



# Fates of *Setaria faberi* and *Abutilon theophrasti* seeds in three crop rotation systems

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## Summary

Weed seeds in and on the soil are the primary cause of weed infestations in arable fields. Previous studies have documented reductions in weed seedbanks due to cropping system diversification through extended rotation sequences, but the impacts of different rotation systems on additions to and losses from weed seedbanks remain poorly understood. We conducted an experiment in Iowa, USA, to determine the fates of *Setaria faberi* and *Abutilon theophrasti* seeds in 2-, 3- and 4-year crop rotation systems when seed additions to the soil seedbank were restricted to a single pulse at the initiation of the study. Over the course of the experiment, seedlings were removed as they emerged and prevented from producing new seeds. After 41 months, seed population densities dropped >85% for *S. faberi* and >65% for *A. theophrasti*, but differences between rotation systems in the

magnitude of seedbank reductions were not detected. Most of the reductions in seedbank densities took place from autumn through early spring in the first 5 months following seed deposition, before seedling emergence occurred, suggesting that seed predation and/or seed decay was important. For *S. faberi*, total cumulative seedling emergence and total seed mortality did not differ between rotation systems. In contrast, for *A. theophrasti*, seedling emergence was 71% lower and seed mortality was 83% greater in the 3- and 4-year rotation systems than in the 2-year system. Results of this study indicate that for certain weed species, such as *A. theophrasti*, crop rotation systems can strongly affect life-history processes associated with soil seedbanks.

**Keywords:** velvet leaf, giant foxtail, crop rotation, seedbank dynamics, seed mortality, seedling emergence, weeds.

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## Introduction

Weed seeds in and on the soil are the primary cause of weed infestations in arable fields (Davis, 2006). Changes in the density of weed seedbanks over time

are determined by seed additions and losses through processes that have been described by Cousens and Mortimer (1995), Mohler (2001), Forcella (2003) and others. Additions of seeds can result from seed dispersal from mature plants (seed rain), contamination

of sown crop seeds and applied manure, and transport by wind, water, animals and machinery. Seed loss may occur via consumption by vertebrates and invertebrates (predation), pathogen attack, physiological collapse due to ageing or germination at soil depths that prevent seedling emergence. Additional losses of seeds from the soil seedbank may occur due to transport by wind, water, animals and machinery, and germination that results in successful seedling establishment.

Although a considerable amount of data exist with regard to how these processes occur and operate individually, there is a dearth of information concerning how they operate together within the context of various cropping systems. In part, this is due to the heavy emphasis placed in conventional weed management strategies on killing germinated seeds and emerged seedlings before they mature and add new seeds to the soil seedbank. As strategies are pursued for reducing reliance on herbicides due to concerns over herbicide resistance and degradation of environmental quality, more attention needs to be focused on additional means of regulating weed seedbank densities (Gallandt, 2006).

Cropping system diversification through the use of longer rotations of dissimilar species can increase the range of stress and mortality factors that regulate weed population dynamics, and thus can be useful for maintaining effective weed control while reducing the burden of crop protection placed on herbicides (Liebman & Staver, 2001; Anderson, 2003; Nazarko *et al.*, 2005). The types of crops grown in rotation sequences over a period of several years and associated management practices can explain a large proportion of the variation observed in weed seed densities in soil (Bohan *et al.*, 2011). Nevertheless, although a number of studies have documented reductions in weed seedbanks due to diversification through crop rotation (Covarelli & Tei, 1988; Schreiber, 1992; Teasdale *et al.*, 2004), the impacts of different rotation systems on processes resulting in seed additions to and losses from the soil seedbank remain poorly understood.

Here, we report on an experiment conducted to quantify the fates of seeds of two annual weed species in three contrasting crop rotation systems. The addition of seeds was restricted to a single pulse at the initiation of the study. The rotation systems differed not only with regard to crop diversity, but also levels of agrochemical inputs and use of manure. Our specific objectives were to quantify rotation system effects on (i) the density of viable seeds within the soil over time, (ii) seedling emergence and (iii) seed mortality. We hypothesised that seed densities would decline in each of the systems, but that declines would be greater in the more diverse systems.

## Materials and methods

### *Experiment site and management practices*

The experiment was conducted at Iowa State University's Marsden Farm (42°01'N; 93°47'W; 333 m above sea level), in Boone County, Iowa, USA, between autumn 2002 and spring 2006, spanning the 2003–2005 crop production seasons. 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). Mean monthly air temperature for the 2003–2005 growing seasons (April–November) was 15°C; mean cumulative seasonal precipitation for April–November of 2003–2005 was 744 mm. Monthly temperature and precipitation data are available in Liebman *et al.* (2008) and Iowa Environmental Mesonet (2013).

We studied the fates of seeds of two annual cropland weeds commonly encountered in the central USA, *Setaria faberi* Herrm. (giant foxtail) and *Abutilon theophrasti* Medik. (velvetleaf), within three crop rotation systems: a 2-year maize (*Zea mays* L.)–soya bean (*Glycine max* (L.) Merr.) system; a 3-year maize–soya bean–triticale ( $\times$  *Triticosecale* Wittmack) + red clover (*Trifolium pratense* L.) system; and a 4-year maize–soya bean–triticale + lucerne (*Medicago sativa* L.)–lucerne system. The 2-year rotation is typical of cash grain farming systems in the region, whereas the 3-year and 4-year rotations are representative of integrated crop–livestock systems in the region. The experiment was arranged in a randomised complete block design with four replicates. Each crop phase of each rotation was present every year, generating nine sequences of crops and crop residues (Table 1). Plot size was 18 × 85 m. Details of all crop management practices and inputs used in the experiment have been provided by Liebman *et al.* (2008) and Davis *et al.* (2012), but are summarised briefly here.

Tillage regimes differed between rotation systems. In the 2-year rotation, a combination of autumn chisel ploughing and spring field cultivation was used between maize harvest and soya bean planting; spring field cultivation was used between soya bean harvest and maize planting. In the 3-year system, a combination of autumn chisel ploughing and spring field cultivation was used between maize harvest and soya bean planting; zero tillage or spring disking was used between soya bean harvest and the planting of triticale and red clover and autumn mouldboard ploughing followed by spring disking and field cultivation were used to incorporate clover residue and prepare a seedbed for maize. Tillage practices in the 4-year

**Table 1** Crops or crop residues present in the different sequences used within the three rotation systems in 2002–2006

Sequence	Rotation system	Spring 2002– spring 2003	Spring 2003– spring 2004	Spring 2004– spring 2005	Spring 2005– spring 2006
		Crop or residue present			
1	2-year	Maize	Soya bean	Maize	Soya bean
2	2-year	Soya bean	Maize	Soya bean	Maize
3	3-year	Maize	Soya bean	Triticale + red clover	Maize
4	3-year	Soya bean	Triticale + red clover	Maize	Soya bean
5	3-year	Triticale + hairy vetch*	Maize	Soya bean	Triticale + red clover
6	4-year	Maize	Soya bean	Triticale + lucerne	Lucerne
7	4-year	Soya bean	Triticale + lucerne	Lucerne	Maize
8	4-year	Triticale + lucerne	Lucerne	Maize	Soya bean
9	4-year	Lucerne	Maize	Soya bean	Triticale + lucerne

\*Hairy vetch was used in 2002 after red clover failed to establish successfully.

system were the same as in the 3-year system, except for a longer period without soil disturbance, from small grain and lucerne establishment until lucerne residue was autumn mouldboard ploughed. The direction of tillage passes generally was reversed in alternate years so as to minimise seed movement from experimentally manipulated subplots (see below).

