DOI: 10.1111/j.1365-3180.2009.00715.x

Over-winter predation of *Abutilon theophrasti* and *Setaria faberi* seeds in arable land

C L WILLIAMS*, M LIEBMAN*, P R WESTERMAN†, J BORZA*, D SUNDBERG* & B DANIELSON‡

**Department of Agronomy, Iowa State University, Ames, IA, USA, †Department Hortofruticultura, Botánica y Jardineria, Universitat de Lleida, Lleida, Spain, and ‡Department of Ecology, Evolution and Organismal Biology, Iowa State University, Ames, IA, USA*

Received 1 December 2008
Revised version accepted 4 March 2009

Summary

To improve understanding of over-winter weed seed predation in arable fields, we used data from winter exclosure trials to determine the amount of predation and the influence of crop habitats on predation of *Abutilon theophrasti* and *Setaria faberi* seed in 2-year (maize/soyabean) and 4-year (maize/soyabean/small grain + lucerne/lucerne) crop rotation systems between 2005 and 2008. Crop habitat influenced seed predation, and had similar impacts on the two weed species. Mean *A. theophrasti* predation ranged from 31% in the 2-year soyabean habitat to 99% in the 4-year lucerne habitat. Mean *S. faberi* predation ranged from 31% in the 2-year soyabean habitat to 97% in the 4-year lucerne habitat. Results suggest that a combination or interaction of cover and substrate may have affected crop habitat preference by seed predators. Future research should further examine the influence of physical habitat on seed predation to determine characteristics of cropping systems that encourage predation, particularly during over-winter periods, so as to routinely incorporate seed predators into long-term weed management strategies.

Keywords: *Abutilon theophrasti*, crop, habitats, over-winter, predation, rodents, seed, *Setaria faberi*, weed.

Williams CL, Liebman M, Westerman PR, Borza J, Sundberg D & Danielson B (2009). Over-winter predation of *Abutilon theophrasti* and *Setaria faberi* seeds in arable land. *Weed Research* **49**, 439–447.

Mammals, birds, and insects are prevalent post-dispersal seed predators (Getz & Brighty, 1986; Brust & House, 1988; Diaz, 1994). However, in winter and early spring granivorous rodents are probably the dominant seed predators in Midwestern USA crop fields (Cromar *et al.*, 1999; Andjelkovic *et al.*, 2007). Granivorous insects exhibit little or no activity during winter (Denlinger & Lee, 1998), and birds' impacts on seed populations are usually low (see Diaz, 1994 and references therein). *Peromyscus maniculatus* (Wagner), the prairie deer mouse, and *Mus musculus* (L.), the house mouse, occur frequently in cultivated fields in the Midwestern USA, throughout the year (Getz & Brighty, 1986). Although *P. maniculatus* can reduce its metabolic requirements via daily torpor, it needs concentrated sources of energy such as seeds to survive winter (Degen *et al.*, 1998). During winter, alternative food sources such as insect larvae are largely absent, and thus weed seeds may be the only food resources available.

Foraging animals trade-off energy gains in feeding with costs of foraging (Stephens & Krebs, 1987), and optimal foraging theory predicts that in environments of equal potential energetic gains, rodents should prefer safer environments. Both predation risk and food availability can influence microhabitat use by rodents, thereby affecting post-dispersal weed seed predation (Diaz, 1992). Predation risk by mammalian and avian species is an important foraging 'cost' and a major factor influencing the behavior of granivorous rodents (Brown & Kotler, 2004; Orrock *et al.*, 2004). Seed predation can be directly related to canopy cover, which conceals rodent foragers (Heggenstaller *et al.*, 2006). However, in winter no canopy cover is available in agricultural fields and protection from predators comes from crop residues and substrate unevenness, including crevices, holes, furrows and soil clods (Mandelik *et al.*, 2003; Orrock *et al.*, 2004). Crop habitats as formed via residues of crop species, tillage and other cropping practices, may differ in safety but also in food availability as soil disturbances such as tillage and ploughing cover seeds, which are then more difficult to find by seed predators (Hulme, 1994).

