

## Symposium

# Are many little hammers effective? Velvetleaf (*Abutilon theophrasti*) population dynamics in two- and four-year crop rotation systems

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To improve understanding of relationships between crop diversity, weed management practices, and weed population dynamics, we used data from a field experiment and matrix models to examine how contrasting crop rotations affect velvetleaf. We compared a 2-yr rotation system (corn–soybean) managed with conventional rates of herbicides with a 4-yr rotation (corn–soybean–triticale + alfalfa–alfalfa) that received 82% less herbicide. In November 2002, a pulse of velvetleaf seeds (500 seeds  $m^{-2}$ ) was added to 7- by 7-m areas within replicate plots of each crop phase–rotation system combination. Velvetleaf seed, seedling, and reproductive adult population densities, seed production, and seed losses to predators were measured during the next year. Velvetleaf seed production was greater in the 4-yr rotation than in the 2-yr rotation (460 vs. 16 seeds  $m^{-2}$ ). Averaged over 12 sampling periods from late May to mid-November 2003, loss of velvetleaf seeds to predators also was greater in the 4-yr rotation than in the 2-yr rotation (32 vs. 17% per 2 d). Modeling analyses indicated that velvetleaf density in the 4-yr rotation should decline if cumulative losses of seeds produced in the soybean phase exceeded 40%. Achieving such a level of predation appears possible, given the observed rates of velvetleaf seed predation. In addition, no tillage occurs in the 4-yr rotation for 26 mo after soybean harvest, thus favoring seed exposure on the soil surface to predators. Models that included estimates of seed predation indicated that to prevent increases in velvetleaf density, weed control efficacy in soybean must be  $\geq 93\%$  in the 2-yr rotation, but could drop to 86% in the 4-yr rotation. These results support the hypothesis that diverse rotations that exploit multiple stress and mortality factors, including weed seed predation, can contribute to effective weed suppression with less reliance on herbicides.

**Nomenclature:** Velvetleaf, *Abutilon theophrasti* Medicus ABUTH; alfalfa, *Medicago sativa* L.; corn, *Zea mays* L.; soybean, *Glycine max* (L.) Merr.; triticale, *Triticosecale* spp.

**Key words:** Crop rotation, matrix population models, seed predation, weed population dynamics.

The concept of population thresholds is well established in the theory and practice of insect pest management but has never been widely implemented for managing weeds. Theoretically, with knowledge of crop prices, weed control costs, and the yield loss that a given density of weeds would cause if left uncontrolled, a weed control measure could be applied whenever the expected economic benefits exceeded the costs of treatment. In reality, such decisions are complicated by (1) the lack of yield loss data for most weed–crop species combinations, (2) the large degree of variation that exists among locations and years in weed density–crop yield loss relationships, and (3) the ability of weed seeds produced in the current crop to contribute to future infestations (Cousens 1987; O’Donovan 1996). Consequently, farmers and crop protection advisors considering threshold-based decisions are confronted not only by considerable uncertainty in how much damage weeds will cause in the short term but also by the prospect of failing to prevent, or even encouraging, weed infestations over the long term.

Cousens (1987) proposed the development of “economic optimum thresholds” that account for weed seed produc-

tion, seed survival, and costs of future infestations. For potentially competitive weed species that produce large numbers of long-lived seeds, economic optimum threshold densities may be an order of magnitude lower than thresholds based on damage to the current season’s crop (Cousens and Mortimer 1995). Norris (1999) suggested that the best approach for managing weeds over the long term is to adopt a “no-seed threshold,” whereby all reproductive weeds in a field are eliminated. This is a logical course of action if it is assumed that most seeds will survive with the potential to germinate and infest future crops. A growing body of evidence suggests, however, that weed seed mortality can have important regulatory effects on weed population density. Moreover, rates of this process may vary substantially among crops and crop management systems.

Weed seed mortality in and on soil varies with weed species, seed burial depth, soil disturbance regime, and other factors (Mohler 2001). Over periods of weeks or years, all weed species lose some proportion of their seeds because of consumption by vertebrate and invertebrate seed predators, attack by pathogens, physiological aging and exhaustion of

reserves, and germination at locations or times of year that are inappropriate for seedling emergence (Mohler 2001).

Farming practices can strongly affect weed seed mortality rates. Brust and House (1988) found that weed seed predation was two- to threefold greater in a no-tillage soybean production system that maintained wheat (*Triticum aestivum* L.) straw on the soil surface than in a conventionally tilled system without residue cover. Davis and Liebman (2003) noted that loss of giant foxtail (*Setaria faberi* Herrm.) seeds to predators was twice as great when wheat was intercropped with red clover (*Trifolium pratense* L.) than when wheat grew alone.

Farming practices can also affect weed fecundity. Kegode et al. (1999) reported that seed production by green and yellow foxtail [*Setaria viridis* (L.) Beauv. and *S. glauca* (L.) Beauv.] in wheat stubble was reduced > 70% when tillage or glyphosate application occurred within 2 wk after wheat harvest, as compared with an untilled, unsprayed fallow treatment. Dowling and Wong (1993) found that heavy grazing of pastures reduced grass weed seed production and seedling densities in a succeeding wheat crop by 91 to 99%, compared with an ungrazed control treatment.

The fact that farming practices can be used to manipulate weed fecundity and weed seed mortality rates suggests that weed populations might be regulated through concerted sets of control tactics and ecological interactions whose individual effects are weak but whose cumulative effects prevent population growth and competition against crops. Liebman and Gallandt (1997) called this concept “many little hammers,” to contrast it with conventional weed management approaches that emphasize single “large hammers,” (e.g., herbicides and cultivation). They suggested that diversified crop rotations were likely to provide the best opportunities for exploiting diverse sets of tactics and ecological processes to suppress weeds.

Population dynamics models can serve as important tools for understanding the effects of diversified crop rotations on weeds at multiple life stages. Models may provide insights into how systems should perform over time under different sets of assumptions, as well as indicate the most sensitive life stages influencing population trajectories. Matrix population models have been used productively by conservation biologists and wildlife ecologists (Caswell 2001) and are now being used with increasing frequency by weed scientists interested in crop rotation effects on weeds (Davis et al. 2003, 2004; Mertens et al. 2002).

In this study, we used weed demographic data from a field experiment and matrix models to explore whether a diverse rotation system receiving reduced quantities of herbicides could prevent weed population growth. Secondarily, we sought to examine the effects of weed seed predation in diverse and less-diverse rotation systems.

Although a large portion of the article is devoted to describing the field trial used to estimate weed demographic parameters, it is not our intent here to conduct an in-depth study of those parameters. Rather, the demographic parameter set is presented so that we can examine the influence of diverse crop rotations and weed seed predation on weed population growth on the basis of realistic data. Only above-ground demographic parameters, which are most likely to be influenced by management and rotation, were estimated. Belowground demographic parameters, which are probably

less prone to short-term crop- and rotation-specific variation, were obtained from the literature.

