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Source: Weed Science, 59(1):76-81.
Published By: Weed Science Society of America
https://doi.org/10.1614/WS-D-10-00065.1
URL: http://www.bioone.org/doi/full/10.1614/WS-D-10-00065.1

Weed Science 2011 59:76–81

Cover Crops and Disturbance Influence Activity-Density of Weed Seed Predators *Amara aenea* and *Harpalus pensylvanicus* (Coleoptera: Carabidae)

Meredith J. Ward, Matthew R. Ryan, William S. Curran, Mary E. Barbercheck, and David A. Mortensen*

The activity-density of *Amara aenea* (DeGeer) and *Harpalus pensylvanicus* (DeGeer) (Coleoptera: Carabidae) was monitored in an experiment that compared five management treatments representing a range of disturbance frequencies, crops, and aboveground biomass production. In 2004 and 2005, three treatments comprised of multiple summer cover crops were compared to bare fallow and soybean, the latter of which used mechanical cultivation to manage weeds. In 2005 weed seed predation was assessed from June to September in two of the treatments (bare fallow and oat–pea/rye–hairy vetch). Beetle activity-density varied with treatment, time of sampling, and year. In 2004 peak activity-density of *A. aenea* was highest in the mustard/buckwheat/canola, but there was no difference in *H. pensylvanicus* activity-density. In 2005 activity-density of *H. pensylvanicus* was higher in oat–pea/rye–hairy vetch than in soybean treatment. Seed predation rates were relatively consistent across treatments, averaging between 38 and 63%. In fallow and oat–pea/rye–hairy vetch, *H. pensylvanicus* activity-density accounted for 29 and 33% of the variation in seed predation, respectively. Our findings suggest cover crops have a positive effect on the activity-density of *A. aenea* and *H. pensylvanicus* and that disturbance negatively influences their activity-density in the absence of cover crops.

Nomenclature: Buckwheat, *Fagopyrum esculentum* Moench; canola, *Brassica napus* L.; field pea, *Pisum sativum* L.; hairy vetch, *Vicia villosa* Roth; mustard, *Sinapis alba* L.; oat, *Avena sativa* L.; red clover, *Trifolium pretense* L.; rye, *Secale cereale* L.; soybean, *Glycine max* Merr.; *Amara aenea* DeGeer; *Harpalus pensylvanicus* DeGeer.

Key words: Seed bank, ground beetles, conservation biocontrol, post-dispersal weed seed predation.

A greater understanding of the effects of crop and soil management on organisms that contribute to biological control of pests may lead to enhanced pest suppressive practices and reduce reliance on pest control chemicals. Weed seed predation, a form of biological control, can contribute significantly to weed population regulation (Menalled et al. 2007; Navntoft et al. 2009; Nurse et al. 2003; O'Rourke et al. 2006; Westerman et al. 2003; Williams et al. 2009). Postdispersal seed predation of summer annual weeds has been shown to be an important population regulator or ''choke point'' period in the weed life cycles (Davis et al. 2003; Jordan et al. 1995). Manipulating ground cover with crop residue and cover crops can increase weed seed predation during this time. For example, giant foxtail (*Setaria faberi* Herrm.) seed removal and field cricket (*Gryllus pennsylvanicus* Burmeister) activity-density in late summer and early fall were more than two times higher in wheat plots that were underseeded with red clover compared to wheat plots that were not (Davis and Liebman 2003). This effect may have been a result of more ground cover after wheat harvest from the living clover compared to the remaining wheat stubble. Despite the observed ability to influence seed predation by altering ground coverage, there is relatively little research on the role summer cover crops may play fostering habitat of weed seed predators or how to implement such systems to maximize efficacy. Incorporating practical knowledge of weed management strategies and their effects on weed seed predators may decrease antagonistic interactions and improve the compatibility of tactics resulting in enhanced system-wide weed suppression.