In this study we examined the effect of crop habitats on over-winter weed seed predation. We studied fields that differed in crop rotation and tillage combinations such that fields provided a range of types and levels of crop residue and soil disturbance (i.e. roughness). The fields were part of an on-going experiment including 2-year rotations of maize (*Zea mays* L.)/soyabean [*Glycine max* (L.) Merr.] and 4-year rotations of maize/soyabean/small grains + lucerne (*Medicago sativa* L.)/lucerne (see Materials and methods). We defined crop habitats according to physical characteristics of the soil surface determined to potentially have an influence on winter seed predation. These characteristics included: type and relative amount of cover (e.g. crop residue), and relative amount of disturbance (i.e. whether or not fall tillage had been applied, and if so, type and timing). To test the hypothesis that higher over-winter weed seed loss would occur in crop habitats with greater cover and surface roughness than habitats with less crop residues and smoother surfaces, we examined the degree of over-winter rodent predation of *Abutilon theophrasti* and *Setaria faberi*, which are commonly troublesome weed species within the study region.

Materials and methods

Experimental site and rotation systems

Seed predation trials were conducted at the Iowa State University Agronomy Farm, located in Boone County, IA, USA (42°0′N, 93°6′W), during three winter seasons (2005–2006, 2006–2007, and 2007–2008). Soils at the site are predominantly Clarion-Nicollet-Webster loam soils. Climate type of the study area is Humid Continental with dry winter and hot, humid summer (Mcknight & Hess, 2004). Details of winter monthly temperature and precipitation are provided in Table 1. Average annual temperature is 9°C, with January usually the coldest month, averaging −7°C, and July usually the warmest month, averaging 23°C (Iowa State University, 2008). Average annual precipitation is 712 mm (Iowa State University, 2008). November is usually the driest month with 17 mm precipitation on average, and June is usually the wettest month with 123 mm precipitation on average (Iowa State University, 2008). The soil seed bank at the experiment site is dominated by *Amaranthus rudis* (common waterhemp). Only low background densities of *A. theophrasti* and *S. faberi* seeds have been shown to be present (Westerman *et al.*, 2005).

The observations on seed predation were carried out in an ongoing cropping systems experiment, which has been described in detail elsewhere (Westerman *et al.*, 2005; Liebman *et al.*, 2008). Briefly, the experiment includes a 2-year (maize/soyabean), a 3-year [maize/soyabean/small grains + red clover (*Trifolium pratense* L.)], and 4-year (maize/soyabean/small grains + lucerne/lucerne) crop rotation system. However, over-winter weed seed predation observations in the present experiment were made only in the 2-year and 4-year crop rotation systems. Small grains in the 4-year crop rotation system were triticale (× *Triticosecale* Wittmack) in the first year of the experiment, and oat (*Avena sativa*) in the second and third years of the experiment. Cropping treatments at the experimental site were initiated in 2001 and all phases of the 2-year and 4-year crop rotation systems were present in every year in four replicate

Table 1 Mean monthly air temperature, total monthly precipitation, number of days with snow depth >25.4 mm, and long-term averages (1951–2008)* at the experiment site

	Temperature (°C)				Precipitation (mm)				Days with snow depth >25.4 mm (d)		
Month	2005–2006	2006–2007	2007–2008	Long-term average	2005–2006	2006–2007	2007–2008	Long-term average	2005–2006	2006–2007	2007–2008
Nov.	5.0	4.4	3.3	2.8	24	14	14	17	2	1	1
Dec.	–6.7	1.1	–6.7	–4.4	24	17	17	24	28	0	28
Jan.	1.1	–5.6	–8.3	–7.2	16	14	9	18	4	21	18
Feb.	–2.8	–8.9	–7.8	–4.4	6	45	18	23	9	28	23
Mar.	3.3	6.1	1.1	2.2	74	81	70	53	4	14	3
Apr.	13.3	8.9	11.6	10.0	109	153	168	89	0	2	0

*Not available for snow depth.

blocks. Plots were 18 m × 85 m and arranged in a randomised complete block design. Blocks were separated by approximately 15 m of mowed, mixed grasses (mostly *Festuca arundinacea* Shreb.).

