Symposium

Integrating measurements of seed availability and removal to estimate weed seed losses due to predation

Paula R. Westerman
Corresponding author. Department of Agronomy, 2501 Agronomy Hall, Iowa State University, Ames, IA, 50011-1010; prwester@iastate.edu

Matt Liebman
Department of Agronomy, 3405 Agronomy Hall, Iowa State University, Ames, IA, 50011-1010

Andrew H. Heggenstaller
Department of Agronomy, 3403 Agronomy Hall, Iowa State University, Ames, IA, 50011-1010

Frank Forcella
North Central Soil Conservation Research Laboratory, USDA-Agricultural Research Service, Morris, MN, 56267

To better understand seed predation and enhance weed seed losses in arable fields, we developed a conceptual model that integrates seed dispersal, seed burial, and seed demand, the three processes that determine the dynamics of summer annual weed seeds on the soil surface in late summer and autumn. Published and unpublished experimental data were used to parameterize a simulation model for a number of crop–weed combinations. Sensitivity analyses of models for giant foxtail in corn and soybean indicated that factors related to seed availability were more important in determining overall seed losses due to predation than those related to seed demand. Delaying harvest date and destroying unshed weed seeds collected at harvest emerged as promising strategies to reduce seed input into the seed bank. The role of plant debris in hiding weed seeds from predators was ambiguous and requires further investigation. Estimates of overall seed losses due to predation based on model simulations in various crops and cropping systems indicated that weed seed predation could serve as an important tool in ecological weed management.

Nomenclature: Giant foxtail, *Setaria faberi* Herrm. SETFA; corn, *Zea mays* L.; soybean, *Glycine max* (L.) Merr.

Key words: Seed predation rate, seed residence time, seed shed, simulation model, weed seed losses.

A growing number of studies indicates that postdispersal losses of weed seeds in arable fields can be substantial. Seed bank studies show that 70 to 99% of the seeds produced in a standing crop do not emerge as seedlings in subsequent crops, nor can they be recovered from the soil (Cardina and Norquay 1997; Gerowitt and Bodendörfer 1998). For example, up to 88% of giant ragweed (*Ambrosia trifida* L.) seeds were lost within 1 yr of exposure on the surface of a no-tillage corn field in Ohio (Harrison et al. 2003), and up to 70% of the weed seeds shed in cereal fields in the Netherlands were lost during one cropping season (Westerman et al. 2003).

Losses of this magnitude can have a substantial impact on weed population dynamics. Sensitivity analyses of models for various weed populations indicate that postdispersal seed losses influence population size more than any other life-cycle process (González-Andujar and Fernandez-Quintanilla 1991; Jordan et al. 1995). In ecologically based weed management systems, where weeds are managed through multiple control tactics, postdispersal seed losses can mean the difference between increasing and decreasing weed populations and may foster substantial reductions in herbicide use. For example, Davis et al. (2003) found in a wheat (*Triticum aestivum* L.)–corn–soybean rotation that if losses of giant foxtail seeds exceeded 63%, populations would decline, even when 10% of the weed's seedlings survived to reproductive maturity. Westerman et al. (2005) showed that in a 4-yr crop rotation system that received only 18% of conventional herbicides rates, removal of 40% of the weed seeds produced in soybean, the phase that allowed the highest weed seed production, would prevent increases in density of velvetleaf

(*Abutilon theophrasti* Medik). Models that included estimates of seed predation indicated that weed control efficacy could drop to 86% without permitting increases in velvetleaf density, whereas without predation > 97% control efficacy was required to prevent increases in velvetleaf density.

The intensity of postdispersal seed losses to predators varies both spatially and temporally (e.g., Cardina et al. 1996; Hulme 1994; Marino et al. 1997; Menalled et al. 2000; Mittelbach and Gross 1984; Tooley et al. 1999; Westerman et al. 2003; Whelan et al. 1991; Willson and Whelan 1990). Furthermore, several studies show that seed predation varies among tillage systems (Brust and House 1988; Cardina et al. 1996; Cromar et al. 1999) and crops (Andersson 1998; Cromar et al. 1999; Davis and Liebman 2003; A. H. Heggenstaller et al., unpublished data; Zhang 1993) and is influenced by the amount and type of crop residue (Cromar et al. 1999). This suggests that farming practices and cropping patterns can be used to maximize weed seed predation. So far, however, this idea has proven difficult to develop into recommendations regarding management practices because of the inconsistency in factors related to predation (Menalled et al. in press), and the magnitude of variation in predation intensity (Hulme 1994).

Studies reporting on seed predation have almost exclusively focused on seed demand, i.e., the proportion of weed seeds removed from a feeding station over a given period of time, and predation characteristics, such as intensity and timing of predation and seed preference (e.g., Marino et al. 1997; Menalled et al. 2000; Tooley et al. 1999). To fully understand the process of seed predation and the factors that influence it, the dynamics of seed availability to predators

must be included, which involves weed seed dispersal and seed incorporation into the soil matrix, in addition to seed demand by predators. At this stage, we have insufficient knowledge of the separate processes to predict the overall effect on season-long seed losses due to predation. In particular, we lack knowledge of whether the processes determining seed availability and seed demand amplify or counteract each other (Cardina et al. 1996). For example, a suitable habitat for predators provided by a certain crop at a certain time might lead to high levels of seed predation because weed seeds just started to disperse and soil conditions were such that seeds remained on the surface for a long time. However, seeds may also be dispersed at a time when seed demand by predators is low or when soil conditions allow seeds to disappear quickly into the subsoil. Various factors, such as crop type and farming practices, may influence several processes simultaneously, but not necessarily in the same direction. Consequently, without the help of a (computer) model, anticipation of how the interplay between these processes affects cumulative seed losses to predators and identification of conditions that favor or hinder seed predation will be difficult, if not impossible.