## Materials and Methods

### Site and Management Practices

We used an ongoing 10-ha cropping systems experiment in Boone, IA, to generate demographic parameters for velvetleaf in 2- (corn–soybean) and 4-yr (corn–soybean–triticale + alfalfa–alfalfa) crop rotation systems. The experiment was initiated in 2001 and contains all phases of each rotation every year in four replicate blocks. Plot size is 18 by 85 m. Soils at the site are Clarion loam (fine-loamy, mixed, superactive, mesic, Typic Hapludolls), Nicollet loam (fine-loamy, mixed, superactive, mesic, Aquic Hapludolls), and Webster silty clay loam (fine-loamy, mixed, superactive, mesic, Typic Endoaquolls). Precipitation and average air temperature from April through October 2003 were 700 mm and 16.8 C, respectively, which was 5% higher and 3% lower than the 50-yr mean values at the site.

The different rotations present in the experiment are suitable for different farming systems and use different sets of management practices. Crops in the 2-yr rotation are typical of cash grain farming systems in North Central Iowa and much of the Corn Belt and are managed with conventional rates of synthetic fertilizers and herbicides (Table 1). The 4-yr rotation is suitable for farming systems that include ruminant livestock and receives reduced rates of fertilizers and herbicides (Table 1). In 2003, herbicide use, calculated as the amount of herbicide applied over the period of the rotation divided by the number of years of the rotation, was 82% lower in the 4-yr than in the 2-yr rotation ( $0.4$  vs.  $2.4$  kg ai ha<sup>-1</sup> yr<sup>-1</sup>). This reduction was achieved by coupling banded sprays with cultivation in corn and soybean and eliminating herbicides in triticale and alfalfa (Table 1). Because of nitrogen fixation by alfalfa and the application of a low rate of manure for corn production, the 4-yr rotation received 72% less synthetic nitrogen fertilizer in 2003 than did the 2-yr rotation (Table 1). Despite differences in input levels, corn and soybean yields did not differ in 2003 between the different rotation systems ( $\bar{x}_{\text{corn}} \pm \text{SE} = 11.8 \pm 0.2$  Mg ha<sup>-1</sup>;  $\bar{x}_{\text{soybean}} \pm \text{SE} = 3.0 \pm 0.1$  Mg ha<sup>-1</sup>).

### Experimental Procedures and Velvetleaf Population Data

We used a “pulse-chase” approach to study the population dynamics of velvetleaf in association with a second weed species, giant foxtail. In October 2002, we determined velvetleaf and giant foxtail seed densities in the soil of 7- by 7-m subplot areas in each main plot (i.e., each replicate of each phase of each rotation system) by drawing cores to a depth of 20 cm and separating seeds from soil with an elutriator (Wiles et al. 1996) and an air column separator. These samples indicated that background densities of the two species were very low:  $4 \pm 2$  and  $21 \pm 7$  viable seeds m<sup>-2</sup> for velvetleaf and giant foxtail, respectively ( $\bar{x} \pm \text{SE}$ ). In November 2002, we added 500 velvetleaf seeds plus 2000 giant foxtail seeds m<sup>-2</sup> to each subplot area. During the 2003 growing season, we measured numbers of seeds, vegetative plants, and reproductive plants of the two species within the 7- by 7-m areas.

TABLE 1. Soil fertility, tillage, cultivation, mowing, and herbicide practices in the cropping systems experiment in Boone, IA, used to generate demographic parameters for velvetleaf in 2-yr (corn–soybean) and 4-yr (corn–soybean–triticale + alfalfa–alfalfa) crop rotation systems in 2003.<sup>a</sup>

Rotation length	2003 crop	Fertilizer applications	Tillage preceding 2003 crop	Cultivation and mowing	Herbicide applications	
					Herbicide	Rate
yr						
2	Corn	PPI: 110 kg N ha <sup>-1</sup> (as urea) POST: 40 kg N ha <sup>-1</sup> (as urea)	Field cultivator (1×)	Rotary hoe (1×, POST)	PPI, broadcast: S-metolachlor + isoxaflutole POST, broadcast: nicosulfuron + rimsulfuron + mesotrione	1.6 + 0.11 0.026 + 0.014 + 0.070
2	Soybean	None	Chisel plow, field cultivator (2×)	None	PPI, broadcast: S-metolachlor POST, broadcast: bentazon + flumichlorac + clethodim	1.6 1.1 + 0.060 + 0.18
4	Corn	PPI: 55 kg N ha <sup>-1</sup> (as urea), 12.5 Mg ha <sup>-1</sup> composted dairy manure (dry wt. basis)	Moldboard plow, field cultivator (2×)	Rotary hoe (1×, POST), interrow cultivation (2×)	POST, banded <sup>b</sup> : nicosulfuron + rimsulfuron + mesotrione	0.026 + 0.014 + 0.070
4	Soybean	None	Chisel plow, field cultivator (2×)	Rotary hoe (1×, POST), interrow cultivation (1×)	PPI, broadcast: S-metolachlor POST, banded <sup>b</sup> : flumichlorac	1.60 0.060
4	Triticale + alfalfa	PRE: 30 kg N ha <sup>-1</sup> (as urea)	None	Stubble mowing (1×)	None	
4	Alfalfa	None	None	Hay removal (3×)	None	

<sup>a</sup> Abbreviations: PPI, preplant incorporated; PRE, preemergence; POST, postemergence.

<sup>b</sup> Bands were 38 cm wide, centered on crop rows, resulting in half of the plot surface area receiving herbicides. Consequently, only half the amount of ai, as listed in the table, was applied.

To make certain that seeds did not move in and out of the subplot areas as a function of tillage and cultivation operations, we placed a line of colored beads, similar in size to giant foxtail seeds, perpendicular to the direction of field traffic in each plot in November 2002. Recovery of the beads in mid-summer 2003 from soil at different distances from the original line of deposition indicated that 99% of all recovered beads had moved less than 2 m; 90% of the beads had moved less than 1 m.

The focus of the work reported here is on the population dynamics of velvetleaf, so no further mention will be made of giant foxtail. It should be recognized, however, that both species were present within the manipulated subplots. Other weed species present in the field, mostly woolly cupgrass [*Eriochloa villosa* (Thunb.) Kunth] and common waterhemp (*Amaranthus rudis* Sauer), produced little biomass (< 32 g m<sup>-2</sup>) and were not believed to influence the results.

Velvetleaf seed densities in the soil were determined in March, 2003, by drawing 40 1.9-cm-diam soil cores to a depth of 20 cm from each subplot, subdividing the cores into four soil strata (0- to 5-cm, 5- to 10-cm, 10- to 15-cm, and 15- to 20-cm depth), and compositing them by subplot and stratum. After separation of seeds from soil, as described above, seeds were counted under a binocular dissection microscope. Seed viability was determined by direct germination in a growth chamber followed by tetrazolium staining of nongerminating seeds.

Repeated censuses were conducted throughout the 2003

growing season to determine densities of velvetleaf seedlings emerging and surviving within the central portion of each manipulated subplot, using toothpicks to mark individual seedlings. Numbers of surviving velvetleaf adults and adult seed production were measured within the central 3- by 3-m area of each subplot before crop harvest. Velvetleaf seed production was determined by collecting all surviving plants and counting the number of fruits on each plant and the number of carpels in each fruit. Mature carpels were found to contain three seeds each. Seeds were counted directly for immature or underdeveloped fruits. After processing, all reproductive plant material was returned to the respective plots and placed on the ground.

