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Postdispersal Weed Seed Predation and Invertebrate Activity Density in Three Tillage Regimes

Rocio van der Laat, Micheal D. K. Owen, Matt Liebman, and Ramon G. Leon*

Field experiments were conducted near Boone, IA, to quantify postdispersal seed predation of common lambsquarters and common waterhemp in corn (2003) and soybean (2004) managed with conventional, reduced, and zero-tillage systems. Seed predation in each tillage regime was quantified using selective exclusion treatments during July through September 2003 and June through October 2004. In addition, the activity density of ground-dwelling invertebrates was estimated with pitfall traps. Choice and no-choice feeding trials were conducted in the laboratory using the most abundant weed seed predators found in the field to determine seed preferences of the potential predator organisms. The greatest seed loss occurred during July and August. In 2003, seed predation was lower in zero tillage than in conventional and reduced tillages, but no differences in seed predation between tillage regimes were observed in 2004. Maximum seed predation for common lambsquarters was 53% in 2003 and 64% in 2004. Common waterhemp seed predation reached 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 field crickets (*Gryllus pennsylvanicus* De Geer [Gryllidae, Orthoptera]) and ground beetles (*Harpalus pensylvanicus* Burmeister [Coleoptera, Carabidae]). In 2003, field crickets were relatively more abundant in conventional and reduced tillage than in zero-tillage plots. In 2004, field crickets were more abundant in the reduced tillage than in the other two tillage regimes. No differences were detected for ground beetles among tillage regimes ($P = 0.57$). Choice and no-choice feeding experiments confirmed the preferences of field crickets and ground beetles for common lambsquarters and common waterhemp seeds over the larger seeds of giant foxtail and velvetleaf. Under field conditions, the activity density of field crickets was a significant predictor of common lambsquarters ($r^2 = 0.47$) and common waterhemp ($r^2 = 0.53$) seed predation. Positive relationships were also detected between the activity density of ground beetles and common lambsquarters ($r^2 = 0.30$) and common waterhemp ($r^2 = 0.30$) seed predation. This research demonstrated that weed seed predation is an important component affecting weed seedbanks and that crop management practices that favor the activity of predators such as field crickets or ground beetles could influence weed populations. Also, the results suggested that tillage is more important in determining the number of weed seeds available on the soil surface to predators than directly affecting predator activity density.

Nomenclature: Common lambsquarters, *Chenopodium album* L.; common waterhemp, *Amaranthus tuberculatus* (Moq.) Sauer.; giant foxtail, *Setaria faberi* Herrm.; velvetleaf, *Abutilon theophrasti* Medik.; corn, *Zea mays* L.; soybean, *Glycine max* (L.) Merr.

Key words: Biological control, field crickets, ground beetles, integrated weed management, seedbank.

The weed seedbank is the main source of weeds in agricultural fields (Rahman et al. 2001). Weed populations in agricultural fields can be reduced by various management practices. However, the number of weed seeds in the soil and the production of new seeds by weeds that escape control are often sufficient 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, decay, and predation, and indirectly by soil and climatic conditions, crop rotation, weed management, and tillage practices (Buhler et al. 1997; Parker et al. 1989; Simpson et al. 1989).

A diverse group of small vertebrates, including field mice and birds (Holmes and Froud-Williams 2005; Hulme and Hunt 1999; Rey et al. 2002; Westerman et al. 2003), as well as ground-dwelling invertebrates such as carabid beetles, field crickets, and ants (Brust and House 1988; Carmona et al. 1999; Cromar et al. 1999; O'Rourke et al. 2006) can consume large numbers of weed seeds. Estimating weed seedbank reductions attributable to vertebrate

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and invertebrate seed predation may improve our ability to identify and design crop production systems that enhance weed seed predation and potentially allow reduced herbicide use, thus lowering production costs as well as possibly improving the environmental sustainability of crop production.

The distribution of weed seeds in the soil profile influences potential 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). Intense soil disturbance can reduce insect populations by affecting their life cycles as well as causing a less favorable habitat (Landis et al. 2000). Therefore, tillage regimes may not only affect soil quality, but also could influence the behaviors and population densities of ground-dwelling organisms, thus making tillage an important agricultural practice to consider when assessing weed seed predation (Baguette and Hance 1997). Although weed seed predation has been previously studied under different tillage systems, it is still unclear which tillage system provides a more suitable habitat for weed seed predators and their activity. Cardina et al. (1996) found no differences in the predation of velvetleaf seeds comparing continuous no-tillage and moldboard-plowed fields. Similarly, Trichard et al. (2013) observed that although zero tillage presented a higher diversity of granivorous carabids, weed seed predation levels were similar to fields with conventional tillage. Cromar et al. (1999) found that predation of barnyardgrass [*Echninochloa crus-galli* (L.) Beauv.] and common lambsquarters seeds was similar in no-tillage and moldboard-plowed systems but was lower in chisel-plowed systems. In contrast, Menalled et al. (2007) reported that fall panicum (*Panicum dichotomiflorum* Michx.) and common lambsquarters seeds were predated at levels up to two times higher in no-tillage systems when compared to tilled systems. In each situation, seed predation was likely determined by refuge provided by crop residues and the mobility of the insects within the tillage system. Therefore, we hypothesized that a reduced tillage system maintaining intermediate levels of plant residue on the ground would be more favorable for weed seed predation by creating a better balance between refuge and seed predator mobility when compared to conventional and no-tillage systems.

