Post-dispersal predation of common lambsquarters and common waterhemp seeds in three tillage regimes

by

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To Ignacio, Ramon and my parents

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ABSTRACT

Post-dispersal predation of common lambsquarters (*Chenopodium album* (Tourn.) L.) and common waterhemp (*Amaranthus tuberculatus* (Moq.) Sauer.) seeds was evaluated in conventional, reduced and no-tillage regimes in Boone, IA. Glyphosate resistant corn and soybean were planted in 2003 and 2004, respectively. The level of seed predation was quantified using different insect exclusion treatments. We also identified some of the potential seed predators in the field and their preference and consumption of weed seeds in laboratory experiments. We observed no consistent differences in common lambsquarters and common waterhemp seed predation among tillage regimes. The main predators of common lambsquarters and common waterhemp seeds were invertebrate organisms. The most abundant invertebrates captured in pitfall traps were field crickets (*Gryllus pennsylvanicus* De Geer [Gryllidae, Orthoptera]) and a ground beetle (*Harpalus pensylvanicus* Burmeister [Coleoptera, Carabidae]). Under field conditions, there was a significant correlation between common lambsquarters and common waterhemp seeds predated and the activity-density of field crickets and ground beetles. Weed seed predation by insects can play an important role in plant population dynamics. Annual weed populations depend primarily on the soil seedbank. Therefore, the reduction of the weed seedbank, as a consequence of insect predation, might play an important role in reducing weed populations in the field. Understanding the impact that the activity-density of weed seed predators has on the weed seedbank can help determine the best management practices for lowering weed populations.

CHAPTER 1

GENERAL INTRODUCTION

Introduction

Research on weed control and weed biology has increased over the years due to the evolution of herbicide resistance and adaptation to control practices. This allowed weeds to thrive in agronomic production systems, becoming one of the most important pests in agricultural fields (Buhler *et al.*, 1997; Monaco *et al.*, 2002). Weeds compete effectively for light, nutrients, and moisture with crops thus causing significant reductions in yields and negatively affecting crop production by increasing weed control costs (Liebman, 2001). Two weeds that have become economically important throughout the North Central Region of the United States are common waterhemp (*Amaranthus tuberculatus* (Moq.) Sauer.) and common lambsquarters (*Chenopodium album* (Tourn.) L.). The success of these weeds is due to their adaptation to agronomic production and weed management systems, making them increasingly difficult to control (Buhler, 1995; Manley *et al.*, 2001; Derksen *et al.*, 2002; Locke *et al.*, 2002).

Common waterhemp is an annual weed that is native of the Midwestern United States. It has become one of the most problematic pest in soybean (*Glycine max* (L.) Merr.) (Mayo *et al.*, 1995) and corn (*Zea mays* L.) (Anderson *et al.*, 1996b) fields in the last decade. Common waterhemp can reduce soybean yields by 43% (Hager *et al.*, 2002) and up to 74% for corn (Steckel and Spague, 2004). Several factors have helped common waterhemp become such a successful weed. It produces large numbers of small seeds (0.9-1.2 mm in diameter) (Stubbenddieck *et al.,* 1995) that can be easily spread throughout the field by water, wind, vertebrates or invertebrates, and machinery. In addition, Buhler and Hartzler (2001) observed that common waterhemp could remain viable after 4 years in the soil seedbank, indicating that it is a persistent seed. Another characteristic of common waterhemp is that its seed dormancy regulation is highly dependent on environmental conditions (Leon and Owen, 2003) and its seedling emergence period is longer than most weeds in the Midwest Region. Also, conservation and no-tillage have increased in soybean and corn production, and they favor weed species that produce small seeds (Buhler, 1992).

Another factor that has made common waterhemp such an important weed is the fact that many populations have evolved herbicide resistance. There are numerous reports of common waterhemp biotypes that are resistant to acetolactate synthase (ALS)-inhibiting herbicides (Horak and Peterson, 1995; Hinz and Owen, 1997; Foes *et al.*, 1998) as well as triazine herbicides (Anderson *et al.*, 1996a, 1996b) and protoporphyrinogen oxidase-inhibiting herbicides (Shoup *et al.*, 2003). Also, common waterhemp populations in Iowa, Illinois and Missouri have demonstrated variable response and consistently incomplete control to commercial doses of glyphosate, suggesting the initial evolution of resistance to this herbicide (Zelaya and Owen, 2000; Smeda and Schuster, 2002).

Common lambsquarters is an annual weed widely distributed all over the world, and a frequent weed in Iowa corn and soybean fields. There are several factors that make this weed difficult to control. For example, it is highly competitive, adaptive and capable of producing thousands of small seeds per plant (Harrison, 1990) that can remain viable in the soil for many years (Conn and Deck, 1995). Common lambsquarters is well adapted to current crop production systems such as crop rotation and reduced tillage systems (Thomas and Frick, 1993; Bàrberi and Mazzoncini, 2001; Shrestha *et al.*, 2002). In addition, common lambsquarters has evolved resistance to herbicides such as atrazine (Dekker and Burmester, 1989; Myers and Harvey, 1993).

The fact that many problematic weeds have evolved resistance to herbicides reduces their effectiveness as a control tactic. Other control tactics must be used, in addition to herbicides, to develop an effective management program for these weeds. Tillage such as conventional tillage, reduced tillage, and no-tillage, can effectively complement other weed control tactics and improve integrated weed management programs. Different tillage regimes disturb the soil at different levels and thus change the soil surface, moisture, temperature, and affect weed emergence patterns and seedbanks (Buhler *et al.*, 1997). For example, in conventional tillage, weed seed distribution is relatively uniform throughout the tillage profile after a period of time (Mohler, 1993). However, in reduced and no-tillage regimes, 60% of weed seeds remain in the upper 5 cm of soil surface (Clements *et al.*, 1996).

Conventional tillage has been a very common crop production practice. In this tillage regime, residues from previous crops are plowed into the soil, and weed seeds are thus concentrated near the depth of plowing after a single moldboard plow (Mohler, 1993; Hoffman *et al.*, 1998; Buhler *et al.*, 2001). Conventional tillage controls weeds by killing emerged weeds and by burying seeds to depths that prevent seed germination or successful seedling emergence (Monaco *et al.*, 2002). Even though this tillage regime controls weeds, it also increases water depletion and soil erosion (Monaco *et al.*, 2002). Therefore, farmers are using reduced and no-tillage to prepare the soil in order to minimize problems. In reduced tillage, more crop residue is left on the soil surface thus protecting soils from erosion, but the impact on weed populations is less. In no-tillage, most plant residues from the previous crop remain on the soil surface. These residues help prevent soil erosion but can become a barrier for preemergence herbicides thus affecting weed control (Locke *et al.*, 2002). Also, the lack of soil disturbance is an advantage for small seeded weeds, such as common lambsquarters and common waterhemp, that germinate shallow in the soil profile (Weaver *et al.*, 1988). In addition, the absence of mortality caused by tillage and cultivation favors population increases of weeds that show early emergence during the growing season, which is the case for common lambsquarters and common waterhemp.

The primary source of annual weed seeds is the soil seedbank (Carvers, 1983). Weed seed viability in the seedbank can be reduced by abiotic factors such as temperature stress, radiation, drought, anoxia, and by biotic factors such as pathogen infection, and predation by vertebrates and invertebrates (Brust and House, 1988; Marino *et al.*, 1997; Cromar *et al.*, 1999; Menalled *et al.*, 2000; Westerman *et al.*, 2003a, b; Holmes and Froud-Williams, 2005). In a study conducted by Westerman *et al.* (2003a), vertebrates, presumably wood mice (*Apodemus sylvaticus* (L.)) were responsible for 30 to 88% of seed predation of *Stellaria media*, common lambsquarters and *Avena fatua*, compared to 4 to 38% by invertebrates such as the ground beetle *Harpalus rufipes* DeGeer. Birds have also been observed to predate weed seeds, consuming an average of approximately 7% of seeds, compared to 51% of seeds predated by other vertebrate and invertebrate organisms (Holmes and Froud-Williams, 2005). Even though weed seed predation by birds might not be as important compared with other organisms, this predation can still have an important negative effect on weed populations (Holmes and Froud-Williams, 2005). Brust and House (1988) also observed important predation rates by vertebrate and invertebrate organisms. They observed that mice (*Peromyscus maniculatus* (Wagner)) and large ground beetles (*H. caliginosus*) predated large seeds and that invertebrates such as smaller ground beetles (*H. pensylvaniscus* and

Selenophorus sp.), ants (*Pheidole* and *Lasius* spp.) and crickets (*Gryllus* spp.) had a preference for small seeds.

In other studies, it was observed that weed seed predation played an important role in modifying weed population dynamics (Cromar *et al*., 1999; Westerman *et al*., 2003b). Insects are considered to be one of the most abundant weed seed predators in agroecosystems. The reduction of the weed seedbank by insect predators can be an effect of the insect consuming the seed or by damaging the seed that later is infected by microorganisms. Kremer and Spencer (1989) observed that 98% of velvetleaf (*Abutilon theophrasti* Medik.) seeds that were attacked by scentless plant bugs (*Niesthrea louisianica* Sailer), had some level of seed-born microorganisms, compared to only 8% for seeds not exposed to the insects.