The longer rotations received less mineral N fertiliser and more organic N than did the 2-year rotation. During the 2003–2005 cropping seasons, mineral N fertiliser inputs, averaged over all phases of the rotations, were 48% and 71% lower in the 3-year (32 kg N ha<sup>-1</sup> year<sup>-1</sup>) and 4-year (18 kg N ha<sup>-1</sup> year<sup>-1</sup>) rotations, respectively, than in the 2-year rotation (63 kg N ha<sup>-1</sup> year<sup>-1</sup>). Composted cattle manure was applied to the 3-year and 4-year rotations, supplying 44 and 33 kg N ha<sup>-1</sup> year<sup>-1</sup>, respectively, but manure was not applied to the 2-year rotation. Nitrogen additions to the more diverse rotation systems also occurred through biological N<sub>2</sub> fixation by red clover and lucerne, which has been shown to often exceed 100 kg N ha<sup>-1</sup> year<sup>-1</sup> (Peoples *et al.*, 1995).

Herbicide use also differed between rotation systems. Averaged over all crop phases within the rotations during the 2003–2005 cropping seasons, herbicide inputs were 71% and 78% lower in the 3-year (0.65 kg a.i. ha<sup>-1</sup> year<sup>-1</sup>) and 4-year (0.48 kg a.i. ha<sup>-1</sup> year<sup>-1</sup>) rotations, respectively, than in the 2-year rotation (2.21 kg a.i. ha<sup>-1</sup> year<sup>-1</sup>). In the 2-year rotation, herbicides were applied at conventional rates, and no inter-row cultivations were conducted. In contrast, in the 3- and 4-year systems, herbicides were applied in 38-cm-wide bands over maize and soya bean rows and inter-row areas were cultivated; no herbicides were applied to triticale + red clover, triticale + lucerne or lucerne crops. Weed suppression in triticale stubble, red clover and lucerne was accomplished through mowing and hay removal.

Choices of herbicides were made depending on the weed species present, their population densities and the size of emerged seedlings. Depending on the year, maize in the 2-year rotation was treated with S-metolachlor, isoxaflutole, nicosulfuron, rimsulfuron and/or mesotrione; maize in the 3- and 4-year rotations was treated with nicosulfuron, rimsulfuron and mesotrione. Soya bean in the 2-year rotation was treated with S-metolachlor, bentazon, flumiclorac pentyl ester and/or clethodim. Soya bean in the 3- and 4-year rotations was treated with S-metolachlor, flumiclorac pentyl ester and/or bentazon. Herbicide rates for the specific products applied to each crop in each year are given in Liebman *et al.* (2008).

#### Methods for studying weed seedbank dynamics

We examined weed seedbank dynamics in 7 × 7 m subplots established within main plots of each sequence of crops and crop residues (Table 1). Following a basic difference equation model, we posited that the number of weed seeds in and on the soil at a particular time would be equal to the number of seeds previously present, plus additions, minus losses.

At the start of our study in late October 2002, prior to manipulating weed seedbank densities, we drew forty 19-mm-diameter soil samples to a depth of 20 cm from each subplot area and separated weed seeds from soil using an elutriator (Wiles *et al.*, 1996) and an air-column separator (Model 757; Seedburo Equipment, Des Plaines, IL, USA). Remaining material was inspected by eye, and seeds were removed by hand. After identification by species, numbers of viable seeds were determined by placing recovered seeds in a germination chamber for 4 days, followed by tetrazolium testing of ungerminated seeds (International Seed Testing Association, 1985). The resulting data represented the initial 'background' seed densities present in each subplot.

We then added a pulse of *S. faberi* and *A. theophrasti* seeds to the surface of each subplot area on 4–7 November 2002 using a calibrated 1-m-wide mechanical drop spreader (Gandy, Owatonna, MN, USA). Seeds of both weed species were harvested locally during the late summer of 2002 and stored in the dark at 4°C. Several days before, seeds were spread in subplot areas, and their status was assessed via direct germination and tetrazolium tests. For *S. faberi*,  $1 \pm 1.3\%$  of seeds spread were readily germinable and  $93 \pm 3.2\%$  were dormant; total seed viability was  $94 \pm 3.2\%$ . For *A. theophrasti*,  $15 \pm 5.8\%$  of seeds spread were readily germinable and  $79 \pm 3.8\%$  were dormant; total seed viability was  $94 \pm 4.7\%$ . Based on these values and the machine calibration, *S. faberi* and *A. theophrasti* seeds were spread at mean rates of 470 and 1876 viable seeds  $\text{m}^{-2}$  respectively. Numbers of added seeds were within the range of values observed by other investigators for seed shed by *S. faberi* and *A. theophrasti* in maize and soya bean fields in the central USA (Forcella *et al.*, 2000; Bussan & Boerboom, 2001a,b).

During the subsequent 2003–2005 growing seasons, we counted the number of *S. faberi* and *A. theophrasti* seedlings emerging each week within the central  $2 \times 2$  m area of each subplot and then removed all seedlings in the full  $7 \times 7$  m subplots before the plants could mature and reproduce. Thus, no new seeds were added through *in situ* seed shed after the initial experimental pulse of seeds was applied, and losses of seeds from the seedbank due to seedling emergence were quantified.

To determine changes in weed seedbank densities over time, we extracted 40 soil cores to a depth of 20 cm from the central  $5 \times 5$  m area of each subplot on 26 March to 4 April 2003, 5 to 8 April 2004, 28 March to 1 April 2005 and 10 to 11 April 2006. Core diameter was 19 mm in 2003–2005 and 32 mm in 2006. Soil sampling was intended to occur before seasonal emergence of *S. faberi* and *A. theophrasti* seedlings had commenced; visual inspection of plots indicated that this was largely true. Samples from each subplot were composited, and seeds were removed using an elutriator, an air-column separator and forceps. Numbers of viable seeds were determined through direct germination in a germination chamber, tetrazolium staining and crush testing of non-germinated seeds (Borza *et al.*, 2007).

After accounting for additions of *S. faberi* and *A. theophrasti* seeds due to experimental supplementation and losses due to seedling emergence, we expected that the remainder of changes in seedbank densities from autumn 2002 to spring 2006 would be due to seed deaths. That is,

$$M = N_{2002} - N_{2006} + A - E \quad (1)$$

where  $M$  represents cumulative seed deaths from 2002 to 2006,  $N_{2002}$  and  $N_{2006}$  are densities of viable seeds in the soil in 2002 and 2006, respectively,  $A$  is the number of viable seeds added intentionally in autumn 2002, and  $E$  is the total of number seedlings emerging in 2003–2005.

