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Cropping system effects on giant foxtail demography

by

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CHAPTER 1. GENERAL INTRODUCTION

Despite more than 50 years of weed control efforts relying primarily upon herbicide applications, weeds continue to impose substantial costs upon agriculture. For example, in the north central corn belt of the Midwestern USA, weeds are responsible for annual crop reductions of 12% (Pike et al., 1995). A growing number of weed scientists have stressed the need for going beyond weed control, based on killing weeds within a single growing season, and embracing the concept of integrated weed management (IWM) (Zimdahl, 1999; Buhler, 2002). Although the definition of IWM may vary somewhat between practitioners, common features of the IWM approach include use of 1) site-specific information about weed populations and communities, 2) biological information about the dominant weed species, 3) and multiple control tactics (Buhler, 2002). In general, IWM practitioners aim to reduce their reliance upon herbicides for weed management, so that herbicides tune, rather than drive, the system.

Increased interest among weed scientists in looking at IWM systems coincides with growing public concerns about unintended environmental impacts of agriculture and consumer demand for food produced with less reliance upon pesticides that have led to rapid growth in low-external-input (LEI) production systems (Geier, 1998). Although producers in LEI systems have indicated that their highest priority for public-funded research is the development of ecologically-based weed management strategies (OFRF, 1998), this research area has received little attention in the weed science literature over the past 50 years (Benbrook, 1996).

Production conditions in LEI systems offer both challenges and opportunities for ecologically-based weed management strategies. One large challenge is the prevention of weed population increases in LEI systems (Jordan, 1996). Weed management based upon

the combined effect of multiple sub-lethal control tactics is most likely to succeed when weed populations are maintained at low levels (Mortensen, 1995), yet without recourse to big-hammer approaches. LEI producers may find it difficult to achieve this goal. Some of the common characteristics of LEI cropping systems, such as diversified crop rotations and use of soil organic amendments, may aid weed prevention by introducing stresses at important points in the weed life cycle (Liebman and Davis, 2000).

The above trends indicate a clear need for research that 1) identifies links between production practices and ecological processes regulating weed population dynamics and 2) highlights the impacts of integrating multiple weed control tactics upon weed populations. Such questions may be addressed with long-term field experiments examining the effect of factorial treatment combinations upon weed populations over time. But because of the large amounts of time and space needed to conduct such experiments, and because of the difficulties associated with the analysis and interpretation of multi-way treatment interactions, a purely empirical approach to answering these questions seems impractical.

The goal of my dissertation work was to integrate the results of short-term empirical experiments of cropping system effects on weed demographic rates into simulations of weed population dynamics under the various cropping systems. I chose giant foxtail (*Setaria faberi* Herrm.) as my model organism because of its economic importance throughout the Midwestern corn producing region (Lindquist et al., 1999) and because it has been well characterized at the morphological (Forcella et al., 2000), genetic (Wang et al., 1995) and physiological (Dekker and Hargrove, 2002) levels.

Dissertation organization

The combined empirical and modeling approach discussed above is reflected in the four studies comprising this dissertation. The first two articles describe field experiments, conducted in parallel, designed to examine how management of organic matter amendments to soil affect demographic rates of giant foxtail. The third and fourth articles describe modeling studies of cropping system effects on giant foxtail population dynamics in systems managed with either no external weed control or some form of external weed control. The following paragraphs provide a synopsis of each article, including title, research questions and general approach.

Cropping system effects on giant foxtail demography: I. Green manure and tillage timing. This study focused on the following research questions: 1) How do residues from a red clover/spring wheat green manure affect giant foxtail life stage transitions?, and 2) Does differential tillage timing, either directly, or by modifying residue freshness, affect giant foxtail life stage transitions? These questions were addressed with a field experiment conducted in 2000 and 2001 in which giant foxtail life stage transitions were measured in the context of a corn-soybean-wheat crop sequence. The wheat phase was grown either as a sole crop (W) or as an intercrop with red clover (R). Residues from the wheat phase were incorporated either in the fall (FT) or in the spring (ST) to form a factorial of four cropping system treatments: FT/W, FT/R, ST/W and ST/R. Life stage transitions measured included seedbank persistence from October through March and from March through October, seedling recruitment, seedling survival to reproductive maturity, seeds produced per mature individual, and proportion of newly shed seeds not consumed by seed predators.

Cropping system effects on giant foxtail demography: II. Compost This study focused on the following research question: Does compost, either directly, or through an interaction with residues from a red clover/spring wheat green manure, affect giant foxtail life stage transitions? This question was addressed with a field experiment conducted in 2000 and 2001 in which giant foxtail life stage transitions were measured in the context of a corn-soybean-wheat crop sequence. The wheat phase was grown either as a sole crop (W) or as an intercrop with red clover (R), and residues from this phase were incorporated in the spring. Prior to incorporation of residues from the wheat phase, composted swine manure was either added to (C) or withheld from (NC) plots in the wheat phase to form a factorial of four cropping system treatments: W/C, R/C, W/NC and R/NC. Life stage transitions measured included seedbank persistence from October through March and from March through October, seedling recruitment, seedling survival to reproductive maturity, seeds produced per mature individual, and proportion of newly shed seeds not consumed by seed predators.

Cropping system effects on giant foxtail demography: III. Retrospective perturbation analysis. This study used a periodic matrix population model to focus on the following research questions: 1) Do the effects of residues from a red clover/spring wheat green manure on giant foxtail life stage transitions result in differential giant foxtail population growth rates when no form of external weed control is applied?, and 2) For which giant foxtail life stages did variation due to cropping system treatment contribute the most to overall treatment differences in giant foxtail population growth rate. This simulation used data for the FT/W and FT/R treatments (see description of article 1, above) in the 2000 field season to parameterize a matrix model of giant foxtail population dynamics. Retrospective

perturbation analysis of the matrix model was performed by weighting treatment differences for each giant foxtail life demographic parameter by the sensitivity of giant foxtail population growth rate to changes in those parameters (Caswell, 2001).

Prospective and retrospective perturbation analysis of cropping system effects on weed demography. This study used a periodic matrix population model to focus on the following research questions: 1) Do the effects of green manure and tillage timing on giant foxtail life stage transitions result in differential giant foxtail population growth rates when some form of external weed control is applied?, and 2) For which giant foxtail life stages did variation due to cropping system treatment contribute the most to overall treatment differences in giant foxtail population growth rate. This simulation used data for the FT/W. FT/R. ST/W and ST/R treatments (see description of article 1, above) in the 2000 and 2001 field seasons to parameterize a matrix model of giant foxtail population dynamics. Prospective perturbation analysis of the matrix model was performed by observing the proportional change in giant foxtail population growth rate when each demographic parameter was varied, in turn, while all other parameters were held constant (de Kroon et al., 2000). Retrospective perturbation analysis of the matrix model was performed as described for article 3.

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CHAPTER 2. CROPPING SYSTEM EFFECTS ON GIANT FOXTAIL

DEMOGRAPHY: I. GREEN MANURE AND TILLAGE TIMING

A paper submitted to Weed Science

Adam S. Davis and Matt Liebman

Abstract

Manipulation of cropping systems to improve weed management requires a better understanding of how crop- and soil-related factors affect weed life cycles. Our objectives were to determine how timing of primary tillage and use of legume green manures affect soil properties and giant foxtail demography in corn. We measured giant foxtail seed mortality and dormancy, seedling emergence and survival, and fecundity, in addition to soil phytotoxicity and chemical and physical properties, within the corn phase of a wheat-corn-soybean crop sequence in Boone, IA. Post-dispersal predation of giant foxtail seeds was measured in all three phases of the crop sequence. Wheat was grown either as a sole-crop ('W'), or as an intercrop with red clover ('R'), and residues from this phase were rototilled either in the fall ('FT') or in the spring ('ST'). There were consistent *Red clover* by *Tillage timing* interaction effects on giant foxtail demography, with the greatest changes in the ST/R treatment. Giant foxtail seedling emergence was 30% lower, and time to 50% emergence was more than 1 wk later, in the ST/R treatment than in the ST/W, FT/W and FT/R treatments. Nevertheless, fecundity of giant foxtail was more than 200% greater in the ST/R treatment than in the other treatments, due to suppressed early corn growth. A 200% increase in daily rates of post-dispersal seed predation in the R treatment, compared to daily seed predation rates in the W treatment, appeared to offset increased giant foxtail fecundity in corn under the ST/R treatment. The degree of soil phytotoxicity from red clover residues, changes in the amount of interference from the corn crop early in the growing season, and

differential suitability of crop residues in the different rotations as habitat for seed predators all contributed to changes in giant foxtail demography. High seed predation and low fecundity in the FT/R treatment suggest that population growth rate of giant foxtail should be lower in this treatment than in the other treatments. Success in cropping-system based weed prevention efforts will depend on improved selectivity, with greater suppressive effects on the weed and fewer negative consequences for the crop.

Nomenclature: giant foxtail, *Setaria faberi* Herrm. SETFA; corn, 'Pioneer 3512'. *Zea mays* L.; red clover, 'Cherokee'. *Trifolium pratense*. L.; soybean, 'IA 2039', *Glycine max* L.; spring wheat. 'Sharp'. *Triticum aestivum* L.

Key words: soil organic amendments, allelopathy, phytotoxicity, integrated weed management. post-dispersal seed predation. arthropod activity-density, seedbank dynamics. mortality, dormancy, seedling recruitment, fecundity.

Introduction

A key priority for integrated weed management research should be to identify cropping system characteristics that prevent weed population growth without sacrificing crop performance (Jordan 1996). This is an especially important goal in low-external-input (LEI) systems, where intensive herbicide use is not an option (Liebman and Davis 2000). Crop sequence, cultivar choice, tillage regime, use of soil organic amendments and other cropping system characteristics can strongly influence weed population densities (Buhler 1995; Buhler et al. 2001; Gallandt et al. 1998; Schreiber 1992). Although producers normally would not base their choice of cropping system entirely on its weed management merits, weed

prevention will benefit from increased understanding of cropping system effects on weed demography (Buhler 2002).

Two areas of limited knowledge hinder the intentional use of cropping systems in weed prevention efforts. First, whole weed life cycles are rarely the unit of study. Despite the proliferation of dynamic models that simulate management effects on weed populations (Bussan and Boerboom 2001 a, b: Blumenthal and Jordan 2001; Fernandez-Quintanilla et al. 2001; Gonzalez-Andujar and Fernandez-Quintanilla 1991; Jordan et al. 1995; Lindquist et al. 1995; Pino et al. 1998; Shea and Kelly 1998), there are few empirical studies of management effects on entire weed life cycles (Cousens and Mortimer 1995), and even fewer focused on weed life cycles in LEI systems (Misra et al. 1992; Ullrich 2000). Because weed life history traits often are highly variable in spatial (Burnside et al. 1996; Forcella et al. 1997), climatological (Benech-Arnold et al. 2000; Ullrich 2000; Weaver et al. 1988) and genetic (Rice and Mack 1991; Wang et al. 1995) dimensions, it may be difficult to reliably assess how management effects on individual demographic rates contribute to changes in weed population growth rate when parameter estimates are pooled from different study sites, years and populations. More unified demographic data sets are necessary to help identify robust weed prevention strategies for LEI systems.

A second research priority is to investigate how agronomic practices affect the ecological factors regulating weed demographic rates (Cousens and Mortimer 1995). The literature on ecological determinants of weed population dynamics is small, but growing (Arntz et al. 2000; Dekker and Hargrove 2002; Teasdale and Mohler 2000; Weaver et al. 1988). Few studies, however, attempt to link ecological effects of specific management practices with changes in weed population ecology in the field (Buhler and Mester 1991;

Menalled et al. 2000; Ullrich 2000). Such an approach is essential to the development of new weed prevention strategies for LEI farming systems.

This study begins a three-part series looking at 1) how much variation in giant foxtail demographic processes can be produced by manipulating cropping system characteristics (present article and Davis and Liebman "SUBMITTED"), and 2) how management effects on demographic rates contribute to overall changes in population growth rate for giant foxtail (Davis et al. "SUBMITTED"). The empirical studies estimate key giant foxtail demographic parameters under contrasting crop sequence, tillage and soil amendment practices. The empirical studies also look at associated soil and crop data to identify possible ecological mechanisms for management effects on giant foxtail demography.

We chose giant foxtail as our model organism for several reasons. First, giant foxtail is a widespread, economically important summer annual weed of the north central corn belt of the USA (Lindquist et al. 1999). Second, much demographic and biological information already exists for this species (Buhler and Hartzler 2001; Bussan and Boerboom 2001a; Dekker and Hargrove 2002; Fausey and Renner 1997; Forcella et al. 1997; Mester and Buhler 1991; Schreiber 1992). Third, the annual life history and ephemeral seedbank of giant foxtail (Buhler and Hartzler 2001) allowed us to avoid the demographic complexity of age and stage structured populations (Caswell 2001). Finally, low genetic diversity in giant foxtail populations (Wang et al. 1995) reduces one source of variability that could obscure management effects on demographic rates.

In previous work (Davis and Liebman 2001; Conklin et al. 2002), we observed reduced wild mustard growth and interference in sweet corn grown in soil amended with a red clover green manure and composted dairy manure compared to sweet corn grown without organic amendments but fertilized with synthetic N. Suppression of wild mustard emergence

and growth diminished with increasing time after amendment incorporation (Conklin et al. 2002). suggesting that tillage timing could play an important role in regulating soil amendment effects on weeds. Following these experiments, we wondered if soil organic amendments could be managed to reduce weed population growth.