Weed seed predation may occur predispersal while seeds are still attached to the parent plant or postdispersal. Rodents, birds, ants, ground beetles and crickets are important postdispersal weed seed predators, contributing up to 90% of weed seed bank loss (Carmona et al. 1999; Cromar et al. 1999; Navntoft et al. 2009). Carabid beetles in particular have been shown to consume impressive amounts weed seeds in agroecosystems (Cardina et al. 1996; Menalled et al. 2007) and are commonly found inhabiting old fields, pastures, cultivated fields, and their borders (Larochelle and Lariviere 2003). These beetles feed on a wide variety of weed seeds; however, they tend to prefer small seeded grasses and broadleaf plants (Best and Beegle 1977).

Tillage and mowing as well as the disturbance from crop harvesting can drastically decrease insect populations (Landis et al. 2000). Carabid populations will also decrease when beetles emigrate from a site before the oncoming disturbance. Additionally, populations can be adversely affected by indirect effects on habitat quality (Thorbek and Bilde 2004). Decreasing the intensity of soil disturbance (Kromp 1999), creating refuge strips, and temporal variation in tillage can result in higher seed predator abundance (Carmona and Landis, 1999). In a recent study in Maine, moldboard plowing and rotary tillage reduced a common carabid beetle, *Harpalus rufipes* (DeGeer), activity-density by 53 and 55%, when compared to no tillage (Shearin et al. 2007). Higher beetle abundance is the likely result of several interacting factors including greater food and shelter, a more suitable microclimate, and ease of movement.

Several studies have examined factors that influence carabid beetle activity-density, including plant density, mobility, and weed seed predation (Gallandt et al. 2005; Hatten et al. 2007; Navntoft et al. 2009; O'Rourke et al. 2006; Shearin et al. 2007; Shearin et al. 2008). Dense canopy cover provides habitat for seed predators and can increase seed predator populations and the amount of seeds consumed (Cromar et al. 1999; Gallandt et al. 2005; Shearin et al. 2008). Higher rates of seed predation have been reported in plots with vegetative cover than those without (Davis and Liebman 2003; Gallandt et al. 2005). Summer annual row crops often have a long period of bare soil or low soil cover in early spring resulting in an extreme soil-surface environment with regard to temperature, moisture, and

DOI: 10.1614/WS-D-10-00065.1

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exposure. As summer annual row crops mature, the habitat becomes more favorable with a dense plant canopy, cooler temperatures near the soil surface, higher humidity, and greater protection from predators. Winter cereals provide a more favorable environment in early spring by providing early canopy cover, lower fluctuations in temperature and moisture, and reduced exposure (Kromp 1999). In the early spring, the fully developed winter cereal canopy provides protection for ground beetles while still allowing good mobility as the ground surface remains open (Melnychuk et al. 2003).

In Pennsylvania, *Amara aenea* (DeGeer) and *Harpalus pensylvanicus* (DeGeer) are two common carabid beetles that inhabit agroecosystems. Both species are omnivorous and can consume pollen, fungi, and other insects; however, they are primarily granivorous and feed on plant seeds (Menalled et al. 2007). The lifecycle of *A. aenea* is poorly understood; however, this species overwinters as an adult in field margins and can be found year-round (Holland 2002). *Amara aenea* is a spring-breeder and actively disperses during the mating season leading to high activity-density at that time (Saska et al. 2007). *Harpalus pensylvanicus* breeds in late summer/autumn and has highest activity-density in summer/autumn in the northeastern United States (Carmona and Landis 1999; Leslie et al. 2009; Pavuk et al. 1997).

Summer cover crops and soil disturbance are used to manage weeds in agroecosystems and thus understanding how they influence resident seed predators is important for conservation biocontrol and overall weed management. Previous research suggests that vegetative ground cover and lower disturbance levels can foster seed predator populations. The objective of this research was to determine how commonly used northeastern U.S. cover cropping practices and associated tillage influence *A. aenea* and *H. pensylvanicus* activity-density and weed seed predation. We hypothesized that *A. aenea* and *H. pensylvanicus* activity-density will (1) be higher in cover crop treatments than in the fallow or soybean treatments; (2) increase as the duration after disturbance increases; (3) be higher in no-till compared to tilled plots; and (4) be positively correlated with *S. faberi* seed predation.