For this relationship to be true, two assumptions needed to be met. First, immigration and emigration of *S. faberi* and *A. theophrasti* seeds to and from the experimental subplots due to tillage and cultivation operations should have been minimal. Second, addition of seeds of the two weed species to the subplot areas via manure application should also have been minimal. We checked these assumptions explicitly.

#### Assessment of seed movement due to tillage and cultivation

To determine possible changes in seed densities in subplot areas due to seed movement through tillage and cultivation operations, we tracked the movement of spherical ceramic beads (Macrolite ML1430; Kinetico, Newbury, OH, USA) used as surrogate seeds, using a protocol similar to one used by Marshall and Brain (1999). Beads were sieved to generate a subset with diameters between 0.8 and 1.4 mm, corresponding *c.* to *S. faberi* and *A. theophrasti* seeds. These beads were then painted with red acrylic screen printing ink (Speedball Art Products, Statesville, NC, USA) to facilitate detection. On 29 October 2002, a 3-m-long  $\times$  7-cm-wide line of painted beads was placed at an identified location within plots of each sequence (Table 1), in three of the four replicate blocks of the experiment, away from the  $7 \times 7$  m subplots. Based on a measured bead number/bead mass ratio, we deposited 218 300 beads per linear metre. Bead lines lay east to west, perpendicular to the direction of tillage and cultivation operations.

During late spring and summer 2003, after tillage and cultivation operations were completed for crop establishment, soil samples were drawn with a 32-mm-diameter soil probe to a depth of 30 cm at measured distances along a transect perpendicular to the centre of each bead line (Table 2). Transects extended to a distance of 10 m both north and south of the line of bead deposition. In triticale and lucerne plots, soil samples were drawn at 0 m and 0.5, 1.0, 1.5, 2.0, 4.0, 6.0, 8.0, 10.0 m north and south of the bead lines. The sampling intensity was greater in maize and soya bean plots due to greater soil disturbance and the expectation of greater bead movement. In those plots, soil samples were taken at 0 m and 0.25, 0.5, 0.75, 1.0, 1.5, 2.0, 4.0, 8.0 and 10.0 m north and south of the bead lines. Soil samples

**Table 2** Soil disturbance and bead sampling events from autumn 2002 through summer 2003 as affected by crop phase and rotation system

Crop during 2002 and rotation system									
	Maize, 2-year (Sequence 1)	Soya bean, 2-year (Sequence 2)	Maize, 3-year (Sequence 3)	Soya bean, 3-year (Sequence 4)	Triticale, 3-year (Sequence 5)	Maize, 4-year (Sequence 6)	Soya bean, 4-year (Sequence 7)	Triticale, 4-year (Sequence 8)	Lucerne, 4-year (Sequence 9)
Date	Beads applied	Beads applied	Beads applied	Beads applied	Beads applied	Beads applied	Beads applied	Beads applied	Beads applied
29 October 2002									
12 November 2002					Mouldboard ploughing				Mouldboard ploughing
13 November 2002	Chisel ploughing		Chisel ploughing			Chisel ploughing			
26 March 2003				No-till drilling of triticale and red clover			No-till drilling of triticale and lucerne		
15 April 2003	Surface cultivation		Surface cultivation		Surface cultivation	Surface cultivation			Surface cultivation
23 April 2003		Surface cultivation and maize planting			Surface cultivation and maize planting				Surface cultivation and maize planting
19 May 2003		Rotary hoeing			Rotary hoeing				Rotary hoeing
23 May 2003					Inter-row cultivation				Inter-row cultivation
29 May 2003	Surface cultivation and soya bean planting		Surface cultivation and soya bean planting		Surface cultivation and soya bean planting				
10 June 2003				Soil sampled for beads			Soil sampled for beads	Soil sampled for beads	
12 June 2003		Rotary hoeing				Rotary hoeing			
16 June 2003					Inter-row cultivation				Inter-row cultivation
24 June 2003						Inter-row cultivation			
6 July 2003		Soil sampled for beads			Soil sampled for beads				Soil sampled for beads
19 July 2003	Soil sampled for beads		Soil sampled for beads			Soil sampled for beads			

Depth of soil disturbed by chisel ploughing: 25 cm; by mouldboard ploughing: 20 cm; by inter-row cultivation: 5–7 cm; and by surface cultivation and rotary hoeing: 3 cm.



from each location were washed separately in an elutriator to remove soil from beads. Washed samples were then dried, and beads were separated by hand from any remaining soil material and counted. In samples with greater than 100 beads, the number of beads was estimated using a bead mass to bead number regression. Samples of weighed beads that were mixed with soil and processed and recovered in this manner showed no more than a 2% loss of beads.

#### *Weed seed movement due to crop harvesting and manure application*

Weed seed movement can occur due to dispersal of mature seeds by crop harvesting machinery (Mohler, 2001). We considered this to be unimportant in our experiment due to the very low amounts of weed biomass present in the plots areas surrounding our subplots (Liebman *et al.*, 2008).

Composted cattle manure was applied in autumn 2002–2005 to plots containing triticale stubble in the 3-year rotation and lucerne in the 4-year rotation, preceding maize production in the following years. We assessed possible additions of seeds in the manure by drawing five or six samples (570 cm<sup>3</sup> per sample in 2002 and 2003, 1455 cm<sup>3</sup> per sample in 2004 and 2005 cm<sup>3</sup>) from manure piles prior to application of manure on the plots, elutriating the samples, isolating seeds from the remaining material by hand and enumerating densities of viable *S. faberi* and *A. theophrasti* seeds after subjecting recovered seeds to germination chamber assays, tetrazolium staining and forceps crush tests (International Seed Testing Association, 1985; Borza *et al.*, 2007). Weed seeds can also be added to fields as contaminants of crop seeds (Mohler, 2001). However, because we planted certified commercial seed that had been cleaned to remove weed seeds, we considered seed contamination to be an unimportant source of weed seeds in our experiment.

#### *Data analysis*

Data were analysed using procedures in JMP 10.0 (SAS Institute, Cary, NC, USA). The level of significance for statistical tests was set at  $\alpha = 0.05$ .

#### *Analyses of seedbank population densities*

We examined changes in *S. faberi* and *A. theophrasti* seedbank densities over time using nonlinear regression and linear mixed-effects models. For each species, we converted the number of viable seeds detected in the soil at each sampling date into proportions of initial seed density (i.e. background seed density plus experimentally

added seeds). We then fitted nonlinear models describing proportional declines in soil seed densities from initial values through the succeeding 41 months until the final soil sampling date in April 2006. We used data from each plot to develop a general model for each species that did not differentiate between sequences and rotation systems (Table 1). Choice of mathematical models was based on parsimony in the number of model parameters and inspection and comparison of residuals and root mean square error values. We then used the two general models (one for each species) to generate predicted values for proportional seedbank densities at each sampling date, that is, a 'time' effect. Next, we used these predicted values in linear mixed-effects models that included seedbank density as the dependent variable and replicate block, time, sequence or rotation, and the interaction of time with sequence or with rotation as independent variables. This is an example of Ross's predicted value parameterisation of nonlinear models (Ross, 1990). Block was treated as a random effect; all other terms were treated as fixed effects.

