

Impact of agricultural management on carabid communities and weed seed predation

Fabián D. Menalled^{a,*}, Richard G. Smith^a, Joseph T. Dauer^b, Tyler B. Fox^c

^a Department of Land Resources and Environmental Sciences, Montana State University, Bozeman, MT 59717, USA

^b Department of Crop and Soil Sciences, Pennsylvania State University, University Park, PA 16802, USA

^c Department of Entomology, Michigan State University, East Lansing, MI 48824, USA

Received 8 December 2005; received in revised form 11 April 2006; accepted 25 April 2006

Available online 12 June 2006

Abstract

This study evaluated the relationship between diversity and activity-density of carabid beetles and invertebrate weed seed predation in conventional, no-till, and organic management systems in the Midwest USA. Carabid beetles were sampled with pitfall traps and invertebrate seed predation rates of fall panicum and common lambsquarters were assayed with exclosure cages. Total carabid activity-density was over two times higher in the conventional systems compared to the no-till and organic management systems. In contrast, activity-densities of seed-predating carabid species were over three times higher in the no-till compared to the conventional and organic systems. Carabid diversity was higher in the no-till and organic systems compared to the conventional system, and a multivariate analysis showed that carabid community structure was distinct among the three systems. Predation of fall panicum and common lambsquarters seeds was often over two times higher in the no-till compared to the conventional and organic systems, and there was a strong correlation ($r > 0.94$) between seed removal rates and the total number of carabid seed predators captured in each system.

© 2006 Elsevier B.V. All rights reserved.

Keywords: Cropping systems; Beetles; Tillage; Organic agriculture; Integrated weed management

1. Introduction

Post-dispersal seed predation represents a significant source of weed mortality that, in combination with other factors, may contribute to effective weed suppression with reduced reliance on synthetic chemical control practices (Liebman and Gallandt, 1997; Menalled et al., 2000; Davis et al., 2003; Gallandt et al., 2005; Westerman et al., 2005).

Carabid beetles (Coleoptera: Carabidae) are significant generalist predators in annual row-crop agricultural systems (Lee et al., 2001; Harrison and Regnier, 2003; Gallandt et al., 2005) and several carabid species consume substantial numbers of weed seeds under laboratory and field conditions (Lund and Turpin, 1977; Harrison and Regnier, 2003). Despite the growing interest in carabids and their potential

role in weed suppression in agricultural systems (Lee et al., 2001), the relative importance of cropping systems on carabid communities and weed seed predation is still not well understood (Westerman et al., 2003).

Several studies have shown that individual management practices such as tillage, crop type, fertilizer, and pesticide inputs could have substantial impacts on weed seed predation (see Menalled et al., 2006 for a review). This study assessed carabid beetle diversity and activity-density in three crop management systems: conventional, no-till, and organic. In addition, rates of weed seed removal were quantified in these three systems using two weed species common to Midwest USA agricultural systems: common lambsquarters (*Chenopodium album* L.) and fall panicum (*Panicum dichotomiflorum* Michx.). These weeds were selected because they were found to be key species characterizing plant communities of conventional, no-till, and organic management systems (Menalled et al., 2001).

* Corresponding author. Tel.: +1 406 9944783; fax: +1 406 9943933.

E-mail address: Menalled@montana.edu (F.D. Menalled).

Specifically, common lambsquarters dominated the organic systems and fall panicum was commonly observed in the conventional and the no-till system. Therefore, a goal of this study was to evaluate if differential seed predation of these two weed species could account for the patterns observed in Menalled et al. (2001). The specific hypotheses were (1) carabid densities and community composition would differ among the three management systems and (2) for each weed species, seed removal rates would differ among the three management systems.

2. Materials and methods

This study was conducted from 23 June to 20 September 2000 at the W.K. Kellogg Biological Station (KBS) Long Term Ecological Research (LTER) project in Agroecology in Hickory Corners, Michigan, USA. Soils at the KBS LTER are primarily Kalamazoo silt loam (Typic hapludalfs) with sand, silt, clay content of 43, 40, and 17%, respectively (Robertson et al., 1997). The site was principally in continuous corn production for more than 20 years prior to the establishment of the LTER project in 1989. Strip-cropping of wheat and corn occurred for 2 years in the 1970s and alfalfa was grown on the western side of the study site for 4 years in the 1980s.