In this article, we first describe in more detail the three processes that determine overall seed losses due to predation: weed seed dispersal, burial, and predation. We then summarize quantitative information regarding the timing and rates at which these processes take place. In addition to published data, we draw from unpublished and preliminary data obtained from our ongoing trials aimed at elucidating and quantifying those processes. Finally, we formulate a model of weed seed predation in arable fields and use it to (1) identify key model parameters; (2) illustrate the role of weed seed dispersal, seed burial, and seed demand for a range of crops, cropping systems, and weed species; and (3) identify approaches that might lead to enhanced weed seed losses due to predation.

Processes Determining Predation

For weed seeds to be consumed, they first have to be available to predators. Predation occurs mainly on the soil surface after seed dispersal (Hulme 1994) and, to a much lesser extent, before dispersal, when seeds reside on the plant (Kjellsson 1985), or after seeds have been incorporated into the soil (Crawley 1992; Thompson 1987; White 2000). The risk of seed predation is, therefore, largely a function of the timing of seed shed and the duration of seed exposure on the soil surface. The amount of seed predation that actually is realized depends on the intersection between the temporal patterns of seed demand and seed availability.

Weed Seed Dispersal

Only a few studies have focused on the timing of weed seed dispersal in arable fields (Forcella et al. 1996; Westerman et al. 2003). In corn, Forcella and coworkers (1996) found that the onset of weed seed dispersal varied between years but could be predicted using accumulated growing degrees days. Seed dispersal ended with crop harvest, and weed species differed with regard to the percentage of seeds that were retained by the seed heads and dispersed by the combine at harvest. Seventy-nine percent of the seeds of the early-maturing species, wild mustard [Brassica napus (D.C.)
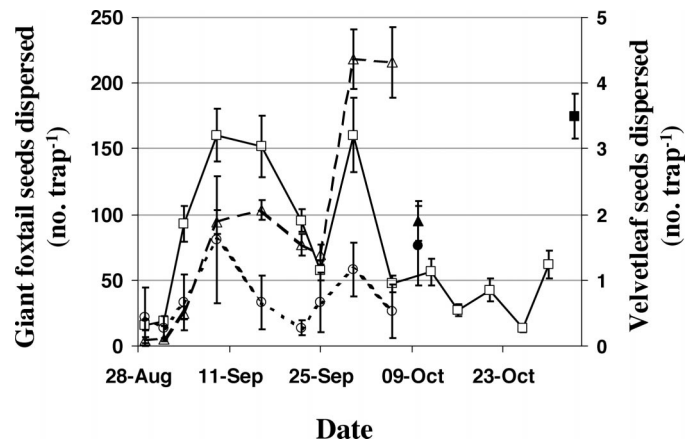

FIGURE 1. The average number (± SE) of giant foxtail seeds in corn (—□—), giant foxtail in soybean (—△—) and velvetleaf seeds in soybean (– –○– –; right y-axis) collected per seed trap (n = 18) between August 29, and October 10, 2004. Corresponding closed symbols (■, ▲, and ●) indicate numbers of seeds collected per seed trap postharvest.

L.C. Wheeler], were dispersed before corn harvest in 1994, but almost 100% were dispersed in 1993. In contrast, only 24% of the seeds of the later-maturing species, common lambsquarters (Chenopodium album L.), were dispersed before crop harvest in 1993, and 69% in 1994 (Forcella et al. 1996).

Using seed traps similar to those used by Forcella et al. (1996) and Westerman et al. (2003), Westerman (unpublished data) found contrasting patterns of weed seed dispersal between corn and soybean grown near Ames, IA (Figure 1). Seed traps were emptied every 3 to 7 d and before and immediately after crop harvest (corn, November 3, 2004; soybean, October 10, 2004). In addition, seed heads containing seeds were sampled from the field postharvest. In corn, 85% of all giant foxtail seeds were dispersed in a 66-d period before harvest. In contrast, in soybean, 90% were dispersed in only a 45-d period before harvest. In the same soybean field, 80% of the velvetleaf seeds were dispersed in the 45-d period before harvest (Figure 1). In the context of seed losses due to predation, temporal differences in weed seed dispersal among crop environments are important because seed demand patterns also vary among crops. Calculations done by Westerman et al. (2003) indicate that differences in the estimates of annual seed losses due to predation in cereal fields may largely stem from differences in the timing of seed shed.

Seed Demand

Numerous studies report on the removal of weed seeds exposed to predators in feeding stations (e.g., Brust and House 1988; Hulme, 1994; Cardina et al. 1996; Marino et al. 1997). Studies of this type essentially report seed demand, i.e., the potential fate of weed seeds if they had been available on the soil surface at that time, at those places, and at those densities. Although it is often implicitly assumed that all removed seeds are destroyed by the granivores, some may be transported and cached without being consumed (Vander Wall et al. 2005).

Interestingly, the pattern of seed demand over the season tends to be crop-specific. For example, in small grains grown in northern temperate areas, seed demand peaks in June
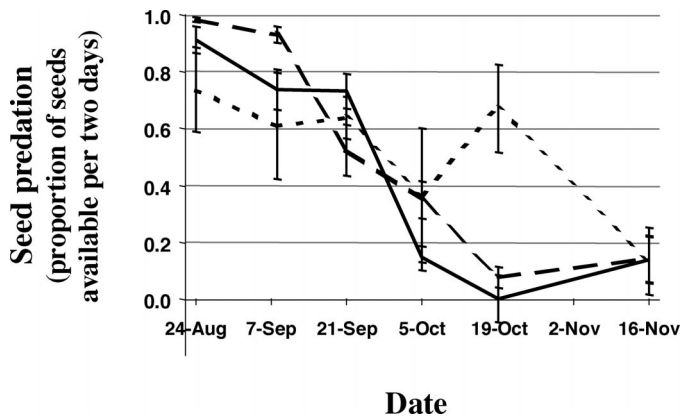
FIGURE 2. The average proportion (±SE) of giant foxtail seeds removed by seed predators in 2 d (n = 16), in corn (——), soybean (– – –), and red clover in triticale stubble (·····), between August 24, and November 16, 2004 (A. H. Heggenstaller et al, unpublished data).