In the absence of significant sequence, rotation or interaction effects, we retained the general model of the nonlinear regression. If sequence, rotation or interaction effects were significant, we developed separate models for individual sequences or rotations using the same general form of the mathematical function as for the general model, but with parameters specific for each sequence or rotation. Because most of the total variation in *S. faberi* and *A. theophrasti* seed densities over the course of the experiment occurred during the first 5 months after seed deposition, and because this large effect of time may have obscured other effects, we further investigated possible differences between sequences and rotations using seedbank data only from months five through 41. We analysed these data with the same linear mixed-effects models used for the full data sets.

#### *Analyses of seedling emergence*

We used linear mixed-effects models to analyse *S. faberi* and *A. theophrasti* seedling emergence in 2003–2005 in two ways. First, we examined annual seedling emergence for each of the 3 years using a repeated measures approach. Models included sequence or rotation system, year, and the interaction of sequence or rotation with year as fixed effects, and replicate block nested within sequence or rotation as a random effect. Second, we examined total cumulative seedling emergence during 2003–2005 with linear mixed-effects models that used sequence or rotation system as a fixed effect and replicate block as a random effect. The same linear mixed-effects models were used to examine background viable seed densities in soil in autumn 2002 and final

viable seed densities in soil in spring 2006. If significant sequence or rotation effects were detected, we conducted mean separations using Student's *t*-test. Seedling and seed density data were square root-transformed before analysis to homogenise variances.

#### Analyses of seed movement and seed contamination data

We assessed seed movement due to tillage and cultivation operations, as indicated by patterns of recovery of painted ceramic beads at locations lying on a transect perpendicular to the original line of bead deposition, by determining the total number of beads collected in each plot and the cumulative proportion of beads collected at each sampling point in each plot from 10 m south to 10 m north of the bead line. For each sequence of crops and crop residues (Table 1), we then calculated means of cumulative proportions of total beads recovered and their SE for transect segments lying  $\pm 1$  and  $\pm 2$  m from the line of bead deposition.

Densities of recovered viable *S. faberi* and *A. theophrasti* seeds in manure samples were converted to seed densities per unit of plot surface area based on measured manure application rates and volume/mass ratios for manure. Assessment of the magnitude of weed seed additions in manure between years and treatments was based on means and their SE.

#### Analyses of seed mortality

We used Eqn (1) and plot-specific data concerning initial and final viable seed densities in and on the soil,

numbers of added seeds and numbers of emerged seedlings to calculate numbers of *S. faberi* and *A. theophrasti* seeds that died in the soil seedbank between autumn 2002 and spring 2006. We then converted these values to proportional mortality values by dividing the number of dead seeds by the initial size of the seedbanks. Seed mortality values were analysed using linear mixed-effects models that included sequence or rotation system as a fixed effect and replicate block as a random effect. If significant sequence or rotation effects were detected, mean separations were conducted using Student's *t*-tests with error terms derived from the relevant linear mixed-effects models.

## Results

#### Viable seed population densities

The background population density of viable *S. faberi* seeds in the surface 20 cm of soil at the start of the experiment in autumn 2002 did not differ significantly between sequences ( $P = 0.54$ ) or rotation systems ( $P = 0.38$ ; Table 3). Mean density ( $\pm 1$  SE) was  $24 \pm 9.6$  seeds  $m^{-2}$ . Addition of 1876 viable *S. faberi* seeds  $m^{-2}$  after measuring background densities was thus assumed to create seedbanks of similar size for each treatment at the initiation of the experiment. Mean *S. faberi* seed density ( $\pm 1$  SE) in spring 2006 was  $138 \pm 24.3$  seeds  $m^{-2}$  (Table 3).

Using data from the entire 41-month course of the experiment, a three-parameter model,  $y = 1/(A + B \times x \times \exp(x \times C))$ , was selected to describe the decline in *S. faberi* seed densities in soil from autumn 2002