Common lambsquarters and common waterhemp are economically important and persistent weeds in corn and soybean fields through the north-central region of the United States. The importance of these weed species derives from their ability to compete with crops and reduce yields (Hager et al. 2002; Steckel and Sprague 2004). In addition, common lambsquarters and common waterhemp produce large numbers of seeds with physiological dormancy, which enables them to form persistent seedbanks and have variable emergence patterns (Baskin and Baskin 2001; Leon and Owen 2006), assuring their continuing presence and economic importance in agricultural fields. Common lambsquarters seed predation by invertebrates consistently surpassed 30% in row-crop systems, and was influenced by tillage regime (Cromar et al. 1999; Menalled et al. 2007). Common waterhemp seed predation has not been studied despite its pervasiveness in agricultural fields in the north-central region. The objectives of this study were to quantify common lambsquarters and common waterhemp seed predation in three tillage regimes (conventional, reduced, and zero tillage), and to identify and quantify the populations of insect species that predate seeds of those species. In addition, we investigated the relative weed seed preference and feeding ability of some of the potential predator organisms observed in the field.

Materials and Methods

A field experiment was conducted to quantify postdispersal common lambsquarters and common waterhemp seed predation at the Iowa State University Agricultural Engineering Research Farm near Boone County, IA, during 2003 and 2004. The experimental area was part of a long-term tillage study under a corn–soybean rotation. The field was divided into plots and subjected to three tillage treatments for 15 yr: conventional tillage (moldboard plow), reduced tillage (chisel plow), and zero tillage (Leon and Owen 2006). Plots were arranged in a randomized complete block design with four replications. Field cultivation was conducted in the spring of 2003 and 2004 for conventional and reduced tillage before crops were planted. Glyphosate-resistant corn and soybean were planted in 76-cm rows in 2003 and 2004, respectively. Glyphosate was applied at 832 g ae ha^{-1} (Roundup Ultra®, 356 g ae L^{-1}, Monsanto Co., St. Louis, MO) in July 2003 and late June 2004 for weed control. The local weed community was comprised predominantly of common lambsquarters, common waterhemp, common cocklebur (*Xanthium strumarium* L.), giant foxtail, green foxtail [*Setaria viridis* (L.) Beauv.], redroot pigweed (*Amaranthus retroflexus* L.), and velvetleaf. Although weed control in the experimental site was effective (> 95%), plants from these species survived and produced new seed every year, so weed seed inputs were part of the ecological processes of the site. The soil was a mixture of Clarion (fine-loamy, mixed, superactive, mesic Typic Hapludoll), Nicollet (fine-loamy, mixed, superactive, mesic Aquic Hapludoll), and Canisteo (fine-loamy, mixed, superactive, calcareous, mesic Typic Endoaquoll) silty clay loams with pH 6.0 and 4.0% organic matter. The size of each treatment plot was 30 m by 30 m and a 3-m grass aisle surrounded individual plots.

The percentage of plant residue coverage on the soil surface in each tillage regime was determined in August 2003 and 2004 by measuring plant residue intercept in a 1-m straight line in 5-cm intervals. These measurements were replicated five times in each plot.

Quantification of Postdispersal Weed Seed Predation in the Field. Predation of common lambsquarters and common waterhemp seeds was evaluated from July through September 2003, and June through October 2004, using two different predator exclusion treatments: vertebrate exclusion and vertebrate + invertebrate exclusion (control). In 2004, in order to test whether 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 predator exclusions allowed vertebrates as well as invertebrates to predate the seeds. Wire cages (25 cm by 25 cm by 5 cm) constructed with galvanized hardware cloth with 1.3-cm by 1.3-cm openings were used for vertebrate exclusion and were fixed permanently on the ground (Menalled et al. 2000). The wire cages allowed invertebrates access to the weed seeds, but excluded vertebrate seed predators. Weed seed predation was evaluated by placing 10-cm by 12-cm sandpaper cards covered with 50 lightly glued weed seeds inside the cages. This seed density is equivalent to low to moderate seed densities observed for common lambsquarters and common waterhemp under field conditions (Bensch et al. 2003; Crook and Renner 1990). 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 feeding on the weed seeds (vertebrate + invertebrate exclusion). The purpose of these vertebrate + invertebrate exclusions was to differentiate between weed seed loss due to predators from losses as a consequence of environmental conditions and manipulation of the cards.

