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Weed seed loss due to predation in Michigan maize fields

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Abstract

The influence of weed seed predation by invertebrates and vertebrates was examined in relation to distance from hedgerows in maize fields of southwestern Michigan. Experiments were conducted in spring and winter and included five common weed species, i.e., velvet-leaf (*Abutilon theophrasti*), redroot pigweed (*Amaranthus retroflexus*), common lamb's-quarters (*Chenopodium album*), fall panicum (*Panicum dichotomiflorum*), and yellow foxtail (*Setaria lutescens*). In the spring post-tillage study, treatments excluding invertebrates, vertebrates, invertebrates + vertebrates plus no exclusion controls were established at 5 and 100 m from the hedgerow. Seeds were placed into the field in trays filled with sterilized soil at low densities to avoid creating a 'super stimulus' for seed predators. The trays were placed in the field for 3–4 weeks and then placed in a heated greenhouse and seed loss was estimated from the number of seedlings that emerged. The design of the winter study was similar except that only control and vertebrate exclusion treatments were used and seeds were left in the field from December to mid-April. Significant differences among exclusion treatments were found in spring in terms of seed loss. Seed loss was lowest in the treatments that excluded both vertebrates + invertebrates and highest under no exclusion. There was some evidence of preferential predation by vertebrates upon seeds of *A. retroflexus* and *C. album*. In winter, significant seed predation by vertebrates on all species except *A. retroflexus* were detected. In both seasons, seed predation was highly patchy among and within fields and there was no consistent effect of distance from hedgerow. © 1997 Elsevier Science B.V.

Keywords: Agroecosystems; Hedgerow; Landscape structure; Weed seed predation

1. Introduction

Non-crop habitats are often assumed to be a major source of weeds invading adjacent crop fields through seed rain (Cavers and Benoit, 1989). Although long-distance dispersal by weeds into crop fields is infrequent (Hume and Archibold, 1986; Marshall, 1988a,b, 1989; Marshall and Hopkins, 1990), there is evidence that seed rain from non-crop habitats can contribute significantly to the seed bank of crop fields (Archibold and Hume, 1983). However, non-crop habitats, also provide shelter and food for many potential seed predators, such as mammals (Pollard and Relton, 1970), birds (Lewis, 1969; Best, 1983) and insects (Thomas et al., 1991, 1992). The abun-

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dance and diversity of both birds (Best, 1983; Castrale, 1987) and small mammals (Castrale, 1987) has been shown to be higher in non-crop environments than in adjacent crop fields. Carabid beetles, which are important seed consumers in temperate agroecosystems (Best and Beegle, 1977; Brust and House, 1988; Johnson and Cameron, 1969; Kjellsson, 1985; Lund and Turpin, 1977; Manley, 1992) are also known to use non-crop habitats as over-wintering sites (Descender, 1982; Southerton, 1984, 1985; Thomas et al., 1991, 1992; Wallin, 1985, 1986).

A field experiment was conducted to determine whether adjacent non-crop habitats enhanced biological control of weeds in Michigan maize fields, focusing on the effect of distance from hedgerows on seed predation. Hedgerows are increasingly removed from agroecosystems to increase field size and it was assumed that weed seed loss would be greater close to hedgerows than distant from hedgerows. The experiments were conducted in spring following tillage and over-winter, because seasonal effects on predation associated with management were expected. Tillage in spring exposes seeds to predation, but also triggers seed germination whereas over-winter seed predation by vertebrates is likely to be high because of scarce food resources (Best, 1983).

2. Methods

Five species of common Michigan agricultural weeds, i.e., velvet-leaf (*Abutilon theophrasti* Medicus), redroot pigweed (*Amaranthus retroflexus* L.), common lamb's-quarters (*Chenopodium album* L.), fall panicum (*Panicum dichotomiflorum* Michaux.) and yellow foxtail (*Setaria lutescens* (L.) Beauv.) were considered. The average seed size for the five species was: *A. theophrasti* = 3–3.5 mm, *S. lutescens* = 2.5–3 mm, *P. dichotomiflorum* = 1.5–1.8 mm, *C. album* = 1–1.5 mm and *A. retroflexus* = 1–1.2 mm (Radford et al., 1968). We had no a priori reason to expect preferences among these species by different types of seed predators and so chose a broad range of weed species to account for this uncertainty. Seeds used in this study came from field populations harvested the previous fall, except for *S. lutescens* which had been collected 2 years previously, but did not germinate in this experiment and was excluded from the analyses of the spring experiment.