**Table 3** Mean *Setaria faberi* viable seed and emerged seedling densities by sequence and rotation

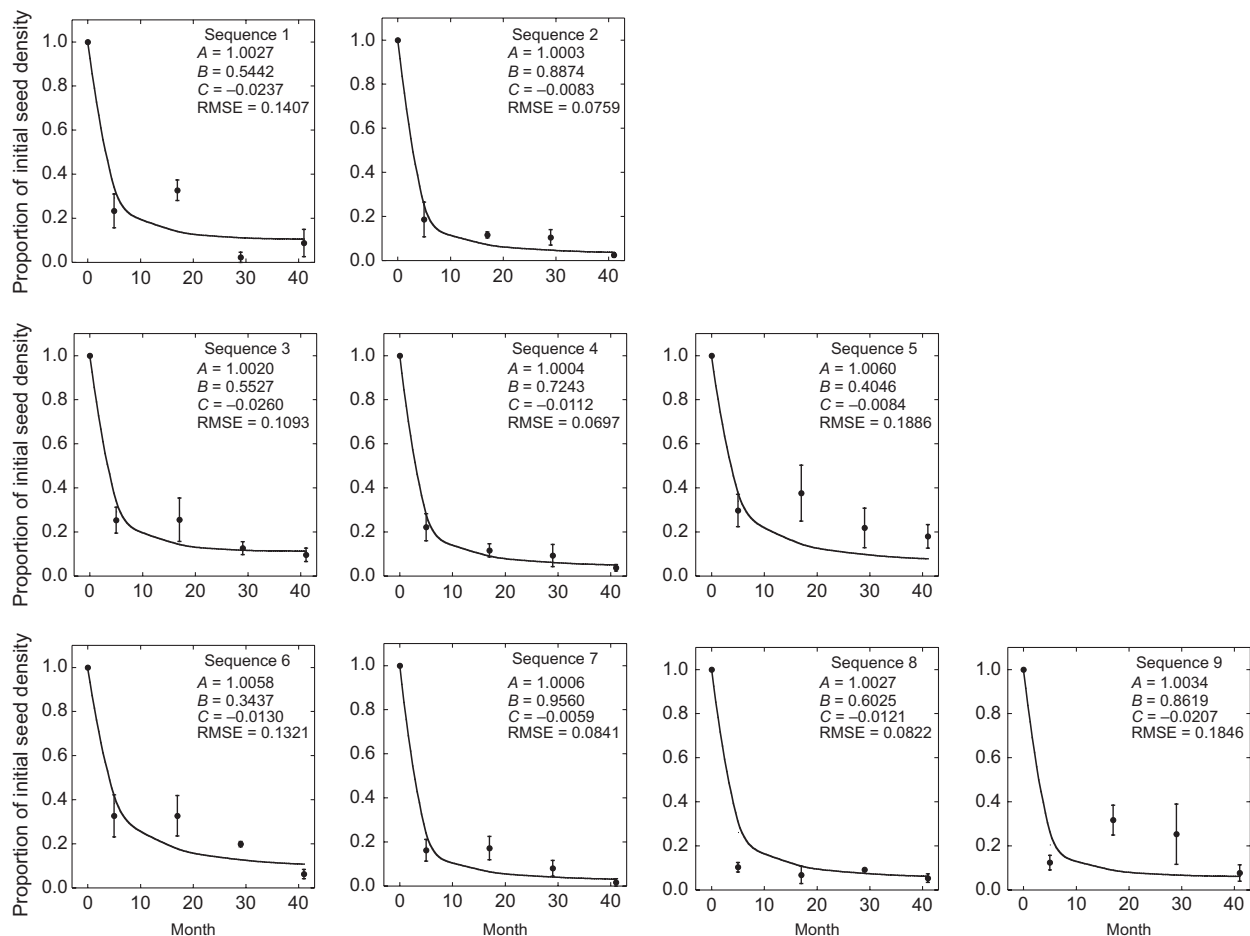
	Background viable seed density in soil to 20 cm, 2002 no. $m^{-2}$	Added viable seeds, 2002 no. $m^{-2}$	Total seedling emergence, 2003–2005 no. $m^{-2}$	Final viable seed density in soil to 20 cm, 2006 no. $m^{-2}$
Sequence				
1	0 (0.0 $\pm$ 0.00)	1876	267 (16.2 $\pm$ 0.61)	166 (9.8 $\pm$ 4.79)
2	0 (0.0 $\pm$ 0.00)	1876	190 (13.7 $\pm$ 0.61)	48 (5.8 $\pm$ 2.12)
3	22 (2.3 $\pm$ 2.35)	1876	262 (16.2 $\pm$ 0.12)	182 (13.0 $\pm$ 1.95)
4	0 (0.0 $\pm$ 0.00)	1876	472 (21.5 $\pm$ 1.77)	71 (7.2 $\pm$ 2.50)
5	88 (6.6 $\pm$ 3.82)	1876	137 (11.4 $\pm$ 1.49)	348 (18.1 $\pm$ 2.55)
6	0 (0.0 $\pm$ 0.00)	1876	265 (16.3 $\pm$ 0.10)	119 (10.4 $\pm$ 1.90)
7	44 (3.3 $\pm$ 3.31)	1876	460 (20.7 $\pm$ 3.27)	32 (3.5 $\pm$ 3.25)
8	22 (2.3 $\pm$ 2.34)	1876	154 (12.4 $\pm$ 0.61)	108 (8.7 $\pm$ 2.98)
9	44 (3.3 $\pm$ 3.31)	1876	115 (10.6 $\pm$ 0.87)	150 (11.0 $\pm$ 3.14)
Rotation system				
2-year	0 (0.0 $\pm$ 0.00)	1876	227 (15.0 $\pm$ 0.62)	107 (7.8 $\pm$ 2.54)
3-year	37 (3.0 $\pm$ 1.58)	1876	290 (16.4 $\pm$ 1.43)	200 (12.8 $\pm$ 1.82)
4-year	27 (2.2 $\pm$ 1.22)	1876	248 (15.0 $\pm$ 1.26)	105 (8.7 $\pm$ 1.46)

Means  $\pm 1$  SE of square root-transformed data are shown in parentheses, except for added viable seeds, for which it was assumed a constant number was added to all treatments.

until spring 2006. Time and sequence effects were highly significant ( $P < 0.0001$  and  $P = 0.0009$ , respectively), but rotation system and time  $\times$  sequence and time  $\times$  rotation effects were not significant ( $P = 0.13$ ,  $P = 0.59$  and  $P = 0.72$  respectively). Consequently, we developed separate models for each sequence (Fig. 1). Three aspects of the observed patterns of *S. faberi* seedbank decline are particularly striking. First, by spring 2006, seedbank density was reduced by  $>85\%$  from the original values for all sequences. Second, also for all sequences, most of the decline in *S. faberi* seedbank density occurred between seed deposition in autumn 2002 and soil sampling in spring 2003, 5 months later, before seedling emergence had commenced. Third, the greatest reductions in *S. faberi* seedbank population densities were observed for those sequences in which no soil disturbance occurred from autumn 2002 until at least spring 2003. More specifically, mean *S. faberi*

seedbank densities over the course of the experiment were lowest in Sequences 2, 4 and 7, which all contained soya bean residue in autumn 2002 and had no soil disturbance until spring 2003, and in Sequence 8, which contained lucerne growing in triticale stubble in autumn 2002 and had no soil disturbance until autumn 2003 (Table 2).

Similar to the analyses of the full data set for *S. faberi* seedbanks, analyses of the subset of data for months five through 41 indicated that time and sequence effects were highly significant ( $P = 0.001$  and  $P = 0.0009$ , respectively), whereas rotation system and time  $\times$  sequence and time  $\times$  rotation effects were not significant ( $P = 0.13$ ,  $P = 0.62$  and  $P = 0.54$  respectively). Thus, from the fifth month of the experiment onwards, *S. faberi* seeds continued to be lost from the soil seedbank, and the pattern of differences between sequences in mean seedbank densities that was detected in the full data set remained.



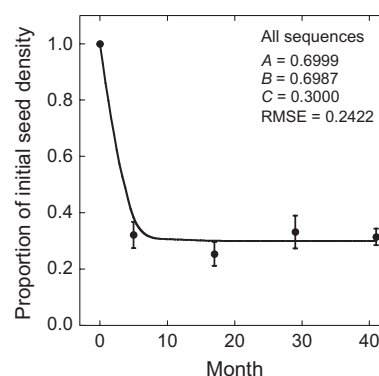
**Fig. 1** Population densities of viable *Setaria faberi* seeds in soil (to 20 cm depth) over time for the nine different crop sequences used within the experiment (see Table 1) shown as proportions of initial seed densities (background seed densities plus experimentally added seeds). Means  $\pm$  1 SE are presented for each of five dates from autumn 2002, when experimental seed additions were made, to spring 2006. Data were fitted to the general model  $y = 1/(A + B \times x \times \exp(x \times C))$ . Curve parameters and the root mean square error for each regression are shown.



No viable *A. theophrasti* seeds were found in the surface 20 cm of soil in autumn 2002 in any of the treatments, prior to experimental additions of seeds (Table 4). Addition of 470 viable *A. theophrasti* seeds  $\text{m}^{-2}$  after measuring background densities was thus assumed to create seedbanks of similar size for each treatment. Mean *A. theophrasti* seed density ( $\pm 1$  SE) in spring 2006 was  $148 \pm 13.7$  seeds  $\text{m}^{-2}$  (Table 4).

A three-parameter model,  $y = A \times \exp(-B \times x) + C$ , was selected to describe the decline in *A. theophrasti* seed densities in soil over the full 41-month course of the experiment. The effect of time was highly significant ( $P < 0.0001$ ), but sequence, rotation, and sequence and rotation interactions with time were not significant ( $P = 0.17$ ,  $P = 0.34$ ,  $P = 0.96$  and  $P = 0.79$  respectively). Thus, we retained the general model for *A. theophrasti* seedbank decline for all sequences and rotations (Fig. 2). The decline in seed densities observed by the end of the experiment for *A. theophrasti* was  $>65\%$ , which was not as large as the declines observed for *S. faberi* (Fig. 1). However, similar to *S. faberi*, most of the decline in *A. theophrasti* seedbank density occurred in the first 5 months after seed deposition (Fig. 2).