Materials and Methods

Management Treatments. A field experiment was initiated in the fall of 2003 and repeated in 2004 to evaluate the effects of cover cropping treatments on ground beetle activity-density and weed seed predation at the Russell E. Larson Agricultural Research Center in Centre County, Pennsylvania (40°44′N, 77°57′W). Conventional corn and soybean had been grown in these fields prior to initiating the experiment. The experiment was conducted on a Hagerstown silt loam soil (fine, mixed, mesic, Typic Hapludalfs).

The experiment was arranged as a randomized complete block with four replicates. Treatments consisted of five cover crop systems representing different crops, levels of soil disturbance, duration of cover, and quantity and quality of biomass production. The plot size of each experimental unit was 12.2 by 12.2 m. Plot size was limited by available space, and although larger plots would have been ideal, we believe this design was adequate for assessing relative differences between treatments.

Five treatments that represented a wide range of disturbance frequencies and disturbance types (tillage and mowing) as well as a range of crop species and levels of dry matter production were tested: (1) fallow: bare fallow where weeds were controlled with tillage and no crop was grown; (2) soybean: organically managed soybean (*Glycine max* Merr. 'Pioneer 93M11') that relied on mechanical weed control; (3) mustard/buckwheat/canola: yellow mustard (*Sinapis alba* L. 'Idagold'), followed by buckwheat (*Fagopyrum esculentum* Moench 'VNS'), followed by winter canola (*Brassica napus* L. 'Dwarf Essex'); (4) oat–pea/rye–hairy vetch: spring oat (*Avena sativa* L. 'Ogle') and field pea (*Pisum sativum* L. 'Maxum'), followed by cereal rye (*Secale cereale* L. 'Aroostook') and hairy vetch (*Vicia villosa* Roth); and (5) oat–red clover: spring oat and red clover (*Trifolium pretense* L. 'Mammoth').

Soybean was planted in 76-cm rows to facilitate inter-row cultivation, whereas all other species were seeded in 20-cm rows or less. In the mustard/buckwheat/canola and oat–pea/rye–hairy vetch treatments, cover crops were flail mowed prior to seed set and incorporated before planting the next crop. Oats were rotary mowed prior to seed set. A more detailed description of field operations is provided in Table 1.

In 2005 management treatment plots from 2004 were planted to sweet corn (*Zea mays* L. 'Kandy Kwik') (Figure 1). For the sweet corn crop, main plots were split into no-till and conventional tillage split-plots (split-plot = 6.1 by 12.2 m) to examine the effects on incorporated vs. surface residues. Cover crops were mowed, rotovated, and cultimulched in the conventional tillage split-plots, and they were treated with an herbicide in mid-May in the no-till split-plots. In the no-till split-plot, 0.84 kg ae ha^{-1} glyphosate plus 0.28 kg ae ha^{-1} 2,4-D ester were applied to control cover crops and any emerged weeds approximately 10 d prior to corn planting. Weeds emerging after crop planting were managed with one interrow cultivation in the conventional tillage split-plots and with a postemergence herbicide (35 g ai ha^{-1} nicosulfuron plus 104 g ai ha^{-1} mesotrione plus 1% crop oil concentrate) in the no-till split-plots. Both the cultivation and the postemergence herbicide application occurred at 4 wk after corn planting.

Activity-Density. Beetle activity-density was defined as the average number of beetles captured per pitfall during a 72-h sampling period. Pitfall traps consisted of a 950-ml plastic container (height 10.9 cm by diameter 11.4 cm) with a 240-ml polystyrene cup filled about a third full with ethylene glycol (killing agent) placed in the bottom of the plastic container. The specimen collection cup allowed the traps to be checked without removing the entire trap from the soil. The top half of a 2,000-ml plastic bottle was inverted and placed into the 950-ml plastic container to direct invertebrate organisms into the specimen cup. Three pitfall traps were placed flush with the soil surface every 3 m along a horizontal transect in the center of each management treatment main plot or each sweet corn tillage split-plot. When not in use, traps were covered to prevent the unnecessary capture of beetles and to exclude debris and water. Pitfall trapping was done each month from July to October in 2004 (total of four times) and from May to September in 2005 (total of six times). Although other insects were captured, we report the activity-density for the two most abundant carabid beetle species (*A. aenea* and *H. pensylvanicus*). Carabid beetle activity-density in sweet corn was only assessed in 2005.