Crop habitats

Observations of over-winter seed predation were conducted in six crop habitats. Crop habitats were characterised by crop rotation system, type and relative amount of cover, and relative amount of soil disturbance (i.e. roughness). Only 2-year and 4-year crop rotation systems were considered. Details of the crop habitats are provided in Table 2. As crop canopy is absent in winter, crop residue was considered as cover. Relative amount of soil disturbance was determined by type and timing of tillage. The six crop habitats were: 2-year maize, 2-year soyabean, 4-year maize, 4-year soyabean, 4-year small grains + lucerne, and 4-year lucerne.

Residue in the 2-year and 4-year maize habitats consisted of stalks and leaves that were partially shredded and incorporated into the soil via autumn chisel ploughing, which resulted in moderate amount of soil disturbance. Residue in the 2-year soyabean habitat consisted of leaves and stems that remained on the soil surface as this habitat type was not autumn tilled, and therefore the soil surface was not disturbed. Residue in the 4-year soyabean habitat consisted of shredded leaves and stems partially incorporated into the soil as this habitat type was lightly disked in the autumn and

Table 2 Crop habitats: crop identities, harvest dates, and fall tillage used in 2005–2007

Crop	Cultivar/hybrid	Harvest date	Rotation (year)	Autumn tillage	Residue	Fall tillage date
Lucerne	FSG 300LH	14 Sept. 2005 25 Sept. 2006 11 Sept. 2007	4	Mold-board ploughed	None	3 Nov. 2005 1 Nov. 2006 14 Nov. 2007
Maize	Agrigold 6395	22. Sept. 2005 2. Oct. 2006 10. Oct. 2007	2*	Chisel-ploughed	Shredded leaves & stalks	1 Nov. 2005 1 Nov. 2006 6 Nov. 2007
Maize	Agrigold 6395	22 Sept. 2005 2 Oct. 2007 10 Oct. 2007	4	Chisel-ploughed	Shredded leaves & stalks	1 Nov. 2005 1 Nov. 2006 6 Nov. 2007
Soyabean	Kruger K-287RR/SCN	4. Oct. 2005 9 Oct. 2006 26 Oct. 2007	2*	None	Standing stubble	None
Soyabean	Kruger K-2918/SCN	4 Oct. 2005 9 Oct. 2006 26 Oct. 2007	4	Lightly disked	Shredded stubble	1 Nov. 2005 1 Nov. 2006 1 Nov. 2007
Triticale + lucerne; oat + lucerne; oat + lucerne	Trical 37812; FSG 300LH IN09201 FSG 300LH IN09201 FSG 300LH	14 Jul. 2005 14 Sept. 2005 18 Jul. 2006 1 Oct. 2006 18 Jul. 2007 14 Oct. 2007	4	None	Standing young lucerne	None

*The 2-year rotation system is a conventional cash grain system; the 4-year crop rotation system is a mixture of cash grains and hay using animal manure input.

therefore the soil was slightly disturbed. The 4-year small grains (triticale or oat) habitat was undersown with lucerne which was subsequently mowed in early September of each year, and was not tilled in the autumn. Therefore, cover in the 4-year small grains habitat consisted of first-year lucerne in the over-winter period, and no soil disturbance. The 4-year lucerne habitat consisted of shredded lucerne leaves and stems completely incorporated into the soil via moldboard ploughing in the autumn, and therefore had the highest amount of soil disturbance among the crop habitats. For all crop habitats, tillage was conducted 2–14 d prior to installation of the weed seed additions (Table 2).

Based on the assumptions that combinations of crop residue and soil disturbance offer varying degrees of cover for seed predators, and that more cover is likely to be associated with greater seed predation, we expected greatest seed predation in the 2-year and 4-year maize habitats, followed by the 4-year lucerne habitat, and the 4-year small grains habitat. We expected least seed predation in the 2-year and 4-year soyabean habitats.