FIGURE 3. The average percentage (± SE) of (A) giant foxtail and (B) velvetleaf seeds remaining on seed cards (n = 16) during a 3-d exposure period (September 7 to September 10) to seed predators in corn (——), soybean (– – –), and red clover in triticale stubble (·····).

(Mauchline et al. 2005; Watson et al. 2003; Westerman et al. 2003). In triticale (×*Triticosecale* spp.) undersown with a forage crop, weed seed demand followed a bimodal pattern, with a peak in June and another one in August, whereas for soybean and corn, weed seed demand tended to be highest in late August (A. H. Heggenstaller et al., unpublished data). Heggenstaller and coworkers measured seed demand by pinning seed cards, consisting of sand paper (4 by 10 cm) with 50 seeds of either velvetleaf or giant foxtail seeds glued to them, to the soil surface for 2 d, in an ongoing 10-ha cropping systems experiment in Boone, IA (Heggenstaller and Liebman 2006; Westerman et al. 2005). This experiment contained a range of crops grown in 2-, 3-, and 4-yr rotations with contrasting intensities of fertilizer and herbicide inputs. The proportion of seeds predated per 2 d for giant foxtail in corn, soybean, and red clover (*Trifolium pratense* L.) is shown for the period mid-August to November 2004 (Figure 2).

To characterize seed predation, Hulme (1994) distinguished seed encounter, the probability that a source of seeds is discovered, from seed exploitation, the intensity of predation once that source is discovered. Westerman and Heggenstaller (unpublished data) characterized seed predation in a slightly different manner, by estimating a delay time, representing the time until a seed source was discovered, and a consumption rate, representing the rate at which seeds were removed from the source, assuming an exponential decline (Mittelbach and Gross 1984; Whelan et al. 1991). Delay times and consumption rates were estimated simultaneously in three trials in the cropping systems experiment in Boone, IA, conducted in June, July, and September 2004, by counting the number of seeds per card on a daily basis in the field, until most seeds had been removed. Results for giant foxtail and velvetleaf in corn, soybean, and red clover in September are shown in Figure 3. The rate at which seeds were removed from seed cards appeared to vary among crops, weed species, and sampling dates.

Seed Burial

Predation by generalist postdispersal predators occurs mainly on the soil surface. Once soil or litter covers the seeds the probability of predation decreases substantially
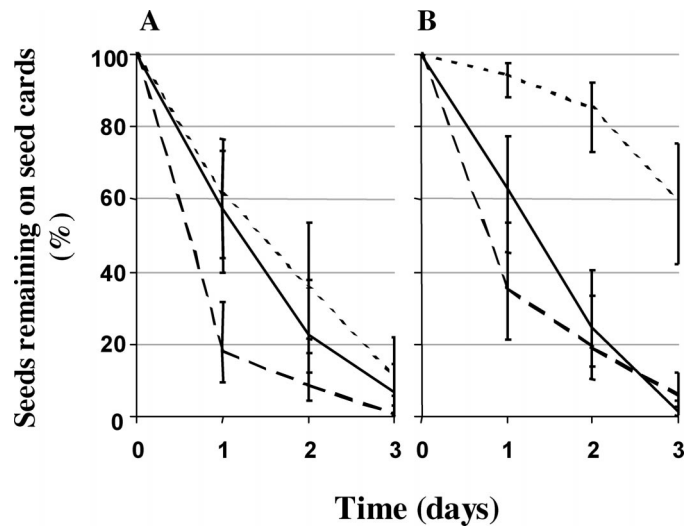
(Hulme 1994; White 2000). Few studies have investigated the fate of seeds on the soil surface or identified factors that influence the rate of entry of seeds into the seed bank (Chambers and MacMahon 1994, and references therein).

Tillage after harvest effectively removes weed seeds from the soil surface and buries them at various depths in the soil profile (Cousens and Moss 1990), thus protecting them from surface dwelling seed predators (Hulme 1994). Seeds also may enter the soil matrix via soil pores, cracks caused by drying–wetting or freezing–thawing cycles, coverage by mud or litter, or the actions of burrowing, hoarding, and caching animals (Chambers and MacMahon 1994).

Trials conducted under Dutch conditions using predator exclosures indicated that 50% of common lambsquarters seeds, which are relatively small, disappeared from the surface of a fallow field in about 2 wk, whereas the rate of burial of large-sized species, such as wild oat (*Avena fatua* L.) and wild buckwheat (*Polygonum convolvulus* L.), was considerably lower (Seguer Millàs 2002). The shape of seeds appeared to be less important than the size and weight (Seguer Millàs 2002).