Weed Seed Predation. In 2005 only, seed predation was assessed in the (1) fallow and in the (4) oat–pea/rye–hairy

Table 1. Timing of management events that occurred in the five management treatments during 2004 and 2005.

System	2004	2005	Management	Implement type
Fallow	12 May	—	Field cultivation	Disk and cultimulch
	24 May	27 May	Field cultivation	Cultimulch
	15 June	29 June	Field cultivation	Cultimulch
	9 July	20 July	Field cultivation	Cultimulch
	17 August	15 August	Field cultivation	Cultimulch
Soybean	12 May	9 May	Field cultivation	Disk and cultimulch
	24 May	20 May	Field cultivation	Cultimulch
	24 May	20 May	Plant soybean	Grain drill
	28 May	27 May	Blind cultivation	Tine weed
	5 June	3 June	Blind cultivation	Tine weed
	20 June	17 June	Inter-row cultivation	S-tine cultivate
	1 July	—	Inter-row cultivation	S-tine cultivate
	1 November	31 October	Harvest soybean grain	Combine
M/BW/C[a]	12 May	5 May	Field cultivation	Disk and cultimulch
	24 May	—	Field cultivation	Cultimulch
	24 May	6 May	Plant yellow mustard	Grass seeder
	9 July	29 June	Mow yellow mustard	Flail mow
	17 July	7 July	Field cultivation	Rotovate and cultimulch
	17 July	7 July	Plant buckwheat	Grass seeder
	5 September	15 September	Mow buckwheat	Flail mow
	11 September	17 September	Field cultivation	Rotovate and cultimulch
	14 September	18 September	Plant canola	Grass seeder
O-P/R-HV	28 April	5 May	Field cultivation	Disk and cultimulch
	30 April	6 May	Plant oats and peas	Grain drill
	9 July	7 July	Mow oats and peas	Rotary mow
	18 August	24 August	Field cultivation	Rotovate and cultimulch
	18 August	29 August	Plant rye and hairy vetch	Grain drill
O/RC	28 April	5 May	Field cultivation	Disk and cultimulch
	29 April	6 May	Plant oats and clover	Grain drill
	9 July	7 July	Mow oats at boot stage	Flail mow
	22 July	19 July	Mow clover	Rotary mow
	2 August	—	Mow clover	Rotary mow
	16 August	—	Mow clover	Rotary mow

[a] Abbreviations: M/BW/C, mustard/buckwheat/canola; O–P/R–HV, oat–pea/rye–hairy vetch; and O/RC, oat/red clover.

vetch management treatments. Weed seed predation was also assessed in sweet corn split-plots that were previously (1) fallow and (4) oat–pea/rye–hairy vetch in 2004. These two management treatments were selected due to extreme differences in vegetative cover (little or none in the fallow and up to 100% in the oat–pea/rye–hairy vetch) during the experiment. In addition, the effect of tillage (no-till vs. conventional as previously described) on weed seed predation was also examined in the sweet corn. Weed seed predation was not assessed in management treatments in 2004 or sweet corn in 2006.

Weed seed predation was assessed using six cages that were randomly positioned along a transect in each plot. Three cages were "closed" consisting of galvanized metal hardware cloth (3.3 by 3.3 cm openings), which prevented access by small mammals and birds, but allowed most invertebrates. Closed cages were cylindrical (14 cm diameter, 9 cm tall) and capped with a clear lid to repel rain. "Open" traps were constructed without metal hardware cloth, and therefore permitted access to vertebrate and invertebrate seed predators. Three 18-cm bolts were used to suspend a 14-cm diameter clear lid to exclude rain. Within each cage a 10-cm Petri dish was placed bottom side up and buried so that the dish was flush with the soil surface. The surface of the Petri dish was covered with double-sided indoor/outdoor carpet tape, and 100 giant foxtail (*S. faberi* Herrm.) seeds were placed on the surface. Approximately 1 to 2 g of field soil was applied to the tape to reduce adhesiveness and better mimic the soil surface. Weed seed predation rate was based on the removal of giant foxtail seed over a 14-d period and was repeated five times during the summer beginning in late May and ending in early September. During the course of the summer, cages were removed then returned to their original position when agronomic management practices (tillage, mowing, sowing, etc.) were performed.