The two weed species were evaluated with separate cards and exclusion treatments. Spray glue (Multi-Purpose 27 Spray Adhesive, 3M, St. Paul, MN) was applied to the cards, then the seeds were sprinkled and a thin layer of soil was added to the cards to better mimic the natural environment and to prevent insects from 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 were used to secure the cards to the ground. After leaving seed cards in the field for 48 h, they were collected and the number of seeds removed was determined. Measurements were conducted every 2 wk.

There were three replications of each exclusion treatment per plot, which were arbitrarily distributed between crop rows in the center of each plot (at least 10 m from the plot edges). Cards were arranged such that there were at least 3 m between cards in the same row and 1.5 m between rows. Seed predation was estimated by subtracting vertebrate + invertebrate exclusion seed loss from the seed loss observed in the other exclusion treatments for each evaluation date.

Pitfall traps consisting of a 500-ml cup filled with 200 ml of 10% ethylene glycol solution were placed in each tillage plot. Also, pitfall traps were located in aisles between tillage plots to monitor weed seed predator activity density outside the experimental plots. Evaluations were done every 2 wk during the growing season by opening the traps for 48 h 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 in 2003 and 2004. 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 (Alexander 1957) using the Iowa State University Insect Collection, Entomology Department in Ames, IA.

Estimating Feeding Ability and Weed Seed Preference of Possible Predators under Laboratory Conditions. Weed seed preference and efficiency of predation for the most abundant insect species found in the field and whose activity density correlated with seed predation 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, and velvetleaf with weights of 0.02, 0.04, 0.16, and 1 mg seed^{-1}, respectively. Adults of the most abundant insect species found in the field experiments were captured using dry pitfall traps in 2013 and 2014. The insects were then placed individually in 500-ml cups with a lid containing holes and fed commercial dry cat food (Purina® Cat Chow® Complete Formula, Société des Produits Nestlé S.A., Vevey, Switzerland); a wet cotton ball was added to the cup for humidity and water (Sanguankeo and Leon 2011). Insects that were actively feeding were chosen for the experiment and food was withheld for 24 h prior to the experiment. Insect feeding ability was evaluated by "no-choice" and "multiple-choice" seed experiments. For the no-choice experiments, a single individual from each insect species were placed in a 500-ml cup with a moist filter paper on the bottom, a wet cotton ball, and 100 seeds of common waterhemp, 100 seeds of common lambsquarters, 25 seeds of giant foxtail, or 10 seeds of velvetleaf. The number of seeds varied per weed species to compensate for differences in seed mass. Weed seed dry weight was determined before each experiment. After 24 h, the remaining seeds were dried at 65 C for 48 h and dry weight was obtained.

The multiple-choice seed experiments were conducted to evaluate whether insects prefer specific weed seeds. A single individual from each insect species was placed alone in a 500-ml cup with moisture paper, a wet cotton ball, and a mixture of seeds from the four weed species (100 seeds of common waterhemp, 100 seeds of common lambsquarters, 25 seeds of giant foxtail, and 10 seeds of velvetleaf). Weed seed dry weight was determined before each experiment. The seeds remaining intact after 24 h were dried for 48 h and dry weight was obtained by species. These experiments were conducted in growth chambers set at 25 C and with a photoperiod of 16 h light and 8 h dark. Both no-choice and multiple-choice feeding experiments were conducted with completely randomized designs, had six replications and were conducted three times.

Statistical Analysis. The field experiment was a randomized complete block design arranged as a split plot with tillage as the main plot and exclusion treatment as the subplot. Seed predation data from the field experiment were subjected to ANOVA using PROC MIXED of SAS (SAS Institute, Cary, NC). Results were analyzed independently by weed species and year. Pitfall trap data were analyzed with a nonparametric ANOVA using a Wilcoxon rank-sum test, which facilitates the analysis of variables that are not normally distributed (Ramsey and Shafer 2002). Total number of individuals per species captured during the entire experiment was used to compare tillage systems, and rare species were pooled and analyzed as a single category to avoid bias due to zeros. There were no differences ($P = 0.57$) among tillage regimes for the number of ground beetles captured per pitfall trap, so these data were combined. The data obtained from the feeding experiments were analyzed with ANOVA using PROC MIXED of SAS. LSD tests were used to separate means of the different weed species in the feeding experiments ($\alpha = 0.05$). Linear regression analyses were conducted to determine the relationship between activity density of potential weed seed predators and observed weed seed predation under field conditions.