Several studies emphasized the existence of pre- and post-dispersal weed seed predation in crops (DeSousa *et al*., 2003; Menalled *et al.,* 2000). In soybean fields, Nurse *et al*. (2003) observed 26% and 4% pre-dispersal seed predation of redroot pigweed (*Amaranthus retroflexus* L.) and common lambsquarters respectively, attributable to invertebrates. Even though pre-dispersal weed seed predation has the potential of reducing the amount of seeds and thus influencing the population of weeds in the field, the insects responsible for the consumption or damage of these seeds are specific to the weed species or family (Crawley, 2000). Thus, given the fact that pre-dispersal seed predators are so specific, other weeds may gain an advantage and increase their populations in the field. In addition, pre-dispersal seed predator insects are small and sedentary. The amount of seeds that they can consume will usually be lower than the amount consumed by more mobile insect species, reducing the possibility of decreasing weed populations. Conversely, post-dispersal weed seed predators are not as specific to the seeds they consume. Such predators are vertebrate and invertebrate organisms, which includes a larger group of seed predators that are more mobile, thus increasing the potential of consuming seeds of various weed species (Crawley, 2000) and significantly influencing weed population dynamics. Davis and Liebman (2003) observed that post-dispersal seed predation by invertebrates was an important factor for reducing giant foxtail (*Setaria faberi* Herrm.) seedbanks. They observed that management practices such as crop rotation, green manure and tillage affected seed predation levels and invertebrate population dynamics. In addition, they also observed a positive correlation between foxtail seed predation and amount of crop residue on the soil. The use of cover crops provided an appropriate habitat for invertebrate seed predators, increasing their populations and as a consequence, the potential for weed seed predation (Gallandt *et al.*, 2005).

Tillage systems have also been observed to indirectly impact weed seed predation (Brust and House, 1988; Cromar *et al.*, 1999). Conventional, reduced and no tillage have characteristics that can influence the incidence and diversity of weed seed predator species. For example, as soil disturbance increases, insect mortality might also increase. Tillage can destroy the habitat for some weed seed predators, thus reducing their presence in the field. There is the need of a favorable environment for increasing the populations and the seed predation potential of insects in the field (Landis *et al.*, 2000). Some of the most common insects that consume weed seeds are ground beetles (Coleoptera: Carabidae) (Brust and House, 1988; Davis and Liebman, 2003; Honek *et al.*, 2003), field crickets (Orthoptera: Gryllidae) (Carmona *et al.*, 1999; Davis and Liebman, 2003), and ants (Formicidae) (Mittelbach and Gross, 1984). Weiss *et al.* (1990) observed that some carabid species were present in higher populations in reduced and no-tillage regimes compared to conventional tillage. Brust and House (1988) observed that 2.3 times more weed seeds were consumed by vertebrates and invertebrates in no-tillage compared to conventional tillage. However, Cromar *et al.* (1999) observed higher common lambsquarters and barnyardgrass (*Echinochloa crus-galli* (L.) Beauv.) seed predation in conventional tillage and no-tillage (32%) than in reduced tillage (24%). Thus, the results of different studies are inconsistent and it is difficult to assess the importance of tillage regime and the potential for weed seedbank reductions due to post-dispersal seed predation.

Understanding the potential ground-dwelling organisms that predate weed seeds can help identify tactics that will increase their populations and movement in fields. Increasing the activity-density of weed seed predators can help reduce the soil weed seedbank and subsequently reduce weed populations in agricultural systems. Despite the research conducted thus far, the relationship between tillage regimes and the post-dispersal predation of small seeded weeds such as common lambsquarters and common waterhemp remain unclear. Understanding this relationship can help design and implement new crop management practices that will complement existent weed management strategies and thus potentially reduce the use of herbicides.

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CHAPTER 2

QUANTIFICATION OF POST-DISPERSAL WEED SEED PREDATION AND INVERTEBRATE ACTIVITY-DENSITY IN THREE TILLAGE REGIMES

A paper to be submitted to *Agriculture, Ecosystems and Environment*

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Abstract

Field experiments were conducted in Boone, IA to quantify post-dispersal seed predation of common lambsquarters (*Chenopodium album* (Tourn.) L.) and common waterhemp (*Amaranthus tuberculatus* (Moq.) Sauer.) in conventional, reduced and no-tillage regimes. Glyphosate resistant corn and soybean were planted in 2003 and 2004, respectively. The level of seed predation in each tillage regime was quantified using selective exclosure treatments. In addition, the activity-density of the most abundant ground-dwelling invertebrates was estimated with pitfall traps. Choice and no-choice feeding trials were conducted in the laboratory with the most abundant weed seed predators found in the field to confirm the consumption of common lambsquarters and common waterhemp seeds, and to determine seed preference of the potential predator organisms.

Seed predation in the field was estimated throughout July and August, 2003 and June through October, 2004. The greatest seed loss for both weed species occurred during July and August. However, there was not a clear difference in the level of seed predation between

tillage regimes. The maximum seed predation level for common lambsquarters was 53% in 2003 and 54% in 2004. In the case of common waterhemp, seed predation was 80% in 2003 and 85% in 2004. The majority of seed predation was by invertebrate organisms.

The most common invertebrate species captured with pitfall traps were a field cricket (*Gryllus pennsylvanicus* De Geer [Gryllidae, Orthoptera]) and a ground beetle (*Harpalus pensylvanicus* Burmeister [Coleoptera, Carabidae]). A significant difference was observed in 2003 and 2004 for the presence of field crickets between tillage regimes (P<.0001). In 2003, field crickets were relatively more abundant in conventional and reduced tillage. In 2004, this insect species was more abundant in the reduced tillage. No significant difference was detected for the ground beetles among tillage regimes (P=0.57). Choice and no-choice feeding experiments confirmed the preference of field crickets and ground beetles for common lambsquarters and common waterhemp seeds over other weed seeds such as giant foxtail (*Setaria faberi* Herrm.) and velvetleaf (*Abutilon theophrasti* Medik.).

Under field conditions, a positive correlation was observed between the presence of field crickets with common lambsquarters (r^2=0.47, P<.0001) and common waterhemp (r^2=0.53, P<.0001) seed predation. Positive correlations were also detected between the presence of ground beetles and common lambsquarters (r^2=0.30, P<.0001) and common waterhemp (r^2=0.30, P<.0001) seed predation in the field.

Introduction

The weed seedbank is a main source of weeds in agricultural fields (Rahman *et al.*, 2001). A seed can germinate under appropriate conditions and if this plant is not controlled, it has the potential to produce thousands of seeds that can become part of the soil seedbank.

Weed populations in agricultural fields can be reduced by various management practices, however, the amount of weed seeds in the soil and the seed production of weeds that escape control are enough to maintain the soil weed seedbank (Buhler *et al.*, 1997). The size and dynamics of the soil weed seedbank are determined by seed rain, dormancy, germination, and predation, and indirectly by the soil conditions, crop rotation, tillage, soil pathogens, and the environment (Parker *et al.*, 1989; Simpson *et al.*, 1989; Buhler *et al.*, 1997). Vertebrate and invertebrate organisms can play an important role in weed population dynamics by consuming weed seeds on the soil surface (Cromar *et al.*, 1999). A diverse group of small vertebrates including several species of field mice and birds (Hulme and Hunt, 1999; Rey *et al.*, 2002; Westerman *et al.*, 2003; Holmes and Froud-Williams, 2005) as well as ground-dwelling invertebrates such as several species of carabids, field crickets, and ants (Brust and House, 1988; Carmona *et al.*, 1999; Cromar *et al.*, 1999; Rey *et al.*, 2002) consume large amounts of post-dispersal weed seeds. Estimating soil weed seedbank reductions due to invertebrate seed predation can help design crop production strategies that may enhance weed seed predation and allow reduced herbicide use, thus lowering production costs as well as possibly improving environmental sustainability. In addition, the presence of weed seed predators in an agricultural system favors organic matter decomposition thus potentially improving soil quality (Brussaard, 1998).

The distribution of weed seeds in the soil profile can influence seed predation. Small vertebrates and ground-dwelling invertebrate seed predators tend to consume seeds on the soil surface before digging for seeds buried in the soil (Crawley, 2000). Intensive soil disturbance can reduce insect populations by affecting their life cycles as well as changing their habitat (Landis *et al.*, 2000). Therefore, tillage regimes may not only affect soil quality, but also could influence the activity and population of ground-dwelling organisms, making tillage an important agricultural practice to consider when assessing the significance of invertebrate seed predation (Baguette and Hance, 1997).

Weed seed predation by insects can play an important role in reducing soil seedbanks. However, weed predation by itself, is not likely sufficient to maintain weed populations below economic threshold levels (Crawley, 2000). More appropriately, weed seed predation should be considered as complementary to other weed management strategies. Weed management practices such as cover cropping and mechanical weeding, in combination with foliar weed pathogens and weed seed predators, can help control weed populations in arable fields (Hatcher and Melander, 2003).

Common lambsquarters (*Chenopodium album* (Tourn.) L.) and common waterhemp (*Amaranthus tuberculatus* (Moq.) Sauer.) are two economically important and persistent weeds in corn and soybean fields thought the North Central Region of the United States. The importance of these weeds is due to their ability to compete with the crop, reducing its yield (Hager *et al.*, 2002; Steckel and Sprague, 2004). In addition, common lambsquarters and common waterhemp produce large amounts of seeds thus considerably increasing the soil seedbank each year. The objectives of this study were to quantify common lambsquarters and common waterhemp seed predation in three tillage regimes (conventional, reduced and no-tillage), and to identify and quantify the populations of important insect predators that predated these weed seeds. In addition, we described the relative feeding ability and weed seed preference of some of the potential predator organisms observed in the field.