Agronomic treatments at the KBS LTER consisted of four management systems: (1) conventional (high external chemical input, tilled), (2) no-till (high external chemical input, no tillage), (3) organic (no external chemical input, tilled), and (4) reduced input system (low chemical input, tilled). Due to the labor-intensive nature of seed predation studies and the similarities between the organic and the reduced input systems, only the conventional, no-till, and organic systems were compared in this study. Since 1990, the organic system has been in an annual rotation of corn–soybean–winter wheat (*Triticum aestivum* L.), with the winter wheat phase underseeded with red clover (*Trifolium pratense* L.) at a rate of 13 kg ha⁻¹. From 1990 to 1993 the conventional and no-till systems were planted to a corn–soybean rotation and from 1994 on to a corn–soybean–wheat rotation in phase with the organic system. Thus, the systems had completed two (conventional and no-till) and three (organic) full rotations prior to the study.

Primary tillage in the conventional and organic systems consisted of moldboard plowing from 1990 until 1997 and chisel plowing in 1999 and 2000. Fertilizer in the conventional and no-till systems was applied at planting (as NH₄NO₃ until 1995, and as 28% UAN after that time) at a rate of 123 kg N ha⁻¹ in corn and 56 kg N ha⁻¹ in winter wheat. Herbicides were used to manage weeds in the conventional and no-till systems and applied at rates recommended for the region. During the study period, glyphosate (420 g ai ha⁻¹) was applied in the no-till system and sethoxydim (110 g ai ha⁻¹) and bentazon (340 g ai ha⁻¹) were applied in the conventional and no-till system for weed control. No

insecticides were applied in the site since the initiation of this long-term study in 1989.

At the time of the study, the entire site was planted to soybean. Soybean was planted in 76 cm rows to facilitate cultivation in the organic system and in 18.75 cm rows in the conventional and no-till systems. Each management system was replicated six times in 1 ha plots in a randomized block design. Within each block, plots were separated by 10 m wide, periodically mowed, grassy strips.

Carabid activity-density and community composition were sampled by placing five pitfall traps (12 cm diameter and 16 cm high) in each of the six plots per management system treatment. The openings of the pitfall traps were flush with the soil surface and traps were filled with approximately 50 ml of a 10% ethylene glycol solution as preservative. Traps were left open for 6 days over seven sampling periods from 23 June to 26 September 2000. After each sampling period, the contents of each trap were emptied and the carabid species identified according to Lindroth's (1969) key. Traps were covered with lids between sampling periods.

2.1. Post-dispersal weed seed predation

Invertebrate weed seed predation was measured five times between 4 August and 7 September 2000, which corresponds to the peak of natural seed dispersal period in the Midwest USA. Seed predation was quantified using the method described in Menalled et al. (2000). Fifty seeds of each weed species were placed on separate 11 cm long × 14 cm wide × 0.5 cm high waterproof pads (3-M Metallic Finishing Pad) level with the soil surface. Fifty seeds per pad (3246 seeds m⁻²) was selected to resemble natural occurring seedbank densities which in Michigan corn, soybean, and wheat fields ranges between 1873 and 5000 seeds m⁻² (Renner et al., 1998).

Individual pads were placed in two types of wire enclosure cages (34 cm long × 34 cm wide × 7 cm high) with the bottom flush with the soil surface: ones that permitted access to the seeds by invertebrate but not vertebrate-sized seed predators (mesh size = 1.25 cm²) and others that restricted access by both invertebrate and vertebrate seed predators (mesh size = 0.1 cm²). Cages that restricted access by both invertebrates and vertebrates served as controls and allowed estimation of the ability to recover seeds left on pads. Within each plot, four cages (two weed species by two enclosure treatments) were placed at each of five sampling points for a total of 120 cages per system. During each sampling period, seeds were left in the field for 5 days, after which time seed pads were collected and the number of seeds remaining on pads were counted in the laboratory.