Weed seed predation

We placed weed seeds in metal screen trays to assess over-winter weed seed predation. Three hundred-fifty *A. theophrasti* and 700 *S. faberi* seeds were added to each tray in each year. Trays were placed on the soil surface in plots (i.e. crop habitats) in November 2005, 2006, and 2007. Trays were intended to provide a barrier between the soil and seeds, and were positioned randomly in plots 2–4 d after tillage and 0–14 d prior to application of seeds (Tables 2 and 3). Recovery of remaining seeds occurred in late March and early April of the subsequent years (Table 3). Seed tray design and materials were similar but not the same among years. In the first year (2005–2006), seed trays were constructed of 0.016 mm mesh hardware cloth and were 60 cm × 60 cm with 4 cm sides. In the second and third years, trays were constructed of 0.017 mm galvanised wire hardware cloth, and they measured 47 cm × 61 cm with 4 cm sides. Additionally, in the second and third years a 3 cm top lip was added to prevent seeds from being blown out of the trays.

Trays were randomly assigned to two sub-plot treatments, each replicated twice, namely a full exclosure and a partial exclosure. The partial exclosure had four openings (15.2 cm × 15.2 cm), one on each side, to exclude large animals and birds but allow access by small mammals (e.g. rodents; Mauchline *et al.*, 2005). Full exclosures were intended to indicate seed loss from extrinsic physical factors such as wind scattering, and to allow estimates of seed predation to be adjusted for experimental error (Cromar *et al.*, 1999; Orrock *et al.*, 2006). The partial exclosure was intended to indicate seed losses from predation while creating the same micro-environment as in the full exclosure. The full exclosure and partial exclosure treatments consisted of 75 cm × 75 cm × 15 cm cages constructed of 1 cm^{-2} wire mesh on the vertical sides and top. The exclosure cages were inserted 10 cm into the soil to prevent entrance by burrowing animals.

Weed biomass was low and presumably weed seed production was therefore also low, thus crop habitats were likely to have low weed seed bank densities (Liebman *et al.*, 2008). Distributions of weed plants and seeds within agricultural fields typically are clumped (Benoit *et al.*, 1989; Wilson & Brain, 1991; Cardina *et al.*, 1997). Consequently, the distribution of artificial seed patches (i.e. trays) in this study likely did not differ greatly from conditions that seed predators normally encounter.

Statistical analysis

The number of seeds remaining per tray was used as an expression of seed loss. Prior to analysis, values from replicate trays in the same plot were averaged. The effects of crop habitat (2-year maize, 2-year soyabean, 4-year maize, 4-year soyabean, 4-year small grains + lucerne, 4-year lucerne), year (2005–2006, 2006–2007, 2007–2008), block (1–4) and exclosure (full or partial) on post-dispersal seed predation were analysed using analysis of variance (ANOVA) (PROC MIXED; SAS, 2002). Crop habitat and exclosure were fixed factors, and block and year were random factors. Weed species were analyzed separately. For this first set of analyses, data were not transformed because they met normality

Table 3 Dates of seed tray and treatment installation and removal, and seed placement and retrieval

Year	Tray installation dates	Treatment installation dates	Seed placement dates	Seed retrieval dates
2005–2006	7–9 Nov.	10–11 Nov.	14–15 Nov.	28–30 Mar.
2006–2007	23–26 Oct.	23–26 Oct.	7–8 Nov.	2 Apr.
	1–2 Nov.	1–2 Nov.		9 Apr.
	6 Nov.	6 Nov.		
2007–2008	2 Nov.	2 Nov.	16 Nov.	9 Apr.
	16 Nov.	16 Nov.		

and homogeneity of variance assumptions for ANOVA. Significant interactions of year with crop habitat and exclosure type made it necessary to analyze effects separately by year. Differences in seed predation among crop habitats were evaluated using Abbott's correction formula: $P = (C - E)/C \times 100$, where P is percentage predation, E is the number of seeds remaining in the partial exclosure treatment, and C is the number of seeds remaining in the full exclosure treatment (Abbot, 1945). Data were arcsine-square root transformed prior to analysis to ensure normality, but untransformed data are reported. Probability values of *post hoc* multiple comparisons between crop habitats were obtained using Tukey pairwise adjustments (PROC MIXED; SAS, 2002).

