the exact meaning was not clear.) Roberts and Feast (1973) conducted a five-year seed longevity study by placing known seed quantities of various weeds in the ground and tilling the soil periodically. Seeds that were closer to the surface were shorter lived than those seeds that were buried deeper. They also found that seed longevity was greater in undisturbed than in tilled soil.

Forcella *et al.* (1997, 1992) studied weed seed bank emergence across the corn belt. They found that average seedbank densities of viable seed ranged from 600 to 162,000 seeds m^{-2} with redroot pigweed and common lambsquarters being the most common in the seedbank. Of the total seeds recovered, 50 to 90% were dead.

There seems to be agreement in the literature that: 1) weed species vary in their ability to maintain a viable population in the soil; 2) weed seed survival increases with depth of burial in soil; and 3) weed seeds dissipate more rapidly in tilled compared to undisturbed soil (Lueschen and Andersen 1980).

MICROFLORA

Fungal colonization of weed seeds has been widely surmised as a factor in seed longevity in the soil. Changes in tillage practices bring changes in placement of plant residues in the soil profile (Bakermans and DeWitt 1970). These changes affect the number and type of soil microflora. Dawson *et al.*

(1948) found that the top 2.5-cm of soil contained greater numbers of fungi, bacteria, and actinomycetes when plant residues were subsurface tilled. When the residues were plowed under, the 2.5- to 15-cm layer contained the greater number of organisms. Gamble *et al.* (1952), Norstadt and McCalla (1969), and Doran (1980a, 1980b) confirmed these results.

Zerfus (1979) found conflicting results in the Soviet Union. He reported a decrease in the number of fungi in fields with a reduction or cessation of mechanical soil cultivation. His determinations were made in the 0 to 76 cm soil depth. A dilution effect may have occurred as he included some soil not affected by tillage implements.

Velvetleaf. Velvetleaf exhibits very low microbial infection in the field due to physical barriers and antimicrobial compounds localized within the seed coats (Halloin 1983; Kremer 1986; Kremer *et al.* 1984). Kremer *et al.* (1984) found abundant growth of microorganisms on both velvetleaf seeds matured on the plant and from seeds dispersed on the soil surface. An association of four sporulating fungi persisted on seeds after dispersal to the soil. In spite of the abundant growth on the seed surface – seed deterioration was infrequent. Approximately 80% of the bacteria isolated from within the seeds were antagonistic to externally borne fungi. The proportion of surface-sterilized seeds with internal fungi was approximately 10%, indicating the seed coat acted as a barrier to most fungal invasions. If the seed coat was punctured, seed deterioration by seedborne organisms readily occurred. In developing seeds, microorganisms readily penetrate the seed coat and decompose the seed contents (Kremer *et al.* 1984).

In 1986, Kremer found some rhizobacteria strains in the field that were able to overcome the tough outer coat of velvetleaf, causing them to rot before they could germinate. If the seed coat could be weakened in the field by feeding, it would allow microflora to invade the mature seed and decompose the seed contents.

Giant foxtail. A study by Pitty *et al.* (1987) found giant foxtail seeds susceptible to fungal colonization. Soil depth had no significant effect on fungal colonization. Fungal colonization of giant foxtail seeds at the 0.0 to 7.5 cm depth was greater in the reduced tillage compared with the plowed plots. Colonization was greater in plowed plots compared to the reduced tillage plots at the 7.5 to 15 cm depth. This can be attributed to crop residue placement by tillage implements.

Two of the most prevalent fungi species found on the exhumed seeds were not isolated from hand-harvested giant foxtail seeds, indicating that the fungi were endemic to the soil. Both of these fungal isolates reduced germination when they colonized a caryopsis and were prevalent in either type of tillage and at various depths. Weed seed populations can be reduced by these isolates, but due to the high number of seeds produced, the fungi effect was minimal (Pitty *et al.* 1987).

IMPACT OF SEED PREDATION. Some authors have indicated that post dispersal seed predation rates are too low to have an impact on plant populations because factors other than seed numbers may limit the size of future populations (Crawley 1989; Harper 1977). However in the absence of a mulch cover, seed predators reduced the number of emerging broadleaf seedlings but not the grass seedlings and the researchers concluded that insect seed predators have a potential importance in reducing weed numbers and biomass (House and Brust 1989). Cardina *et al.* (1996) found the daily predation rate for all sample periods over four years was 11%. At this rate, surface seed density would be reduced nearly 80% in four weeks which could have a significant impact on seedling populations. This level of predation of surface seeds indicates that predation could be encouraged by delaying tillage as long as possible to allow predators a longer period of time to destroy seeds before they become part of the seed bank. However, rates of predation would vary with weed species, available predators and availability of other food sources (Crawley 1992; 1989).

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CHAPTER 2

WEED SEED PREFERENCE AND BURIAL DEPTH CHOICES OF THREE GROUND BEETLES (COLEOPTERA: CARABIDAE) AND THE NORTHERN FIELD CRICKET (ORTHOPTERA: GRYLLIDAE)

ABSTRACT

The fate of weed seeds in the soil include germination, dormancy, degradation by microbes, or consumption by seed predators. We determined the feeding preference of four insect species for seeds of three weed species common in Michigan corn fields and determined if burial depth in soil affects seed predation. Feeding choice studies were conducted with three species of common ground beetle species (*Amara aenea* DeGeer, *Anisodactylus sanctaecrucis* F., and *Harpalus pensylvanicus* DeGeer) and the northern field cricket (*Gryllus pennsylvanicus* Burmeister). There were significant differences among these species in their weed seed feeding preferences. All insect species consumed fewer velvetleaf (*Abutilon theophrasti* Medicus) compared to redroot pigweed (*Amaranthus retroflexus* L.) and giant foxtail (*Setaria faberi* Herrm.) seeds. *Gryllus pennsylvanicus*, *A. sanctaecrucis*, and *H. pensylvanicus* consumed more redroot pigweed than giant foxtail seeds, whereas *A. aenea* did not show a preference between these two species. *Gryllus pennsylvanicus* consumed a greater weight (mg) of redroot pigweed seed when compared to giant foxtail and velvetleaf seed, whereas *H. pensylvanicus* consumed a greater weight of velvetleaf compared to giant foxtail seed.

The depth of seed burial influenced feeding preferences. *Anisodactylus sanctaecrucis* consumed more velvetleaf and redroot pigweed seeds from the soil surface compared to seeds buried at a 0.5 or 1.0 cm depth, whereas *Amara aenea* consumed more redroot pigweed and giant foxtail seeds from the soil surface compared to seeds buried at a 0.5 or 1.0 cm depth. *Harpalus pensylvanicus* consumed large numbers of giant foxtail and redroot pigweed seeds with no feeding differences among seeding depths. These results show that ground-dwelling arthropods predate weed seeds on or near the soil surface thereby influencing the composition of the resulting weed community in agroecosystems.

INTRODUCTION

Seed consumption by seed predators can occur both on the plant (pre-dispersal) and in the soil seed bank (post-dispersal). Annual plant populations depend on seed production, dispersal, and germination to initiate new populations. Therefore, predators may influence the input and output of seed at virtually every stage of the plants' life cycle thereby impacting the composition of the weed seed bank.

An important source of seed loss in deserts, forests, pastures, and old fields is post-dispersal seed predation (Crawley 1989; Louda 1989). Predation can be intense, resulting in 90% seed loss in desert systems (Brown *et al.* 1975; Reichman 1979). Louda (1989) suggests that seed predation changes density and relative abundance of dominant species that have annual life histories. She also suggests that seed predation influences recruitment, occurrence, and distribution of moderately large-seeded plants with fugitive life histories.

Weed seed predation also occurs in agroecosystems (Reader 1991, 1993; Campbell 1966; Nelson *et al.* 1970; Borchert and Jain 1978; Louda *et al.* 1989; Sagar and Harper 1961; Campbell 1968; Putwain and Harper 1970). Seed predators include invertebrates (carabid beetles, field crickets, and ants) and vertebrates (rodents and birds). Weed seed predation rates of 1 to 5% day^{-1} were reported in no-tillage and moldboard-plowed fields during a five-week period in autumn in Indiana (Brust and House 1988). Cromar *et al.* (1999) conducted field experiments in southern Ontario to determine the influence of tillage and ground cover on the quantity of postdispersal seed predation of common lambsquarters and barnyardgrass (*Echinochloa crus-galli* L. (Beauv)). Predation was highest in no-till and moldboard-plowed environments (32%) and lowest in chisel-plowed environments (24%). In no-till, the type of crop residue also influenced the quantity of predation with greater predation occurring in corn residue than soybean and wheat residues. Ground dwelling invertebrates were found to have consumed 25% of the available seed while mice and other vertebrates consumed 10 to 22% of the available seed.

Cardina *et al.* (1996) measured velvetleaf seed predation in no-tillage and moldboard plow corn fields in Ohio. Predation was low in winter months and increased in mid-summer. The daily predation rate for all sample periods was 11%. Marino *et al.* (1997) conducted a field experiment to determine if adjacent non-crop habitats enhanced biological control of weeds in corn fields. Because hedgerows are being removed from farming systems to increase field size, their research focused on whether the distance between fields and hedgerows had an effect on seed predation. Although seed predation rates were high at this site, their results did not support the expectation that seed loss in crop fields would be higher nearer the hedgerows than in the field interior. The inability to detect this difference may be due to low rates of seedling emergence, experimental design, the presence of crop residue in the fields, and the small size of the fields when looking at the diverse landscape surrounding the fields. They concluded that the impact of post-dispersal predators was patchy and not consistently related to field location relative to hedgerows.