2.2. Statistical analyses

For each pitfall trap, the number of individuals and species of carabid beetles captured during the 6 days of each trapping interval was recorded and captures were pooled across plots.

Table 1

Carabid beetle (Carabidae) activity-density and diversity in three agricultural management systems at the W.K. Kellogg Biological Station Long Term Ecological Research project in Michigan, USA

	Conventional	No-till	Organic
Number of individuals			
Total	143.8 (35.1) a	67.3 (29.7) b	57.2 (8.7) b
Seed predators only	6.2 (1.4) a	21.8 (6.3) b	6.2 (1.6) a
Diversity			
Number of species	8.6 (0.6)	9.7 (1.6)	7.8 (1.2)
<i>E</i> (evenness)	0.32 (0.08) b	0.76 (0.06) a	0.67 (0.07) a
<i>H'</i> (Shannon diversity)	0.68 (0.14) b	1.63 (0.10) a	1.33 (0.18) a
<i>D</i> (Simpson diversity)	0.28 (0.08) b	0.72 (0.03) a	0.61 (0.06) a

Samples were obtained by pitfall trapping between 23 June and 20 September 2000. Values are means \pm 1 S.E. ($n = 6$). Within a row numbers followed by the same letter are not significantly different at $P \leq 0.05$ (LSD test).

Differences in activity-density of all carabid beetles, activity-density of carabid beetles that are known to predate weed seeds, total number of species, diversity, and evenness were analyzed as a single factor (management system) randomized complete block design ANOVA using SAS[®] Version 9.0 (SAS/STAT, 2002).

Three indices were used to quantify carabid beetle community characteristics: (1) Shannon diversity: $H' = -\sum p_i(\log p_i)$, where p_i is the proportion of individuals accounted by species i per sample (Magurran, 1988); (2) evenness: $E = H'/\ln(\text{species richness})$ (Pielou, 1969); (3) and Simpson's index of diversity: $D = 1 - \sum p_i^2$ (McCune and Grace, 2002). These indices were estimated using the PC-ORD multivariate statistical software program (McCune and Mefford, 1999).

The effect of management system on carabid beetle community composition was further explored by means of a multivariate Nonmetric Multidimensional Scaling (NMS) ordination utilizing the Sorensen distance measure and 400 iterations. For each species, total capture in the five pitfall traps per plot was pooled and plots were ordinated using the PC-ORD multivariate statistical software program (McCune and Mefford, 1999). The first two most explanatory axes were used to graphically display ordination scores for the plots in carabid species space and for the carabid species data in plot space. Spearman correlation coefficients were used to examine relationships between the first two NMS axes and the management treatments and carabid community structure (i.e. activity-density, number of species, diversity).

For each weed species, the percentage of weed seeds removed from each individual pad was compared across management systems, enclosure type, and sampling period by means of a repeated measures analysis of variance. All analyses were conducted using SAS[®] Version 9.0 (SAS/STAT, 2002). To increase data normality and homoscedasticity, percentage weed seed removal was arcsin transformed prior to analysis. Treatment means were separated with a protected LSD test at the $P < 0.05$ level of probability.

3. Results

A total of 1609 individuals comprising 33 species were collected in the three management systems. Three species, *Poecilus chalcites* (Say), *Poecilus lucumblundus* (Say), and *Anisodactylus rusticus* (Say) made up 82.5% of the total capture. However, only one omnivorous species, *A. rusticus* accounted for more than 2% of total capture.

Overall, there were more beetles captured in the conventional compared to organic and no-till systems (Table 1). *P. chalcites* was dominant in the conventional and organic systems, making up 87 and 56%, respectively, of the total number of individuals (Table 2). In contrast two species, *P. lucumblundus* and *A. rusticus* were dominant in the no-till system, together making up 62% of the total capture.

Although more carabids were collected in the conventional system than in the no-till and organic systems, more weed seed predators were found in the no-till system (Table 1). Seed predators made up 32% of the total individuals captured in the no-till system, with the majority being *A. rusticus*. In contrast, seed predators made up only 10% of the individuals in the organic system and 4% in the conventional system (Table 2).