Materials and Methods

A field experiment was conducted to quantify post-dispersal weed seed predation of common lambsquarters and common waterhemp at the ISU Agricultural Engineering Research Center in Boone County, IA during 2003 and 2004. The field was divided into three tillage treatments: conventional tillage (moldboard plow), reduced tillage (chisel plow) and no-tillage, which were arranged in a randomized complete block design with 4 replications. Field cultivation was conducted in 2003 and 2004 for conventional and reduced tillage before planting in the spring. Plots had been under these tillage regimes for 15 years. Glyphosate resistant corn and soybean were planted in 76 cm rows in 2003 and 2004, respectively. Glyphosate was applied in July 2003 for weed control, although this herbicide was applied before the experiment was conducted. In 2004, glyphosate was applied on June 23. The soil was a Clarion (fine-loamy, mixed, superactive, mesic Typic Hapludolls), Nicollet (fine-loamy, mixed, superactive, mesic Aquic Hapludolls), and Canisteo (fine-loamy, mixed, superactive, calcareous, mesic Typic Endoaquolls) association consisting of silty clay loam with a pH 5.95 and 4.0% organic matter. The size of each treatment plot was 30 by 30 m. A 3 m grass aisle surrounded the plots.

The percent of plant residue coverage on the soil surface in each tillage regime was determined in August 2003, by measuring plant residue in a one-meter straight line. These measurements were replicated five times in each tillage regime. Conventional tillage had approximately 10% residue coverage on the soil surface, reduced tillage had 29%, and no-tillage had 97%.

Quantification of post-dispersal weed seed predation in the field

Common lambsquarters and common waterhemp seed predation was evaluated in July and August, 2003 and June through October, 2004 using three different predator exclusion treatments: vertebrate exclusion, vertebrate + invertebrate exclusion (control), and no exclusion. Wire cages (25 x 25 x 5 cm) for vertebrate exclusion were constructed with galvanized hardware cloth with 1.3 by 1.3 cm openings, and were fixed permanently on the ground (Menalled *et al.*, 2000). The wire cages allowed insects access to the weed seeds, but excluded vertebrate seed predators. Weed seed predation was evaluated using sandpaper cards with weed seeds, placed inside the cages. Both weed species were evaluated with separate cards and exclusion treatments. Fifty seeds were glued to 12 x 10 cm sandpaper cards. Soil was also added to the cards to better mimic the natural environment and to avoid insects sticking on the cards. The glue was strong enough to keep the seeds attached to the card during manipulation and under field conditions, but insects could remove the seeds during feeding (Westerman *et al.*, 2003). Nails in the corners of the card were used to secure the cards to the ground. The cards were left in the field for 48 hours and then removed and the number of seeds predated was determined. Evaluations were done biweekly. In 2004, in order to confirm that most of the predation was caused by invertebrates, the total level of predation (no exclusion) was determined by placing the same number of cards for each weed species in the plot, but without the cages. The absence of exclusions allowed any invertebrate as well as vertebrates to predate the seeds. Furthermore, for each weed species, three controls that consisted of cards enclosed in window screen bags were placed in each plot in a similar manner to the rest of the exclusion treatments. These screen bags prevented any vertebrate or invertebrate from feeding on the weed seeds (vertebrate + invertebrate exclusion). The purpose of these controls was to differentiate between weed seed loss due to predators from losses as a consequence of environmental conditions and manipulation of the cards. The maximum seed loss was estimated by calculating the difference between the vertebrate exclusion seed loss and the vertebrate + invertebrate exclusion seed loss data. There were three replications of each exclusion treatment per block, which were randomly distributed between crop rows in the center of each plot (at least 10 meters from the plot edges). Finally, the cards were arranged such that there were at least 3 meters between cards in the same row and 1.5 meters between rows.

Identification and quantification of possible insect seed predators

Permanent pitfall traps were placed in each tillage plot. Pitfall traps consisted of a 500 ml cup filled with 200 ml of 10% ethylene glycol solution. Evaluations were done biweekly during the growing season by opening the traps for 48 hours to capture potential weed seed predators. These evaluations were conducted at the same time that the seed cards were placed in the field for weed seed predation evaluation. The ethylene glycol solution and insects from each pitfall trap were recovered, and the traps then closed until the next evaluation. The insects recovered were identified to genus and species with identification keys (Alexander, 1957), and the Iowa State University Insect Collection, Entomology Department, Ames, IA 50010, USA. Dr. Kirk Larsen (Luther College, Iowa) also helped in the identification of the carabid species.

Estimating feeding ability and weed seed preference of possible predators under laboratory conditions

Weed seed preference and efficiency of predation of the most abundant insect species found in the field were evaluated in laboratory experiments. Weed species with different seed sizes were used to assess insect preferences. The experiments included seeds of common waterhemp, common lambsquarters, giant foxtail (*Setaria faberi* Herrm.), and velvetleaf (*Abutilon theophrasti* Medik.) with weights of 0.2, 0.4, 1.6, and 10 mg per seed, respectively. Adults of the most abundant insect species found in the field were captured using dry pitfall traps. The insects were then placed individually in 500 ml cups with a lid with holes. They were fed commercial dry cat food [1] and a wet cotton ball was added to the cup for humidity and water supply. Insects that were actively feeding during this time were chosen for the experiment and food was removed for 24 hours prior to the experiment. Insect feeding ability was evaluated by "no-choice" and "multiple-choice" seed experiments. For the "no-choice" experiments, insects were placed in 500 ml cups with a moist filter paper on the bottom, a wet cotton ball and either 50 seeds of common waterhemp, 50 seeds of common lambsquarters, 25 seeds of giant foxtail, or 10 seeds of velvetleaf. The number of seeds varied to provide insects with the same seed mass of all weed species. The dry weight of the seeds was determined before each experiment. Twenty-four hours later, the remaining seeds were dried for 48 hours and dry weight was obtained. The "multiple-choice" seeds experiments were conducted to evaluate weed seed preference. Insects were placed in 500 ml cups with moisture paper, a wet cotton ball and a mixture of seeds from the four weed species (50 seeds of common waterhemp, 50 seeds of common lambsquarters, 25 seeds of giant foxtail, and 10 seeds of velvetleaf). The seeds remaining after 24 hours were dried for 48 hours and dry weight was obtained by species. These experiments were conducted in growth chambers set at 25 C and with a photoperiod of 16 hours light and 8 hours dark. Feeding experiments had six replications and were repeated three times.

Statistical Analysis

The field experiment was a randomized complete block design with four replications arranged in a split plot designed. An analysis of variance (ANOVA) using the Proc Mixed Model of SAS (Statistical Analysis Systems 1995) was used to compare seed predation in conventional, reduced and no-tillage regimes. Pitfall trap data were analyzed with a non-parametric ANOVA, using a Wilcoxon rank-sum test, which facilitates the analysis of variables that are not normally distributed (Ramsey and Shafer, 2002). There were no significant differences (P=0.57) among tillage regimes for the number of ground beetles captured per pitfall trap, so these data were combined. The no-choice and multiple-choice laboratory feeding trials consisted of a completely randomized design with 6 replications. The data obtained from the feeding experiments were compared with an analysis of variance (ANOVA) using the Proc Mixed Model of SAS. Least significant difference was used to determine significant difference between feeding experiments and species.

Results

Post-dispersal weed seed predation in the field

Seed loss was similar in the no exclusion and vertebrate exclusion treatments throughout the whole season (Figures 1 and 2). The exclusion cage that allowed insects access to the seeds had larger seed losses compared to the cards inside the screen bag (Figures 1 and 2). There was seed loss throughout the period of evaluation (July through

September, 2003 and June through October, 2004), but most of the seed loss occurred during July and August (Figures 1 and 2). In 2003, seed loss for common lambsquarters ranged from 4% to 53% in conventional tillage, 4% to 48% in reduced tillage and 5% to 41% in the no-tillage regime. A similar pattern was observed in 2004, when seed losses ranged between 1% to 52% in conventional tillage, 1% to 64% in reduced tillage and 2% to 48% in no-tillage (Figure 1). In the case of common waterhemp, seed losses during the growing season were approximately 5% to 80% in 2003 and 0% to 70% in 2004 for both conventional and reduce tillage regimes. The range of common waterhemp seed predation in no-tillage was approximately 2% to 57% in 2003 and 1% to 68% in 2004. Most seed predation for common waterhemp occurred in mid-July (Figure 2), and declined early in September.

There was a significant effect of tillage regime on common lambsquarters ($P<0.0001$) and common waterhemp ($P=0.0004$) seed predation in 2003 but not in 2004 (Table 1). In 2003, we observed significantly lower seed predation in the no-tillage regime compared to the conventional and reduced regimes. Differences in corn and soybean canopy structures in 2003 and 2004 respectively, may have contributed to differences in light, temperature, relative humidity, and wind speed. These differences might have influenced the activity-density of seed predator organisms, thus affecting seed predation (Gallandt *et al.*, 2005).