Menalled *et al.* (1997) conducted a field experiment looking at the effect of agricultural landscape structure on post-dispersal weed seed removal. Known weed seed numbers of four common agricultural weeds were placed in complex and simple landscape fields. The seed removal rate was higher in a complex landscape (52%) compared to the simple landscape (32%), suggesting that landscape complexity influences the effectiveness of natural enemies of weed seeds in agroecosystems. In all of these seed predation studies, weed seed was placed on the soil surface.

Crawley (1989) and Harper (1977) have indicated that factors other than seed density may limit future densities of weed populations. These factors may include safe sites for germination, seedling competition, and herbivory (Harper 1977; White 1980; Crawley 1983, 1989; Fenner 1985; Hendrix 1989; Andersen 1988,1989; Louda 1983, 1989). However, seed predators may play a critical role in weed populations of agricultural systems because of predation of seeds of multiple weed species on the soil surface. The degree of seed predation below the soil surface in agroecosystems has not been reported.

The objectives of our research were two-fold. We wanted to determine the feeding preferences of invertebrate seed predators common in Michigan, and secondly, we wanted to determine if these insects would feed on buried weed seed, since much of the weed seed bank is buried beneath the soil surface. We compared seed consumption by three common species of carabid beetles: *Amara aenea*, *Anisodactylus sanctaecrucis*, and *Harpalus pensylvanicus*, and the northern field cricket (*Gryllus pennsylvanicus*) when given a choice of three weed seeds commonly found in agroecosystems in the Midwest. These weed species were giant foxtail, redroot pigweed, and velvetleaf.

MATERIALS AND METHODS

General insect collection. The spring active carabid beetle species (*A. aenea* and *A. sanctaecrucis*) were collected in a fallow corn field and a fallow soybean field while the fall active carabid beetle species (*H. pensylvanicus*) was collected in a soybean field using pitfall traps at Michigan State University. Pitfall traps (11 mm diameter by 14 mm deep) were placed 1 cm below the soil surface. Male and female northern field crickets were caught by hand after disturbing 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 in the same time period (Carmona 1998; Carmona *et al.* 1999).

Feeding Choice Study

Ground beetle assays. Carabid beetles were placed individually in 7.5 L feeding dishes (18 mm diam. x 8 mm deep) containing 300 g of moist sterilized sandy loam soil (84% sand, 10% silt, and 6% clay) with 2% organic matter. The soil was sifted using USA Standard testing sieve #16 and Tyler equivalent #14 mesh screens to remove organic matter the insects may feed upon. The beetles were placed in a growth chamber (22° C, 60% humidity, photoperiod 16:8 Light:Dark) and starved for 24 h prior to testing. After starvation, a mixture of giant foxtail, redroot pigweed, and velvetleaf seed was placed on the soil surface. *Anisodactylus sanctaecrucis* were given a mixture of 100 velvetleaf, 100 giant foxtail, and 100 redroot pigweed seeds. *Amara aenea* and *H. pensylvanicus* were given a mixture of 50 velvetleaf (decreased due to low consumption with *A. sanctaecrucis*), 100 giant foxtail, and 100 redroot pigweed seeds. Carabid beetles remained in the dish for 48 h before they were removed. Carabid beetles tested in these studies were sent to Dr. Foster Purrington at The Ohio State University for positive identification. There were ten replications of each insect species and two control dishes to measure seed recovery from the soil in the absence of insects.

Northern field crickets assays. The crickets were acclimated and handled as above prior to testing. A mixture of 100 giant foxtail, 400 redroot pigweed, and 100 velvetleaf seeds was placed on the soil surface. A higher number of redroot pigweed seeds was necessary due to documentation of higher consumption rates by crickets, especially by females (Carmona 1998; Carmona *et al.* 1999).

Analysis. There were ten replications of the insect species in a completely randomized design. Uneaten seeds were removed from the soil by sifting with a Tyler equivalent #14 mesh screen. The recovered seeds were counted and the number of seeds consumed was calculated. Data was transformed using ARCSINE. An analysis of variance was conducted on both transformed and nontransformed data. Similar results were obtained using transformed and nontransformed data in detecting significant differences among treatments. Therefore only the results for the nontransformed data are reported. Analysis of variance was used to analyze for differences in seed consumption by insect and weed species and the differences were separated by Fisher's LSD at P=0.05 (Table 5-6). All analyses were conducted using Statistical Analysis System (SAS Institute 1996).

Total seed consumption was converted to seed weight consumption for each insect species using seed weight data by Carmona (1998). Data was transformed using ARCSINE. An analysis of variance was conducted on both transformed and nontransformed data. Similar results were obtained using transformed and nontransformed data in detecting significant differences among treatments. Therefore only the results for the nontransformed data are reported. The analysis of variance determined seed weight consumption of each weed seed species and compared the weight of each weed seed species consumed (Table 7).

Feeding Depth Study. Seeds were placed on the soil surface, 0.5 cm, or 1.0 cm below the soil surface. A 1.5 cm layer of moist sterilized sandy loam soil (as above) was placed in the bottom of all 7.5 L feeding dishes (18 mm diam. x 8 mm deep). If the seeds were placed on the soil surface, the insects were allowed to acclimate in the dishes for 24 h before adding the seeds and then allowed to forage for 48 hours. If the seeds were buried below the soil surface, the seeds were placed on the 1.5 cm soil layer and covered with either 0.5 cm or 1.0 cm of soil. The insects were then placed in the dish and allowed a total of 72 hours in which to acclimate and forage for the seeds. The dishes were placed in a growth chamber (22° C, 60% humidity, photoperiod 16:8 L:D) and remained there for the duration of the experiment. In these experiments, seed of one species was placed in each dish and there were six replications of each insect/seed/depth combination. 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 on the soil surface or at one of the seeding depths. *Harpalus pensylvanicus* were given 50 giant foxtail, 100 redroot pigweed, or 50 velvetleaf seed. Carabid beetles tested in this feeding study were sent to Dr. Foster Purrington at The Ohio State University for positive identification. Northern field crickets were not tested in this study. A control was also included to measure seed recovery from the soil in the absence of insects.

Analysis. There were six replications of the four carabid beetle species, seed species, and depth of seed combination in a completely randomized design. The soil was sifted with a Tyler equivalent #14 mesh screen to remove the remaining seeds. The recovered seeds were counted and the number of seeds consumed was calculated. Data was transformed using ARCSINE. An analysis of variance was conducted on both transformed and nontransformed data. Similar results were obtained using transformed and nontransformed data in detecting significant differences among treatments. Therefore only the results for the nontransformed data are reported. The analysis of variance determined differences in seed consumption by soil depth and weed species and these differences were separated by Fisher's LSD at P=0.05 (Table 8).

RESULTS AND DISCUSSION

Feeding Choice Study

Seed preference. Seed consumption of the three species differed for each invertebrate (*A. aenea* (F=22.21, P=0.0001); *A. sanctaecrucis* (F=78.92, P=0.0001); *H. pensylvanicus* (F=72.71, P=0.0001); *G. pennsylvanicus* female (F=93.79, P=0.0001); and *G. pennsylvanicus* male (F=38.04, P=0.0001)) (Table 1). *Amara aenea* consumed a greater percentage of giant foxtail and redroot pigweed seeds (32%) compared with velvetleaf seeds (4%). This could be caused by density-dependent consumption since the number of velvetleaf seed was half that of giant foxtail and redroot pigweed seed. *Amara aenea* did not show a preference between giant foxtail and redroot pigweed seed.

Anisodactylus sanctaecrucis also consumed a greater percentage of giant foxtail and redroot pigweed compared with velvetleaf seeds. This was not due to density dependent availability since 100 weed seeds of each species were presented. *Anisodactylus sanctaecrucis* consumed almost two times more redroot pigweed (77%) than giant foxtail (41%) seeds (Table 5). These two carabid species are spring breeders (Carmona 1998) and previous studies have shown they prefer smaller seeds such as redroot pigweed and common ragweed (Brust and House 1988), but feeding preferences have not been tested.

Harpalus pensylvanicus consumed a greater percentage of redroot pigweed (89%) when compared to giant foxtail (61%) and velvetleaf (13%) seed consumption (Table 5). All seeds were present in equal numbers. *Harpalus pensylvanicus* has been reported to predate small grass weed seeds (Barney and Pass 1986), common ragweed, and redroot pigweed seeds (Brust and House 1988), but preference for redroot pigweed seed has not been previously reported. *Harpalus pensylvanicus* is a fall breeder so their populations are naturally highest when these summer annual weed species would be dispersing seed (Carmona 1998; Carmona *et al.* 1999).

Female *G. pennsylvanicus* consumed more redroot pigweed (81%) compared to giant foxtail (63%) and velvetleaf (4%) seed. Male *G. pennsylvanicus* consumed similar amounts of redroot pigweed (65%) and giant foxtail (56%) seed (Table 6). Density dependent feeding may have occurred since redroot pigweed seed numbers were four times that of giant foxtail or velvetleaf seed. Since female crickets consumed similar amounts of redroot pigweed and giant foxtail seeds, it may suggest a preference for giant foxtail seed compared to velvetleaf seed. Field crickets, *Gryllus* species, have been reported to remove a substantial portion of small-seeded weed seeds, especially common ragweed and redroot pigweed (Brust and House 1988). Female crickets alone have been reported to consume an average of 223 redroot pigweed seeds in a 24 hour period (Carmona 1998). 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.