Results and Discussion

Postdispersal Weed Seed Predation in the Field. Greater seed loss was observed in the vertebrate exclusion than in the vertebrate + invertebrate exclusion treatments, confirming invertebrate seed predation in 2003 and 2004 ($P < 0.01$). Also, because the vertebrate-exclusion and no-exclusion treatments exhibited similar seed loss in 2004 ($P > 0.11$), it was concluded that most of the observed seed predation was due to invertebrates. There was invertebrate seed predation throughout the periods of evaluation (July through September 2003 and June through October 2004), but most of the seed predation occurred during July and August (Figures 1 and 2). In 2003, seed losses for common lambsquarters ranged from 19 to 53% in conventional tillage, 19 to 48% in reduced tillage, and 6 to 41% in the zero-tillage regime (Figure 1). A similar pattern was observed in 2004, when seed losses ranged from 0 to 52% in conventional tillage, 1 to 64% in reduced tillage, and 0 to 48% in zero tillage. Common waterhemp seed losses during the growing season were 14 to 80% in 2003 and 0% to close to 70% in 2004 for both conventional and reduced-tillage regimes (Figure 2). The range of common waterhemp seed predation in zero tillage was 5 to 57% in 2003 and 0 to 68% in 2004. Most seed predation for common waterhemp occurred in mid-July, and seed losses declined early in September.

Our hypothesis that reduced tillage would support greater weed seed predation than conventional and

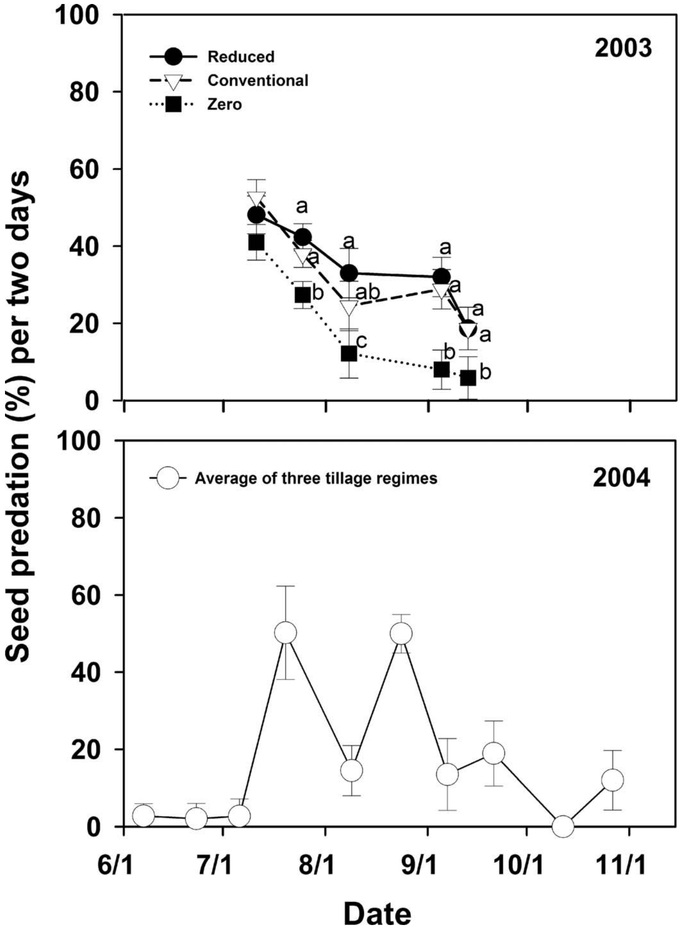

Figure 1. Common lambsquarters seed predation by invertebrates in conventional, reduced, and zero-tillage regimes determined during periods of 48 h in different dates in 2003 and 2004, in Boone County, IA. Seed predation was estimated by subtracting seed loss in the vertebrate + invertebrate exclusion from the seed loss in the vertebrate exclusion. Error bars represent SEM. No differences between tillage regimes were observed in 2004, so the data are presented as an average of tillage regimes. Tillage regimes with different letters were statistically different ($P < 0.05$) within each evaluation date. The absence of letters indicates that no differences between tillage regimes were detected within evaluation date.