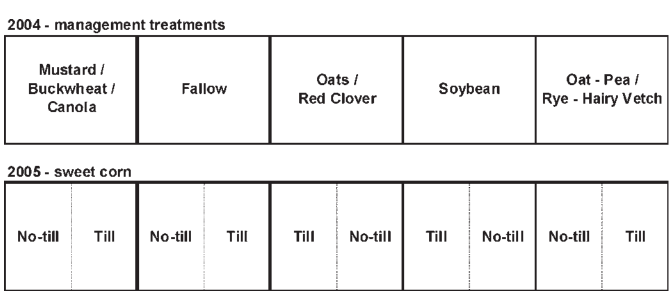

Figure 1. Diagram of one replicate block showing treatments in 2004 and the same plots in 2005 planted to sweet corn with tillage split-plots. In the five management treatments, crops that are separated with a dash "-" were grown in combination, whereas crops separated with a slash "/" were grown in sequence with disturbance (i.e., tillage) between them.

Statistical Analysis. Beetle activity-density was analyzed using repeated measures ANOVA with the mixed procedure in SAS 9.1.[1] Appropriate covariance structures were selected using Akaike Information Criteria to determine the best model. Sampling dates with zero-rich data (e.g., May and June 2005) were excluded from the analysis to meet the assumption of homogenous variance. Activity-density data were square-root transformed and seed predation data were arc-sine transformed prior to analysis to better meet the assumption of

Table 2. Monthly temperature and precipitation at the Russell E. Larson Research Farm during the 2004 and 2005 growing seasons.

	Temperature (°C)		Precipitation (cm)	
Month	2004	2005	2004	2005
May	18.7	12.9	9.5	5.2
June	18.9	21.9	8.1	4.8
July	21.1	23.6	18.5	7.6
August	20.5	22.1	18.2	0.9
September	18.2	19.1	26.9	2.2
October	10.6	11.6	5.5	14.4

homogenous variance and normality. Treatment mean comparisons were made using the Tukey–Kramer method, and significance was set at $P \leq 0.05$, unless otherwise stated. Activity-density sampling did not occur on the same dates each year because of differences in timing of field activities and rainfall. For this reason, activity-density data were not pooled across years.

The effect of disturbance on activity-density of *H. pensylvanicus* in 2005 was tested using linear regression. For each management treatment, the number of days since the last disturbance event was calculated by subtracting the day of the year of each sample by the day of the year of the last disturbance event (tillage, mowing, sowing, harvesting, etc.). For example, if traps were sampled on September 15 (day 258) and the last disturbance was on July 7 (day 188), then the variable "days since the last disturbance event" would be 70.

Results and Discussion

Activity-densities of two carabid beetle species were quantified across a range of management treatments that differed in crop cover diversity, residue production, and degree of disturbance. Weather conditions varied substantially between 2004 and 2005. Total rainfall was near normal for May and June of 2004, but was two to three times above average from July through September (Table 2) and resulted in standing water in the field experiment during some of the sampling times. Fortunately, several activity-density sampling times in 2004 were rain-free. In contrast, crops were under drought stress for much of the season in 2005, with severe drought conditions in August and September. Air temperatures during summer 2004 were near normal and slightly elevated throughout the summer in 2005 (Table 2).

