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Agronomic productivity of conventional and low-external-input cropping systems and their effect on giant foxtail (*Setaria faberi*) population dynamics

by

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A dissertation submitted to the graduate faculty in partial fulfillment of the requirements for the degree of

Doctor of Philosophy

Major: Sustainable Agriculture

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Chapter 1. General Introduction

In the last decade there has been a growing body of literature focused on cropping systems that use less external inputs, such as fertilizer and pesticides, but maintain or increase crop yield and pest control (Bastiaans et al., 2008; Liebman et al., 2008). Such cropping systems, called low-external-input (LEI) systems, are proposed as an alternative to conventional farming systems and are intended to reduce environmental, economic and social problems caused by current agricultural practices (Liebman and Davis, 2000).

LEI systems rely on intensive management of ecological relationships within the agroecosystem to establish a favorable environment for the crops but an unfavorable one for weeds. Instead of relying on herbicide applications to control weeds in current crops, LEI systems incorporate a broader perspective of weed management to include a prevention component (Anderson, 2007; Bastiaans et al., 2000). Weeds are usually controlled by enhancing natural loss of weed seeds in soil, reducing weed seedling establishment, and minimizing seed production by established plants (Anderson, 2005). Crop rotations comprised of crops with different life cycles have a detrimental effect on weed population growth (Anderson, 2007; Bastiaans et al., 2000). Different planting and harvest dates among crops prevent either plant establishment or seed production by weeds (Bastiaans et al., 2008; Liebman et al., 2001).

The impact of rotations on weed community density is also related to seed survival in soil. If fewer seeds enter the soil seedbank each season due to the stresses conveyed by crops and their associated management practices, the mortality rate of the seeds that are currently in the soil strongly affects future seedling emergence. Seed mortality depends on factors such as soil moisture, burial depth, and soil cover, which are influenced by tillage operations, and on morphological and physiological characteristics of the seeds (Schutte et al., 2008).

To test the hypothesis that yield, weed suppression, and profit characteristics of LEI cropping systems can match or exceed those of conventional systems, a multiyear, 9-ha field experiment was established at Iowa State University's Marsden Farm in 2002 (Liebman et al., 2008). The experiment includes three cropping systems: a conventional 2-year corn-soybean rotation, a 3-year corn-soybean-small grain/red clover rotation, and a 4-year corn-soybean-small grain/alfalfa-alfalfa rotation. Triticale was planted in 2002-2005 and oats from 2006-2011 as the small grains. Results from this long-term study has indicate that diversified cropping systems that require less external inputs such as synthetic fertilizer and herbicides are a solid agronomic and economic alternative to conventional agriculture. Several questions regarding the agronomic performance of these cropping systems and their effect on weed population dynamics, however, remain unanswered.

First, little research has been done to evaluate the rotation effect on yield of genetically engineered crop varieties compared to conventional varieties, in part because LEI

systems are designed precisely to reduce pesticide applications while from a weed management perspective most of the transgenic varieties are engineered to tolerate herbicide spraying. But because the majority of the corn and soybean genotypes sown in the U.S. are transgenic, and also because farmers should assess a wide range of options in order to choose hybrids and varieties that they consider fits their farming system best, transgenic corn and soybean genotypes may be included in LEI systems whenever there is a judicious reason for doing so. In 2008 the plots corresponding to corn and soybean of each rotation in the Marsden Farm experiment were split in half and planted with a conventional and a transgenic genotype of each crop. Chapter 2 is dedicated to answer the question: is the rotation effect the same for the two genotypes evaluated? It is important to note that this comparison is not between conventional and transgenic genotypes *per se*, but between corn and soybean genotypes that were paired with different agricultural practices associated with their particular genetic characteristics.

Second, there is debate whether beneficial effects that diversified crop rotations might have on soil physical and chemical characteristics, such as increased organic matter content, greater aggregate stability, higher water retention in drought conditions, and slower nutrient release (Buyer and Kaufman, 1996; Chee-Sanford et al., 2006), might also affect soil microbial population distribution and community structure (Buyer et al., 1999; Garbeva et al., 2004) and thereby affect the colonization and decay of weed seeds. Seed mortality can have an important regulatory effect on weed population density, and seed decay rates can vary substantially among crops and crop

management systems (Chee-Sanford et al., 2006; Davis et al., 2006; Kremer, 1993; Westerman et al., 2005). In LEI systems, the incorporation of livestock manure and green manure can reduce weed emergence through the release of allelochemicals or by providing substrates for other organisms that inhibit seedling growth (Davis and Liebman, 2003; Kremer, 2006; Liebman and Gallandt, 1997; Menalled et al., 2005). Chapter 3 deals with the following set of questions regarding weed seed decay in contrasting cropping systems: Do differences in management practices among crop rotations result in differential rates of weed seed decay? Is there a burial depth effect on seed decay? What are the most frequent fungi and Oomycetes genera colonizing weed seeds? Are these microorganisms related to seed decay?

Third, various ecological studies have been carried out in different crop rotations to understand weed population dynamics in these complex agroecosystems (Jordan et al., 1995; Mertens et al., 2002). Key processes in weed life history are seed viability and germination, seed predation, seedling establishment, plant fecundity, and seed dispersal (Colbach and Debaeke, 1998; Holst et al., 2007; Westerman et al., 2006). Farming practices can strongly affect weed seed mortality and weed fecundity. As suggested by Liebman and Gallandt (1997), diversified cropping systems present the best opportunities to target the most vulnerable steps in the weed life histories and mitigate the impact of weeds on crop growth and yield. O'Rourke et al. (2006) reported, for example, that higher giant foxtail seed predation rates by invertebrates occurred in low-external-input soybean compared to conventionally managed soybean.

Projection matrix models of weed population dynamics are useful for two main purposes: to project weed population dynamics under different management scenarios and to evaluate long term consequences of hypothetical changes in the weed life cycle (van Groenendael et al., 1988). In Chapter 4 I used matrix population models to answer the question: does a diverse rotation that affect multiple processes of a weed life cycle decreases weed persistence by depleting giant foxtail seed bank?

In summary, these studies found similar or higher corn and soybean yield in low-external-input (LEI) cropping systems that included small grain and legumes than in a simpler 2-year corn-soybean rotation. Economic return was highest in a three year corn-soybean-oat+red clover LEI rotation. In the LEI systems, giant foxtail seed decay was higher than in the 2-year rotation during one year but not in the other two years, which was attributed to differences in the seed lots evaluated, environmental conditions, and seed pathogen dynamics in the soil. Finally, giant foxtail seed bank density was projected to decrease in the 2-year rotation and increase in the 4-year rotation over time, and it was suggested that summer seed decay values above 20% would affect negatively the population growth rate.

Dissertation organization

The first two articles describe field studies carried out at the Marsden Farm cropping systems experiment. The third article comprises a matrix model study of giant foxtail

population dynamics in a 2-year corn-soybean and in a 4-year corn-soybean-small grain+alfalfa-alfalfa rotation.

Comparison of crop management strategies involving crop genotype and weed management practices in conventional and low-external-input cropping systems. Chapter 2 is dedicated to answer the question: is the rotation effect the same for the two genotypes evaluated? It is important to note that this comparison is not between conventional and transgenic genotypes *per se*, but between corn and soybean genotypes that were paired with different agricultural practices associated with their particular genetic characteristics.

Weed seed decay in conventional and low-external-input cropping systems. Chapter 3 deals with the following set of questions regarding weed seed decay in contrasting cropping systems: Do differences in management practices among crop rotations result in differential rates of weed seed decay? Is there a burial depth effect on seed decay? What are the most frequent fungi and Oomycetes genera colonizing weed seeds? Are these microorganisms related to seed decay?

Cropping system effects on giant foxtail (*Setaria faberi*) population dynamics: modeling analyses .In Chapter 4 I used matrix population models to answer the question: does a diverse rotation that affect multiple processes of a weed life cycle decreases weed persistence by depleting giant foxtail seed bank?

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Chapter 2. Comparison of crop management strategies involving crop genotype and weed management practices in conventional and low-external-input cropping systems

A paper submitted to Renewal Agriculture and Food Systems

Robin Gómez, Matt Liebman, David N. Sundberg, Craig A. Chase

Abstract

Low-external-input (LEI) cropping systems that include forage legumes and small grains in addition to corn (*Zea mays* L.) and soybean [*Glycine max* (L.) Merr.] can achieve similar or higher crop productivity and economic return than conventional corn-soybean rotations. We hypothesized that this rotation effect occurs regardless of the crop genotype planted and the herbicide and cultivation regime selected for weed management. To test this hypothesis, we compared over a 3-year period three cropping systems: a conventional 2-year corn-soybean rotation, a 3-year corn-soybean-oat (*Avena sativa* L.)/red clover (*Trifolium pretense* L.) rotation, and a 4-year corn-soybean-oat/alfalfa-alfalfa (*Medicago sativa* L.) rotation. Within each cropping system, two management strategies were contrasted: (i) genetically engineered (GE) corn with resistance to European corn borer (*Ostrinia nubilalis* Hübner*)* and corn rootworms (*Diabrotica* spp.) plus the broadcast application of preemergence herbicides (PRE), followed in the rotation by a genetically engineered soybean variety with resistance to the herbicide glyphosate plus the postemergence broadcast application of glyphosate

(GLY); and (ii) conventional (non-GE) corn plus the banded application of postemergence herbicides (POST), followed in the rotation by a conventional soybean variety and banded application of a mixture of postemergence herbicides (MIX). Corn yield was higher in the LEI systems than in the conventional 2-yr rotation, and it was also slightly higher in the PRE/GE strategy than in the POST/non-GE strategy. Soybean yield was similar between rotations in 2008, but higher in the LEI systems in 2009 and 2010. Soybean yield was also similar between management strategies in 2008, higher in the GLY/GE strategy in 2009, and similar between strategies in the 3- and 4-yr rotations in 2010. Economic return was highest for the 3-yr rotation, lowest for the 2-yr rotation, and intermediate for the 4-yr rotation. The economic return for both management strategies was similar in the 3-yr rotation, whereas it was 3% higher for the non-GE strategy in the 4-yr rotation and 12% higher for the GE strategy in the 2-yr rotation. Our results indicate that LEI systems can be as profitable as conventional systems while providing farmers with greater flexibility in crop management.

Key words: Low-external-input cropping systems; Forage legumes; Crop rotation; Weed management; Economic return.

Introduction

Crop diversity at farm and regional levels in the U.S. has diminished markedly during the last 50 years [1, 2], and monocultures and short rotation sequences are the prevalent cropping systems there and in many other developed countries [3, 4]. Concomitantly, use

of synthetic pesticides and fertilizer has risen while conservation practices are sometimes abandoned to increase production [5]. Contamination of underground and surface water by nitrogen, herbicides, and soil sediment is an on-going concern for agriculturalists [6, 7].

In the last three decades there has been an effort among researchers and policy makers to raise awareness of environmental, social, and economic consequences of intensive agriculture[8, 9]. This effort has led to attempts to improve agricultural sustainability through the design and management of agroecosystems that exploit ecological processes to maintain soil productivity, improve crop yield, and manage pest and weed populations [10-13].

Low external input (LEI) cropping systems are intended to reduce environmental, economical, and social problems related to intensive pesticides and fertilizer applications [14, 15]. LEI cropping systems rely on manipulations of ecological processes, and the agricultural practices performed in these more diverse systems can lead to improvement in soil structure [16], reduction in carbon and nitrogen losses [17, 18], added organic matter [19], fixation of atmospheric nitrogen by legumes [20], reduction in the incidence and severity of crop diseases [21, 22], reduction in weed density [23, 24], increase in soil microbial biomass [25 26], and higher fossil energy efficiency [27]. LEI systems use green and animal manures and other organic matter amendments as principal nutrient sources for crops, and to improve soil structure. Weed management, an important concern in LEI and organic systems, can be addressed through the application of small

quantities of herbicides, cultivation, and other cropping practices, which expose weeds to multiple stress and mortality factors [10].

Various studies have reported higher crop productivity and economic return in more diverse crop rotations than in simpler conventional systems [28, 29], while other experiments indicated the contrary [30]. Previously, we reported the results of a multiyear cropping systems experiment established in Iowa to test the hypothesis that yield, weed suppression, and profit characteristics of LEI cropping systems can match or exceed those of conventional systems [31]. The experiment included a conventional 2-year corn-soybean rotation, and two LEI rotations: a 3-year corn-soybean-small grain/red clover system, and a 4-year corn-soybean-small grain/alfalfa-alfalfa system. Over a four-year period (2003-2006), net returns were highest for the 4-yr rotation, lowest for the 3-yr rotation, and intermediate for the 2-yr system, with lower use of synthetic N fertilizer and herbicide in the more diverse rotations [31]. Within that study, however, corn and soybean genotypes were not necessarily the same in the different rotation system, i.e., rotation systems and management practices were confounded with crop genetic identity. To address this issue, an experiment was initiated to determine whether the rotation effect on crop productivity was similar for management strategies that differ in the crop genotype planted and the weed management program implemented. We hypothesized that (i) more diverse crop rotations can achieve similar or higher corn and soybean yields than a conventional rotation regardless of the genotype planted and the herbicide and cultivation regime selected for weed management, and (ii) the total economic return of the more diverse rotations is similar or higher than the conventional 2-yr rotation.

There are several implications of having a similar rotation effect regardless of the crop genotype and weed management strategy implemented. First, it would enhance the flexibility of choosing the crop genotype to be planted according to the needs of each production unit, either for resistance to insects, diseases, or tolerance to certain herbicides. Second, it would reduce the inherent risk of depending on fixed external outputs and consequent price fluctuations. Third, the risk of developing herbicide resistance in weeds might be minimized by allowing the use of small quantities of herbicides with different active ingredients over time. And fourth, by favoring a more resilient agroecosystem, it might be possible to reduce the potential negative impacts of environmental and biotic factors on crop yield.

Materials and Methods

Experimental site

The experiment was conducted at Iowa State University's Marsden Farm, located in Boone County, Iowa. The site characteristics, management history, and agronomic performance of the crops from 2003 to 2008 are reported by Liebman et al. (2008) and Cruse et al. (2010).

In 2008-2010, the experiment was arranged as a split-plot design. The main plot size was 18 by 85 m. Each crop of each rotation was grown each year, constituting nine main plots for each of the four replicate blocks. The main plots corresponding with corn and soybean were split in halves and one of two different crop management strategies

was assigned to each subplot. Corn management strategies consisted of either genetically engineered (GE) corn plus the broadcast application of preemergence herbicides (PRE), or conventional (non GE) corn plus the application of postemergence herbicides in a 38-cm band over the crop row (POST). The GE corn was a stacked hybrid with genes to control both European corn borer, *Ostrinia nubilalis* Hübner, and corn rootworms, *Diabrotica* spp. Soybean management strategies were a genetically engineered variety with resistance to the herbicide glyphosate plus the postemergence broadcast application of glyphosate (GLY), or alternatively, a conventional, non-GE, variety and application of a mixture of postemergence herbicides in a 38-cm-band over the crop row (MIX). Details of the corn hybrids and soybean varieties planted, and the pre- and postemergence herbicides applied are provided in Tables 1 and 2.

Crop Management

Tillage operations varied among rotation systems. Fall chisel plowing occurred in all the rotations after corn harvest, to partially incorporate corn residue, and a shallow fall disking was performed after soybean harvest in the 3- and 4-yr rotations to level the plots. Fall moldboard plowing was carried out in the 3-yr rotation to incorporate the red clover and in the 4-yr rotation to incorporate the second-year alfalfa. Spring cultivation was performed in all corn plots before planting in 2008-2010, and in soybean plots in 2009 and 2010.

Oat was planted with red clover in the 3-yr rotation or with alfalfa in the 4-yr rotation in the spring of each year. Oat straw was baled and removed after grain harvest, and red

clover was used as a green manure. First-year alfalfa was harvested once in each seeding year and second-year alfalfa was harvested three times in 2008 and four times in 2009 and 2010. Crop hybrid or cultivar, planting and harvest dates, seed density, and row spacing are provided in Table 1.

Fertilizer rates were based on soil tests from each rotation. We applied synthetic fertilizers in the 2-yr rotation, whereas we used composted cattle manure and reduced rates of synthetic fertilizers in the 3- and 4-yr rotations. Soil samples (0-20 cm depth) were collected each fall and submitted to the Iowa State University (ISU) Soil and Plant Analysis Laboratory for analysis. Synthetic nitrogen was applied as urea to corn plots in the 2-yr rotation before planting, and the late spring nitrate test was used to determine rates for post-emergence side-dress nitrogen applications in all corn plots [32]. In 2009 and 2010, no synthetic nitrogen was applied to corn plots in the 3- and 4-yr rotations due to the presence of adequate amounts of nitrate in the soil, according to fertilizer recommendations for Iowa [33]. Composted cattle manure was applied to plots of red clover and alfalfa each fall preceding corn in the 3- and 4-yr rotations at a rate of 16.2 Mg ha^{-1} (fresh weight basis). Synthetic fertilizer rates and total calculated N, P, and K applied with the composted manure, following analyses conducted by the Iowa State University Soil and Plant Analysis Laboratory, are shown in Table 3.

As noted previously, weed management differed among rotations and management strategies in corn and soybean plots, with POST/non GE corn and MIX/non GE soybean subplots receiving markedly less herbicide than PRE/GE corn and GLY/GE soybean

subplots (Table 2). Interrow cultivation for weed control was carried out in the POST/non-GE corn and MIX/non-GE soybean subplots. This cultivation occurred once in corn and twice in soybean in 2008, and two times in corn and soybean in 2009 and 2010. Oat stubble in the 3- and 4-year rotations was mowed 28 to 35 days after grain harvest to control weeds (Table 2). No explicit weed control was performed in established alfalfa plots.

To control soybean aphid (*Aphis glycines* Matsumura), we applied the insecticides lambda-cyhalothrin (0.027 kg a.i. ha^{-1}) on 13 August 2008 and chlorpyrifos (0.531 kg a.i. ha^{-1}) on 14 August 2009 to all soybean plots.

Yield determination and data analysis

Six rows (382 m^2) of each corn and soybean subplot were harvested using a combine and the grain yield was measured in a weigh wagon. Corn weight was adjusted to reflect a moisture content of 155 g kg^{-1}, whereas soybean weight was adjusted to a moisture content of 130 g kg^{-1}. Oat grain was harvested from entire plots (1530 m^2) using a combine, and the weight was adjusted to a moisture content of 140 g kg^{-1}. Alfalfa and oat straw were clipped and baled from entire plots, and the weight of the bales was determined and adjusted to a moisture content of 150 g kg^{-1} and 100 g kg^{-1}, respectively.

Yield of each crop was analyzed separately. Analyses of variance of corn and soybean yields were performed using the MIXED procedure of SAS, specified for analysis of a split-plot experiment repeated over three years [34]. Rotation and management strategy were considered fixed factors, and replication and year as random factors. The triple interaction between year, rotation, and management was considered the error term for the main plot, while the residual was used as the error term for the subplot. Orthogonal contrasts were used to analyze corn and soybean yield of (i) the 2-yr rotation vs. the average of the 3- and 4-yr rotations (conventional vs. low external input systems) and (ii) the 3-yr rotation vs. the 4-yr rotation (comparison between diverse rotations). Oat yield was analyzed using the GLM procedure of SAS, with rotation as a fixed factor and replication and year as random factors. Alfalfa yield over the three years was analyzed using the GLM procedure.

Weed biomass sampling and data analysis.

In corn plots, above-ground weed biomass in eight 3.05 x 0.76 m areas per sub-plot was clipped on 30 September 2008, 23 September 2009, and 14 September 2010, and then dried and weighed. The same methodology was used to determine weed biomass in soybean sub-plots on 2 October 2008, 24 September 2009, and 30 September 2010. In oat stubble with red clover, oat stubble with alfalfa, and second year alfalfa plots, weed biomass was collected, and later dried and weighed, from eight 0.25m^2 randomly placed quadrats per plot on 10 October 2008, 6 October 2009, and 15 October 2010. Weed biomass values were transformed (ln [x+1]) to meet the ANOVA requirement for

normal distribution. The same ANOVA and orthogonal contrasts performed in the crop yield analyses were used to test for differences in weed biomass, within the same crop, among years, rotations, and management strategies.

Economic analysis

Labor requirements, costs, and returns for the different crops and rotation systems were assessed using data from various sources. Machinery operations conducted were assigned both labor times based on publications by Hanna [35] and cost estimates per field operation based on reports by Duffy [36]. Fertilizer, seed, and herbicide costs were calculated using data from Duffy [36] and local agricultural dealers. Manure was assumed to be generated by on-farm livestock and therefore free, but the costs of spreading it, i.e., labor and machinery, were calculated using data from Hanna [35] and Duffy[36]. Iowa market year crop prices were obtained from the National Agricultural Statistics Service [37]. The 2010 marketing year prices were based on estimates as of April 2011. General crop input estimates for labor wage rates, land rental rates, interest rates, crop insurance, and miscellaneous expenses were estimated using data from Duffy [36].Economic analyses of returns to land and management for the different crops and rotations systems were conducted for individual years and then averaged for the period 2008-2010.