Analyses of the subset of *A. theophrasti* seedbank data for months five through 41 indicated that time, sequence, rotation and time  $\times$  rotation effects were not significant ( $P > 0.39$ ,  $P = 0.17$ ,  $P = 0.33$  and  $P = 0.21$  respectively). However, a significant time  $\times$  sequence interaction ( $P = 0.04$ ) was detected. This interaction reflected differences in *A. theophrasti* seed



**Fig. 2** Population densities of viable *Abutilon theophrasti* seeds in soil (to 20 cm depth) over time for all crop sequences used within the experiment shown as proportions of initial seed densities (background seed densities plus experimentally added seeds). Means  $\pm 1$  SE are presented for each of five dates from autumn 2002, when experimental seed additions were made, to spring 2006. Data were fitted to the general model  $y = A \times \exp(-B \times x) + C$  because significant sequence and rotation effects were not detected. Curve parameters and the root mean square error for the general model are shown.

population densities that were inconsistent between sequences and dates and which might have resulted from sampling seedbanks with low densities and non-homogeneous spatial distributions. In general, *A. theophrasti* seeds did not continue to be lost from the soil seedbank after the initial steep decline, and no differences were evident between sequences and rotations in seed densities during months five through 41. This general pattern differed substantially with the one observed for *S. faberi*, described above.

**Table 4** Mean *Abutilon theophrasti* viable seed and emerged seedling densities by sequence and rotation

	Background viable seed density in soil to 20 cm, 2002 no. $\text{m}^{-2}$	Added viable seeds, 2002 no. $\text{m}^{-2}$	Total seedling emergence, 2003–2005 no. $\text{m}^{-2}$	Final viable seed density in soil to 20 cm, 2006 no. $\text{m}^{-2}$
<b>Sequence</b>				
1	0 (0.0 $\pm$ 0.00)	470	196 (14.0 $\pm$ 0.52)	134 (11.4 $\pm$ 1.25)
2	0 (0.0 $\pm$ 0.00)	470	219 (14.8 $\pm$ 0.53)	110 (10.2 $\pm$ 1.41)
3	0 (0.0 $\pm$ 0.00)	470	67 (8.2 $\pm$ 0.22)	126 (11.2 $\pm$ 0.58)
4	0 (0.0 $\pm$ 0.00)	470	80 (8.9 $\pm$ 0.85)	158 (11.7 $\pm$ 2.67)
5	0 (0.0 $\pm$ 0.00)	470	38 (6.1 $\pm$ 0.39)	111 (9.9 $\pm$ 2.01)
6	0 (0.0 $\pm$ 0.00)	470	68 (8.1 $\pm$ 0.72)	118 (10.5 $\pm$ 1.72)
7	0 (0.0 $\pm$ 0.00)	470	75 (8.6 $\pm$ 0.43)	137 (11.6 $\pm$ 1.18)
8	0 (0.0 $\pm$ 0.00)	470	48 (6.8 $\pm$ 0.50)	205 (14.1 $\pm$ 1.43)
9	0 (0.0 $\pm$ 0.00)	470	46 (6.8 $\pm$ 0.39)	229 (14.8 $\pm$ 1.86)
<b>Rotation system</b>				
2-year	0 (0.0 $\pm$ 0.00)	470	207 (14.4 $\pm$ 0.38)	122 (10.8 $\pm$ 0.90)
3-year	0 (0.0 $\pm$ 0.00)	470	62 (7.7 $\pm$ 0.46)	132 (10.9 $\pm$ 1.05)
4-year	0 (0.0 $\pm$ 0.00)	470	59 (7.6 $\pm$ 0.31)	175 (12.8 $\pm$ 0.87)

Means  $\pm 1$  SE of square root-transformed data are shown in parentheses, except for added viable seeds, for which it was assumed a constant number was added to all treatments.

### Seedling emergence

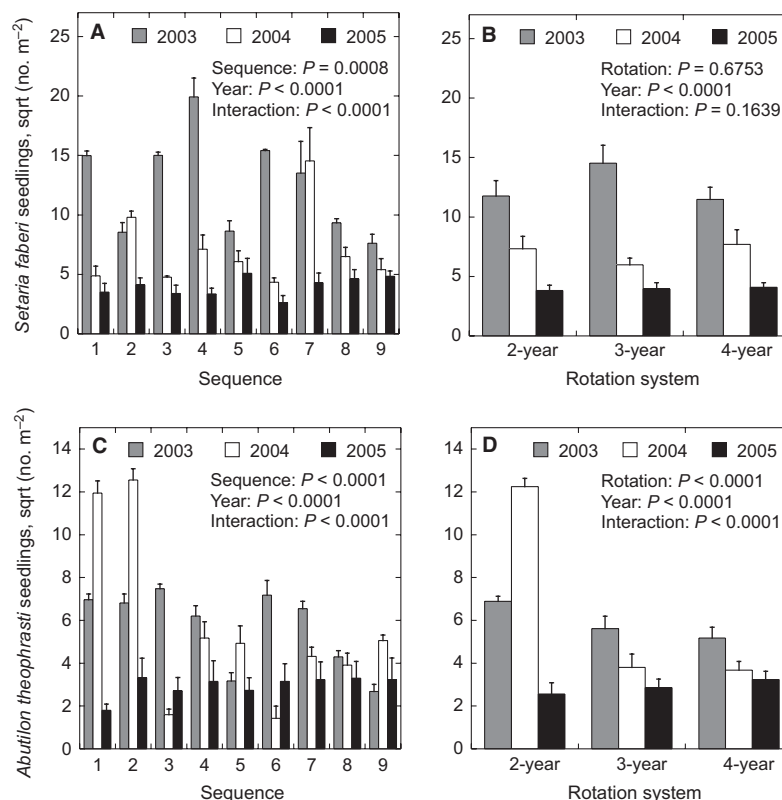
Cumulative emergence of *S. faberi* seedlings during 2003–2005 differed between crop sequences ( $P < 0.0001$ ), being greatest in Sequences 4 and 7 and least in Sequences 5 and 9 (Table 3). Cumulative emergence of *S. faberi* seedlings did not differ between rotation systems ( $P = 0.70$ , Table 3). In assessing *S. faberi* emergence between treatments and years, strong effects of sequence ( $P = 0.0008$ ), year ( $P < 0.0001$ ) and sequence  $\times$  year ( $P < 0.0001$ ) were detected, but there were no significant effects of rotation ( $P = 0.68$ ) or rotation  $\times$  year ( $P = 0.16$ ; Fig. 3A and B). In general, *S. faberi* seedling emergence was greatest in 2003 and declined in the subsequent 2 years (Fig. 3B). The higher levels of cumulative seedling emergence noted for Sequences 4 and 7 were characterised by high levels of seedling emergence in 2003 in the former sequence, and in 2004 in the latter sequence (Fig. 3A).