While the number of carabid species was similar across the three management systems, the diversity and evenness of carabid beetle communities was over two times greater in the no-till and organic systems than in the conventional system (Table 1). The NMS ordination of management systems provided visual confirmation of the differences in carabid community structure between the three systems. The first NMS axis separated the three management systems and was strongly correlated ($P < 0.001$) with the abundance of seed predators, the two diversity indices and the evenness index (Table 3). The second NMS axis further separated plots within the no-till system and was most strongly correlated ($P < 0.001$) with the two diversity indices and the number of seed predators. NMS ordination of carabid species indicated that while seed- and non-seed predating species were associated with

Table 2

Total species abundance of carabid beetles (Carabidae) sampled in three agricultural management systems at the W.K. Kellogg Biological Station Long Term Ecological Research project in Michigan, USA

Carabid beetle species	Omnivorous	Management system		
		Conventional	No-till	Organic
<i>Poecilus chalcites</i> (Say)	No	749	19	192
<i>Poecilus lucublandus</i> (Say)	No	35	175	77
<i>Anisodactylus rusticus</i> (Say)	Yes	1	74	6
<i>Harpalus herbivagus</i> (Say)	No	5	30	8
<i>Harpalus pensylvanicus</i> (DeGeer)	Yes	13	15	12
<i>Amara aenea</i> (DeGeer)	Yes	2	32	1
<i>Agonum placidum</i> (Say)	No	15	3	10
<i>Anisodactylus santaecrusis</i> (Fabricius)	Yes	9	6	2
<i>Clivina bipustulata</i> (Fabricius)	No	9	2	4
<i>Clivina impressifrons</i> (LeConte)	Yes	4	0	11
<i>Cyclotrachelus sodalis</i> (LeConte)	No	1	13	1
<i>Pterostichus melanarius</i> (Illiger)	No	4	4	5
<i>Agonum cupripenne</i> (Say)	No	2	8	2
<i>Acupalpus partarius</i> (Say)	No	4	5	0
<i>Harpalus affinis</i> (Schränk)	Yes	2	1	4
<i>Stenolophus comma</i> (Fabricius)	Yes	5	0	0
<i>Calleida punctata</i> (Fabricius)	No	0	5	0
<i>Selenophorus pedicularius</i> (Dejean)	No	0	3	1
Other (seed predators) ^a		0	3	5
Other (non-seed predators)		3	6	1
Total individuals		863	404	342

Samples were obtained by pitfall trapping between 23 June and 20 September 2000.

^a Include *Amara cupreolata* Putz., *Harpalus compars* LeConte, and *Stenolophus rotundicollis* (Haldeman).

the conventional and organic systems, seed predating species, such as *A. rusticus* and *Amara aenea* (DeGeer) were associated with the no-till system. Together, these two species accounted for 70% of all seed predators captured during this study.

3.1. Weed seed removal

More seeds were removed from the vertebrate exclosures than from control cages (common lambsquarters:

Table 3

Spearman correlation coefficients between management and ground beetle community variables and the first two axes of an NMS ordination

Variable	Axis 1	Axis 2
Management system	0.866***	0.669**
No. of individuals	0.530*	−0.346
No. of seed predators	−0.684**	0.562*
Number of species	−0.017	0.092
<i>E</i> (evenness)	−0.703**	0.523*
<i>H'</i> (Shannon diversity)	−0.863***	0.597**
<i>D</i> (Simpson diversity)	0.814***	0.598**

Carabid beetle samples were obtained by pitfall trapping between 23 June and 20 September 2000 in three agricultural management systems at the W.K. Kellogg Biological Station Long Term Ecological Research project in Michigan, USA; *n* = 18.

* *P* < 0.05.