Activity-Density in Management Treatments. In 2004 activity-density of *A. aenea* was low (mean < 1 beetle trap^{-1}) across four of the five management treatments. Activity-density was higher in the mustard/buckwheat/canola system, which accounted for 88% of all *A. aenea* captured (total captured across all systems, $n = 89$) and averaged 4.9 beetles trap^{-1} over the four sampling events. Most beetles were captured in July (71% of total) and no beetles were captured in September, which may have been a result of heavy rains and cooler temperatures (Table 2). In the mustard/buckwheat/canola system, the lack of soil disturbance and dense canopy cover of the flowering yellow mustard in early July may have provided good habitat. Although relatively little is known about *A. aenea* diet preferences, pollen can be an exceptional forage resource for polyphagous carabid beetles (Mullin et al. 2005). In 2005 *A. aenea* activity-density declined to near zero (total across all treatments, $n = 4$).

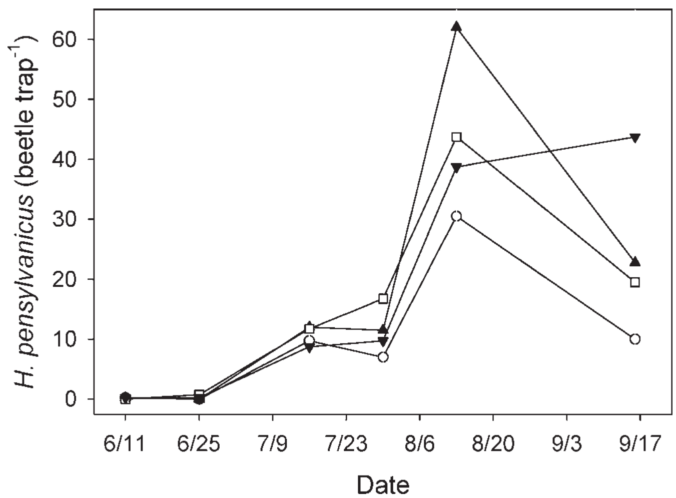

Figure 2. Activity-density of *Harpalus pensylvanicus* in soybean (○), oat–pea/rye–hairy vetch (▲), mustard/buckwheat/canola (□), and oat/red clover (▼) treatments in 2005. Repeated measures ANOVA showed higher activity-density in oat–pea/rye–hairy vetch than soybean ($P = 0.012$). Activity-density was marginally different between mustard/buckwheat/canola and soybean ($P = 0.062$) and oat/red clover and soybean ($P = 0.057$). The fallow treatment did not differ ($P > 0.1$) from the other treatments and thus was excluded from this figure.

In both years, *H. pensylvanicus* was more abundant than *A. aenea* in the study system. In 2004 the average activity-density of *H. pensylvanicus* was 1.9 beetles trap^{-1} (total captured across all systems, $n = 115$); however, we did not detect a difference in activity-density across management treatments in 2004. In 2005 *H. pensylvanicus* activity-density increased greatly (total captured, $n = 1{,}792$) averaging 15.1 beetles trap^{-1} over the six sampling dates and across the five treatments (Figure 2). Peak activity-density for *H. pensylvanicus* occurred in early August in both years of the cover crop treatments and in the sweet corn crop in 2005. The increase in activity-density of *H. pensylvanicus* in 2005 compared to 2004 suggests an important difference in how environmental factors affect populations of these two carabid species. We speculate that weather conditions may have contributed to the large variation in carabid beetle activity-density across years. *Amara aenea* is most active in early spring and the larval stage dominates in late summer (Larochelle and Lariviere 2003). Heavy rains and flooding in late summer 2004 may have caused high mortality for the soil dwelling larvae, resulting in the lower *A. aenea* activity-density in 2005. Greater activity-density of *H. pensylvanicus* in 2005 may have been the result of the drier, warmer weather compared to the wet conditions, particularly during July through September, in 2004.