In a study using artificial seeds, Westerman and Liebman (unpublished data) observed that seeds were lost from the soil surface in one of four ways: (1) entrance into cracks and passage beneath litter immediately following dispersal, (2) gradual incorporation into the soil matrix, (3) sudden disappearance due to severe rain, and (4) coverage by crop residue following harvest or by application of manure. Losses of seeds were estimated by using three sizes of ceramic beads (1.1 to 1.5 mm, 1.5 to 2.0 mm, and 2.25 to 3.0 mm in diameter) to simulate seeds in various crops in the cropping system experiment in Boone, IA, described above. Two small arenas (25 cm diameter) were created in each plot and sets of 50 beads of each size category were scattered over the surface in early September. By counting visible beads immediately after application and twice a week thereafter, the fate of the beads was followed over time in several crops. The rate at which the beads disappeared from the soil surface is illustrated for corn and for alfalfa growing in triticale stubble (Figure 4). Many beads were lost instantaneously
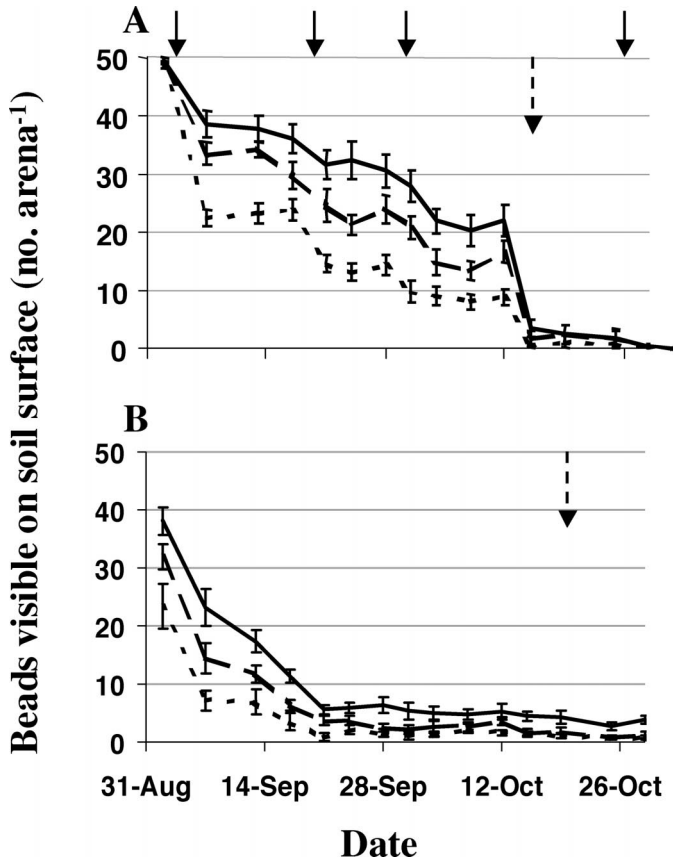
FIGURE 4. Counts of small (1.1 to 1.5 mm; ·····), medium (1.5 to 2.2 mm; – – –), and large (2.25 to 3.0 mm; ——) beads (± SE) over the course of time in small arenas (25 cm in diameter) in (A) corn and (B) alfalfa in triticale stubble (n = 8). Solid arrows indicate dates with rain; striped arrows indicate (A) corn harvest or (B) the application of composted manure.

during application and following rain and harvest. These events are indicated by the arrows in the figure.

Model Development

Model Concept

We propose, here, a model that describes the fates of summer annual weed seeds on the soil surface from the onset of seed shed in late August until the time of tillage in mid-November. The model includes the three major processes already discussed (seed shed, seed incorporation into the soil matrix, and seed removal by predators), and uses a daily time step (Figure 5). There are four state variables: (1) seeds on weed plants, W; (2) seeds on the soil surface, U; (3) seeds in the soil matrix, S; and (4) seeds consumed by seed predators, R. Flows between state variables are described by three major processes: dispersal, burial, and demand.

The rate at which ripe seeds are lost from weed plants can be described by

$$\frac{dW}{dt} = d(t) \cdot W \qquad [1]$$

with d being a relative dispersal rate that describes seed shed over time and which is crop- and weed-specific. A proportion, i, of the dispersed seeds disappears immediately into cracks or underneath litter and is considered to be inacces-
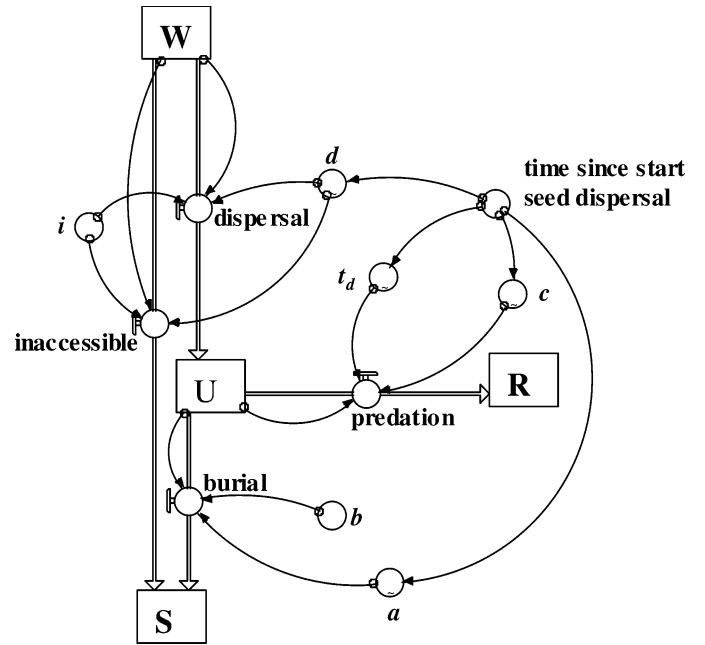