We measured rates of seed loss to seed predators in each phase of both rotation systems, using the large areas of each plot that did not receive pulses of velvetleaf seeds, to avoid disturbance and trampling of weeds in the subplots. Seed predation was measured using techniques developed by Westerman et al. (2003). Velvetleaf seeds were glued lightly to cards made of sand paper (4 by 10 cm) and then covered with a thin layer of sifted soil. Four replicate cards were placed in each 18- by 85-m plot and pinned to the soil surface for 2 d. Seed loss due to causes other than predation (e.g., wind, rain, and loss of adhesive) was assessed using two replicate control cards that were protected within narrow-mesh metal screen cages. After recovery, numbers of intact seeds remaining on each card were determined in the laboratory. Measurements were conducted during twelve 2-

TABLE 2. Velvetleaf demographic parameters obtained from the cropping systems experiment in Boone, IA, with 2-yr (corn–soybean) and 4-yr (corn–soybean–triticale + alfalfa–alfalfa) crop rotation systems in 2003.

Parameter	Symbol	2-yr rotation		4-yr rotation				Data source
		Corn	Soybean	Corn	Soybean	Triticale + alfalfa	Alfalfa	
Proportion emergence, <sup>a</sup> seedlings seed <sup>-1</sup>	<i>c</i>	0.31	0.22	0.11	0.22	0.33	0.17	A. H. Heggenstaller (unpublished data)
Proportion summer seed survival, seeds seed <sup>-1</sup>	<i>n</i>	0.73 <sup>b</sup>	0.73 <sup>b</sup>	0.73 <sup>b</sup>	0.73 <sup>b</sup>	0.73 <sup>b</sup>	0.73 <sup>b</sup>	Buhler and Hartzler (2001)
Proportion plant survival, reproductive plants seedling <sup>-1</sup>	<i>p</i>	0.0000 <sup>c</sup>	0.0028	0.0157	0.0414	0.0116	0.0032	A. H. Heggenstaller (unpublished data)
Fecundity, seeds plant <sup>-1</sup>	<i>f</i>	0 <sup>c</sup>	230	186	822	23	0 <sup>c</sup>	A. H. Heggenstaller (unpublished data)
Proportion overwinter seed survival, <sup>a</sup> seeds seed <sup>-1</sup>	<i>o</i>	0.62 <sup>d</sup>	0.77 <sup>e</sup>	0.62 <sup>d</sup>	0.77 <sup>e</sup>	0.77 <sup>e</sup>	0.77 <sup>e</sup>	Buhler and Hartzler (2001)

<sup>a</sup> Averaged over all soil layers (see Table 3).

<sup>b</sup> Summer seed survival in the top 5 cm of the soil in soybean in the first year of a soybean–corn crop rotation trial, assuming that all nonviable seeds in autumn died but did not decompose during the summer, recalculated from Buhler and Hartzler (2001).

<sup>c</sup> For modeling purposes, a survival rate or fecundity of 0.001 was used.

<sup>d</sup> Winter seed survival in the top 5 cm of the soil after a corn crop, averaged over 2 yr in a soybean–corn crop rotation trial, assuming that all seeds that died during winter decomposed during summer, recalculated from Buhler and Hartzler (2001).

<sup>e</sup> Winter seed survival in the top 5 cm of the soil after a soybean crop, averaged over 2 yr in a soybean–corn crop rotation trial, assuming that all seeds that died during winter decomposed during summer, recalculated from Buhler and Hartzler (2001).

d periods between late May and late November 2003: May 20 to 22, June 3 to 5, June 16 to 18, June 30 to July 1, July 15 to 17, July 28 to 30, August 11 to 13, August 25 to 27, September 15 to 17, September 29 to October 1, October 15 to 17, and November 18 to 20.

### Calculation and Estimation of Velvetleaf Demographic Parameters

Three crop- and rotation-specific parameter values were estimated from the data collected in the field trial. Overall velvetleaf emergence rate, *c*, was calculated by dividing the average total number of emerged seedlings by the average spring seed bank density. Proportion plant survival, *p*, was calculated by dividing the average number of reproductive plants by the average number of emerged seedlings. Fecundity, *f*, was determined as the average number of seeds per reproductive plant (Table 2).

The estimated emergence rate, *c*, is an overall rate representing total weed emergence from different soil layers:

$$c = c_1d_1 + c_2d_2 + c_3d_3 + c_4d_4 \quad [1]$$

with  $c_x$ , the probability of emergence from a specific depth  $x$ , and  $d_x$ , the relative seed density in soil layer  $x$  ( $b_x/\sum_{x=1}^4 b_x$ , with  $b_x$  the number of seeds in layer  $x$ ), assuming four 5-cm soil strata. The overall rate changes with changing seed distribution in the soil profile, for example, as a result of seed shed or tillage. Seed density per soil layer was estimated during soil sampling in spring. The overall emergence rate will furthermore change with, for example, weather and soil conditions in spring. However, the ability to emerge from a certain depth is species specific (Benvenuti et al. 2001); therefore, the overall emergence reflects the relative emergence probability throughout the soil profile. The depth-

specific emergence probability can be described as a proportion of the emergence from the topsoil layer,  $c_1$ . Using the relationship between emergence rate and soil depth for velvetleaf (Benvenuti et al. 2001), we expressed the depth-specific emergence rates as:

$$c_x = l_x c_1 \quad [2]$$

with  $l_1 = 1.00$ ,  $l_2 = 0.42$ ,  $l_3 = 0.02$ , and  $l_4 = 0.00$  (estimated after Benvenuti et al. 2001). Emergence rate from the top 5 cm,  $c_1$ , was solved from the equation:

$$c = l_1 c_1 d_1 + l_2 c_1 d_2 + l_3 c_1 d_3 + l_4 c_1 d_4 \quad [3]$$

The other depth-specific emergence rates were calculated according to Equation 2 (Table 3). In the alfalfa crop, we assumed that all weeds had emerged from the top 5 cm of the soil because the soil had not been disturbed between harvest of the triticale + alfalfa crop in the preceding year and regrowth of the alfalfa crop the next year. Soil disturbance is a primary cause of weed emergence from deeper soil layers (Mohler 1993).

Velvetleaf overwinter seed survival,  $o_1$ , and summer seed survival,  $n_1$ , in the top 5 cm of the soil in corn and soybean were recalculated from Buhler and Hartzler (2001) (Table 2). We assumed that dead seeds recovered by Buhler and Hartzler (2001) during autumn seed bank sampling had died during summer, whereas those unaccounted for had died during the preceding winter and decomposed during summer. We adopted 0.73, the survival rate in first-year soybean, as an estimate of  $n_1$  in both soybean and corn because we were unable to distinguish between effects caused by the two crops or by seed aging. No published data were available for velvetleaf survival in triticale or alfalfa and, therefore, we used the highest summer and overwinter survival rates as parameter values for these crops (Table 2).



TABLE 3. Velvetleaf seedling emergence rate,  $c$ , summer seed survival rate,  $n$ , and winter seed survival rate,  $o$ , in the cropping systems experiment in Boone, IA, in 2- and 4-yr crop rotation systems in 2003, subdivided over four soil layers.