Results

Crop yields

Corn

The main effect of year was not significant (p=0.2743), and no interactions were detected among years, rotations or management strategies. In 2008, standing water in one plot corresponding to the 3-yr rotation, PRE/GE management strategy caused a reduction in plant density and therefore a reduction in corn yield. This particular value was considered an outlier in the data set after testing the normality of the distribution. We then performed an analysis of variance and orthogonal contrasts with and without the outlying observation, and with the data transformed ($\log_e x$) and untransformed. The outlier made the rotation main effect in the ANOVA not significant, whether or not the data were transformed. However, this value was not removed from the data set because the significant rotation main effect remained evident through orthogonal contrasts (Table 4).

Corn yield was highest in the 4-yr rotation, lowest in the 2-yr rotation, and intermediate in the 3-yr rotation (Table 4). There were significant differences in corn yield between the conventional 2-yr rotation and the low-external-input 3- and 4-yr rotations, but no differences among LEI systems (Table 4). We also detected higher corn yield in the PRE/GE management strategy compared to the POST/non-GE management strategy, in all the rotations (Table 4), although this difference was small.

Soybean

Soybean yield was affected by a significant three-way interaction among year, rotation, and management strategy (p=0.0022), therefore, soybean yield was analyzed separately each year. Orthogonal contrasts for each year highlighted the higher soybean yield in the low-external-input rotations versus the conventional corn-soybean rotation in 2009 and 2010 (Table 5).

The ANOVA for each year detected significant differences in soybean yield between management strategies in 2009 and 2010 (Table 5). These differences could be the result of abiotic and biotic factors affecting the soybean plants in those years. In 2009 we observed severe temporary defoliation in the MIX/non-GE subplots sprayed with lactofen, but no precise quantification was made on each plot. In 2010, low soil temperatures at planting and high soil moisture during the summer favored the attack of the soil pathogen *Fusarium solani* f. sp. *glycines*, which caused the disease known as Sudden Death Syndrome (SDS). This attack affected 96% of the soybean plants in the MIX/non-GE management strategy and 27% of the soybean plants in the GLY/GE strategy in the 2-yr rotation. In the 3- and 4-yr rotations, fewer than 9% of the soybean plants of either management strategy were affected by SDS.

Oat and alfalfa

Oat grain yield was similar between rotations (p=0.1018) and between years 2008 and 2010, but higher in 2009 (p=0.0250) (Table 6). Alfalfa hay yield differed among years

($p<0.0001$): it was highest in 2010, lowest in 2009, and intermediate in 2008 (Table 6). The differences in alfalfa yield among years could be attributed to extreme environmental conditions, such as flooding in spring of 2008 and summer of 2009.

Weed biomass

Overall, weed biomass in all the corn and soybean plots was very low (Table 7). Because of the few weeds present and their patchy distribution, the data were not normally distributed and the variability was high. This situation is common in agricultural fields with low weed density [38]. The dominant weeds were *Taraxacum officinale* F.H. Wigg. aggr., *Setaria faberi* R.A.W. Herrm., *Amaranthus rudis* J.D. Sauer, *Abutilon theophrasti* Medik., and *Chenopodium album* L. The triple interaction of year, rotation, and management strategy was significant for weed biomass in corn plots ($p=0.0079$), therefore weed biomass was analyzed by year. Weed biomass in corn was greater in the 4-yr rotation, POST/non-GE subplots in 2008, and in the 2-yr rotation, PRE/GE subplots in 2010. Higher weed biomass was detected in the POST/non-GE than PRE/non-GE corn subplots in 2009 (Table 7). In soybean plots, no differences in weed biomass were evident between rotations or management strategies (Table 7). Weed biomass in oat intercropped with a legume was affected by the interaction between year and rotation ($p=0.0289$). Weed biomass in oat did not differ between rotations in 2008 and 2010, but was lower in the 3-yr rotation in 2009 (Table 7).

Economic analysis

In corn, gross revenue was higher in the PRE/GE management strategy than the POST/non-GE strategy in all rotations, but the production cost was also higher (Table 8), mainly because of the higher cost of the GE seed. In soybean, gross revenue was higher and the production cost was lower for the GLY/GE management strategy than the MIX/non-GE strategy, where more expensive herbicides were applied and interrow cultivation was used. For both corn and soybean, gross revenue was highest in the 4-yr rotation, lowest in the 2-yr rotation, and intermediate in the 3-yr rotation, whereas production cost was highest in the 2-yr rotation, lowest in the 3-yr rotation, and intermediate in the 4-yr rotation, regardless of the management strategy (Table 8). Higher quantities of synthetic nitrogen and herbicides applied in the 2-yr rotation, and lower quantities of P and K applied in the 3-yr rotation explain these differences (Table 3). Labor cost was higher in the POST/non-GE and MIX/non-GE management strategies in corn and soybean, respectively, because of a higher number of hours devoted to weed control through cultivation. Labor cost in corn was highest in the 4-yr rotation, lowest in the 2-yr rotation, and intermediate in the 3-yr rotation, whereas in soybean labor cost was similar among rotations (Table 8). The higher labor cost in corn in the 3- and 4-yr rotations was related to added work in plowing legume sod and spreading manure before planting.

The rotation total gross revenue was highest in the conventional 2-yr rotation regardless of the management strategy, specifically because of the low revenue of oat in the 3- and

4-yr rotations. Production cost was also higher in the 2-yr rotation due to greater application of synthetic nitrogen and herbicides. Returns to land and management, however, were higher for the 3-yr rotation for both management strategies. Lower P and K fertility requirements and the inclusion of clover and manure as nitrogen sources led to much lower production costs in the 3-yr rotation. The economic return of both strategies was similar in the 3-yr rotation, whereas it was 3% higher in the non-GE strategy in the 4-yr rotation and 11.5% higher in the GE strategy in the 2-yr rotation (Table 8). It is important to note that these two management strategies do not constitute a comparison between genetically engineered and conventional crop performance, but rather an evaluation of two specific sets of management tactics in which particular genotypes were coupled with chemical and/or physical weed control practices.

Discussion

This study and previous publications [27, 31] have been consistent in showing higher productivity of corn and soybean in low external input cropping systems over an eight-year period (2003-2010), despite the lower use of synthetic fertilizer and herbicides. Mineralization of the composted manure and legume residues provided sufficient quantities of nitrogen so that no synthetic fertilizer was applied to the 3- and 4-yr rotations in 2009 and 2010. The N made available by the legumes and the manure in the more diverse rotations is released more slowly than the N provided by commercial fertilizers and can therefore be less susceptible to leaching into subsurface drainage lines that discharge into streams and lakes [18]. This represents an important potential

advantage at a time when reducing water contamination by nitrate comprises an important goal for the design of sustainable agricultural systems[8]. In the present study, the economic return of LEI systems was also higher than the conventional 2-yr rotation, even when the labor requirement was higher in the LEI systems. Higher economic return in the 3-yr rotation than the 4-yr rotation was due to the application of lower quantities of P and K in the 3-yr rotation. The alfalfa hay harvested from plots of the 4-yr rotation removed P and K that was not offset sufficiently by manure application, while the red clover was not removed but incorporated into the soil in the 3-yr rotation.

We also found that in the more diversified 3- and 4-yr rotation systems it was possible to implement management strategies that differ in crop genotypes and weed management activities, including the herbicides applied, without altering substantially the economic return of the cropping system. In the conventional 2-yr rotation system, in contrast, choice of management strategy strongly affected the economic return.

More diverse cropping systems that include crops with different botanical characteristics and the addition of organic matter increase microbial biomass and enhance the functional diversity of microbial communities that affect multiple processes within the soil, limiting the impact of some crop pathogens [22, 39] and potentially making the system more resilient. As an example, in the present work we observed in 2010 a severe outbreak of Sudden Death Syndrome of soybean, in the 2-yr rotation. The appearance of this disease was widespread in soybean fields in Iowa in 2010 and favored by certain weather and soil conditions. In the soybean plants of the 3- and 4-yr rotations, however,

SDS incidence was much lower and similar between management strategies, suggesting a rotation effect that operates similarly regardless of the crop genotype planted. In a similar cropping systems experiment, Porter et al.[1] suggested an association between higher disease incidence observed in a 2-yr corn-soybean rotation with lower soybean yield, compared to a 4-yr corn-soybean-oat/alfalfa-alfalfa rotation, although they didn't identify the diseases affecting soybean plants or quantify disease incidence or severity.

Having similar economic return regardless of the management strategy implemented gives the farmer higher flexibility when choosing the corn and soybean genotype to be planted and the herbicides to be applied, and decreases the risk associated with depending on a specific management strategy over time. Similarly, the N supplied by composted manure and legumes made the LEI systems less reliant on synthetic N, and therefore less affected by the variability in fertilizer prices.

Oat productivity in the 3- and 4-yr rotations and alfalfa productivity in the 4-yr rotation had important impacts on the rotation total economic return. Oat grain and alfalfa hay yields varied significantly among years, and both were less profitable than corn or soybean. In order to maintain high rotation economic return, it is important to maximize the productivity of oat and alfalfa. Although weed biomass was low in both crops, when cold weather conditions reduced the alfalfa stand in 2009, weed seedlings emerged and colonized empty spaces, affecting crop growth. Weed biomass was significantly higher in 2009 because of the successful colonization of *Taraxacum officinale* F.H. Wigg. aggr.

in certain areas of the plots where the alfalfa plants were damaged. Nonetheless, weed management was generally successful in both conventional and LEI systems, and in both management strategies. The implications of these results are that farmers who plant non-genetically engineered genotypes in more diverse cropping systems could achieve the same weed control as with GE hybrids, and would be less likely to depend on a single herbicide as the control method, thereby reducing the risk of selection for herbicide resistant weeds.

We conclude that low input cropping systems can be as profitable as conventional systems, require less synthetic nitrogen and herbicide use, give greater crop management flexibility to farmers, and be more resilient to biotic factors that affect the crops. We acknowledge, however, that broad-scale shifts to diversified systems from the conventional corn-soybean system will favor changes in crop prices, due to changes in supply, which may create economic forces that countervail diversification. Policy and economic incentives that encourage cropping system diversification as a means of reducing agrichemical use, retarding the evolution of herbicide resistance in weeds, and improving environmental quality will likely be required to promote substantial change on a landscape level.

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Table 1.1. Hybrid or cultivar grown, planting and harvest date, seed density, seed mass, and interrow spacing used in contrasting crop rotations.

Crop[a]	Year	Management Strategy	Hybrid or cultivar	Planting date	Harvest date	Seed density	Seed mass	Interrow spacing
						seeds ha^{-1}	kg ha^{-1}	cm
Corn	2008	Post / non-GE	Agrigold 6395	19 May.	3 Nov.	80,500	-	76
Corn	2009	Post / non-GE	Agrigold 6395	23 Apr.	21 Oct.	80,501	-	76
Corn	2010	Post / non-GE	Agrigold 6395	20 Apr.	8 Oct.	80,502	-	76
Corn	2008	Pre / GE	Agrigold 6395 Yield Guard Plus	19-May	3 Nov.	80,503	-	76
Corn	2009	Pre / GE	Agrigold 6395 Yield Guard Plus	23 Apr.	21 Oct.	80,504	-	76
Corn	2010	Pre / GE	Agrigold 6395BtRW	20 Apr.	9 Oct.	80,505	-	76
Soybean	2008	GLY / GE	Kruger 287RR/SCN	21-May	6 Oct.	387,500	-	76
Soybean	2009	GLY / GE	Kruger 287RR/SCN	12-May	27 Oct.	400,000	-	76
Soybean	2010	GLY / GE	Kruger 287RR/SCN	19 May[b]	5 Oct.	400,750	-	76
Soybean	2008	MIX / non-GE	Kruger 2918SCN	21-May	6 Oct.	387,500	-	76
Soybean	2009	MIX / non-GE	Kruger 2918SCN	12-May	27 Oct.	400,000	-	76
Soybean	2010	MIX / non-GE	Kruger 2918SCN	19 May[b]	5 Oct.	400,750	-	76
Oat	2008	-	IN09201	16 Apr.	4 Aug.	-	84	20
Oat	2009	-	IN09201	1 Apr.	20 Jul.	-	79	20
Oat	2010	-	IN09201	1 Apr.	16 Jul.	-	82	20
Red clover	2008	-	Cherokee	16 Apr.	-	-	14	20
Red clover	2009	-	Duration	1 Apr.	-	-	14	20
Red clover	2010	-	Medium	1 Apr.	-	-	14	20
Alfalfa	2008	-	FSG 400LH	16 Apr.	20 June, 1 Aug, 17 Sept.	-	17	20
Alfalfa	2009	-	Freedom	1 Apr.	3 Jun, 6 Jul, 17 Aug, 15 Sept.	-	18	20
Alfalfa	2010	-	FSG 400LH	1 Apr.	28 May, 12 Jul, 20 Aug, 30 Nov.	-	17	20

[a] Corn and soybean were planted in all the rotation systems, oat was planted with either red clover in the 3-yr rotation or with alfalfa in the 4-yr rotation

[b] In 2010, soybean was planted on 19 May in blocks 1 to 3 and on 25 May in block 4

Table 1.2. Weed management practices for each crop rotation from 2008 to 2010. Rate (kg ha^{-1}) of herbicide active ingredients shown in parentheses.

Crop	Management strategy	2008	2009	2010
		2-yr rotation		
Corn	Pre / GE	PRE, broadcast: S-metolachlor (1.981), isoxaflutole (0.088)	PRE, broadcast: S-metolachlor (1.820), isoxaflutole (0.070)	PRE, broadcast: S-metolachlor (1.820), isoxaflutole (0.070)
Corn	Post / non-GE	POST, banded: nicosulfuron (0.013), rimsulfuron (0.007), mesotrione (0.053); interrow cultivation (1x)	POST, banded: nicosulfuron (0.013), rimsulfuron (0.007), mesotrione (0.053); interrow cultivation (2x)	POST, banded: nicosulfuron (0.013), rimsulfuron (0.007), mesotrione (0.053); interrow cultivation (1x)
Soybean	GLY / GE	POST, broadcast: glyphosate (1.121)	POST, broadcast: glyphosate (0.121)	POST, broadcast: glyphosate (1.401)
Soybean	MIX / non-GE	POST, banded: clethodim (0.051), lactofen (0.053), flumiclorac pentyl ester (0.015); interrow cultivation (2x)	POST, banded: clethodim (0.051), lactofen (0.070), flumiclorac pentyl ester (0.015); interrow cultivation (2x)	POST, banded: clethodim (0.051), lactofen (0.088), flumiclorac pentyl ester (0.023); interrow cultivation (2x)
		3-yr rotation		
Corn	Pre / GE	PRE, broadcast: S-metolachlor (1.981), isoxaflutole (0.088)	PRE, broadcast: S-metolachlor (1.820), isoxaflutole (0.070)	PRE, broadcast: S-metolachlor (1.820), isoxaflutole (0.070)
Corn	Post / non-GE	POST, banded: nicosulfuron (0.013), rimsulfuron (0.007), mesotrione (0.053); interrow cultivation (1x)	POST, banded: nicosulfuron (0.013), rimsulfuron (0.007), mesotrione (0.053); interrow cultivation (2x)	POST, banded: nicosulfuron (0.013), rimsulfuron (0.007), mesotrione (0.053); interrow cultivation (1x)
Soybean	GLY / GE	POST, broadcast: glyphosate (0.121)	POST, broadcast: glyphosate (0.121)	POST, broadcast: glyphosate (1.401)
Soybean	MIX / non-GE	POST, banded: clethodim (0.051), lactofen (0.053), flumiclorac pentyl ester (0.015); interrow cultivation (2x)	POST, banded: clethodim (0.051), lactofen (0.070), flumiclorac pentyl ester (0.015); interrow cultivation (2x)	POST, banded: clethodim (0.051), lactofen (0.088), flumiclorac pentyl ester (0.023); interrow cultivation (2x)
Oat + red clover	-	Stubble mowing (1x)	Stubble mowing (1x)	Stubble mowing (1x)
		4-yr rotation		
Corn	Pre / GE	PRE, broadcast: S-metolachlor (1.981), isoxaflutole (0.088)	PRE, broadcast: S-metolachlor (1.820), isoxaflutole (0.070)	PRE, broadcast: S-metolachlor (1.820), isoxaflutole (0.070)
Corn	Post / non-GE	POST, banded: nicosulfuron (0.013), rimsulfuron (0.007), mesotrione (0.053); interrow cultivation (1x)	POST, banded: nicosulfuron (0.013), rimsulfuron (0.007), mesotrione (0.053); interrow cultivation (2x)	POST, banded: nicosulfuron (0.013), rimsulfuron (0.007), mesotrione (0.053); interrow cultivation (1x)
Soybean	GLY / GE	POST, broadcast: glyphosate (0.121)	POST, broadcast: glyphosate (0.121)	POST, broadcast: glyphosate (1.401)
Soybean	MIX / non-GE	POST, banded: clethodim (0.051), lactofen (0.053), flumiclorac pentyl ester (0.015); interrow cultivation (2x)	POST, banded: clethodim (0.051), lactofen (0.070), flumiclorac pentyl ester (0.015); interrow cultivation (2x)	POST, banded: clethodim (0.051), lactofen (0.088), flumiclorac pentyl ester (0.023); interrow cultivation (2x)
Oat + alfalfa	-	Stubble mowing; hay removal (1x)	Stubble mowing; hay removal (1x)	Stubble mowing; hay removal (1x)
Alfalfa	-	Hay removal (3x)	Hay removal (4x)	Hay removal (4x)

Table 1.3. Fertilization regimes for crops grown in contrasting crop rotations from 2008 to 2010.

Crop	2008	2009	2010
	2-yr rotation		
Corn	34 kg P + 86 kg K ha^{-1} as TSP[a] and KCl before planting; 114 kg N ha^{-1} as urea at planting; 102 kg N ha^{-1} after planting as UAN[b]	112 kg N ha^{-1} as urea at planting; 56 kg N ha^{-1} after planting as UAN	178 kg K ha^{-1} before planting as KCl; 59 kg P ha^{-1} before planting as TSP; 112 kg N ha^{-1} as urea at planting; 63 kg N ha^{-1} after planting as UAN
Soybean	34 kg P + 86 kg K ha^{-1} as TSP and KCl before planting	none	178 kg K ha^{-1} before planting as KCl; 59 kg P ha^{-1} before planting as TSP
	3-yr rotation		
Corn	119 kg N + 69 kg P + 92 kg K ha^{-1} as composted manure before planting; 102 kg N ha^{-1} after planting as UAN	122 kg N + 52 kg P + 113 kg K ha^{-1} as composted manure before planting	83 kg N + 43 kg P + 73 kg K ha^{-1} as composted manure before planting; 90 kg K ha^{-1} before planting as KCl
Soybean	none	none	90 kg K ha^{-1} before planting as KCl
Oat + red clover	none	none	90 kg K ha^{-1} before planting as KCl
	4-yr rotation		
Corn	34 kg P + 86 kg K ha^{-1} as TSP and KCl before planting; 119 kg N + 69 P + 92 kg K ha^{-1} as composted manure before planting; 102 kg N ha^{-1} after planting as UAN	122 kg N + 52 kg P + 113 kg K ha^{-1} as composted manure before planting	83 kg N + 43 kg P + 73 kg K ha^{-1} as composted manure before planting; 178 kg K ha^{-1} before planting as KCl
Soybean	34 kg P + 86 kg K ha^{-1} as TSP and KCl before planting	none	178 kg K ha^{-1} before planting as KCl
Oat + alfalfa	34 kg P + 86 kg K ha^{-1} as TSP and KCl before planting	none	178 kg K ha^{-1} before planting as KCl
Alfalfa	34 kg P + 86 kg K ha^{-1} as TSP and KCl before planting	none	178 kg K ha^{-1} before planting as KCl

[a] TSP: triple super phosphate

[b] UAN: urea ammonium nitrate

Table 1.4. Mean corn yield over the years 2008-2010.

	Management strategy	
	PRE / GE	POST / non-GE
	Mg ha^{-1}	
Rotation system		
2-yr	12.49	11.82
3-yr	12.59	12.43
4-yr	12.82	12.75
SE	0.24	
	P	
Effects		
Rotation	0.0846	
Management	0.0330	
Rotation*Management	0.2949	
Contrasts		
2-yr vs. (3-yr + 4-yr)/2	0.0391	
3-yr vs. 4-yr	0.4036	

Table 1.5. Soybean yield from 2008 to 2010 involving three rotations and two management strategies.