** *P* < 0.001.

*** *P* < 0.0001.

$F_{1,113} = 70.92$, $P < 0.0001$; fall panicum: $F_{1,103} = 159.22$, $P < 0.0001$). A large number of weed seed coats were observed on pads, suggesting that seed removal was due primarily to predation. Removal rates of common lambsquarters and fall panicum seed varied during the course of the study and were slightly higher for fall panicum than lambsquarters (Fig. 1). While seed removal rates remained more or less constant during the course of this study in the no-till system, removal rates decreased through time in the conventional and organic system. The repeated measures ANOVA indicated that predation rates of both species were affected by management system (common lambsquarters: $F_{2,113} = 11.65$, $P < 0.0001$; fall panicum: $F_{2,103} = 27.79$, $P < 0.0001$), sampling date (common lambsquarters: $F_{4,452} = 60.62$, $P < 0.0001$; fall panicum: $F_{4,412} = 40.92$, $P < 0.0001$), and their interaction (common lambsquarters: $F_{8,452} = 9.74$, $P < 0.0001$; fall panicum: $F_{8,412} = 9.50$, $P < 0.0001$). For fall panicum, more seeds were removed in the no-till system compared to the conventional and organic systems in all sampling periods (Fig. 1A). For common lambsquarters, removal rates were higher in the no-till compared to the conventional and organic system in the last two sampling periods only (30 August and 6 September; Fig. 1B). Pooled across management systems and sampling periods, there was a strong correlation between the total number of seed predators captured and the percentage seed removed for both fall panicum ($r = 0.96$) and common lambsquarters ($r = 0.94$).

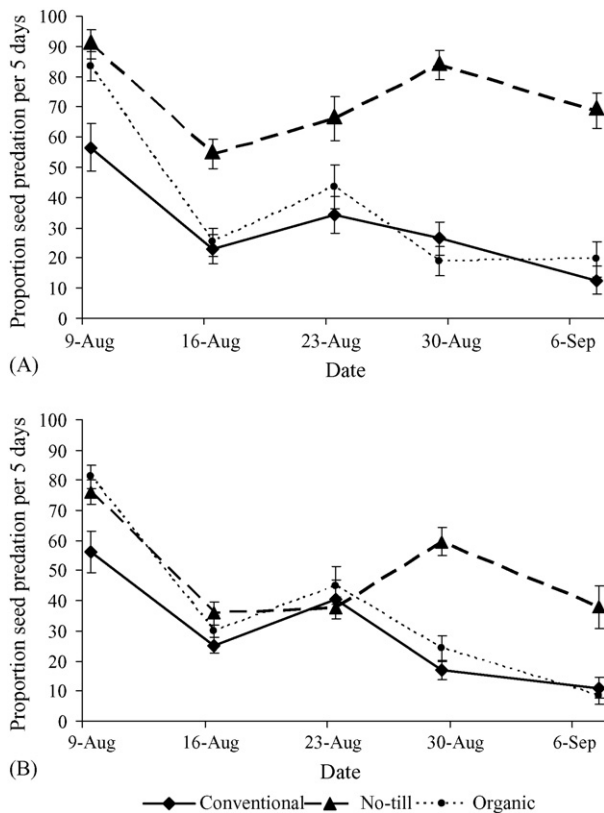


Fig. 1. Proportion of (A) fall panicum and (B) common lambsquarters seeds removed by invertebrate seed predators per 5 days in three agricultural systems at the Long Term Ecological Research site project in agricultural ecology at the W.K. Kellogg Biological Station, Michigan USA (means $1 \pm \text{S.E.}$, $n = 6$).

4. Discussion

The differences in carabid community composition and diversity between the three management systems support the findings that agronomic practices can have significant impacts on generalist predator communities (Thomas et al., 1992; Kromp, 1999). Tillage and herbicide applications reduced carabid abundance and diversity through direct mortality and disruption of overwintering sites (Kromp, 1999; Purvis and Fadl, 2002) and through a decrease in the availability of suitable prey and alternative food sources (Brust, 1990; Chiverton and Sotherton, 1991). The relatively high densities of the native spring breeder *P. chalcites* in both the conventional and organic systems, which were annually tilled, may reflect a tolerance in this particular species to intensive soil disturbance.