Results

Analysis of variance (Table 4) indicated that all main factors (year, block, crop habitat, and exclosure) and most of their interactions had significant effects on predation of *A. theophrasti*. Only year × block × habitat was not significant. Main factors of year, crop habitat, and exclosure had significant effects on predation of *S. faberi* seed (Table 4). Interactions of year × block, year × exclosure, habitat × exclosure, and year × habitat × exclosure had significant effects on predation of *S. faberi* seeds (Table 4).

Non-predation seed losses

Significantly higher mean numbers of seeds were recovered from the full exclosure treatment compared with the partial exclosure treatment (Table 5). Seed loss in full exclosure trays ranged from 16–43% compared with 75–93% in partial exclosure treatment trays (Table 5). Loss of seeds from the full exclosure trays was greatest in the first year (Table 5), when the trays lacked the upper lip and thus seeds inside the trays were more vulnerable to displacement because of rain and wind. The difference between years was not substantial in the case of *A. theophrasti* seeds (20%, 18% and 17% for first, second and third, winters respectively). Loss of *S. faberi* seed, the lighter of the two species, from full exclosure trays was 43% in the first winter, then 16% and 28% in the second and third, winters respectively (Table 5). These results indicate that over-winter predation of *A. theophrasti* and *S. faberi* seed accounted for the majority of seed loss from partial exclosure trays.

Effects of year and crop habitat on overwinter seed predation

Considerable interannual variability of predation of *A. theophrasti* and *S. faberi* occurred, but there was an overall trend of considerable amounts of predation of both species across years. Mean predation of *A. theophrasti* was 0.72 (±0.05) in the first winter, 0.91 (±0.01) in the second winter, and 0.69 (±0.04) in the third winter. Mean predation of *S. faberi* was 0.61 (±0.04) in the first winter, 0.85 (±0.02) in the second winter, and 0.77 (±0.03) in the third winter. In all three winters, predation of both species was highest in the 4-year lucerne habitat and was least in the 2-year and 4-year soyabean habitats (Table 6).

Table 4 Results of ANOVA for the effects of crop habitat (2-year maize, 2-year soyabean, 4-year maize, 4-year soyabean, 4-year small grains + lucerne, 4-year lucerne), year (2005–2006, 2006–2007, or 2007–2008), block (1–4), exclosure (full or partial) and interactions on post-dispersal predation of *Abutilon theophrasti* and *Setaria faberi* seeds (PROC MIXED; SAS, 2002)

		A. theophrasti		*S. faberi*	
Effect	d.f.	*F*	*P*-value	*F*	*P*-value
Year	2	12.77	<0.0001	14.88	<0.0001
Block	3	3.46	0.0432	0.29	0.8315
Year × block	6	3.09	0.0113	3.39	0.0066
Habitat	5	3.63	0.0237	7.85	0.0010
Block × habitat	15	1.91	0.0429	1.16	0.3325
Year × habitat	10	2.84	0.0066	1.85	0.0742
Year × block × habitat	30	1.41	0.1326	0.60	0.9361
Exclosure	1	1897.5	<0.0001	1409.23	<0.0001
Year × exclosure	2	14.65	<0.0001	49.98	<0.0001
Habitat × exclosure	5	12.71	<0.0001	3.96	0.0040
Year × habitat × exclosure	10	3.69	0.0008	2.39	0.0200

Table 5 Recovery of *Abutilon theophrasti* and *Setaria faberi* seeds in full and partial exclosure treatments, averaged across all crop habitats (d.f. = 15)

		Mean number of seeds recovered (% loss)	
Years	Treatment	*A. theophrasti*	*S. faberi*
2005–2006	Exclosure	282.1 (20)	401.6 (43)
	Partial exclosure	75.5 (79)	148.8 (79)
	t	23.74*	15.81*
2006–2007	Exclosure	290.9 (18)	594.1 (16)
	Partial exclosure	27.6 (93)	92.31 (87)
	t	32.88*	29.92*
2007–2008	Exclosure	291.8 (17)	509.4 (28)
	Partial exclosure	89.7 (75)	115.4 (84)
	t	20.65*	19.89*

There were 350 *A. theophrasti* and 700 *S. faberi* seeds added to all treatments.
*Significant at the 0.0001 level.