	2-yr rotation		4-yr rotation			
	Corn	Soybean	Corn	Soybean	Triticale + alfalfa	Alfalfa
Proportion emergence, $c^a$ seedlings seed <sup>-1</sup>						
0–5 cm	0.333	0.315	0.368	0.315	0.356	0.170
5–10 cm	0.140	0.132	0.155	0.132	0.150	0
10–15 cm	0.007	0.006	0.007	0.006	0.007	0
15–20 cm	0	0	0	0	0	0
Proportion summer seed survival, $n^b$ seeds seed <sup>-1</sup>						
0–5 cm	0.730	0.730	0.730	0.730	0.730	0.730
5–10 cm	0.887	0.887	0.887	0.887	0.887	1.000
10–15 cm	0.995	0.995	0.995	0.995	0.995	1.000
15–20 cm	1.000	1.000	1.000	1.000	1.000	1.000
Proportion overwinter seed survival, $o^b$ seeds seed <sup>-1</sup>						
0–5 cm	0.620	0.770	0.620	0.770	0.770	0.770
5–10 cm	0.840	0.903	0.840	0.903	0.903	1.000
10–15 cm	0.992	0.995	0.992	0.995	0.995	1.000
15–20 cm	1.000	1.000	1.000	1.000	1.000	1.000

<sup>a</sup> Depth-specific emergence probabilities were calculated as a proportion of the emergence probability from the 0 to 5 cm soil layer,  $c_x = l_x c_1$ , with  $l_1 = 1.00$ ,  $l_2 = 0.42$ ,  $l_3 = 0.02$  and  $l_4 = 0.00$  (estimated after Benvenuti et al. 2001), assuming fixed relative emergence probabilities.

<sup>b</sup> Depth-specific seed survival probabilities were calculated as a proportion of the seed survival probability in the 0–5 cm soil layer  $n_1$ ,  $o_1: n_x = 1 - l_x(1 - n_1)$  and  $o_x = 1 - l_x(1 - o_1)$ , with  $l_x$  as in <sup>a</sup>.

Seed survival rates in deeper soil strata were calculated as a proportion of the survival rate in the top 5 cm (Table 3):

$$o_x = 1 - l_x(1 - o_1) \quad \text{for overwinter survival, and} \quad [4]$$

$$n_x = 1 - l_x(1 - n_1) \quad \text{for summer survival} \quad [5]$$

with  $x$  the designation for a 5-cm soil stratum ( $x = 1, \dots, 4$ ) and  $l_x$  as described for emergence (see above), assuming that the probability of emergence,  $c_x$ , and the probability of seed mortality,  $1 - o_x$  or  $1 - n_x$ , relative to the top 5 cm of the soil ( $l_x$ ), are linked. In other words, mortality of biologically active seeds is assumed higher than that of dormant seeds. The assumption is based on an observed close

correlation between percentage mortality and emergence, for example, in data by Roberts and Feast (1972), who studied emergence, recovery, and viability for 20 weed species over a 5-yr period.

Seed predation data were analyzed using generalized linear mixed models (procedure IRREML, logit link function; Genstat 5 Committee 1993) that included the fixed effects of sampling time, crop in the rotation, control vs. uncaged status, and interaction terms and the random effects of block, plot within block, and replication within plot. The test criterion for significance was the Wald statistic (Genstat 5 Committee 1993), which is a squared  $z$  statistic ( $b/SE$  for each coefficient,  $b$ , in the model) that

TABLE 4. Examples of published ranges of parameter values for velvetleaf recruitment, plant survival, and fecundity.

Parameter	Value range and conditions	Source(s)
Proportion emergence, <sup>a</sup> seedlings seed <sup>-1</sup>	0.11 in soybean	Bauer and Mortensen (1992)
	0.11–0.38 in soybean	Buhler and Hartzler (2001)
	0.17–0.22 in corn	
	0.08 in soybean and corn	Hartzler et al. (1999)
	0.07 in soybean	Lindquist et al. (1995)
	0.21–0.38 no crop	Mester and Buhler (1991), at 10 C
Proportion plant survival, reproductive plants seedling <sup>-1</sup>	0.19–0.40 no crop	Mohler and Galford (1997)
	0–0.22 in corn, herbicides	Buhler et al. (1994)
	0–0.35 in corn, herbicides + interrow cultivation	
	0.0055–0.072 in corn, full herbicide dose	Bussan et al. (2001)
	0.097–0.15 in corn, half herbicide dose	
	0.0023–0.0039 in soybean, full herbicide dose	
Fecundity, seeds plant <sup>-1</sup>	0.012–0.21 in soybean, half herbicide dose	Lindquist et al. (1995)
	0.0167–0.037 in soybean	
	4,300 in soybean	Bauer and Mortensen (1992)
	33–38 in corn, full herbicide dose	Bussan et al. (2001)
	54–408 in corn, no herbicides	
	214–408 in soybean, full herbicide dosage	
	118–335 in soybean, no herbicides	
	40–49 in soybean	Lindquist et al. (1995)
	3–683 in corn	Zanin and Sattin (1988)

has a chi-square distribution. For significant effects, the  $t$  test was used to separate means. The predation rate,  $r$ , was calculated as the mean proportion predation survival per 2 d, corrected for seed losses from the caged control cards (Abbott 1945):

$$r = \frac{(s_{c,2} - s_2)}{s_{c,2}} \quad [6]$$

with  $s_2$  the proportion seed survival per 2 d, and  $s_{c,2}$  the proportion seeds remaining on the control cards per 2 d.

## Model Structure and Analytical Procedures

We used periodic matrix population models (Caswell 2001; Davis et al. 2004; Jordan et al. 1995; Mertens 2002) to examine the fates of weed seeds and plants in the different rotation systems. Here, the population vector,  $N$ , describes the numbers of plants, and the number of seeds in four soil strata: 0 to 5, 5 to 10, 10 to 15, and 15 to 20 cm (Gonzalez-Andular 1997; Jordan et al. 1995). This approach allows us to keep track of changes in the vertical seed distribution caused by plowing, and differential rates of emergence and seed mortality rates associated with soil depth. We assumed spatially homogenous weed populations. In some studies, velvetleaf plant mortality and seed production seem to be regulated by density-dependent feedback (Bussan et al. 2001; Zanin and Sattin 1988) but not in others (Bussan et al. 2001; Lindquist et al. 1995). Here, no density-dependent feedback was assumed during seedling recruitment and seed production, resulting in linear models. No distinction was made between weed cohorts emerging at different times or between seeds belonging to different age classes, although we realize that cohorts differ in survival probabilities and fecundity (Lindquist et al. 1995), and seed age classes may differ in emergence probabilities (Burnside et al. 1981) and mortality rates (Buhler and Hartzler 2001; Lueschen et al. 1993). To date, insufficient data are available to parameterize such extensive models for velvetleaf.