Repeated measures ANOVA of *H. pensylvanicus* activity-density data from 2005 showed a treatment and date effect, but no interaction between treatment and date. An equal slopes model was fit using an unstructured covariance structure because it provided the best fit to the data. In 2005 *H. pensylvanicus* activity-density was higher ($P = 0.012$) in the oat–pea/rye–hairy vetch treatment (24.0 beetles trap^{-1}) than the soybean treatment (11.7 beetles trap^{-1}) (Figure 2). Mean activity-density of *H. pensylvanicus* was 20.9 beetles trap^{-1} in the mustard/buckwheat/canola treatment and 21.1 beetles trap^{-1} in the oat–red clover treatment, and although beyond our criteria for statistical significance of $P = 0.05$, the

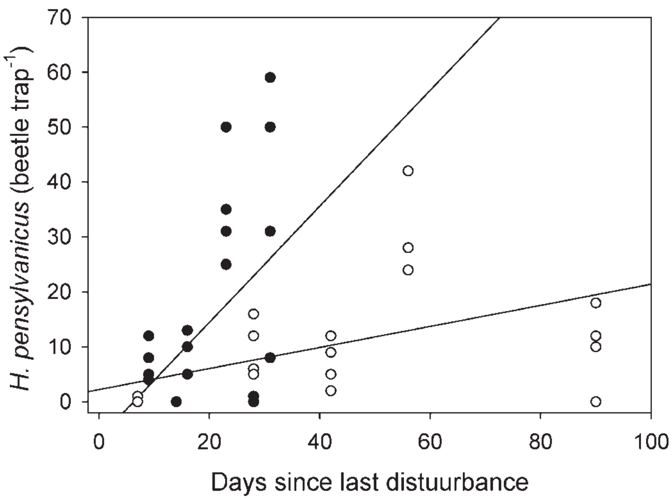

Figure 3. Linear regression of 2005 *Harpalus pensylvanicus* activity-density in fallow (●, $P = 0.024$, $r^2 = 0.21$) and soybean (○, $P = 0.012$, $r^2 = 0.25$) treatments as a function of the duration of time since the last disturbance event.

mustard/buckwheat/canola ($P = 0.062$) and oat–red clover ($P = 0.057$) treatments displayed enough divergence from the soybean treatment that they deserve recognition. Results from *A. aenea* in 2004 and *H. pensylvanicus* in 2005 provide partial support for our first hypothesis and suggest that summer cover crops may provide a more suitable habitat than soybean. Wider row spacing and reduced soil coverage in soybean compared to the other treatments may have contributed to this effect.

In the fallow treatment in 2005, we found a positive correlation between the days since last disturbance and activity-density of *H. pensylvanicus* (slope of 1.6 beetles trap^{-1} day^{-1}, $P = 0.024$) and accounted for 21% of the variance in activity-density (Figure 3). In the soybean treatment, the effect of disturbance was less pronounced (slope of 0.2 beetles trap^{-1} day^{-1}, $P = 0.012$), but accounted for 25% of the variance in activity-density (Figure 3). Despite the significant effect of disturbance in these treatments, this factor was not a significant predictor in the cover crop treatments. This result partially supports our second hypothesis that activity-density will increase with days since last disturbance, and suggests that when surface residue and ground coverage is low, disturbance may play an important role in mediating activity-density of *H. pensylvanicus.*

Activity-Density in Sweet Corn. In 2005 although the management treatments (start year) and sweet corn (second year) experiments were in different fields (c. 0.5 km apart), *A. aenea* was absent in both. Activity-density of *H. pensylvanicus* in sweet corn was similar to that observed in the management experiment. In sweet corn in 2005, *H. pensylvanicus* activity-density averaged 13.5 beetles trap^{-1} and neither the previous management treatment ($P = 0.920$) nor tillage treatment ($P = 0.242$) affected activity-density. As in the management experiment, peak activity-density in the sweet corn occurred in August and declined in September. Prior to planting sweet corn, cover crops from 2004 were either mechanically incorporated with tillage or killed with herbicides in mid-May, so large differences in the amount of plant residue on the soil surface were present early in the season depending on the treatment. The tilled plots were disturbed again in early July with row cultivation; the no-till plots received a postemergent herbicide application. Although management activities were quite different in the no-till and tilled treatments, these differences did not influence beetle activity-density. By mid-July, sweet corn was actively growing and some weeds were present in both the tilled and no-till systems, potentially providing suitable habitat for *H. pensylvanicus.* Overall, early season soil disturbance (till vs. no-till) did not influence mid and late season activity-density of *H. pensylvanicus*, and thus we reject our third hypothesis that activity-density would be higher in no-till plots.