Weed seed predation was highest in the 4-year lucerne habitat (Table 6). No significant differences in predation of either weed species were observed among the 4-year lucerne and 2-year maize habitats (Table 6). Similarly, no significant differences in predation were detected between the 4-year lucerne and the 4-year maize habitats, except for *A. theophrasti* in the second winter (Table 6). Predation did not differ significantly between the 2-year and 4-year maize habitats (Table 6).

Weed seed predation was least in the 2-year soyabean habitat, except for *A. theophrasti* in the second winter when predation was least in the 4-year soyabean habitat (Table 6). Significant differences in predation of both weed species were observed between the 4-year lucerne and the 2-year soyabean habitats, except for *S. faberi* in the second winter (Table 6). Predation did not differ significantly between the 4-year lucerne and the 4-year soyabean habitats, except for *A. theophrasti* in the first and third winters (Table 6). No differences in predation were detected between the 2-year and 4-year soyabean habitats (Table 6).

Predation differed between the 2-year soyabean and 2-year maize habitats only in the first winter (Table 6). Predation in the 4-year soyabean and 4-year maize habitats did not differ (Table 6), and there were no differences observed between the 2-year maize and 4-year soyabean habitats, except for *A. theophrasti* in the first winter (Table 6). A significant difference between the 2-year soyabean and 4-year maize habitats was observed only in the first winter (Table 6).

Predation differed significantly between the small grain and 4-year lucerne habitats for *A. theophrasti* in the first and second winters, and for *S. faberi* in the second winter (Table 6). Predation in the small grain habitat did not differ from that in the 2-year maize, 4-year maize, 2-year soyabean or 4-year soyabean habitats, except for *A. theophrasti* in the first winter when the difference was significant with the 2-year maize habitat, and for *S. faberi* in the first winter when the difference was significant with the 2-year soyabean habitat (Table 6).

Mean *A. theophrasti* predation declined from the first year to the third year in the 2-year maize habitat (95%, 91%, and 67%; Table 6). In all other crop habitats, mean *A. theophrasti* predation was greatest in the second year (Table 6). The range of differences among years was substantial in the 2-year and 4-year soyabean habitats (55 and 47 percentage points respectively; Table 6), whereas the difference was moderate in the small grains + lucerne habitat (22 percentage points; Table 6), and slight in the 4-year lucerne habitat (seven percentage points; Table 6). Mean *S. faberi* predation was greatest in second year in all crop habitats except the 4-year maize and 4-year small grains + lucerne habitats (Table 6). In the 4-year maize habitat mean predation was highest in the second and third years (85%; Table 6). In the 4-year small grains + lucerne habitat mean predation was highest in the third year (77%, Table 6). Differences in mean predation of *S. faberi* among years were least in the 2-year maize and 4-year small grains/lucerne habitats (10 and 11 percentage points, respectively; Table 6). Difference in mean predation of *S. faberi* among years was substantial in the 2-year soyabean habitat (52 percentage points; Table 6). The difference in mean predation of *S. faberi* among years was moderate in the 4-year lucerne, 4-year

Table 6 Means and standard errors of post-dispersal predation of *Abutilon theophrasti* and *Setaria faberi* in crop habitats within winter study periods

Rotation (years)	Crop	Winter (2005–2006)	(2006–2007)	(2007–2008)
Abutilon theophrasti				
2	Maize	0.95 (±0.02)a	0.91 (±0.02)ab	0.67 (±0.11)ab
	Soyabean	0.31 (±0.05)c	0.86 (±0.04)b	0.59 (±0.04)b
4	Lucerne	0.98 (±0.002)a	0.99 (±0.007)a	0.92 (±0.06)a
	Maize	0.78 (±0.11)ab	0.87 (±0.06)b	0.74 (±0.13)ab
	Oat or triticale + lucerne	0.67 (±0.05)bc	0.89 (±0.02)b	0.82 (±0.05)ab
	Soyabean	0.62 (±0.09)bc	0.90 (±0.05)ab	0.43 (±0.06)b
Setaria faberi				
2	Maize	0.73 (±0.04)a	0.87 (±0.04)ab	0.83 (±0.02)ab
	Soyabean	0.31 (±0.13) b	0.83 (±0.09)ab	0.60 (±0.09)b
4	Lucerne	0.74 (±0.04)a	0.97 (±0.02)a	0.90 (±0.05)a
	Maize	0.69 (±0.10)a	0.85 (±0.04)ab	0.85 (±0.03)ab
	Oat or triticale + lucerne	0.66 (±0.09) a	0.66 (±0.08)b	0.77 (±0.02)ab
	Soyabean	0.57 (±0.04)ab	0.88 (±0.05)ab	0.66 (±0.09)ab