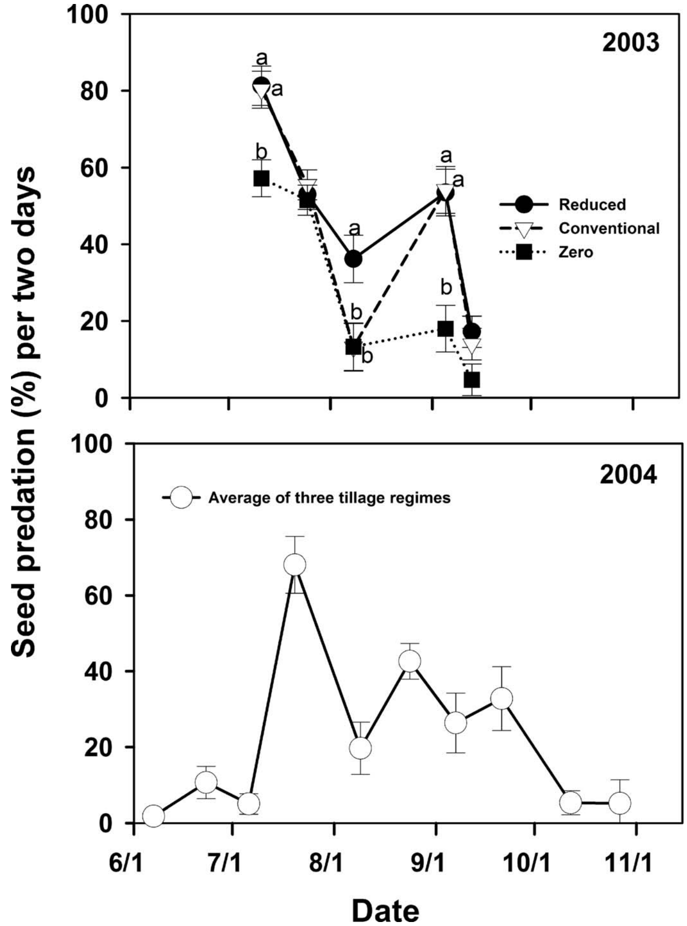

Figure 2. Common waterhemp seed predation by invertebrates in conventional, reduced, and zero-tillage regimes determined during periods of 48 h in different dates in 2003 and 2004, in Boone County, IA. Seed predation was estimated by subtracting seed loss in the vertebrate + invertebrate exclusion from the seed loss in the vertebrate exclusion. Error bars represent SEM. No differences between tillage regimes were observed in 2004, so the data are presented as an average of tillage regimes. Tillage regimes with different letters were statistically different ($P < 0.05$) within each evaluation date. The absence of letters indicates that no differences between tillage regimes were detected within evaluation date.

zero tillage was rejected. 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 several evaluation dates in 2003, seed predation for both weed species was lower in zero tillage than in conventional and reduced tillage (Figures 1 and 2). These findings are in contradiction with reports by Cromar et al. (1999) and Menalled et al. (2007), in which zero tillage favored common lambsquarters seed predation when compared to other tillage systems. Therefore, it seems that tillage system alone is not the determinant factor for predation of weed seeds located on the soil surface. Instead, tillage may influence seed predation through its effects on the total number of weed seeds that remain on the soil surface and are accessible to predators (Yenish et al. 1992). The lack of a consistent tillage effect was likely influenced by differences in crop and environmental conditions in 2003 and 2004, but the specific factor (or factors) was not determined due to the confounded effect of crop and year. However, 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, thus changing the microclimate and consequently affecting the life cycle and activity density of

Table 1. Effect of tillage (conventional, reduced and zero tillage), predator exclusion treatments (vertebrate, vertebrate + invertebrate, and no exclusion), and evaluation date on seed predation of common lambsquarters and common waterhemp in 2003 and 2004 in Boone County, IA.

Factor	Common lambsquarters 2003	Common lambsquarters 2004	Common waterhemp 2003	Common waterhemp 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

ground-dwelling organisms (Gallandt et al. 2005; Holland and Luff 2000; Norris and Kogan 2000). Therefore, the different microclimates that these crops generated might have influenced the populations of ground-dwelling organisms and their movement in the field, potentially altering patterns of weed seed predation.

Identification and Quantification of Possible Insect Seed Predators. In 2003 and 2004, the most common insect 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 pitfall traps. 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 were carnivorous species (data not shown). Even though ants were also caught in the pitfall traps, we found no one species that dominated the ant fauna. In addition, no correlation between the presence of ants and weed seed predation was observed for either common lambsquarters ($r^2 = 0.03$) or common waterhemp ($r^2 = 0.01$). For this reason, ants were not included in the laboratory experiments. It is possible that ant activity densities were related with the activity densities of field crickets and carabids but we were unable to detect this association.

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; O'Rourke et al. 2006). Field cricket population densities differed between tillage regimes (Table 3), with zero tillage

Table 2. Total number of invertebrates captured in pitfall traps in conventional, reduced, and zero-tillage regimes in Boone County, IA.

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

[a] Tillage regimes with different letters are statistically different ($P < 0.05$) within family, based on a nonparametric ANOVA using a Wilcoxon rank-sum test. The absence of letters indicates that no differences between tillage regimes were detected.

Table 3. Effect of tillage (conventional, reduced, and zero tillage), sampling location within plot, evaluation date within year, and year on field crickets (*Gryllus pennsylvanicus*) and ground beetles (*Harpalus pensylvanicus*) populations in Boone County, IA, in 2003 and 2004.