FIGURE 5. Flow diagram illustrating the dynamics of weed seeds on the soil surface within a cropping season. Boxes represent the state variables for seeds on weed plants (W), seeds on the soil surface (U), seeds in the seed bank (S), and seeds removed and consumed by predators (R). The valves represent the dispersal, burial, and predation rates; and the circles represent intermediate variables, the relative dispersal rate, d, relative burial rate, b, etc. The block arrows represent flows of seed, and the line arrows flows of information. For further explanation of the symbols, see text.

sible to surface-dwelling seed predators. The remainder, $1 - i$, is exposed to seed predators on the soil surface. The rate at which seeds on the soil surface disappear into the subsurface can be described by

$$\frac{dS}{dt} = [a(t) + b] \cdot U \qquad [2]$$

with b, a constant relative burial rate, describing the gradual disappearance of seeds into the subsoil as mediated by wind and rain; and a, a time-specific relative rate describing sudden and instantaneous disappearance due to, for example, harvest and tillage operations, or the application of composted manure. Alternatively, seeds on the soil surface may become prey to seed predators. The rate at which seeds are consumed by predators at any given time can be described by

$$\begin{cases} \dfrac{dR}{dt} = 0 & \text{for } t \leq t_d \\[2mm] \dfrac{dR}{dt} = c(t - t_d) \cdot U & \text{for } t > t_d \end{cases} \qquad [3]$$

with c, a relative consumption rate, which varies over time as a result of changes in, for example, the number of seed predators, availability of weed seeds, alternative food sources, energy or dietary requirements of the seed predators, changes in habitat quality, etc. Also included is t_d, a delay time, representing the time it takes seed predators to locate and exploit a seed source. Consequently, the overall dynamics of seeds on the soil surface can be described by

$$\begin{cases} \dfrac{dU}{dt} = (1 - i) \cdot d(t) \cdot W - [b + a(t)] \cdot U \quad \text{for } t \le t_d \\[2mm] \dfrac{dU}{dt} = (1 - i) \cdot d(t) \cdot W - [b + a(t) + c(t - t_d)] \cdot U \quad [4] \\[1mm] \hspace{4cm} \text{for } t > t_d \end{cases}$$

A simulation model was constructed in STELLA ® (ISEE systems, version 7.0.3). Model calculations integrating seed dispersal, burial, and demand were used to estimate the overall percentage of weed seeds consumed by predators, Y = 100 · R/S %. All calculations started with W = 1,000 seeds, all other state variables were set at zero, and t, the time-step for integration, was set at 0.05 day ($\approx$1/10 of the smallest time coefficient in the system).

Parameter Values

We estimated the relative dispersal rate, d, from the seed dispersal data by Forcella et al. (1996) and by Westerman (unpublished data). The relative consumption rate, c, and the delay time until a seed source is discovered by predators, t_d, were estimated by Westerman and Heggenstaller (unpublished data) in three trials during the 2004 growing season. Because the values for c and t_d change over time, we used regression lines between either c and t_d and the proportion seed predation per 2 d, to estimate c and t_d from the trials of A. H. Heggenstaller et al. (unpublished data) for the period late August to mid-November 2004. Values for the proportion of the dispersed seeds that is immediately inaccessible to predators, i, the relative burial rate, b, and relative rate describing the sudden loss of seeds at harvest, a_h, were estimated by Westerman and Liebman (unpublished data) for three bead sizes. We used the estimates for the smallest bead size (1.1 to 1.5 mm) as parameter values of seed behavior in our model, except in the case of velvetleaf, for which we used the estimates for the largest bead size (2.15 to 3.0 mm). Estimates of seed loss due to severe rain events, a_r, were not included in the model because the fate of the missing beads was unknown; they may have either been covered by mud or washed into cracks, or splashed or washed out of the arenas (Westerman and Liebman, unpublished data). In the latter case, the beads may still have been on the soil surface.

Model Calculations and Sensitivity Analysis

Crop- and weed-specific parameters values of $a(t)$, b, $c(t)$, $d(t)$, $t_d(t)$, and i were available for giant foxtail in corn and soybean and for velvetleaf in soybean. Models parameterized for these crop–weed combinations were used in initial model calculations. Models parameterized for giant foxtail in corn and in soybean were used to measure model sensitivity, which we determined by calculating the relative change in Y as a result of a 20% change in one of the parameters $a(t)$, b, $c(t)$, $d(t)$, $t_d(t)$, and harvest date, t_h ([$\Delta Y/Y$]/[$\Delta z/z$], with z being one of the parameters). Changing $c(t)$ or $d(t)$ results in increased or decreased consumption of seeds or accelerated or decelerated seed shed over the entire period. The parameter, $a(t)$, describing sudden seed burial as a result of management practices, was changed for each event separately. Shifting harvest date, t_h, to an earlier date caused all remaining unshed seeds to be dispersed, whereas shifting it

to a later date prolonged natural dispersal. Because estimates of the relative seed dispersal rate, d, after the official harvest day were, obviously, lacking, the value of d on the day preceding harvest was used postharvest.

To investigate the effect of a wider range of crops on overall seed predation, Y, we parameterized the model with values of a_h, b, $c(t)$, i, and $t_d(t)$, estimated for giant foxtail in red clover growing in triticale stubble, in alfalfa growing in triticale stubble, and in a second-year stand of alfalfa but assumed that the relative dispersal rate, d, in those crop environments was similar to that of giant foxtail in corn. Seeds on the soil surface were not lost due to harvest activities but due to the application of composted manure on the red clover crop and second-year alfalfa stand, as depicted by a_m.