2.1. Seed predation after spring tillage

This experiment was conducted in four conventional tillage and one no tillage maize field having a hedgerow on the south, east or west side on the Diehl farm in Dansville, MI, USA (42°50″N, 84°30″W). In each field, three parallel transects perpendicular to the hedgerow were established, separated from one another by 25 m. Hedgerows were an unmanaged row of trees or shrubs enclosing or separating fields (Forman and Baudry, 1984). At 5 and 100 m along each transect (six replicates), four treatments were established which excluded different types of seed predators: vertebrates only, invertebrates only, invertebrate + vertebrate, and a control plot (no exclusion). To exclude vertebrates, plots were covered with 50 cm × 50 cm, 12 cm high 0.67 cm hardware cloth cages sunk ≈ 5 cm into the soil. Invertebrates were excluded by placing a 60 cm diameter circular ring of plastic garden edging painted with fluon™, a teflon-like material that prohibits insects from crawling up vertical surfaces (Mittelbach and Gross, 1984), 5 cm into the soil. Both vertebrates and invertebrates were excluded by containing the vertebrate exclusion cages within the circular invertebrate exclosures. Any invertebrate observed within the exclosures were removed. The four treatments were distributed at random in a linear array parallel to hedgerows and separated 1 m from each other.

A 32 × 20 cm flat filled with steam sterilized field soil was placed in the center of each exclusion or control plot and sunk into the soil so that 1 cm of the edge was raised above the soil surface. Twenty-five seeds of each species (a total of 125 seeds) were scattered on the surface of the sterilized soil. All cages and exclosures were placed into the fields within 1 week after maize planting (20 May–7 June). After 3–4 weeks, flats were removed from the fields and brought to a heated greenhouse at Michigan State University where they were watered. The number of seedlings of each species that emerged in each

flat were recorded 3 times at ≈ 2 week intervals, i.e., lower emergence = higher seed predation. Seedlings were removed at each census and the surface 1 cm of soil of each flat was stirred to enhance germination of remaining seeds. After 6 weeks, all flats were removed from the greenhouse to a cold chamber (4°C) for 1 month to break dormancy of any remaining ungerminated seeds, and then returned to the greenhouse. The top 1 cm of soil on each flat was turned over to enhance germination and the number of seedlings that emerged was recorded 2 weeks later.

2.2. Over-winter seed predation

The second experiment examined over-winter seed predation in four of the five maize fields used in spring. Following crop harvest (December), four flats filled with sterilized field soil were placed at each site as described above, the soil being sterilized with methyl bromide to reduce soil odor, as caused by steam sterilization and subsequent disruption of the experiment by raccoons (*Procyon lotor*). Two of the flats were covered with vertebrate exclusion cages as described above and two were left uncovered as controls. Vertebrate exclosures only were used as invertebrates were not expected to be active over-winter. The position of both treatments at each site was as for the spring experiment. All seed used in this experiment were freshly harvested, 25 seed of each species (a total of 125 seeds) being placed on the surface of the sterilized soil. Flats remained in the field until mid-April prior to plowing. After removal from the field, the flats were placed in a heated greenhouse and kept well watered over the next 4 months. Seedlings of each species that emerged in the flats were recorded and removed at ≈ 2-week intervals. After each census, the surface 1 cm of soil was stirred to enhance germination of any remaining seeds. Flats were not exposed to cold treatment because cold-induced dormancy would have already been broken by exposure to winter temperatures and the results from the spring study showed that cold treatment only increased germination by $< 5\%$.

Data were analyzed using a split–split-plot design, with field split on position (edge vs. interior) and the second split on exclusion treatment (Montgomery, 1991). Because seeds of all species were scattered together in each treatment weed species were not independent in the experimental design and species differences in predation loss could not be legitimately examined. However, we present the species data to illustrate the magnitude of potential species differences in predation loss. MANOVA was used for data analysis to account for the potential effect of differential seed predation, and MANOVA optimizes the r^2, making it more likely to find significant differences among treatments. ANOVA was also used, with weed species pooled, to compare to the MANOVA results. No differences between the two analyses being observed, results of MANOVA only are presented.