Biomass consumption. *Amara aenea* consumed a similar biomass of velvetleaf, giant foxtail and redroot pigweed (Table 7). *Anisodactylus sanctaecrucis* consumed greater biomass of velvetleaf (34 mg) and redroot pigweed (29 mg) when compared to giant foxtail (16 mg) seed. *Harpalus* *pensylvanicus*, however, consumed more velvetleaf biomass (60 mg) compared with giant foxtail (24 mg) biomass consumption (Table 7). Total seed weight consumed by *H. pensylvanicus* exceeded that of the smaller carabid species, *A. aenea* and *A. sanctaecrucis*. Female *G. pennsylvanicus* consumed similar weights of velvetleaf (34 mg) and giant foxtail (25 mg) but consumed a greater amount of redroot pigweed (119 mg) seed. Male *G. pennsylvanicus* consumed similar amounts of velvetleaf (8 mg) and giant foxtail (22 mg) while consuming a greater amount of redroot pigweed (97 mg) seed. Female cricket biomass consumption exceeded that of male crickets by 45% over all weed seed species (Table 7).

Brust and House (1988) found that weed seed resource partitioning among soil arthropod groups was due to the size of both the arthropod and the seed size. Seed predators tend to consume seeds with a high protein content and caloric content, thus providing the predator with a high energy return for time spent in handling seeds (Brust and House 1988). Small seeds are easily transported but low in energy while large seeds are high in energy but difficult to transport (Brown *et al.* 1975). Larger carabid beetles harvested large-seeded species such as wheat (*Triticum aestivum* L.) and sicklepod (*Cassia obtusifolia* L.), while small carabid beetles, field crickets, and ants harvested redroot pigweed and common ragweed (*Ambrosia artemisiifolia*), the small-seeded species (Brown *et al.* 1975; Brust and House 1988). Velvetleaf has a hard seed coat (Kremer *et al.* 1984; Kremer 1986) and is a relatively large seed (~8.5 mg seed^{-1}). This combination makes the seed less attractive to seed predators that do not have the strength necessary to penetrate the seed coat or move the seed easily to another site (Brust and House 1988). Giant foxtail (~0.4 mg seed^{-1}) and redroot pigweed (~0.37 mg seed^{-1}) are much smaller seeds and their seed coats are easier to crack, allowing the insect to penetrate the seed coat more easily with their mandibles and to transport them to other sites for later consumption.

Feeding Depth Study. The depth of seed placement influenced consumption of velvetleaf and redroot pigweed seed by *Anisodactylus sanctaecrucis* (F=4.88, P=0.0232 for velvetleaf; F=4.73, P=0.0287 for redroot pigweed), and redroot pigweed and giant foxtail by *Amara aenea* (F=16.62, P=0.0002 for redroot pigweed; F=4.53, P=0.0289 for giant foxtail) (Table 2).

Amara aenea consumed 23% of the redroot pigweed seed sown on the soil surface while consuming less than 1% of seed placed below the soil surface. Giant foxtail consumption was greater on the soil surface (12%) compared to predation of seed 0.5 cm (4%) below the soil surface. There was no difference in velvetleaf consumption at the various depths. Consumption of velvetleaf and redroot pigweed by *A. sanctaecrucis* occurred only on the soil surface. Giant foxtail seed consumption was higher on the surface (17%) than at the 1.0 cm (1%) depth (Table 8).

Anisodactylus sanctaecrucis and *Amara aenea* consumed 78% less seed placed the soil surface in this study compared to seed placed on the surface in the feeding preference study (Table 5). 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. sanctaecrucis* exists and is yet undocumented. A feeding difference has been found between male and female northern field crickets (Carmona 1998; Carmona *et al.* 1999). Another possibility is the insects were at a different maturity level in each study. The insects may consume fewer seeds as they approach diapause compared to seed consumption during the breeding and egg-laying season.

Harpalus pensylvanicus consumed seed from all depths, with no difference in consumption due to depth for any weed species (Table 8). Consumption of the three seed species on the surface was similar to seed consumption in the feeding preference studies. The fact that there are no differences in seed consumption due to burial depths indicates that these larger carabid beetles are able to burrow into the soil and consume seeds.

In conclusion, two carabid beetle species and the female northern field cricket consumed more redroot pigweed seeds followed by giant foxtail seeds and lastly velvetleaf seeds. The smallest carabid beetle species, *A. aenea*, did not show a preference between redroot pigweed and giant foxtail seeds. However when seed biomass was measured, one carabid beetle species consumed similar amounts of redroot pigweed and velvetleaf seeds while another preferred velvetleaf over giant foxtail seeds. The northern field crickets consumed a higher biomass of redroot pigweed seeds. The smallest carabid beetle species consumed a similar biomass of all three seeds. From a weed management standpoint, less weed seeds could reduce weed populations, and consuming a few large seeds may have less impact on the weed community compared with consumption of many small seeds.

The smaller carabid beetle species, *A. aenea* and *A. sanctaecrucis*, primarily consume seeds on the soil surface and would appear to have minimal impact on the buried seeds in the seed bank. However, the larger carabid beetle species, *H. pensylvanicus* consumed seeds to a 1.0 cm depth in soil and therefore could have a greater impact on seeds that have moved into the upper one centimeter of the soil profile.

Only a small percentage (5 to 20%) of weed seeds in the soil-seed bank germinate each year depending on the site and weed species (Forcella *et al.* 1997; Kropac 1986; Wilson *et al.* 1985). Insect predation may not only reduce the old shallow seed bank but may strongly influence the fate of new seed rain each year. In no-tillage systems, most seeds that germinate in a single season are on or within 2 cm of the soil surface, exposing them to consumption by seed predators (Brust and House 1988). Seed predation may be one reason why weed pressure declines over time in no-till agroecosystems (Radosevich *et al.* 1997). Cromar *et al.* (1999) found that ground dwelling invertebrates and small animals consumed 10 to 25% of the available seed in a field experiment. Consumption of weed seeds in the spring and fall by these ground-dwelling arthropods and other predators may influence the composition of the weed community in agroecosystems.

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Table 1. Completely randomized design ANOVA (treatment being a mixture of velvetleaf, giant foxtail, and redroot pigweed seeds) on the feeding preferences of three species of common ground beetles (*Amara aenea, Anisodactylus sanctaecrucis*, and *Harpalus pensylvanicus*) and female and male northern field cricket (*Gryllus pennsylvanicus).*

Amara aenea

Source	df	MS	F	P
Treatment	2	0.2568	22.21	**0.0001**

Anisodactylus sanctaecrucis

Source	df	MS	F	P
Treatment	2	1.3322	78.92	**0.0001**

Harpalus pensylvanicus

Source	df	MS	F	P
Treatment	2	1.4484	72.71	**0.0001**

Gryllus pennsylvanicus (female)

Source	df	MS	F	P
Treatment	2	1.5021	93.79	**0.0001**

Gryllus pennsylvanicus (male)

Source	df	MS	F	P
Treatment	2	0.6010	38.04	**0.0001**

Table 2. Completely randomized design ANOVA (treatment is depth of seed burial: soil surface, 0.5 cm, or 1.0 cm) of the feeding depth study analyzing the ability of the common ground beetle species, *Anisodactylus sanctaecrucis*, to feed on three species of weed seeds (velvetleaf, giant foxtail, or redroot pigweed).

Velvetleaf

Source	df	MS	F	P
Treatment	2	0.0038	4.88	**0.0232**

Giant foxtail

Source	df	MS	F	P
Treatment	2	0.0481	2.98	0.0816

Redroot pigweed

Source	df	MS	F	P
Treatment	2	0.0693	4.73	**0.0287**

Table 3. Completely randomized design ANOVA (treatment is depth of seed burial: soil surface, 0.5 cm, or 1.0 cm) of the feeding depth study analyzing the ability of the common ground beetle species, *Amara aenea*, to feed on three species of weed seeds (velvetleaf, giant foxtail, or redroot pigweed).

Velvetleaf

Source	df	MS	F	P
Treatment	2	0.0003	0.43	0.6573

Giant foxtail

Source	df	MS	F	P
Treatment	2	0.0214	4.53	**0.0289**

Redroot pigweed

Source	df	MS	F	P
Treatment	2	0.0955	16.62	**0.0002**

Table 4. Completely randomized design ANOVA (treatment is depth of seed burial: soil surface, 0.5 cm, or 1.0 cm) of the feeding depth study analyzing the ability of the common ground beetle species, *Harpalus pensylvanicus*, to feed on three species of weed seeds (velvetleaf, giant foxtail, or redroot pigweed).

Velvetleaf

Source	df	MS	F	P
Treatment	2	0.0111	2.11	0.1614

Giant foxtail

Source	df	MS	F	P
Treatment	2	0.0060	1.06	0.3697

Redroot pigweed

Source	df	MS	F	P
Treatment	2	0.0931	1.59	0.2361

Table 5. Feeding preferences of three species of common ground beetles (*Amara aenea*, *Anisodactylus sanctaecrucis*, and *Harpalus pensylvanicus*) for three species of weed seeds (velvetleaf, giant foxtail, and redroot pigweed).

	Percentage of seeds consumed		
Weed species	***A. aenea***	***A. sanctaecrucis***	***H. pensylvanicus***
Velvetleaf	4^{b}	4^{c}	13^{c}
Giant foxtail	32^{a}	41^{b}	61^{b}
Redroot pigweed	32^{a}	77^{a}	89^{a}

Means with the same letter are not significantly different.