To investigate the effect of a wider range of weed species on Y, we parameterized the model with values of a_h, b, $d(t)$, and i for common lambsquarters and wild mustard in corn, given by Forcella et al. (1996) but assumed that the relative predation rate, $c(t)$ and the delay time $t_d(t)$ for those weeds were similar to values for giant foxtail in corn. This is a reasonable assumption given the fact that the patterns of seed demand over time in a specific crop always tend to be very similar for different weed species, although the level of seed demand can differ among weed species (A. H. Heggenstaller et al., unpublished data; Mauchline et al. 2005; Watson et al. 2003; Westerman et al. 2003).

In the preceding analyses, parameter values used for a_h, b, $c(t)$, i and $t_d(t)$, involving corn and soybean, had been estimated in a 4-yr rotation (corn–soybean–triticale + alfalfa–alfalfa) managed with reduced chemical inputs and increased tillage intensity. To investigate whether cropping system has an effect on overall seed predation, Y, we included data from a conventionally managed 2-yr rotation (corn–soybean) and compared models parameterized with values estimated for giant foxtail in corn grown in 2-yr vs. 4-yr rotations and in soybean grown in 2-yr vs. 4-yr rotations. A similar comparison was conducted for velvetleaf in soybean grown in 2-yr vs. 4-yr rotations.

Model Results and Discussion

The simulation model, combining estimates of seed dispersal, burial, and demand, calculated Y at 65% for giant foxtail in corn (Figure 6A; Table 1A). Few seeds were present on the soil surface at any given time before harvest because seed input by dispersal was balanced by seed output by predation and burial. Corn harvest had an important effect on both seed dispersal and seed burial. Up to the harvest date, Y was about 75% but decreased to 65% at harvest. Seeds retained by the seed heads (15% of total) were dispersed at once; however, most were immediately covered by soil and plant debris (a_h). Consequently, almost all seeds that had been retained by the seed heads up to harvest ended up in the seed bank and became inaccessible to predators.

The relationship between the proportion of unshed seeds and Y was not always as clear-cut as described above. In the case of giant foxtail in soybean, Y was 60%. We expected a higher Y, based on the low percentage of seeds retained by seed heads at harvest (10.5%). However, an additional 6.3% of the seeds had accumulated on the soil surface. In soybean, giant foxtail seeds were dispersed in a very short period of
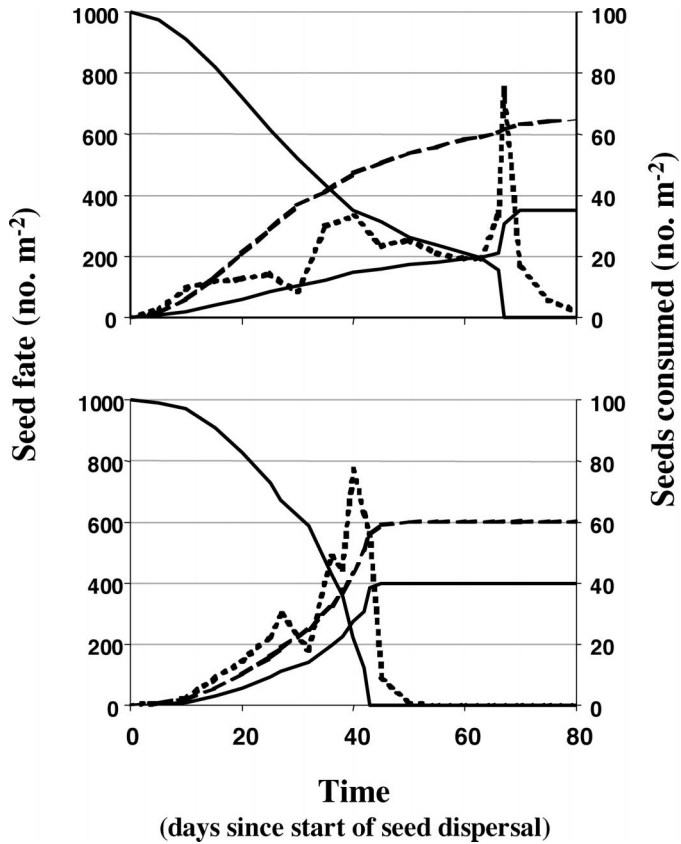
FIGURE 6. Number of seeds on the plant (——), on the soil surface (·····), in the soil matrix (left y-axis; ——), or consumed by predators (right y-axis; – – ·) for giant foxtail in (A) corn or (B) soybean.

TABLE 1. The percentage of seed predation, Y, as affected by (A) weed species, (B) crop type, and (C) cropping system, as calculated by the simulation model.

A. Effect of weed species on percentage of predation in corn.

Giant foxtail	Common lambsquarters		Wild mustard	
2004	1993	1994	1993	1994
65	32	61	65	78

B. Effect of crop type on percentage of predation in giant foxtail seeds.

Corn	Soybean	Red clover in stubble	Alfalfa in stubble	Alfalfa
65	60	32	35	64

C. Effect of cropping system on percentage of predation

	2-yr	4-yr
Giant foxtail in corn	67	65
Giant foxtail in soybean	80	60
Velvetleaf in soybean	82	79

and stronger seed dispersal earlier in the season (Figure 1) when seed demand was higher.

The above examples illustrate the complexity of interactions between seed dispersal, seed burial, and seed demand. They show that a similar result (Y) can be obtained through different routes but also that combinations of slightly different settings of the three processes may result in very different levels of overall predation. The above examples also suggest that there is ample room for manipulation of predation because many parameters are directly or indirectly related to cropping systems and farming practices. To identify the most influential parameters, we conducted a sensitivity analysis on the model parameterized for giant foxtail in corn and soybean.

