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Annual Postdispersal Weed Seed Predation in Contrasting Field Environments

Adam S. Davis, Erin C. Taylor, Erin R. Haramoto, and Karen A. Renner*

Interest in weed seed predation as an ecological weed management tactic has led to a growing number of investigations of agronomic and environmental effects on predation rates. Whereas the measurements in most of these studies have taken place at very short timescales, from days to weeks, measurements at longer timescales (from several months to a year) have greater relevance to the demographic impact of weed seed predation and potential contributions from this process to ecological weed management. Our aim was to quantify the impact of crop phase, within a corn–soybean–wheat crop sequence, on quarterly and annual seed predation rates of giant foxtail, giant ragweed, and velvetleaf. The study took place in areas of the northern U.S. Corn Belt contrasting in dominant land use: Savoy, IL (2005–2007), where corn and soybean production predominates, and East Lansing, MI (2005–2008), where crop production occurs within an old field/forest landscape matrix. Mean annual rates of weed seed predation by the combined action of invertebrate and vertebrate predators were 31 ± 1.6% for giant ragweed, 37 ± 1.4% for velvetleaf, and 53 ± 1.4% for giant foxtail. Crop phase had negligible effects upon long-term seed predation rates, accounting for less than 2% of observed variation. Weed species and site-year, in contrast, contributed 35% and 40%, respectively, of the variation in cumulative annual seed predation. These results are consistent with the spatial variability in best management practices seen at spatial scales greater than the county level: weed seed predation appears to be an inherently site-specific phenomenon. New developments in managing weed seed predation as an ecosystem service are therefore likely to have local recommendation domains or to be driven by stochastic annual variation related to weather or granivore demography.

Nomenclature: Giant foxtail, *Setaria faberi* Herrm.; giant ragweed, *Ambrosia trifida* L.; velvetleaf, *Abutilon theophrasti* Medik.; corn, *Zea mays* L., red clover, *Trifolium pratense* L.; soybean, *Glycine max* (L.) Merr.; wheat, *Triticum aestivum* L.

Key words: arable habitat, carabid beetles, cropping system, demography, ecological weed management, ecosystem services, granivory, interannual variation, interspecific, rodents.

Postdispersal predation of weed seeds in arable fields is a ubiquitous phenomenon, observed in many types of farming systems and at many temporal and spatial scales (Bohan et al. 2011; Davis et al. 2011; Lundgren 2009). Despite increased scientific attention over the past decade to underlying causes of variation in postdispersal weed seed predation rates, guidelines for intentional regulation of this ecosystem service as a component of ecological weed management remain elusive (Baraibar et al. 2011). Among the issues needing clarification are dependence of foraging on seed and granivore population densities (Westerman et al. 2008), abiotic and biotic environmental determinants of predator activity (Booman et al. 2009; Davis and Raghu 2010; Meiss et al. 2010; Saska et al. 2010), cumulative rates of long-term seed predation (Davis et al. 2011; Harrison et al. 2003; Williams et al. 2009), temporal overlap between seed rain and predator activity (Westerman et al. 2011), and agronomic factors such as soil disturbance and cropping system as they pertain to seed predation rates (Baraibar et al. 2009; Bohan et al. 2011; Heggenstaller et al. 2006; Menalled et al. 2007; Ward et al. 2011).

We focused on the effects of crop sequence on quarterly (3-mo duration) and annual rates of postdispersal weed seed predation in the present study. Whereas most published studies of weed seed predation have relied on observations made at very short timescales, from days to weeks (Davis et al. 2011), demographic models projecting the contribution of variation in weed vital rates to integrated weed management strategies underscore the importance of longer-term predation effects, at the timescale of several months to a year (Harrison et al. 2003; Liebman and Davis 2009; Westerman et al. 2006). We chose the sequence of crop species as our management variable of interest because it is a farming system variable readily under grower control, and because short-term weed seed predation rates, on the order of days, have been observed to be influenced by the crop in which they occur. In both annual and perennial cropping systems, the amount of living vegetative cover is positively correlated with daily weed seed removal rates (Davis and Liebman 2003; Heggenstaller et al. 2006; Meiss et al. 2010), possibly due to predator avoidance behavior by granivores. Additionally, crops with different life histories will mature at different times in relation to the phenology of dominant weeds, and will disrupt seed feeding activities with different farming schedules (Westerman et al. 2011). Crop sequence effects on short-term weed seed predation rates may thus arise from variation in suitability of crop habitat for granivore activity, and from secondary effects of crop phenology and agronomic operations on the temporal overlap of weed seed dispersal and granivory.

Our primary goal was to test the hypothesis that crop sequence influences quarterly and annual rates of postdispersal weed seed predation in weed species common to field crops in the northern U.S. Corn Belt. In particular, we were interested in knowing whether such effects were consistent across experimental locales and study years. If such a hypothesis were supported by the data, it would provide guidance for intentional manipulation of long-term weed seed predation rates by producers as a component of an ecological approach to weed management.