A. aenea: velvetleaf n = 50, giant foxtail n = 100,
redroot pigweed n = 100

A. sanctaecrucis: velvetleaf n = 100, giant foxtail n = 100,
redroot pigweed n = 100

H. pensylvanicus: velvetleaf n = 50, giant foxtail n = 100,
redroot pigweed n = 100

Table 6. Feeding preferences of the female and male northern field cricket (*Gryllus pennsylvanicus*) for three species of weed seeds (velvetleaf, giant foxtail, and redroot pigweed).

	Percentage of Seeds Consumed	
Weed species	***G. pennsylvanicus*** **(female)**	***G. pennsylvanicus*** **(male)**
Velvetleaf	4^{c}	1^{c}
Giant foxtail	63^{b}	56^{a}
Redroot pigweed	81^{a}	65^{a}

Means with the same letter are not significantly different.

G. pennsylvanicus: velvetleaf n = 100, giant foxtail n = 100, redroot pigweed n = 400

Table 7. Biomass (mg) consumed of three weed seeds (velvetleaf, giant foxtail, and redroot pigweed) in feeding preference study by three carabid beetle species (*Amara aenea*, *Anisodactylus sanctaecrucis*, *Harpalus pensylvanicus*) and the female and male northern field cricket (*Gryllus pennsylvanicus*).

	Biomass consumed				
Weed species	***A. aenea***	***A. sanctaecrucis***	***H. pensylvanicus***	***G. pennsylvanicus* (female)**	***G. pennsylvanicus* (male)**
Velvetleaf	17^{a}	34^{a}	60^{a}	34^{b}	8^{b}
Giant foxtail	13^{a}	16^{b}	24^{b}	25^{b}	22^{b}
Redroot pigweed	12^{a}	29^{a}	33^{ab}	119^{a}	97^{a}

Means with the same letter are not significantly different.

Table 8. Seed consumption of three weed seed species (velvetleaf, giant foxtail, and redroot pigweed) at 0.0, 0.5, and 1.0 cm burial depths by one carabid beetle species, *A. aenea*, *A. sanctaecrucis*, or *H. pensylvanicus*.

	Percentage of Seeds Consumed								
	A. aenea			***A. sanctaecrucis***			***H. pensylvanicus***		
Soil Depth	ABUTH[1]	SETFA[2]	AMARE[3]	ABUTH	SETFA	AMARE	ABUTH	SETFA	AMARE
0.0 cm	2^{a}	12^{a}	23^{a}	4^{a}	17^{a}	22^{a}	2^{a}	72^{a}	57^{a}
0.5 cm	1^{a}	4^{ab}	1^{b}	0^{b}	3^{ab}	0^{b}	8^{a}	78^{a}	33^{a}
1.0 cm	0^{a}	0^{b}	0^{b}	0^{b}	1^{b}	0^{b}	11^{a}	76^{a}	40^{a}

Means with the same letter are not significantly different.

[1] ABUTH = *Abutilon theophrasti* (velvetleaf)
[2] SETFA = *Setaria faberi* (giant foxtail)
[3] AMARE = *Amaranthus retroflexus* (redroot pigweed)

CHAPTER 3

WEED SEED PREDATION INFLUENCES WEED COMMUNITY COMPOSITION

ABSTRACT

Weed seed predators include some species of carabid beetles and crickets. Predation of weed seeds on our near the soil surface may reduce weed seedling emergence and influence the resulting weed community. The influence of post-dispersal seed predation by three carabid beetle species and the northern field cricket on weed seedling emergence was determined in greenhouse and field experiments. Velvetleaf (*Abutilon theophrasti* Medicus) emergence in the greenhouse was greater when seed was buried at 0.5 cm compared to seed placed on the surface in experiments with four of five insect species. Giant foxtail (*Setaria faberi* Herrm.) emergence was also greater from the 0.5-cm depth in the studies with spring-breeding carabid beetles. Redroot pigweed emergence from 0.5-cm was lower compared to surface sown seed in the seeding for the fall-breeding carabid beetle *Harpalus pensylvanicus*. *Anisodactylus sanctaecrucis* decreased redroot pigweed (*Amaranthus retroflexus* L.) emergence by 18% compared to emergence in the absence of this carabid beetle species. Male and female *Gryllus pennsylvanicus*, (northern field cricket) reduced seedling emergence by 16% and 5%, respectively, compared to seedling emergence in the absence of these insects. *Amara aenea* and

Harpalus pensylvanicus did not influence weed seedling emergence in the greenhouse.

In the 1997-98 field study, vertebrate/invertebrate predation decreased emergence of fall-seeded velvetleaf by 9% (P=0.0001). Giant foxtail emergence from the fall-seeding was decreased by 15% (P=0.0597) in the presence of vertebrate/invertebrates compared to the exclusion of all predators. There were no significant differences in weed emergence due to exclosure during the spring-seeded field trial. In the 1998-99 field studies, redroot pigweed, giant foxtail, or velvetleaf seed was sown at three sites and weed emergence was monitored for 12 months in three exclosure treatments. Giant foxtail emergence decreased at two of three sites and velvetleaf emergence decreased at three of three sites when all predators could access the seed compared to complete exclosure. Invertebrates decreased velvetleaf emergence at two of three sites and giant foxtail at one of three sites. Redroot pigweed did not emerge in any exclosure at any site. Seed predator captures were low at all sites. Predation influenced the weed community in greenhouse and field research.

INTRODUCTION

Annual plants depend on seed set, dispersal, and germination for the initiation of new populations. Thus, seed must be both produced and dispersed for a plant species to be successful (Harper 1977; Louda, 1989). Seed input into the soil as well as seed loss influence the composition of seed banks. Seed predation is one cause of seed loss that occurs on the plant and on the soil surface (Louda 1989). Therefore, seed predators may potentially influence the life cycle of an annual plant at several stages. Seed predators may differentially select certain seed types and sizes, therefore impacting the characteristics of the seed bank (Louda 1989). By finding and exploiting clusters of seeds and/or larger seeds, predators may reinforce other pressures that select for seed traits characteristic of persistent seed banks, including small seed size and hard seed coats. Additionally, the moving and caching of propagules by predators may change seed distribution and recruitment of seed (Louda 1989).

Louda (1989) suggests that seed predation can change density and relative abundance of dominant annual species. She also suggests that seed predation influences recruitment, occurrence, and distribution of moderately large-seeded plants with fugitive life histories. Generally, the risk of predator activity and impact increases as the canopy matures, because a denser canopy provides greater cover.

Brown *et al.* (1975) found that rodents and ants were important and efficient seed predators in desert systems. The spatial distribution of foraging activity and the sizes and species of seeds taken were similar for these predators. Inouye *et al.* (1980) and Reichman (1979) examined the impact of ants and rodents on plant density in desert plots. Seed predation greatly reduced plant densities but granivorous ants and rodents had qualitatively different affects on the plant community (Inouye et al. 1980). Rodents preyed selectively on larger-seeded species while the ants harvested the smaller seeds of certain abundant species.

Some species of carabid beetles are known predators of weed seed. Carabid beetles had the greatest impact in removing weed seeds in both no-till and conventional tillage soybean fields (Brust and House 1988). Velvetleaf seed loss from the soil surface ranged from 1 to 57% day^{-1} in continuous no-till and moldboard plow systems (Cardina et al. 1996). Mice and small animals were responsible for 15% of this seed loss. Cromar *et al.* (1999) studied the influence of tillage and crop residue on postdispersal predation of the seed of common lambsquarters (*Chenopodium album* L.) and barnyardgrass (*Echinochloa crus-galli* Beauv.) and found that ground-dwelling invertebrates consumed 25% of the available seed while mice and small animals were responsible for 10 to 22% of seed loss. In all of these studies weed seed was placed on the soil surface in the fields for certain time periods and then removed. Similarly, in an alfalfa system, Radosevich *et al.* (1997) observed that 99.8% of a current year's seed rain of barnyardgrass, redroot pigweed (*Amaranthus retroflexus* L.), and common lambsquarters was eliminated by the field mouse (*Peromyscus* spp.).

More recently, the field cricket *Gryllus pennsylvanicus* has been found to consume weed seeds. In a laboratory no-choice test, both male and female *G. pennsylvanicus* readily consumed the seeds of small and large-seeded annual weeds (Carmona *et al.* 1998, 1999). In a choice test discussed in the previous chapter, females preferred redroot pigweed compared to giant foxtail and velvetleaf seed while males preferred redroot pigweed and giant foxtail compared to velvetleaf seed.

House and Brust (1989) conducted a greenhouse experiment to determine whether seed predators could reduce weed-seed germination and weed numbers in the presence or absence of a mulch cover. Three common broadleaf weed seeds (redroot pigweed, common lambsquarters, and common ragweed) and two common grass weed seeds (fall panicum *Panicum dichotomiflorum* Michx. and large crabgrass *Digitaria sanguinalis* (L.) Scop.) were used in the study. The carabid beetles *Amara* species, *Anisodactylus* species, and *Harpalus pensylvanicus,* and ten crickets (*Gryllus* species) were included in this study. In the absence of a mulch cover, seed predators reduced broadleaf seedling emergence but not grass seedling emergence. They concluded that insect seed predators could potentially reduce weed numbers and biomass.