Our objectives in the present study were to assess the effects of red clover green manure and tillage timing on soil properties and giant foxtail demographic rates in corn (Fig. 1.1). We tested two hypotheses. First, we predicted that including a red clover green manure in the wheat phase of a wheat-corn-soybean crop sequence would have negative effects on all stages of the giant foxtail life cycle. Second, we predicted that incorporation timing of red clover residues would interact with residue-mediated effects on giant foxtail demographic processes, such that more recently incorporated residues would have greater effects on demographic rates than less recently incorporated residues.

Materials and Methods

Field procedures

Management effects on giant foxtail life stage transitions and soil characteristics were measured in 2000 and 2001 within the context of a wheat-corn-soybean crop sequence. initiated in 1999, at the Iowa State University Agronomy and Agricultural Engineering Farm in Boone, IA. Soil type was Nicollet clay loam (Aquic Hapludolls), which was 35% sand. 45% silt. 30% clay, and which had a pH of 6.3 and 4.7 % organic matter. A split plot experimental design was used, comprising four replications of *Tillage timing* (fall vs. spring: main plot) and *Red clover* (red clover present or absent in wheat phase: subplot). Each replication was composed of two adjacent 3.8 m by 12.2 m main plots, each of which contained two 3.8 m by 6.1 m subplots.

Spring wheat was grown either as a sole crop ('W') or in an intercrop with red clover ('R'). Wheat was drilled in 17.8 cm rows at 112 kg seeds ha^{-1} and red clover, pre-inoculated with *Rhizobium*, was broadcast over subplots in the R treatment with a push-spreader at 16.8 kg seeds ha^{-1}. Corn was planted on April 27 in 0.76 m wide rows at 64.500 seeds ha^{-1} in 2000. Due to variable establishment in 2000, this procedure was modified in 2001 so that corn was planted on April 27 at 72,000 seeds ha^{-1} and then thinned on May 15 to a common density of 64.500 plants ha^{-1}. Soybean was planted in 0.76 m wide rows at 395.000 seeds ha^{-1}. Urea was broadcast at wheat planting at 60 kg N ha^{-1} and banded 2.5 cm from the corn row at 90 kg N ha^{-1} on June 5. Soil tests indicated that background soil levels of P and K were sufficient for wheat, corn and soybean production in 2000 and 2001 (Voss et al. 1999), so P and K fertilizers were not applied.

In late October of 1999 and 2000, compost was spread on subplots transitioning from the wheat to the corn phase at 25,000 kg C ha^{-1} (compost dry-weight C content was 11% in 1999 and 15% in 2000). Compost was obtained from a deep-bedded swine production system maintained at the Iowa State University Rhodes Research Farm (Honeyman and Kent 2001) and was aged for six months prior to application. After compost application, in late October, subplots assigned to the fall tillage treatment ('FT') were tilled to a depth of 20 cm with a power takeoff-driven rototiller; subplots assigned to spring tillage ('ST') were tilled in mid-April.

Soil and weather data

Corn subplots were sampled on June 1 of 2000 and 2001 for NO_3-N, P, K, OM, and pH. Fifteen soil cores per plot were taken to a depth of 20 cm and then bulked to form a composite sample. All analyses were performed by the Iowa State University Soil Testing

Laboratory using a Cd-reduction assay for NO_3-N, the Bray-1 method for P, a NH_4OAc extractant for K, a SMP buffer for pH, and the combustion method for percent organic matter (Brown et al. 1998).

Soil moisture, surface roughness, and bulk density were measured within the corn rotation phase in 2000 and 2001. Gravimetric water content was measured for subplots from bulked samples of fifteen 20-cm-deep cores at two dates during the first 4 wk of giant foxtail seedling recruitment. Surface roughness was measured on May 8 in 2000 and 2001 using a soil surface profiler (Harper et al. 1965). A series of twenty 7.5-cm-long metal pins passing through holes spaced 1 cm apart along the length of a 30 cm by 4 cm strip of plexiglass were allowed to fall perpendicular to the soil surface. Surface roughness was estimated as log_e of the variance of pin displacement.

Soil phytotoxicity during giant foxtail and corn seedling recruitment was assessed with bioassays (Dabney et al. 1996). Forty giant foxtail seeds or 10 corn seeds were spaced in a line 10 cm from the top edge of two 25 cm by 38 cm sheets of germination paper moistened with 20 mL distilled deionized H_2O. The field-moist equivalent of 100g dry weight soil, collected from subplots on May 10, 2000 and May 17, 2001, was spread in a 1 cm deep band starting 2 cm above, and extending 12 cm below, the line of seeds. A third, pre-moistened sheet of germination paper was placed on top of the soil layer, and the entire assembly was rolled up along the short axis, wrapped in plastic film and secured with rubber bands. Units were incubated vertically for 4 d at 25 C in the light (16 hrs.)/15 C in the dark (8 hrs.), after which the number of germinated seedlings was counted and seedling radicle length was measured.

Monthly air temperature and precipitation data for the Iowa State University Agronomy Research Farm for 1999, 2000 and 2001, as well as the 30 yr mean for each

month, were obtained from weather records made available through the Iowa State

University Ag Climate website (Todey and Herzmann 2002).

Recruitment, growth, fecundity and survival

Giant foxtail recruitment, growth, fecundity and survival were measured in the period

from the end of the wheat phase to the end of the corn phase. Post-dispersal predation of

giant foxtail seeds was measured in all phases of the crop sequence. Giant foxtail seeds were

planted in two different ways to examine different parts of the life cycle. For precise

measurements of weed seedbank dynamics, including seed mortality, dormancy and

recruitment, we used synthetic seedbanks. These consisted of 7.5 cm lengths of PVC pipe

30.5 cm in diameter driven into the soil, to which giant foxtail seeds were added at a rate of

5,480 seeds m^{-2}. To look at plant survival, growth and fecundity, we planted after-ripened

seeds (see below) at 50 seeds m^{-2} in rows parallel to, and offset 4 cm from, the corn row.

Seedbank dynamics

Ambient weed seedbank density was estimated in April 1999 by collecting thirty 2.5

cm diameter soil cores to a depth of 20 cm from each subplot, and then sieving and washing

soil to recover seeds. No giant foxtail seeds were found at the site. Mature giant foxtail seed

was collected in fall of 1999 and 2000 from a nearby location. Non-viable seed was removed

with an air-column separator, and remaining seed was tested for viability using a tetrazolium

dye test. Seed for row plantings of weeds was buried in the field in nylon stocking bags to

allow after-ripening under field conditions.

All synthetic seedbanks were interred in late October. To place PVC rings into

rototilled soil, we stepped on the rim of the rings until the lip protruded about 0.5 to 1 cm

above the soil surface. Pre-weighed seed aliquots were then mixed into the soil to a depth of 5 cm by hand. We chose this depth because giant foxtail germination declines rapidly below a depth of 5 cm (Mester and Buhler 1991). To drive PVC rings into untilled soil, we used a sharp spade to cut a trench around the perimeter of the ring and drove it to within 1 cm of its full depth with a hammer. Giant foxtail seed was then sprinkled into surface plant residue to simulate seed dispersal without tillage.

Seed mortality and physiological state. Two sets of synthetic seedbanks were interred in late October: one was used for determination of percentage seed mortality from October through March $(\mu_{s(w)})$, and the second was used for determination of recruitment and seed mortality from March through October $(\mu_{s(s)})$. We did not distinguish between causes of mortality. Prior to the onset of seed rain, synthetic seedbanks were covered with Agribon[©] AG-19[1], a breathable, translucent vegetable row cover, to exclude newly shed seed.

Seedbanks were removed from the soil in mid March after the soil had thawed but no germination had begun. Those to be used in determining $\mu_{s(w)}$ were stored at 5 C until seed extraction took place. Seedbanks for determining seedling emergence and $\mu_{s(s)}$ were moved to the field margin, after which spring tillage was performed. Immediately after tillage, seedbanks were mixed manually in bags to simulate rototilling action, and poured back into PVC rings placed between where corn rows would be located.

Seedbanks were processed by mechanically washing in an elutriator (Wiles et al. 1996), removing most of the remaining residue with an air column separator and then using a forceps to recover giant foxtail seeds. To test germinability, recovered seed were incubated for 96 h on moist filter paper at 30 C for 16 h (light) and 20C for 8 h (dark). Empty or rotted

seeds were counted as non-viable. Ungerminated, but intact, seeds that were classified as viable with a tetrazolium test (Peters 2000) were counted as dormant.

We calculated $\mu_{s(w)}$ as $[(N_{OCT}-N_{MAR})/N_{OCT}]$ x 100%, where N_{OCT} was the number of viable seeds added to the seedbank in late October and N_{MAR} was the number of viable seeds recovered from the seedbank in March. We calculated $\mu_{s(s)}$ as $[(N'_{MAR}-N_g-N'_{OCT})/N'_{MAR}]$ x 100%, where N'_{MAR} was an estimated value calculated from the treatment mean of seeds recovered in March. N_g was the total number of seedlings that emerged, and N'_{OCT} was the number of viable seeds recovered in early October.

Recruitment. Corn recruitment was measured as the density of plants within 3 m of row on May 12 and Sept. 9 in 2000 and 2001. Giant foxtail seedling recruitment from synthetic seedbanks was measured weekly from April 27 through June 21 in both 2000 and 2001. Two subsequent censuses indicated that giant foxtail seedling emergence had ceased by June 21. Emerged seedlings were counted and removed with sharp forceps, with minimal soil disturbance, to eliminate confounding between soil management and emergence-order effects on recruitment. Percent emergence (γ) was calculated for each plot as $[N_g/N'_{MAR}]$ x 100%. Thermal time to 50% seedling emergence (T_{50}) was calculated in two steps using nonlinear regression (Weaver et al. 1988). First, a four-parameter Gompertz function was fit to emergence data for each plot:

$$Y = ae^{-be^{-cx}} + d \qquad [1]$$

where Y = cumulative number of emerged seedlings m^{-2}, x = growing degree days (base 10 C), e represents the exponential constant 2.7471 and a, b, c and d are parameters to be estimated. All curve fits were generated using the least squares subroutine of Kaleidagraph[®]

v. 3.0.8 (Synergy Software 1998). and inspected for goodness of fit. Equation 1 described the progress of seedling recruitment well, with R^2 values between 0.91 and 0.99. In a second step. equation 1 was solved for x when Y was set equal to 50% of cumulative seedling emergence to give T_{50}.

Growth, survival and biomass production

Red clover shoot biomass and wheat stubble were clipped in late October of 1999 and 2000 from two 0.125 m^{-2} quadrats per subplot and dried at 65 C for 96 h. Red clover root biomass estimates were obtained by digging up 30 plants, calculating a root:shoot ratio. and applying this ratio to shoot biomass estimates from each experimental unit. Red clover total tissue C and N content were determined using a CHN combustion analyzer.

Giant foxtail seedlings emerging in row plantings were tagged with toothpicks and dead seedlings noted in weekly counts that continued through June 21. Height of giant foxtail and corn plants was measured every two weeks through late August. Plant survival (μ_p) was calculated as the percentage of seedlings that emerged by June 21 that were present as mature plants in late August. Giant foxtail shoot biomass was harvested within subplots in early September and dried at 35 C for 72 h before weighing.

Fecundity

In each experimental unit, a subset of mature giant foxtail panicles was enclosed in bags made of Agribon AG-19[®1]. Panicle length was regressed on seed number for bagged panicles. We used this method each year to convert measurements of giant foxtail panicle length in the rest of the experimental unit into an estimate of fecundity per plant (ϕ) and per

m^2 (f) (Forcella et al. 2000). Corn was hand harvested and adjusted to 13% moisture to determine yield.

Seed predation

Unlike the other demographic parameters in this study, $\mu_{s(pred)}$ was measured in the corn, soybean and wheat sole-crops and the wheat + red clover intercrop. Our rationale for this change in protocol was that seed predators would be more likely to be influenced by the different habitats represented by the different types of crop residue (Carmona and Landis. 1999; Carmona et al., 1999) than changes in soil characteristics associated with different green manure and tillage timing treatments.

Estimates of seed predation ($\mu_{s(pred)}$) and arthropod seed predator activity-density were obtained using the methods of Menalled et al. (2000). Every two weeks after onset of seed rain in August 2001 and 2002, 200 giant foxtail seeds were placed on a 10 cm by 10 cm piece of Bemis[2] humidifier filter that lay flush with the soil surface. As a control treatment, feeding stations were placed in fine wire mesh cages to determine seed losses when predators were excluded. Feeding stations were inspected daily and recovered before all seeds were removed. Daily probability of seed removal due to predation was calculated as $[1-R^{1/t}]-C$, where R = proportion of seeds remaining when the seed pads were recovered. t was the number of days the seed pads were left in the field, and C was the proportion of seeds removed in the control treatment (Mittelbach and Gross 1984).

Pitfall traps filled with a 10% aqueous solution of ethylene glycol were placed in the field on August 20-23 and September 7-10 in 2001 and 2002. Traps were covered to inactivate them between collection dates. Collected insects were frozen until they were identified with help from the Iowa State University Extension Entomology program.

Data analysis

We used both Cochran's test (Underwood 1997) and the modified Levene's test (Neter et al. 1996) to assess homogeneity of error variances. All variables passed both tests within and between years except for f, ϕ, $\mu_{s(s)}$ and $\mu_{s(w)}$, which failed the modified Levene's test across years. Square root (f and ϕ) and arcsine ($\mu_{s(s)}$) transformations (Neter et al. 1996) rectified this situation. No transformation worked for $\mu_{s(w)}$, therefore data for this variable were analyzed within years. Raw data are presented in tables for ease of interpretation.