Materials and Methods

Our study was located in contrasting areas of the northern U.S. Corn Belt to provide a means of assessing the generality of crop sequence effects on long-term weed seed predation

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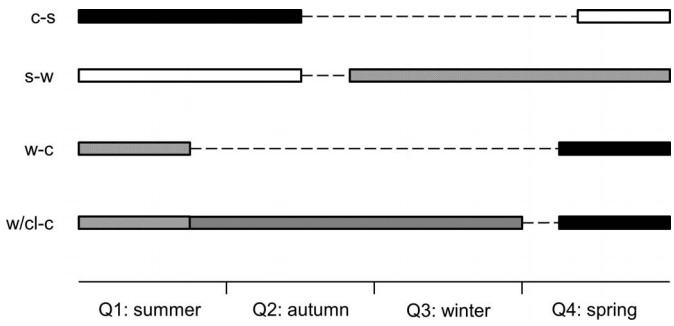


Figure 1. Contrasting crop sequences featured in the study, where boxes denote periods in which there is living cover in a particular crop sequence. Explanation of abbreviations: c = corn, s = soybean, w = wheat, w/cl = wheat underseeded with red clover. Bars correspond to standing biomass of different crops: black = corn, white = soybean, stippled = wheat, and gray = red clover.

rates. A northern study site was established at the Michigan State University Crop and Soil Science Farm in East Lansing, MI (42.737N, 84.484W; soil description: Capac fine sandy loam [fine-loamy, mixed, mesic Aquic Glossudalf] 55% sand, 24% silt, 21% clay, 2.5% organic carbon (OC), and pH of 6.9), where agriculture takes place within an old-field and forest landscape matrix. A more southerly study site was established at the University of Illinois Crop Science Research and Extension Center in Savoy, IL (40.048000N, 88.236489W; soil description: Catlin silt loam [fine-silty, mixed, mesic Oxyaquic Argiudoll], 7% sand, 68% silt, 25% clay, pH 7.2 and 4.2% soil OC), where corn and soybean production is the dominant land use and comprises the broader landscape context in which weed seed predation occurs.

The experiment was implemented as a hierarchical nested design, with four replicated blocks of weed species, crop phase, location, and year arranged in the following nesting order: year{location{block{crop sequence{weed species}}}}. At both study sites, we established a corn–soybean–wheat crop sequence. All entry points of the crop sequence were present in each study year (2005–2007 in Illinois, and 2005–2008 in Michigan), representing contrasting crop phases differing in crop growth period (Figure 1): corn–soybean, soybean–wheat, and wheat–corn. The wheat phase of the crop sequence was underseeded with red clover at both locations; in Michigan, the wheat phase also included a wheat sole-crop as a treatment level, to permit comparisons of seed predation within the wheat phase in ± red clover treatments.

Main plots, each containing a different level of crop phase, were 9.2 m long by 12.2 m wide in Illinois and 76.2 m long by 6.1 m wide in Michigan. Corn was planted in 76-cm rows at 75,000 seeds ha^{-1} in mid-April in Illinois and in late April in Michigan. Soybean was planted in 76-cm rows at 432,250 seeds ha^{-1} in early May in Illinois and in mid-May in Michigan. Wheat was drilled in 19-cm rows at 2×10^6 seeds ha^{-1} in early October in Illinois and Michigan. Red clover was frost-seeded into wheat in mid-February in Illinois and mid-March in Michigan at 13.5 kg seed ha^{-1}. Crops were fertilized according to local extension recommendations. Weed control was accomplished with a combination of POST herbicide applications made at labeled rates (glyphosate in corn and soybean, and 2,4-D low-volatility ester in wheat and wheat/red clover plots) and hand labor.

We chose giant foxtail, giant ragweed, and velvetleaf because of their economic importance in the northern U.S. Corn Belt (Bridges and Baumann 1992), and because seed predation in these species has been extensively studied at shorter temporal scales in this region (Heggenstaller et al. 2006; Menalled et al. 2007). Weed seeds were collected in late September of each study year from plants in neighboring production fields by gently shaking mature inflorescences over a paper bag and allowing the seeds to air dry at room temperature for 2 wk. After removing light or damaged seeds with an air column separator (757 South Dakota seed blower, Seedburo Equipment, Chicago, IL), clean seeds were stored at 4 C in an airtight plastic container before use. Mean hundred seed weights for giant foxtail, giant ragweed, and velvetleaf were 0.18 g, 4.35 g, and 0.87 g, respectively.

Predation Measurements. Weed seed predation measurements were focused at two temporal scales: quarterly (removal during a 3-mo period) and cumulative annual seed removal. Within each experimental replicate, estimates of quarterly and annual seed predation were made for each weed species using 40-cm-diam by 40-cm-tall cylindrical wire mesh exclosures providing one of two levels of predator access: control/no predators (1-mm by 1-mm openings) or invertebrates plus small vertebrates (8-cm by 15-cm openings). Each exclosure was set among crop plants (between crop rows for corn and soybean, and displacing several wheat rows in the wheat phase) within a 2.5-cm-deep excavation in the soil and the bottom panel was covered by soil to meet the surrounding soil surface at the same level. This allowed predators unimpeded access to exclosure openings.