Our experiment includes three hierarchical sequences of environments: crop rotation system, rotation phase within rotation system, and period of the weed life cycle within rotation phase. We followed the same hierarchy in our modeling. First, we constructed five matrices ( $R_{j,k}$  for seedling recruitment,  $SS_{j,k}$  for summer seed bank and seedling survival,  $SP_{j,k}$  for seed production and seed predation,  $WS_{j,k}$  for winter seed survival, and  $T_{j,k}$  for seed movement within the soil profile by plowing; see Appendix 1) to describe one period in the annual life cycle of a weed seed or plant for a specific crop rotation ( $j$ ) and phase ( $k$ ). The aggregate annual change for a specific phase in a rotation is the matrix product of the period-specific matrices:

$$P_{j,k} = T_{j,k}WS_{j,k}SP_{j,k}SS_{j,k}R_{j,k} \quad [7]$$

Weed population dynamics differ between phases (e.g., corn and soybean) in a rotation, so the net change over a rotation cycle is the product of the phase-specific matrices:

$$A_2 = P_{2,2} * P_{2,1} \quad \text{for the 2-year rotation} \quad [8]$$

$$A_4 = P_{4,4} * P_{4,3} * P_{4,2} * P_{4,1} \quad \text{for the 4-year rotation} \quad [9]$$

The periodic matrix models provided estimates of the population growth rate,  $\lambda_j$ , for the entire rotation and estimates of the contributions to  $\lambda$  from each phase and each life-

cycle period within each phase. Annualized population growth rates were calculated as  $^2\sqrt{\lambda_2}$  for the 2-yr rotation and  $^4\sqrt{\lambda_4}$  for the 4-yr rotation. Elasticities of the population growth rate,  $\lambda$ , i.e., proportional sensitivity, were computed for elements ( $o_{j,k}$ ,  $c_{j,k}$ ,  $n_{j,k}$ ,  $p_{j,k}$ ,  $f_{j,k}$ , or  $s_{j,k}$ ) of the life cycle-specific matrices,  $R_{j,k}$ ,  $SS_{j,k}$ ,  $SP_{j,k}$ , and  $WS_{j,k}$ , according to the periodic matrix algorithm of Caswell and Trevisan (1994). All the elasticities were adjusted to compensate for rotation length by dividing the elasticities for the entire rotational cycle by the appropriate rotation length.

In this study, we investigated the role of crop rotations in the dynamics of velvetleaf by comparing population growth rates and elasticities in the population growth rates to changes in the demographic parameters of the two crop rotation systems, assuming zero seed predation. Next, we investigated the role of seed predation by exploring the possibilities to further decrease the population growth rate in the 4-yr rotation as opposed to the 2-yr rotation. Furthermore, we investigated to what degree the efficacy of various control tactics can be replaced by seed predation. We conducted an elasticity analysis and three modeling exercises. In the first exercise, we added 40% seed predation to one of the crop phases and calculated the effects on  $\lambda_2$  and  $\lambda_4$ . Forty percent was chosen because it is well within the range of values commonly found in the weed seed predation literature (Brust and House 1988; Cromar et al. 1999; Harrison et al. 2003; Westerman et al. 2003). In the second exercise, we investigated the trade-off between control efficacy (weed mortality) and seed predation in the 4-yr rotation by determining how much velvetleaf seed predation in the soybean or corn phases would be required to prevent the seed bank density from increasing ( $\lambda > 1$ ), while plant survivorship increased from 0.001 to 0.1 (i.e., by reducing the efficacy of direct weed control tactics from 0.999 to 0.900). In the third exercise, we simulated velvetleaf dynamics using estimates of cumulative predation rates for each of the crop phases in the 4-yr rotation. Finally, we determined elasticities of the reparameterized model and monitored velvetleaf population response to a relaxation of weed control, as indicated by the plant mortality rate.

## Results and Discussion

### Weed Demographic Parameters

#### *Velvetleaf Seedling Recruitment and Survival and Fecundity*

There were clear differences in velvetleaf response to the 2- and 4-yr crop rotations. Seed return was greater in the 4-yr rotation (460 seeds  $m^{-2}$ ) than in the 2-yr rotation (16 seeds  $m^{-2}$ ) because of higher plant survival and higher fecundity in every phase of the 4-yr rotation (Table 2). Proportion seedling emergence was equivalent in the 2- and 4-yr soybean phases, lower in the 4-yr compared with the 2-yr corn phase, but relatively high in the 4-yr triticale and alfalfa phases. More details on the estimation of demographic parameters will be reported elsewhere. The obtained parameter estimates were well within the range of values commonly reported in the literature for velvetleaf and other broadleaf weed species (Table 4).

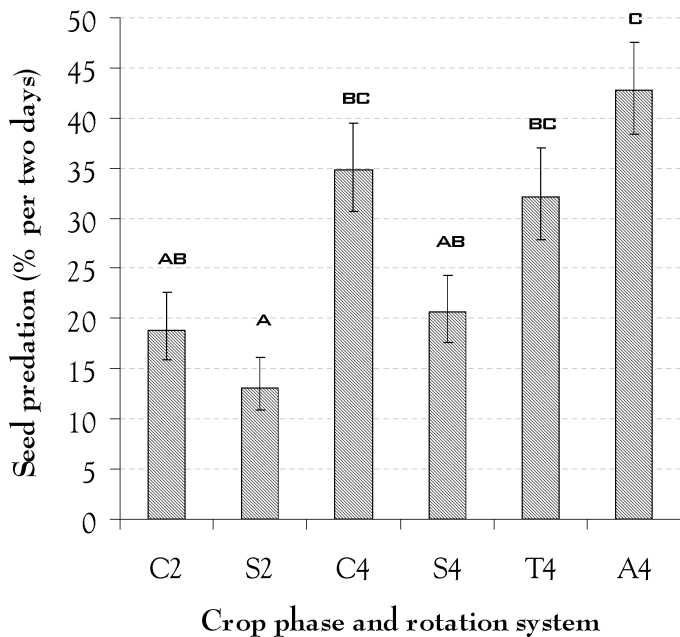


FIGURE 1. Percentage seed loss due to predation over a 2-d period, in the corn and soybean phases of the 2-yr rotation (C2 and S2) and in the corn, soybean, triticale + alfalfa and alfalfa phases of the 4-yr rotation (C4, S4, T4, and A4), averaged over 12 sampling periods from the end of May to mid-November 2003, in Boone, IA. Error bars indicate the standard error of the mean (SE). Bars with the same letter are not significantly different.

#### Postdispersal Seed Predation

Seed predators were active in all phases of both crop rotations (Figure 1). However, averaged over 12 sampling periods from late May to late November 2003, loss of velvetleaf seeds to predators was greater in the 4-yr rotation (32% per 2 d) than in the 2-yr rotation (17% per 2 d) (Figure 1). The data also suggest that triticale and alfalfa provide a better habitat for seed predators than does soybean. Although not all crop rotation-system combinations differed significantly in predation rate, differences among crops and rotation systems will magnify when rates are compounded over a longer time period. Field crickets (e.g., *Gryllus pennsylvanicus* Burmeister), carabid beetles (e.g., *Harpalus pennsylvanicus* De-Geer), and prairie deer mice [*Peromyscus maniculatus* (Wagner)] were the dominant seed predators recovered in traps. More detail on the estimation of seed predation rates and seed predator densities will be reported elsewhere.