All variables, with the exception of soil temperature and cumulative giant foxtail emergence, were analyzed with ANOVA models that included *Year*. *Tillage timing* and *Red clover* main effects and interaction terms using the GLM subroutine of SYSTAT® 9.0 (Wilkinson 1999). Means were separated by Fisher's Protected LSD test at $P<0.05$ (Gomez and Gomez 1984). Soil temperatures and cumulative giant foxtail seedling emergence were analyzed by repeated measures using the GLM: REPEAT subroutine of SYSTAT® 9.0 (Wilkinson 1999). No significant within-subjects treatment by date interactions existed. therefore only between-subjects effects are reported.

A path analysis of the *Red clover* and *Tillage timing* effects on ϕ was performed using methods described by Mitchell (2001). Data were analyzed across years, since the component variables in the models, including corn height. giant foxtail biomass and ϕ did not fail tests for homogeneity of error variances, nor were there year by treatment interactions for these variables. Candidate models including manifest and latent variables were compared using the RAMONA subroutine of SYSTAT 9.0 (Wilkinson 1999), and the most parsimonious hypothesis-testing model was chosen based on minimization of Akaike's information criterion (Burnham and Anderson 1998). Path coefficients were computed using the RAMONA subroutine of SYSTAT 9.0 (Wilkinson 1999).

Results and Discussion

Weather and green manure biomass

Weather varied substantially between study years (Table 1.1). In 1999, when the crop sequence was established, temperatures were warmer, and precipitation was much greater, than the 30-yr mean. The 2000 growing season had a warmer, drier spring than the 30-yr mean, followed by a very dry summer with average temperatures. Finally, the 2001 growing season had a cool, moist spring, followed by a dry summer with air temperatures close to the 30-yr mean.

Green manure biomass production followed annual precipitation patterns, with 40% more red clover biomass produced in the R treatment in 1999 than in 2000 (Table 1.2). Wheat shoot biomass was 25% greater in 1999 than in 2000 (P < 0.05), but did not differ between the W and R treatments. Consistent with the pattern of red clover biomass production, there was a *Year* by *Red clover* effect (P < 0.001) on total N content of residues from the wheat phase, with 12 and 8 times more N in the R treatment than in the W treatment in 1999 and 2000, respectively.

Soil properties

The only soil chemical properties that varied with the management treatments imposed in this experiment were NO_3-N and K on June 1 (Table 1.3). Soil NO_3-N levels in 2000 were greater in the FT/R treatment than in all other treatments, whereas soil NO_3-N levels in 2001 were greater in the ST/R treatment than in all other treatments. There was a small increase in soil K levels associated with spring tillage in both years. Soil P, pH and percent organic matter were unaffected by years or management treatments, with mean values (± se) of 37 ± 3, 6.6 ± 0.1, and 4.6 ± 0.2, respectively.

Soil moisture on April 12, prior to spring amendment incorporation, was subject to a
Year by *Tillage timing* by *Red clover* interaction (P < 0.05) (Table 1.3). In 2000, soil H_2O
content was 13% greater in the ST treatment than in the FT treatment, and 8% greater in the
R level than the W level of the ST treatment. In 2001, soil H_2O content was 21% lower in
the ST treatment than in the FT treatment. Snow was trapped by red clover residues in the
ST treatment in late winter of 2000, but not in 2001 (data not shown). Spring tillage of red
clover residues may have led to in drier soils in April 2001 due to prolonged transpiration
(Tiffin and Hesterman, 1998) and low winter precipitation.

There was a *Year* by *Tillage timing* by *Red clover* interaction on soil surface
roughness (Table 1.3): in 2000, surface roughness was greater in the ST treatment than in the
FT treatment, and greater in the R level than the W level of the ST treatment, whereas in
2001, there were no management effects on surface roughness. Surface roughness was
correlated with soil moisture prior to spring amendment incorporation in 2000 (r = 0.62, P <
0.001), but not in 2001 (r = 0.09, P = 0.63).

Bioassays showed a consistent inhibitory effect of *Red clover* on corn and giant
foxtail radicle length (Table 1.4). There was also a *Tillage timing* effect on corn radicle
length, with a 27% reduction in the ST treatment compared to the FT treatment. Since this
effect was averaged across soil amended with residues from both the wheat sole crop and the
wheat + red clover intercrop, these data suggest that phytotoxicity from wheat residues may
have been present in the field in mid May. A *Year* by *Tillage timing* by *Red Clover* effect (P
< 0.05) on giant foxtail germination in bioassays indicated that fresher residues were more
suppressive in 2000, but not in 2001 (Table 1.4).

Crop growth and weed demography

Interannual variation in most plant growth and demographic variables was greater than variation due to management effects (Tables 1.5, 1.6, 1.7 and 1.8). These data agree with those of Ullrich (2000), who found that weather far outweighed the effects of crop sequence, cultivation and tillage on the population dynamics of common lambsquarters (*Chenopodium album* L.), low cudweed (*Gnaphalium uliginosum* L.), birdsrape mustard (*Brassica rapa* L.), wild mustard (*Brassica kaber* (D.C.) L.C. Wheeler), and wild radish (*Raphanus raphanistrum* L.) in Maine potato cropping systems. We did, however, see management effects on plant growth and demography pertinent to our hypotheses.

Seed mortality and dormancy

Due to non-constant error variance across years, $\mu_{s(w)}$ was analyzed within years. There was a *Tillage timing* by *Red clover* interaction effect (P < 0.05) on $\mu_{s(w)}$ in 2000 (Table 1.5): $\mu_{s(w)}$ was 56% greater in the FT/R treatment, which was similar to the ST/W and ST/R treatments, than in the FT/W treatment. This suggests that incorporating fresh red clover residues into the soil constitutes a seed mortality factor comparable to, but not greater than, exposure to the elements, pathogens and seed predators. In 2001, there was a *Tillage timing* main effect (P < 0.05) on $\mu_{s(w)}$, which was 25% greater in the ST treatment than in the FT treatment. Greater values of $\mu_{s(w)}$ in the ST treatment than in the FT treatment were consistent with the observation that seed mortality factors tend to be strongest at the soil surface (Cousens and Mortimer 1995).

Less variation was observed for $\mu_{s(s)}$ than for $\mu_{s(w)}$. There was a *Year* by *Tillage timing* effect (P < 0.05) on $\mu_{s(s)}$, which did not differ between tillage treatments in 2000, but which was 39% greater in the FT treatment than in the ST treatment in 2001 (Table 1.5). It is

unclear why $\mu_{s(s)}$ should been affected by tillage timing, since seeds in both the FT and ST treatments were distributed evenly throughout the top 5 cm of soil during the period from March through October and therefore exposed equally to mortality factors.

There was a *Year* by *Tillage timing* by *Red clover* interaction effect on d_w (P < 0.05). In 2000, d_w was 13 and 29% greater in the FT/R and ST/R treatments, respectively, than in the FT/W and ST/W treatments, which were similar (Table 1.5). In 2001, d_w was 38% greater in the FT treatment than in the ST treatment, and 38% greater in the R treatment than in the W treatment. Percentage dormancy of seeds recovered in October (d_s) did not differ between any of the management treatments.

Seedling recruitment and mortality

Corn. There was a *Year* by *Tillage timing* by *Red clover* effect (P < 0.05) on corn density both early (Table 1.6) and late (Table 1.7) in the growing season. Spring tillage was associated with lower corn densities in both 2000 and 2001 than fall tillage. Red clover was associated with reduced corn densities in the ST treatment in 2001, but not in 2000.

Giant foxtail. Repeated measures analysis of cumulative giant foxtail seedling emergence revealed a *Tillage timing* by *Red clover* interaction (Figure 1.2). Cumulative emergence was 30% lower in the ST/R treatment than in the FT/R, FT/W and ST/W treatments. There was also a *Year* by *Tillage timing* by *Red clover* effect on γ(P < 0.05) (Table 1.6). In 2000, γ was lowest in the FT/W and ST/R treatments, intermediate in the FT/R treatment and greatest in the ST/W treatment. In 2001, γ was 25% lower in the ST/R treatment than in the FT/R, FT/W and ST/W treatments, which were similar. Red clover was associated with a decrease in recruitment only in the spring tillage regime.

Thermal time to 50% emergence followed a pattern similar to that for seedling emergence (Table 1.6). In 2000, the R treatment was associated with delayed T_{50} compared to the W treatment, but the delay was greater in the ST treatment (40 GDD_{10}) than in the FT treatment (30 GDD_{10}). In 2001, red clover residues were associated with a delay in T_{50} in the ST treatment, but not in the FT treatment.

Mortality of giant foxtail seedlings was 57% and 40% lower in the ST treatment than in the FT treatment in 2000 and 2001, respectively ($P < 0.05$). We speculate that the reduction in giant foxtail mortality associated with spring tillage may have been due to reduced early corn growth in the ST treatment compared to the FT treatment (Table 1.7).

Growth and fecundity

Corn. Both spring tillage and red clover residues were associated with reduced corn height early in the growing season (Table 1.7). *Tillage timing* modified the effect of *Red Clover* on corn height at June 5 and 22 ($P < 0.05$), such that corn height was reduced within the ST/R, but not the FT/R, treatment. Despite early height reductions, corn yield was unaffected by *Red clover* (Table 1.7). Corn yield was lower in the ST than the FT treatment (Table 1.7).

Giant foxtail. Crop and soil management did not influence giant foxtail height at June 5 (Table 1.8). There was, however, a *Tillage timing* by *Red clover* interaction effect ($P < 0.05$) on giant foxtail height at June 22, which was greater in the ST treatment than the FT treatment, and greater in the R level than the W level of the FT treatment (Table 1.8). There was also a *Tillage timing* by *Red clover* interaction effect on giant foxtail shoot biomass and

fecundity ($P < 0.05$). These variables were greater within the ST treatment than the FT treatment, and were greater in the R than in the W level of the ST treatment.

We were interested in knowing whether *Tillage timing* and *Red clover* effects on giant foxtail biomass and seed production were due to changes in interference from the corn crop or due to direct treatment effects on giant foxtail. We tested these alternate explanations using path analysis, within tillage treatments, of red clover effects on corn height at June 5 and mature giant foxtail biomass, and the relationship of these intermediate variables to giant foxtail seed production (Figure 1.3).

In both the FT and the ST treatments, corn height, giant foxtail biomass and giant foxtail seeds m^{-2} formed a strong causal pathway. There was, however, only one causal link between red clover and this pathway: the R treatment was negatively correlated ($r = -0.24$, $P < 0.05$) with corn height on June 5. The large value of latent variable U_1 indicates that there was much unexplained variation in corn height in both models. Nonetheless, these analyses suggest that reduced interference from corn was the more plausible explanation for increased giant foxtail growth and fecundity in the ST and R treatments compared to the FT and W treatments. Other work has also shown limitation of giant foxtail fecundity by early corn growth (Campbell et al. 1981; Perera and Hartwig 1980).

Post-dispersal seed predation

Giant foxtail daily seed removal rate ($\mu_{s(pred)}$) in the wheat phase increased from mid-August through late September and then declined through mid-October (Fig. 1.4). At the first four sampling dates in 2001, $\mu_{s(pred)}$ was greater in the wheat + red clover intercrop than in the wheat sole crop (Fig. 1.4), after which, $\mu_{s(pred)}$ was similar for the two crops. The temporal pattern of seed predation was similar for the corn and soybean phases (data not

shown). During the period of September 26-29. 2001. $\mu_{s(pred)}$ was lowest in soybean (5% of

seeds eaten d^{-1}), intermediate in corn (18% of seeds eaten d^{-1}) and wheat (25% of seeds eaten

d^{-1}). and greatest in the wheat + red clover intercrop (58% of seeds eaten d^{-1}) (Fig. 1.5).

During the period of September 7-10. 2001. activity-density of field crickets (*Gryllus*

pennsylvanicus Burmeister) in the wheat + red clover intercrop was more than twice that in

corn and wheat. but there were no differences in the activity-density of ground beetles

(Coleoptera: Carabidae) in the three crops (Fig. 1.6). This suggests that field crickets may

have been at least partially responsible for the high rates of giant foxtail seed predation

observed in the wheat + red clover intercrop compared to the corn and wheat crops. In

laboratory feeding studies. adult female and male field crickets ate an average of 26 and 9

giant foxtail seeds. respectively. in a 24 h period (Carmona et al. 1999). The ground beetle

species most often found in our pitfall traps, *Harpalus pennsylvanicus* De Geer. is also

known to be an important seed predator in agricultural systems (Carmona and Landis 1999).

We believe that differences in habitat quality may have been responsible for varying

activity densities of seed predators in the different phases of the crop sequence. Following

harvest. wheat. corn and soybean all had relatively low amounts of residue on the soil

surface. whereas large amounts of live red clover biomass remained (6.0 ± 0.8 x 10^3 kg red

clover shoot biomass ha^{-1} was harvested in late October). Our results corroborate previous

studies in which habitat diversification through refuge strips, cover crops and hedgerows

promoted greater post-dispersal seed predation and greater activity-density of arthropod seed

predators (Carmona and Landis 1999; Menalled et al. 2000).

Plant-soil interactions

The fixed root habit and soil seedbank of annual plants render them highly responsive to soil characteristics. Here, we examine patterns of variation in soil variables and identify possible links to plant growth and demography. Since soil properties were not controlled, but were measured as dependent variables of crop and soil management, the proposed links are speculative.