The objective of our research was to examine the impact of post-dispersal seed consumption by vertebrates and invertebrates on annual weed seedling establishment in the greenhouse and in no-till corn fields. The insects selected for the greenhouse study were three species of common ground beetles (*Amara aenea* DeGeer, *Anisodactylus sanctaecrucis* F., and *Harpalus pensylvanicus* DeGeer) and the male and female northern field cricket (*Gryllus pennsylvanicus* Burmeister), all known to be granivores (Carmona *et al.* 1999, Brust and House 1988, House and Brust 1989). Both male and female crickets were evaluated because females consumed greater numbers of weed seeds than males in the same time period (Carmona 1998; Carmona *et al.* 1999). The objective of the field exclusion studies in no-till corn fields was to determine if predation (vertebrate and invertebrate) could influence weed emergence in no-till corn fields the year following simulated weed seed rain.

MATERIALS AND METHODS

Greenhouse. The study was conducted from April to June 1999 and August to October 1999 at the Michigan State University greenhouse. The timing of the experiment was based on the time of optimal activity of the seed predators. *Amara aenea* and *Anisodactylus sanctaecrucis* are active in spring (April to June) while *Harpalus pensylvanicus* and *Gryllus pennsylvanicus* are active in the fall (August to October). The spring active carabid beetle species (*A. aenea* and *A. sanctaecrucis*) were collected in a fallow corn field and a fallow soybean field while the fall active carabid beetle species (*H. pensylvanicus*) was collected in a soybean field using pitfall traps at Michigan State University. Pitfall traps (11 mm diameter by 14 mm deep) were placed 1 cm below the soil surface. Northern field cricket (*G. pennsylvanicus*) males and females were caught by hand after disturbing their diurnal resting areas (beneath boards, under debris, etc). Collected insects were placed in 7.5 L feeding dishes (18 mm diam. x 8 mm deep) containing 1 cm of moist sterilized sandy loam soil (84% sand, 10% silt, and 6% clay) containing 2% organic matter. Soil was sifted using USA Standard testing sieve #16 and Tyler equivalent #14 mesh screens to remove non-decayed organic matter the insects may feed upon. The dishes were left at room temperature while insects were starved for 24 h prior to testing.

Sterilite® (Sterilite Corporation, Townsend, Massachusetts) blanket boxes measuring (40 w x 60 l x 25 h 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 (small enough to prevent insects from escaping). The bottom 14 cm of the boxes was painted black to eliminate the effect of light on root growth near the perimeter of the box. Fourteen 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 x 68 cm hole was cut out of the plastic lid and screen was hot-glued on the inside of the lid taking care to eliminate any space between the screen and the plastic that would allow insects to escape from the box. Lids remained on all boxes until the first seedling count at seven days and daily watering took place through the screened lid.

The experimental design was a three factor factorial with six replications. The first factor was the presence or absence of an insect, the second factor was the weed species (giant foxtail, velvetleaf, and redroot pigweed), and the third factor was the seeding depth (surface or 0.5 cm). Two carabid beetle species (*Amara aenea* and *Anisodactylus sanctaecrucis*) were studied in the spring and one carabid beetle species (*Harpalus pensylvanicus*) and males and females of the northern field cricket (*Gryllus pennsylvanicus*) were studied in the fall when adults of the respective species were active. Four *A. sanctaecrucis*, six *A. aenea*, four *H. pensylvanicus*, or one male or one female *G. pennsylvanicus* were added to a box. (Male field crickets are territorial therefore, only one cricket was placed in each box (personal observation)). Seed mixtures for the carabid beetle species consisted of 150 redroot pigweed, 150 giant foxtail, and 60 velvetleaf. Due to the high consumption rate of redroot pigweed by field crickets (Carmona 1998; Carmona *et al.* 1999), redroot pigweed was increased to 510 seeds in the cricket experiments. In preliminary germination tests, velvetleaf, giant foxtail, and redroot pigweed seed had germination percentages of 54, 40, and 55, respectively (data not shown).

The third factor was imposed by sowing seed on the soil surface or 0.5 cm below the soil surface. If the seed was sown on the soil surface, the soil was soaked with 1.3 cm of water (representing a 1.3 cm rainfall) and the insects were placed in the box for a 24 h acclimation period prior to sowing the seed mixture. After seed placement on the base soil layer, the seed was lightly scratched into the surface with a Goody® (Goody Products, Inc., Peachtree City, Georgia) hair pik (six tines 0.8 cm apart) simulating a 'natural' soil surface. Insects remained in the box for 48 hours after seed distribution on the soil surface. 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 water applied. The insects were added at this time, minimizing the effect of seed germination and water imbibition on seed predation by the insects. These insects remained in the box for 72 hours to allow for the 24 hour acclimation period and 48 hour feeding period. At the end of the feeding period insects were killed by the addition of the soil insecticide, terbufos, at 0.17 g per box to the soil surface. The insecticide was leached into the soil with 1.3 cm of water.

Newly emerged weed seedlings were counted weekly for five weeks. Seedlings were marked by placing a dot on the leaf surface using a fine point permanent marker. These markings assured that seedlings would not be counted twice during this process. Five weeks after planting, a final weed count was taken in each box.

Analysis. The experimental design followed a three-factor factorial model in a randomized complete block design with six replications. The factors were the presence/absence of a seed predator, weed seed species, and the seed placement depth of 0.0 or 0.5 cm. Analysis of variance was performed on transformed (ARCSINE transformation) and nontransformed data for total weed emergence in both spring and fall experiments. Data transformation did not alter treatment significance and therefore the results of nontransformed data are presented. Data is presented separately by depths because of a significant seed predator by seeding depth interaction. The analysis of variance was used to analyze for differences among treatments and the differences were separated by

Fisher's LSD test (P=0.05). All analyses were conducted using Statistical Analysis System (SAS Institute 1996).

Field studies. Field studies were conducted in fallow no-till corn fields in 1997-98 and 1998-99. Weed seeds were placed in the field on the soil surface in the fall or spring and exclosures (cages) were then placed over the seeds to exclude vertebrates only; exclude vertebrates and invertebrates (no predation); or exclude neither (no cages to allow both vertebrate and invertebrate access). Weed seedlings were then counted in the spring and summer following seed placement.

Exclosure (cage) construction. Wire cages measuring 38 x 69 x 25 cm were constructed of 1.3 cm hardware cloth. Openings measuring approximately 20 x 15 x 20 cm were cut in the top of each cage, allowing for removal of weed seedlings. The cut hardware cloth openings were held shut with cable ties. Cages that excluded both vertebrates and invertebrates had an eight-inch strip of thick plastic treated with a Teflon® spray (to minimize the possibility of insects entering the experimental area) placed around the bottom of the cage with four inches of plastic located on the inside and the outside of the cage. Cage placement in the field was dependent on tire spacing on the combines (see Figure 1 for field design) to prevent cage disturbance during corn harvest.

Field insertion. Cage edges were placed 2.5 cm into the soil to minimize burrowing of predators into feeding area. To ease placement of cages into the soil, a 15 x 27 cm metal 'L' (courtesy of K. A. Nelson) 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 exclosure) were marked with four yellow flags. Cages, flags, and seeds were placed in the field in August to coincide with the time of seed rain and the time of emergence of the fall-breeding ground beetles. Exclosures remained in the field for 12 months.

1997-1998 Season. This study was conducted from August 1997 to August 1998 in a fallow no-till corn field on the Michigan State University Crop and Soil Science farm. The design was a two factor factorial arranged in a randomized complete block design with nine replications. The factors were exclosure type and weed seed species. The treatments consisted of 200 giant foxtail, 200 velvetleaf, a mixture of 200 giant foxtail and 200 velvetleaf seeds, or no seeds sprinkled into the feeding area after the cages were set. A second study identical to the fall study was set out in the same field (leaving one row of corn stubble between matching treatments) in April 1998 to determine spring seed predation only.

1998-1999 Season. This research was conducted as a complete randomized design from August 1998 to August 1999 in three fallow no-till corn fields located at three sites in southern Michigan. The sites were: Site 1) Michigan State University Crop and Soil Science Farm, East Lansing; Site 2) Gary Powell, private farm, Sunfield; and Site 3) Saginaw Valley Dry Bean and Sugar Beet Research Farm, Saginaw (Table 1).

There were 12 replications at Site 1 and 2, and nine replications at Site 3. The cage types were as described in the 1997-1998 study. Weed seed species were velvetleaf, redroot pigweed, or giant foxtail. Seed treatments were increased to 400 velvetleaf, 400 redroot pigweed, or 400 giant foxtail seeds. Preliminary tests showed germination percentages of 72, 34, and 48 for velvetleaf, redroot pigweed, and giant foxtail, respectively. The seeds were sprinkled into the feeding area after the cages were set.

Pitfall traps. In order to monitor the presence/absence of invertebrate seed predators, pitfall traps (11 mm diameter by 14 mm deep) were set 1 cm below the soil surface at each field site. Cups contained no killing agents and beetles were released close to their capture location to avoid depletion of seed predators. The number of beetles caught in the traps was used to estimate a combination of activity and density of seed predator beetles in the plots.

In the 1997-98 field season, sixteen pitfall traps were placed in each block. Eight traps were placed in each eight row buffer strip. Four traps were placed 3 m apart between rows two/three and five/six. During the 1998-99 field season, 20 pitfall traps were placed at each site (four on each side and four down the center of the field). Trap numbers were changed in 1998-1999 because of the change in the field plot design. In both seasons, pitfall traps were monitored daily for five consecutive days per month August to November and March to August for a total of 50 trap days.