Identification and quantification of possible insect seed predators

The most common species recovered from pitfall traps were carabids, crickets, ants, and spiders (Table 2). Field crickets (*Gryllus pennsylvanicus* Burmeister, Gryllidae, Orthoptera), ground beetles (*Harpalus pensylvanicus* De Geer, Carabidae, Coleoptera) and ants in general, were the most abundant insect species found in the field. Field crickets represented 89% of the Orthoptera species recovered from the pitfall traps; *H. pensylvanicus* represented 35% of all the carabid species captured. *Harpalus pensylvanicus* was the most abundant omnivorous carabid species caught throughout the season. The majority of the other carabids species were carnivorous species (data not shown). Even though ants were also a large family of insects caught with pitfall traps, we found no predominant species present. In addition, no correlation in the presence of ants and weed seed predation was observed with common lambsquarters (r^2= 0.03) and common waterhemp (r^2=0.01). For this reason, ants were not included in the laboratory experiments.

Field crickets and ground beetles are considered important weed seed predators in agricultural systems (Brust and House, 1988; Carmona *et al.*, 1999; Davis and Liebman, 2003). There was a difference in field cricket populations between tillage regimes in both years (Table 3) and the differences were observed at three evaluation dates (Figure 3). Field cricket populations were at least 10 times higher on July 20 compared to the other evaluation dates. We considered that this high number was a consequence of an oat (*Avena sativa* L.) field next to the experiment being harvested the day before the evaluation. Crop harvest is an important habitat alteration for organisms that are in that area, likely causing them move to less disturbed or more suitable areas. There was no significant difference for ground beetle density among tillage regimes in 2003 and 2004 (Table 3). The population density of field crickets and ground beetles approached zero in late September (Figures 3 and 4).

A peak in seed predation was observed when the insect populations were the highest. A significant correlation was observed between the presence of field crickets with common lambsquarters (r^2=0.47, P<0.0001) (Figure 5) and common waterhemp (r^2=0.53, P<0.0001) (Figure 6) seed predation. Similarly, there was a significant correlation between ground beetles populations and common lambsquarters (r^2= 0.30, P<0.0001) (Figure 5) and common waterhemp (r^2=0.30, P<0.0001) (Figure 6) seed predation in the field. However, seed predation was still observed even when low numbers of ground beetles and field crickets were captured in the field. This suggests that there are other insect species that predate common lambsquarters and common waterhemp seeds that were not captured.

We confirmed the presence of the mice *Peromyscus maniculatus* (Wagner), which is a small vertebrate that has been reported to feed on weed seeds (Getz and Brighty, 1986; Brust and House, 1988). Using exposed cards in the field in one evaluation date with larger seeds like giant foxtail and oats, approximately 68% and 98% of giant foxtail and oat seeds, respectively, were predated. Based on seed residues and the disturbance of the card area after predation, we concluded that the main predators of these seeds were mice, presumably *P. maniculatus*. It seems that there are larger seed predators in the field that tend to consume larger seeds and not smaller seeds like common lambsquarters and common waterhemp (Brust and House, 1988). This observation was consistent in the three tillage treatments (data not shown).

Feeding ability and weed seed preference under laboratory conditions

Both *G. pennsylvanicus* and *H. pensylvanicus* consumed common lambsquarters and common waterhemp seeds in laboratory feeding trials. Field crickets consumed approximately 60% more seeds compared to ground beetles (Table 4). In general, there was a preference for common waterhemp seeds in the multiple and no-choice experiments. Field crickets consumed 71% of common waterhemp seeds in the multiple choice experiment and 85% in the no-choice experiments. These insects also consumed 48% of common lambsquarters seeds in the multiple choice and 66% in the no-choice seed experiment. Field crickets showed similar giant foxtail and velvetleaf seed predation in either multiple or no-choice seed experiments. Ground beetles demonstrated a significant preference for common waterhemp over common lambsquarters, giant foxtail and velvetleaf seeds, consuming 43% and 72% in the multiple and no-choice experiments respectively. The second weed seed preferred by ground beetles was common lambsquarters, followed by giant foxtail and velvetleaf. In the multiple choice seed experiment, ground beetles did not consume any velvetleaf seeds (Table 4).

Discussion and Conclusions

High levels of predation of common lambsquarters and common waterhemp seeds were observed in 2003 and 2004 in the field, as has been observed in other studies with various weed species (Brust and House, 1988; Cromar *et al.*, 1999; Menalled *et al.*, 2000; Harrison *et al.*, 2003; Westerman *et al.*, 2003; Gallandt *et al.*, 2005; Mauchline *et al.*, 2005). Post-dispersal weed seed predation may thus play an important role as part of weed management strategies by maintaining lower weed populations. Seeds are necessary for maintaining an existing weed population (Louda, 1989). If a population of a given weed species is significantly reduced due to seed predation, changes in weed community composition can occur by population increases of other weed species seeds that are not predated (Louda, 1989).

According to our field data, invertebrate organisms are the main predators of common lambsquarters and common waterhemp seeds. If vertebrate organisms were predating the seeds, seed loss in the no-exclusion would be higher than in the exclusion treatment because in the former, seed loss would be the result of both vertebrate and invertebrate predation. Our results show that invertebrate organisms, and not vertebrates, are consuming small weed seeds such as common lambsquarters (1.2-1.3 mm in diameter) and common waterhemp (0.9-1.2 mm in diameter), in contrast to larger weed seeds such as giant foxtail (1.5-1.7 mm in diameter) and velvetleaf (3.0-3.5 mm in diameter). This pattern was observed in both multiple choice and no-choice feeding experiments under laboratory conditions, where field crickets and ground beetles preferred the smaller seeds like common lambsquarters and common waterhemp over larger seeds like giant foxtail and velvetleaf. It has been observed that weed seed consumption is related to the predator size (Brust and House, 1988). This is a very important aspect because insects tend to consume a larger amount of smaller weed seeds than larger weed or crop seeds. In addition, there was no significant difference between common lambsquarters and common waterhemp seed predation in the field, indicating that there is no preference by invertebrates, and that seed consumption might be solely a seed size effect. Given the potential for insects to reduce weed seed populations, it is important to increase the populations of these beneficial insects. Further research will be important to determine how selective invertebrate seed predators are and how this selectivity might be involved in weed community shifts in the field.

A peak in weed seed predation was observed late in June, representing the moment in which there was the highest demand for weed seeds by ground-dwelling organisms. However, seed supply resulting from seed rains of common lambsquarters and common waterhemp occurs from August to October (data not shown). Therefore, more realistic predation levels would be not the ones observed in June, but the ones in October, which can produce approximately a 50% and 45% seed loss in a two-day period for common lambsquarters and common waterhemp seeds, respectively. Reduced seed predation was observed in mid-July, which coincided with reductions in activity-density of field crickets and ground beetles. This reduction might be a consequence of weather conditions. Changes in temperature, rainfall, humidity, wind and light influence the activity of invertebrate organisms (Drake, 1994). As observed in Figure 7, during the first two weeks of July in both years, there were significant rainfall events. A similar situation occurred during the first week of August in 2004. These weather conditions might have reduced field crickets and ground beetles activity and subsequently weed seed predation.

In 2003, we found significant differences in predation for common lambsquarters and common waterhemp seeds among tillage regimes. Cromar *et al.* (1999) observed that seed predation of common lambsquarters and barnyardgrass was higher in no-tillage and conventional tillage than in reduced tillage. The same pattern was observed by Brust and House (1988) who observed that 2.3 times more weed seeds were predated in a no-tillage regime, when compared to a conventional tillage. The lower predation of common lambsquarters and common waterhemp seeds in the no-tillage regime, compared to the conventional and reduced regimes observed in 2003, can be a consequence of the amount of crop residue on the soil surface. The no-tillage regime had considerably higher amount of residue compared to the conventional and reduced tillage regimes. This higher amount of crop residue might have reduced insect mobility throughout the field (Cromar *et al.*, 1999). Also, no-tillage regime provides a more diverse habitat and microenvironment than conventional or reduced tillage, which may benefit different insect species as well as diseases (Landis *et al.*, 2000). The presence of some of these insect species might have an antagonistic effect on the populations of insect predators of weed seed. Reduced seed predator populations in the no-tillage regime will obviously reduce weed seed predation.

The tillage regime can play an important role in determining insect populations and subsequent activity density. However, ground beetles populations did not differ significantly among tillage regimes in 2003 and 2004. With respect to field crickets, there was a significant difference in insect numbers captured among tillage regimes in 2003 and 2004. These differences were not consistent between years; however there was a tendency to observe more field crickets in reduced tillage. Insects have different habitat requirements; therefore their population dynamics may differ in movement and preference of habitats, and can respond in different ways to these changes (Baguette and Hance, 1997). More carabid species were observed throughout the season in the aisles between the crop areas (data not shown). The aisles were mainly covered with grass and with a larger number of weeds species when compared to the area of evaluation. This would suggest that carabids prefer less disturbed areas. The intense management of the crop might have a negative effect on the insect populations in the crop area. The soil disturbance produced by conventional and reduced tillage, changes the soil structure and reduces earlier crop residues, and as a consequence, reduces shelter and food availability, and changes the microclimate for ground-dwelling organisms (Baguette and Hance, 1997; Landis *et al.*, 2000). Such soil disturbance can reduce the abundance and diversity of invertebrate species in the field. On the other hand, a no-tillage condition preserves the soil structure and maintains crop residues on the soil surface, providing a more stable environment for invertebrates (Stinner and House, 1990). Another way to potentially increase invertebrate seed predator populations is the use of cover crops that create a habitat favorable for these organisms (Stinner and House, 1990;

Cromar *et al.*, 1999; Gallandt *et al.*, 2005). However, more research is required to determine appropriate habitats that will increase these predators populations and benefit agroecosystem sustainability and crop profitability.