The effects of summer cover crop on activity-density did not persist when the plots were planted to sweet corn in the following year. In other words, a preferred habitat in 1 yr leaves little in the way of a legacy with respect to carabid beetle abundance in the following year. Alternatively, any legacy that a preceding crop might leave is scale-dependent and can be overcome by carabid dispersal. Previous research in a related study has shown that beetles will migrate to new locations that promise greater opportunities for survival (Shearin et al. 2008).

Weed Seed Predation. In the cover crop experiment in 2005, seed predation did not differ between the fallow and the oat–pea/rye–hairy vetch treatments. In these systems, the average seed removal rate was 55%. Similar to activity-density, weed seed removal varied by sampling period ($P = 0.008$). Giant foxtail seed removal ranged from 38 to 63%, with lower levels of predation early in the season, peak predation early in August, then a decline through the end of the sampling period in October. Average seed removal was higher ($P = 0.014$) in open cages (58%) than in closed cages (52%) indicating larger seed predators were accounting for a small increase in seed predation and that invertebrates played a major role in seed removal. Carmona and Landis (1999) found that invertebrates were responsible for 80 to 90% of seed predation in long-term tillage and crop rotations studies that included corn, soybean, and wheat and attributed 10 to 22% of total seed predation to vertebrates. We did not identify the animals responsible for weed seed removal in this study—an important research goal that was recently achieved with the use of videography (Navntoft et al. 2009). Birds were the most important seed predator in that study.

We tested the hypothesis that activity-density would be positively correlated with seed predation using linear regression. Activity-density of *H. pensylvanicus* was positively correlated with seed removal in the fallow ($r^2 = 0.29$; $P = 0.028$) and the oat–pea/rye–hairy vetch ($r^2 = 0.33$; $P = 0.019$) treatments, and at least partially explained variance in removal rates. This result is interesting in light of recent literature suggesting little correlation between carabid beetle activity-density and weed seed predation (Saska et al. 2008). However, carabid beetle activity-density was strongly correlated with common lambsquarters (*Chenopodium album* L.) ($r = 0.94$) and fall panicum (*Panicum dichotomiflorum* Michx.) ($r = 0.96$) seed removal in a separate experiment (Menalled et al. 2007). Furthermore, previous research evaluating the role of other invertebrates in weed population regulation showed that activity-density of *G. pennsylvanicus* and *Allonemobius allardi* (Orthoptera: Gryllidae) explained 66% of the variation in *S. faberi* seed removal (O'Rourke et al. 2006).

In sweet corn in 2005, weed seed predation averaged between 38 and 61% and peaked in late-July to early-August. Similar to our results for activity-density, management treatments (fallow or oat–pea/rye–hairy vetch) in 2004 did not influence seed predation ($P > 0.05$) once the plots were rotated to sweet corn in 2005. Weed seed predation results from this research should be interpreted with caution because predation was not assessed in management treatments in 2004 or sweet corn in 2006, limiting our ability to determine year-to-year variation.

Conclusion

Our findings support an on-going research focus that has begun to elucidate the contribution of seed predation to weed population and community regulation. Improving our understanding of organisms that contribute to weed seed predation brings us one step closer to manipulating these interactions to improve agricultural productivity and decrease the negative effects of current weed management practices. Results generated from this experiment and other on-farm research projects should guide mechanistic research aimed at developing strategies that accelerate the turnover of weed seeds prior to being incorporated in the soil seed bank (Holland et al. 2008). Further research strategies for actively manipulating weed seed predators is needed to move this form of biological control toward grower integration.

Sources of Materials

[1] SAS version 9.1, SAS Institute, Inc., Cary, NC.

Acknowledgments

We would like to thank Steven Mirsky and Eric Gallandt for assistance with this experiment and acknowledge the U.S. Department of Agriculture Northeast Region Integrated Pest Management and Sustainable Agriculture Research and Education programs for financial support of this research.

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Received May 6, 2010, and approved September 2, 2010.