For the third modeling exercise and the second part of the elasticity analysis, we needed realistic predation rates to evaluate the effect of seed predation on weed population growth. However, the above predation rates cannot be used as estimates of the annual proportion of weed seeds consumed by predators. Rather, they reflect the relative demand for weed seeds if exposed to predators in different habitats at particular points in time. The duration of exposure to seed predators potentially varies greatly among rotations due to differences in crop sequence and tillage practices. Predation rates of seeds are significantly reduced when covered by soil (Hulme 1994; Thompson 1987). Tillage, especially plowing, thus provides protection from predation. In no-till situations, as in the triticale + alfalfa and the alfalfa phases of this study, seeds will be covered only slowly by soil (Seguer Millàs 2002) and a portion of the weed seeds may be exposed to predators all year round. Consequently, part of the velvetleaf seeds pro-

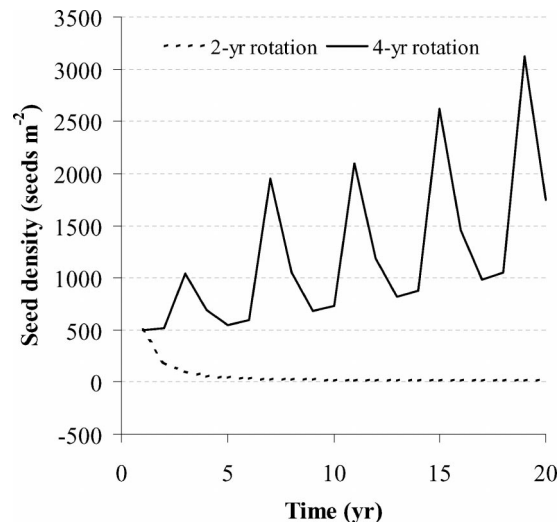


FIGURE 2. Simulated velvetleaf seed bank densities to a depth of 20 cm in the 2- and 4-yr rotations over a period of 20 yr, with 500 seeds applied to the soil surface in November of Simulation Year 1, assuming no seeds are lost because of predation.

duced in the soybean phase of the 4-yr rotation may have been exposed to predators for two additional years after seed shed, those produced in the triticale + alfalfa phase for one additional year, and those in the other crops for just a few months before plowing in late autumn (Table 1).

The potential duration of seed exposure to predators in the various crops was combined with the predation rates to produce the following ranking of the probability of seed losses due to predation: soybean, 4-yr > triticale, 4-yr > alfalfa, 4-yr > corn, 4-yr ≈ soybean, 2-yr ≈ corn, 2-yr. Harrison et al. (2003) reported 39 and 88% removal of giant ragweed (*Ambrosia trifida* L.) seeds in no-till corn when exposed for a winter or a year, respectively, and Cromar et al. (1999) reported 22 to 43% predation of common lambsquarters (*Chenopodium album* L.) and barnyardgrass [*Echinochloa crus-galli* (L.) Beauv.] in different crops and tillage regimes when weed seeds were exposed to predators for periods varying from 1 to 2.5 mo. Applying these rates as guides for the present rotation experiment yielded the following conservative “estimates” of seed mortality rates in the different phases of the two rotation systems: 0.8 for velvetleaf seeds produced in soybean, 0.6 in triticale + alfalfa, and 0.4 in alfalfa of the 4-yr rotation; 0.2 for seeds produced in corn of the 2- and 4-yr rotations; and 0.2 for seeds produced in soybean of the 2-yr rotation. These numbers were used as predation rates in the third modeling exercise and the second part of the elasticity analysis (see below).

#### The Role of Crop Rotations in Velvetleaf Population Dynamics

When assuming no velvetleaf seeds were lost because of predation in any of the crops, the annualized population growth rate was 0.97 for the 2-yr rotation ( $\lambda_2$ ) and 1.05 for the 4-yr rotation ( $\lambda_4$ ), indicating that the velvetleaf seed bank density was decreasing in the 2-yr rotation and increasing in the 4-yr rotation (Figure 2). In the 4-yr rotation, the velvetleaf population increased after corn and soybean phases, and decreased after triticale + alfalfa and alfalfa phases, resulting in a continuous cyclic pattern repeating on 4-yr intervals.

In the 2-yr rotation, the highest elasticities were obtained for changes in summer and winter seed survival and, to a lesser extent, to seedling recruitment in both crop phases (Table 5). The population growth rate for the 4-yr rotation ( $\lambda_4$ ) was considerably more elastic to changes in demographic parameters than was the growth rate for the 2-yr rotation ( $\lambda_2$ ). Elasticities were highest for demographic parameters in crop phases with the highest seed production (soybean > corn > triticale + alfalfa > alfalfa). In crop phases with low velvetleaf seed output (triticale + alfalfa and alfalfa), the elasticities were higher for demographic parameters related to seed survival rather than seed production (Table 5).

It is notable that  $\lambda$  over the entire 4-yr rotation was as low as 1.05. Growth rate for the soybean-specific matrix in the 4-yr rotation was very high ( $\lambda_{4,2} = 8.64$ ) because of the combination of a relatively high plant survival rate (0.0414 reproductive plants per seedling) and high fecundity (822 seed per plant). The more diverse 4-yr rotation displayed lower population growth rates than would be anticipated on the basis of the individual demographic parameters alone. At the same time, the possibility to further decrease the population growth rate through the manipulation of individual demographic parameters is preserved, as indicated by the high elasticities.

The pattern just described is typical for periodic matrices that create an asymptotically cyclic pattern in population densities (Caswell 2001, pp. 349–356). This outcome is explained by the fact that “the matrix at one phase in the rotational cycle operates on the stage distribution from the previous phase and produces a new stage distribution that is operated on by the next matrix” (Caswell 2001, p. 354). At no point during the rotation does the population converge to the stable stage distribution and the associated dominant eigenvalue,  $\lambda$ . In this study, periodicity occurred at two levels: the crop phase within the rotation system, and seasonal phase within the rotation phase, causing cyclic patterns at two time scales. Although the phase-specific growth rate  $\lambda_{4,2}$  is potentially high, this growth rate will not be attained in the context of the 4-yr rotation. The biological explanation underlying such model behavior is that weeds are exposed to very diverse environments during crop rotations. For example, in triticale + alfalfa, velvetleaf emergence was high because of a high seed density in the topsoil layer and a high emergence rate, but the subsequent plant survival rate and fecundity were low. Vavrek et al. (1997) provide another example of this principle for dandelion (*Taraxacum officinale* Weber). Of particular interest is that this set of mathematical relationships both demonstrates and provides an explanation for the observation that crop rotation represents an extremely effective means of controlling weeds, while reducing requirements for herbicide inputs (Leighty 1938; Liebman and Staver 2001).

### The Role of Seed Predation in Velvetleaf Population Dynamics

As predicted by the elasticities (Table 5), adding 40% seed predation to either the corn or soybean phases of the 2-yr rotation did not affect the overall population growth rate ( $\lambda_2$ ). Similarly,  $\lambda_4$  was hardly affected by 40% predation of seeds produced in the triticale + alfalfa or alfalfa phases of the 4-yr rotation ( $\lambda_4 = 1.04$  and 1.05, respectively). In contrast,  $\lambda_4$  was more strongly affected by 40% predation

TABLE 5. Population growth rates in the 2-yr ( $\lambda_{2,k}$ ) and 4-yr ( $\lambda_{4,k}$ ) rotations and elasticities of population growth rates to demographic parameters, when no seeds are lost to predation (left) and when seeds are lost to predation at an annual rate of 0.2 in the corn, 0.8 in the soybean, 0.6 in the triticale + alfalfa, and 0.4 in the alfalfa phases (right).