	2008		2009		2010	
	GLY/GE	MIX/non-GE	GLY/GE	MIX/non-GE	GLY/GE	MIX/non-GE
	Mg ha^{-1}					
Rotation system						
2-yr	3.61	3.32	3.56	3.24	2.83	1.45
3-yr	3.73	3.58	4.18	3.43	3.64	3.73
4-yr	3.94	3.99	4.05	3.85	3.69	3.59
SE	0.18		0.26		0.44	
	P					
Effects						
Rotation	0.0968		0.1046		0.0003	
Management	0.0580		0.0307		0.0034	
Rotation * Management	0.1308		0.3941		0.0012	
Contrasts						
2-yr vs. (3-yr + 4-yr)/2	0.0819		0.0460		<0.0001	
3-yr vs. 4-yr	0.1508		0.5315		0.8227	

Table 1.6. Oat grain and alfalfa hay yield from 2008 to 2010.

Crop	Year	Rotation system			SE
		2-yr	3-yr	4-yr	
		Mg ha^{-1}			
Oat[a]	2008	-	3.17	3.30	0.15
Oat[a]	2009	-	3.56	3.69	0.10
Oat[a]	2010	-	3.23	3.50	0.13
Alfalfa[b]	2008	-	-	9.96	0.35
Alfalfa[b]	2009	-	-	5.48	0.17
Alfalfa[b]	2010	-	-	12.12	0.35

[a] Mean yield of harvested oat straw in the 3-yr rotation was 2.82, 2.81, and 1.86 Mg ha^{-1} in 2008, 2009, and 2010, respectively, and 2.59, 2.67, and 1.74 Mg ha^{-1} in the 4-yr rotation.

[b] Alfalfa hay yield for second-year stands. Mean first-year alfalfa hay yield was 1.03, 1.21, and 1.13 Mg ha^{-1} in 2008, 2009, and 2010, respectively

Table 1.7. Weed biomass in crop rotations involving two management strategies from 2008-2010. Transformed (ln [x+1]) means are in parentheses.

Crop	Rotation system	Management strategy	Year		
			2008	2009	2010
			g m^{-2}		
Corn	2-yr	POST/non-GE	0.11 (0.10)	0.65 (0.44)	0.18 (0.15)
Corn	2-yr	PRE/GE	0.26 (0.22)	0.23 (0.20)	1.18 (0.71)
Corn	3-yr	POST/non-GE	2.81 (0.78)	1.15 (0.73)	0.70 (0.44)
Corn	3-yr	PRE/GE	6.18 (0.96)	0.28 (0.24)	0.17 (0.15)
Corn	4-yr	POST/non-GE	2.24 (1.09)	1.44 (0.85)	0.25 (0.22)
Corn	4-yr	PRE/GE	0.16 (0.15)	0.40 (0.32)	0.17 (0.15)
	SE[a]		(0.39)	(0.13)	(0.15)
Soybean	2-yr	GLY/GE	0.06 (0.06)	0.25 (0.22)	0.17 (0.16)
Soybean	2-yr	MIX/non-GE	0.50 (0.40)	0.26 (0.22)	0.40 (0.32)
Soybean	3-yr	GLY/GE	0.37 (0.28)	0.22 (0.19)	0.05 (0.05)
Soybean	3-yr	MIX/non-GE	0.26 (0.21)	4.48 (0.85)	0.25 (0.21)
Soybean	4-yr	GLY/GE	0.07 (0.07)	0.06 (0.06)	0.02 (0.02)
Soybean	4-yr	MIX/non-GE	0.24 (0.17)	0.07 (0.06)	0.24 (0.20)
	SE		(0.09)	(0.28)	(0.07)
Oat	3-yr	-	10.09 (2.17)	0.31 (0.26)	9.12 (1.77)
Oat	4-yr	-	7.04 (1.82)	6.88 (2.04)	10.14 (2.38)
	SE		(0.40)	(0.11)	(0.51)
Alfalfa	4-yr	-	1.27 (0.76)	51.50 (3.93)	7.93 (2.18)
	SE		(3.81)	(3.81)	(3.81)

[a] Transformed (ln [x+1]) standard error of the mean

Table 1.8. Economic return of crop rotations and management strategies from 2008-2010.

Rotation	Gross revenue	Production cost	Labor cost	Return to land and management
	——— $ ha^{-1} yr^{-1} ———			
2-yr				
Corn Pre/GE	2096.39	1089.07	18.30	989.03
Corn Post/non-GE	2018.36	916.57	22.11	1079.70
Soybean GE	1266.71	535.00	20.11	711.60
Soybean non-GE	996.74	543.29	28.36	425.10
Rotation aver. GE strategy	1681.55	812.04	19.20	850.31
Rotation aver. non-GE strategy	1507.55	729.93	25.23	752.40
3-yr				
Corn Pre/GE	2155.63	797.29	37.12	1321.20
Corn Post/non-GE	2125.85	632.17	41.84	1451.80
Soybean GE	1467.78	405.99	19.66	1042.13
Soybean non-GE	1376.11	415.38	27.89	932.84
Oat / red clover	808.90	324.73	19.66	464.51
Rotation aver. GE strategy	1477.44	509.34	25.48	942.61
Rotation aver. non-GE strategy	1436.95	457.43	29.80	949.72
4-yr				
Corn Pre/GE	2201.60	892.83	37.59	1271.19
Corn Post/non-GE	2183.65	728.58	42.29	1412.79
Soybean GE	1486.76	497.53	20.11	969.13
Soybean non-GE	1455.09	507.26	28.36	919.48
Oat / alfalfa	974.56	630.64	36.14	307.79
Alfalfa	1239.89	387.10	49.72	803.07
Rotation aver. GE strategy	1475.70	602.03	35.89	837.79
Rotation aver. non-GE strategy	1463.30	563.39	39.12	860.78

Chapter 3. Weed seed decay in conventional and low-external-input cropping systems

A paper submitted to Weed Research

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Abstract

Diversified cropping systems can have high soil microbial biomass and thus strong potential to reduce the weed seed bank through seed decay. This study, conducted in Iowa, U.S.A., evaluated the hypothesis that weed seed decay is higher in a low-external-input 4-year maize–soyabean–oat /lucerne-lucerne cropping system than in a conventional 2-year maize-soyabean rotation. Mesh bags filled with either *Setaria faberi* or *Abutilon theophrasti* seeds and soil were buried at two depths in the maize phase of the two cropping systems and sampled over a 3-yr period. *Setaria faberi* seed decay was higher in the more diverse rotation than in the conventional rotation, and at 2 cm than at 20 cm burial depth, only during one year. *A. theophrasti* seeds decayed very little over the three years. Separate laboratory and field experiments confirmed differences in germination and seed decay among the seed lots evaluated each year. *Fusarium, Pythium, Alternaria, Cladosporium, and Trichoderma* were the most abundant genera colonizing seeds of both species. A greenhouse experiment determined a possible relationship between *P. ultimum* and *S. faberi* seed decay. These differences in seed susceptibility to decay indicate the necessity to evaluate weed

population dynamics in different cropping systems in order to make weed management programs as effective as possible.

Keywords: weed management, *Giant foxtail*, *Abuthilon theophrasti*, diversified crop rotations, soil microorganisms, weed pathogens.

Introduction

Crop rotations comprised of crops with different life cycles can have a detrimental effect on weed population growth (Bastiaans et al., 2000, Anderson, 2007), with different planting and harvest dates among crops preventing or reducing either plant establishment or seed production by weeds (Liebman et al., 2001, Bastiaans et al., 2008). In low-external-input (LEI) cropping systems, the use of forage legumes as green manure and livestock manure to provide organic sources of nutrients and organic matter can reduce weed emergence by affecting small seeded weeds through the release of allelochemicals or by providing substrates for other organisms that inhibit seedling growth (Liebman & Gallandt, 1997, Davis & Liebman, 2003, Menalled et al., 2005, Kremer, 2006).

Because weed management represents a challenge for organic and LEI cropping systems, a long-term experiment was established in Iowa, U.S.A., to assess the effect of three cropping systems on weed population dynamics. Over a four year period, decline of an experimentally supplemented seed bank of *Setaria faberi* Herrm. (giant

foxtail) was greatest in a conventional 2-yr maize (*Zea mays* L.) – soyabean [*Glycine max* (L.) Merr.] rotation, least in a LEI 3-yr maize/soyabean/small grain + red clover (*Trifolium pretense* L.) rotation, and intermediate in a LEI 4-yr maize/soyabean/small grain + lucerne (*Medicago sativa* L.)/lucerne rotation (Liebman et al., 2008). *Abutilon theophrasti* Medik. (velvetleaf) seed densities in this experiment declined significantly in the 2-yr and 4-yr systems, but remained unchanged in the 3-yr system (Liebman et al., 2008). The seed decay process, however, remains poorly understood.

Weed seed decay rates can vary substantially among crops and crop management systems (Kremer, 1993, Westerman et al., 2005, Chee-Sanford et al., 2006, Davis et al., 2006). Beneficial effects of diversified cropping systems on soil physical and chemical characteristics, such as increased organic matter content, greater aggregate stability, higher water retention in drought conditions, and slower nutrient release (Buyer & Kaufman, 1996, Chee-Sanford et al., 2006), can impact the soil microbial population distribution and community structure (Buyer et al., 1999, Garbeva et al., 2004, De Cauwer et al., 2011), influencing the colonization and decay of weed seeds by soil microorganisms. Several studies have addressed the potential of organic and other agricultural systems that are less dependent on external, non-renewable resources to reduce the weed seed bank through enhanced weed seed decay or reduced seedling recruitment (Liebman & Davis, 2000, Gallandt, 2006, Ullrich et al., 2011). Contrasting results, however, were obtained. Davis et al. (2006) found higher *S. faberi* and *A. theophrasti* decay in soil from a conventionally managed system than in soil from a cropping system with low external resources. They suggested that soil organic

amendments had an inhibitory effect upon weed seed decay. Ullrich et al. (2011) did not find a consistent system effect on weed seed decay when they compared conventional cropping systems to organic systems with higher organic amendments and soil microbial biomass. De Cauwer et al. (2011), on the other hand, determined that ambient seed bank density was lowest in plots amended with compost with a low C:N ratio, whereas Kremer and Li (2003) associated higher proportions of weed-inhibiting bacteria with cropping systems with soils containing high levels of organic matter.

The present study was conducted to test the hypothesis that a more diverse 4-yr crop rotation system would promote higher weed seed decay by enhancing the development of a more diverse soil microbial community that facilitates greater seed colonization by fungi and Oomycetes, as compared with a simpler 2-yr crop rotation system. The experiment evaluated seed decay of *S. faberi* and *A. theophrasti*, two important weeds in maize and soyabean in the U.S. Midwest (Forcella et al., 1992, Buhler & Hartzler, 2001) with different seed coat thickness, which is an important factor that may influence the ability of soil microorganisms to decay seeds (Mohamed-Yasseen et al., 1994). The seed coat of *A. theophrasti*, formed by a cutinized palisade layer, is an important barrier for pathogen, gas, and water penetration (Kremer & Schulte, 1989, Nurse & DiTommaso, 2005, Davis et al., 2008), and is the main reason for the formation of persistent seed banks of this species. Mature seeds of *S. faberi*, in contrast, are capable of freely imbibing water and dissolved gases (Dekker, 2003). The hypothesis that *S. faberi* and *A. theophrasti* seed decay would be higher when seeds are buried in the soil at 2 cm than at 20 cm was also tested. Burial of *S. faberi* and *A. theophrasti*

seeds increases both the level of dormancy and viability and the longevity of the seeds, possibly because of decreased oxygen at greater depths or within soil aggregates (Stoller & Wax, 1974, Webster et al., 1998, Dekker & Hargrove, 2002, Davis & Renner, 2007). Finally, the identity of the most predominant fungi and Oomycetes colonizing the seeds, and potentially causing seed decay, was investigated. These microorganisms are known to be important seed decay causal agents for weeds (Wagner & Mitschunas, 2008) and crops (Agarwal & Sinclair, 1988).

Materials and methods

Description of site, crop management, and seeds

The study was carried out from 2008 to 2010 at Iowa State University's Marsden Farm, in Boone County, Iowa, U.S.A. (42°01'N, 93°47'W; 33 3 m above sea level). The experiment in which the study was conducted was initiated in 2002 to evaluate crop productivity, weed productivity and density, energy use efficiency, and economic performance characteristics of three crop rotation systems: a 2-year maize/soyabean rotation, a 3-year maize/soyabean/red clover+oats, and a 4-year maize/soyabean/lucerne+oat/lucerne rotation (Liebman et al., 2008, Cruse et al., 2010). A randomized complete block design with four replicates was used, and each crop phase of each rotation system was grown every year in a separate plot, for a total of nine plots per block. The plot size was 18 x 85 m. In 2008, the maize and soyabean plots were split in halves to plant (i) one genetically engineered (GE) maize hybrid

followed by a GE soyabean variety and (ii) one conventional (non-GE) maize hybrid followed by a non-GE soyabean variety on each plot (Gómez et al., *in review*). Seed decay of *S. faberi* and *A. theophrasti* was studied over a 3-year period in the maize plots of the 2- and 4-year cropping systems planted with the GE hybrid. The GE maize was a stacked hybrid with genes to control both *Ostrinia nubilalis* Hübner (European corn borer) and *Diabrotica* spp. (maize rootworms). Weed seeds were buried in these particular plots because there was no soil disturbance after the maize was planted and therefore the risk of disturbing the seeds was minimal. Weed management was performed in these plots by applying a mixture of the preemergence herbicides S-metolachlor [acetamide, 2-chloro-*N*-(2-ethyl-6-methylphenyl)-N-(2-methoxy-1-methylethyl)-(S)] and isoxaflutole [5-cyclopropyl-4-(2-methylsulfonyl-4-trifl uoromethylbenzoyl) isoxazole]. The identities of the crops planted, seed density, and inter-row spacing are shown in Table 1.

Crop management practices varied among rotation systems. Synthetic fertilizers were applied in the 2-yr rotation, whereas composted cattle manure and reduced rates of synthetic fertilizers were applied in the 4-yr rotation, based on soil tests from each crop rotation (Table 2). No synthetic nitrogen was applied to maize plots in the 4-yr rotation in 2009 and 2010. Composted cattle manure was applied to lucerne plots during the fall preceding maize in the 4-yr rotation at a rate of 16.2 Mg ha^{-1} (fresh weight basis). Details of the farming practices carried out in the 2-yr and 4-yr crop rotations, as well as crop productivity and economic returns from 2008 to 2010 are provided by Gómez et al. (*in review*).

Setaria faberi and *A. theophrasti* seeds evaluated in 2008, 2009, and 2010 were collected from a field located 13 km east of the experimental site in October of 2006, 2008, and 2009, respectively. It was not possible to harvest and test seeds produced at the Marsden Farm site due to the paucity of plants of *S. faberi* and *A. theophrasti* that survived control practices until the end of each crop season. The seeds collected were stored in a cold room at a temperature of 5℃ and 40 % relative humidity until one day before burial. Germination of each seed lot was evaluated by placing six batches of 50 seeds each in petri plates with moist filter paper for 14 days. The plates were placed in a growth chamber in cycles of 30/20℃ for 15.5 and 8.5 hours, respectively. Germinated seeds were counted and discarded on a daily basis and seeds that did not germinate after 14 days were tested for their viability with a solution of tetrazolium (2,3,5 triphenyl tetrazolium chloride) at 1% m/v (Baalbaki et al., 2009). Another sample of seeds from each seed lot was tested for seedborne fungi and Oomycetes using two different growth media: four batches of 15 seeds were placed in petri plates containing potato dextrose agar (PDA, 39 g per liter of water) plus the antibiotics streptomycin sulfate (33 mg l^{-1}) and neomycin sulfate (40 mg l^{-1}), while four other batches of 15 seeds were placed in petri plates with maize meal agar (CMA, 17 g per liter of water), quintozene (130 mg l^{-1}), and the antibiotics vancomycin (300 mg l^{-1}) and pimaricin (5 mg l^{-1}). The PDA medium was selected to isolate several fungi and Oomicetes (Agarwal & Sinclair, 1988) that colonize seeds, whereas the CMA medium was chosen as a *Pythium* selective media (Pieczarka & Abawi, 1978).

Seed burial

The experiment was laid out as a split-plot design with four blocks. The main plot treatment was the crop rotation system (2-yr and 4-yr). Subplots were arranged in a completely randomized design in both rotation systems to evaluate the effects of weed species identity (*S. faberi* and *A. theophrasti*), at two burial depths (2 and 20 cm) at 11 extraction times during the crop season.

Eleven sets of 32 nylon mesh bags (10 x 19 cm, pore size of 0.08 cm) were prepared each year. Sixteen of the bags in each set were filled with 30 seeds per bag of *S. faberi* mixed with 458 cm^3 of soil collected from either the 2-yr or the 4-yr rotation, whereas the other 16 bags were filled with *A. theophrasti* seeds and soil following the same procedure. Mixing soil with seeds in the bags was intended to reduce seed-to-seed contamination by soil fungi and Oomycetes, which can happen when high densities of seeds are buried within mesh bags (Van Mourik et al., 2005). Soil from the first 2 cm and from 18-20 cm was collected the day before the bag filling, in each of the plots where the bags were going to be buried. Once filled, the bags were stored in a cold room at 4 C until they were taken to the field, 12 hours later. The seed density within each bag was equivalent to 6550 seeds per square meter, at 0-10 cm depth. Previous field studies have reported *S. faberi* seed densities ranging from 100 to 25500 and *A. theophrasti* seed densities of 100-7000 seeds per square meter (Forcella et al., 1992, Lindquist et al., 1995).

Bags were placed into the soil by marking a 4.1 x 1.9 m grid on the ground with 45 squares of 0.45 x 0.38 m each (the longer side oriented parallel to maize rows). Bags were randomly assigned to grid squares and buried at either 2 or 20 cm in-between the crop rows. Bag burial areas were then covered with continuous sheets of non-colored plastic for one hour to protect the seeds while preemergence herbicides were applied to the rest of the plot area. Seed burial occurred on 21 May 2008, 1 May 2009, and 21 April 2010, one day after the maize was planted.

Seed recovery and classification

Every two weeks for the first 14 weeks after burial, and every four weeks for the subsequent 12 weeks, one bag per weed species, burial depth, and crop rotation was recovered from each of the four replicates. The initial 2-week interval between extractions was intended to make a more precise differentiation between decayed and germinated seeds; some non-infected seeds that germinate but do not reach the surface could be mistaken for decayed seeds once the vegetative parts that emerged from them decompose in the soil (Gallandt et al., 2004). One set of bags remained in the soil overwinter and was extracted on 23 April 2009, 9 April 2010, and 10 April 2011. To allow tillage operations in the plots in preparation for the next crop season, however, this last group of bags was temporarily removed from the soil in the fall of each year, placed in individual plastic bags, stored inside a dark plastic bag in a cold room at 4℃, and buried again in the same micro-plot three or four days later.

All the bags recovered from the soil were placed individually inside mesh tubes and washed in an elutriator (Wiles et al., 1996) for 120 minutes. The bags were then placed on top of laboratory benches and air dried overnight using two 60 W fans. The seeds were recovered manually using nested sieves, and classified as germinated, dormant, or decayed. The following criteria were followed to classify *S. faberi* seeds: (i) those seeds that exhibited root or shoot growth, separation between the palea and the lemma larger than 0.1 cm, or aperture of the placental pore, were classified as germinated; (ii) seeds that appeared intact but collapsed under a pressure of approximated 0.832 kg cm^{-2} (measured with the Wagner FDX Algometer) done with forceps, a method known as the crush test (Borza et al., 2007), were classified as decayed; and (iii) seeds that looked intact and did not collapse under pressure in the crush test were considered dormant. Dormant seeds recovered at 6 and 10 weeks after burial, and those that had overwintered, were tested for viability with tetrazolium, as described above. Classification of decayed and dormant *A. theophrasti* seeds was performed similarly to that for *S. faberi* seeds, whereas intact *A. theophrasti* seeds that showed a lateral seed coat opening, signs of root or shoot emergence, or seed shells showing signs of a similar lateral aperture were considered germinated.

Identification of fungi and Oomycetes colonizing the seeds

All the recovered seeds were placed on the two growth media described above. Half of the seeds recovered from each bag were placed on petri plates containing PDA plus antibiotics and the other half were plated in CMA plus antibiotics. These two media were

selected to isolate *Fusarium, Alternaria, Cladosporium,* and *Pythium*, which have been associated with *S. faberi* and *A. theophrasti* seeds in previous studies and can cause seed decay (Kirkpatrick & Bazzaz, 1979, Kremer, 1986, Davis & Renner, 2007). Seed colonization by *Trichoderma* was also recorded because some strains within this genus are used as biocontrol agents against some pathogenic *Pythium* species (Naseby et al. 2000).The petri plates were then placed in a growth chamber for 7 days at a temperature of 25℃, with constant light. Seeds were e valuated at 2, 4 and 7 days after plating, and the cumulative proportion of seeds colonized by each microorganism was determined by the end of the evaluation period. Fungi and Oomycetes were visually identified by analyzing their mycelia and spores under the microscope, and by observing their mycelia color and growth patterns on the growth media.