In the analysis of both experiments, seedling emergence was used as the response variable, i.e., lower emergence = higher seed predation. Ungerminated seeds were not counted as it was not possible to recover seeds from the soil. Seedling emergence was low across all treatments including the treatment in which we expected the most emergence (vertebrate + invertebrate exclusion). Low emergence was likely a consequence of low seed viability as even viability of fresh seeds grown on potting medium in the greenhouse was low (45–65%). Emergence may have also been low because of pathogens. The data could not be normalized with standard transformations and rank-transformations were used for both analyses (Conover and Iman, 1981). The use of rank-transformations was criticized (Seaman et al., 1994) because they obscure the magnitude of differences between treatment effects. However, they are effective in identifying trends in the data. Figures are plotted using untransformed data.

3. Results

In the spring experiment, a significant effect of exclosure treatment on seed loss/seedling emergence was detected (Table 1). Seedling emergence was highest in vertebrate + invertebrate exclosure (indicating low seed loss), intermediate in the vertebrate and invertebrate exclosure treatments, and low-

Table 1
Results of MANOVA comparing total seedling emergence among fields, positions within fields and exclusion treatments, spring study. Wilks' lambda was the test statistics used to examine treatment effects and to calculate an approximate F test

Source of variation	Wilks' lambda	F	df	P
Field	0.0059	1.0	16	0.5647
Error = field × position				
Position	0.6848	0.1151	4	0.9579
Error = field × position				
Field × position	0.6247	2.17	16	0.0071
Exclusion treatment	0.2497	2.75	12	0.0064
Error = field × exclusion (position)				
Position × exclusion	0.4247	1.52	12	0.1480
Error = field × exclusion (position)				
Field × exclusion (position)	0.3503	0.9813	84	0.5301

est in the no exclosure treatments (Fig. 1). Although field or position had no significant effect, there was a significant interaction between field and position (edge vs. interior). This interaction (Table 1) indicated higher seed loss in the interior vs. the edge of fields 2 and 5 but no difference in seed loss between edge vs. interior in the other fields (Fig. 2). Graphs of differential seed loss in the treatments suggest that vertebrates account for much of the seed loss in *A. retroflexus* and *C. album* whereas seedling emergence was approximately the same in the four treatments for *A. theophrasti* or *P. dichotomiflorum* (Fig. 3).

In the over-winter experiments, field and exclosure had a significant effect of on average seedling emergence from the flats (Table 2). Seed loss was lower in field 1 than in the remaining fields and seed

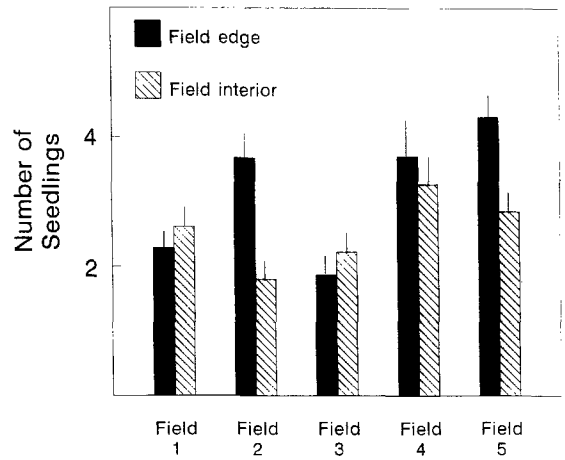

Fig. 2. Average number of seedlings ($\bar{X} \pm 1$ SE) emerging from field edge and interior treatment in the five study fields averaged across species and exclusion treatment in the spring study.

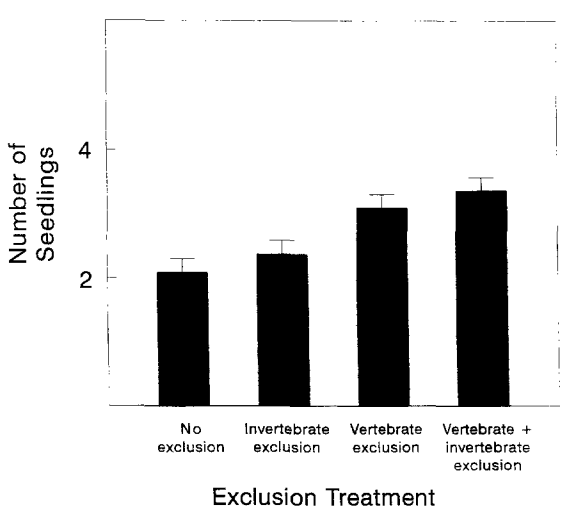

Fig. 1. Average number of seedlings ($\bar{X} \pm 1$ SE) emerging per individual exclusion treatment averaged across species, distance from the field edge and field in the spring.