Conversely to the significant differences observed among tillage regimes in 2003, no significant difference in seed predation among tillage regimes was observed in 2004. This study was conducted in corn in 2003 and soybean in 2004; two crops, which canopies differed. Different environmental variables, such as light, day and night temperatures, radiation, wind speed, and relative humidity, will change depending on the canopy of the crop, thus changing the microclimate around it (Norris and Kogan, 2000). Changes in the microclimate can affect the life cycle and activity-density of ground-dwelling organisms (Holland and Luff, 2000). Therefore, the different microclimates that these crops generated might have influenced the populations of ground-dwelling organisms, as well as their movement in the field. Therefore, there will be differences in seed predation as well.

We observed a significant correlation between field crickets population density and seeds predated. This correlation is a good indicator that field crickets were responsible for a high percentage of common waterhemp and common lambsquarters seed predation. The laboratory experiments confirmed that field crickets consumed common lambsquarters and common waterhemp seeds and preferred these seeds over other weed species. The same seed predation trend was observed in the field with ground beetles, however, no significant correlation between their density and seed predation in the field was detected. Although this correlation indicates that ground beetles might not be a predominant feeder of common lambsquarters and common waterhemp seeds under field conditions, laboratory feeding trials suggest that they are responsible for some weed seed predation. This may suggest that carabid species feed on a variety of seeds, depending on seed availability in the field (Lund and Turpin, 1977).

This study showed that weed seed predation by invertebrates was not significantly influenced by tillage regime. In addition, weed seed predation by invertebrates, presumably field crickets and ground beetles, can play an important role in reducing common lambsquarters and common waterhemp soil seedbanks. Invertebrate seed predation can contribute to maintaining these weed populations at manageable levels.

Sources of Materials

[1] Purina® Cat Chow® Complete Formula, Société des Produits Nestlé S.A., Vevey, Switzerland.

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Table 1. Statistical significance of the effect of tillage (conventional, reduced and no-tillage), predator exclusion treatments (vertebrate, vertebrate+invertebrate and no-exclusion), and evaluation date on seed predation of common lambsquarters (*Chenopodium album*) and common waterhemp (*Amaranthus tuberculatus*) in 2003 and 2004 in Boone, IA.

Source	Common lambsquarters		Common waterhemp	
	2003	2004	2003	2004
	P-value			
Tillage	< 0.0001	0.2390	0.0004	0.1295
Exclusion	< 0.0001	< 0.0001	< 0.0001	< 0.0001
Date	< 0.0001	< 0.0001	< 0.0001	< 0.0001
Tillage * Exclusion	0.0001	0.0352	0.0001	0.2634
Tillage * Date	0.8048	0.0635	0.1147	0.3701
Exclusion * Date	< 0.0001	< 0.0001	< 0.0001	< 0.0001
Tillage * Exclusion * Date	0.9769	0.7274	0.1609	0.9960
Block	0.1717	0.1455	0.9828	0.3061
Sample (Block)	0.9624	0.9144	0.7180	0.8702

Table 2. Total number of invertebrates captured in pitfall traps in conventional, reduced and no-tillage regimes during the period of mid-July through mid-September, 2003, in Boone, IA.

Insect Order	**Family**	**Tillage regime**			**Total #**
		Conventional	**Reduced**	**No-tillage**	**of insects**
Coleoptera	Carabidae	64 [a]	40 [a]	38 [a]	142
	Lampyridae	8 [a]	1 [a]	9 [a]	18
	Scarabidae	11 [a]	17 [a]	10 [a]	38
	Others	21 [a]	22 [a]	41 [a]	84
Orthoptera	Field cricket	247 [a]	303 [a]	131 [b]	681
	Grasshoppers	18 [b]	20 [b]	44 [a]	82
Formicidae	Various	125 [a]	102 [a]	170 [a]	397
Diptera	Various	42 [a]	41 [a]	47 [a]	130
Hymenoptera	Various	5 [a]	2 [a]	0 [a]	7
Lepidoptera	Various	47 [a]	61 [a]	19 [b]	127
Others	Spiders	95 [a]	132 [a]	93 [a]	320
	Others	78 [a]	71 [a]	61 [a]	210

* Tillage regimes with different letters are significantly different ($P<0.05$) within Family, based on a non-parametric ANOVA, using a Wilcoxon rank-sum test.

Table 3. Statistical significance of the effect of tillage (conventional, reduced and no-tillage), sampling location within plot, evaluation date within year, and year on field crickets (*Gryllus pennsylvanicus*) and ground beetles (*Harpalus pensylvanicus*) populations in Boone, IA, in 2003 and 2004.

Source	**Field crickets**	**Ground beetles**
	P-value	
Tillage	<.0001	0.5656
Date	<.0001	0.1284
Block	0.4693	0.6517
Sample x Block	0.5570	0.1403
Year	<.0001	<.0001
Tillage x Year	0.0002	0.5264
Block x Year	0.5592	0.4060
Sample x Year (Block)	0.3672	0.1685
Tillage x Date	0.0232	0.8184
Date x Block	0.4514	0.5075
Date x Sample (Block)	1.0000	0.9988
Tillage x Date x Year	<.0001	0.0535
Tillage x Date x Block	1.0000	0.9951
Tillage x Date x Sample (Block)	1.0000	0.9998

Table 4. Percentage of weed seeds consumed by field crickets (*Gryllus pennsylvanicus*) and ground beetles (*Harpalus pensylvanicus*) after 24 hours in a multiple choice and no-choice feeding experiment[1].

Weed species	**Field crickets**		**Ground beetles**	
	Multiple Choice	No-Choice	Multiple Choice	No-Choice
Setaria faberi	13 c[2]	38 b	9 c	25 c
Chenopodium album	48 b	66 a	29 b	45 b
Abutilon theophrasti	10 c	43 b	0 d	11 d
Amaranthus tuberculatus	71 a	85 a	43 a	72 a

[1] The experiments were conducted three times, but experiment repetition effect was not significant ($P>0.5$). Therefore, experiment repetitions were combined for the statistical analysis. Thus, each percentage represents the average of 18 replications.

[2] Weed species with the same letter are not significantly different based on LSD ($\alpha=0.05$) within experiments and insect species.

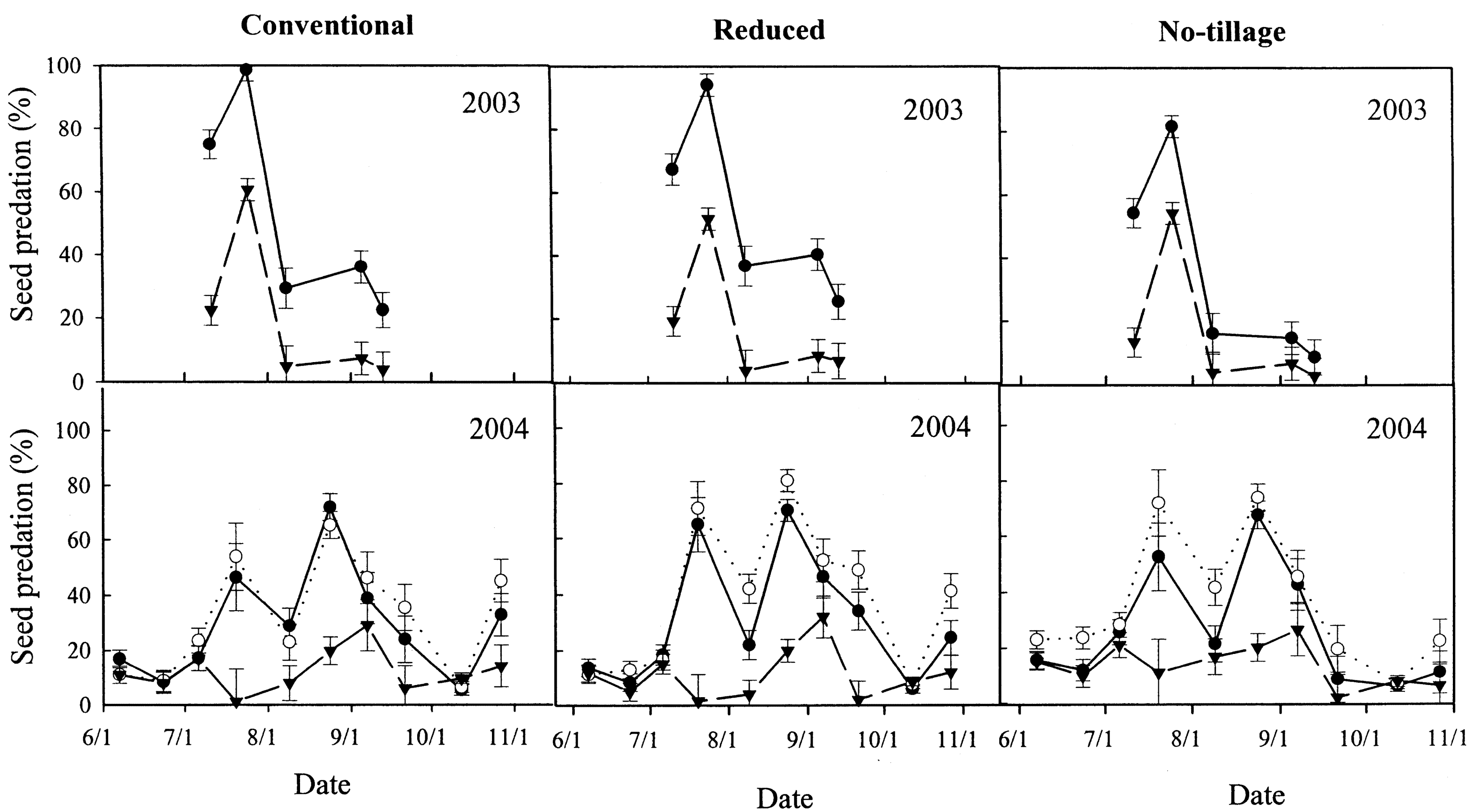

Figure 1. Average of the percentage of common lambsquarters (*Chenopodium album*) seed predation from vertebrate exclusion (—•—) and vertebrate + invertebrate exclusion (--▼--) seed cards in conventional, reduced and no-tillage regimes determined during periods of 48 hours in different dates in 2003 and 2004, in Boone, IA. In 2004, a no-exclusion (···o···) treatment was added to the experiment.