Long-term estimates of seed predation were made within 10-cm by 10-cm by 3-cm-deep trays made of 1-mm wire mesh located within the long-term predation exclosures. Each exclosure held four trays, one for each 3-mo quarter, with only a single species represented per exclosure. Trays were filled with soil and buried to the level of the surrounding soil surface in the exclosure, leaving a 1-cm wire mesh lip protruding above the soil to prevent seed loss to water movement. On one side of the tray, soil was built up to the level of the wire mesh lip to allow unrestricted invertebrate access. Soil used to fill the trays was obtained from underneath a long-term grass sward at each location with very low weed seedbank density (no seeds of the study species were found in 20 elutriated samples of this soil). Weed seeds of a single species were placed weekly on the soil surface of predation trays, using concurrent measurements of seed rain (Davis and Raghu 2010) to guide seed placement rate. Mean weekly seed rain densities across site years for giant foxtail, giant ragweed, and velvetleaf were 2,850 ± 300, 430 ± 50, and 1,600 ± 200 seeds m^{-2}, respectively. Germinated seedlings were counted and removed weekly.

Every exclosure contained four seed trays placed in the field at the start of each study year, on July 1. Each tray was randomly assigned to one of four quarterly predation study periods lasting 3 mo each (Q1 = July through September, Q2 = October through December, Q3 = January through March, Q4 = April through June). Seeds of a given species were placed on all trays in the same quantity throughout the study. At the end of a given quarter, the corresponding tray was removed from the field, the soil washed through 1-mm sieves, and intact seeds enumerated.

Estimates of quarterly seed predation rates were calculated from seed placement, recovery, and germination data in two

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steps. First we estimated seed loss in the jth quarter (L_j) as

$$L_j = 1 - \frac{r_j}{\sum_{1}^{j} n_i - \sum_{1}^{j-1} l_i - \sum_{1}^{j} g_i} \quad [1]$$

where r_j = seeds recovered in the jth quarter, n_i = seeds placed in the field in the ith quarter, l_i = seeds removed from the seed tray in the ith quarter, and g_i = seeds lost to germination in the ith quarter. This step was performed for seeds recovered from exclosures allowing seed predator access as well as for control exclosures excluding predators. Quarterly predation (P_j) was then calculated as $P_j = L_{j(\text{pred})} - L_{j(\text{control})}$. Cumulative annual predation in the fourth quarter tray (Q4) was calculated in two steps. First, cumulative annual seed loss (L_{ann}) was calculated as

$$L_{\text{ann}} = 1 - \frac{r_j}{\sum_{1}^{j} n_i - \sum_{1}^{j} g_i} \quad [2]$$

where n_i and g_i have the same meanings as in Equation 1, and $j = 4$. Next, cumulative annual predation (P_{ann}) was calculated as $P_{\text{ann}} = L_{\text{ann(pred)}} - L_{\text{ann(control)}}$.

Statistical Analysis. Quarterly and cumulative weed seed predation rates were analyzed with general linear mixed-effects models with location, year, quarter, and weed species, and their interactions, as fixed effects and block-nested within location within year as a random effect. Proportion data were $\sin^{-1}(x^{0.5})$-transformed to meet assumptions of normality and constant error variance (Crawley 2007). Variance partitioning analyses were performed in the nlme package of R v. 2.13.0 (R Development Core Team 2009) on general linear models containing the same terms as above, with all terms treated as random variables (Crawley 2007). Variance proportions for individual terms were then estimated as a proportion of total model variance.

Results and Discussion

Crop Sequence and Seed Predation. The central hypothesis driving this study, that phase of crop sequence consistently influences long-term weed seed predation rates, was motivated by previous observations of short-term predation, at a timescale of days, being affected by the amount of living vegetative crop cover at the time of the predation event (Heggenstaller et al. 2006; Meiss et al. 2010). On the basis of this line of reasoning, our expectations were that we would see one of the following types of evidence. First, we would have expected a significant quarter-by-crop sequence interaction term in quarterly predation rates, consistent with seasonal variation in the amount of living crop tissue in different crop sequences providing contrasting habitats for seed predators. Second, we would have expected a significant main effect of crop sequence in cumulative predation rates, indicating that crop habitats varied enough over time in the different crop sequences to result in differential long-term seed removal by granivores. In particular, we expected the long duration of living cover in the wheat/red clover–corn sequence (Figure 1), provided by red clover growth subsequent to wheat harvest, to support higher predation rates than in the other crops (Davis and Liebman 2003).

Table 1. ANOVA of quarterly postdispersal weed seed predation rates in Urbana, IL and East Lansing, MI.