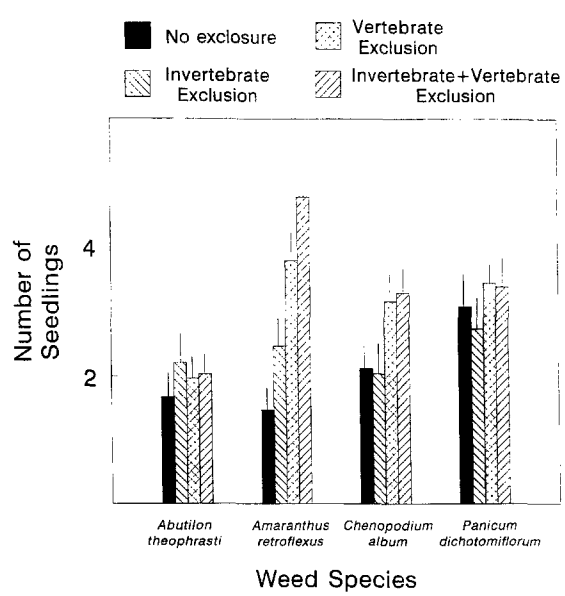

Fig. 3. Average number of seedlings ($\bar{X} \pm 1$ SE) of each of the four weed species that emerged per individual exclusion treatment in the spring study.

Table 2
Results of MANOVA examining total seedling emergence among fields, positions within fields and exclusion treatment (±vertebrates) in the over-winter study. Wilks' lambda was the test statistics used to examine treatment effects and to calculate an approximate F test

Source of variation	Wilks' lambda	F	df	P
Field	0.0116	3.06	15	0.0312
Error = Rep (field)				
Rep (field)	0.4136	1.41	40	0.0615
Position	0.3954	1.22	5	0.4349
Error = field × position				
Field × position	0.1686	0.70	15	0.7524
Field × position × rep	0.4339	1.32	40	0.1025
Exclusion treatment	0.6753	5.48	5	0.0003
Position × exclusion	0.8581	1.88	5	0.1113
Field × exclusion	0.6511	1.77	15	0.0435
Field × position × exclusion	0.6728	1.62	15	0.0730

loss was higher in the control treatment than in the vertebrate exclosure treatment (Fig. 4). Graphs of differential seed loss among species suggest that vertebrates preyed upon all species except *A. retroflexus* (Fig. 4). As observed in the spring study, there was no significant effect of position (edge vs. interior) on seed loss in these fields (Table 2).

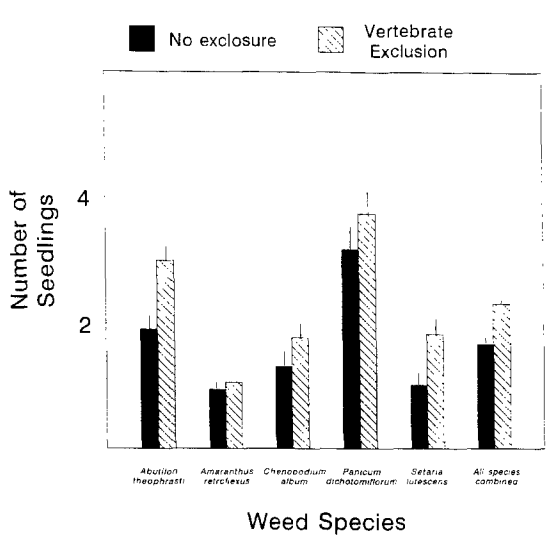

Fig. 4. Average number of seedlings ($\bar{X} \pm 1$ SE) of each of the five weed species alone and all species combined that emerged per exclusion treatment in the over-winter study.

4. Discussion

Although significant weed seed removal due to predators (especially vertebrates) was detected, the results did not support the expectation that seed loss in crop fields would be higher near hedgerows than in the field interior. The inability to detect differences in seed removal in edge vs. interior may be due to: (1) low rates of seedling emergence, (2) the presence of crop residue in the fields, particularly in the over-winter experiment, and (3) the small size of these fields and the diversity of the surrounding landscape.