Sensitivity Analysis

Not surprisingly, sensitivity analysis of the model for giant foxtail in both corn and soybean showed that Y was most sensitive to changes in the date of harvest, t_h (Table 2). Advancing t_h in corn by 13 d (from November 3 to October 21) reduced Y from 65 to 61% because a larger proportion of the weed seed (21%) was not yet dispersed. The reduction in Y was greater in soybean; advancing t_h in soybean by 9 d (from October 1 to October 10) reduced Y from 60 to 50%. Sensitivity ranking of the remaining parameters was

time (45 d; Figure 1), and seed burial and seed consumption together were not high enough to prevent the accumulation of seeds on the soil surface (Figure 6B). Both unshed seeds and accumulated seeds on the soil surface were worked into the soil and underneath litter at crop harvest. In the case of velvetleaf in soybean, Y was 79%. Here, we expected a lower Y, based on the high percentage of seeds retained by seed heads at harvest (19%). Seed burial at harvest was compensated by conditions favorable for seed consumption before harvest: a lower value for the relative burial rate, b, for the larger velvetleaf seeds; a lower crop-specific proportion of the seeds that was immediately inaccessible to predators, i;

TABLE 2. The relative change (%) in the overall proportion of seeds consumed by seed predators, Y, as a result of a 20% increase or decrease in one of the parameter values, z, for giant foxtail in corn and soybean ([$\Delta Y/Y$]/[$\Delta z/z$]·100%).

			Giant foxtail in corn			Giant foxtail in soybean		
Description	Parameter	Dimensions	Standard value	−20%	20%	Standard value	−20%	20%
Relative rate of								
—dispersal	d	d^{-1}	*	33	24.9	*	8.1	8.2
—burial	b	d^{-1}	$3.64·10^{-2}$	−6.4	−6.1	$4.67·10^{-2}$	−6.9	6.8
—seed loss due to crop harvest	a_h	d^{-1}	1.52	−7.2	−5.5	0.62	−4.7	4.5
—consumption	c	d^{-1}	*	12.4	9.1	*	15.2	13.8
Proportion immediately inaccessible	i	d^{-1}	0.218	−24.4	−24.4	0.365	−45.5	45.5
Delay time	t_d	d	*	−0.2	−0.2	*	0.04	0.07
Harvest date	t_h	d	67	28.8	43.3	43	79.9	100.6

* Variable over the season.

different for the two crops. In corn, the second most-influential parameter was the relative dispersal rate, d, for reasons again connected to harvest. Accelerating seed dispersal by 20% caused only 11% of the seeds to be on the plant at harvest, resulting in 60% predation. The Y was almost as sensitive to i (proportion of dispersed seeds immediately inaccessible) as it was to d. Obviously, seeds that disappear into the soil straight from the plant were never exposed to seed predators and, thus, never at risk of predation. The smaller this proportion, the higher the Y. The relative consumption rate, c, was ranked fourth. In soybean, the second most-influential parameter was i, followed at great distance by c and d. Even if c is doubled, Y would only increase from 65 to 69% in corn and from 60 to 64% in soybean. Future analyses are necessary to determine whether critical periods might exist where c has a disproportionally large effect on Y. In that case, research involving seed demand could focus on removing constraints for seed predator abundance and activity during those critical periods.

The above analysis leads to the interesting conclusion that the actual rate at which seeds were consumed by predators wasn't nearly as important as the phenology of the weed in combination with the timing of farming practices, notably harvest. The results suggest that, other factors being equal, fields containing seed-bearing weeds should be harvested last. In fact, weed seed losses may potentially be very high in perennial forage crops without any harvest or tillage activity. Obviously, whether or not postponing harvest date is a feasible option depends on many factors other than weeds, such as local weather forecast, soil conditions, the availability of labor and machinery, crop prices, etc., which fall beyond the scope of this article. However, increasing weed seed predation may become an additional consideration in planning harvest dates. Removing nondispersed weed seeds at harvest is another option to increase weed seed loss because nondispersed seeds have the highest probability of reaching the safety of the seed bank. Potentially, combine harvesters could be designed or modified for weed seed removal and destruction (Ballaré et al. 1987; Slagell Gossen et al. 1998).

The Effect of Weed Species, Crop Type, and Cropping System

To investigate the effect of weed phenology on Y, we conducted model simulations in corn, comparing giant foxtail with common lambsquarters (late maturing) and wild mustard (early maturing), using the seed dispersal patterns near Morris, MN, reported by Forcella et al. (1996) (Table 1B). Model calculations confirm that, in general, the later weed seeds are dispersed and the higher the proportion of seeds retained in the seed heads at harvest, the lower the Y (table 1B). This finding implies a strong selective pressure toward late seed shattering, in particular in systems that allow some weed seed production. Studies on the timing of weed seed shed are rare, and to our knowledge, no studies have ever checked whether the timing of seed shed has indeed changed over time. In climates that allow prolonged seedling emergence, seedling cohorts may differ in the timing of seed maturation (Recasens et al. 2005). Selective pressure by seed predators may be one of the mechanisms by which the persistence of late emerging and maturing cohorts can be explained, despite lower quantity and quality of seeds

produced by these cohorts. Weed phenology is usually tightly linked with crop phenology and the management activities that steer them, e.g., planting date, timing of weed control measures, and fertilizer applications. In the current study, a higher percentage of giant foxtail seed were retained by the seed heads at harvest in the corn field than in the soybean field, despite the later harvest date for corn compared with soybean. Trying to manipulate weed phenology may prove impossible without manipulating crop phenology.