Source[a]	d.f.n.	d.f.d.	F	P
(intercept)	1	571	553	< 0.0001
Year	1	2	4.9	0.16
Crop sequence	2	571	0.55	0.57
Quarter[b]	3	571	26	< 0.0001
Location	1	2	4.9	0.16
Weed species	2	571	3.1	0.04
Q × L	3	571	15	< 0.0001
Q × W	6	571	2.4	0.03
L × W	2	571	0.62	0.54
Q × × L × W	6	571	6.6	< 0.0001

[a] The most parsimonious general linear mixed-effects model contained interaction effects only between quarter (Q), location (L), and weed species (W). All other interactions were nonsignificant at $P > 0.50$.

[b] Explanation of quarters: Q1 = July–September, Q2 = October–December, Q3 = January–March, Q4 = April–June.

We did not observe either of these types of support in the data from our field study for the role of crop sequence in quarterly or annual weed seed predation rates. Neither main effects of crop sequence nor interactions between crop sequence and observation quarter or location influenced quarterly weed seed predation rates (Table 1, Figures 2 and 3). Preplanned 1 d.f. contrasts of seed predation rates in the wheat/red clover–corn sequence compared with the other crop sequences also did not support the hypothesis (Illinois: $F_{1,279} = 0.66$, P = 0.42; Michigan: $F_{1,279} = 0.003$, P = 0.96). Limiting data to Michigan only, and performing a preplanned 1 d.f. contrast of the wheat–corn and wheat/red clover–corn crop sequences also gave no support for our hypothesis ($F_{1,170} = 0.46$, P = 0.50), nor was there an interaction between the presence of red clover in the crop sequence and quarter in Michigan ($F_{3,164} = 1.61$, P = 0.20). Lack of observed significance of crop sequence was therefore not due to averaging across temporal variation in seed predation rates influenced by variable crop biomass. These results are consistent with the lack of cover-crop effect on weed seed predation by invertebrates observed by Gallandt et al. (2005) in contrasting vegetable cropping systems in Maine.

Crop sequence did not have a significant main effect on cumulative annual rates of weed seed predation; however, there was a significant interaction between crop sequence and location (Table 2, Figure 4). Upon examining cumulative predation rates by location, it became apparent that the interaction term was driven by lack of a crop sequence effect in Michigan ($F_{2,70} = 0.72$, P = 0.49) and a significant main effect of crop sequence in Illinois ($F_{2,62} = 4.82$, P = 0.01). Separation of means at this stage by Bonferroni-protected multiple comparisons indicated that cumulative predation rates in Illinois for the corn–soybean sequence (38 ± 4%) were lower than in the soybean–wheat (51 ± 4%) and wheat/red clover–corn (53 ± 4%) sequences, which were similar. The crop phases that included wheat, or wheat and red clover, may have attracted additional granivore activity by providing a high-quality habitat with green plant tissues at times when grain production fields in Illinois would otherwise be covered in dead plant residues (Heggenstaller et al. 2006). Although this result demonstrated that crop sequence can influence long-term seed predation rates, it did not support our hypothesis that this effect would be spatiotemporally consistent. One difference among the experimental locations that may have led to inconsistent predation rates was that field