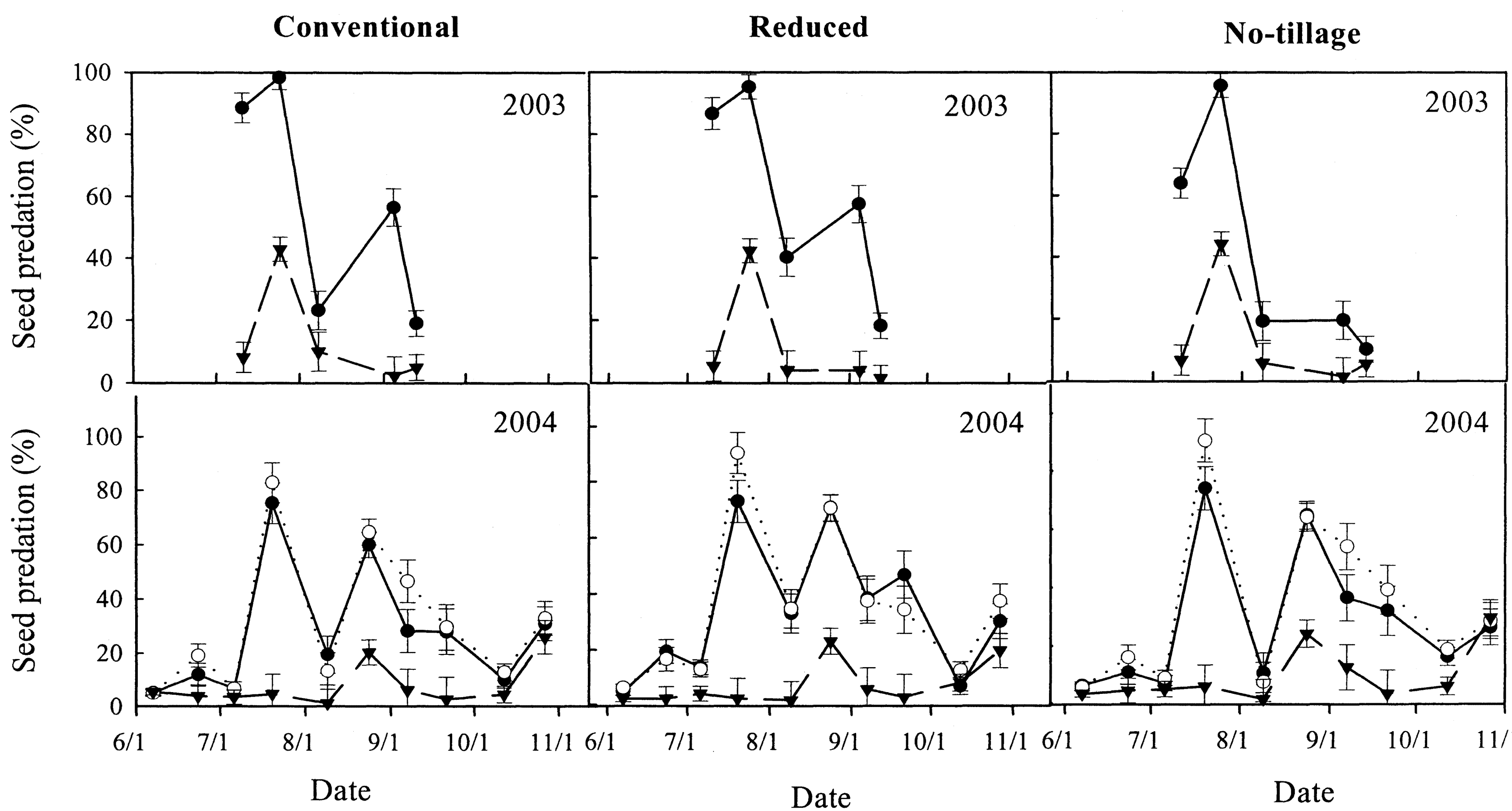

Figure 2. Average of the percentage of common waterhemp (*Amaranthus tuberculatus*) seed predation from vertebrate exclusion (—•—) and vertebrate + invertebrate (--▼--) seed cards in conventional, reduced and no-tillage regimes determined during periods of 48 hours in different dates in 2003 and 2004, in Boone, IA. In 2004, a no-exclusion (···o···) treatment was added to the experiment.

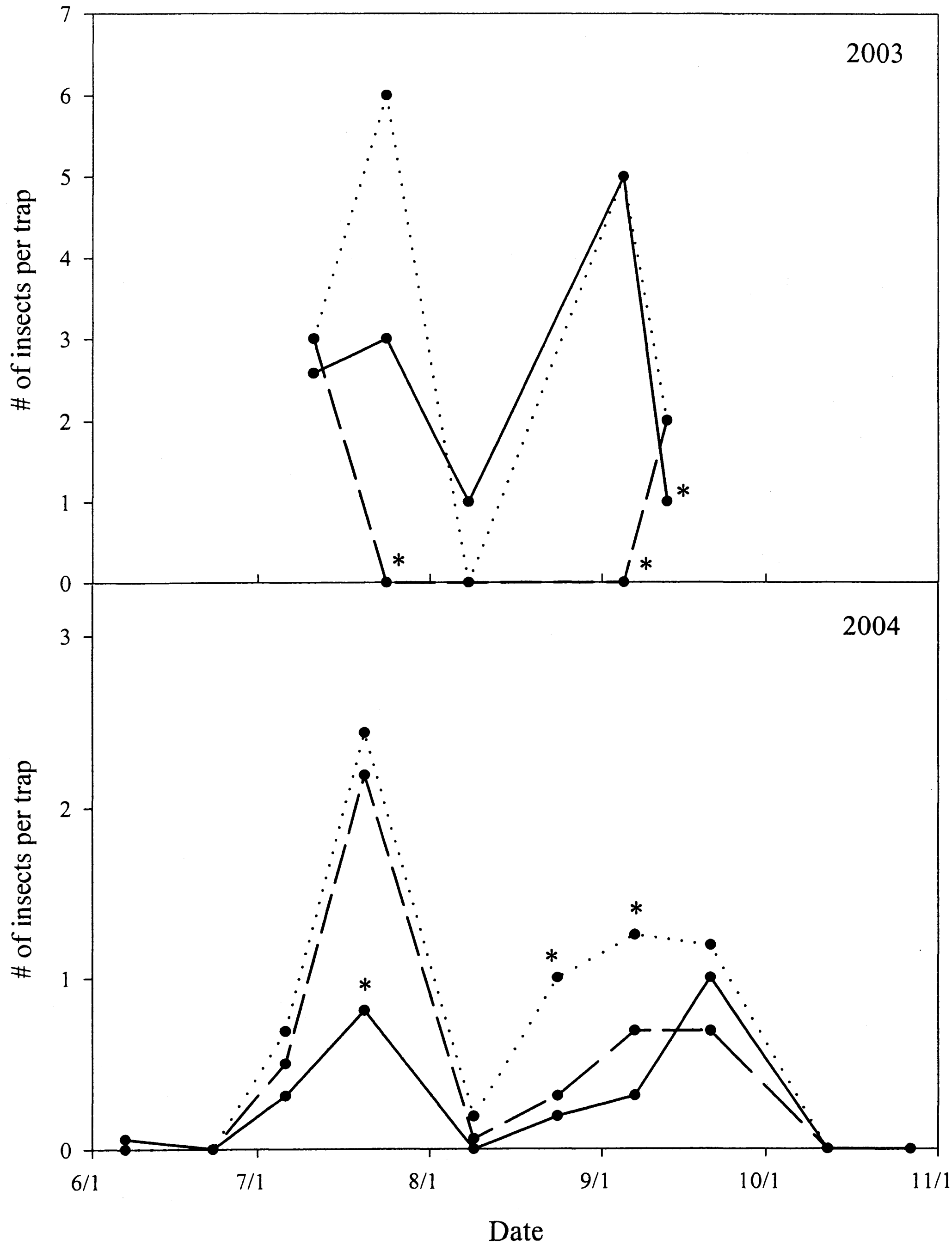

Figure 3. Average of field crickets (*Gryllus pennsylvanicus*) captured using pitfall traps in conventional (——), reduced (······), and no-tillage (----) regimes determined during periods of 48 hours in different dates in 2003 and 2004, in Boone, IA. Significant difference among treatments is represented by asterisks.