The generality of the relationship between tillage intensity and activity-density of omnivorous carabids could have important implications for ecologically based weed management in no-till systems, as these systems often rely heavily on herbicides (but see Cromar et al., 1999). Additional increases in predator abundance and predation rates in these systems might be achieved through maintenance of beetle banks (MacLeod et al., 2004) or

refuge habitat (Lys and Nentwig, 1992; Carmona and Landis, 1999).

For each weed species, seed predation differed across management systems. Moreover, there was a very high correlation between seed predator activity-density and overall weed seed removal. This result is particularly significant because it further supports the notion that increasing predator abundance may lead to enhanced weed suppression in many agricultural systems (Westerman et al., 2005; Gallandt et al., 2005). It also highlights the important linkage between agronomic management practices and generalist predator activity. Other studies have found similar correlations between natural enemy abundance and predation rates of insect pests (Menalled et al., 1999; Collins et al., 2002; Frank and Shrewsbury, 2004). Collectively, these studies provide positive evidence of a shift in pest control from chemical-based to biotic-based that is hypothesized to accompany reductions in the intensity of management practices and increases in cropping-system diversity (Altieri, 1999).

Acknowledgements

We would like to thank D. Landis, K. Gross, A. Gould, A. Costamagna, and J. Lee for their help in conducting this experiment. L. Rew, P. Marino and the Mortensen lab (Pennsylvania State University) provided helpful comments on an earlier draft of this manuscript. Support for this research was provided by the NSF Long-Term Ecological Research Program at the Kellogg Biological Station and by the Michigan Agricultural Experiment Station. JTD was supported by the NSF Research Experiences for Undergrads (REU) program.

References

- Altieri, M.A., 1999. The ecological role of biodiversity in agroecosystems. *Agric. Ecosyst. Environ.* 74, 19–31.
- Brust, G.E., 1990. Direct and indirect effects of 4 herbicides on the activity of carabid beetles (Coleoptera: Carabidae). *Pesticide Sci.* 30, 309–320.
- Carmona, D.M., Landis, D.A., 1999. Influence of refuge habitats and cover crops on seasonal activity-density of ground beetles (Coleoptera: Carabidae) in field crops. *Environ. Entomol.* 28, 1145–1153.
- Chiverton, P.A., Sotherton, N.W., 1991. The effects on beneficial arthropods of the exclusion of herbicides from cereal crop edges. *J. Appl. Ecol.* 28, 1027–1039.
- Collins, K.L., Boatman, N.D., Wilcox, A., Holland, J.M., Chaney, K., 2002. Influence of beetle banks on cereal, aphid predation in winter wheat. *Agric. Ecosyst. Environ.* 93, 337–350.
- Cromar, H.E., Murphy, S.D., Swanton, C.J., 1999. Influence of tillage and crop residue on postdispersal predation of weed seeds. *Weed Sci.* 47, 184–194.
- Davis, A.S., Dixon, P.M., Liebman, M., 2003. Cropping system effects on giant foxtail (*Setaria faberi*) demography. II. Retrospective perturbation analysis. *Weed Sci.* 51, 930–939.
- Frank, S.D., Shrewsbury, P.M., 2004. Effect of conservation strips on the abundance and distribution of natural enemies and predation of *Agrotis ipsilon* (Lepidoptera: Noctuidae) on golf course fairways. *Environ. Entomol.* 33, 1662–1672.