Parameter	Symbol	No seed losses to predation						With seed losses to predation					
		2-yr rotation		4-yr rotation		2-yr rotation		4-yr rotation		Triticale + alfalfa		Alfalfa	
Lambda	$\lambda$	0.94	1.00	0.99	8.64	1.00	0.86	0.94	1.00	0.97	2.04	1.00	0.86
Elasticity of $\lambda$ (%) for demographic parameters													
Proportion emergence	$c$	-0.16	-0.12	4.51	8.81	-3.03	-2.08	-0.15	-0.12	2.29	2.97	-2.24	-0.88
Proportion summer seed survival	$n$	0.33	0.31	2.83	0.90	8.50	10.09	0.33	0.31	2.23	1.46	4.76	4.28
Proportion plant survival	$p$	0.00	0.02	6.10	9.22	1.64	0.00	0.00	0.02	3.54	3.63	0.35	0.00
Fecundity	$f$	0.00	0.02	6.10	9.22	1.64	0.00	0.00	0.02	3.54	3.63	0.35	0.00
Proportion predation survival	$s$	0.00	0.02	6.10	9.22	1.64	0.00	0.00	0.02	3.54	3.63	0.35	0.00
Proportion overwinter seed survival	$o$	0.28	0.35	8.15	10.14	10.16	7.53	0.28	0.34	4.30	5.12	5.14	5.09



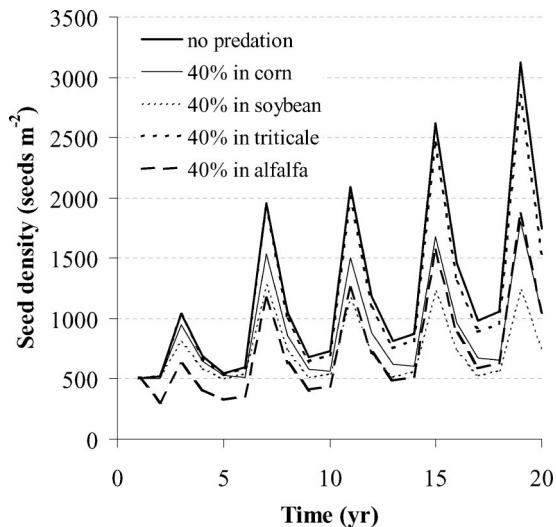


FIGURE 3. Simulated velvetleaf seed bank densities to a depth of 20 cm in the 4-yr rotation over a period of 20 yr, with 500 seeds applied to the soil surface in November of simulation year 1, assuming no seed predation, or 40% predation of seeds produced in the corn, soybean, triticale + alfalfa, or alfalfa phases.

in the soybean and corn phases (Figure 3) ( $\lambda_4 = 1.00$  and 1.02, respectively).

To compensate for a small decrease in control efficacy from 0.9945 to 0.986 in the corn phase of the 4-yr rotation, an increase in the seed predation rate from 0 to 0.60 was required (Figure 4). However, any further decrease in control efficacy required a much smaller increase in the seed predation rate. A similar trend was obtained for soybean, but lower predation rates sufficed to compensate for the decrease in control efficacy. If seed predation rates are sufficiently high (soybean  $\geq 0.70$ , corn  $\geq 0.95$ ), weed control through cultivation and herbicides could allow 10% survivorship without leading to uncontrollable velvetleaf population growth, i.e.,  $\lambda > 1$ . High predation rates have been reported in the literature (Harrison et al. 2003); therefore, a 70% predation rate of the weed seeds produced in soybean seems feasible.

The annualized population growth rate for the 2-yr rotation ( $\lambda_2$ ) remained unchanged at 0.97 when the estimated cumulative seed predation rates were added to the model, compared with the model without seed predation rates (Table 5). However, the population growth rate for the 4-yr rotation ( $\lambda_4$ ) was reduced from 1.05 to 0.93. The growth rate for the soybean-specific matrix in the 4-yr rotation ( $\lambda_{4,2}$ ) was reduced from 8.64 to 2.04, whereas the other phase-specific matrices remained unchanged. Clearly, weed management benefited from the high elasticity for losses of newly produced seeds in the soybean phase of the 4-yr rotation (Table 5). Elasticity analysis of the reparameterized 4-yr model that included estimates of the cumulative seed predation rates showed that although the elasticity values were all lower compared with the “no predation” situation, relative ranking changed little. With the addition of seed predation, the population growth rate of the 4 yr ( $\lambda_4$ ) was equally elastic to changes in demographic parameters in the corn and soybean phases and more elastic to summer and winter seed survival in the soybean phase (Table 5). The elasticities show that there is room for further reduction of the population growth rate in the 4-yr rotation, through reductions in summer and winter seed survival in the soil.

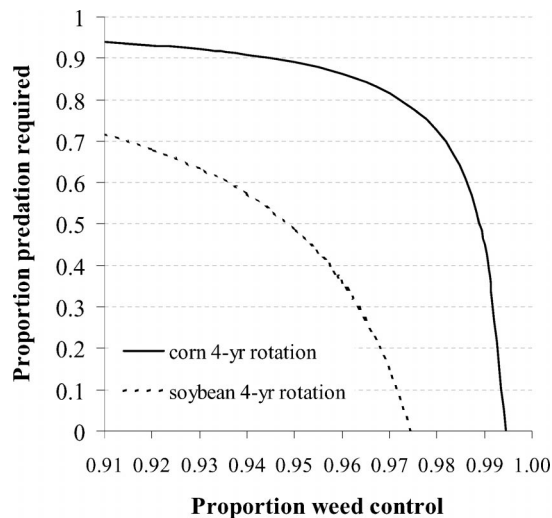


FIGURE 4. Zero population growth isocline ( $\lambda = 1$ ) for velvetleaf in corn and soybean phases for given combinations of proportional seed predation ( $1 - s$ ) and control efficacy ( $1 - p$ ), indicating the seed predation rate that is required to replace plant mortality caused by weed control to prevent the velvetleaf population from either increasing or decreasing.

However, these demographic parameters are difficult to manipulate. Seed survival can be reduced through disruptive practices, such as fumigation and inundation, while less disruptive alternatives such as seed pathogenic microorganisms and allelopathy are as yet in the experimental stage (Einhellig 1995; Kremer 1993).

Finally, we investigated the effect of a reduction in control efficacy from 0.999 to 0.75 in the soybean phases of the 2- and 4-yr rotations, on the annualized population growth rates ( $\lambda_2$  and  $\lambda_4$ , respectively) of the reparameterized model, while keeping all other parameter values constant (Table 2). Compared with the 4-yr rotation ( $\lambda_4$ ), population growth in the 2-yr rotation ( $\lambda_2$ ) responded much more strongly to this reduction in control efficacy, yielding annualized population growth rates of 1.04 and 1.73, respectively, at a control efficacy of 75% (Figure 5). These results indicate that the 4-yr rotation is more resilient with respect to velvetleaf population

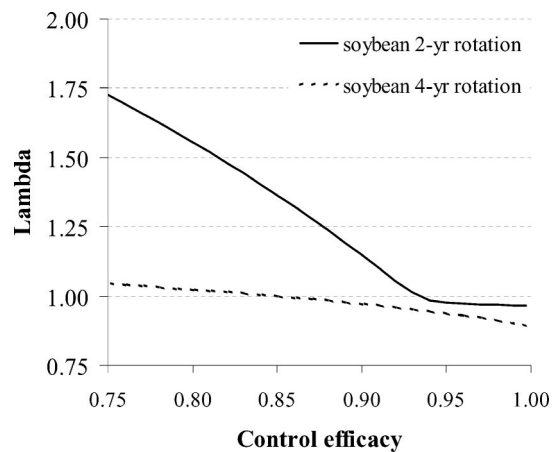


FIGURE 5. Velvetleaf population growth rates ( $\lambda$ ) associated with given levels of control efficacy ( $1 - p$ ) in the soybean phase of the 2- and 4-yr rotations, assuming seed predation rates of 0.8 for velvetleaf seeds produced in soybean, 0.6 in triticale + alfalfa, and 0.4 in alfalfa of the 4-yr rotation; 0.2 for seeds produced in corn of the 2- and 4-yr rotations; and 0.2 for seeds produced in soybean of the 2-yr rotation.