Changes in soil NO_3-N and K, the only soil chemical properties that varied with management (Table 1.3), did not appear to be important factors determining giant foxtail demographic parameters in this study. Red clover contributions to soil NO_3-N were minor, and overall soil NO_3-N levels prior to urea application were insufficient to support commercially acceptable corn yields without additional N fertilizer (Voss et al., 1999). Background soil K levels were in the "very high" range for corn production (Voss et al., 1999), and the increase in K levels associated with spring tillage was quite small (3% in 2000 and 8% in 2001).

Soil moisture and soil surface roughness, the only soil physical properties affected by management in this study, have been linked to variation in dormancy and seedling recruitment (Benech-Arnold et al. 2002; Harper et al. 1965). The effects of Red clover and Tillage timing on d_w (Table 1.5) may have been due in part to differential soil moisture during the winter months, since d_w was positively correlated with soil H_2O content prior to spring tillage (r = 0.72, P < 0.001). Increased soil moisture content would have decreased the amount of gaseous O_2 in soil pores, thereby decreasing the after-ripening dose received by dormant giant foxtail seeds in the soil seedbank (Dekker and Hargrove, 2002) and increasing d_w.

Soil surface roughness followed a pattern in 2000 that matched *Tillage timing* by *Red clover* effects on seedling recruitment: surface roughness was greater in the ST treatment than in the FT treatment, and greater in the R level than the W level of the ST treatment (Table 1.3). In controlled environment experiments, Pareja and Staniforth (1985) found that soil aggregate size (a correlate of surface roughness) interacted with irrigation frequency so that larger aggregates inhibited giant foxtail recruitment more in drier soil. Surface roughness on May 8 and giant foxtail recruitment were negatively correlated ($r = -0.63$, $P < 0.001$) in 2000, but were unrelated in 2001. Soil moisture on May 10 was 19% lower in 2000 than 2001 ($P < 0.05$), suggesting that under drier soil conditions in 2000, management effects on surface roughness may have been a factor in seedling recruitment.

Bioassays using field soil collected in mid May (Table 1.4) suggest that phytotoxicity from both red clover and wheat residues may have negatively affected seedling recruitment and early growth under field conditions. Despite consistent *Tillage timing* by *Red clover* interaction effects on corn and giant foxtail recruitment and early growth in the field (Tables 1.6, 1.7 and 1.8), bioassays did not show consistent *Tillage timing* by *Red clover* interaction effects on corn or giant foxtail germination and radicle growth. This suggests that the *Tillage timing* by *Red clover* effects on giant foxtail recruitment, growth and fecundity observed in the field may not have been due solely to the effects of red clover phytotoxicity, but may have been influenced by other factors, such as reduced corn recruitment and growth due to spring tillage.

Lower corn yields in the ST treatment may have resulted from poor stand establishment associated with the cool soil temperatures that result when large amounts of crop residue are left to overwinter on the soil surface (Drury et al. 1999; Kaspar and Erbach 1998). Alternatively, phytotoxic effects of wheat residue on corn recruitment may have been

more pronounced in the ST treatment than in the FT treatment. We do not have data to assess the first hypothesis, but bioassay results support the latter one.

Identifying mechanisms by which associated changes in soil properties affected seed mortality was beyond the scope of this study. There are many putative abiotic and biotic factors affecting the mortality of seeds in the soil seedbank (Cousens and Mortimer 1995), and there remains much work to do in determining how agronomic management practices affect ecological determinants of seed mortality.

Management implications

The goal of this experiment was to improve understanding of how cropping system characteristics, such as use of green manures and timing of primary tillage, can be manipulated to inhibit weed population growth. We drew three main conclusions related to cropping system management from this study.

First, we found that intercropping wheat with red clover during the wheat phase of a wheat-corn-soybean crop sequence reduced successful transitions between some giant foxtail life stages, and increased successful transitions between others. The red clover green manure was associated with greater giant foxtail seed losses to predation and overwinter mortality, and decreased giant foxtail germination, yet there was also a large increase in giant foxtail seed production associated with the ST/R treatment. We weighed management effects on giant foxtail demographic rates against one another using a matrix simulation model (Davis et al. "SUBMITTED"), and found that management effects on seed predation made the largest contribution to changes in population growth rate. The model projected that use of red clover green manure would lead to decreased rates of giant foxtail population growth under fall tillage.

Second, we found that tillage timing had direct and indirect effects on weed demography by regulating the degree of residue-mediated weed suppression, and by influencing corn growth and interference against the weed. Residue-mediated weed suppression was stronger with spring tillage, presumably because of shorter residue decomposition time (Breland 1996). Spring tillage, however, inhibited corn recruitment and early growth, thereby reducing the strength of corn interference against giant foxtail.

Third, we found that levels of interannual variation in giant foxtail demographic parameters greatly exceeded the amount of variation created by the different management practices studied here. Stochastic simulations of weed population dynamics under these and other management scenarios will help determine if cropping system effects on weed demographic parameters contribute enough to changes in weed population growth rate across growing seasons to constitute important cropping system design factors.

One concern we have is the relatively low selectivity observed in residue-mediated suppression of crop and weed recruitment and growth. Not only giant foxtail, but corn recruitment and growth, were consistently suppressed in the ST/R treatment. The large increase in giant foxtail fecundity in this treatment due to release from early corn interference was unacceptable, especially if the goal was weed prevention. It is possible that the ST/R treatment, which showed the greatest suppression of giant foxtail recruitment, may be more suitable for a vegetable production system. In high-value cropping systems, transplanting large seedlings into the field is a routine practice and would render the crop less susceptible to residue-mediated suppression and more capable of interfering with weed growth and seed production.

The effort to develop integrated suites of management tactics for weed prevention in LEI production systems is in its beginning stages. Future studies along these lines will

benefit from treating demographic rates for the entire weed life cycle as an emergent property of climatological and management effects on the plant growth environment.

Source of Materials

[1] Agribon AG-19 floating row cover, PGI Nonwovens, 111 Excellence Way. Mooresville, NC 28115.

[2] Bemis 4035 humidifier filter belt. Bemis Manufacturing Company. 300 Mill Street. P.O. Box 901. Sheboygan Falls, Wisconsin 53085-0901.

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Figure captions

Fig. 1.1. Flow chart of giant foxtail life cycle. Boxes represent state variables and valves

represent rate variables. Symbols representing demographic parameters are as follows: $\mu_{s(w)}$

= % seed mortality from October through March. $\mu_{s(s)}$ = % seed mortality from March

through October. γ = % emergence, μ_p = % plant mortality from June through September. ω =

seeds produced per plant, and $\mu_{s(pred)}$ = % seed mortality due to post-dispersal seed predation.

Fig. 1.2. Giant foxtail seedling emergence from synthetic seedbanks under contrasting crop

sequence and tillage timing treatments. Treatment abbreviations are the same as described in

Table 1.3. Data were analyzed using repeated measures analysis of variance. Vertical bars

represent ± one standard error of the mean of four replicates.

Fig. 1.3. Path analysis of tillage timing and red clover effects on crop and weed factors

related to weed seed production. The relative strength of causal pathways is represented by

the thickness of solid arrows, and the symbols *, ** and *** represent the significance of

path coefficients at the P<0.05, 0.01, and 0.001 levels, respectively. Non-significant

pathways are represented by dotted arrows. Latent variables, or unexplained sources of

variation, are represented by U_n.

Fig. 1.4. Post-dispersal predation of giant foxtail seeds at five dates during the period from

Aug. 15. 2001, through Oct. 18. 2001, in a wheat sole-crop and a wheat + red clover

intercrop. Predation rate was expressed as mean percentage of seeds (out of 200) removed

per day from feeding stations. Vertical bars represent ± one standard error of the mean of

four replicates. The symbols '*' and '**' represent means that are significantly different at

the P < 0.05 and P < 0.01 levels, respectively.

Fig. 1.5. Post-dispersal predation of giant foxtail seeds from 26-29 Sept., 2001 in soybean,

corn, wheat and a wheat + red clover intercrop. Predation rate was expressed as mean

percentage of seeds (out of 200) removed per day from feeding stations. Vertical bars

represent ± one standard error of the mean of four replicates. Means identified by different

lower case letters were different as determined by a Fisher's Protected $LSD_{0.05}$ multiple

comparison test.

Fig. 1.6. Activity-density of field cricket (*Gryllus pennsylvanicus* Burmeister) and ground

beetles (Coleoptera: Carabidae) in corn and wheat sole-crops and a wheat + red clover

intercrop, measured in pitfall traps from 7-10 Sept., 2001. Vertical bars represent ± one

standard error of the mean of four replicates. Within insect groups, means identified by

different lower case letters were different as determined by a Fisher's Protected $LSD_{0.05}$

multiple comparison test.

Table 1.1. Monthly mean air temperature and precipitation in Boone. IA, for 2000, 2001 and 30-yr. average from 1970-2000.

Month	Mean air temperature			Mean precipitation		
	2000	2001	30-yr mean	2000	2001	30-yr mean
	C			mm		
March	6.6	-6.7	2.4	11	0	52
April	11.0	11.8	9.9	21	85	89
May	18.2	16.0	16.3	120	159	110
June	20.4	21.0	21.3	104	42	127
July	22.4	24.2	23.3	72	43	112
August	22.9	22.6	22.0	34	64	110
September	19.7	16.3	17.9	26	134	78

Table 1.2. Biomass and tissue N content of a wheat sole-crop or wheat + red clover intercrop sampled in October 1999 and 2000 in Boone, IA.

Treatment	Red clover root + shoot residue		Wheat shoot residue		Residue total N content[a]	
	1999	2000	1999	2000	1999	2000
	10^3 kg ha^{-1}				kg N ha^{-1}	
W[b]	0 a[c]	0 a	2.0	1.4	9 a	11 a
R	4.9 b	3.5 b	1.5	1.4	111 b	89 b
SE	0.6	0.5	0.2	0.1	2	2

[a] Total N content includes wheat and (where applicable) red clover residues.

[b] Abbreviations: 'W' = wheat sole-crop, 'R' = wheat + red clover intercrop

[c] Within columns for each year, means followed by different lower case letters were different as determined by a Fisher's Protected LSD$_{0.05}$ multiple comparison test.

Table 1.3. Selected soil chemical and physical properties measured within a corn crop grown under management treatments varying in tillage timing and crop sequence.

Treatment	NO₃-N[a]		P		K		Gravimetric water content				Surface roughness	
							April 12		May 10			
	2000	2001	2000	2001	2000	2001	2000	2001	2000	2001	2000	2001
	ppm						%				$\log_e(mm^2)$	
FT/W[b]	10 a[c]	8 a	43	36	130	110	23 a	19 b	21	25	1.0 a	1.6
FT/R	15 b	9 a	36	33	130	120	23 a	20 b	20	25	1.0 a	1.2
ST/W	10 a	8 a	43	42	130	130	25 b	16 a	21	25	1.5 b	1.6
ST/R	11 a	13 b	44	33	140	120	27 c	14 a	22	26	1.9 c	1.4
SE	0.7	0.6	3	2	2	2	0.8	1.0	0.6	0.5	0.1	0.2
Main effect: Tillage timing												
FT	12	11	39	34	130 a	115 a	23	19	21	25	1.0	1.4
ST	9	10	43	38	135 b	125 b	26	15	21	26	1.7	1.5
Main effect: Red clover												
W	10	8	43	39	130	120	24	17	21	25	1.3	1.6
R	13	11	40	33	135	120	25	17	21	26	1.5	1.3

[a] Soil NO₃-N, P and K were measured on June 1, 2000 and 2001, and surface roughness was measured on May 8, 2000 and 2001.

[b] Abbreviations: 'FT' = fall tillage, 'ST' = spring tillage, 'W' = wheat sole crop prior to corn phase, 'R' = wheat + red clover intercrop prior to corn phase.

[c] Within columns for each year, means followed by different lower case letters were different as determined by a Fisher's Protected LSD₀.₀₅ multiple comparison test.

Table 1.4. Bioassay of phytotoxic properties of soil collected[a] within a corn crop grown under management treatments varying in tillage timing and crop sequence.

Treatment	Radicle length			Germination		
	SETFA		Corn	SETFA		Corn
	2000	2001	2001	2000	2001	2001
	— mm —			— % —		
FT/W[b]	21	20	84	37 b	45 b	99
FT/R	14	13	70	39 b	33 a	100
ST/W	18	19	70	42 b	50 b	100
ST/R	11	12	43	26 a	33 a	100
SE	0.9	1.1	4.8	2.4	2.3	0.2
Main effect: Tillage timing						
FT	17	17	77 b	38	39	99
ST	15	16	56 a	34	41	100
Main effect: Red clover						
W	19 b[c]	20 b	77 b	39	47	99
R	13 a	13 a	57 a	33	33	100

[a] Soil was collected on May 10, 2000 and May 17, 2001.

[b] Abbreviations follow the pattern described in Table 1.3.

[c] Within columns for each year, means followed by different lower case letters were different as determined by a Fisher's Protected $LSD_{0.05}$ multiple comparison test.

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Table 1.5. Giant foxtail seed mortality and dormancy measured within a corn crop grown under management treatments varying in tillage timing and crop sequence.