After analyzing results from 2008, a secondary field experiment was carried out in 2009 to determine whether the fungi and Oomycetes were internal or external colonizers of the seeds. Following the procedure described above, one set of 32 bags was filled with *S. faberi* and *A. theophrasti* seeds mixed with soil, and then buried at 2 cm next to the micro-plots of the main study. The bags were exhumed 26 weeks after burial and the seeds recovered by washing the soil in the elutriator. Dormant seeds were surface sterilized by submersion in a solution of 0.1 % v/v of sodium hypochlorite for 2 minutes followed by a 5 minute rinse with deionized water on a strainer (Leon et al., 2004). The seeds were then placed either in PDA plus streptomycin sulfate and neomycin sulfate or CMA plus vancomycin and pimaricin. They were then placed in a growth chamber, and

colonizing fungi and Oomycetes were visually identified following the procedure previously described.

Greenhouse study

Decayed seeds of *S. faberi* recovered in 2008 and 2009 from the main experiment were mostly colonized by the pathogens *Fusarium* spp. and *Pythium* spp. A greenhouse experiment was then set out in 2010 to answer the questions (i) are *Fusarium* and *Pythium* species causing *S. faberi* seed decay?, and (ii) is the soil from the studied crop rotations enhancing or suppressing the decay process? Soil from plots corresponding to the 2- and 4-yr rotations was collected, and half of the soil from each rotation was pasteurized by microwaving 4 kg of soil at a time for eight minutes to eliminate soilborne pathogens but not other soil microorganisms (Ferriss, 1984). Each type of soil, pasteurized and non-pasteurized, was separated into three fractions. One fraction was inoculated with *Pythium ultimum* Trow, another fraction was inoculated with *Fusarium sporotrichoides* Sherb., and the third fraction was used as a control with no microbial inoculation. These pathogens were selected for this experiment due to their high incidence on the plated seeds. *Pythium ultimum* inoculum was obtained from *S. faberi* seeds that remained buried in the soil for 8 weeks and were placed on CMA plus antibiotics after being recovered. *Fusarium sporotrichoides* inoculum was obtained following the same procedure except that PDA plus antibiotics was used instead of CMA. Inoculum was prepared by transferring the microorganisms to 9 cm-diameter petri

plates that were placed in a growth chamber for 7 days at 25℃, with constant light, to allow them to fill the plate.

The soil needed to fill a one liter pot was mixed with the inoculum finely sliced, in a ratio of one petri plate with inoculum per pot (Zhang & Yang, 2000). The control treatment consisted of soil mixed with CMA only. Thirty *S. faberi* seeds were placed in each pot at approximately 2 cm below the soil surface. The soil in each plot remained saturated with water at all times. The pots were placed on greenhouse benches in a completely randomized design. After five weeks, the soil was washed and the seeds recovered and classified as germinated, dormant, or decayed following the procedure described above.

Seed lot differentiation

Setaria faberi seed decay was considerably higher in 2008 than in 2009. Considering that seed decay might be influenced by the maternal environment because the seed coat is maternally derived (Schutte et al., 2008), and that the seed lots evaluated in 2008 and 2009 were harvested in different years, a field and a laboratory experiment were carried out in 2010 to determine a possible seed lot effect on the *S. faberi* and *A. theophrasti* seeds that could explain differences in seed decay and germination among years. One set of mesh bags was prepared to test in the field seed lots of *S. faberi* and *A. theophrasti* harvested in 2006, 2008, and 2009. These seed lots were evaluated in the main study from 2008 to 2010. The bags were buried at 2 and 20 cm in micro-plots within the maize plots of the 2- and 4-year crop rotations. The bags were filled and

buried following the procedure previously described. All the bags were exhumed 26 weeks after burial and the seeds recovered and classified as germinated, dormant, and decayed following the criteria previously explained.

A Saturated Salt Accelerated Aging (SSAA) test (Jianhua & McDonald, 1997) was also performed in 2010 to evaluate, in controlled conditions, the vigor of the three seed lots of *S. faberi* and *A. theophrasti* evaluated in the field trial from 2008 to 2010. The SSAA test provides a more sensitive index of small seed quality than the germination test as well as a consistent ranking of seed lot performance (Bennett et al., 2004). A sample of 200 seeds of each seed lot was surface sterilized by submersion in a solution of 0.1% v/v of sodium hypochlorite for 2 minutes followed by a 5-minute rinse with deionized water. The salt solution used in the SSAA test was prepared by dissolving 135 g of sodium chloride in 400 ml of water. This solution was stored for 3 days in an oven at 30℃ before it was used. One SSAA box per seed lot was used and 40 ml of the saturated salt were poured on the bottom of the box. The boxes were then placed in the aging chamber for 72 hours at 41℃. Once the aging pr ocess was completed, two replicates of 100 aged seeds each per seed lot were transferred to plastic boxes with blotter paper. The boxes with the seeds were then placed in a growth chamber with a temperature set to oscillate between 14 and 26℃ on a 16- and 8-hours cycle, respectively. The seeds were observed daily and the germination percentage was recorded after 11 days.

Data analysis

Proportions of germinated, dormant, decayed, and viable seeds were arcsin (√x) transformed to meet analysis of variance requirements for normal distribution. Analyses of variance were then performed using the Mixed procedure of SAS for analysis of split-plot experiments (Littell et al., 2002). Crop rotation system, weed species identity, burial depth, and extraction time were considered fixed factors, and replication and year were considered random factors. Non-linear regression was used to analyze the 2008 seed decay in the two crop rotations and depths, using DataFit software (version 9.0, Oakdale Engineering, Oakdale, PA).The proportion of weed seeds colonized by each microorganism was transformed and analyzed similarly to proportion of germinated, dormant, and decayed seeds. The greenhouse experiment was analyzed using the GLM procedure of SAS; treatment (microorganisms and control), soil type (pasteurized and non-pasteurized), and crop rotation were considered fixed factors, whereas replication was treated as a random factor.

Results

Initial viability of *S. faberi* and *A. theophrasti* seed lots ranged from 96 to 100% and from 95 to 100%, respectively. Germination of *S. faberi* seeds was 14, 11, and 0%, whereas *A. theophrasti* germination was 11, 20, and 5% for 2008, 2009, and 2010, respectively. *Fusarium* spp., *Alternaria* spp., and *Cladosporium* spp. were the main colonizers of the

seeds before burial; *Penicillium* spp. was found colonizing *S. faberi* seeds only in 2008 (Table 3). *Pythium* was not detected colonizing the seeds before burial.

Germination, decay, and dormancy of recovered seeds

A significant year effect ($P<0.05$) was detected for the response variables germinated, dormant, and decayed. Because interactions between species and the other factors were significant ($P<0.05$) within years, data were analyzed by species.

Setaria faberi. In 2008, germination at 2 cm was 42% higher than at 20 cm ($P<0.0001$, Table 4). No significant differences in seed germination were determined between crop rotations. Seed decay was higher in the 4 year rotation than in the 2-yr rotation ($P=0.009$), and also higher at 2 cm than at 20 cm ($P=0.014$) (Table 4). Seed dormancy was lowest in the 4-yr rotation at 2 cm due to higher seed decay and germination ($P=0.0162$).

In 2009 seed decay was again higher at 2 cm than at 20 cm ($P=0.002$), although it was much lower than in 2008. No differences between rotations were determined. Germination was three times higher at 2 cm than at 20 cm ($P<0.0001$). Related to this finding, there was a lower proportion of dormant seeds at 2 cm than at 20 cm ($P<0.0001$), in both rotations.

Seed decay varied among extraction times in 2008 and 2009. A Gompertz function fitted the data of seed decay in 2008 but not in 2009. Seed decay increased over time in

2008 until reaching a maximum value of 29.4% at 14 weeks in the 4-yr rotation and 26.8% at 22 weeks in the 2-yr rotation (Fig. 1). When compared among burial depths, seed decay was highest at 2 cm (31.8%) after 22 weeks since burial (Fig. 1). In 2009, only burial depth had an effect on seed decay over time (Table 4).

In 2010, significant differences in germinated, dormant, and decayed seeds between burial depths were detected. The number of germinated (P=0.039) and decayed (P=0.027) seeds was higher at 2 cm than at 20 cm, although these values were several orders of magnitude lower than in the two previous years (Table 4). Likewise, dormancy was slightly lower at 2 cm than at 20 cm (P=0.005).

Abutilon theophrasti. Differences in germination of *A. theophrasti* seeds among extraction times in 2008 were significant (P<0.0001), but no particular trend occurred over time. No significant differences were found between crop rotations and burial depths (P>0.05). Germination and decay were lower than 6 and 2%, respectively, which indicated that *A. theophrasti* seeds remained mostly dormant in 2008 (Table 4).

Germination of *A. theophrasti* seeds was highest in 2009 (Table 4), and the significant 3-way interaction among crop rotation, burial depth, and extraction time (P=0.046) indicated high variability of seed germination throughout the season. Overall, germination at 2 cm was higher in the 4-yr rotation than in the 2-yr rotation, but the differences only were significant during certain times of the season. In the 4-yr rotation, germination at 2 cm was generally higher than at 20 cm, and significant differences

were observed during certain extraction times. In the 2-yr rotation, on the other hand, no differences in seed germination between depths were observed (Table 4). Seed decay, although very low, also varied among extraction times (P<0.0001). *Abutilon theophrasti* seed dormancy was lowest in the 4-yr rotation at 2 cm (P=0.0002) (Table 4). In 2010, *A. theophrasti* germination was slightly higher at 2 cm than at 20 cm (P=0.014), although more than 96% of the seeds remained dormant (Table 4).

Viability of dormant seeds

Viability of dormant seeds recovered at 6, 10, and 14 weeks after burial was analyzed similarly to germination, decay, and dormancy. The triple interaction between year, species, and depth was significant (P=0.0073), therefore the data were analyzed by year and species. All *A. theophrasti* seeds classified as dormant were viable every year; likewise, all *S. faberi* seeds classified as dormant in 2009 and 2010 were viable. In 2008, viability of *S. faberi* seeds recovered from 2 cm was lower than viability of seeds recovered from 20 cm (P=0.0134), 81 vs. 91%, respectively. No significant differences were found between crop rotations or extraction times.

Overwintering seeds

Setaria faberi seeds that remained buried in the soil over the 2008-2009 winter continued to decompose. Over 42% of the seeds recovered from 2 cm and over 27% of the seeds recovered from 20 cm were decayed (Table 5). However, no significant differences (P>0.05) were determined between rotations or burial depths. Decay of

seeds of *S. faberi* overwintering in 2009-2010 and 2010-2011, on the other hand, was lower than 4% (Table 5). Overall, germination of *S. faberi* seeds that remained buried in the soil over the winter was higher than germination during the growth season. This occurred mostly because some of the seeds that were dormant by the end of the crop season germinated early in the spring, before the bags were pulled out from the soil. Germination was highest at 2 cm in 2008-2009 and 2009-2010 (P<0.03). No significant differences were determined between rotations. Viability of *S. faberi* dormant seeds was 97, 98, and 99% in 2008-2009, 2009-2010, and 2010-2011 winters, respectively.

Abutilon theophrasti seeds remained mostly dormant in 2008-2009 and 2010-2011 winters, similar to the 2008 and 2010 growing seasons. Seed germination and decay were less than 9 and 2%, respectively, during those winters (Table 5). Germination of *A. theophrasti* seeds in 2009 was higher than in the other years (Table 4), but it did not increase over the winter of 2009-2010 (Table 5). No significant differences were determined between crop rotations and burial depths for germinated, decayed, or dormant seeds in any of the three years. Viability of dormant *A. theophrasti* seeds was 99, 99, and 100% in 2008-2009, 2009-2010, and 2010-2011 winters, respectively.

Fungi and Oomycetes colonizing S. faberi and A. theophrasti seeds

Seed colonization by fungi and Oomycetes was analyzed by year and species due to the significant interactions (P<0.05) between these two factors. *Pythium*, *Fusarium*, *Alternaria*, *Trichoderma*, and *Cladosporium* were the predominant genera from both *S. faberi* and *A. theophrasti* seeds.

Setaria faberi. Overall, there was higher colonization of *S. faberi* seeds by *Pythium*, *Fusarium*, and *Trichoderma* in 2008 than in 2009 or 2010 (Table 6). In 2008, seed colonization by *Pythium* was slightly higher in the 2-yr rotation than in the 4-yr rotation (P<0.0001), whereas in 2009 seed colonization was highest at 2 cm regardless of the crop rotation (P=0.013). *Pythium* incidence on recovered seeds varied among extraction times in each of the three years (P<0.001) (Fig. 2). There were significant differences in seed colonization by *Fusarium* between extraction times (P<0.0001), but not between crop rotations or burial depths (Fig. 3). *Trichoderma* seed colonization was highest at 2 cm in the 2-yr rotation and at 20 cm in the 4-yr rotation (P<0.05) (Fig. 2); higher colonization in the 2-yr rotation than in the 4-yr rotation was observed in certain extraction times (P<0.05). Seed colonization by *Alternaria* varied between extraction times every year (P<0.0001) (Fig. 2); it was also higher at 20 cm than at 2 cm, although this difference was significant only in 2010 (P=0.024). *Cladosporium* seed colonization also fluctuated between extraction times (P<0.0001) (Fig. 2).

Abutilon theophrasti. Similar to *S. faberi* seed colonization, *A. theophrasti* seed colonization by *Pythium, Fusarium*, and *Trichoderma* was highest in 2008 (Fig. 3). *Pythium* colonization was higher in the 2-yr rotation than in the 4-yr rotation at certain extraction times in 2008, 2009, and 2010 (P<0.05). Seed colonization by *Fusarium* and *Alternaria* varied among extraction times (P<0.05), but not between burial depth or crop rotation, whereas *Trichoderma* colonization was highest at 2 cm in the 2-yr rotation over the three years (P<0.05). Colonization of *A. theophrasti* seeds by *Cladosporium* was

higher in the 2-yr rotation than in the 4-yr rotation during certain extraction times in 2008 (P=0.003); in 2009, it was highest at 20 cm in the 2-yr rotation, and in 2010 it fluctuated among extraction times (P<0.0001).

In the field experiment designed to identify fungi and Oomycetes colonizing *S. faberi* seeds internally, it was found that over 50 and 20% of the seeds were colonized by *Fusarium* and *Alternaria*, respectively (Fig. 4). No significant differences were determined between crop rotations. *Trichoderma* growth was observed in less than 9% of the seeds recovered from the 2-yr rotation.

Greenhouse study

The proportion of decayed seeds was higher in soil inoculated with *Pythium ultimum* (0.14) than in soil inoculated with *Fusarium sporotrichoides* (0.08) or the control (0.09) (P=0.02; SE = 0.015). No significant differences were determined between crop rotation or soil type (pasteurized or non-pasteurized).

Seed lot differentiation

Setaria faberi. *Setaria faberi* seed germination was highest in the seed lot harvested in 2008, lowest in the seed lot harvested in 2009, and intermediate in the seed lot harvested in 2006 (P<0.0001) (Table 7). Germination of the seeds buried at 2 cm was significantly higher than germination of seeds buried at 20 cm (P=0.013). Seed decay of

S. faberi seeds was highest in the seed lot harvested in 2006 (Table 7). Within this seed lot, seed decay was higher in the 4-yr rotation than in the 2-yr rotation (P=0.014). A similar result was obtained in our 3-year field experiment when this particular seed lot was evaluated in 2008 (Table 4).

Abutilon theophrasti. Germination of *A. theophrasti* seeds was low for the three seed lots evaluated in the field (Table 7). The seeds harvested in 2008 and buried in the 4-yr rotation at 2 cm had the highest germination percentage by the end of the season (P=0.019). Concomitantly, seed dormancy was high for all seed lots, and it was slightly lower for seeds harvested in 2008 and buried in the 4-yr rotation at 2 cm (P=0.029). *Abutilon theophrasti* seed decay was negligible for either seed lot (Table 7).

When the seeds were aged in the laboratory, significant differences (P<0.001) in germination among *S. faberi* and *A. theophrasti* seed lots were also determined. Similarly to what was observed in the field, seed germination was highest in the 2008 seed lot, lowest in the 2009 seed lot, and intermediate in the 2006 seed lot (Fig. 5). These findings support the hypothesis that inherent seed lot differences could potentially affect the germination, decay, and dormancy of the seeds once they are buried in the field.

Discussion

It has been suggested that microbial seed decomposition plays an important role in reducing the persistence of the soil weed seed bank (Chee-Sanford et al., 2006, Wagner & Mitschunas, 2008), but the great number of factors that influence weed seed decay make this phenomenon so variable over time, location, weed species, and cropping systems that determining a consistent effect of a particular cropping system on weed seed decay is extremely difficult. It is established in seed and plant pathology that the key elements that need to be considered when analyzing a disease are the environment, the host, and the pathogen, also known as the disease triangle (Agrios, 1995). The study of weed seed decay needs to be done following similar criteria.

Applying the concept of the disease triangle, this study found that environmental conditions might have affected *S. faberi* seed decay when we compared burial depths, cropping systems with contrasting soil management practices, and crop seasons. This study also determined differences in host (seed) susceptibility to microbial-related decay, both among *S. faberi* seed lots and between weed species. Weed seed germination, dormancy, and decay in the soil are influenced by genetic traits, the maternal environment in which the seed develops, and the environment that the seed encounters once it enters the soil seed bank (Bazzaz et al., 1992, Mousseau & Fox, 1998, Wolf et al., 1998, Schutte et al., 2008). Considering that *S. faberi* and *A. theophrasti* seeds evaluated in this study from 2008 to 2010 were harvested in the same field but in different years, it is possible that intrinsic seed lot differences related to the maternal environment might be the cause of the observed differences in germination

and decay (Bewley & Black, 1994), as suggested by the SSAA test and the parallel seed lots field experiment carried out in 2010. *Setaria faberi* seeds have a great deal of plasticity in phenotypic expression, and even genetically identical seeds might differ in their dormancy characteristics (Dekker, 2003), making them more or less susceptible to microbial decay. Differences in seed decay among years could also be attributed to physiological and chemical factors. Although we did not determined the concentration of seed exudates in the spermosphere of *S. faberi* or *A. theophrasti* seeds, it is known that the presence and quantity of specific exudate components released during seed germination are directly correlated to disease incidence, particularly for diseases caused by *Pythium* and *Fusarium* species (Begonia & Kremer, 1994, Kageyama & Nelson, 2003, Nelson, 2004). Seed age, seed coat integrity, and environmental variables such as temperature may influence the concentration of certain organic molecules in the spermosphere (Bewley & Black, 1994, Nelson, 2004). Thus, it is plausible that physiological differences among seed lots and environmental fluctuations between years could have affected the microbial-mediated seed decay process. Finally, a possible relationship between the pathogen *P. ultimum* and *S. faberi* seed decay was determined by following Koch's postulates: we found *P. ultimum* growing in buried *S. faberi* seeds, we isolated the pathogen in pure media, and we determined, in our greenhouse experiment, that *P. ultimum* caused higher *S. faberi* seed decay than the control when inoculated in pasteurized soil. Incidence of *P. ultimum* on *S. faberi* weed seeds was highest in 2008, concurring with higher seed decay, than in 2009 and 2010. Despite the high proportion of *S. faberi* seeds colonized internally by *Fusarium* species, determined in our parallel field experiment, the effect of *F. sporotrichoides* on

seed decay was not as important as the effect of *P. ultimum*. It is important to note that *P. ultimum* might not be the primary agent causing seed decay but a pathogen that would colonize the seed once another microorganism triggers the decay process.

Abutilon theophrasti seeds, conversely, remained viable or germinated during the season, even when a high proportion of seeds was colonized by *Pythium* and *Fusarium* species. High persistence of *A. theophrasti* seed in the seed bank was also reported in studies by Kremer (1986) and Kirkpatrick and Bazzaz (1979), whereas other studies suggest that once the integrity of *A. theophrasti* seed coat is compromised, microbial mediated seed decay occurs readily (Kremer & Spencer, 1989, Davis & Renner, 2007).

Setaria faberi and *A. theophrasti* population dynamics must be considered when designing weed management strategies in agricultural landscapes. This study found that *S. faberi* seed decay can be as important to seed bank depletion as seed germination, which suggests that any effort done towards enhancing microbial decomposition of seeds would reduce significantly the pressure on the performance of postemergence weed management tactics. Similar decay rates for *S. faberi* were determined by Davis et al. (2006) in controlled conditions, but field experiments by Buhler and Hartzler (2001) and Schutte et al. (2008) reported seed decay rates of up to two times higher, depending on seed lot, burial location, and year. These previous studies, however, did not account for mortality attributable to fatal germination. This study also found that certain *S. faberi* seed lots can exhibit very low decay rates. *A. theophrasti* seed decay has been found to range from 16 to 60% (Buhler & Hartzler,

2001, Davis et al., 2006, Schutte et al., 2008), whereas this study determined that it was not an important seed bank depletion factor. These differences among studies show a high ecological variability in agricultural fields, and indicate the necessity to evaluate weed population dynamics in multiple cropping systems in order to make weed management programs as effective as possible.