Rodent trapping. To monitor the presence/absence of rodents, 36 Sherman traps were placed in a 6 x 6 grid over each field site. The traps were opened once for 5 consecutive days 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 (AUF# 01/99-001-00).

Analysis. Weed seedlings were counted every two weeks from September to November and again from April to August. Emerged seedlings were accessed through the hole 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.

Analysis of variance was performed on transformed (ARCSINE) and nontransformed data on total weed emergence in both spring and fall experiments. Significant differences among treatments were not altered due to transformation. Therefore only the results for the nontransformed data are presented. The analysis of variance was used to analyze for differences among treatments and the differences were separated by Fisher's LSD test (P=0.05). All analyses were conducted using Statistical Analysis System (SAS Institute 1996).

1997-98. The experimental design was a two-factor factorial arranged in a randomized complete block design. The factors were weed seed species sown and cage type and there were nine replications. Seedlings were counted and removed monthly during the growing season and the total percentage of weed emergence was calculated.

1998-99. The experimental design was a two-factor factorial arranged in a randomized complete block design. There were 12 replications at Sites 1 and 2 and nine replications at Site 3. Seedlings were counted and removed bimonthly during the growing season and the total percentage of weed emergence was calculated.

RESULTS AND DISCUSSION

Greenhouse Study. There was a significant weed by depth interaction for all three weed species at both depths, when averaged over the presence/absence of insects for each insect experiment (Tables 2 to 6). In four of the five studies, velvetleaf had greater emergence (18 to 28%) from a seeding depth of 0.5 cm below the soil surface compared to emergence from the soil surface (Table 7). These results support those of Buhler *et al.* (1997) in which velvetleaf germination decreased when placed on the soil surface.

Redroot pigweed emergence declined slightly at 0.5 cm when compared to surface sown seed (Table 7). Wiese and Davis (1987) and Siriwardana and Zimdahl (1983) concluded that 1-cm was optimal for redroot pigweed emergence. Giant foxtail emergence was greatest from seeds placed on the soil surface in three of five treatments, while seedling emergence was greatest from seeds placed at the 0.5 cm depth in one treatment, and emergence was similar regardless of seed placement in one treatment (Table 7). In previous research, emergence of giant foxtail decreased as seeding depth increased (Dawson and Bruns 1962), while Fausey and Renner (1997) found the greatest giant foxtail emergence at one cm.

In the study with *A. sanctaecrucis*, the presence of the insect had a significant effect (F = 5.43, P = 0.0235) on weed seedling emergence, and there was an insect by weed interaction as well (F = 7.88, P = 0.0010) (Table 3). Redroot pigweed emergence decreased by 18% in the presence of *A. sanctaecrucis* when compared to the no insect treatment (Table 8). Emergence of giant foxtail and velvetleaf was not influenced by the presence/absence of *A. sanctaecrucis* (Table 3).

Gryllus pennsylvanicus females and males (F = 40.38, P = 0.0001 (Table 5); F = 5.85, P = 0.0189 (Table 6), respectively) decreased weed emergence when averaged over all weed species and seeding depth. The presence of males decreased emergence by 5% while the presence of females decreased emergence by 16% when averaged over the three weed species (Table 9). There was no weed by insect interaction for female or male *Gryllus pennsylvanicus* (Tables 5 and 6).

The presence of *Harpalus pensylvanicus* (F = 1.62, P = 0.2087 (Table 4) and *Amara aenea* (F = 2.83, P = 0.0985 (Table 2)) did not affect weed seedling emergence. In Chapter 2, we reported *H. pensylvanicus* consumed 89% of the available redroot pigweed seed and 61% of the available giant foxtail seed when given a choice of redroot pigweed, giant foxtail, and velvetleaf seeds. We also found in the seed placement study that *H. pensylvanicus* consumed redroot pigweed and giant foxtail seed placed 0.5 or 1 cm below the soil surface. It is possible that the carabid beetles were closer to diapause in this study which may lead to lower seed consumption. In *Gryllus pennsylvanicus*, females consumed greater numbers of seeds when compare to seed consumption by the males. This may be an additional factor that may influence seed consumption by *H. pensylvanicus* . Based on the conclusions in Chapter 2, we did not expect to see *Amara aenea* influence weed seedling emergence because this carabid beetle species consumes weed seed only on the soil surface and in addition, has a low rate of seed consumption compared to the other carabid beetle species studied and the northern field cricket.

Field Study.

1997-98. Emergence of velvetleaf from the fall seeding was affected by predator exclosure type (F = 12.89, P = 0.0001) (Table 10). Giant foxtail emergence from the fall seeding was also influenced by exclosure type (F=3.03, P=0.00597) (Table 11). However, velvetleaf and giant foxtail emergence from the spring seeding did not differ due to exclosure type (Tables 12 and 13). For the fall seeding, vertebrate access significantly lowered velvetleaf emergence from 16 to 7% (Table 14). Giant foxtail emergence decreased in the presence of invertebrates from 36 to 23%, and decreased by an additional 2% when all seed predators were allowed access to the seeds (Table 14). These results infer that invertebrates were largely responsible for the decrease in giant foxtail emergence the following spring. When seeds were placed in the field in the spring, there were no differences in weed seedling emergence between exclosure treatments, suggesting weed seed predation occurred in the fall and winter months. Cardina *et al.* (1996) found velvetleaf seed predation was generally low in the winter months, increased in mid-summer and declined in late summer. In no-till treatments, the percent of seed predation averaged 43% in the fall and decreased to 24% in the spring (Cromar *et al.* 1999).

1998-99.

Emergence. At each site, exclosures influenced weed seedling emergence. The effect of the exclosures was dependent on exclosure type and weed species. The main effects for weed and exclosure and the weed by exclosure interaction at each site are presented in Tables 15, 16, and 17 for Sites 1, 2, and 3, respectively.

Redroot pigweed emergence was very low at all three sites and no significant differences were detected among treatments (Table 18). Velvetleaf emergence decreased by 4% at Site 1 when invertebrates were allowed into the feeding area (Table 18). Vertebrate predation decreased emergence by an additional 4%, as compared to the total exclosure treatment. At Site 2, invertebrates decreased velvetleaf emergence by 6% compared to the total exclosure treatment, while vertebrates were responsible for a decrease in velvetleaf emergence (8%) at Site 3 compared to the total exclosure treatment (Table 18).

At Site 1, vertebrates were responsible for a 7 to 8% reduction in giant foxtail emergence compared to the total exclosure treatment, whereas invertebrates were responsible for the 4% decrease in emergence at Site 2. At site 3 giant foxtail emergence decreased by 4% when vertebrates were allowed access to the seed (Table 18).

In summary, vertebrate predation decreased velvetleaf and giant foxtail emergence at Site 1 and velvetleaf emergence at Site 3. Invertebrates decreased velvetleaf emergence at Site 1 and Site 2 and invertebrates decreased giant foxtail emergence at Site 2.

Further experimentation with different cage exclosures may be of interest in future research. Did the exclosure deter either predator or plant movement? When no cage was present, we marked the plot with a flag in each corner. Insertion of a 2.5 tall strip the size of the cage into the soil and constructing a 'roof' over the seeded area could determine the effect of exclosures on weed seedling emergence.

Seed predator presence/absence. At all three sites, the activity/density of the carabid beetle seed predators (*A. aenea*, *A. sanctaecrucis*, and *H. pensylvanicus*) was low (Table 19). Only the carabid beetle species studied in the growth chamber and greenhouse studies were recorded and these numbers were not an accurate reflection of all insect seed predators in the field. In addition, a pitfall trap does not effectively trap the northern field cricket; therefore their activity/density is not reflected in this table. Only one rodent species, the white-footed mouse (*Peromyscus leucopus* Fischer), was captured and released at all of our field sites. This rodent is common in agricultural fields and belongs to the family Cricetidae (Burt and Grossenheider 1980).

Excavation. The complete exclosure plots at Sites 1 and 2 were excavated in the fall of 1999 to a 2.5 cm depth. Only data from Site 1 is included in this discussion. The intact seed remaining in the soil was extracted and the seed counted (Table 20). The germination percentages for each weed seed species in the laboratory were 33% for velvetleaf, 31% for redroot pigweed, and 41% for giant foxtail. Maximum germination in the field for velvetleaf, redroot pigweed, and giant foxtail could have approached 132, 124, and 164 seeds, respectively. The average number of seeds germinating in the control exclosures were 37, 2, and 42 seedlings of velvetleaf, redroot pigweed, and giant foxtail, respectively, and the average number of seeds excavated from these sites were 9 velvetleaf, 25 redroot pigweed, and 1velvetleaf seed, respectively. This resulted in 354 velvetleaf, 373 redroot pigweed, and 357 giant foxtail seeds unaccounted for within the control exclosures. It is unlikely that seed loss occurred through wind erosion or surface soil erosion as 7.6 cm of plastic were above the soil surface in the total exclosure treatments to prevent washing and blowing, and the cage edges were set 2.5 cm in the soil. However, seeds may have moved past the 2.5 cm excavation depth during rainfall events, or from the soil surface cracking due to freezing of the soil as well as soil dryness during the summer. Alternatively, seeds may have decayed on the soil surface. In addition, seed loss may have occurred by predation of other invertebrates such as earthworms and burrowing insects or by microbial decomposition.