Cumulative emergence of *A. theophrasti* seedlings during 2003–2005 differed between crop sequences ( $P < 0.0001$ ) and rotation systems ( $P < 0.0001$ ), being greatest in Sequences 1 and 2 of the 2-year rotation and least in Sequence 5 of the 3-year rotation (Table 4). Cumulative emergence of *A. theophrasti* seedlings was

71% lower in the 3- and 4-year rotation systems than in the 2-year system ( $P < 0.0001$ ; Table 4). Strong differences in temporal patterns of *A. theophrasti* seedling emergence were detected between treatments (Fig. 3C and D), with the effects of sequence, rotation, year and interactions of sequence and rotation with year all highly significant ( $P < 0.0001$  for each). The highest levels of *A. theophrasti* seedling emergence occurred in 2004 in Sequences 1 and 2 of the 2-year rotation (Fig. 3C and D).

### Movement of surrogate seeds

Recovery of painted ceramic beads from the soil in 2003 suggested that tillage and cultivation activities had a small or negligible effect on weed seed movement into and out of the subplot areas used to study weed seed-banks. For all sequences, the majority of beads recovered were within 1 m of the original bead locations (Table 5). With the exception of Sequence 6, the proportion of beads recovered within 2 m of the original bead locations was  $\geq 0.97$ ; for Sequence 6, the proportion of beads recovered within 2 m was 0.90 (Table 5). Based on these results, we chose to ignore seed movement via tillage and cultivation in subsequent analyses of seed-



**Fig. 3** Emergence of *Setaria faberi* seedlings by sequence (A) and by rotation system (B), and emergence of *Abutilon theophrasti* seedlings by sequence (C) and rotation system (D) in 2003, 2004 and 2005. See Table 1 for the order of crops within each sequence. Means  $\pm$  1 SE of square root-transformed data are presented.

**Table 5** Proportions of ceramic beads recovered from the soil in summer 2003 along transect segments lying  $\pm 1$  and  $\pm 2$  m from lines of bead deposition on the soil surface in autumn 2002

	$\pm 1$ m	$\pm 2$ m
Sequence		
1	0.91 $\pm$ 0.040	0.99 $\pm$ 0.005
2	0.82 $\pm$ 0.123	0.99 $\pm$ 0.006
3	0.84 $\pm$ 0.077	0.97 $\pm$ 0.018
4	1.00 $\pm$ 0.003	1.00 $\pm$ 0.002
5	0.81 $\pm$ 0.152	0.98 $\pm$ 0.006
6	0.71 $\pm$ 0.081	0.90 $\pm$ 0.075
7	1.00 $\pm$ 0.000	1.00 $\pm$ 0.000
8	1.00 $\pm$ 0.001	1.00 $\pm$ 0.000
9	0.92 $\pm$ 0.043	0.99 $\pm$ 0.005

Proportions were calculated relative to the total number of beads recovered per replicate plot in transects  $\pm 10$  m from lines of bead deposition. Bead lines lay perpendicular to the direction of tillage and planting operations. Data are shown for the nine different crop sequences used within the experiment (see Table 1). Means  $\pm 1$  SE are presented.

bank dynamics within the central  $5 \times 5$  m areas of the subplots.

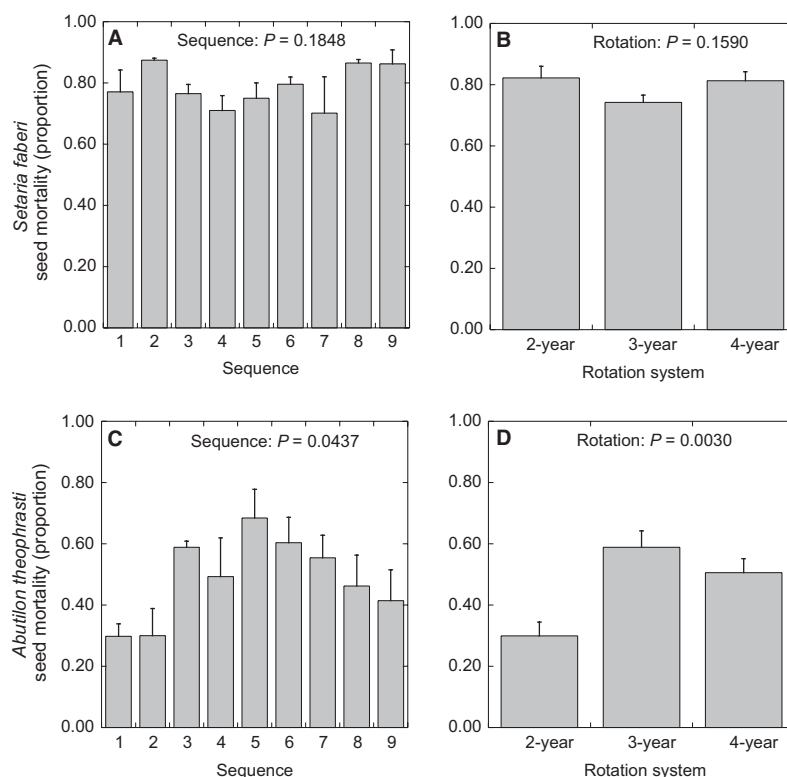
#### Seeds in manure

Analyses of composted manure applied in autumn 2002–2005 indicated that densities of viable seeds of

*S. faberi* and *A. theophrasti* were low or nil (data not shown). No viable *A. theophrasti* seeds were detected in manure in any year, and no viable *S. faberi* seeds were detected in manure in 2002, 2003 and 2004. In 2005, the density of viable *S. faberi* seeds added to plots receiving manure was  $0.3 \pm 0.25$  seeds  $m^{-2}$ . These seed additions occurred preceding maize production in 2006 in the 3- and 4-year rotation systems. However, because the value was small in comparison with the initial input of *S. faberi* seeds, we chose to ignore seed additions via manure application in our subsequent analyses of seedbank dynamics.

#### Seed mortality

Mortality of *S. faberi* seeds during the period of 2002–2006 was unaffected by sequence ( $P = 0.18$ ) or rotation ( $P = 0.16$ ; Fig. 4A and B). Averaged across treatments, mean *S. faberi* mortality ( $\pm 1$  SE), assessed as a proportion of original seedbank density, was  $0.79 \pm 0.018$ . In contrast to the pattern observed for *S. faberi*, there were significant effects of both sequence ( $P = 0.04$ ) and rotation ( $P = 0.003$ ) on *A. theophrasti* seed mortality during 2002–2006 (Fig. 4C and D). Seed mortality was greatest in Sequence 5 and least in Sequences 1 and 2 (Fig. 4C). Comparing rotations, mean proportional seed mortality



**Fig. 4** Cumulative mortality of *Setaria faberi* seeds by sequence (A) and by rotation system (B), and mortality of *A. theophrasti* seeds by sequence (C) and rotation system (D) from autumn 2002 until spring 2006. See Table 1 for the order of crops within each sequence. Means  $\pm 1$  SE are presented.

was 83% greater ( $P = 0.001$ ) in the 3-year ( $0.59 \pm 0.053$ ) and 4-year ( $0.51 \pm 0.046$ ) systems than in the 2-year system ( $0.30 \pm 0.045$ ; Fig. 4D).