	Mortality				Dormancy			
	Oct.-Mar. ($\mu_{s(w)}$)		Mar.-Oct. ($\mu_{s(s)}$)		Mar. (d_w)		Oct. (d_s)	
Treatment	2000	2001	2000	2001	2000	2001	2000	2001
				%				
FT/W[a]	9 a[b]	38	50	41	57 a	10 b	40	11
FT/R	14 b	41	44	43	63 b	14 c	37	13
ST/W	13 b	50	46	29	55 a	6 a	34	7
ST/R	15 b	49	44	31	72 c	9 b	31	7
SE	1.1	1.9	1.2	2.5	1.9	1.0	2.2	1.4
Main effect: Tillage timing								
FT	12	40 a	47	42 b	60	12	39	12
ST	14	50 b	45	30 a	64	8	33	7
Main effect: Red clover								
W	11	44	48	35	56	8	37	9
R	15	46	44	37	68	12	34	10

[a] Abbreviations follow the pattern described in Table 1.3.

[b] Within columns for each year, means followed by different lower case letters were different as determined by a Fisher's Protected $LSD_{0.05}$ multiple comparison test.

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Table 1.6. Giant foxtail and corn recruitment within a corn crop grown under management treatments varying in tillage timing and crop sequence.

	SETFA recruitment				SETFA plant		Corn density	
	Cumulative $(\gamma)^a$		T_{50}^b		mortality $(\mu_p)^c$		May 12	
Treatment	2000	2001	2000	2001	2000	2001	2000	2001
	— % —		GDD_{10}		—%—		10^3 plants ha^{-1}	
FT/W	15 a^d	33 b	240 a	170 a	8.9	5.3	62 b	70 b
FT/R	18 ab	33 b	270 b	170 a	8.2	6.0	65 b	73 bc
ST/W	19 b	29 b	240 a	170 a	4.9	3.2	44 a	78 c
ST/R	14 a	24 a	280 c	220 b	2.6	3.6	41 a	62 a
SE	1.0	1.7	4	5	1.8	1.0	3.0	2.0
Main effect: Tillage timing								
FT	17	33	260	170	8.6 b	5.7 b	64	72
ST	17	27	260	200	3.7 a	3.4 a	43	70
Main effect: Red clover								
W	17	31	240	170	6.9	4.2	53	74
R	16	29	280	200	5.4	4.8	53	68

[a] Seedling recruitment through June 21, when new emergence had ceased, expressed as the percentage of viable seeds in March giving rise to established seedlings.

[b] Abbreviations: T_{50} = growing degree days (base 10 C) required to reach 50% emergence: treatment abbreviations the same as described in Table 1.3.

[c] Seedling mortality was expressed as (number of mature plants in late August)/(number of seedlings that had emerged in row plantings by June 21) x 100%.

[d] Within columns for each year, means followed by different lower case letters were different as determined by a Fisher's Protected LSD$_{0.05}$ multiple comparison test.

Table 1.7. Growth and yield of a corn crop grown under management treatments varying in tillage timing and crop sequence.

| | Corn height | | | | Corn population at harvest | | Corn yield | |
| | June 5 | | June 22 | | | | | |
Treatment	2000	2001	2000	2001	2000	2001	2000	2001
	cm				10^3 plants ha^{-1}		10^3 kg ha^{-1}	
FT/W[a]	63 c[b]	33 c	140 c	70 b	61 b	64 b	15.3	15.3
FT/R	61 c	34 c	140 c	73 b	62 b	65 b	15.3	15.3
ST/W	46 b	29 b	120 b	70 b	49 a	66 b	12.8	13.4
ST/R	42 a	23 a	110 a	60 a	46 a	60 a	12.2	12.8
SE	0.7	1.3	2	1	1.7	0.6	0.6	0.5
Main effect: Tillage timing								
FT	62	34	140	70	62	65	15.3 b	15.3 b
ST	44	26	120	65	47	63	12.8 a	13.1 a
Main effect: Red clover								
W	55	31	130	70	55	65	14.0	14.4
R	51	29	125	67	54	63	13.8	14.0

[a] Abbreviations follow the pattern described in Table 1.3.

[b] Within columns for each year, means followed by different lower case letters were different as determined by a Fisher's Protected LSD$_{0.05}$ multiple comparison test.

Table 1.8. Giant foxtail growth and fecundity within a corn crop grown under management treatments varying in tillage timing and crop sequence.

Treatment	SETFA height				SETFA biomass		SETFA fecundity			
	June 5		June 22				ϕ^a		f	
	2000	2001	2000	2001	2000	2001	2000	2001	2000	2001
	——— cm ———				g m^{-2}		10^3 sds. plt.$^{-1}$		10^3 sds. m^{-2}	
FT/W[b]	3.5	9.9	16 a[c]	26 a	6 a	190 a	0.1 a	0.9 a	0.5 a	30 a
FT/R	2.8	9.9	21 b	30 b	6 a	210 a	0.2 a	1.1 a	0.6 a	34 a
ST/W	2.4	9.5	25 b	33 b	22 b	300 b	0.6 b	1.3 a	3.4 b	47 b
ST/R	2.2	9.9	23 b	31 b	74 c	460 c	2.4 c	2.0 b	12.1 c	72 c
SE	0.2	0.4	0.8	0.8	8	28	0.2	0.2	1.6	3.7
Main effect: Tillage timing										
FT	2.9	9.9	19	28	6	200	0.2	1.0	0.5	32
ST	2.5	9.7	24	32	48	380	1.5	1.6	7.8	59
Main effect: Red clover										
W	3.1	9.7	21	30	14	240	0.4	1.1	1.9	38
R	2.3	9.9	22	31	40	340	1.3	1.5	6.3	53

[a] The symbols ϕ and f represent giant foxtail fecundity in seeds per plant and seeds per m^2, respectively.

[b] Treatment abbreviations follow the pattern described in Table 1.3.

[c] Within columns for each year, means followed by different lower case letters were different as determined by a Fisher's Protected $LSD_{0.05}$ multiple comparison test.
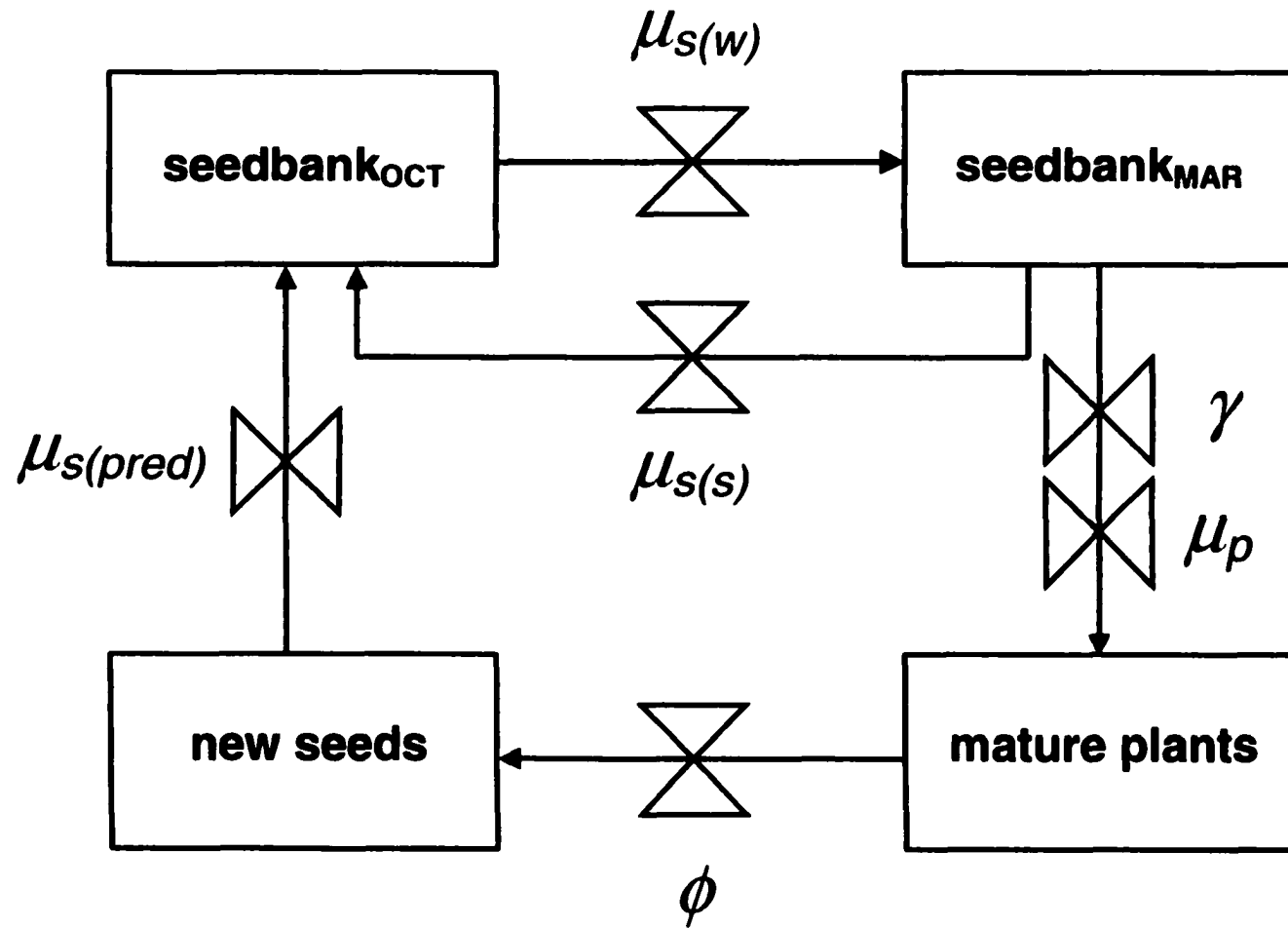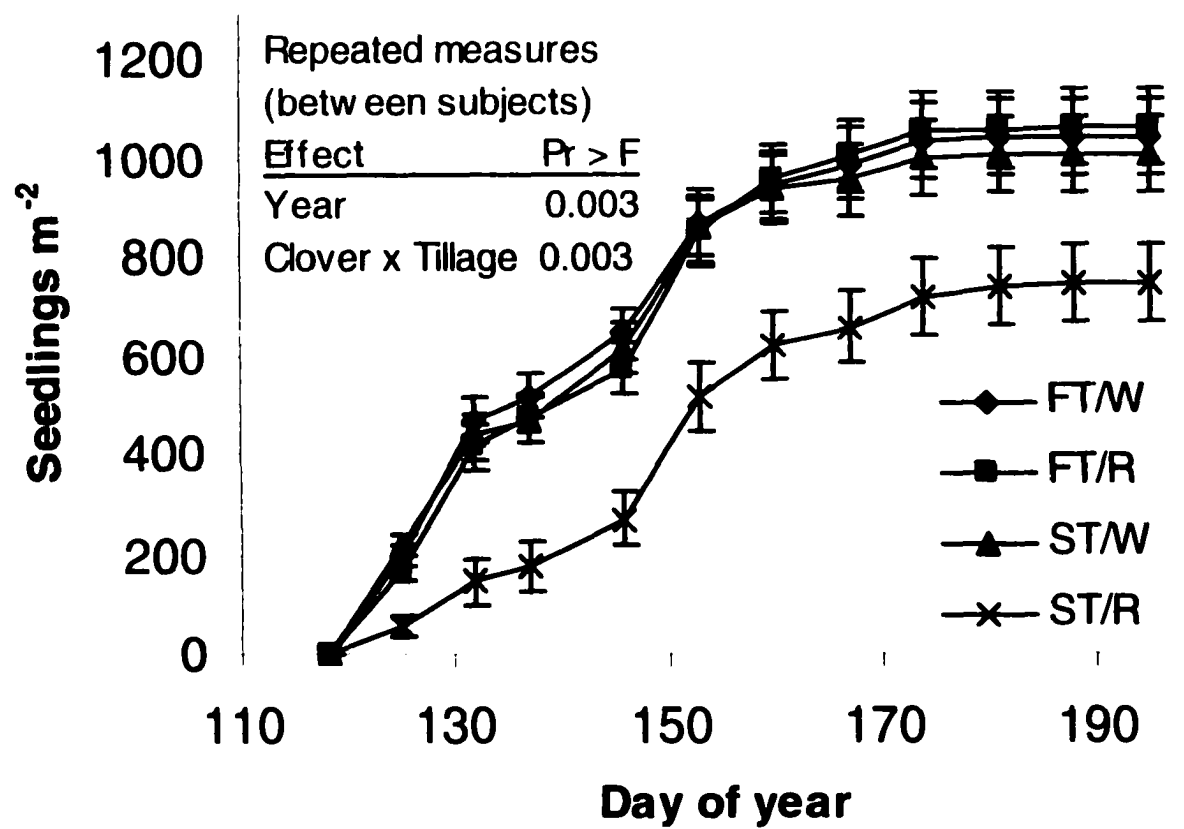
$\mu_{S(w)}$