dynamics than the 2-yr rotation and therefore more robust. If for some reason weed control is less successful in a particular year, velvetleaf densities should increase rapidly in the 2-yr rotation but much more slowly in the 4-yr rotation. An occasional failure of weed control in the 2-yr rotation is associated with high costs because of yield loss and increased weed control efforts in subsequent crops. In contrast, an occasional weed control failure in the 4-yr rotation would only cause a small increase in the population growth rate (Figure 5). Furthermore, there are more opportunities to intervene in the 4-yr than in the 2-yr system, varying from an (temporary) increase in the intensity of chemical or mechanical weed control in the corn and the soybean phases to the use of the alfalfa as a 'weed trap', which allows emergence and thus depletion of the seed bank but prevents seed return, thanks to frequent mowing and hay removal. The 2-yr rotation lacks the latter possibility for weed management. Similarly, matrix model analyses conducted by Davis et al. (2004) indicated that adding red clover to a corn-soybean-wheat rotation helped buffer the system against failures of control tactics directed at giant foxtail.

The analyses conducted in this study are based on a single year's data set and comprise only one weed species. Nevertheless, the results suggest that Liebman and Galland's (1997) concept of many little hammers may work in the case of velvetleaf in a 4-yr crop rotation. Using only 18% of the herbicide input of the 2-yr rotation, velvetleaf population growth could nearly be halted ( $\lambda = 1.05$ ) simply through a more diverse crop rotation that exposed the weed to multiple stress factors. In addition, the more diverse 4-yr crop rotation favored the actions of weed seed predators, resulting in higher mortality rates of velvetleaf seeds. In conjunction with reduced rates of herbicides and tillage, a more diverse crop rotation and increased weed seed predation could effectively contain velvetleaf populations ( $\lambda = 0.93$ ), and provide an alternative to conventional approaches that require a high herbicide input or intensive cultivation. Obviously, additional observations involving more years and other weed species are needed for confirmation.

Norris' (1999) argument for zero seed thresholds is primarily based on the high fecundity of weeds, which passes on the danger of crop loss from current to future crops. If, however, the majority of newly produced seeds does not enter the soil seed bank but is instead lost to predators, as appears from this study and others (Brust and House 1988; Cromar et al. 1999; Harrison et al. 2003; Westerman et al. 2003), there should perhaps be alternative, higher thresholds for weed densities in more diverse cropping systems. Higher weed densities in fields might help to sustain a resident population of seed predators, ensuring their presence during weed seed shed, whereas in systems that maintain a zero seed threshold seed predators are likely to be lost because of the lack of food and suitable habitat. Moreover, it would seem from the results of this study that weed densities, including threshold densities, are context dependent: higher weed densities can be tolerated in more diverse cropping systems because they are better buffered against sudden and uncontrollable weed population increases than are simple systems.

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## Appendix 1

Matrix models are composed of population vectors describing numbers of individuals within different weed life stage classes (e.g., seeds within the soil seed bank, seedlings, reproductive adults, newly produced seeds) and projection matrices that specify the probabilities of making transitions between those life stages. Transition probabilities can be adjusted to reflect effects of different crops and associated management practices on weed survivorship and fecundity. Simulation of population dynamics over time, indicating rates of population increase or decrease, is accomplished by repeated multiplication of the population vector by sets of transition matrices.

Population vector:

$$N = \begin{pmatrix} \# \text{ seeds } 0\text{--}5 \text{ cm} \\ \# \text{ seeds } 5\text{--}10 \text{ cm} \\ \# \text{ seeds } 10\text{--}15 \text{ cm} \\ \# \text{ seeds } 15\text{--}20 \text{ cm} \\ \# \text{ plants} \end{pmatrix}$$

Recruitment matrix ( $R_{jk}$ ) describing germination probabilities from specific soil depths and losses of seeds from those depths resulting from germination:

$$R_{jk} = \begin{pmatrix} 1 - e_1 & 0 & 0 & 0 & 0 \\ 0 & 1 - e_2 & 0 & 0 & 0 \\ 0 & 0 & 1 - e_3 & 0 & 0 \\ 0 & 0 & 0 & 1 - e_4 & 0 \\ e_1 & e_2 & e_3 & e_4 & 0 \end{pmatrix}$$

Summer seed and plant survival ( $SS_{jk}$ ) matrix containing survival rates for seeds in soil at four depths and plants survival during summer:

$$SS_{jk} = \begin{pmatrix} n_1 & 0 & 0 & 0 & 0 \\ 0 & n_2 & 0 & 0 & 0 \\ 0 & 0 & n_3 & 0 & 0 \\ 0 & 0 & 0 & n_4 & 0 \\ 0 & 0 & 0 & 0 & p \end{pmatrix}$$

Seed production and seed predation matrix ( $SP_{jk}$ ) combining individual plant fecundity with the proportion surviving predation:

$$SP_{jk} = \begin{pmatrix} 1 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & f^*s \end{pmatrix}$$

Winter seed survival matrix ( $WS_{jk}$ ) containing the proportion survival rates for seeds in soil at four depths during winter:

$$WS_{jk} = \begin{pmatrix} o_1 & 0 & 0 & 0 & 0 \\ 0 & o_2 & 0 & 0 & 0 \\ 0 & 0 & o_3 & 0 & 0 \\ 0 & 0 & 0 & o_4 & 0 \\ 0 & 0 & 0 & 0 & 0 \end{pmatrix}$$

Tillage matrices ( $T_{jk}$ ) describing vertical seed movement resulting from moldboard plowing, chisel plowing (i.e., rigid-tine tillage), as per Coussens and Moss (1990), and no tillage:

$$T_{jk} = \begin{pmatrix} 0.70 & 0.33 & 0.02 & 0 & 0 \\ 0.23 & 0.50 & 0.15 & 0 & 0 \\ 0.06 & 0.15 & 0.68 & 0.16 & 0 \\ 0.02 & 0.01 & 0.16 & 0.84 & 0 \\ 0 & 0 & 0 & 0 & 0 \end{pmatrix} \quad \text{chisel plow matrix}$$

$$T_{jk} = \begin{pmatrix} 0.02 & 0.211 & 0.365 & 0.294 & 0 \\ 0.112 & 0.274 & 0.255 & 0.100 & 0 \\ 0.404 & 0.304 & 0.200 & 0.122 & 0 \\ 0.464 & 0.211 & 0.180 & 0.484 & 0 \\ 0 & 0 & 0 & 0 & 0 \end{pmatrix} \quad \text{moldboard plow matrix}$$

$$T_{jk} = \begin{pmatrix} 1 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 1 \end{pmatrix} \quad \text{no-till matrix}$$

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