The variability of *S. faberi* and *A. theophrasti* seed decay results in this study suggest that other factors, which were not measured, might be also involved in the seed decay process. Those factors include the effect of soil bacteria on the seed coat and embryo (Owen & Zdor, 2001, Chee-Sanford et al., 2006, Kremer, 2006); the presence of antimicrobial compounds on the seeds that prevent microbial colonization (Kremer, 1986, Davis et al., 2008); the C:N ratio in the soil (De Cauwer et al., 2011); the existence of “safe-sites” in the soil that prevent the decay of certain seeds (Conn & Werdin-Pfisterer, 2010); spatial heterogeneity and patchiness in microbial population distributions (Chee-Sanford, 2007); the effect of the competition for light, water, and N by the crop on nutrient composition of the weed seed (Cardina & Sparrow, 1997, Nurse & DiTommaso, 2005); and seed damage by insects and vertebrates (Kremer & Spencer, 1989, Schutte et al., 2008). It is important, therefore, that future research on seed decay takes a broad view of the biological interactions that weed seeds, and the weed plant itself, encounter during weed life cycles.

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Fig. 2.1. Gompertz function fitted to *Setaria faberi* seed decay among crop rotations and burial depths over the 2008 crop season. Seed decay in 2009 and 2010 was significantly lower and did not follow any specific pattern. Vertical bars represent the standard deviation of the mean.

Fig. 2.2. Mean *S. faberi* seed colonization by fungi and Oomycetes over crop seasons 2008-2010.

Fig. 2.3. Mean *A. theophrasti* seed colonization by fungi and Oomycetes over crop seasons 2008-2010.

Fig. 2.4. Proportion of *S. faberi* seeds colonized by fungi. Seeds were exhumed from soil after 26 weeks and surface sterilized before being placed in growth media. Vertical bars respresent means and standard errors.

Fig. 2.5. Proportion of seeds germinated in the Saturated Salt Accelerated Aging test. Vertical bars represent means and standard errors.

Table 2.1. Hybrid or cultivar grown, planting and harvest date, seed density, seed mass, and interrow spacing used in contrasting crop rotations.

Crop*	Year	Hybrid or cultivar	Planting date	Harvest date	Seed density	Seed mass	Interrow spacing
					seeds ha^{-1}	kg ha^{-1}	cm
Corn	2008	Agrigold 6395 Yield Guard Plus	19-May	3 Nov.	80,503	-	76
Corn	2009	Agrigold 6395 Yield Guard Plus	23 Apr.	21 Oct.	80,504	-	76
Corn	2010	Agrigold 6395BtRW	20 Apr.	9 Oct.	80,505	-	76
Soybean	2008	Kruger 287RR/SCN	21-May	6 Oct.	387,500	-	76
Soybean	2009	Kruger 287RR/SCN	12-May	27 Oct.	400,000	-	76
Soybean	2010	Kruger 287RR/SCN	19 May†	5 Oct.	400,750	-	76
Oat	2008	IN09201	16 Apr.	4 Aug.	-	84	20
Oat	2009	IN09201	1 Apr.	20 Jul.	-	79	20
Oat	2010	IN09201	1 Apr.	16 Jul.	-	82	20
Alfalfa	2008	FSG 400LH	16 Apr.	20 June, 1 Aug, 17 Sept.	-	17	20
Alfalfa	2009	Freedom	1 Apr.	3 Jun, 6 Jul, 17 Aug, 15 Sept.	-	18	20
Alfalfa	2010	FSG 400LH	1 Apr.	28 May, 12 Jul, 20 Aug, 30 Nov.	-	17	20

* Corn and soybean were planted in the two rotation systems, oat was planted with alfalfa in the 4-yr rotation

† In 2010, soybean was planted on 19 May in blocks 1 to 3 and on 25 May in block 4

Table 2.2. Fertilization regimes for crops grown in contrasting crop rotations from 2008 to 2010.

Crop	2008	2009	2010
	2-yr rotation		
Corn	34 kg P + 86 kg K ha^{-1} as TSP* and KCl before planting; 114 kg N ha^{-1} as urea at planting; 102 kg N ha^{-1} after planting as UAN†	112 kg N ha^{-1} as urea at planting; 56 kg N ha^{-1} after planting as UAN	178 kg K ha^{-1} before planting as KCl; 59 kg P ha^{-1} before planting as MAP‡; 112 kg N ha^{-1} as urea at planting; 63 kg N ha^{-1} after planting as UAN
Soybean	34 kg P + 86 kg K ha^{-1} as TSP and KCl before planting	none	178 kg K ha^{-1} before planting as KCl; 59 kg P ha^{-1} before planting as MAP
	4-yr rotation		
Corn	34 kg P + 86 kg K ha^{-1} as TSP and KCl before planting; 119 kg N + 69 P + 92 kg K ha^{-1} as composted manure before planting; 102 kg N ha^{-1} after planting as UAN	122 kg N + 52 kg P + 113 kg K ha^{-1} as composted manure before planting	83 kg N + 43 kg P + 73 kg K ha^{-1} as composted manure before planting; 178 kg K ha^{-1} before planting as KCl
Soybean	34 kg P + 86 kg K ha^{-1} as TSP and KCl before planting	none	178 kg K ha^{-1} before planting as KCl
Oat + alfalfa	34 kg P + 86 kg K ha^{-1} as TSP and KCl before planting	none	178 kg K ha^{-1} before planting as KCl
Alfalfa	34 kg P + 86 kg K ha^{-1} as TSP and KCl before planting	none	178 kg K ha^{-1} before planting as KCl

* TSP: triple super phosphate

† UAN: urea ammonium nitrate

‡ MAP: monoammonium phosphate

Table 2.3. Seed colonization (proportion of seeds) by fungi before burial. Standard errors are shown in parenthesis.

Year	Species	*Fusarium*	*Alternaria*	*Cladosporium*	*Penicillium*
2008*	*S. faberi*	0.00	0.00	0.47	0.60
2008	*A. theophrasti*	0.60	0.20	0.67	0.00
2009	*S. faberi*	0.65 (0.05)	0.62 (0.07)	0.57 (0.04)	0.00 -
2009	*A. theophrasti*	0.95 (0.03)	0.40 (0.09)	0.95 (0.05)	0.00 -
2010	*S. faberi*	0.97 (0.03)	0.09 (0.06)	1.00 0.00	0.00 -
2010	*A. theophrasti*	0.94 (0.04)	0.00 -	0.91 (0.06)	0.00 -

* In 2008 only one replicate was evaluated due to contamination of the growth media on the other three replicates.

Table 2.4. Incidence (proportion of seeds) of germinated, decayed, and dormant *S. faberi* and *A. theophrasti* seeds recovered from 2008-2010, averaged over 10 extraction times. Transformed [arcsin (?x)] means are shown in parentheses.

Seed condition	Year	2-yr rotation		4-yr rotation		ANOVA*			SE†
		2 cm	20 cm	2 cm	20 cm	Rotation	Depth	Rot*Depth	
		S. faberi							
Germinated	2008	0.2580 (0.5230)	0.1738 (0.4120)	0.3194 (0.5916)	0.1637 (0.4029)	0.3327	**<0.0001**	0.0834	(0.0474)
	2009	0.3484 (0.6266)	0.1098 (0.3234)	0.2737 (0.5266)	0.1087 (0.3046)	0.2002	**<0.0001**	**0.0501**	(0.0295)
	2010	0.0407 (0.1607)	0.0254 (0.1244)	0.0592 (0.2015)	0.0367 (0.1523)	0.2213	**0.0390**	0.7522	(0.0214)
Decayed	2008	0.2288 (0.4482)	0.1954 (0.4051)	0.2782 (0.5160)	0.2168 (0.4605)	**0.009**	**0.014**	0.7532	(0.0148)
	2009	0.0221 (0.0920)	0.0175 (0.0629)	0.0336 (0.1351)	0.0094 (0.0484)	0.3147	**0.0015**	0.1075	(0.0152)
	2010	0.0085 (0.0410)	0.0061 (0.0340)	0.0165 (0.0806)	0.0052 (0.0264)	0.2177	**0.0268**	0.0870	(0.0122)
Dormant	2008	0.5131 (0.8037)	0.6269 (0.9344)	0.4015 (0.6829)	0.6195 (0.9126)	0.0654	**<0.0001**	**0.0162**	(0.0218)
	2009	0.6265 (0.9180)	0.8709 (1.2161)	0.6836 (0.9832)	0.8819 (1.2472)	0.3373	**<0.0001**	0.3847	(0.0329)
	2010	0.9508 (1.3877)	0.9685 (1.4210)	0.9243 (1.3217)	0.9581 (1.4043)	0.098	**0.0049**	0.2255	(0.0189)
		A. theophrasti							
Germinated	2008	0.0280 (0.1136)	0.0366 (0.1323)	0.0533 (0.1850)	0.0315 (0.1282)	**0.0502**	0.3418	0.0612	(0.0163)
	2009	0.2197 (0.4775)	0.2168 (0.4657)	0.3219 (0.5956)	0.2179 (0.4778)	0.0903	**0.0004**	**0.0036**	(0.0225)
	2010	0.0252 (0.1167)	0.0211 (0.0923)	0.0309 (0.1335)	0.0152 (0.0751)	0.9935	**0.0142**	0.3076	(0.0222)
Decayed	2008	0.0114 (0.0549)	0.0079 (0.0389)	0.0119 (0.0478)	0.0068 (0.0286)	0.3926	0.1259	0.8915	(0.0102)
	2009	0.0110 (0.0401)	0.0101 (0.0312)	0.0059 (0.0240)	0.0045 (0.0207)	0.1313	0.5269	0.7674	(0.0081)
	2010	0.0000 0.0000	0.0017 (0.0065)	0.0008 (0.0046)	0.0000 0.0000	0.8537	0.8002	0.1662	(0.0043)
Dormant	2008	0.9607 (1.4196)	0.9555 (1.4150)	0.9348 (1.3554)	0.9617 (1.4204)	0.0727	0.1047	0.0627	(0.0150)
	2009	0.7722 (1.0874)	0.7705 (1.0791)	0.6722 (0.9688)	0.7887 (1.1093)	0.2220	**0.0009**	**0.0002**	(0.0246)
	2010	0.9748 (1.4543)	0.9772 (1.4719)	0.9682 (1.4328)	0.9848 (1.4957)	0.9664	**0.0193**	0.1848	(0.0211)

* Analysis of variance of transformed data

† Standard error of transformed [arcsin (?x)] means

Table 2.5. Condition of overwintering seeds of *S. faberi* and *A. theophrasti* (values are proportions of total seed sample).

Seed condition	Year	2-yr rotation		4-yr rotation		Source of variability*			SE†
		2 cm	20 cm	2 cm	20 cm	Rotation	Depth	Rot*Depth	
					S. faberi				
Germinated	2008	0.2029	0.1653	0.3724	0.1495	0.2673	**0.0266**	0.1186	0.0600
	2009	0.4279	0.1238	0.2801	0.1123	0.3877	**0.0030**	0.2433	0.0600
	2010	0.0536	0.0083	0.0684	0.0175	0.4630	0.0927	0.7916	0.0756
Decayed	2008	0.4152	0.2693	0.4466	0.3358	0.4601	0.0568	0.7741	0.0585
	2009	0.0268	0.0173	0.0353	0.0083	0.7327	0.2844	0.7316	0.0600
	2010	0.0000	0.0170	0.0172	0.0089	0.8965	0.2417	0.0968	0.0571
Dormant	2008	0.3819	0.5653	0.1810	0.5147	**0.0228**	**0.0059**	0.2216	0.0522
	2009	0.5453	0.8589	0.6845	0.8794	0.4107	**0.0030**	0.3342	0.0664
	2010	0.9464	0.9747	0.9143	0.9735	0.6568	0.1667	0.4646	0.0944
					A. theophrasti				
Germinated	2008	0.0441	0.0417	0.0880	0.0374	0.0666	0.6772	0.4341	0.0385
	2009	0.1137	0.1985	0.2501	0.2427	0.1117	0.2740	0.1792	0.0491
	2010	0.0230	0.0083	0.0342	0.0259	0.3748	0.6474	0.9324	0.0766
Decayed	2008	0.0000	0.0000	0.0182	0.0000	0.1819	0.1342	0.1342	0.0000
	2009	0.0000	0.0000	0.0089	0.0000	0.3910	0.3559	0.3559	0.0000
	2010	0.0000	0.0000	0.0000	0.0000	-	-	-	0.0000
Dormant	2008	0.9559	0.9583	0.9023	0.9626	0.0618	0.6052	0.3892	0.0450
	2009	0.8863	0.8015	0.7409	0.7573	0.0904	0.3409	0.1703	0.0487
	2010	0.9770	0.9917	0.9658	0.9741	0.3748	0..6474	0.9324	0.0766

* Analysis of variance of transformed data

† Standard errors

Table 2.6. Proportion of recovered seeds colonized by fungi and Oomycetes. Transformed [arcsin (?x)] means are shown in parentheses.

Seed colonizer	Year	2-yr rotation		4-yr rotation		SE
		2 cm	20 cm	2 cm	20 cm	
			S. faberi			
Pythium	2008	0.7203 (1.0459)	0.6932 (1.0171)	0.6798 (1.0087)	0.6496 (0.9716)	(0.0364)
	2009	0.3020 (0.5489)	0.1776 (0.4037)	0.1705 (0.3702)	0.1363 (0.3171)	(0.0699)
	2010	0.0871 (0.2443)	0.0447 (0.1388)	0.0298 (0.1064)	0.0957 (0.2436)	(0.0279)
Fusarium	2008	0.7451 (1.0964)	0.6617 (0.9831)	0.7364 (1.1289)	0.7672 (1.1598)	(0.0616)
	2009	0.4958 (0.7969)	0.5025 (0.7986)	0.4634 (0.7559)	0.5276 (0.8195)	(0.0390)
	2010	0.4958 (0.7847)	0.4317 (0.6803)	0.5322 (0.8180)	0.5360 (0.8208)	(0.0500)
Trichoderma.	2008	0.4368 (0.7267)	0.3267 (0.6054)	0.2958 (0.5391)	0.3440 (0.6126)	(0.0249)
	2009	0.1457 (0.3204)	0.0621 (0.1886)	0.0310 (0.1021)	0.0557 (0.1651)	(0.0355)
	2010	0.0999 (0.2367)	0.0236 (0.0905)	0.0258 (0.0722)	0.0326 (0.0879)	(0.0282)
Alternaria	2008	0.0858 (0.1929)	0.0933 (0.1644)	0.0486 (0.1080)	0.0514 (0.1201)	(0.0384)
	2009	0.2477 (0.4651)	0.2968 (0.5144)	0.3014 (0.5208)	0.3063 (0.5737)	(0.0448)
	2010	0.1313 (0.2855)	0.2314 (0.4613)	0.2251 (0.4474)	0.2371 (0.4727)	(0.0406)
Cladosporium	2008	0.1157 (0.1954)	0.0978 (0.2142)	0.0289 (0.0760)	0.0686 (0.1480)	(0.0425)
	2009	0.3312 (0.5981)	0.3759 (0.6417)	0.3736 (0.6621)	0.4288 (0.7078)	(0.0391)
	2010	0.3107 (0.5592)	0.2824 (0.4890)	0.2998 (0.5230)	0.3140 (0.5377)	(0.0664)
			A. theophrasti			
Pythium	2008	0.5031 (0.7780)	0.4722 (0.7728)	0.4517 (0.7281)	0.4424 (0.7264)	(0.0619)
	2009	0.3933 (0.6602)	0.3435 (0.6177)	0.3478 (0.6083)	0.3292 (0.6017)	(0.0349)
	2010	0.0716 (0.1926)	0.0850 (0.2210)	0.0258 (0.0933)	0.0681 (0.1779)	(0.0269)
Fusarium	2008	0.6283 (0.9450)	0.6270 (0.9215)	0.5930 (0.8689)	0.6067 (0.8936)	(0.0391)
	2009	0.6813 (0.9863)	0.5964 (0.9003)	0.6778 (0.9948)	0.6696 (0.9812)	(0.0256)
	2010	0.6754 (0.9862)	0.6582 (0.9877)	0.7356 (1.0636)	0.6978 (1.0255)	(0.0616)
Trichoderma	2008	0.5338 (0.8001)	0.4173 (0.6364)	0.4022 (0.6707)	0.4148 (0.6813)	(0.0528)
	2009	0.2286 (0.4647)	0.1127 (0.3055)	0.0363 (0.1024)	0.0531 (0.1564)	(0.0322)
	2010	0.1631 (0.3741)	0.0776 (0.2098)	0.0028 (0.0109)	0.0250 (0.0980)	(0.0235)
Alternaria	2008	0.2334 (0.4447)	0.3314 (0.5719)	0.3008 (0.5058)	0.2872 (0.5061)	(0.0496)
	2009	0.3275 (0.5864)	0.4058 (0.6768)	0.3774 (0.6534)	0.4118 (0.6904)	(0.0376)
	2010	0.3312 (0.5699)	0.3287 (0.5906)	0.4189 (0.6987)	0.4446 (0.7246)	(0.0460)
Cladosporium	2008	0.0823 (0.1246)	0.1052 (0.2135)	0.0347 (0.0749)	0.0435 (0.0980)	(0.0405)
	2009	0.1779 (0.3598)	0.2535 (0.4825)	0.2254 (0.3956)	0.1583 (0.3384)	(0.0440)
	2010	0.1108 (0.2450)	0.0858 (0.1978)	0.1028 (0.2063)	0.0972 (0.1919)	(0.0373)

Table 2.7. Condition of *S. faberi* and *A. theophrasti* seeds of three seed lots after exhumation in 2010 (values are proportions of total seed sample). Transformed [arcsin (?x)] means are shown in parentheses.