Means within columns followed by the same letter are not significantly different according to Tukey's test ($P < 0.05$).

maize, and 4-year soyabean habitats (23, 16 and 31 percentage points respectively; Table 6).

Discussion

The results of this study indicate that: (1) considerable predation occurred in all three winters; (2) different crop habitats were associated with different levels of predation; and (3) there was considerable variation in the magnitude of predation among years and among crop habitats.

Although we did not evaluate cover quantity and quality, or substrate quality, our results, that a combination of cover and substrate may result in crop habitat preference by seed predators, are generally supported by the findings of others (Meyer & Valone, 1999; Kotler *et al.*, 2001; Mandelik *et al.*, 2003; Brown & Kotler, 2004; Orrock *et al.*, 2004). However, in our study tillage seemed to have a bigger effect than crop residues; seed predation was consistently highest in the moldboard ploughed habitat (i.e. the 4-year lucerne habitat), lowest in the habitat that was not tilled (i.e. the 2-year soyabean habitat), and intermediate in the habitats with intermediate soil disturbance regimes. Although it lacked residue cover, the relatively rough texture of the substrate in the 4-year lucerne habitat may have provided refuge or other means for avoiding capture from predators (e.g. crevices and large soil clods). It is also possible that the rough substrate texture created a mosaic of shapes and shadows of different sizes that foragers were able to use as camouflage as suggested by Mandelik *et al.* (2003), either while feeding or while traversing to seed trays, as suggested by Mandelik *et al.* (2003).

Our results differ markedly from those of Brust & House (1988) and Cromar *et al.* (1999) who found greater seed predation in no-till treatments, as well as Cardina *et al.* (1996) who found no effect of tillage on seed predation. However, Brust & House (1988), Cromar *et al.* (1999), and Cardina *et al.* (1996) did not study over-winter seed predation exclusively by vertebrates. Habitat preference can change in response to changes in predation risk (Lima & Bednekoff, 1999) as related to seasons. It may differ among seed predators; for example, vertebrates may prefer rough soil surfaces that invertebrates may avoid.

The effect of crop residues seemed secondary; seed predation in maize stubble was higher than in small grain + lucerne residues, which in turn was higher than in soyabean stubble. However, predation in the 4-year lucerne habitat was not significantly different from predation in the 2-year and 4-year maize habitats (except for *A. theophrasti* in the second winter). These results are more or less in agreement with those of Cromar *et al.* (1999), who found that seed predation was highest in no-till maize residue and lowest in soyabean and wheat residue that had been disk tilled. However, the actual ranking of crop habitats was different from what we had anticipated. Either our assessment of the suitability of crop habitats was not entirely correct, or predation risk was not the only factor influencing habitat selection by seed predators.

Alternative explanations have been suggested. For example, Cromar *et al.* (1999) concluded that the dense ground cover in disked wheat residue may have reduced predation by reducing vertebrate mobility compared with no-till maize residue. They also suggested that the higher predation in the moldboard ploughed treatment as compared with the chisel ploughed treatment could be explained by greater mobility of seed predators and fewer food choices, leading to more seeds consumed per predator. However, metabolic costs of foraging (e.g. locomotion) are thought to be less of an influence on forager behavior than risk of being attacked by other species (Brown & Kotler, 2004).