Low rates of seedling emergence were an unexpected result. Prior to placing seeds in the field, seed viability was tested in the lab and ranged between 45 and 65%. This level of viability should have resulted in 10–15 seedlings emerging in those treatments having no predation (i.e., summer: invertebrate + vertebrate exclusion; winter: vertebrate exclusion).

In addition, all treatments were exposed to conditions favorable to seedling emergence as all treatments were returned to the greenhouse where they were kept watered, free from further seed or seedling predation and had the soil periodically stirred. The summer treatments were also given a cold shock to further enhance germination. Yet despite these efforts, seedling emergence was low.

Pathogens may have been responsible for the low seedling emergence. Because seeds were not surface sterilized and were left in the field for an extended period, exposure to microorganisms was likely. On the one hand, low seedling emergence, probably as a result of pathogens, negatively affected our ability to detect the effects of vertebrate and invertebrate seed predation by reducing the power of our statistical analyses. Low emergence resulted in an inability to normalize the data hence the use of rank transformations as discussed in Section 2. On the other hand, the effects of mortality caused by microorganisms should not have differed across treatments because all treatments were equally exposed to potential pathogens. Despite low emergence, seed predation did differ among treatments and weed species. In retrospect, there was an unexpected trade-off associated with the experimental design. The design avoided unnatural aggregations of large numbers of seeds that may have acted as 'super stimuli' to seed

predators at the cost of reduced power in identifying treatment effects.

Groundcover is another factor that may have affected our ability to detect differences in seed predation between the field edge vs. the interior. Crop fields with groundcover (cover crops, no-till cultivation, post-harvest debris), offer greater protection and have higher rodent and invertebrate populations than conventional-till fields that are disked after harvest (Castrale, 1984, 1987; Warburton and Klimstra, 1984; Wooley et al., 1987). Post-harvest debris was left on all four fields (no fields were disked in the fall) used in the over-winter experiment and there were prolonged periods of snow cover. These conditions may have provided cover for rodents and facilitated foraging throughout fields equalizing seed predation between field edges and interiors.

A striking result of this study was high variability within and among fields, in seed removal. Other studies of seed predators have found similar variability (Mittelbach and Gross, 1984; Thompson et al., 1991) and attribute this to the ability of predators to find seed patches which are often at high densities in these experiments (e.g., Mittelbach and Gross, 1984). In this study, seeds were at low densities (as opposed to clumps of seeds in small dishes) and were left in the field for an extended period in both experiments (3–4 weeks in spring; 4 months over-winter) which should have increased the probability of their being discovered by predators. Thus, the high variability in seed predation observed in this study probably reflects realistic spatial and temporal variability in the foraging habits of potential seed predators in agroecosystems. This along with variability in seed predation may contribute to the observed spatial variability of weeds in agricultural fields (Dessaint et al., 1991; Forcella et al., 1992; K.L. Gross, unpublished).

The Diehl farm used for this study is located in a complex matrix of relatively small (mean ≈ 18.2 ha) agricultural fields, woodlots, hedgerows and oldfields in southcentral Michigan. Within such a complex landscape, a field edge vs. field interior comparison may not be the appropriate scale with which to examine landscape influences on weed seed predation. A more appropriate scale may be a comparison of weed seed predation in complex agricultural landscapes (small crop fields embedded in a matrix of numerous hedgerows and woodlots) vs. simple agricultural landscapes (large crop fields embedded in a matrix of widely scattered woodlots and hedgerows) as used by Marino and Landis (1996) when examining rates of parasitism on the true armyworm (*Pseudaletia unipuncta* Haworth). Future studies of weed seed predation in agroecosystems should address the larger landscape level because source populations of potential weed seed predators may be responding to landscape structure at this larger landscape level.

Seed predation by invertebrates was expected to be highest near field edges. Several studies have shown that carabid beetles are abundant in agroecosystems (Esau and Peters, 1975; Gholson et al., 1978; Dritschillo and Wanner, 1980; Dritschillo and Erwin, 1982; Southerton, 1985; Thomas et al., 1991, 1992), and a number of carabid species are known to be seed predators (Lund and Turpin, 1977; Kjellsson, 1985). Carabids often use hedgerows and fencerows as over-wintering sites (Descender, 1982; Southerton, 1984, 1985; Wallin, 1985, 1986; Thomas et al., 1991, 1992) and so might be expected to be more abundant, and contribute significantly to weed seed loss near field edges. No difference in the level of invertebrate predation was found between field edges and interior which may be a consequence of the time of year (late May to early June) the spring experiments were conducted and the rapid dispersal of carabids from hedgerow over-wintering sites into agricultural fields (Thomas et al., 1991). By the time the spring post-tillage experiment was established, carabids may have already dispersed throughout the fields.