Seed condition	Seed lot	2-yr rotation		4-yr rotation		SE
		2 cm	20 cm	2 cm	20 cm	
		Giant foxtail				
Germinated	2006	0.4150 (0.6985)	0.2157 (0.4653)	0.2214 (0.4876)	0.1981 (0.4563)	(0.0339)
	2008	0.6087 (0.8503)	0.4488 (0.7328)	0.6643 (0.9578)	0.5000 (0.7854)	(0.0969)
	2009	0.0684 (0.2647)	0.0349 (0.1603)	0.0537 (0.1654)	0.0675 (0.2212)	(0.0690)
Decayed	2006	0.1214 (0.3580)	0.1358 (0.3789)	0.2207 (0.4882)	0.2567 (0.5265)	(0.0357)
	2008	0.0457 (0.1468)	0.0396 (0.1425)	0.0263 (0.1147)	0.0089 (0.0475)	(0.0668)
	2009	0.0083 (0.0459)	0.0000 0.0000	0.0262 (0.1409)	0.0000 0.0000	(0.0300)
Dormant	2006	0.4637 (0.7739)	0.6485 (0.9293)	0.5578 (0.8433)	0.5452 (0.8308)	(0.0445)
	2008	0.3456 (0.6754)	0.5116 (0.7983)	0.3094 (0.5852)	0.4911 (0.7762)	(0.0827)
	2009	0.9232 (1.2910)	0.9651 (1.4105)	0.9201 (1.2993)	0.9325 (1.3496)	(0.0514)
		Velvetleaf				
Germinated	2006	0.0000 (0.0000)	0.0000 (0.0217)	0.0256 (0.1128)	0.0000 (0.0000)	(0.0360)
	2008	0.0000 (0.0000)	0.0208 (0.0732)	0.0707 (0.3009)	0.0143 (0.0289)	(0.0386)
	2009	0.0259 (0.1137)	0.0250 (0.1112)	0.0096 (0.0494)	0.0000 (0.0000)	(0.0544)
Decayed	2006	0.0000 (0.0000)	0.0000 (0.0000)	0.0000 (0.0000)	0.0000 (0.0000)	(0.0000)
	2008	0.0000 (0.0000)	0.0000 (0.0000)	0.0000 (0.0000)	0.0077 (0.0000)	(0.0000)
	2009	0.0000 (0.0000)	0.0000 (0.0000)	0.0000 (0.0000)	0.0000 (0.0000)	(0.0000)
Dormant	2006	1.0000 (1.5708)	1.0000 (1.5491)	0.9744 (1.4580)	1.0000 (1.5708)	(0.0360)
	2008	1.0000 (1.5708)	0.9792 (1.4976)	0.9293 (1.2786)	0.9780 (1.4972)	(0.0279)
	2009	0.9741 (1.4571)	0.9750 (1.4596)	0.9904 (1.5214)	1.0000 (1.5708)	(0.0544)

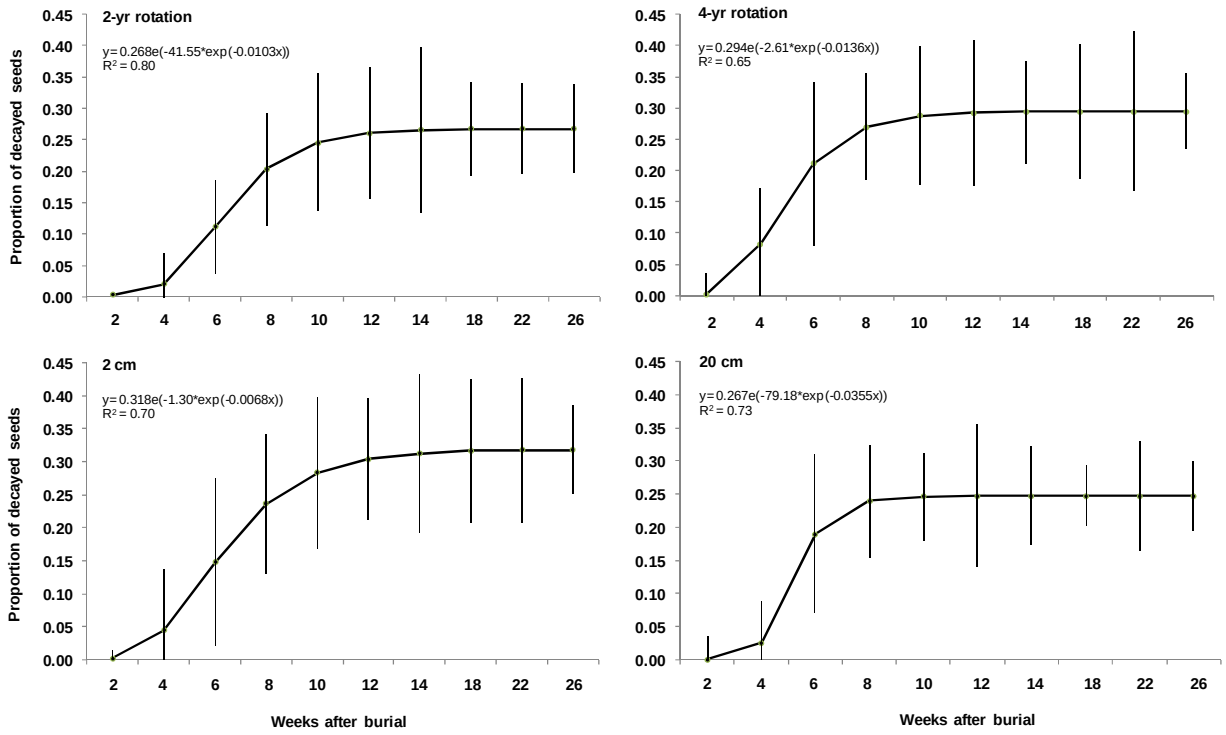
2-yr rotation
y = 0.268e(-41.55*exp(-0.0103x))
R² = 0.80
4-yr rotation
y = 0.294e(-2.61*exp(-0.0136x))
R² = 0.65
2 cm
y = 0.318e(-1.30*exp(-0.0068x))
R² = 0.70
20 cm
y = 0.267e(-79.18*exp(-0.0355x))
R² = 0.73
Proportion of decayed seeds
Weeks after burial
0.45
0.40
0.35
0.30
0.25
0.20
0.15
0.10
0.05
0.00
2
4
6
8
10
12
14
18
22
26

Fig. 2.1.

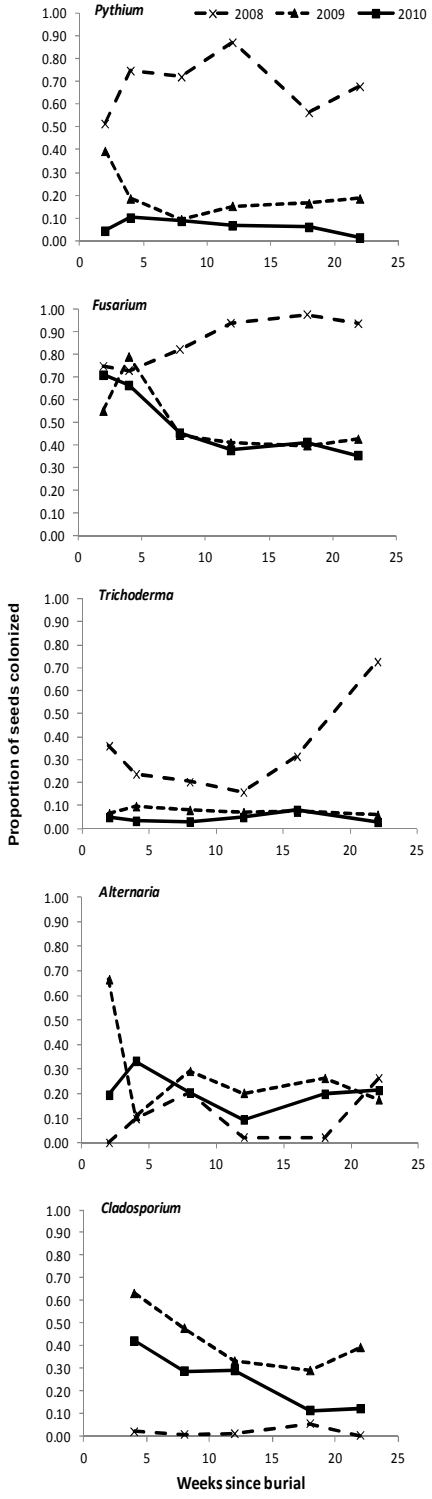
Pythium
2008
2009
2010
Fusarium
Trichoderma
Alternaria
Cladosporium
Proportion of seeds colonized
Weeks since burial

Fig. 2.2.

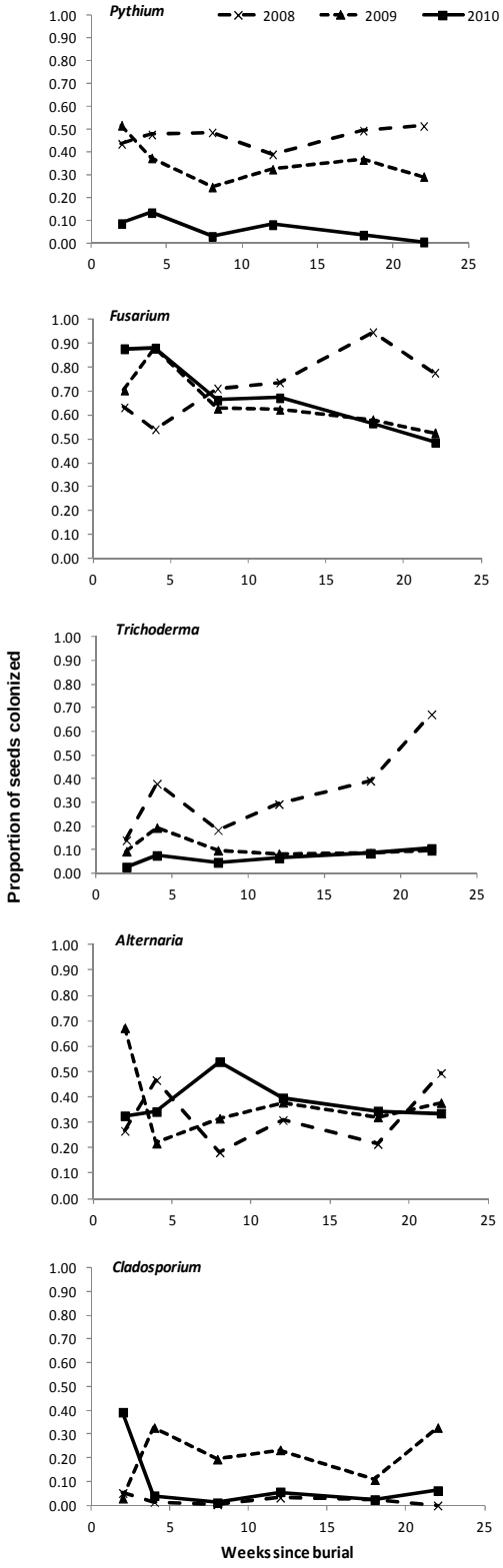
Pythium
2008
2009
2010
Fusarium
Trichoderma
Alternaria
Cladosporium
Proportion of seeds colonized
Weeks since burial

Fig. 2.3.

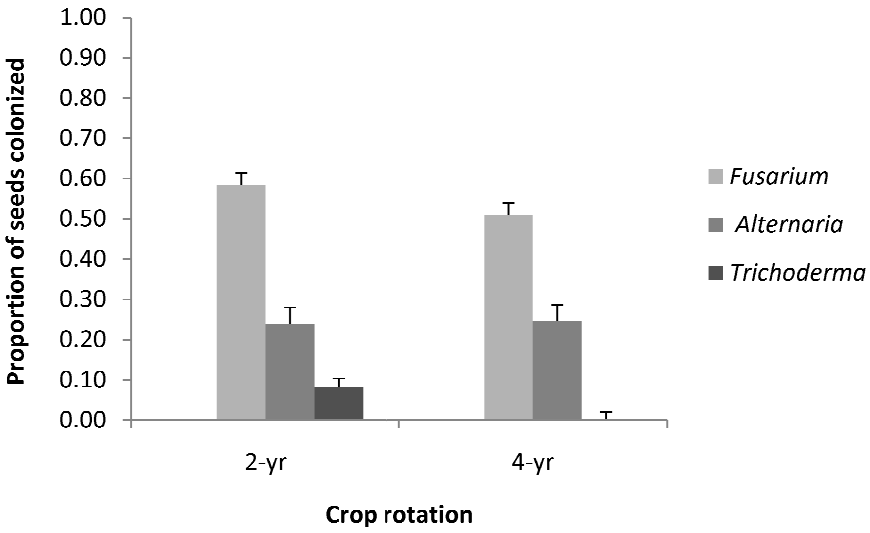
1.00
0.90
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
Proportion of seeds colonized
2-yr
4-yr
Crop rotation
Fusarium
Alternaria
Trichoderma

Fig. 2.4.

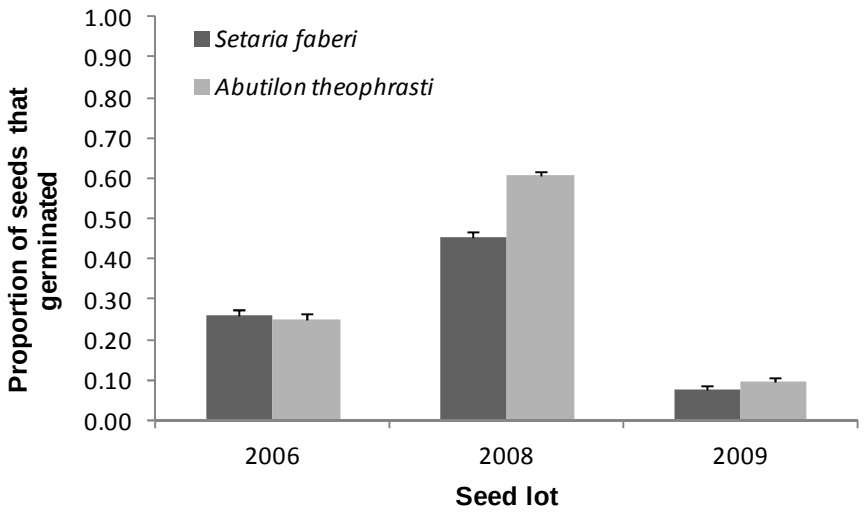
1.00
0.90
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
Setaria faberi
Abutilon theophrasti
Proportion of seeds that germinated
2006
2008
2009
Seed lot

Fig. 2.5.

Chapter 4: Cropping system effects on giant foxtail (Setaria faberi) population dynamics: modeling analyses

A paper to be submitted to Weed Science

Robin Gómez, Matt Liebman, Mike Colvin

Abstract

Crop rotation sequences create complex agroecological environments that affect weed population dynamics by altering key processes of the weed life cycle. We investigated the effects of a conventionally managed 2-year rotation (corn-soybean) and a low-external-input 4-year rotation (corn-soybean-small grain+alfalfa-alfalfa) on giant foxtail seed bank dynamics using matrix population models and demographic data collected in 2003-2005 and 2008-2010 from a field study in Boone, IA. Using mean values for seed decay from three years of observations, modeling analyses projected that over a 20-year period, giant foxtail seed banks would decline in the 2-year rotation (λ=0.83) and increase in the 4-year rotation (λ=1.04). Elasticity analysis indicated that changes in the proportion of over-winter and summer seed survival at a depth of 11-20 cm would have the greatest impacts on the population growth rate in the 2-year rotation, whereas several parameters, including over-winter and summer seed survival, and seedling emergence and survival, would have strong effects on the population growth rate in the 4-year rotation. Modeling analyses also showed that giant foxtail summer seed decay values higher than 20% would reduce the seed bank in the 4-year rotation. These

findings highlight the importance of preventing or reducing the incorporation of weed seeds into deep soil layers, and focusing attention on ecological processes that occur at the soil surface and below ground, such as seed predation and seed decay.

Nomenclature: Giant foxtail, *Setaria faberi* Herrm. SETFA; alfalfa, *Medicago sativa* L.; corn, *Zea mays* L.; soybean, *Glycine max* (L.) Merr.; oat (*Avena sativa* L.); triticale (x *Triticosecale* Wittmack).

Key words: Matrix population models, elasticity analysis, seed bank, weed population dynamics, crop rotations.

Introduction

Weed population dynamics depend on the nature of the biotic and abiotic environment experienced by individual plants (Cousens and Mortimer, 1995). Crop rotation sequences create complex agroecological environments that affect particular aspects of weed demography and therefore population dynamics (Cardina et al., 2002; Jordan et al., 1995; Liebman and Gallandt, 1997; Mertens et al., 2002). The length of the rotation sequence and the identity, order, and attendant management practices of crops within it determine weed habitat characteristics and variability (Bohan et al., 2011; Liebman et al., 2001). For example, crop rotations affect soil properties such as organic matter content (Campbell and Zentner, 1993) and soil structure (Raimbault and Vyn, 1991), that influence water movement and aeration, and consequently can have an impact on

weed seed decomposition (Schafer and Kotanen, 2003) and seedling emergence (Boyd and Van Acker, 2003). Agricultural operations performed in each crop phase of a rotation sequence have different effects on weed seed burial (Buhler and Mester, 1991; Mohler et al., 2006), seedling survival, and mature plant fecundity (Davis et al., 2004; Heggenstaller and Liebman, 2006). Diversified crop rotations that include forage legumes can provide a favorable habitat for seed predators (Heggenstaller et al., 2006; O'Rourke et al., 2006), and, under certain conditions, seed predation can be an important factor affecting seed depletion on the soil surface (Westerman et al., 2005; Westerman et al., 2003; Williams et al., 2009). Organic compounds released by legumes after they are incorporated into the soil, together with the incorporation of livestock manure, can affect weed seed germination (Menalled et al., 2005). A longer rotation may thus be considered a complex environment for annual weed species that have relatively non-persistent seed banks (Cousens and Mortimer, 1995).

Matrix population models can be used to study weed population dynamics and to identify mechanisms and ecological interactions that are especially stressful or fatal for weeds at different life history stages (Mertens et al., 2002; Westerman et al., 2005). Such models can also be used to project the consequences of hypothetical life history changes (Caswell, 2001; Davis, 2006). We developed a matrix population model to explore the effects on giant foxtail seed bank dynamics of a conventionally managed 2-year rotation (corn-soybean) and a low-external-input 4-year rotation (corn-soybean-small grains+alfalfa-alfalfa). The seed bank is of special interest in weed management because it is the main means of persistence of annual weed species (Gallandt, 2006;

Holst et al., 2007). The number of factors that affect seed banks and the variability encountered in the soil, however, make assessment of seed bank effects on weed populations difficult, especially in complex systems such as crop rotations (Mertens et al., 2002; Mohler, 2001).

The focal organism of the present study was giant foxtail (*Setaria faberi*), an important weed in corn and soybean in the U.S. Midwest whose seed bank persistence can vary from few months to several years (Buhler and Hartzler, 2001; Dekker, 2003; Forcella et al., 1992). Seedling emergence of giant foxtail is limited to seeds within the first 10 cm of the soil, and greatest emergence occurs from a depth of 0-5 cm (Buhler and Mester, 1991; Dekker, 2003). Our model incorporated parameter values for seed predation, decay, and germination, seedling survival, and plant fecundity from observations made over several years in an ongoing field experiment at Iowa State University's Marsden Farm, in Boone, IA. We also included in the model values obtained from the literature for vertical seed movement within the soil due to tillage. We constructed a set of transition matrices to project weed plant and seed bank populations through simulated crop rotation cycles, and conducted perturbation analyses (Caswell, 2001; van Groenendael et al., 1988) to test the sensitivity of the population growth rate to changes in certain model parameters, holding all others constant. Because model parameters are often measured on different scales, e.g. fecundity as seeds per plant and survival proportions, we analyzed the proportional effect of changes in the matrix elements, that is, the elasticities of the population growth rate.

Materials and Methods

Description of site

A 9-ha cropping systems study was initiated in 2001 at Iowa State University's Marsden Farm in Boone, Iowa, to evaluate crop productivity, weed productivity and density, energy use efficiency, and economic performance characteristics of three crop rotation systems: a 2-year corn soybean rotation, a three-year corn-soybean-small grain + red clover rotation, and a 4-year corn-soybean-small grain + alfalfa-alfalfa rotation. Triticale was used as the small grain crop in 2002-2005 and oat was used in 2006-2010. The experiment used a randomized complete block design with four replicates, with all phases of each rotation present each year. Plot size was 18 m x 85 m. We obtained estimates of giant foxtail emergence, seedling survival, and seed recruitment from the 2-year and 4-year rotations over the period 2003-2005. Seed decay estimates were generated over the period 2008-2010. Details of the farming practices carried out in both rotations and their performance characteristics are provided by Liebman et al. (2008), Cruse et al. (2010) and Gómez et al. (*in review*).

Model structure

Considering that processes such as seed germination and emergence, seed predation, and seed decay by microorganisms can vary with depth, and that tillage operations redistribute seeds in the soil, the seed bank in the model was divided into three layers:

the surface, 1-10 cm, and 11-20 cm. Numbers of seeds in and on the soil and numbers of plants were represented by the population vector n(t) (Figure 1), where n_1 is the number of seeds on the surface, n_2 the number of seeds at 1-10 cm, n_3 the number of seeds at 11-20 cm, n_4 the number of emerged seedlings, and n_5 the number of mature plants, modeled on a per m^2 basis. We called each year of a rotation system associated with a different crop a 'phase.' The model considered the two crop rotation systems (*j*) mentioned above, the rotation phase within each rotation system (*k*), and period of the weed life cycle within each rotation phase.

We constructed six transition matrices that described events or processes that occurred during a specific period of a phase and affected the seed bank and plant population. The matrices that we used were (Figure 1): *plant fecundity,* representing seeds produced by mature plants and dispersed onto the surface of the soil; *survival of seed predation,* containing the survival probabilities of seeds on the surface of the soil subject to predation by various vertebrates and invertebrate animals; *tillage,* used to describe the effects of various forms of soil disturbance resulting from tillage on vertical seed movement within the soil; o*ver-winter seed survival,* representing the probabilities of seeds surviving microbial seed decay; e*mergence,* containing the probabilities of seedling emergence from each of the three soil layers and losses of seeds from those layers resulting from germination; *summer survival to decay,* containing survival probabilities to microbial decay for seeds in the three soil layers; and *seedling survival*, representing the probabilities for seedlings to become reproductive plants during the summer.

The timeline used in the model began in October with plant fecundity, followed by seed predation on the surface from October to November; then either chisel plowing (in corn) or surface disking (in soybean) after harvest), no-till (following small grains + alfalfa), or moldboard plowing (at the end of the alfalfa phase) in late November; followed by over-winter seed decay from late November to April. Seedling emergence occurred from April to June, summer seed decay happened from May to October, and seedling survival from June to October. We used R software (R Development Core Team 2011) to implement the model.