The 1998-99 velvetleaf emergence data at Site 3 validates fall velvetleaf emergence in the 1997-98 study. The decrease in velvetleaf emergence was due mainly to the vertebrate predators in 1997-98 and at Site 3 in 1998-99. At Site 1 in 1998-99, invertebrates and vertebrates were equally responsible for a decrease in velvetleaf emergence. Cardina *et al.* (1996) observed that velvetleaf predation was generally low in the winter months, increased in mid-summer, and declined in late summer in continuous no-tillage and moldboard plow corn fields. In their study, exclosures set in the field to exclude mice, large carabid beetles and slugs reduced predation 48 to 69%, suggesting these animals were responsible for about half of the seed predation. Our data suggests that rodent and insect predation of velvetleaf seed influenced the weed community in this agroecosystem the following year.

Giant foxtail emergence decreased when both vertebrates and invertebrates were allowed access to the seed in fall seed placement 1997-98 and 1998-99. Our data suggests that vertebrates consume greater numbers at Site 1 (7%) while Site 2 data infers that insects consume greater numbers of giant foxtail (4%). Unfortunately, data obtained from pitfall traps and Sherman traps were not able to support our findings.

Further field studies should confirm the influence of weed seed predation on weed communities. In all of our field sites the presence of *A. aenea, A. sanctaecrucis*, and *H. pensylvanicus* was low. Sites 1 and 3 were agronomic research farms with rotating soybean and corn crops. Site 1 was bordered by two mown grassy borders and two field sides planted to no-till soybeans. 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 seven years and had a grassy/weedy border along one edge, a road on one edge, and the remaining edges planted to soybeans. The grassy borders should provide cover for potential insect predators. However by mowing the strips, rodent activity may decrease.

Menalled *et al.* (1997) conducted a field experiment looking at the effect of the agricultural landscape structure on post-dispersal weed seed removal. The mean seed removal rate was 52.1% in a complex landscape compared to 31.8% in a simple landscape suggesting that landscape complexity influences the effectiveness of natural enemies of weed seeds in agroecosystems. In Ontario, Cromar *et al.* (1999) found that predation was highest in no-till and moldboard-plowed environments (32%) and lowest in chisel-plowed environments (24%). Low numbers of predators at all sites may have occurred because the grassy borders offered a refuge more attractive to the predator than the open field.

In August 1998, we placed 400 velvetleaf, redroot pigweed, or giant foxtail seeds into the field. When soil was excavated from the complete exclosures at Site 1, we found 88% of the seeds were unaccounted for. Where did they go? Were they swept out of the exclosure by the wind or washed out by the water? No seedling clumps were noted around exclosure edges and edged penetrated 2.5 cm into the soil and the plastic strip was 7.6 cm above the soil surface. However, the seeds may have moved further than 2.5 cm into the soil and therefore would not have been excavated. No evidence of large predators in these cages were noted. It is possible that tunneling insects or earthworms could have removed the seed. Seeds may have undergone microbial degradation during the year. There is no published information that the authors could find on seed degradation on the soil surface.

Weed seed banks decline rapidly over time. The longer the seed is buried in the soil, the greater the seed longevity. In no-tillage systems, the majority of seed is concentrated in the top 2.5 cm of soil, particularly if weeds have been allowed to go to seed at any time since the field has been in no-tillage. In a study by Roberts and Dawkins (1967) measuring the decline of viable seeds in undisturbed and cultivated soil, the mean decrease in viable seeds was 12% per year in undisturbed soil and 32% per year in cultivated soil. At the end of one year, Buhler (D. Buhler, Leopold Center for Sustainable Agriculture, Iowa State University, Ames) found that giant foxtail seed viability rapidly dissipated to 7% after one year and declined to less that 1% after two years. However, they found that 50% of common waterhemp (another *Amaranthus* species) seed and 42% of velvetleaf seed remained viable after one year. Our greenhouse studies and our field studies indicate that the presence of common ground beetles impact seedling emergence and the weed community. A study involving the degradation of seeds in the surface seed bank would be a natural follow-up to these studies to further verify the impact of seed predation and seed decay on the weed seedbank and weed community.

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Figure 1. Basic design of field studies.

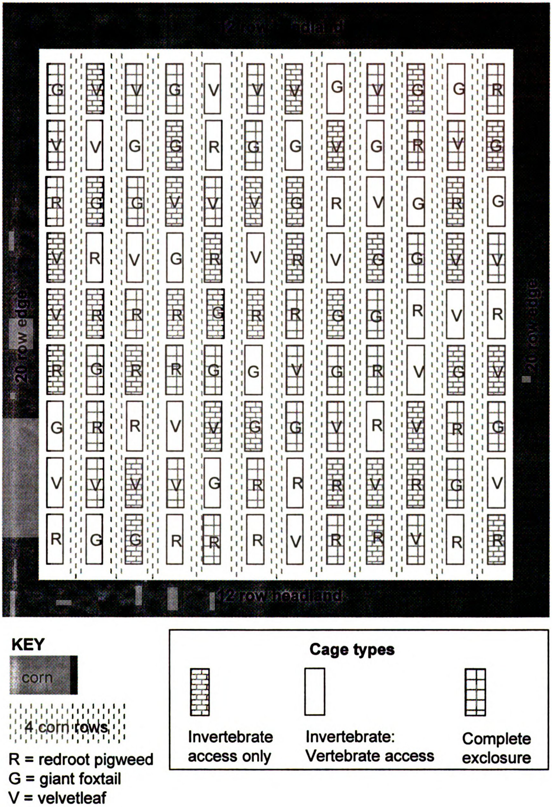

Table 1. History of field sites.

Year	Location	Crops	Tillage	Soil Type
1997-98	Campus	corn, soybean	no-till	sandy loam
1998-99	Site 1	corn, soybean	no-till	sandy loam
	Site 2	corn, soybean	no-till	loam
	Site 3	corn, soybean	no-till	silty loam

Table 2. Analysis of variance for the effect of feeding by the common ground beetle, *Amara aenea*, on weed seedling emergence in the spring greenhouse studies. The three-factor factorial included weed seed (velvetleaf, giant foxtail, and redroot pigweed), insect (presence/absence), and weed seed placement in soil (0.0 or 0.5 cm).

Source	df	MS	F	P
Weed	2	0.4996	96.95	**0.0001**
Insect	1	0.0146	2.83	0.0985
Depth	1	0.1254	24.33	**0.0001**
Weed * insect	2	0.0012	0.24	0.7869
Weed * depth	2	0.1065	20.66	**0.0001**
Insect * depth	1	0.0024	0.47	0.4968
Weed * insect * depth	2	0.0020	0.40	0.6738

Table 3. Analysis of variance for the effect of feeding by the common ground beetle, *Anisodactylus sanctaecrucis*, on weed seedling emergence in the spring greenhouse studies. The three-factor factorial included weed seed (velvetleaf, giant foxtail, and redroot pigweed), insect (presence/absence), and weed seed placement in soil (0.0 or 0.5 cm).

Source	df	MS	F	P
Weed	2	0.7424	62.02	**0.0001**
Insect	1	0.0650	5.43	**0.0235**
Depth	1	0.5026	41.99	**0.0001**
Weed * insect	2	0.0943	7.88	**0.0010**
Weed * depth	2	0.2172	18.15	**0.0001**
Insect * depth	1	0.0428	3.57	0.0640
Weed * insect * depth	2	0.0339	2.83	0.0674

Table 4. Analysis of variance for the effect of feeding by the common ground beetle, *Harpalus pensylvanicus*, on weed seedling emergence in the spring greenhouse studies. The three-factor factorial included weed seed (velvetleaf, giant foxtail, and redroot pigweed), insect (presence/absence), and weed seed placement in soil (0.0 or 0.5 cm).

Source	df	MS	F	P
Weed	2	0.3630	11.66	**0.0001**
Insect	1	0.0504	1.62	0.2087
Depth	1	0.0054	0.17	0.6781
Weed * insect	2	0.0505	1.62	0.2067
Weed * depth	2	0.1498	4.81	**0.0118**
Insect * depth	1	0.0629	2.02	0.1608
Weed * insect * depth	2	0.0689	2.21	0.1190

Table 5. Analysis of variance for the effect of feeding by the female northern field cricket, *Gryllus pennsylvanicus*, on weed seedling emergence in the spring greenhouse studies. The three-factor factorial included weed seed (velvetleaf, giant foxtail, and redroot pigweed), insect (presence/absence), and weed seed placement in soil (0.0 or 0.5 cm).

Source	df	MS	F	P
Weed	2	0.4412	32.07	**0.0001**
Insect	1	0.5556	40.38	**0.0001**
Depth	1	0.0146	1.06	0.3080
Weed * insect	2	0.0092	0.67	0.5147
Weed * depth	2	0.0929	6.75	**0.0024**
Insect * depth	1	0.0018	0.13	0.7198
Weed * insect * depth	2	0.0079	0.58	0.5655

Table 6. Analysis of variance for the effect of feeding by the male northern field cricket, *Gryllus pennsylvanicus*, on weed seedling emergence in the spring greenhouse studies. The three-factor factorial included weed seed (velvetleaf, giant foxtail, and redroot pigweed), insect (presence/absence), and weed seed placement in soil (0.0 or 0.5 cm).