Although our analysis did not allow seed predation among these five weed species to be compared, the data suggest there may be differences. In spring, vertebrates were the predominant predators eating mainly seeds of the two smaller-seeded species (*A. retroflexus* and *C. album*). In the over-winter study, all species except *A. retroflexus* had higher seed loss when exposed to vertebrate predators. In spring, significant carabid predation was expected because carabids, such as *Harpalus pensylvanicus*, are abundant (Manley, 1992) and readily consume *C. album* (Lund and Turpin, 1977) and *A. retroflexus* seeds (Lund and Turpin, 1977; Brust and House, 1988). Results of this study may differ from previous studies because vertebrate exclusion cages may have

interfered with the movement of larger carabids such as *H. pensylvanicus*.

5. Conclusion

This study shows that weed seeds are vulnerable to seed predators in agricultural fields even when cryptically placed into maize fields at low densities. In spring, vertebrates appeared to prefer seeds of *A. retroflexus* and *C. album*. Seed losses attributable to vertebrate predators over-winter were more generalized as seeds of all weed species except *A. retroflexus* were eaten. At both times of the year, seed loss was highly variable both within and among fields and was not influenced in a consistent way by the location of seeds relative to hedgerows. The impact of post-dispersal seed predators is, therefore, patchy and not consistently related to field location relative to hedgerows.

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References

Archibold, O.W., Hume, L., 1983. A preliminary survey of seed input into fallow fields in Saskatchewan. Can. J. Botany 61, 1216–1221.

Best, L.B., 1983. Bird use of fencerows: implications of contemporary fencerow management practices. Wildl. Soc. Bull. 11, 343–347.

Best, R.L., Beegle, C.C., 1977. Food preferences of five species of carabids commonly found in Iowa cornfields. Environ. Entomol. 6, 9–12.

Brust, G.E., House, G.J., 1988. Weed seed destruction by arthropods and rodents in low-input soybean agroecosystems. Am. J. Alt. Agric. 3, 19–25.

Castrale, J.S., 1984. Impacts of conservation tillage practices on farmland wildlife in southeastern Indiana. Federal Aid Annual Report. Project Number W-26-R-15, Job XXXV-M-2-3, Population levels and habitat use. Indiana Department of Natural Resources, Fish and Wildlife Division, Indianapolis, 11 pp.

Castrale, J.S., 1987. Wildlife use of cultivated fields set aside under the payment of kind (PIK) program. Indiana Acad. Sci. 97, 173–180.

Cavers, P.B., Benoit, D.L., 1989. Seed banks of arable land. In: Leck, M.A., Parker, V.T., Simpson, R.L., (Eds.), Ecology of Soil Seed Banks. Academic Press, San Diego, pp. 309-328.

Conover, W.J., Iman, R.C., 1981. Rank transformations as a bridge between parametric and nonparametric statistics. Am. Statistician 35, 124–129.

Descender, K., 1982. Ecological and faunal studies on Coleoptera in agricultural land: II. Hibernation of Carabidae in agroecosystems. Pedobiologia 23, 295–303.

Dessaint, F., Chadoeuf, R., Barralis, G., 1991. Spatial pattern analysis of weed seeds in the cultivated soil seed bank. J. Appl. Ecol. 28, 721–730.

Dritschillo, W., Erwin, T.L., 1982. Responses in abundance and diversity of cornfield carabid communities to differences in farm practices. Ecology 63, 900–904.

Dritschillo, W., Wanner, D., 1980. Ground beetle abundance in organic and conventional corn fields. Environ. Entomol. 9, 629–631.

Esau, K.L., Peters, D.C., 1975. Carabidae collected in pitfall traps in Iowa cornfields, fencerows, and prairies. Environ. Entomol. 4, 509–513.

Forcella, F.R., Wilson, G., Renner, K., Dekker, A., Harvey, J., Alm, R.G., Buhler, D.A., Cardina, D.D., 1992. Weed seedbanks of the U.S. cornbelt: magnitude, variation, emergence, and application. Weed Sci. 40, 636–644.

Forman, R.T.T., Baudry, J., 1984. Hedgerows and hedgerow networks in landscape ecology. Environ. Manag. 8, 495–510.