Parameter values used

Giant foxtail demographic data obtained from the Marsden Farm cropping systems experiment yielded 12 distinctive data sets (3 years *x* 4 replicate blocks). We used in our model the average of years and replicates for the parameter values of seed recruitment, over-winter and summer seed decay, emergence, and seedling survival (Table 1); we show the variability of the data in Tables 2 and 3. Values for vertical seed movement due to tillage were recalculated from Cousens and Moss (1991) (Table 1). Fecundity, *r*, was calculated as the average number of seeds per reproductive plant. The proportion of seeds surviving predation in each crop within each rotation, *p*, was estimated by Westerman et al. (2006) using a model that linked seed dispersal, seed burial, and seed demand as the main processes determining giant foxtail seed survival on the soil surface. Overall emergence, *e*, was calculated by dividing the average total number of emerged seedlings by the average spring seed bank density. Assuming that

giant foxtail seedlings emerged from the first 10 cm of soil (Dekker, 2003), and that tillage systems influence emergence of giant foxtail from certain depth (Buhler and Mester, 1991), we estimated the probability of emergence from the first soil layer, e_1, as a proportion of the overall emergence, expressed as:

$$e_1 = l_1 e \quad (1)$$

where l_1= 0.03 when moldboard plowing was performed, l_1= 0.08 when chisel plowing or disking were completed, and l_1= 0.2 when there was no tillage carried out (Buhler and Mester 1991). Emergence from 11-20 cm (e_3) was considered to be nil, and emergence from 1-10 cm (e_2) was solved from the equation:

$$e = e_1 + e_2 + e_3 \quad (2)$$

Values for over-winter and summer seed survival to decay at 1-10 cm (w_2 and s_2) and 11-20 cm (w_3 and s_3) were obtained in corn plots of each rotation from Gómez et al. (*in review*). Because no published data concerning survival to decay in soybean, small grains, and alfalfa were available, we used the same values as in corn for these parameters. We estimated over-winter seed survival (w_1) and summer seed survival at the surface (s_1) as a proportion of the respective survival rate in the 1-10 cm layer:

$$w_1 = l_1 w_2 \quad (3)$$

$$s_1 = l_1 s_2 \quad (4)$$

with l_1 as described for emergence (see above), assuming that the probability of emergence and the probability for seed decay at the surface were linked. Proportion

plant survival, *m*, was calculated by dividing the average number of reproductive plants by the number of emerged seedlings.

Our model does not differentiate between seeds belonging to different age classes or between weed cohorts emerging at different times. We recognize that survival probabilities and seed recruitment may vary among cohorts, and seed age classes may differ in emergence probabilities and decay rates, but such specific parameter values were not available.

Model analysis

We examined the effects of the two crop rotations on giant foxtail population dynamics, starting in the corn phase of both rotations, in three steps. We first calculated the population growth rate for the entire rotation and the annual population growth rate (as $\sqrt[2]{\lambda_2}$ for the 2-year rotation and $\sqrt[4]{\lambda_4}$ for the 4 year rotation), and the projected weed seed bank dynamics over a 20-year period, for (i) a no seed decay scenario and (ii) a scenario using estimates of seed decay obtained from the Marsden Farm cropping systems experiment (Table 1). Second, we performed elasticity analyses of the model parameters to identify the processes and events whose proportional change would have a major impact on the population growth rate under each scenario. Finally, we studied the role of summer seed decay on giant foxtail population dynamics in the 4-year rotation by projecting the seed bank and analyzing population growth rate elasticities under three different scenarios with higher decay values than the values observed in our field plots: (i) 20% seed decay in the 1-10 cm layer and 15% seed decay in the 11-

20 cm layer, (ii) 25% decay at 1-10 cm and 20% at 11-20 cm, and (iii) 30% decay at 1-10 cm and 25 % decay at 11-20 cm. The assumed percentages of summer seed decay in each layer are similar to results obtained during 2008 in our cropping systems experiment, and are within the lower end of giant foxtail seed mortality ranges obtained by different studies carried out in the US Midwest (Buhler and Hartzler 2001, Davis et al. 2006, Schutte et al. 2008). Over-winter seed decay was observed to be very low each year, therefore we did not modified these values in the model for these last seed bank projections.

Results and Discussion

Model simulations over a 20-year period under the scenario of no over-winter and no summer seed decay showed a decreasing giant foxtail seed bank in the 2-year rotation, and an increasing seed bank in the 4-year rotation (Figure 2). Total population growth rate was 0.94 for the 2-year rotation and 1.17 for the 4-year rotation. Annualized population growth rate for each phase of the rotation indicated that the seed bank would decrease similarly in corn and soybean in both rotations, but it would increase in small grains + alfalfa and alfalfa phases of the 4-year rotation (Table 4). Such an increase in the giant foxtail seed bank is associated with the high proportion of seedling emergence in those two phases of the 4-year rotation and a higher proportion of seedling survival to control methods in the small grain + alfalfa phase (Table 1). Moreover, when there is no seed decay, the proportion of seedlings that emerge becomes the most important factor affecting the population growth rate in the 2-year rotation, as shown by the elasticities

analysis (Table 4). In the 4-year rotation, on the other hand, several parameters would have a strong effect on the population growth rate of each phase (Table 4).

Projection of the giant foxtail seed bank using over-winter and summer seed decay estimates obtained from the field experiment showed, again, that the seed bank would decrease in the 2-year rotation (λ_2=0.83) and increase in the 4-year rotation (λ_4=1.04), but the lower population growth rates calculated for both rotations indicate that seed decay is an important biological process that affects giant foxtail seed bank density (Figure 3). The elasticities of λ_2 indicated that any change in the proportion of over-winter and summer seed survival in the 11-20 cm layer would have the highest effect on the whole-rotation population growth rate (Table 5). Over-winter seed survival was also noted by Jordan et al. (1995a) and Davis (2006) to be particularly important in determining the population growth rate of annual weeds.

In the 4-year rotation of the present study several parameters would affect the population growth rate of each phase, including seed decay at 1-10 cm and 11-20 cm (Table 5), suggesting that in a diversified rotation multiple factors contribute to the population growth rate, although individually each of them may have a lower impact on λ than in the simpler 2-year rotation. In a similar population dynamics study, Westerman et al. (2005) reported that velvetleaf (*Abutilon theophrasti*) population growth rate for the 4-year rotation was more elastic to changes in demographic parameters than was the population growth rate for the 2-year rotation.

Giant foxtail seed bank projections under three scenarios of increasing summer seed decay illustrated how the seed bank would decrease (λ_4=0.99) in the 4-year rotation if a

minimum of 20% and 15% seed decay were to occur at 1-10 cm and at 11-20 cm, respectively (Figure 4). Estimates of giant foxtail summer seed death reported in various studies carried out in the US Midwest range from 27% to 91% (Buhler and Hartzler 2001, Davis et al. 2006, Schutte et al. 2008), although those studies did not account for mortality attributable to fatal germination. Empirical observations obtained in the Marsden Farm plots and reported by Liebman et al. (2008) indicated that giant foxtail seed banks diminished over a four-year period in both rotations. It is possible, therefore, that the very low seed decay estimates obtained in our study were related to particular interactions among the seed lots evaluated, the environment, and soil microbial populations, as suggested by Gómez et al. (*in review*).

Elasticities analysis of giant foxtail population growth rate for the 4-year rotation in the three increasing summer seed decay scenarios showed again how multiple demographic parameters affect the growth rate (Table 6). As seed decay increased, elasticities of the different parameters in each phase of the rotation decreased, supporting the concept that in a diversified crop rotation, multiple weed management alternatives that target different weed life stages would have an effect in reducing population density similar to a conventional single postemergence control tactic (e.g., herbicide application) used in a simpler rotation (Liebman and Gallandt 1997), but with the benefit of decreasing the risk of failing to control the weed when one tactic fails.

Our findings support the importance of the seed decay process in regulating giant foxtail population growth. Because decomposition of seeds of certain species is favored by saturated soil conditions (Boyd and Van Acker, 2003), one could speculate that in dry years seed decay would be low, and therefore preventing and controlling seedling

emergence would be particularly important in drier years for reducing future recruitment of new seeds and population growth, as suggested by the calculated elasticities in the no decay scenario. When seed decay is high, the importance of post-emergence weed control methods diminishes, which has agricultural and environmental implications regarding the frequency and intensity of chemical and physical weed control operations. Various studies have reported that seed decay depends on the composition and abundance of soil microbial populations (Chee-Sanford, 2007; Chee-Sanford et al., 2006; Kremer, 1993). Diversified cropping system effects on soil physical and chemical characteristics, such as increased organic matter and higher water retention in drought conditions, could potentially influence positively the soil microbial biomass and thus favor the seed decay process, having a direct effect on giant foxtail population growth rate.

It is also important to note that we used high values of seed predation in our matrix population model. These values can be achieved in the field but, as previously mentioned, depend on factors such as the timing of seed dispersal, seed burial, and seed demand by predators (Westerman et al., 2006). As an example, plowing early in the fall would bury most of the seeds that were on the surface, making them unavailable for predators. For this reason, weed management in agricultural fields should be seen as a multidimensional challenge, in which ecological processes such as seed predation and seed decay that occur in various seasons at the soil surface and below ground require the same or greater attention as the events that happen above ground.

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Figure 3.1. Population vector [n(t)] and transition matrices used in the giant foxtail matrix model. n_1: number of seeds on the surface, n_2: number of seeds at 1-10cm, n_3: number of seeds at 11-20 cm, n_4: number of seedlings, and n_5: number of mature plants. R_{jk}: plant fecundity; SP_{jk}: survival to seed predation; T_{jk}: tillage matrices for chisel plow, moldboard plow, and no-till, respectively from left to right; SW_{jk}: survival to over-winter seed decay; E_{jk}: emergence; SS_{jk}: survival to summer seed decay.

Figure 3.2. Projection of giant foxtail seed bank dynamics in a conventional 2-year corn-soybean rotation and a low-external-input 4-year corn-soybean-small grain + alfalfa-alfalfa rotation, assuming there is no occurrence of over-winter and summer seed decay.

Figure 3.3. Projected seed bank density for a 2-year corn-soybean rotation and a 4-year low-external-input corn-soybean-small grain + alfalfa-alfalfa rotation over a 20 year period, using baseline demographic parameters.

Figure 3.4. Projected seed bank density for a 4-year corn-soybean-small grain + alfalfa-alfalfa rotation under three seed decay scenarios: 20% seed decay in the 1-10 cm layer and 15% seed decay in the 11-20 cm layer, 25% decay at 1-10 cm and 20% at 11-20 cm, and 30% decay at 1-10 cm and 25 % decay at 11-20 cm.

Table 3.1. Baseline demographic parameters for giant foxtail growing in a 2-yr corn-soybean rotation and a 4-yr corn-soybean-small grains+alfalfa-alfalfa rotation.

		2-yr rotation		4-yr rotation			
Parameter	Symbol	Corn	Soybean	Corn	Soybean	Small grain + alfalfa	Alfalfa
Fecundity (seeds plant^{-1})	r	119	25	130	4708	156	97
Proportion survival to seed predation	p	0.3500	0.4000	0.3500	0.4000	0.6500	0.3600
Seed movement							
remaining at surface	t_{11}	0.0100	0.0100	0.0100	0.0100	0.0100	1.0000
surface to 1-10 cm	t_{21}	0.9200	0.9200	0.1300	0.9200	0.9200	1.0000
surface to 11-20 cm	t_{31}	0.0700	0.0700	0.8600	0.0700	0.0700	1.0000
remaining at 1-10 cm	t_{22}	0.8300	0.8300	0.4800	0.8300	0.8300	1.0000
1-10 cm to 11-20 cm	t_{32}	0.1600	0.1600	0.5100	0.1600	0.1600	1.0000
1-10 cm to surface	t_{12}	0.0100	0.0100	0.0100	0.0100	0.0100	1.0000
remaining at 11-20 cm	t_{33}	0.8300	0.8300	0.3800	0.8300	0.8300	1.0000
11-20 cm to 1-10 cm	t_{23}	0.1700	0.1700	0.6200	0.1700	0.1700	1.0000
11-20 cm to surface	t_{13}	0.0000	0.0000	0.0000	0.0000	0.0000	1.0000
Proportion over-winter seed survival to decay							
Surface	w_1	0.9965	0.9965	0.9993	0.9982	0.9982	0.9955
1-10 cm	w_2	0.9567	0.9567	0.9776	0.9776	0.9776	0.9776
11-20 cm	w_3	0.9738	0.9738	0.9816	0.9816	0.9816	0.9816
Proportion of emergence							
Surface	e_1	0.0098	0.0149	0.0039	0.0064	0.0275	0.0694
1-10 cm	e_2	0.1129	0.1716	0.1252	0.0742	0.3165	0.2778
11-20 cm	e_3	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Proportion summer seed survival to decay							
Surface	s_1	0.9914	0.9914	0.9957	0.9885	0.9885	0.9712
1-10 cm	s_2	0.8927	0.8927	0.8559	0.8559	0.8559	0.8559
11-20 cm	s_3	0.9250	0.9250	0.9007	0.9007	0.9007	0.9007
Proportion seedling survival	m	0.0011	0.0005	0.0071	0.0039	0.0997	0.0308

Table 3.2. Variability on parameter values of giant foxtial growing in the 2-year rotation of the cropping systems experiment.

Parameter	Symbol	Corn				Soybean			
		Mean	*SE*	*min.*	*max.*	*Mean*	*SE*	*min.*	*max.*
Fecundity (seeds plant^{-1})	r	119	112.2500	0	343	25	22.7800	0	70
Proportion over-winter seed survival to decay									
1-10 cm	w_2	0.9567	0.0294	0.8900	1.0000	0.9567	0.0294	0.8900	1.0000
11-20 cm	w_3	0.9738	0.0079	0.9557	0.9830	0.9738	0.0079	0.9557	0.9830
Proportion of emergence	e	0.1227	0.0618	0.0534	0.2459	0.1865	0.0544	0.0798	0.2586
Proportion of summer seed survival to decay									
1-10 cm	s_2	0.8927	0.0857	0.6947	0.9917	0.8927	0.0857	0.6947	0.9917
11-20 cm	s_3	0.9250	0.0649	0.7750	1.0000	0.9250	0.0649	0.7750	1.0000
Proportion of seedling survival	m	0.0011	0.0006	0.0000	0.0021	0.0005	0.0004	0.0000	0.0012

Table 3.3. Variability on parameter values of giant foxtial growing in the 4-year rotation of the cropping systems experiment.

Parameter	Symbol	Corn				Soybean				Small grain + alfalfa				Alfalfa			
		Mean	*SE*	*min.*	*max.*	*Mean*	*SE*	*min.*	*max.*	*Mean*	*SE*	*min.*	*max.*	*Mean*	*SE*	*min.*	*max.*
Fecundity (seeds plant^{-1})	r	130	91.65	1	308	4708	4333.9	0	13365	156	65.85	24	229	97	91.86	0	281
Proportion over-winter seed survival to decay																	
1-10 cm	w_2	0.9776	0.0216	0.9249	1.0000	0.9776	0.0216	0.9249	1.0000	0.9776	0.0216	0.9249	1.0000	0.9776	0.0216	0.9249	1.0000
11-20 cm	w_3	0.9816	0.0123	0.9537	1.0000	0.9816	0.0123	0.9537	1.0000	0.9816	0.0123	0.9537	1.0000	0.9816	0.0123	0.9537	1.0000
Proportion of emergence	e	0.1291	0.0620	0.0385	0.2477	0.0806	0.0564	0.0162	0.1929	0.344	0.1527	0.0594	0.5822	0.3472	0.0521	0.2431	0.3996
Proportion of summer seed survival to decay																	
1-10 cm	s_2	0.8559	0.0985	0.6285	0.9738	0.8559	0.0985	0.6285	0.9738	0.8559	0.0985	0.6285	0.9738	0.8559	0.0985	0.6285	0.9738
11-20 cm	s_3	0.9007	0.0824	0.7105	1.0000	0.9007	0.0824	0.7105	1.0000	0.9007	0.0824	0.7105	1.0000	0.9007	0.0824	0.7105	1.0000
Proportion of seedling survival	m	0.0071	0.0020	0.0032	0.0100	0.0039	0.0026	0.0000	0.0088	0.0997	0.0179	0.0783	0.1353	0.0308	0.0204	0.0065	0.0714

Table 3.4. Giant foxtail annualized growth rate in two crop rotations and elasticities of the population growth rate to changes in demographic parameters, assuming that no over-winter or summer seed decay occur.

Parameter	Symbol	2-yr rotation		4-yr rotation			
		Corn	Soybean	Corn	Soybean	Small grains + alfalfa	Alfalfa
Population growth rate	λ	0.95	0.93	0.93	0.96	1.04	1.01
Plant fecundity (seeds plant^{-1})	r	0.0012	0.0004	0.2439	0.5989	0.0276	0.0276
Proportion seed predation	p	0.0024	0.0016	0.5218	0.6013	0.0333	0.3608
Prorportion emergence	e_1	0.0012	0.0011	0.0023	0.0057	0.0619	0.2779
Prorportion emergence	e_2	0.3065	0.3028	0.3181	0.8678	0.5654	0.4044
Prorportion seedling survival	m	0.0004	0.0012	0.5989	0.0276	0.2989	0.2439

Table 3.5. Giant foxtail annualized growth rate in two crop rotations and elasticities of the population growth rate to changes in specific demographic parameters, holding all others constant.

Parameter	Symbol	2-yr rotation		4-yr rotation			
		Corn	Soybean	Corn	Soybean	Small grains + alfalfa	Alfalfa
Population growth rate	λ	0.84	0.82	0.8	0.83	0.92	0.88
Plant fecundity (seeds plant^{-1})	r	0.0010	0.0003	0.1836	0.4319	0.0220	0.0220
Proportion seed predation	p	0.0019	0.0013	0.4126	0.4337	0.0266	0.2994
Proportion of overwinter survival	w_1	0.0010	0.0009	0.0042	0.0048	0.0687	0.2994
Proportion of overwinter survival	w_2	0.2297	0.2273	0.6270	0.6133	0.5879	0.3572
Proportion of overwinter survival	w_3	0.5997	0.6021	0.4896	0.5028	0.4642	0.4642
Prorportion of emergence	e_1	0.0010	0.0009	0.0018	0.0046	0.0538	0.2290
Prorportion of emergence	e_2	0.2294	0.2263	0.1975	0.5915	0.3572	0.2440
Proportion summer seed survival	s_1	0.0010	0.0009	0.0018	0.0046	0.0538	0.2290
Proportion summer seed survival	s_2	0.2294	0.2263	0.1975	0.5915	0.3572	0.2440
Proportion summer seed survival	s_3	0.5997	0.6021	0.4896	0.5028	0.4642	0.4642
Proportion of seedling survival	m	0.0003	0.0010	0.4319	0.0220	0.2457	0.1836

Table 3.6. Giant foxtail annualized growth rate (λ) in two crop rotations and elasticities of the population growth rate to changes in demographic parameters, in three summer seed decay scenarios.