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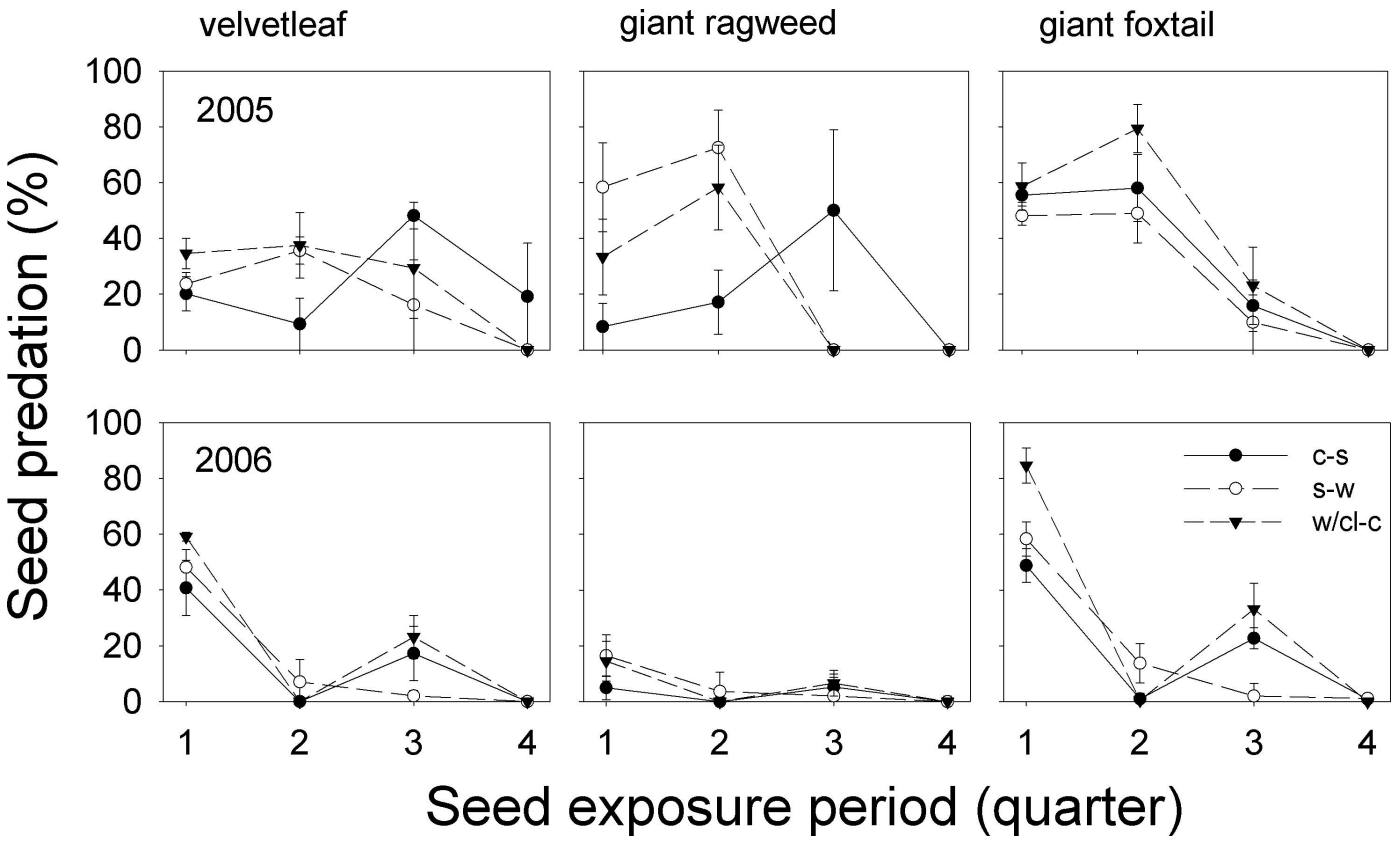


Figure 2. Quarterly postdispersal weed seed predation rates in Urbana, IL in 2005 and 2006. Symbols represent the mean (± standard error) of four replicate observations. Explanation of quarters: Q1 = July–September, Q2 = October–December, Q3 = January–March, Q4 = April–June.

plots were substantially longer and narrower in Michigan than they were in Illinois. Another potential limitation of the data was the relatively large amount of statistical noise due to the low number of replications ($N = 4$) per species in each crop sequence per site-year. However, we would argue that any tool being considered for addition to the ecological weed management tool kit should be robust enough to show clear effects even at low levels of replication. It may be possible for weed scientists to find locally suited crop sequences that will promote higher rates of weed seed predation, but our results do not provide evidence for a more general principle for cropping system design (e.g., choosing crop sequences with long-lasting vegetative cover) applying to broader geographic scales.

Abiotic and Biotic Determinants of Long-Term Predation. Quarterly seed predation rates in both Illinois and Michigan were highly variable, with means ranging from 0 to 100% removal of seeds placed in the field per quarter (Figures 2 and 3). In Illinois, quarterly seed predation rates generally declined over time, with greatest rates observed in quarter 1 (July through September), and lowest predation rates observed in quarter 2 (October through December) and quarter 4 (April through June) (Figure 2). In Michigan, seed predation rates remained high in at least one crop phase during each observation quarter, but no consistent trends were observed for rates within species or crop phase (Figure 3). Annual rates of postdispersal weed seed predation were somewhat less variable, with means ranging from 16 to 90% (Figure 4). As shown above, the considerable amount of observed variation in predation rates was organized in ways other than we first hypothesized.

A variance partitioning analysis indicated that abiotic and biotic factors other than crop sequence made the largest contributions to variation in long-term weed seed predation rates (Figure 5). For quarterly predation rates, quarter and weed species contributed 40 and 55%, respectively, to overall variation (Figure 5A). For cumulative predation rates, weed species was again the most important factor, contributing 35% to overall variation (Figure 5B), with smaller but substantial contributions from spatiotemporal variables including year (19%), location (20%), and block (16%). These results were consistent with ANOVA, which showed significant main effects of quarter and weed species on quarterly seed predation, and significant interactions between quarter, location, and weed species (Table 1). Cumulative predation rates were subject to main effects of weed species, and interactions between weed species, year, and location (Table 2).

In Illinois, cumulative seed predation in 2005 was lowest for velvetleaf (35 to 50%), intermediate for giant foxtail (45 to 55%), and greatest for giant ragweed (30 to 75%), whereas cumulative seed predation rates were more similar among weed species in 2006, ranging from 50 to 75%. In contrast, cumulative rates of seed predation in Michigan were similar for giant foxtail and velvetleaf in all three study years, ranging from 45 to 85%, but substantially lower for giant ragweed in each of those years (19 to 40%). The seeds of velvetleaf and giant foxtail are considerably smaller than those of giant ragweed, and more likely to be handled by both invertebrates and vertebrates (Davis and Raghu 2010; White et al. 2007; Williams et al. 2009). Giant ragweed seed predation is driven primarily by small invertebrate feeding activity (Harrison et al.