seedbank$_{OCT}$

seedbank$_{MAR}$

$\mu_{S(pred)}$

$\mu_{S(s)}$

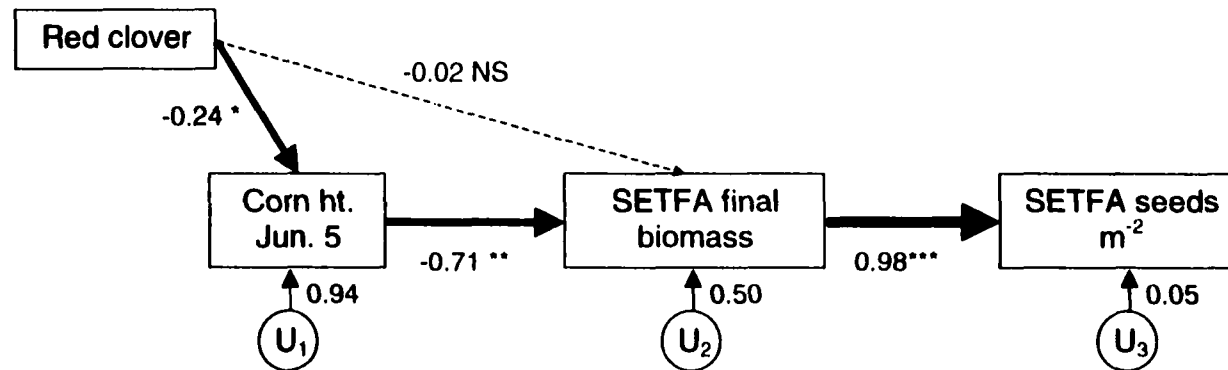γ

μ_p

new seeds

mature plants

ϕ

Fig. 1.1

Fig. 1.2

A. Spring tillage

B. Fall tillage

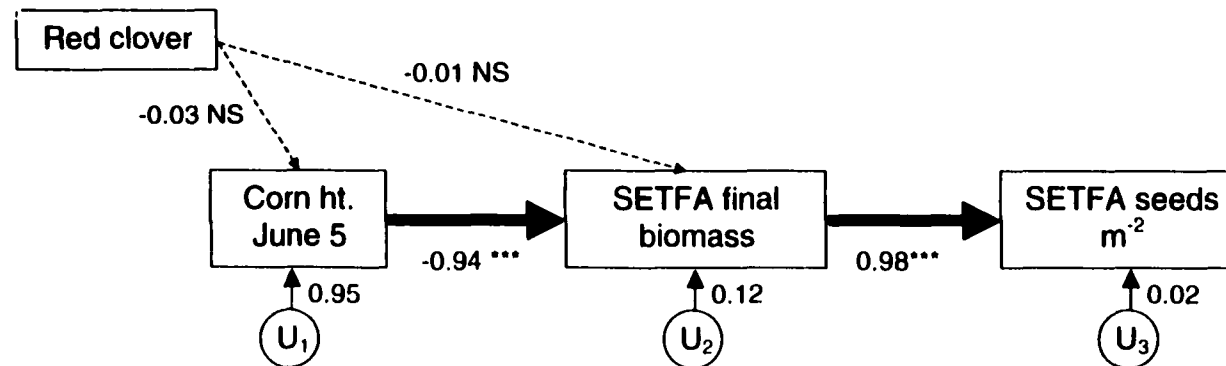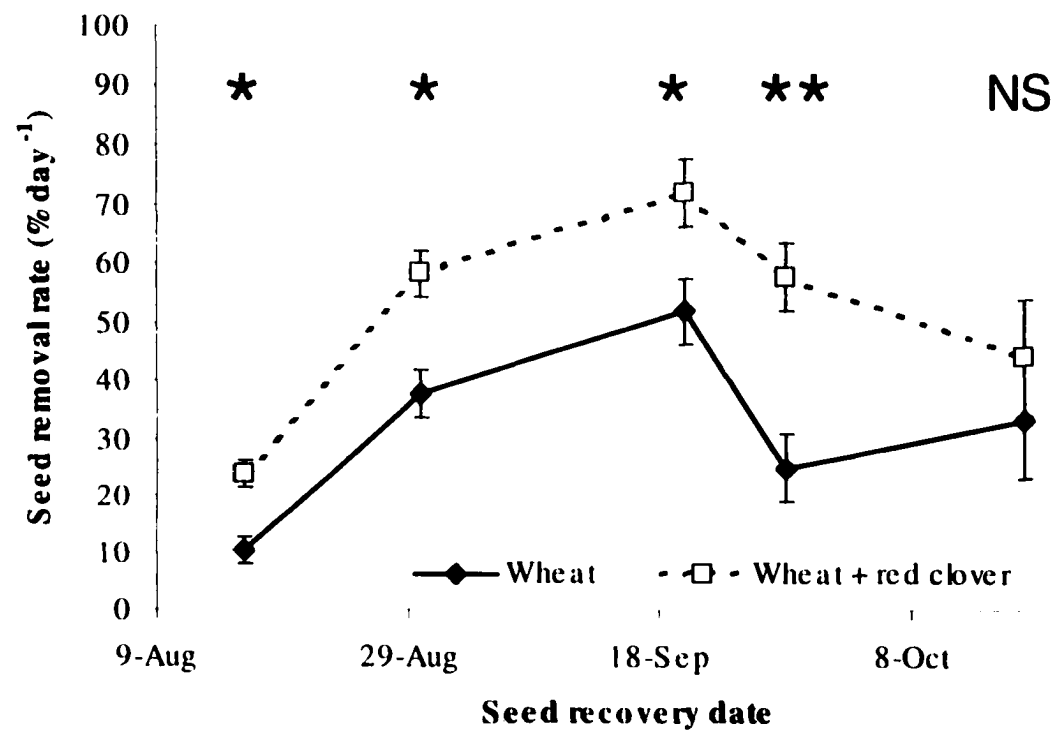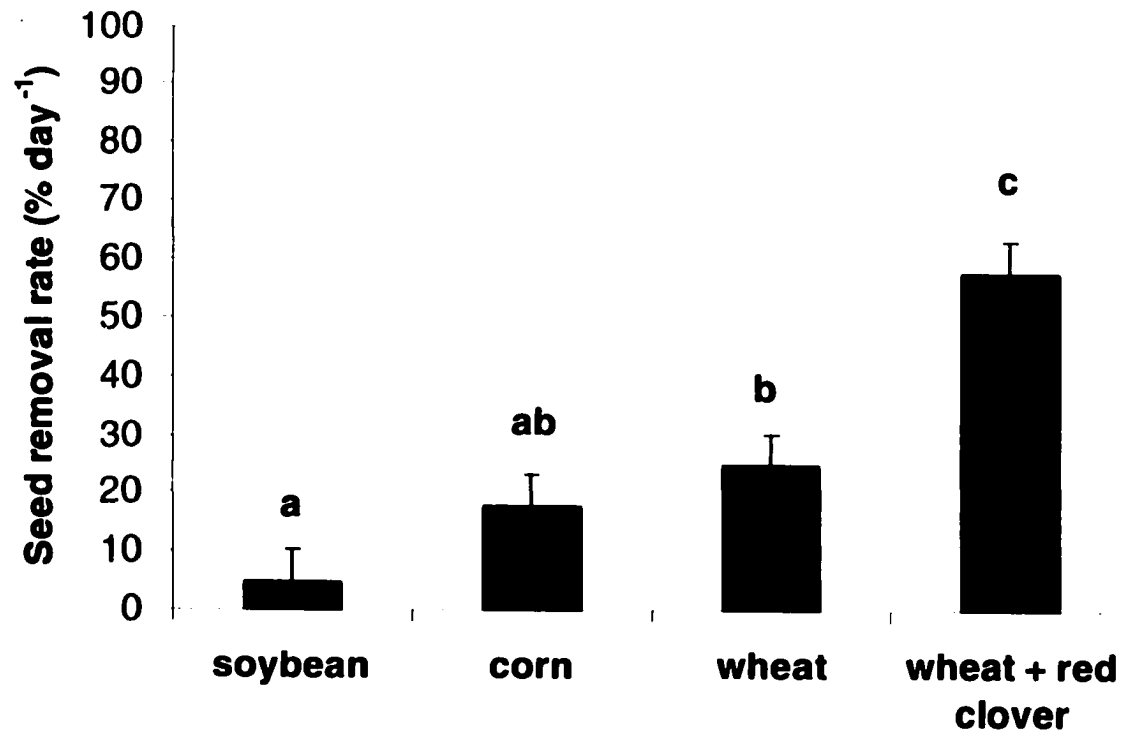Fig. 1.3

Fig. 1.4

Fig. 1.5

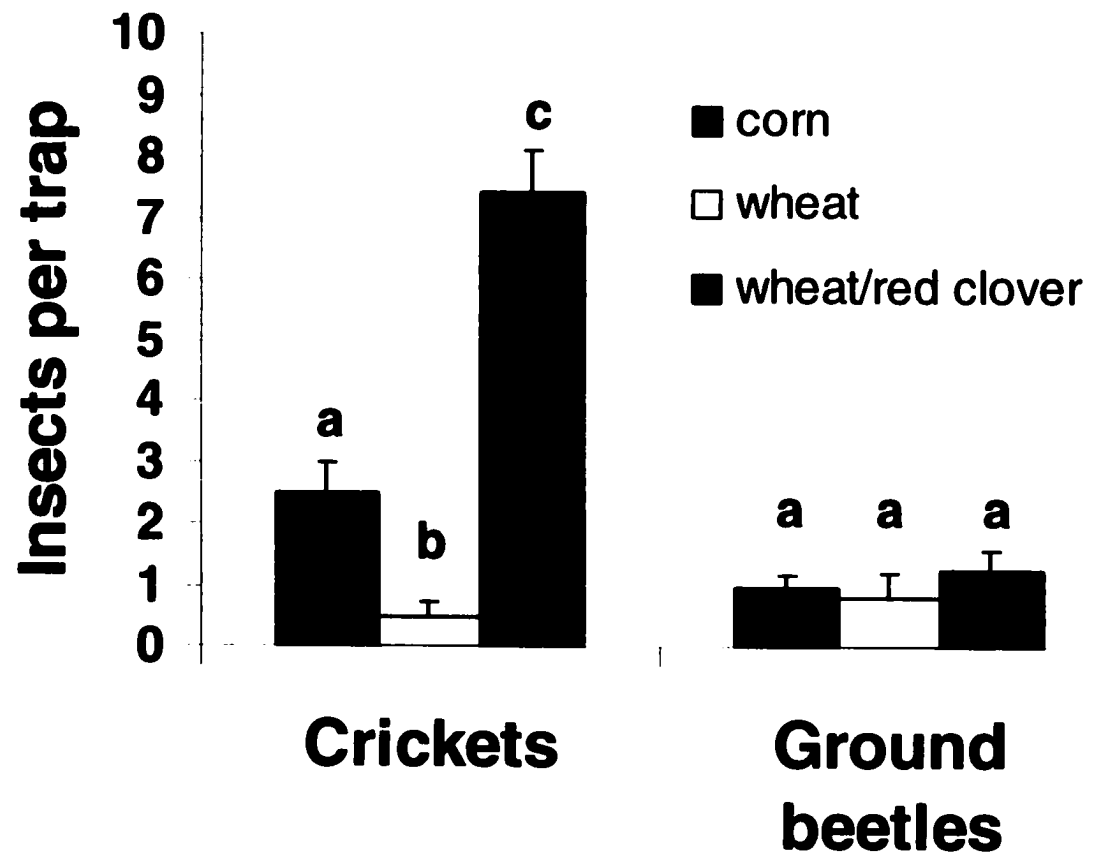Fig. 1.6

CHAPTER 3. CROPPING SYSTEM EFFECTS ON GIANT FOXTAIL

DEMOGRAPHY: II. COMPOST

A paper submitted to Weed Science

Adam S. Davis and Matt Liebman

Abstract

Soil organic amendments, such as legume green manures and composted animal manure, play a fundamental role in maintaining the fertility and tilth of soils in low-external-input agricultural systems, but little is known about their effects on weed population dynamics. Our objectives in this experiment were to determine whether red clover residues and compost affected demographic rates of giant foxtail in corn, and whether they interacted in their effects on giant foxtail demography. We measured giant foxtail seed mortality and dormancy, seedling recruitment and survival, fecundity and post-dispersal seed predation in the corn phase of a wheat-corn-soybean crop sequence in Boone, IA. Prior to the corn phase of the crop sequence, spring wheat was grown either as a sole crop or as an intercrop with red clover. Composted swine manure was applied in late fall at a rate of 0 or 25,000 kg C ha^{-1} to residues from the wheat phase to form a factorial of four soil organic amendment regimes for the corn phase: ± red clover by ± compost. Red clover residues were associated with a 21% reduction in cumulative giant foxtail seedling emergence and a 30 GDD$_{10}$(5 d) delay in thermal time to 50% emergence, with no interaction from compost. Red clover residue-mediated phytotoxicity was also associated with reductions in early corn growth that led to increases in giant foxtail fecundity. Soil amendment with compost, alone or in combination with red clover residues, did not have consistent effects on corn growth or giant foxtail demography. More work is necessary to understand how soil organic amendments affect the population and community dynamics of a wider range of weed species.

Nomenclature: giant foxtail, *Setaria faberi* Herrm. SETFA: corn, 'Pioneer 3512'. *Zea mays*

L.; red clover, 'Cherokee', *Trifolium pratense*, L.; soybean, 'IA 2039', *Glycine max* L.; spring

wheat, 'Sharp', *Triticum aestivum* L.

Key words: legume green manures, compost, phytotoxicity, integrated soil, crop and weed

management, weed demography, life stage transitions

Introduction

Amendment of agricultural soils with plant residues and animal wastes for the

purpose of improving soil fertility and structure is a time-honored practice (Parr and Hornick

1992). More recently, research studies have shown that soil organic amendments may also

contribute to weed management in agricultural systems by reducing weed interference

against crops (Davis and Liebman 2001; Dyck et al. 1995). Determining whether soil

organic amendments can also affect weed population dynamics is of potential interest to

producers in low-external-input (LEI) farming systems, who make substantial use of these

materials (Liebman and Davis 2000). Herbicides are used either in limited amounts, or not at

all, in LEI systems, and preventing the buildup of weed populations is therefore a central

weed management priority (Jordan 1996).