Factor	Field crickets	Ground beetles
	P value	
Tillage	< 0.0001	0.5656
Date	< 0.0001	0.1284
Block	0.4693	0.6517
Sample × block	0.5570	0.1403
Year	< 0.0001	< 0.0001
Tillage × year	0.0002	0.5264
Block × year	0.5592	0.4060
Sample × year × block	0.3672	0.1685
Tillage × date	0.0232	0.8184
Date × block	0.4514	0.5075
Date × sample × block	1.0000	0.9988
Tillage × date × year	< 0.0001	0.0535
Tillage × date × block	1.0000	0.9951
Tillage × date × sample × block	1.0000	0.9998

more frequently exhibiting the lowest population densities (Figure 3). Field cricket populations were at least 10 times higher during the last week of July in both years compared to the other evaluation dates. There was no difference for ground beetle density among tillage regimes in either 2003 or 2004 (Table 3). The activity densities of field crickets and ground beetles approached zero in late September (Figures 3 and 4).

A peak in seed predation was observed when insect activity densities were highest. Linear regression analyses showed a positive relationship between field cricket activity densities and common lambsquarters ($r^2 = 0.47$, $P < 0.0001$) and common waterhemp ($r^2 = 0.53$, $P < 0.0001$) seed predation (Table 4). Similarly, there was a positive relationship between ground beetle activity densities and common lambsquarters ($r^2 = 0.30$, $P < 0.0001$) and common waterhemp ($r^2 = 0.30$, $P < 0.0001$) seed predation in the field (Table 4). 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 were other invertebrate species that predated common lambsquarters and common waterhemp seeds that were at lower population densities than field crickets and ground beetles.

Feeding Ability and Weed Seed Preference under Laboratory Conditions. Both field crickets and ground beetles consumed common lambsquarters

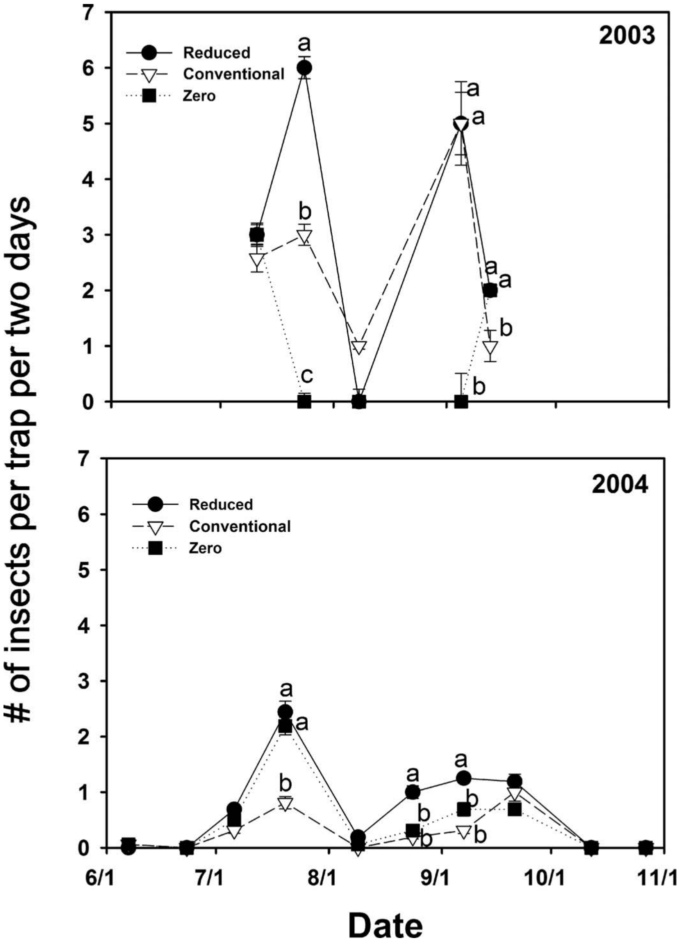

Figure 3. Number of field crickets (*Gryllus pennsylvanicus*) captured using pitfall traps in conventional, reduced, and zero-tillage regimes determined during periods of 48 h in different dates in 2003 and 2004, in Boone County, IA. Error bars represent SEM. Tillage regimes with different letters were statistically different ($P < 0.05$) within each evaluation date. The absence of letters indicates that no differences between tillage regimes were detected within evaluation date.

and common waterhemp seeds in laboratory feeding trials. Field crickets consumed approximately 60% more seeds compared to ground beetles (Table 5). In general, there was a preference for common waterhemp seeds in the multiple-choice 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-choice or no-choice seed experiments. Ground beetles preferred common waterhemp over common lambsquarters, giant foxtail, and velvetleaf seeds, consuming 43 and 72% in the multiple-choice and no-choice experiments, respectively. The second weed seed preferred