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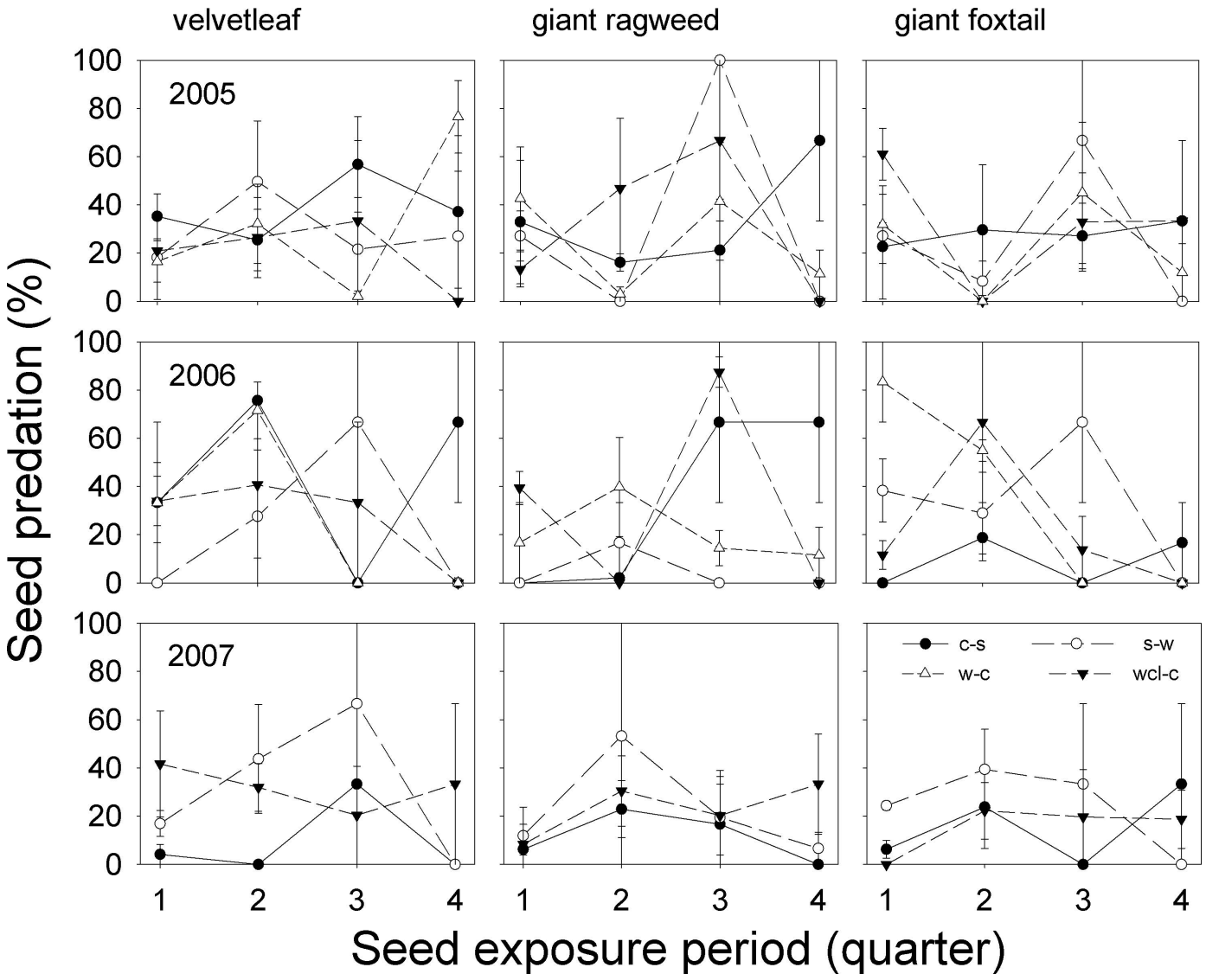


Figure 3. Quarterly postdispersal weed seed predation rates in East Lansing, MI in 2005, 2006, and 2007. Symbols represent the mean (± standard error) of four replicate observations. Explanation of quarters: Q1 = July–September, Q2 = October–December, Q3 = January–March, Q4 = April–June.

2003), and thus subject to different environmental constraints than that of velvetleaf and giant foxtail. The consistently low rates of cumulative predation of giant ragweed seeds in Michigan suggest that seed feeding activity of small vertebrates at this location was less focused on agricultural fields than in Illinois. Such a pattern could arise from landscape-level differences in field margin habitat complexity, with remnant woods and fencerows in Michigan acting as sinks rather than sources for predators (Menalled et al. 2001); in contrast, vertebrate granivores do not have a choice of feeding location in the largely undifferentiated grain production landscapes of central Illinois.