## Discussion

Seedling emergence, seed shed from mature *in situ* plants, seed mortality and seed immigration and emigration mediated by farm machinery, wind, water, animals and other agents can all affect weed seed densities in soil. Based on (i) our success in removing emerged *S. faberi* and *A. theophrasti* seedlings before they reproduced, (ii) the minimal numbers of *S. faberi* and *A. theophrasti* seeds contained within the manure we applied and (iii) the minimal displacement of beads used as surrogate seeds (Table 5), we believe that additions of new seeds, immigration and emigration were not important in our experiment. Consequently, our results provide insights into the impacts of different cropping systems and crops on weed seedling emergence and seed mortality. Nevertheless, because our study involved the application of a pulse of *S. faberi* and *A. theophrasti* seeds only once, the seed fates we observed might have been affected by the particular set of environmental conditions that were present during the course of the experiment. Mickelson *et al.* (2004) added *Eriochloa villosa* (Thunb.) Kunth seeds to field plot soil in two separate years and found differences due to time of seedbank establishment for seedling emergence, seed mortality and seedbank density. Thus, different patterns of seedling emergence and seed mortality might have occurred had we started our 41-month-long experiment in multiple years. Future studies could address this issue, although costs and logistics might be prohibitive.

Despite the potential environmental specificity of our results, they are concordant with those of Buhler and Hartzler (2001), who placed *S. faberi* and *A. theophrasti* seeds into the top 5 cm of field soil and measured seedling emergence, seed disappearance and seed survival over the ensuing 4 years. In both Buhler and Hartzler's (2001) study and ours, there were large reductions in soil seedbank densities of both *S. faberi* and *A. theophrasti* by the end of the experiments.

Most of the reductions in seedbank densities in our study occurred during the cold months of November 2002 to March 2003 (Figs 1 and 2), before seedling emergence had commenced. Fatal germination within the soil was probably not a substantial source of seed loss during that period, because average soil temperature at 10 cm depth was  $-0.5^{\circ}\text{C}$  (Iowa Environmental Mesonet, 2013). Instead, we believe seed predation and/or seed mortality due to pathogens was important in determining seed fates. Williams *et al.* (2009) quanti-

fied rates of overwinter loss of *S. faberi* and *A. theophrasti* seeds from screen trays placed on the soil surface in a subset of the plots in which we conducted our measurements and reported seed removal rates of 31–97% for *S. faberi* and 31–98% for *A. theophrasti*, depending on crop habitat and year. Seed losses were attributed to rodent seed predators. Gómez *et al.* (2014) buried *S. faberi* and *A. theophrasti* seeds in soil of a subset of the plots we used in the present study and reported mean overwinter pathogen-related mortality rates of 0–45% for the former species and 0–2% for the latter, depending on burial depth and year. As noted earlier, reductions in *S. faberi* seed population densities were greatest for those sequences (2, 4, 7 and 8) in which there was no soil disturbance for multiple months after seed deposition in autumn 2002 (Table 2). Because seed predators can remove substantial numbers of *S. faberi* and *A. theophrasti* seeds from the soil surface within several days following crop harvest in autumn (Cardina *et al.*, 1996; Westerman *et al.*, 2006), and because retention of weed seeds on the soil surface by delaying tillage operations can increase seed predation (Westerman *et al.*, 2006), we suggest that the majority of reductions in *S. faberi* and *A. theophrasti* seed densities in our experiment occurred shortly after seeds were deposited on the soil surface on 4–7 November 2002, or in the subsequent winter and early spring months.

Although our study indicated that the largest declines in *S. faberi* and *A. theophrasti* seed population densities occurred in the initial 5 months after seed deposition (Figs 1 and 2), our use of fitted functions to describe seed population densities over time may have interfered with our ability to discern later patterns of seedbank decline. That is, by capturing large initial declines in seed population densities with selected mathematical functions, finer scale changes in months 5 through 41 may have been obscured. We attempted to address this concern by analysing subsets of the data from after the initial 5 months and found no major inconsistencies with the analyses of the full data sets. Nonetheless, more attention should be directed in future investigations towards understanding the fates of older seeds in the soil seedbank, including the potential role of density-dependent factors.

A primary goal of our study was to determine whether there were differences in weed seedbank dynamics between rotation systems in the absence of repeated seed inputs. Other investigators have observed differences in rates of decline of weed seedbanks between different cropping systems when weed seed production has been prevented. Four years after initiating continuous maize, maize–soya bean and maize–soya bean–wheat

cropping systems managed with high levels of herbicide inputs that presumably greatly suppressed weed growth and seed production, Schreiber (1992) found lower viable seed densities of *S. faberi* in the two and three crop rotations than continuous maize; no difference was detected between the diversified systems. Seed densities continued to decline over the subsequent 2 years, although relative differences between the rotation systems were maintained. Lueschen *et al.* (1993) measured changes in *A. theophrasti* seedbank densities for continuous lucerne, continuous maize, continuous oat and a maize–soya bean rotation when *A. theophrasti* seed production was prevented by herbicides, cultivation and hand pulling. Four years after the initiation of the experiment, *A. theophrasti* viable seed densities were higher in the continuous lucerne treatment, which was untilled, than in the other treatments, which were tilled periodically and whose *A. theophrasti* seed densities did not differ. As in Schreiber's (1992) study, *A. theophrasti* seed densities in Lueschen *et al.*'s (1993) study continued to decline over subsequent years, and relative differences between the cropping systems were maintained. This differed from the patterns seen in the present study for *A. theophrasti*, in which differences in seedbank decline were not observed between rotation systems, and little or no seedbank decline was detected in months five to 41.

In a companion study in which seed inputs due to reproduction by weeds surviving cultivation, herbicides, mowing and crop competition were permitted, we found that reductions in *S. faberi* and *A. theophrasti* seed densities were greatest in the 2-year maize–soya bean rotation, least in the 3-year maize–soya bean–triticale + red clover rotation and intermediate in the 4-year maize–soya bean–triticale + lucerne–lucerne rotation (Liebman *et al.*, 2008). In the present study, in which recurrent seed additions were prevented, we did not detect differences between rotation systems in viable seed densities for either *S. faberi* ( $P = 0.17$ ) or *A. theophrasti* ( $P = 0.24$ ) at the final sampling date, 41 months after the initiation of the experiment (Tables 3 and 4). However, we did find that the two weed species differed distinctly in how they responded to rotation systems. For *S. faberi*, cumulative seedling emergence from the seedbank (Table 3) and cumulative seed mortality (Fig. 4B) did not differ between rotation systems. In contrast, for *A. theophrasti*, cumulative seedling emergence was higher in the 2-year rotation than in the 3- and 4-year rotations (Table 4), and seed mortality was lower in the 2-year rotation than in the other rotation systems (Fig. 4D). The mechanisms determining differential seedling emergence and seed mortality are not yet clear and merit more research attention.

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