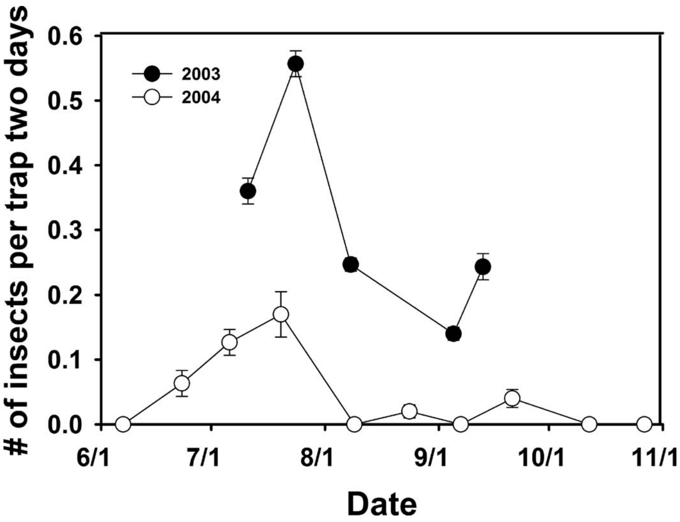

Figure 4. Number of ground beetles (*Harpalus pensylvanicus*) captured using pitfall traps in conventional, reduced, and zero-tillage regimes determined during periods of 48 h in different dates in 2003 and 2004, in Boone County, IA. Error bars represent SEM. No difference was observed among tillage regimes, so data are presented as an average of tillage regimes.

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 5).

Implications for Management. Other studies have reported seed predation levels similar to those observed in the present study (Brust and House 1988; Cromar et al. 1999; Gallandt et al. 2005; Harrison et al. 2003; Mauchline et al. 2005; Menalled et al. 2000; Westerman et al. 2003). Postdispersal weed seed predation thus may play an important role in regulating weed population densities. In the absence of repeated immigration events, local seed production and survival are necessary for maintaining annual weed populations (Louda 1989). If a given weed species population density is reduced by seed predation, changes in weed community composition can occur by population increases of other weed species whose seeds are not predated (Louda 1989).

According to our field data, invertebrate organisms were the main predators of common lambsquarters and common waterhemp seeds during summer and early autumn. Our laboratory results showed that invertebrate organisms consumed small weed seeds such as common lambsquarters (1.2 to 1.3 mm in diam) and common waterhemp (0.9 to 1.2 mm in diam), in contrast to larger weed seeds such as giant foxtail (1.5 to 1.7 mm in diam) and velvetleaf (3.0 to 3.5 mm in diam). It has been observed that weed seed consumption is related to the predator size (Brust and House 1988). Consequently, insect predators tend to consume a larger number of smaller weed seeds than larger weed or crop seeds. Given the potential for insects to reduce weed seed populations, it is important to support and possibly increase the populations of these beneficial insects.

A peak in weed seed predation was observed late in July, 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 (Forcella et al. 1996; Sellers et al. 2003). Therefore, predation levels more likely affecting common lambsquarters and common waterhemp would be not the ones observed in July, but the ones in October, which can produce approximately 20% seed loss in a 2-d period. Reduced seed predation was observed in mid-August, which coincided with reductions in activity density of field crickets and ground beetles. These reductions in activity density and predation coincided with the most intense rainfall events ($>$ 23 mm in less than 12 h) that occurred during the study.

In 2003, we found 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 zero 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 zero-tillage regime, when compared to conventional tillage. In contrast to those

Table 4. Relationship between activity density (number of insects per trap per 48 h) of field crickets (*Gryllus pennsylvanicus*) and ground beetles (*Harpalus pensylvanicus*) and seed predation (%) of common lambsquarters and common waterhemp in 2003 and 2004, in Boone, IA.[a]

	Field crickets			Ground beetles		
Weed species	Model	r^2	P value	Model	r^2	P value
Common lambsquarters	$y = 17.92x + 19.54$	0.47	< 0.0001	$y = 77.44x + 24.75$	0.30	< 0.0001
Common waterhemp	$y = 21.63x + 18.30$	0.53	< 0.0001	$y = 87.98x + 26.11$	0.30	< 0.0001

[a] Data were pooled for the 2 yr and three tillage regimes.

Table 5. Percentage of weed seeds consumed by field crickets (*Gryllus pennsylvanicus*) and ground beetles (*Harpalus pensylvanicus*) after 24 h in a multiple-choice and no-choice feeding experiment under laboratory conditions.[a]

	Field crickets		Ground beetles	
Weed species	Multiple choice	No choice	Multiple choice	No choice
Common lambsquarters	48 b[b]	66 a	29 b	45 b
Common waterhemp	71 a	85 a	43 a	72 a
Giant foxtail	13 c	38 b	9 c	25 c
Velvetleaf	10 c	43 b	0 d	11 d

[a] 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.

[b] Within a column, weed species with the same letter are not statistically different based on LSD ($\alpha = 0.05$).