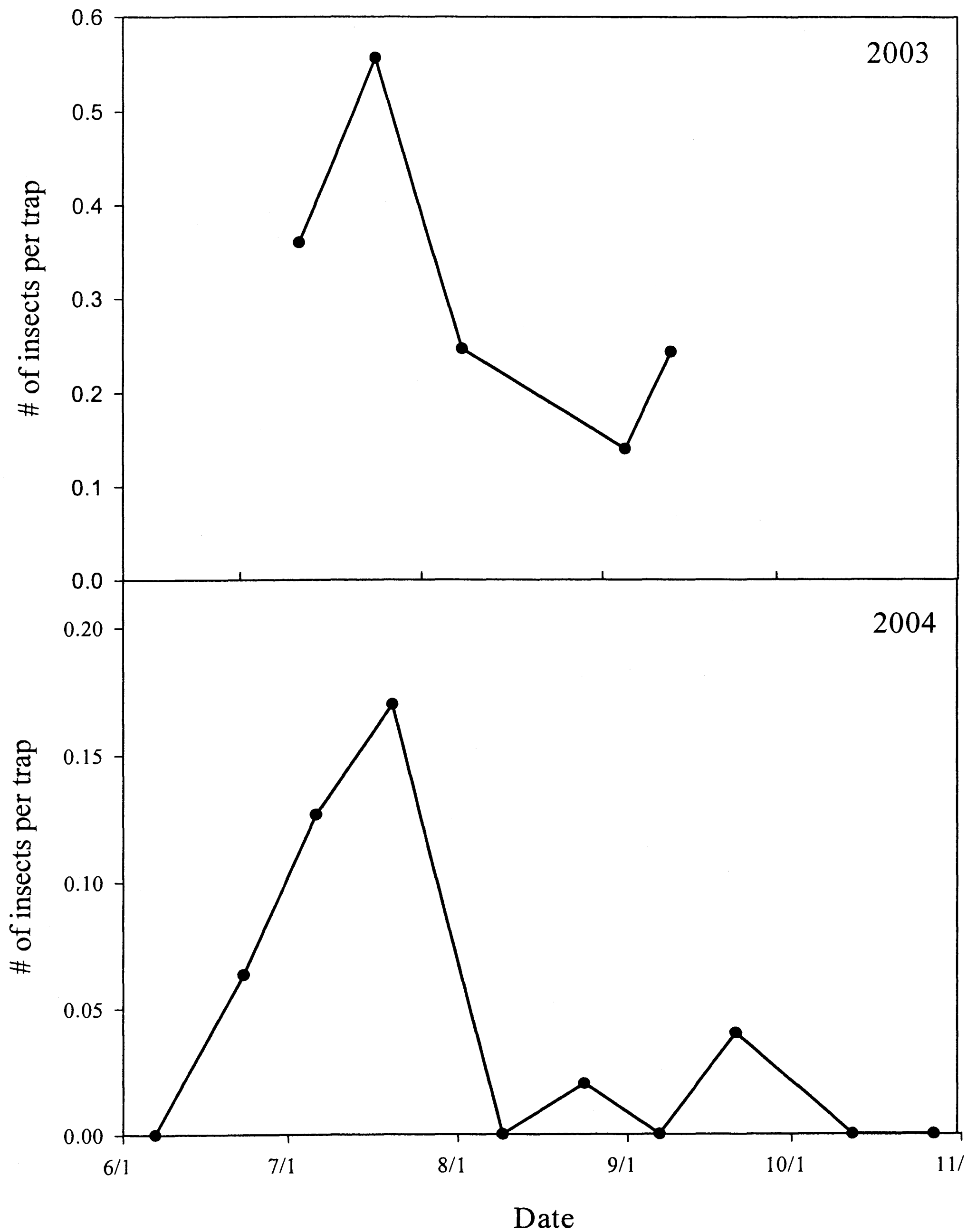

Figure 4. Average of ground beetles (*Harpalus pensylvanicus*) captured using pitfall traps in conventional, reduced and no-tillage regimes determined during periods of 48 hours in different dates in 2003 and 2004, in Boone, IA. No significant difference was observed among tillage regimes, so data are presented as an average of the treatments.

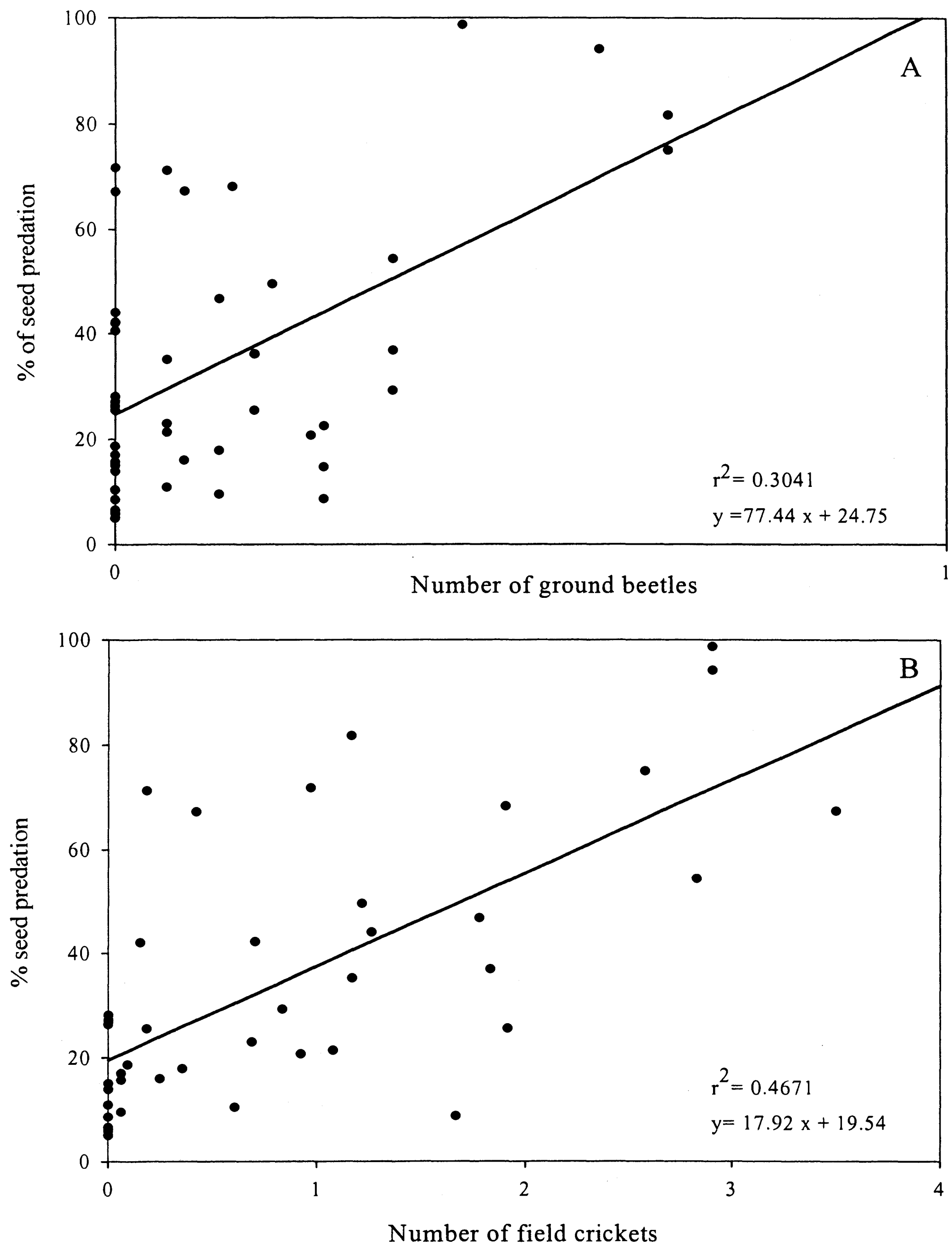

Figure 5. Correlation of seed predation of common lambsquarters (*Chenopodium album*) seeds and ground beetle (*Harpalus pensylvanicus*) (A) and field cricket (*Gryllus pennsylvanicus*) (B) populations in conventional, reduced and no-tillage regimes, during 2003 and 2004, in Boone, IA. No significant year effect was observed, so data of the two years are shown combined.