Gholson, L.E., Beegle, C.C., Best, R.L., Owens, J.C., 1978. Effects of several commonly used insecticides on cornfield carabids in Iowa. J. Econ. Entomol. 71, 416–418.

Hume, L., Archibold, O.W., 1986. The influence of a weedy habitat on the seed bank of an adjacent cultivated field. Can. J. Botany 64, 1879–1883.

Johnson, H.E., Cameron, R.S., 1969. Phytophagous ground beetles. Ann. Ent. Soc. Am. 62, 909–914.

Kjellsson, G., 1985. Seed fate in a population of *Carex pilulifera* L: II. Seed predation and its consequences for dispersal and the seedbank. Oecologia 67, 424–429.

Lewis, T., 1969. The distribution of insects near a low hedgerow. J. Appl. Ecol. 6, 443–452.

Lund, R.D., Turpin, F.T., 1977. Carabid damage to weed seeds found in Indiana cornfields. Environ. Entomol. 6, 695–698.

Manley, G.V., 1992. Observations on *Harpalus pensylvanicus* (Coleoptera: Carabidae) in Michigan seed corn fields. Newsletter of the Michigan Entomological Society 37, 1–2.

Marino, P.C., Landis, D.L., 1996. Effect of landscape structure on parasitoid diversity and parasitism in agroecosystmes. Ecol. Applications 6, 276–284.

Marshall, E.J.P., 1989. Distribution patterns of plants associated with arable field edges. J. Appl. Ecol. 26, 247–257.

Marshall, E.J.P., 1988a. The ecology and management of field margin floras in England. Outlook Agric. 17, 178–182.

Marshall, E.J.P., 1988b. The dispersal of plants from field margins. In: J.R. Park (Ed.), Environmental management in agriculture. Belhaven Press, London, pp. 136-143.

Marshall, E.J.P., Hopkins, A., 1990. Plant species composition and dispersal in agricultural land. In: Bunce, R.G.H., Howard, D.C., (Eds.), Dispersal in agricultural habitats. Belhaven Press, London, pp. 98-116.

Mittelbach, G.G., Gross, K.L., 1984. Experimental studies of seed predation in old-fields. Oecologia 65, 7–13.

Montgomery, D., 1991. Design and Analysis of Experiments, 3rd edn. Wiley, USA.

Pollard, E., Relton, J., 1970. Hedges: V. A study of small mammals in hedges and uncultivated fields. J. Appl. Ecol. 7, 549–557.

Radford, A.E., Ahles, A.E., Bell, C.R., 1968. Manual of the Vascular Flora of the Carolinas. Univ. of North Carolina Press, Chapel Hill, NC, USA.

Seaman, J.W., Walls, S.C., Wise, S.E., Jaeger, R.G., 1994. Caveat emptor: rank transform methods and interaction. Trends Ecol. Evol. 9, 261–263.

Southerton, N.W., 1984. The distribution and abundance of predatory arthropods over wintering on farmlands. Ann. Appl. Biol. 105, 423–429.

Southerton, N.W., 1985. The distribution and abundance of predatory Coleoptera over wintering in field boundaries. Ann. Appl. Biol. 105, 17–21.

Thomas, M.B., Wratten, S.D., Sotherton, N.W., 1991. Creation of island habitats in farmland to manipulate populations of beneficial arthropods: predator densities and emigration. J. Appl. Ecol. 28, 906–917.

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 emigration. J. Appl. Ecol. 29, 524–531.

Thompson, D.B., Brown, J.H., Spencer, W.D., 1991. Indirect facilitation of granivorous birds by desert rodents: experimental evidence from foraging patterns. Ecology 72, 852–863.

Wallin, H., 1985. Spatial and temporal distribution of some abundant carabid beetles (Coleoptera: Carabidae) in cereal fields and adjacent habitats. Pedobiologia 28, 19–34.

Wallin, H., 1986. Habitat choice of some field inhabiting carabid beetles (Coleoptera: Carabidae) studied by recapture of marked individuals. Ecol. Entomol. 11, 457–466.

Warburton, D.B., Klimstra, W.D., 1984. Wildlife use of no-till and conventionally tilled corn fields. J. Soil Water Conserv. 39, 327–330.

Wooley, J.B. Jr., Best, L.B., Clark, W.R., 1987. Impacts of no-till row cropping on upland wildlife. Trans. N. Am. Wildl. Natl. Resour. Conf. 50. 157–168.