- Gallandt, E.R., Molloy, T., Lynch, R.P., Drummond, F.A., 2005. Effect of cover-cropping systems on invertebrate seed predation. *Weed Sci.* 53, 69–76.
- Harrison, S.K., Regnier, E.E., 2003. Postdispersal predation of giant ragweed (*Ambrosia trifida*) seed in no-tillage corn. *Weed Sci.* 51, 955–964.
- Kromp, B., 1999. Carabid beetles in sustainable agriculture: a review on pest control efficacy, cultivation impacts and enhancement. *Agric. Ecosyst. Environ.* 74, 187–228.
- Lee, J.C., Menalled, F.D., Landis, D.A., 2001. Refuge habitats modify impact of insecticide disturbance on carabid beetle communities. *J. Appl. Ecol.* 38, 472–483.
- Liebman, M., Gallandt, E.R., 1997. Many little hammers: ecological management of crop–weed interactions. In: Jackson, L.E. (Ed.), *Ecology in Agriculture*. Academic, San Diego, CA, pp. 291–343.
- Lindroth, C.H., 1969. The Ground Beetles (Carabidae, excl. Cicindelinae) of Canada and Alaska, Parts 1–6. *Opuscula Entomologica*, Entomologiska Sällskapet, Lund, Sweden.
- Lund, R.D., Turpin, F.T., 1977. Carabid damage to weed seeds found in Indiana cornfields. *Environ. Entomol.* 6, 695–698.
- Lys, J.A., Nentwig, W., 1992. Augmentation of beneficial arthropods by strip management. *Oecologia* 92, 373–382.
- MacLeod, A., Wratten, S.D., Sotherton, N.W., Thomas, M.B., 2004. Beetle banks' as refuges for beneficial arthropods in farmland: long-term changes in predator communities and habitat. *Agric. For. Entomol.* 6, 147–154.
- Magurran, A.E., 1988. *Ecological Diversity and Its Measurement*. Princeton University Press, Princeton.
- McCune, B., Grace, J.B., 2002. *Analysis of Ecological Communities*. MjM Press, Gleneden Beach, OR, USA.
- McCune, B., Mefford, M.J., 1999. *PC-ORD. Multivariate Analysis of Ecological Data*, Version 4. MjM Software Design, Gleneden Beach, OR, USA.
- Menalled, F.D., Lee, J.C., Landis, D.A., 1999. Manipulating carabid beetle abundance alters prey removal rates in corn fields. *Biocontrol* 43, 441–456.
- Menalled, F.D., Marino, P.C., Renner, K.A., Landis, D.A., 2000. Post-dispersal weed seed predation in Michigan crop fields as a function of agricultural landscape structure. *Agric. Ecosyst. Environ.* 77, 193–202.
- Menalled, F.D., Gross, K.L., Hammond, M., 2001. Weed aboveground and seedbank community responses to agricultural management systems. *Ecol. Appl.* 11, 1586–1601.
- Menalled, F., Liebman, M., Renner, K., 2006. The ecology of weed seed predation in herbaceous crop systems. In: Batish, D. (Ed.), *Handbook of Sustainable Weed Management*. The Haworth Press, Inc., Binghamton, NY.
- Pielou, E.C., 1969. *An Introduction to Mathematical Ecology*. Wiley/Interscience, New York, NY, USA.
- Purvis, G., Fadl, A., 2002. The influence of cropping rotations and soil cultivation practice on the population ecology of carabids (Coleoptera: Carabidae) in arable land. *Pedobiologia* 46, 452–474.
- Renner, K.A., Halstead, S.J., Gross, K.L., 1998. Weed seed bank dynamics at the LTER (long term ecological research) agroecosystem site. In: *Abstr. 1998 Meeting Weed Sci. Soc. Am.*, Chicago, IL.
- Robertson, G.P., Klingensmith, K.M., Klug, M.J., Paul, E.A., Crum, J.R., Ellis, B.G., 1997. Soil resources, microbial activity, and primary production across and agricultural ecosystem. *Ecol. Appl.* 7, 158–170.
- SAS/STAT, 2002. *Users Manual*, Version 9.0. SAS Institute, Cary, NC, USA.
- Thomas, M.B., Wratten, S.D., Sotherton, N.W., 1992. Creation of island habitats in farmland to manipulate populations of beneficial arthropods—predator densities and species composition. *J. Appl. Ecol.* 29, 524–531.
- Westerman, P.R., Wes, J.S., Kropff, M.J., Van der Werf, W., 2003. Annual losses of weed seeds due to predation in organic cereal fields. *J. Appl. Ecol.* 40, 824–836.
- Westerman, P., Liebman, M., Menalled, F.D., Heggenstaller, A.H., Hartzler, R.G., Dixon, P.M., 2005. Are many little hammers effective?—velvetleaf (*Abutilon theophrasti*) population dynamics in two- and four-year crop rotation systems. *Weed Sci.* 53, 382–392.