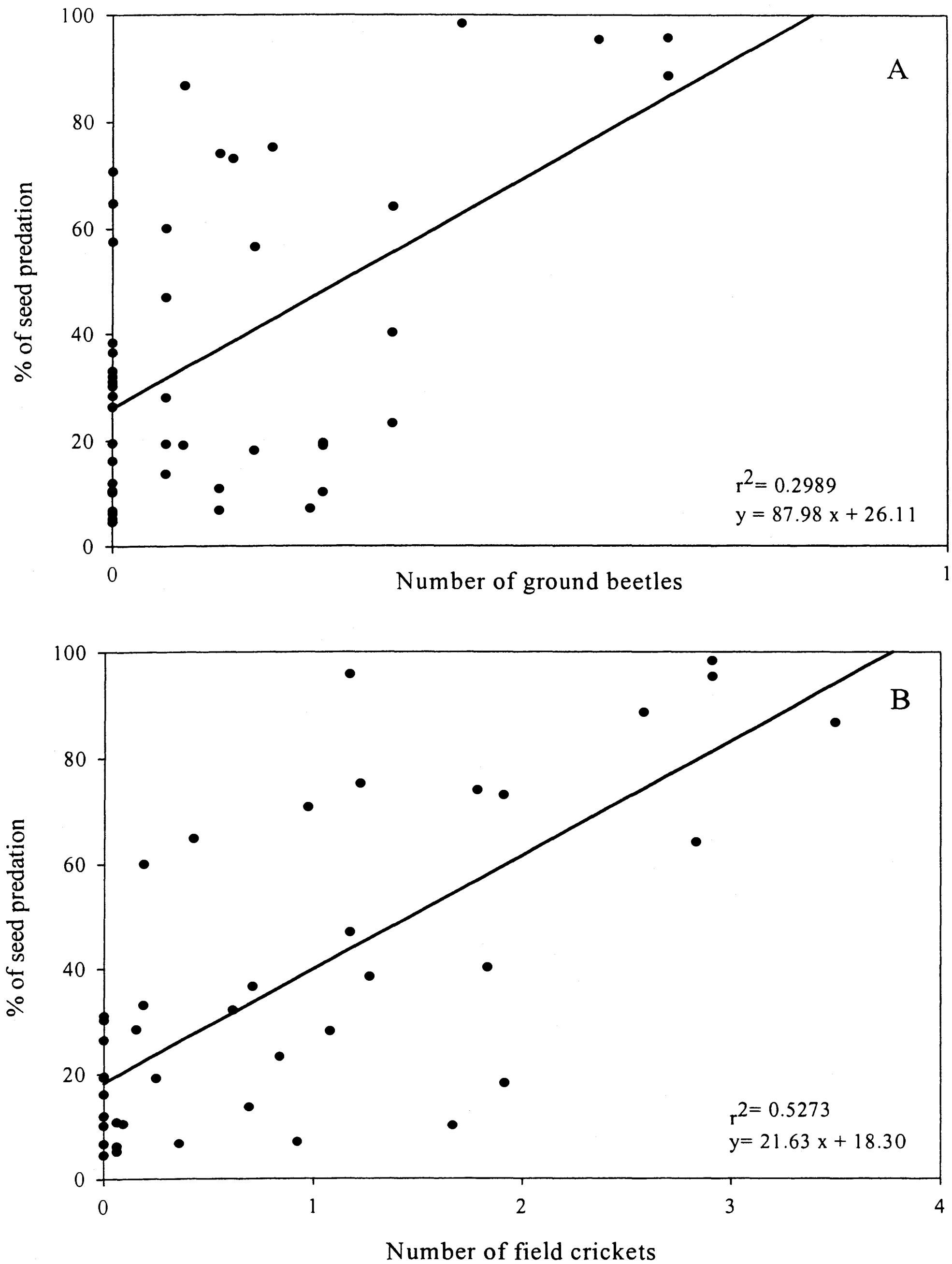

Figure 6. Correlation of seed predation of common waterhemp (*Amaranthus tuberculatus*) seeds and ground beetle (*Harpalus pensylvanicus*) (A) and field cricket (*Gryllus pennsylvanicus*) (B) populations in conventional, reduced and no-tillage regimes, during 2003 and 2004, in Boone, IA. No significant year effect was observed, so data of the two years are shown combined.

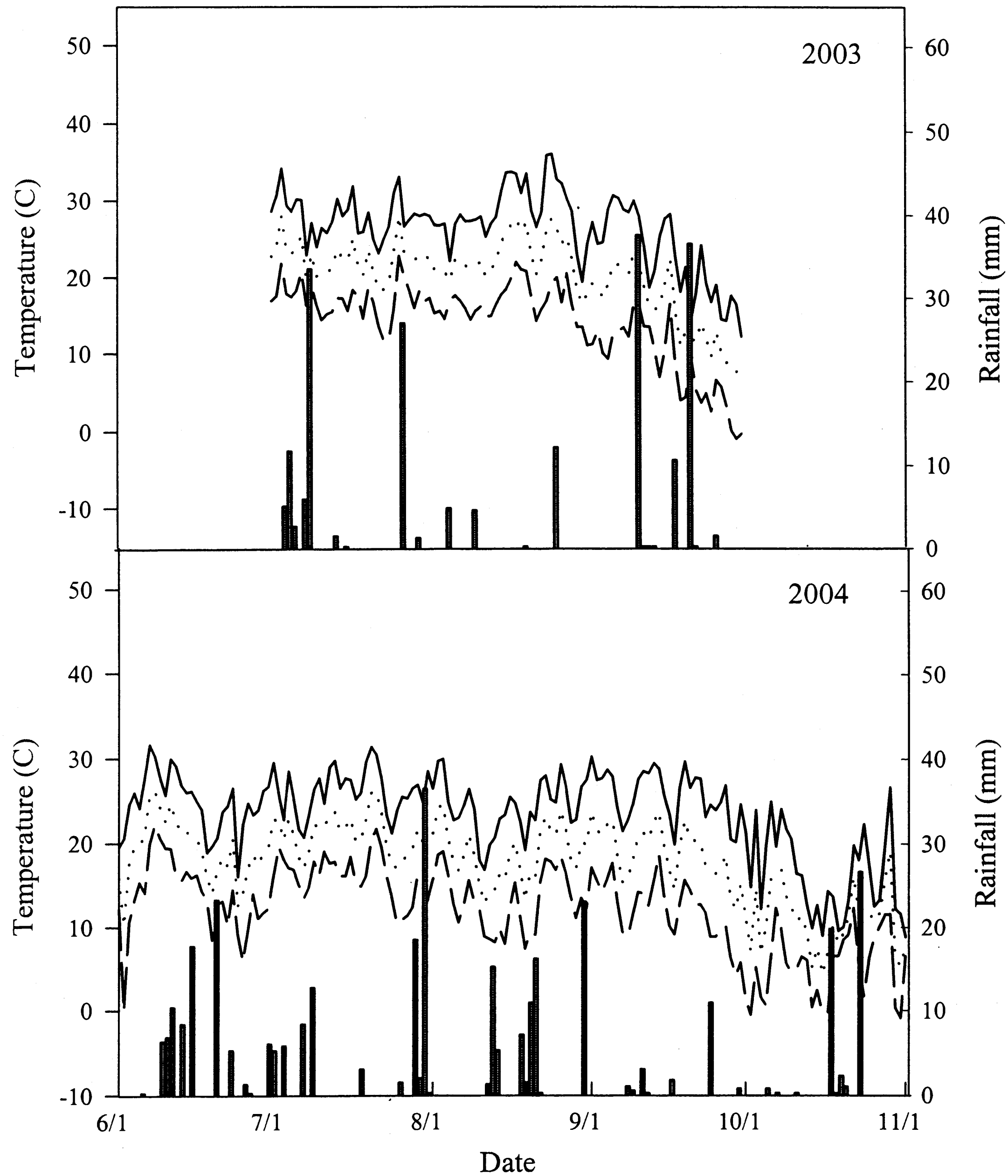

Figure 7. Maximum (solid line), average (dotted line) and minimum (dashed line) temperatures and rainfall (columns) from July through October, 2003 and June through November, 2004, in Boone, IA.

CHAPTER 3

GENERAL CONCLUSIONS

Conclusions

- Predation of common lambsquarters and common waterhemp seeds may play a very important role in reducing seed input into the soil seedbank of these weeds under field conditions.
- The main predators of common lambsquarters and common waterhemp seeds were invertebrate organisms. Two of the most abundant invertebrates captured with pitfall traps were field crickets (*Gryllus pennsylvanicus*) and ground beetles (*Harpalus pensylvanicus*) and are considered important seed predators.
- Under laboratory conditions, field crickets (*Gryllus pennsylvanicus*) and ground beetles (*Harpalus pensylvanicus*) preferred common lambsquarters and common waterhemp seeds over other weed seeds.
- Under field conditions, there was a significant correlation between common lambsquarters and common waterhemp seeds predated and the abundance of field crickets and ground beetles.
- We observed no consistent difference in seed predation of common lambsquarters and common waterhemp among tillage regimes. However, we observed a difference between years, indicating that the crop type might be influencing seed predators and so their level of predation. Different crops provide different microclimates, influencing the activity-density of seed predators. Therefore, by understanding the

habitat requirements of seed predators, we can modify our cropping systems and potentially increase insect seed predator populations, as well as their activity-density.

- Post-dispersal weed seed predation may not control large weed populations, but is definitively an important component of agricultural systems for the prevention of dramatic increases in weed populations.

Recommendations for Future Research

In this study, no evaluation of the reduction of the weed seed bank was conducted. Therefore, it will be necessary to conduct seed predation experiments that determine the reduction of the weed seedbank, and the impact of this reduction on weed populations in the field. In addition, it will be important to determine if such reductions in weed populations could prevent crop yield losses due to weed competition.

It would be important to determine appropriate habitats that will increase seed predators populations. For example, it would be important to conduct experiments to determine the effect that crop shading and canopy microclimate have on the abundance and activity or movement of ground dwelling invertebrates. Other experiments can determine the influence of "grass cover traps" within the plot in relation to seed predators and the level of weed seed predation in the field.

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