The fixed root habit and soil seedbank of annual weed species make them acutely

sensitive to changes in soil characteristics (Liebman and Davis 2000). Soil organic

amendments can alter the biological (Craft and Nelson 1996; Dabney et al. 1996), physical

(Drury et al 1999; Jacobowitz and Steenhuis 1984) and chemical (Tiquia and Tam 1998;

Conklin et al. 2002) properties of soil in different ways, depending upon what types of

amendments are used and how they are handled. Because there are many ways in which soil

organic amendments can be managed, it is important to know if some choices are more effective for weed prevention than others.

This article is the second in a three-part series of empirical and modeling studies looking at the life cycle of giant foxtail as an emergent property of LEI cropping system characteristics. In article 1 (Davis and Liebman "SUBMITTED"), we showed that growing red clover in an intercrop with spring wheat in a wheat-corn-soybean crop sequence can have both negative and positive consequences for giant foxtail population growth, depending upon the timing of incorporation of red clover residues. Our objective in the present study was to determine whether soil amendment with composted swine manure would 1) have direct effects upon giant foxtail demographic rates and 2) modify the effect of red clover residues upon giant foxtail demographic rates. Because the phytotoxicity of compost decreases with increasing age (Tiquia and Tam 1998), we hypothesized that soil amendment with swine manure composted for six months prior to application would not directly affect giant foxtail life stage transitions, but could alter other soil properties that would affect red clover residue-mediated effects on giant foxtail demography. Consequently, we measured a number of soil characteristics with potential to affect weed and crop performance.

Materials and Methods

All experimental procedures are described fully in Davis and Liebman ("SUBMITTED"), and are therefore given only in brief detail here.

Soil amendment effects on giant foxtail life stage transitions and soil properties were measured in 2000 and 2001 in the corn phase of a wheat-corn-soybean crop sequence, initiated in 1999, at the Iowa State University Agronomy Farm in Boone, IA. Although this is the same experimental site used for the study described in the first article in this series,

there was no overlap in field plots between the two experiments. A randomized complete block experimental design was used. including four replications of a factorial of *Red clover* (wheat sole crop. 'W'. vs. red clover + wheat intercrop. 'R'. in the wheat phase). *Compost* (applied at 0 kg C ha^{-1} ('NC') or 25.000 kg C ha^{-1} ('C')) and *N rate* (0, 90 or 200 kg N ha^{-1} from urea applied to the corn phase in mid-June). Compost was obtained from a deep-bedded hoophouse swine production system maintained at the Iowa State University Rhodes Research Farm (Honeyman and Kent 2001). It was aged for six months prior to application. in late October. to plots transitioning from the wheat to the corn phase. Because total C and N proportions of the compost varied between 1999 (10.5% C and 0.76% N) and 2000 (14.7% C and 1.3% N). total N application rate from compost was greater for the 2001 cropping season (220 kg N ha^{-1}) than for the 2000 cropping season (180 kg N ha^{-1}). All plots in the corn phase were tilled to a depth of 20 cm in early April with a power takeoff-driven rototiller.

Soil type in both years was Nicollet clay loam (Aquic Hapludolls). 35% sand. 45% silt. 30% clay. pH 6.3 and 4.7 % organic matter. Soil NO_3-N. P. K. OM. and pH were determined from samples taken on June 1 in both years. Gravimetric water content was measured at two dates during the first 4 wk of giant foxtail seedling recruitment. Soil temperature was measured with Cu-Cn thermocouples at 2.5 and 10 cm depths during the first 5 wk after corn planting (on April 27 of both years). Surface roughness was estimated on May 8 in 2000 and 2001 as log_e of the variance of the pin heights of a soil surface profiler (Harper et al. 1965). Soil phytotoxicity during giant foxtail and corn seedling recruitment was assessed with bioassays measuring effects of field soil on germination percentage and radicle growth (Dabney et al. 1996).

Plant growth and demography

All plant growth and demographic measurements were made following the methods detailed in Davis and Liebman ("SUBMITTED"). Measurements of giant foxtail demographic rates included percentage mortality of seeds in the soil seedbank from October through March ($\mu_{s/w}$) and from March through October ($\mu_{s(s)}$). percentage recruitment of seedlings (γ). percentage survival of seedlings to reproductive maturity (μ_p). fecundity (φ). and percentage seed mortality due to post-dispersal seed predation ($\mu_{s(pred)}$).

Data analysis

Tests for homogeneity of error variance were described in Davis and Liebman (in prep.). Data for $\mu_{s/w}$ were analyzed separately for 2000 and 2001 due to non-homogeneity of error variance. All variables, except for soil temperature and cumulative giant foxtail emergence, were analyzed using the GLM subroutine of SYSTAT$^{®}$ 9.0 (Wilkinson 1999) with ANOVA models that included *Year. Red Clover. Compost* and *N Rate*. Normal probability plots of residuals from each analysis were inspected, but no serious departures from normality were found. Mean separation was by Fisher's Protected LSD test at $P < 0.05$ using appropriate error terms for significant main effects and interactions (Gomez and Gomez 1984). Soil temperatures and cumulative giant foxtail seedling emergence were analyzed by repeated measures using the GLM: REPEAT subroutine of SYSTAT$^{®}$ 9.0 (Wilkinson 1999) with model terms consistent with those described above.

To streamline data presentation, and because there were no significant interactions between *N rate* and other variables, *N rate* was not included in tables. Untransformed means and main effects were reported in tables and figures for clarity of interpretation.

Results and Discussion

Soil properties

Chemical properties

Red clover residues and compost both affected soil nutrients. but in different ways. Soil NO_3-N was 53% greater in the R treatment than in the W treatment on June 1. prior to urea application (Table 2.1). We were surprised not to see a main effect of *Compost* on soil NO_3-N. since the total N loading rate from compost was 180 and 220 kg N ha^{-1} in 2000 and 2001. respectively. Eghball and Powers (1999) estimated that 20% of the total N from composted beef manure should become available to plants during the first year of decomposition. Because the compost that was applied in this experiment had already decomposed for over six months prior to application. it is possible that the mineralization rate had already slowed down substantially. leading to less NO_3-N accumulation than would have been obtained with a less decomposed material.

Soil P was twice as great in the C treatment as in the NC treatment on June 1 in both years (Table 2.1). This is consistent with reports of high P concentration in composted manure (Reider et al. 2000). There was a *Red clover* by *Compost* interaction effect (P < 0.05) on soil K, which was greater in the R/C treatment than in the other three treatments. which were similar. Soil organic matter concentration and pH were not affected by *Year*. *Red clover* or *Compost*, and had mean values (± se) of 4.4 ± 0.2 and 6.3 ± 0.1. respectively.

Physical properties

Soil gravimetric water content was greater in the R treatment (27 % ± 0.8) than in the W treatment (25 % ± 0.8) on April 10, 2000, but was unaffected by *Red clover* or *Compost* on May 12, 2000 (22 % ± 0.6). At these same dates in 2001, soil moisture contents were

14% ± 0.8 and 26 % ± 1.8, respectively, and were unaffected by *Red clover* or *Compost*. We believe that the greater soil moisture in the R treatment at the early date in 2000 may have been a result of snow trapping by red clover residues, whereas low winter precipitation in 2001 precluded such an effect.

Soil surface roughness was 19% greater in the R treatment than in the W treatment in 2000. but not in 2001 (Table 2.1). This result was consistent with our observations in the first article in this series (Davis and Liebman "SUBMITTED"), in which spring-tilled red clover residues were associated with greater surface roughness in 2000 than 2001. Compost amendments did not did not modify this effect.

Bulk density was unaffected by *Year, Red clover* or *Compost*, with a mean (± se) value of 1.20 ± 0.04 g cm^{-3}. Repeated measures analysis of average soil temperatures at a depth of 2.5 and 10 cm for the first five weeks after corn planting indicated that soil temperatures were also unaffected by *Red clover* or *Compost*, but did differ by *Year* (P < 0.05). Mean soil temperatures at 2.5 cm were 20.8 ± 0.4 C and 19.9 ± 0.4 C at 2.5 cm in 2000 and 2001, respectively. Mean soil temperatures at 10 cm were 19.7 ± 0.2 C and 19.1 ± 0.2 C in 2000 and 2001, respectively. These results agree with those of Drury et al. (1999), who found that soil amendment with red clover residues did not alter soil temperature, but differ from those of Jacobowitz and Steenhuis (1984), who found that soil amendment with compost slowed soil warming in the spring.

Phytotoxicity

Controlled-environment bioassays showed a consistent suppressive effect of *Red clover* on giant foxtail and corn radicle elongation and giant foxtail germination, but no effect on corn germination (Table 2.2). Giant foxtail radicle lengths and germination were 32% and

22% lower, and corn radicle lengths were 30% lower in the R treatment than in the W treatment. These results differ somewhat from those of Conklin et al. (2002), who found that soil amended with red clover residues and composted manure suppressed radicle elongation and germination of wild mustard seedlings, but did not negatively affect the growth and germination of corn. Soil amendment with compost had no effect on our bioassay results (Table 2.2), suggesting that the compost used in our experiment may also have had little or no phytotoxicity in the field.

Crop growth and weed demography

Seed mortality and dormancy

Giant foxtail seed mortality from October through March ($\mu_{s(w)}$) was unaffected by *Red clover* or *Compost* (Table 2.3). In contrast, there was a *Year* by *Red clover* by *Compost* interaction effect (P < 0.05) on giant foxtail seed mortality from March through October ($\mu_{s(s)}$). The pattern of treatment effects on $\mu_{s(s)}$ was inconsistent: in 2000, $\mu_{s(s)}$ was greatest in the R/NC treatment, intermediate in the W/C and R/C treatments, and lowest in the W/NC treatment; in 2001, $\mu_{s(s)}$ was greatest in the W/NC and R/C treatments, intermediate in the R/NC treatment, and lowest in the W/C treatment. Red clover residues appeared to be associated with greater levels of seed mortality in both years, although this pattern was somewhat obscured by the interaction with compost.

Percentage dormancy of giant foxtail seeds following burial from October through March (d_w) was subject to an interaction between *Year*, *Red clover* and *Compost* (P < 0.05). In 2000, d_w was lowest in the R/NC treatment, intermediate in both levels of the W treatment, and greatest in the R/C treatment, whereas in 2001, d_w was greater in the R treatment than in the W treatment for both levels of compost (Table 2.3). The increase in d_w associated with

red clover residues in compost-amended soils corroborates the findings of Davis and

Liebman ("SUBMITTED"). We do not have sufficient data to determine why this pattern

was reversed for soils that did not receive compost amendments in 2000. Percentage

dormancy of giant foxtail seeds in October following one year of burial (d_s) was unaffected

by *Red clover* or *Compost*.

Seedling recruitment and mortality

Soil amendment with composted swine manure did not directly affect seedling

recruitment or mortality (Table 2.4). There was a *Year* by *Red clover* by *Compost* interaction

effect on γ(P < 0.05): in 2000, γ was lower in the R treatment than the W treatment for both

levels of compost; in 2001, γ was lower in the R/C treatment than the W/C treatment, and

was intermediate in the W/NC and R/NC treatments, which were similar (Table 2.4).

Thermal time to 50% giant foxtail recruitment (T_{50}) was delayed by 30 GDD_{10} in both 2000

and 2001 (Table 2.4). Repeated measures analysis of cumulative giant foxtail recruitment

showed a main effect of *Red clover* (P < 0.01) on total recruitment, which was 21% lower in

the R treatment than in the W treatment, with no interaction with compost (Fig. 2.1).

Seedling mortality was unaffected by *Red clover* or *Compost* (Table 2.4). These results

corroborate those of the first article in this series (Davis and Liebman "SUBMITTED").

where we found that giant foxtail recruitment was suppressed by spring-tilled red clover

residues, but seedling mortality was unaffected by red clover residues.

Compost did not directly affect corn recruitment (Table 2.4). There was a *Year* by

Red clover by *Compost* interaction effect on corn recruitment (P < 0.001). Corn population

on May 12, 2000, was lowest in the R/NC treatment, intermediate in the W/C and R/C

treatments and greatest in the W/NC treatment. Corn population on May 12, 2001, was

greater in W/C and W/NC treatments. which did not differ. than in R/C and R/NC treatments. which also did not differ. These results agree with those of Davis and Liebman ("SUBMITTED"), who found that red clover residues had the potential to suppress corn recruitment. Although soil amendment with compost may have slightly mitigated suppression of corn recruitment by red clover residues in 2000. this effect was small and not repeated in 2001.

Growth and fecundity

   Giant foxtail. Giant foxtail height was unaffected by *Red clover* or *Compost* on June 5 and June 22. Giant foxtail final biomass. however. was 50 and 18% greater in the R treatment than in the W treatment in 2000 and 2001, respectively (Table 2.5). There was a *Year* by *Red clover* by *Compost* interaction effect on giant foxtail fecundity per plant (ϕ). such that in 2000. ϕ was greatest in the R/NC treatment. intermediate in the R/C treatment and lowest in the W/NC and W/C treatments. which did not differ; in contrast. in 2001. ϕ was unaffected by *Red clover* or *Compost*. Giant foxtail fecundity per m^2 (f) was 71 and 15% greater in the R treatment than in the W treatment in 2000 and 2001, respectively (Table 2.5). These results support concurrent work (Davis and Liebman "SUBMITTED"). in which we found that spring-tilled red clover residues were associated with an increase in f compared to fall-tilled red clover residues. or treatments which did not receive red clover residues. Using path analysis. we demonstrated in that study that the increase in f was not due to a direct stimulation of giant foxtail growth. but rather an indirect result of phytotoxic suppression of early corn growth. which released giant foxtail from crop interference early in the growing season.