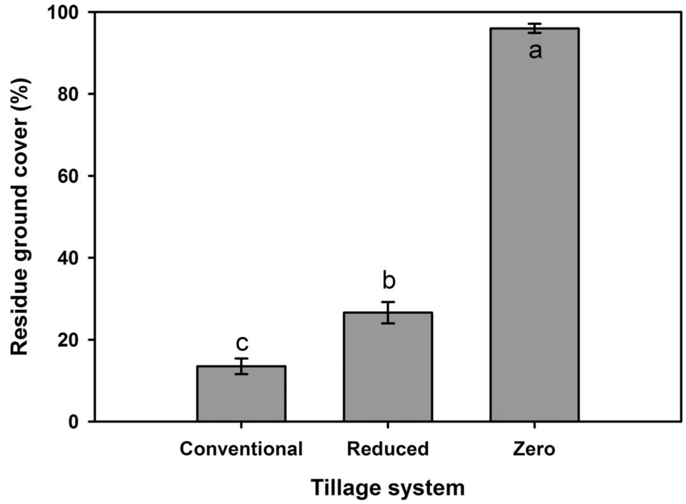

Figure 5. Crop residue cover in three tillage regimes, in Boone County, IA. No year effect was observed, so values represent the average of 2 yr (2003 and 2004). Error bars represent SEM. Tillage regimes with different letters were statistically different ($P < 0.05$).

reports, we observed lower predation of common lambsquarters and common waterhemp seeds in the zero-tillage regime, compared to the conventional and reduced regimes in 2003. This may be a consequence of the amount of crop residue on the soil surface. The zero-tillage regime had at least three times more crop residue compared to the conventional and reduced-tillage regimes (Figure 5). This higher amount of crop residue might have reduced insect mobility throughout the field (Cromar et al. 1999). If this was the case and considering that we did not find clear differences in insect activity density among tillage systems, then it is also possible that insect populations were similar or higher in the zero tillage, but their ability to reach seed cards and pitfall traps was lower than in the other tillage regimes. Another possibility is that there were more food sources (e.g., more seeds remaining on the soil surface) in the zero-tillage regime, making it less likely for predators to feed from the seeds provided in the cards.

Tillage is believed to play an important role in determining insect populations and subsequent activity densities by providing different microhabitats for insects (Baguette and Hance 1997). In the present study, however, ground beetle populations did not differ among tillage regimes. With respect to field crickets, there was a difference in insect numbers captured among tillage regimes in 2003 and 2004. These differences were not consistent between years, but there was a tendency to observe more field crickets in reduced tillage. Because the characteristics of the landscape surrounding agricultural fields can influence weed seed predation levels (Trichard et al. 2013), it is worth noting that activity density of carabid species in the aisles between experimental plots was up to 10 times higher throughout the season than within experimental plots. The aisles were mainly covered with grass and with a larger number of weed species when compared to the study area. Therefore, aisles and field edges might be important reservoirs of invertebrate weed seed predators. Therefore, it might be possible to increase invertebrate seed predator populations by maintaining plant cover on aisles and field edges or by using cover crops that create a habitat favorable for these organisms (Cromar et al. 1999; Gallandt et al. 2005; Heggenstaller et al. 2006; Sanguankeo and Leon 2011). However, it is also possible that if these vegetated areas, especially aisles and borders provide enough food, predators might not need to forage for weeds seeds within agricultural fields.

The lack of clear differences in seed predation between tillage treatments could be the result of a combination of competing processes between insect population densities and activity of insect individuals. It is possible that the abundant plant residue in the zero-tillage regime represented an important barrier for the mobility of insect seed predators making it difficult for them to reach the cards even if the populations were higher than in the other tillage regimes. Conversely, conventional and reduced-tillage systems could provide a ground surface with fewer obstacles (i.e., less crop residue), thus allowing seed predators to scout and forage a larger area (Cromar et al. 1999; Sanguankeo and Leon 2011; Thomas et al. 2006). Also, because tillage buries seeds and reduces food supply for seed predators, it is possible that insect populations with fewer individuals but with a higher need to find food will be more actively foraging, and in zero tillage, where most seeds remain on the soil surface, insects might not need to move much to find food (Dixon and McKinlay 1992).

This study showed that tillage regime may influence weed seed predation by invertebrates, and that zero tillage might limit weed seed predation. In addition, weed seed predation by invertebrates, primarily field crickets and ground beetles, can play an important role in reducing the soil seedbanks of weed species with small seeds such as common lambsquarters and common waterhemp. Our results in combination with multiple previous studies clearly indicate that invertebrate seed predation can provide an important ecological service in agricultural fields by reducing weed seedbank inputs. However, weed seed predation under current agricultural practices is highly variable, and its contribution to the overall weed management in agricultural fields is uncertain. Future research should focus on directly manipulating predator populations to clarify the complicated relations between predator activity density and food and refuge availability over space and time, but more importantly to determine whether higher predator populations can decrease weed populations enough to reduce herbicide use in agricultural fields.

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