Food availability is another main component of habitat use, as rodents need to balance risk (of being attacked, starvation, etc.) with gain (nutrients, calories, etc.) (Jensen *et al.*, 2003; Gutman *et al.*, 2007). Two sources of seeds were available in our study, namely weed seeds and grain spilled from harvest operations. Natural densities of weed seeds on the soil surface were expected to be low because weed densities had been low among crop habitats (Liebman *et al.*, 2008). Grain spill during crop harvest may have provided an additional food source in each of our crop habitats, although the question is whether these crop seeds were available on the soil surface, because buried seeds have a much lower probability of being found than surface seeds (Hulme, 1994; Hulme & Borelli, 1999). Seeds can be buried via tillage and via natural causes (Chambers & MacMahon, 1994; Mohler *et al.*, 2006; Westerman *et al.*, 2009). Tillage buries most seeds, although a larger proportion is buried by moldboard plough than by chisel plough or disk (Mohler *et al.*, 2006). In our study, tillage may have reduced the amount of available seeds in all crop habitats, except in the 2-year soyabean and the 4-year small grain cereals. Natural seed burial is influenced by crop habitat, and appears to be lower in row crops (maize and soyabean) than in forage crops (lucerne and small grain cereals undersown with lucerne) (Westerman *et al.*, 2009). So apparently seed availability is inversely related to habitat use by the rodents, namely highest in 2-year soyabean and the 4-year small grain + lucerne and lowest in 4-year lucerne. Larger seeds appear to be at greater risk of being predated, because natural seed burial is slower (Westerman *et al.*, 2009) and seed recovery by rodents is higher for larger seeds (Jennings, 1976). This strongly suggests that food availability is not the primary driver for habitat selection.

Reliable estimation of the causes of differences in predation among crop habitats with regard to cover, substrate texture and food availability, and their possible interactions is not possible as we did not directly measure these habitat characteristics. Repeated over-winter observations and rodent trapping could provide information for a better evaluation of predator behavior with regard to extrinsic environmental conditions (e.g. weather) and influence of cover and substrate on relative risk among crop habitats.

A consequence of the mismatch between seed availability and habitat selection by rodents is that over-winter seed predation may not be optimal. Nonetheless, the results of this study emphasise the high potential rates of over-winter predation of weed seeds on the soil surface in arable lands. Our results suggest that over-winter seed predation may have a significant effect on weed population dynamics in cropping systems by reducing over-winter survival of seeds. The magnitude of seed losses observed in this study exceeds those predicted by modeling to have a non-trivial contribution to regulation of weed population dynamics (e.g. Westerman *et al.*, 2005).

Several studies suggest that weed seed predation may be enhanced through delayed tillage (Fryer, 1981; Davis *et al.*, 2003; Westerman *et al.*, 2006), use of cover crops or legume small grain intercrops (Davis & Liebman, 2003; Gallandt *et al.*, 2005; Heggenstaller *et al.*, 2006), increase in landscape complexity in areas surrounding fields (Menalled *et al.*, 2000; Booman *et al.*, 2009), or a combination of these activities (Davis *et al.*, 2003). Future research efforts should focus on the extent to which these actions impact winter seed predation by rodents.

Results of this study support the idea that mammalian seed predators could be exploited for ecological process-based approaches to weed management. There is a growing literature on landscape and interspecific competition effects on presence and survival of mammals and their predation of weed seed in agricultural systems (e.g. Menalled *et al.*, 2001; Westerman *et al.*, 2003a; Pearson & Callaway, 2008). Understanding the habitat requirements and characteristics of cropping systems that encourage predation by mammals, particularly that of over-winter periods, needs to be improved to routinely enable incorporation of mammalian predators into long-term weed management strategies.

Acknowledgements

Financial support was provided by the USDA National Research Initiative (Project 2006-35320-16548) and the Leopold Center for Sustainable Agriculture (Project 2004-E6). The authors wish to thank Dr Philip Dixon for his guidance, and Dr Andrew Heggenstaller, Mr Michael Cruse and Mr Robin Gomez for their insightful comments. We also gratefully acknowledge lab and field assistance from Mr Daryl Reed, Mr David Williams, Ms Augustina Sanchez-Parada, Mr José Gutierrez-Lopez, and Ms Vilma Mateo.

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