Parameter	20% decay at 1-10 cm and 15% at 11-20 cm				25% decay at 1-10 cm and 20% at 11-20 cm				30% decay at 1-10 cm and 25% at 11-20 cm			
	Corn	Soybean	grains + alfalfa	Alfalfa	Corn	Soybean	grains + alfalfa	Alfalfa	Corn	Soybean	grains + alfalfa	Alfalfa
λ	0.75	0.78	0.87	0.83	0.75	0.78	0.87	0.83	0.66	0.69	0.78	0.74
r	0.1648	0.3835	0.0205	0.0205	0.1482	0.3415	0.0192	0.0192	0.1324	0.3023	0.0179	0.0179
p	0.3767	0.3851	0.0248	0.2778	0.3440	0.3431	0.0231	0.2573	0.3125	0.3038	0.0216	0.2373
w_1	0.0039	0.0044	0.0638	0.2778	0.0037	0.0041	0.0590	0.2573	0.0035	0.0038	0.0544	0.2373
w_2	0.5450	0.5344	0.5157	0.3017	0.4759	0.4684	0.4551	0.2568	0.4129	0.4080	0.3992	0.2163
w_3	0.4272	0.4373	0.3966	0.3966	0.3718	0.3788	0.3373	0.3373	0.3213	0.3259	0.2840	0.2840
e_1	0.0017	0.0042	0.0500	0.2119	0.0016	0.0039	0.0462	0.1958	0.0015	0.0037	0.0425	0.1801
e_2	0.1638	0.5141	0.3017	0.2028	0.1365	0.4494	0.2568	0.1701	0.1126	0.3902	0.2163	0.1411
s_1	0.0017	0.0042	0.0500	0.2119	0.0016	0.0039	0.0462	0.1958	0.0015	0.0037	0.0425	0.1801
s_2	0.1638	0.5141	0.3017	0.2028	0.1365	0.4494	0.2568	0.1701	0.1126	0.3902	0.2163	0.1411
s_3	0.4272	0.4373	0.3966	0.3966	0.3718	0.3788	0.3373	0.3373	0.3213	0.3259	0.2840	0.2840
m	0.3835	0.0205	0.2279	0.1648	0.3415	0.0192	0.2112	0.1482	0.3023	0.0179	0.1948	0.1324

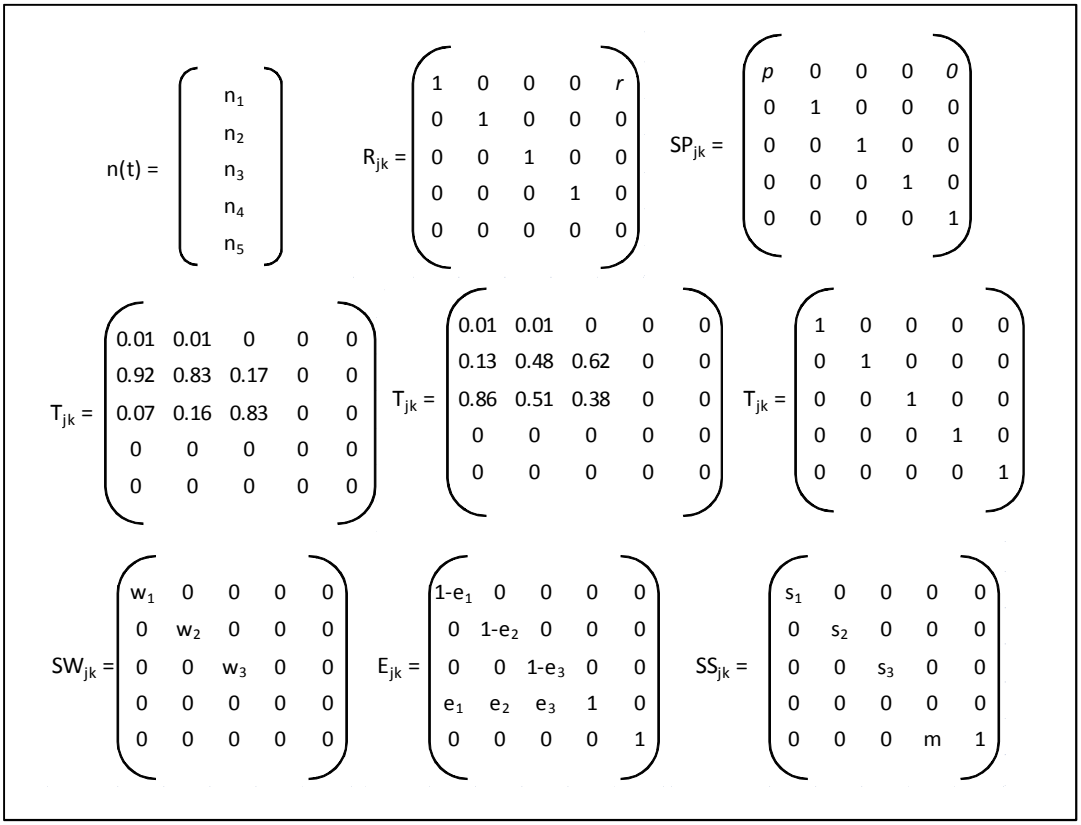
n(t) = (n1 n2 n3 n4 n5)
Rjk = (1 0 0 0 r; 0 1 0 0 0; 0 0 1 0 0; 0 0 0 1 0; 0 0 0 0 0)
SPjk = (p 0 0 0 0; 0 1 0 0 0; 0 0 1 0 0; 0 0 0 1 0; 0 0 0 0 1)
Tjk = (0.01 0.01 0 0 0; 0.92 0.83 0.17 0 0; 0.07 0.16 0.83 0 0; 0 0 0 0 0; 0 0 0 0 0)
Tjk = (0.01 0.01 0 0 0; 0.13 0.48 0.62 0 0; 0.86 0.51 0.38 0 0; 0 0 0 0 0; 0 0 0 0 0)
Tjk = (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)
SWjk = (w1 0 0 0 0; 0 w2 0 0 0; 0 0 w3 0 0; 0 0 0 0 0; 0 0 0 0 0)
Ejk = (1-e1 0 0 0 0; 0 1-e2 0 0 0; 0 0 1-e3 0 0; e1 e2 e3 1 0; 0 0 0 0 1)
SSjk = (s1 0 0 0 0; 0 s2 0 0 0; 0 0 s3 0 0; 0 0 0 0 0; 0 0 0 m 1)

Figure 3.1

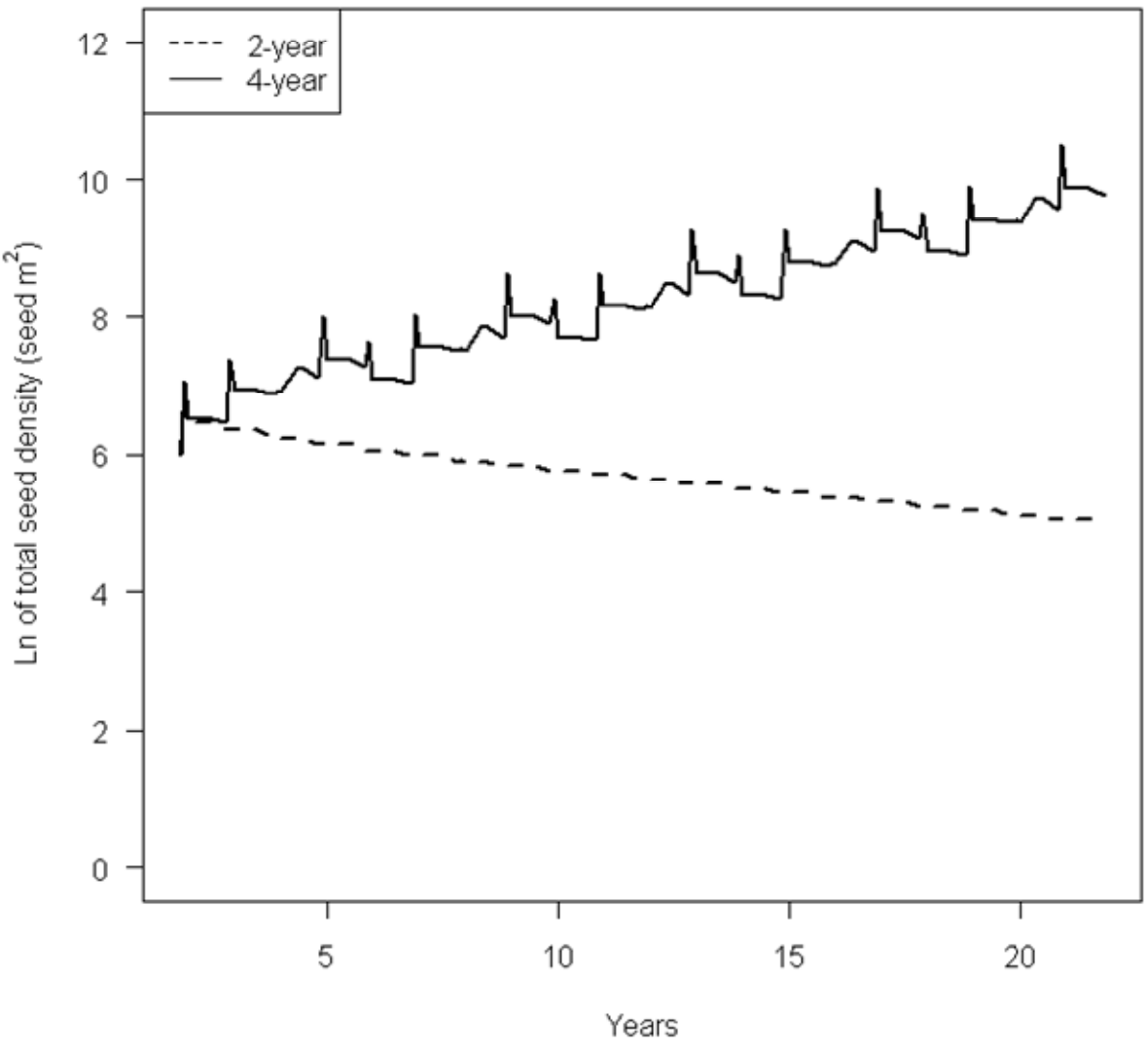
2-year
4-year
12
10
8
6
4
2
0
Ln of total seed density (seed m^2)
5
10
15
20
Years

Figure 3.2

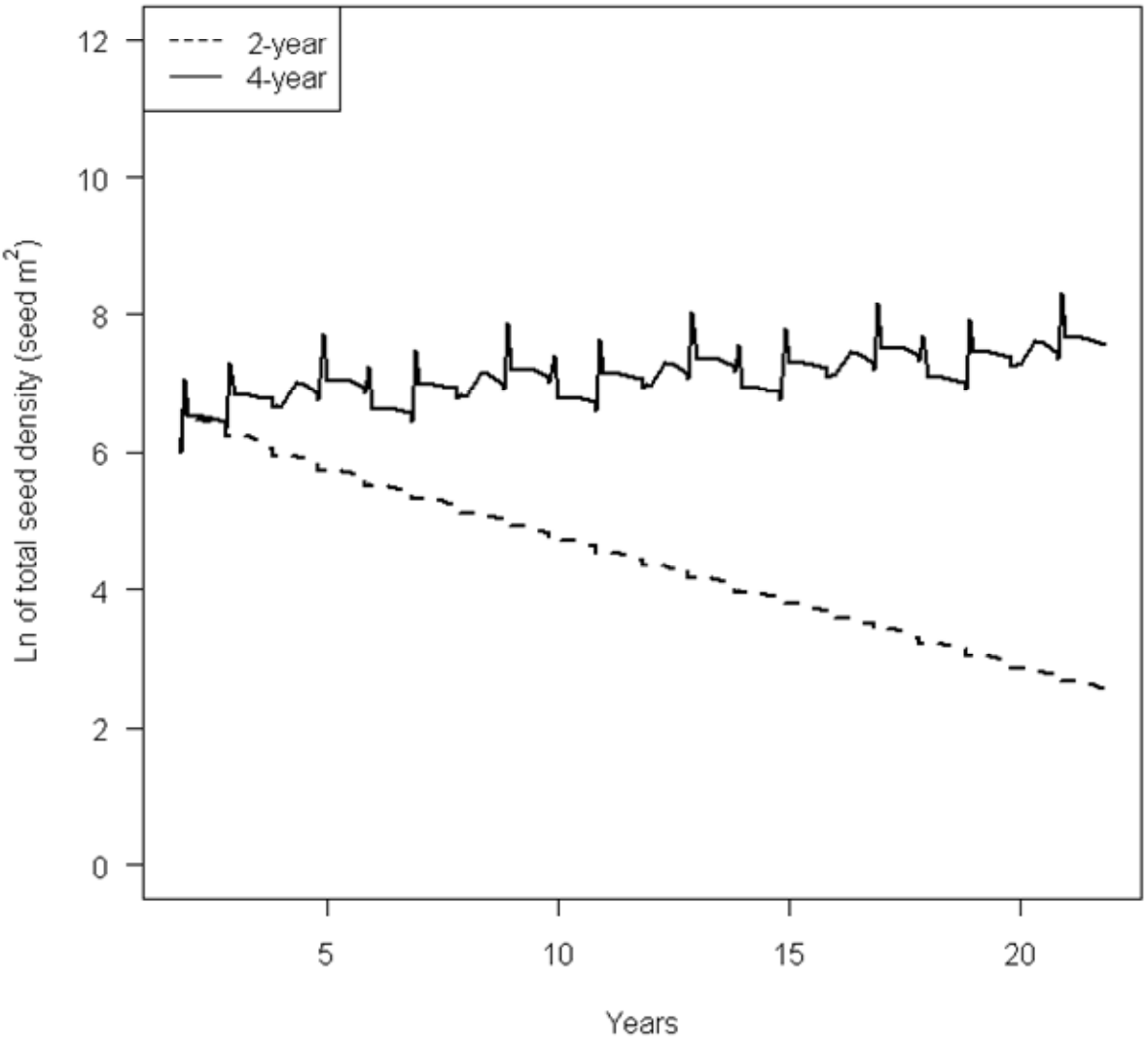
2-year
4-year
12
10
8
6
4
2
0
Ln of total seed density (seed m^2)
5
10
15
20
Years

Figure 3.3

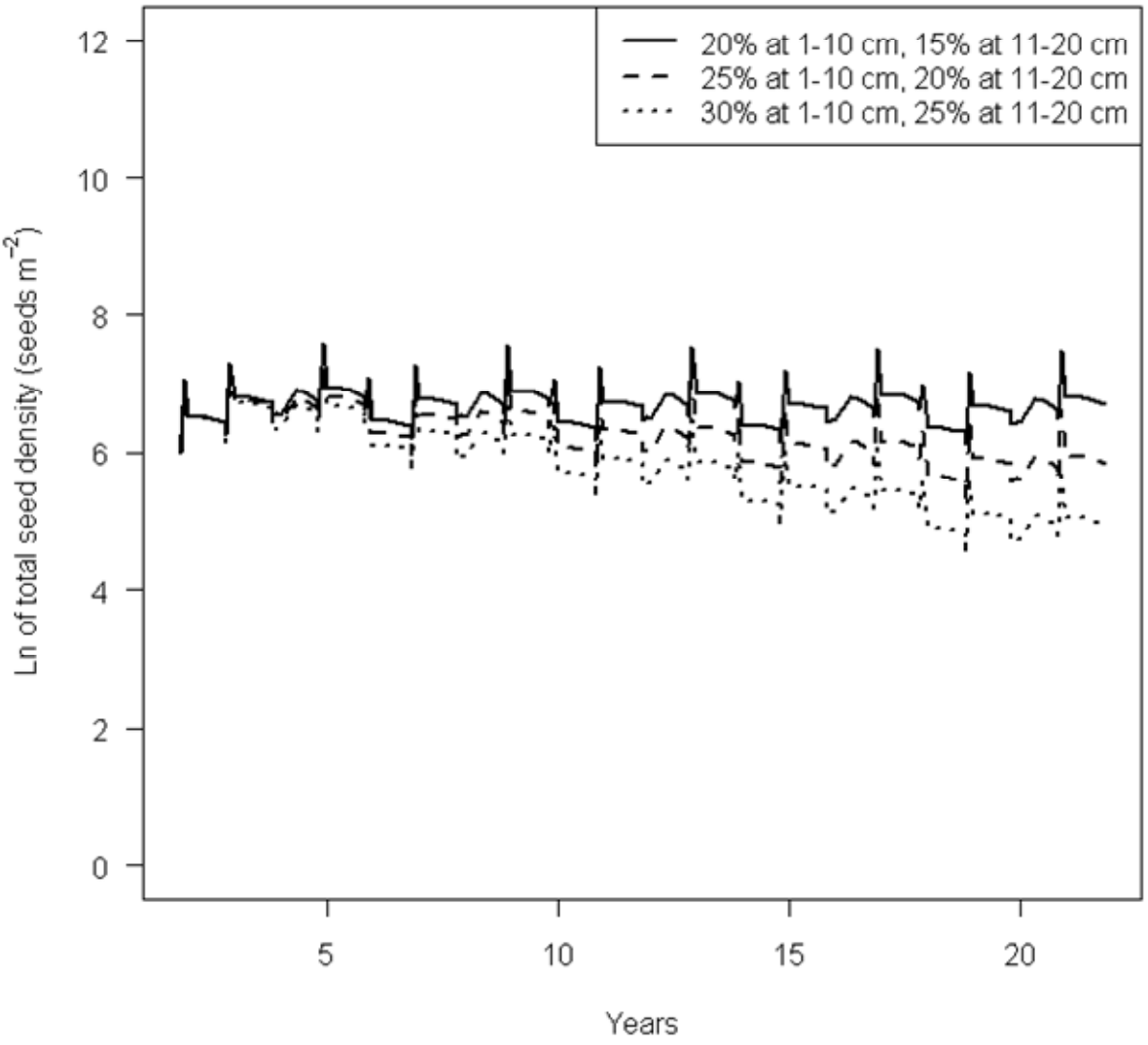
20% at 1-10 cm, 15% at 11-20 cm
25% at 1-10 cm, 20% at 11-20 cm
30% at 1-10 cm, 25% at 11-20 cm
Ln of total seed density (seeds m^{-2})
0
2
4
6
8
10
12
5
10
15
20
Years

Figure 3.4

Chapter 5. General Conclusions

Agricultural alternatives intended to reduce negative impacts on agroecosystems due to heavy reliance on pesticides and synthetic fertilizers are much needed. Concerns about the environment, human and animal health, increased production costs, and high use of energy from non-renewable sources have catalyzed efforts to seek farm management practices that enhance ecological interactions to sustain and improve agricultural production. Despite these efforts, practices that reduce dependency on off-farm chemical inputs are not commonly adopted by farmers who perceive them to be in their infancy where science is concerned or, on the other hand, obsolete. It is, therefore, imperative that we continue to explore the mechanisms that drive the beneficial effects of agricultural alternatives such as diversified cropping systems, because it can provide scientific legitimacy for adopting and implementing a variety of farming practices, in contrast to the ‘silver bullet’ approach.

This research proved that higher corn and soybean yields can be achieved in 3- and 4-year diversified rotations that include small grains and legumes, than in a 2-year simpler rotation. Furthermore, we determined a higher economic return for the 3-year corn-soybean-oats+red clover rotation. These findings have not only economic implications for farmers but also environmental benefits derived from the management practices associated to more diversified cropping systems: less herbicide applications over time reduce the risk of both water contamination and evolution of weed resistance; incorporation of organic matter into the soil improves soil structure and favors multiple

physical and chemical processes that affect plants and microorganisms. Furthermore, we found that the strength of these diverse cropping systems is their resiliency, this is, their capacity to recover from significant change in a way that fluctuation in profits and environmental impact remain minimal. We observed this resiliency when we evaluated contrasting corn and soybean varieties and determined a similar positive rotation effect on both crops, and also when we observed lower damage of the disease Sudden Death Syndrome on soybean varieties planted in the diverse rotations compared to the conventional rotation. The cropping system resiliency allows farmers to reduce the inherent risk of depending on fixed external outputs and consequent price fluctuations, and enhance the flexibility of choosing the crop genotype to be planted according to the needs of each production unit.

A key factor that should be considered when proposing agricultural alternatives intended to reduce pesticide and synthetic fertilizer use and their impact on the environment and human health, is the role of ecological interactions within the agroecosystem. Numerous studies have been conducted in the cropping systems experiment at Marsden Farm to understand the effect of green and animal manure on weed population dynamics, the impact of the rotation on weed demography and weed population dynamics, and the phenomenon of winter and summer weed seed predation. This thesis contributed to the increasing understanding of ecological interactions by analyzing the cropping system effect on the decomposition of weed seeds by fungi and Oomycetes. The initial research question, does the difference in management practices among crop rotations result in a differential seed decay rate?, could not be answered in

a conclusive way due to the complexity of the seed decay process. Instead, the phenomenon of seed decay was approached from a plant pathology perspective, considering the components of the 'disease triangle': the environment, the pathogen, and the host. Higher seed decay in shallower layers of the soil and considerable differences in decay rates among years proved that the environment plays an important role on the seed decay process. The identification of *Pythium ultimum* as a possible causal agent of giant foxtail seed decay, and the finding that giant foxtail seed decay was the lowest in years when *P. ultimum* incidence was very low highlights the role of the pathogen in the seed decay process. Finally, and most fascinating from the weed management perspective, is the finding of differential susceptibilities to seed decay between weed species and within giant foxtail seed lots. We determined higher seed decay in the 4-year rotation than in the 2-year rotation when seed lot susceptibility and pathogen incidence were high, but found no differences between rotations when these conditions were not met.

The importance of studying ecological interactions within cropping systems is having the possibility to identify those processes or events that are especially stressful or fatal in certain stages of the life cycle of an organism, in our case the weeds. Applying this concept, we sought to investigate the effect of two contrasting crop rotations on giant foxtail seed bank dynamics using a matrix population model parameterized with data obtained from the Marsden Farm cropping systems experiment. Two important findings must be highlighted from this study: (i) model simulations showed decreasing giant foxtail seed bank in both the 2-year and the 4-year rotations, which reveals efficient

weed management in a rotation where considerably less herbicides and synthetic fertilizer were applied, and (ii) elasticity analyses suggest that in a diversified crop rotation multiple factors contribute to the population growth rate, although individually each of them may have a lower impact on the population growth rate than in the simpler 2-year rotation. These results confirm the necessity of considering ecological processes such as seed decay and seed predation when developing weed management practices.

I believe that a holistic approach is required when we look at agriculture on a broader scale, and reflect on its impact on the environment, the farmers' life, public health, and the society wellbeing. The debate about the unintended consequences of industrial agriculture that gave birth to the "Alternative Agriculture" movement in the late 1970s is still relevant, although in my opinion the myriad of interests among those who pursue a tangible change in the agricultural system have limited its success. I also believe in the importance of developing agricultural alternatives tailored to the farm or region, and that according to the interests, resources, and capabilities of the farmer or inhabitants of a region those alternatives might or might not include the judicious use of pesticides, genetically engineered crops, and synthetic fertilizers. I am aware of the existence of political and economic forces that impose their interest in a particular agricultural system, but by completely opposing them, rather than working with them and most importantly, working with farmers and consumers, little progress will be achieved. I perceive sustainability in agriculture as a moving target, there is always opportunity for improvement, and it should be pursued with a range of technological and management options that seek to reduce costs, protect human and animal health, maintain

environmental quality, and enhance beneficial ecological interactions and natural processes.

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