Source	df	MS	F	P
Weed	2	0.5633	60.14	**0.0001**
Insect	1	0.0548	5.85	**0.0189**
Depth	1	0.0930	9.93	**0.0026**
Weed * insect	2	0.0021	0.22	0.8026
Weed * depth	2	0.0978	10.44	**0.0001**
Insect * depth	1	0.0201	2.15	0.1480
Weed * insect * depth	2	0.0047	0.5	0.6074

Table 7. The emergence of weed species by soil depth averaged over the presence/absence of an insect in each of the greenhouse studies.[a]

	Percentage of weed emergence									
	A. aenea[b]		*A. sanctaecrucis*[b]		*H. pensylvanicus*[b]		*G. pennsylvanicus*[c] (female)		*G. pennsylvanicus*[c] (male)	
	cm		cm		cm		cm		cm	
Weed species	0.0	0.5	0.0	0.5	0.0	0.5	0.0	0.5	0.0	0.5
Velvetleaf	43^{bc}	65^{a}	35^{c}	72^{a}	48^{ab}	57^{a}	36^{b}	54^{a}	42^{b}	64^{a}
giant foxtail	41^{c}	48^{b}	36^{c}	49^{b}	29^{cd}	35^{bcd}	43^{b}	36^{b}	45^{b}	44^{b}
Redroot pigweed	28^{d}	23^{d}	19^{d}	19^{d}	41^{bc}	21^{d}	20^{c}	18^{c}	23^{c}	23^{c}

[a] The comparison of weed emergence across insect species is not valid. Each insect was evaluated separately.

[b] Seed sown in the containers for these species:
velvetleaf n=60; giant foxtail n=150; redroot pigweed n=150

[c] Seed sown in the containers for these species:
velvetleaf n=60; giant foxtail n=150; redroot pigweed n=510

Table 8. The emergence of weed species as influenced by the presence/absence of an insect, averaged over soil depth.

	Percent of weed emergence		
Insect	**velvetleaf**	**giant foxtail**	**redroot pigweed**
A. sanctaecrucis	57^{a}	39^{c}	10^{e}
No insect	50^{ab}	47^{bc}	28^{d}

Table 9. The effect of the presence/absence of insects on the emergence of weed seedlings.

	Percent of weed emergence	
Insect	**presence**	**absence**
Amara aenea	38^a	41^a
Anisodactylus sanctaecrucis	34^a	40^b
Harpalus pensylvanicus	34^a	39^a
Gryllus pennsylvanicus (female)	25^b	41^a
Gryllus pennsylvanicus (male)	36^b	41^a

Table 10. Analysis of variance for the effect of exclosure types on the emergence of velvetleaf following fall seeding in the 1997-98 field study. The two-factor factorial included weed seed (velvetleaf only or velvetleaf plus giant foxtail) and exclosure type (exclude vertebrates, exclude vertebrates and invertebrates) or no exclosure (allow both vertebrate and invertebrate access).

Source	df	MS	F	P
Rep	8	22.4387	0.64	0.7422
Seed	1	0.5602	0.02	0.9003
Exclosure	2	454.4491	12.89	**0.0001**
Seed*Exclosure	2	7.2269	0.21	0.8155

Table 11. Analysis of variance for the effect of exclosure types on the emergence of giant foxtail following fall seeding in the 1997-98 field study. The two-factor factorial included weed seed (giant foxtail only or giant foxtail plus velvetleaf) and exclosure type (exclude vertebrates, exclude vertebrates and invertebrates) or no exclosure (allow both vertebrate and invertebrate access).

Source	df	MS	F	P
Rep	8	426.0394	1.01	0.4474
Seed	1	1143.5602	2.70	0.1083
Exclosure	2	1283.0046	3.03	0.0597
Seed*Exclosure	2	542.3935	1.28	0.2892

Table 12. Analysis of variance for the effect of exclosure types on the emergence of velvetleaf following spring seeding in the 1997-98 field study. The two-factor factorial included weed seed (velvetleaf only or velvetleaf plus giant foxtail) and exclosure type (exclude vertebrates, exclude vertebrates and invertebrates) or no exclosure (allow both vertebrate and invertebrate access).

Source	df	MS	F	P
Rep	8	38.1227	2.65	**0.0198**
Seed	1	2.0417	0.14	0.7086
Exclosure	2	30.5880	2.12	0.1330
Seed*Exclosure	2	22.2639	1.55	0.2257

Table 13. Analysis of variance for the effect of exclosure types on the emergence of giant foxtail following spring seeding in the 1997-98 field study. The two-factor factorial included weed seed (giant foxtail only or giant foxtail plus velvetleaf) and exclosure type (exclude vertebrates, exclude vertebrates and invertebrates) or no exclosure (allow both vertebrate and invertebrate access).

Source	df	MS	F	P
Rep	8	1771.1574	1.23	0.3098
Seed	1	111.2269	0.08	0.7829
Exclosure	2	1194.7546	0.83	0.4450
Seed*Exclosure	2	2673.3380	1.85	0.1706

Table 14. The percentage of velvetleaf and giant foxtail seed that emerged in the field according to exclosure type at the 1997-98 field site.

	Total Emergence			
	Fall 1997		Spring 1998	
Exclosure type	**Velvetleaf**	**Giant foxtail**	**Velvetleaf**	**Giant foxtail**
Invertebrate:Vertebrate access	7^{b}	21^{b}	9^{a}	27^{a}
Invertebrate access only	16^{a}	23^{ab}	12^{a}	27^{a}
Complete exclosure	16^{a}	36^{a}	12^{a}	41^{a}

Means with the same letter are not significantly different.

Table 15. Analysis of variance for the effect of exclosure types on the emergence of weed seedlings in the 1998-99 field study at Site 1. The two-factor factorial included weed seed (velvetleaf, giant foxtail, or redroot pigweed) and exclosure type (total exclosure, invertebrate access only, or invertebrate:vertebrate access).

Source	df	MS	F	P
Rep	11	0.0005	0.90	0.5410
Seed	2	0.0400	75.03	**0.0001**
Exclosure	2	0.0304	57.09	**0.0001**
Seed*Exclosure	4	0.0075	14.12	**0.0001**

Table 16. Analysis of variance for the effect of exclosure types on the emergence of weed seedlings in the 1998-99 field study at Site 2. The two-factor factorial included weed seed (velvetleaf, giant foxtail, or redroot pigweed) and exclosure type (total exclosure, invertebrate access only, or invertebrate:vertebrate access).

Source	df	MS	F	P
Rep	11	0.0005	0.82	0.6194
Seed	2	0.0132	21.71	**0.0001**
Exclosure	2	0.0164	25.67	**0.0001**
Seed*Exclosure	4	0.0036	5.71	**0.0004**

Table 17. Analysis of variance for the effect of exclosure types on the emergence of weed seedlings in the 1998-99 field study at Site 3. The two-factor factorial included weed seed (velvetleaf, giant foxtail, or redroot pigweed) and exclosure type (total exclosure, invertebrate access only, or invertebrate:vertebrate access).

Source	df	MS	F	P
Rep	8	0.0011	0.93	0.4987
Seed	2	0.0341	29.78	**0.0001**
Exclosure	2	0.0120	10.45	**0.0001**
Seed*Exclosure	4	0.0047	4.10	**0.0051**

Table 18. Average weed seedling emergence (velvetleaf, giant foxtail or redroot pigweed) in each exclosure treatment in three fallow no-till corn fields located in Michigan.[a]

	Average emergence								
	SITE 1[1]			SITE 2[2]			SITE 3[3]		
Cage type	ABUTH	SETFA	AMARE	ABUTH	SETFA	AMARE	ABUTH	SETFA	AMARE
Invertebrate:Vertebrate access	1^{c}	2^{c}	0^{c}	2^{bcd}	2^{bc}	0^{d}	0^{c}	5^{b}	0^{c}
Invertebrate access only	5^{b}	9^{a}	0^{c}	2^{bcd}	3^{b}	1^{cd}	8^{a}	8^{ab}	0^{c}
Complete exclosure	9^{a}	10^{a}	0^{c}	8^{a}	7^{a}	1^{cd}	8^{a}	9^{a}	0^{c}

Means with the same letter are not significantly different.

[1] Site 1 = MSU, East Lansing, MI; [2] Site 2 = Private farm, Sunfield, MI; [3] Site 3 = Saginaw Valley Dry Bean and Sugar Beet Research Farm

[a] ABUTH = *Abutilon theophrasti* (velvetleaf) n = 400 seeds; SETFA = *Setaria faberi* (giant foxtail) n = 400 seeds; AMARE = *Amaranthus retroflexus* (redroot pigweed) n = 400 seeds

Table 19. The total number of spring common ground beetles (*A. aenea* and *A. sanctaecrucis*), fall common ground beetle species (*H. pensylvanicus*), and white footed-mice (*Peromyscus leucopus*) captured and released at Sites 1, 2, and 3 in the 1998-99 field study.*

Predator	**Site 1**	**Site 2**	**Site 3**
Common ground beetles			
Spring[a]	2	13	1
Fall[b]	5	14	3
White footed-mice[c]	39	30	69

*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. A pitfall trap does not effectively trap the northern field cricket, therefore their activity/density is not reflected in this table. Only one rodent species, the white-footed mouse (*Peromyscus leucopus* Fischer), was captured and released in the Sherman traps at all three field sites.

Number of trapping days:
[a] 30 days
[b] 20 days
[c] 30 days

Table 20. A summary of seed fate for velvetleaf, redroot pigweed, and giant foxtail seeds at Site 1 in the 1998-99 field study.

	Velvetleaf	**Redroot pigweed**	**Giant foxtail**
Total seeds sown	400	400	400
Percent germination on soil surface in the greenhouse	33%	31%	41%
Predicted field seedling numbers	132	124	164
Actual number of seedling	37	2	42
Seed recovered from soil	9	25	1
Seeds not accounted for	**354**	**373**	**357**