Variation in long-term seed predation associated with differences in weed species, quarter, and site-year has ample precedents in the weed science literature. Weed seeds vary in their palatability to granivores on the basis of seed size, seed coat strength, and secondary metabolite profile and nutritive value (Lundgren 2009; Lundgren and Rosentrater 2007), with significant intraspecific variation in palatability as well (Honek et al. 2011). Temporal variation in shelter for seed predators, due to changes in crop growth and management over time (Heggenstaller et al. 2006), and activity-density of predators due to seasonal changes in abiotic conditions (Davis and Raghu 2010; Saska et al. 2010) help explain quarterly variation in seed predation rates. The interplay between shifting crop habitat and granivore activity assumes an additional layer of complexity when the degree of overlap between temporal feeding windows of granivores and the phenology of weeds palatable to them is taken into account (Westerman et al. 2011).

Can Weed Seed Predation be "Managed"?. Due to the ubiquity of weed seed predation in arable systems (Menalled et al. 2006) and its potential for large contributions to weed demography (Davis 2006), there is much hope among weed ecologists that empirical studies will help identify a set of rules by which weed seed predation rates may be enhanced through application of a set of management principles. Some management guidelines, such as delaying primary tillage to allow predators time to consume recently dispersed seeds before they are protected through burial, appear to have strong theoretical and empirical validity (Harrison et al. 2003;

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Table 2. ANOVA of cumulative postdispersal weed seed predation rates in Urbana, IL and East Lansing, MI.

Source[a]	$d.f._{num}$	$d.f._{den}$	F	P
(intercept)	1	126	501	< 0.0001
Year	1	2	0.22	0.68
Crop sequence	2	126	1.55	0.22
Location	1	2	4.3	0.17
Weed species	2	126	17.1	< 0.0001
Y × W	2	126	4.7	0.01
L × W	2	126	14.7	< 0.0001
C × L	2	126	6.7	0.002

[a] The most parsimonious general linear mixed-effects model contained interaction effects only between year (Y) and weed species (W), location (L) and weed species, and crop sequence (C) and location. All other interactions were nonsignificant at $P > 0.20$.

Westerman et al. 2006). Others, such as the provision of habitat conducive to high rates of granivory, remain elusive. This question has been approached from several directions, yet none has provided conclusive results to date. For example, the construction of "beetle banks" (high plant species diversity field margins or peninsulas) can increase the diversity of beneficial arthropods within the plant-species-enriched area (MacLeod et al. 2004), but it is unclear whether such areas act as a source or sink for granivores acting within the crop field. Varying crop habitats within a diversified cropping system can exert strong influence on short-term seed predation rates (Heggenstaller et al. 2006), and have been projected through modeling exercises to have strong impacts on demography through differential long-term seed removal (Heggenstaller and Liebman 2006). The current study examined this possibility empirically, but our results did not support the existence of crop habitats that reliably promote high long-term weed seed removal rates in a variety of site-years.

The strong importance of site-year and weed species in determining postdispersal seed predation rates observed in this study offers two insights for weed management. First, as with much of agronomy, there is unlikely to be a universally successful recipe for managing habitat in arable fields for weed seed predators. Reliable approaches to managing granivore activity may need to be tailored to local weed flora and environmental conditions. Second, strong interannual variation in seed predation rates for different weed species in different crop phases suggests that a bet-hedging strategy may be helpful with respect to crop species represented in a crop sequence. Complementary crop phenologies and habitat structures may support better spatiotemporal overlap between granivore activity and weed seed dispersal (Heggenstaller et al. 2006; Westerman et al. 2011), especially when varying abiotic environments favor reproduction of different weeds in different years. In this way, a diversified rotation may provide