We conducted two sets of simulations to investigate the effects on Y of soil surface structure and plant debris on the soil surface, both of which influence i. In the first, we compared giant foxtail in crops with a thick layer of litter on the soil surface (red clover in triticale stubble and alfalfa in triticale stubble) vs. a thin layer or no litter on the soil surface (corn, soybean, and established alfalfa) (Table 1A). The parameter i was estimated at 0.61 to 0.65 in the forage crops and 0.20 to 0.31 in the other crops. The overall percentage of predation, Y, was indeed much lower for the forage crops in triticale stubble (32 to 35%) than for the other crops (60 to 65%) (Table 1B). Next, we compared model simulations for giant foxtail and velvetleaf in corn and soybean in a 2-yr rotation system vs. a 4-yr rotation system (Table 1C). Soil surface characteristics differed between the systems as a result of differences in the intensity of tillage, crop rotation sequence, input of organic matter, and so on, resulting in a smaller i, b, and a_h in the 2-yr relative to the 4-yr corn and soybean. For foxtail in soybean, the simulations showed that the overall percentage of predation, Y, was higher in the 2-yr rotation (80%) than in 4-yr rotation (60%) (Table 1C).

Diversified crop-rotation systems, such as the 4-yr crop rotation system used above, can represent an effective means of controlling weeds, reducing requirements for herbicide inputs (Leighty 1938; Liebman and Staver 2001). For this reason, diverse crop rotations are one of the foundations of ecological weed management (Liebman and Gallandt 1997). Seed predation would fit in well as an additional tool in the ecological toolbox for suppressing weeds. Measures to accommodate and enhance predation are, therefore, more likely to be adopted in low–external input systems and in organic systems than in systems that use conventional weed management. Moreover, seed mortality due to predation or other causes represents an essential and necessary component in controlling weeds in these more-diverse cropping systems (Westerman et al. 2005). Westerman et al. (2005) calculated that in a corn–soybean–triticale + alfalfa–alfalfa crop-rotation system, seed losses of 40% in the soybean phase or 27% in each phase would be sufficient to stabilize velvetleaf populations (Westerman et al. 2005); seed losses in excess of that would result in declining velvetleaf populations. Our simulations using the model described in the present article indicate that the minimum conditions are easily met (65, 60, 35, and 64% predation were predicted to occur in corn, soybean, triticale + alfalfa, and alfalfa, respectively). Thus, further enhancing seed predation in the 4-yr rotation system would not seem to be a necessity.

Importance and Implications

The preceding discussion points to two important questions: how realistic are our simulation estimates of Y, and

what may have caused errors in its estimation? Harrison et al. (2003) reported 39 and 88% removal of giant ragweed seeds in no-till corn when exposed for a winter (November to February) or a year (November to November), respectively, and Cromar et al. (1999) reported 22 to 43% predation of common lambsquarters and barnyardgrass [*Echinochloa crus-galli* (L.) Beauv.] in different crops (wheat, corn, soybean) and tillage regimes (moldboard plow, chisel plow, no-till) when weed seeds were exposed to predators for periods varying from 1 to 2.5 mo. Higher seed-loss estimates come from discrepancies in seed-bank studies. For example, Cardina and Norquay (1997) showed that 70 to 99% of the velvetleaf seeds produced in a standing crop could not be accounted for and were probably lost due to a combination of infections, fatal germination, and predation. Relative to those results, our estimates of seed losses due to predation lie in the middle. Based on our estimates, it seems likely that giant foxtail populations will decrease in both corn–soybean rotations and in corn–soybean rotations extended with small grains and forage crops. This is precisely what seems to be happening in the ongoing 10-ha cropping-systems experiment in Boone, IA, from which most of the parameter estimates used here were derived (M. Liebman, unpublished data). Future comparisons of field observations with the results from demographic models will be necessary to confirm the contribution of seed predation to weed suppression. Moreover, additional research is required to quantify seed losses due to predation in commercially sized fields and in multiple years to verify our estimates and to further improve the simulation model presented here.

We recognize the need for further scrutiny of several parameter values used here, which were based on preliminary and unpublished data, and we are aware of problems and inaccuracies in a number of parameter estimates that may have led to under- or overestimation of *Y*. For example, the effect of severe rains on bead disappearance was not included in the model because the burial rate could not be estimated correctly due to beads splashing out of observation arenas. We assumed that seeds, once covered by soil or litter, were safe from predators, but burial does not necessarily eliminate predation risk (Hulme 1994). This may be especially true for coverage by crop residue (Cromar et al. 1999; Harrison et al. 2003). Unknown is the fate of seeds trapped in litter once the litter degrades or once diminishing supplies force winter-active predators, such as rodents, to intensify searching effort (Harrison et al. 2003). Furthermore, there are many issues in relation to the methodology used to estimate seed removal by predators that have not been fully resolved, such as the influence of spatial arrangement and density dependence (e.g., Marino et al. 2005). Fortunately, our sensitivity analyses showed that the estimate of seed-consumption rate is not especially important with regard to the overall level of predation, *Y*.

At this point, the exact numerical outcome of the calculations is not as important as the conceptual basis of the model and its implications. The integration of seed dispersal, seed burial, and seed demand into one system creates a unifying conceptual framework in which it becomes easier to study and evaluate factors that simultaneously influence multiple aspects of the system. In that sense, the model gives us a much fuller understanding of the interactions determining seed predation. The simulations showed how these interactions may materialize in a range of situations and allowed us to generate testable questions. Most important, the model signifies a next step toward the possible use of seed predation as a means of controlling weeds by identifying opportunities to manipulate seed predation through changes in farming practices. For example, it may be worthwhile to investigate how tillage and residue management can be used to decrease the proportion of dispersed seeds that becomes immediately inaccessible to predators. The results of this study justify a shift in attention from a singular focus on seed demand and attempts to increase seed demand by, for example, enhancing predator habitat quality or predator numbers, to a more integrated approach in which impacts on seed dispersal, seed burial, and seed demand are evaluated simultaneously.

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