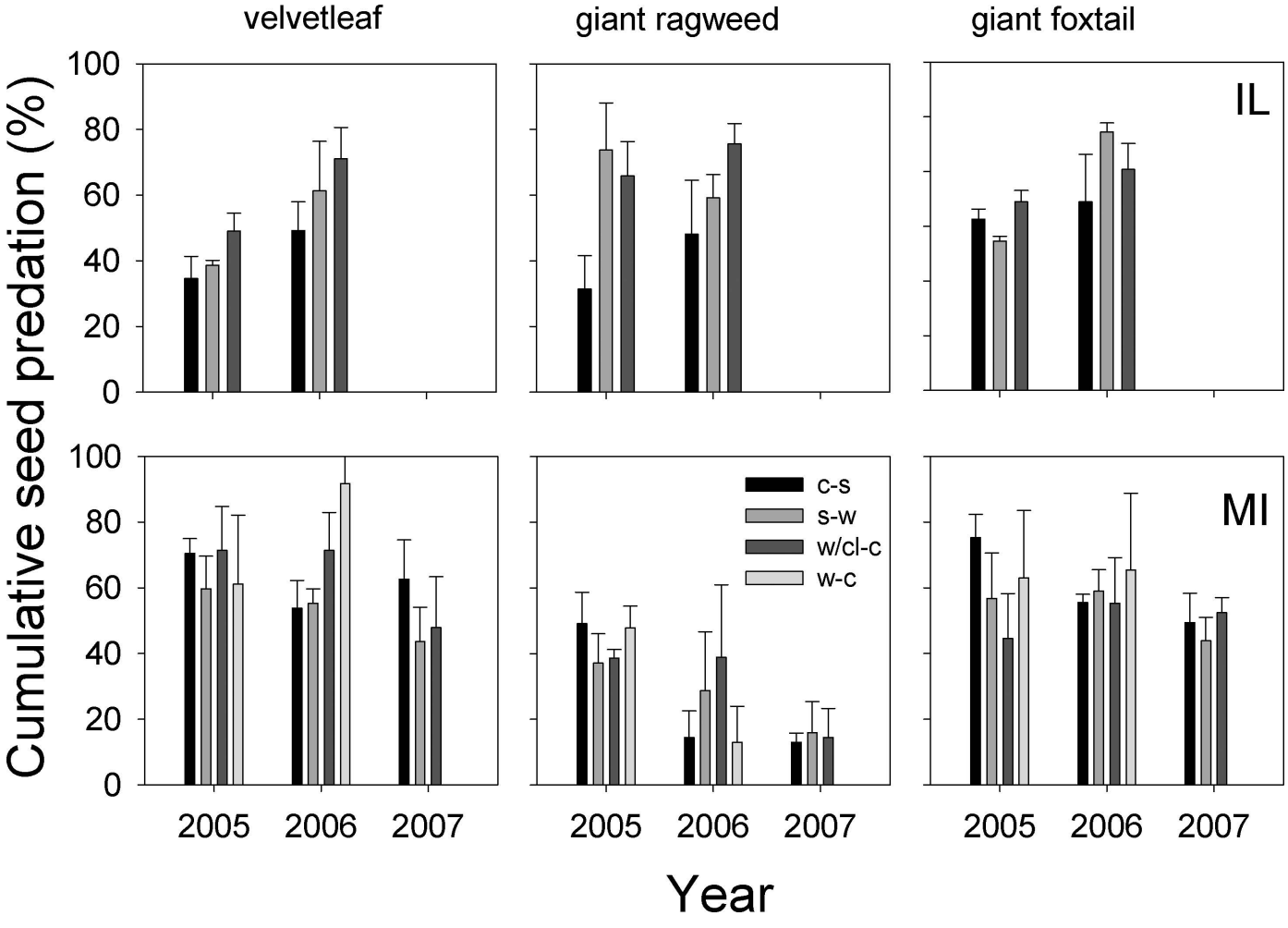


Figure 4. Cumulative annual rates of postdispersal weed seed predation in Urbana, IL and East Lansing, MI in 2005 through 2007. Measurements were made in four contrasting crop sequences, including corn–soybean (c-s), soybean–wheat (s-w), wheat underseeded with red clover followed by corn (w/cl–c), and wheat–corn (w-c). Bars represent the mean (± standard error) of four replicate observations.

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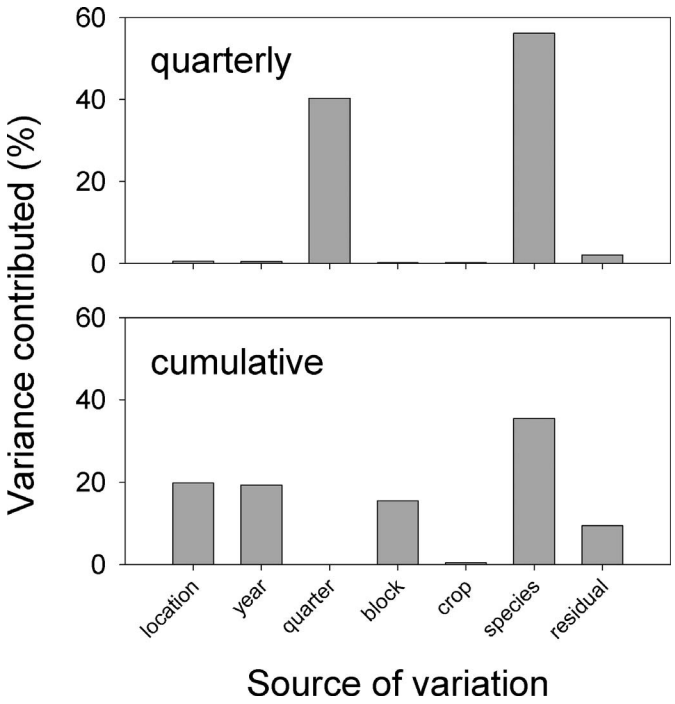


Figure 5. Variance components for quarterly and cumulative rates of postdispersal weed seed predation across site-years for Urbana, IL and East Lansing, MI from 2005 through 2007.

stability in seed predation rates by supporting granivory in some phases when others are performing poorly in a given year. Understanding the sources and mechanisms of site-year variation in weed seed predation among contrasting crop habitats remains a challenge for future investigations.

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