Corn. Corn heights on June 5 and June 22 were subject to *Year* by *Red clover* by *Compost* interaction effects (P < 0.05). On June 5, 2000, corn height was lowest in the R/NC treatment, intermediate in the W/C and R/C treatments and greatest in the W/NC treatment (Table 2.6). On June 22, 2000, corn height was lower in the R/NC treatment than in the other three treatments, which were similar. In 2001, at both dates, corn height was lower in the R treatment than in the W treatment. These results are consistent with the suppression of corn height early in the growing season by red clover residues observed in article 1 (Davis and Liebman "SUBMITTED").

Corn population at final harvest was lower in the R treatment than in the W treatment in 2000 (Table 2.6), but was unaffected by *Red clover* or *Compost* in 2001. There was a *Year* by *Red clover* by *Compost* interaction effect on corn grain yield (P < 0.05): in 2000, red clover residues were associated with a yield reduction in the NC treatment, but not in the C treatment, whereas in 2001, corn grain yield was lower in the W/NC treatment than in the other three treatments, which were similar. The C treatment gave similar, or improved, grain yields in both years, compared to the NC treatment (Table 2.6).

Plant-soil interactions

Analysis of plant and soil data in Davis and Liebman ("SUBMITTED") suggested that red clover residue-mediated inhibition of plant recruitment and growth was due primarily to red clover phytotoxicity, with the possibility of additional inhibition from changes in the texture of the seedbed. In the present study, we were interested in knowing whether composted swine manure, applied alone or in combination with red clover residues, influenced crop growth and giant foxtail demography through changes in associated soil properties.

Soil amendment with composted swine manure did not have significant main effects on any of the plant variables that we measured. However, *Compost* did interact with *Red clover* to influence several growth and demographic variables. Although these interaction effects varied between years, they were either inconsequential or beneficial from a production standpoint, but never detrimental. For example, in 2000, the *Compost* by *Red clover* interactions for corn recruitment, height growth and giant foxtail fecundity (Tables 2.5 and 2.6) suggested a situation in which soil amendment with compost may have reduced the suppression of corn recruitment and growth by red clover residues. This, in turn, appeared to prevent the increase in giant foxtail fecundity, due to reduced interference from corn, that was documented in Davis and Liebman ("SUBMITTED"). In 2001, *Compost* was associated with greater corn yields in the W treatment, but did not affect corn growth or giant foxtail fecundity. We will not speculate about edaphic factors responsible for the interaction between compost and red clover residues in 2000 since the effect was small and inconsistent.

Management implications

As demonstrated in article 1 of this series (Davis and Liebman "SUBMITTED"), there were both benefits and risks associated with including a spring-tilled red clover green manure as an intercrop with wheat in a wheat-corn-soybean crop sequence. Giant foxtail recruitment was both reduced and delayed due to phytotoxicity from red clover residues. We also observed a *N Rate* by *Red Clover* interaction effect ($P < 0.05$), indicating a substantial N contribution from the green manure to corn grain yield. Corn yield did not differ between the R treatment fertilized at 0 kg N ha^{-1} (grain yield = 12,600 ± 550 kg grain ha^{-1}) and the W treatment fertilized at 90 kg N ha^{-1} (grain yield = 12,600 ± 550 kg grain ha^{-1}) (Fig. 2.2). This result suggests that the red clover fertilizer N equivalence value to the following corn crop

was 90 kg N ha^{-1}, which agrees well with published values (Bruulsema and Christie 1987: Hesterman et al. 1992). Soil amendment with compost did not make a detectable N contribution to corn grain yield. One negative consequence of the R treatment was that early corn growth was reduced due to phytotoxic effects of red clover residues (Table 2.6) allowing giant foxtail seed production per m^2 to increase by as much as 50% in the R treatment compared to the W treatment (Table 2.5).

Soil amendment with composted swine manure, either alone or in combination with a red clover green manure, did not have negative effects on either crop growth or giant foxtail demography. These results suggest that producers wishing to obtain the nutrient and waste management benefits of amending crop land with composted swine manure may do so without incurring a weed management penalty. It is important to note, however. that other weed species may respond differently to soil amendment with composted manure. Because of the central importance of soil organic amendments to LEI production systems. there is a need for more information on how these materials affect weed management outcomes through their effects on weed demography and community dynamics.

Acknowledgements

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Figure Captions

Fig. 2.1. Giant foxtail seedling emergence from synthetic seedbanks under contrasting soil

organic amendment treatments. Treatment abbreviations are the same as described in Table

2.1. Data were analyzed using repeated measures analysis of variance. Vertical bars

represent ± one standard error of the mean of four replicates.

Fig. 2.2. Corn grain yield at different rates of N fertilization with urea in a corn crop

following either a wheat sole-crop (solid rectangles) or a wheat + red clover intercrop (open

rectangles). Vertical bars represent ± one standard error of the mean of four replicates.

Table 2.1. Selected soil chemical and physical properties measured[a] within a corn crop grown under varying soil amendment treatments.

Treatment	NO₃-N 2000	NO₃-N 2001	P 2000	P 2001	K 2000	K 2001	Surface roughness 2000	Surface roughness 2001
	ppm						$\log_e(mm^-)$	
W/NC[b]	7	7	19	17	110 a[c]	110 a	1.5	1.7
R/NC	10	12	18	14	110 a	110 a	1.9	1.6
W/C	9	7	44	26	120 a	110 a	1.6	1.3
R/C	11	11	37	30	150 b	120 b	1.8	1.5
SE	0.7	1	4	2	6	3	0.1	0.1
Main effect: Red clover								
W	8 a	7 a	31	21	115	110	1.6 a	1.5
R	11 b	12 b	27	22	130	115	1.9 b	1.6
Main effect: Compost								
NC	8	10	18 a	16 a	110	110	1.7	1.7
C	10	9	40 b	28 b	135	115	1.7	1.4

[a] Soil NO₃-N, P and K were measured in top 20 cm of the soil profile on June 1, and surface roughness was measured on May 8.

[b] Abbreviations: 'W' = wheat sole crop prior to corn phase, 'R' = wheat + red clover intercrop prior to corn phase, 'NC' = no compost applied in fall prior to corn phase, 'C' = compost applied in fall prior to corn phase.

[c] Within columns for each year, means followed by different lower case letters were different as determined by Fisher's Protected LSD₀.₀₅ multiple comparison test.

Table 2.2. Bioassay of phytotoxic properties of soil collected[a] within a corn crop grown under varying soil amendment treatments.

Treatment	Radicle length			Germination		
	SETFA		Corn	SETFA		Corn
	2000	2001	2001	2000	2001	2001
	mm			%		
W/NC[b]	21	17	80	38	39	100
R/NC	11	15	67	28	36	100
W/C	17	20	81	36	46	100
R/C	9	17	47	21	44	100
SE	1.3	0.9	3.9	2.5	2.1	0.2
Main effect: Red clover						
W	19 b[c]	19 b	81 b	37 b	52 b	100
R	10 a	16 a	57 a	24 a	45 a	100
Main effect: Compost						
NC	16	16	73	33	50	100
C	13	18	65	28	47	100

[a] Soil was collected on May 10 in 2000 and May 17 in 2001.

[b] Abbreviations follow the pattern described in Table 2.1.

[c] Within columns for each year, means followed by different lower case letters were different as determined by Fisher's Protected $LSD_{0.05}$ multiple comparison test.

Table 2.3. Giant foxtail seed mortality and dormancy measured within a corn crop grown under varying soil amendment treatments.

	Mortality				Dormancy			
	Oct.-Mar.($\mu_{s(w)}$)		Mar.-Oct.($\mu_{s(s)}$)		Mar. (d_w)		Oct. (d_t)	
Treatment	2000	2001	2000	2001	2000	2001	2000	2001
				%				
W/NC[a]	16	46	43 a[b]	33 c	60 b	7 a	36	5.8
R/NC	14	49	55 b	26 bc	51 a	12 bc	32	6.9
W/C	13	54	48 ab	20 ab	61 b	10 ab	34	9.7
R/C	19	48	47 ab	34 c	68 c	15 c	25	7.8
SE	1.0	1.7	1.6	2.3	1.6	1.4	2.1	0.8
Main effect: Red clover								
W	15	50	46	27	61	9	35	7.8
R	17	49	51	30	60	14	29	7.4
Main effect: Compost								
NC	15	48	49	30	56	10	34	6.4
C	16	51	48	27	65	13	29	8.7

[a] Abbreviations follow the pattern described in Table 2.1.

[b] Within columns for each year, means followed by different lower case letters were different as determined by Fisher's Protected $LSD_{0.05}$ multiple comparison test.

Table 2.4. Giant foxtail and corn recruitment within a corn crop grown under varying soil amendment treatments.

Treatment	SETFA recruitment Cumulative $(\gamma)^a$ 2000	2001	$T_{50}{}^b$ 2000	2001	SETFA seedling mortality $(\mu_p)^c$ 2000	2001	Corn density May 12 2000	2001
	%		GDD_{10}		%		10^3 plants ha^{-1}	
W/NC	20 b^d	29 ab	250	170	4.2	1.9	54 c	72 b
R/NC	11 a	34 ab	280	200	1.4	2.9	27 a	67 a
W/C	18 b	38 b	260	170	2.0	2.2	39 b	72 b
R/C	14 a	26 a	290	200	1.7	2.3	41 b	66 a
SE	1	4	4	5	2.0	0.8	3.5	0.9
Main effect: Red clover								
W	19	34	260 a	170 a	3.1	2.1	47	72
R	13	30	290 b	200 b	1.5	3.1	34	67
Main effect: Compost								
NC	16	32	270	190	2.8	2.4	41	70
C	16	32	280	190	1.8	2.8	40	69

[a] Seedling recruitment through June 21, expressed as the percentage of viable seeds in March giving rise to established seedlings.

[b] Abbreviations: T_{50} = growing degree days (base 10 C) required to reach 50% emergence; treatment abbreviations are the same as described in Table 2.1.

[c] Seedling mortality was expressed as (number of mature plants in late August)/(number of seedlings that had emerged in row plantings by June 21) x 100%.

[d] Within columns for each year, means followed by different lower case letters were different as determined by Fisher's Protected LSD$_{0.05}$ multiple comparison test.

Table 2.5. Giant foxtail growth and fecundity within a corn crop grown under varying soil amendment treatments.

Treatment	SETFA height				SETFA biomass		SETFA fecundity			
	June 5		June 22				ϕ^a		f	
	2000	2001	2000	2001	2000	2001	2000	2001	2000	2001
	cm				$g\ m^{-2}$		10^3 sds. plt.$^{-1}$		10^3 sds. m^{-2}	
W/NC[b]	2.6	9.6	24	30	25	330	1.2 a	1.2	4.1	51
R/NC	2.7	9.4	22	31	54	380	4.0 c	1.4	9.5	59
W/C	2.9	9.1	25	30	36	340	1.5 a	1.3	6.2	54
R/C	2.9	9.4	23	33	41	400	2.2 b	1.8	8.2	62
SE	0.1	0.3	1	1	8	30	0.3	0.2	1.8	3
Main effect: Red clover										
W	2.8	9.4	25	30	31 a[c]	330 a	1.4	1.3	5.2 a	53 a
R	2.8	9.4	23	32	47 b	390 b	3.1	1.6	8.9 b	61 b
Main effect: Compost										
NC	2.7	9.5	23	30	39	350	2.6	1.3	6.8	55
C	2.9	9.3	24	31	39	370	1.9	1.6	7.2	58

[a] The symbols ϕ and f represent giant foxtail fecundity in seeds per plant and seeds per m^{-2}, respectively.

[b] Treatment abbreviations follow the pattern described in Table 2.1.

[c] Within columns for each year, means followed by different lower case letters were different as determined by Fisher's Protected LSD$_{0.05}$ multiple comparison test.

Table 2.6. Growth and yield of a corn crop grown under varying soil amendment treatments.

Treatment	Corn height				Corn population at harvest		Corn grain yield	
	June 5		June 22					
	2000	2001	2000	2001	2000	2001	2000	2001
	cm				10^3 plants ha^{-1}		10^3 kg ha^{-1}	
W/NC[a]	42 c[b]	30 b	108 b	65 b	51	65	12.2 b	11.0 a
R/NC	33 a	23 a	92 a	58 a	47	62	11.0 a	13.4 b
W/C	35 ab	28 b	102 b	63 b	51	63	12.8 bc	12.8 b
R/C	38 bc	24 a	106 b	59 a	47	62	13.4 c	12.8 b
SE	1.4	1.0	2.4	1.6	1.2	1.0	0.5	0.7
Main effect: Red clover								
W	39	29	105	64	51 b	64	12.2	12.2
R	36	24	99	58	47 a	62	12.2	13.4
Main effect: Compost								
NC	38	26	100	62	49	64	11.6	12.2
C	37	26	104	61	49	63	12.8	12.8

[a] Abbreviations follow the pattern described in Table 2.1.

[b] Within columns for each year, means followed by different lower case letters were different as determined by Fisher's Protected LSD$_{0.05}$ multiple comparison test.
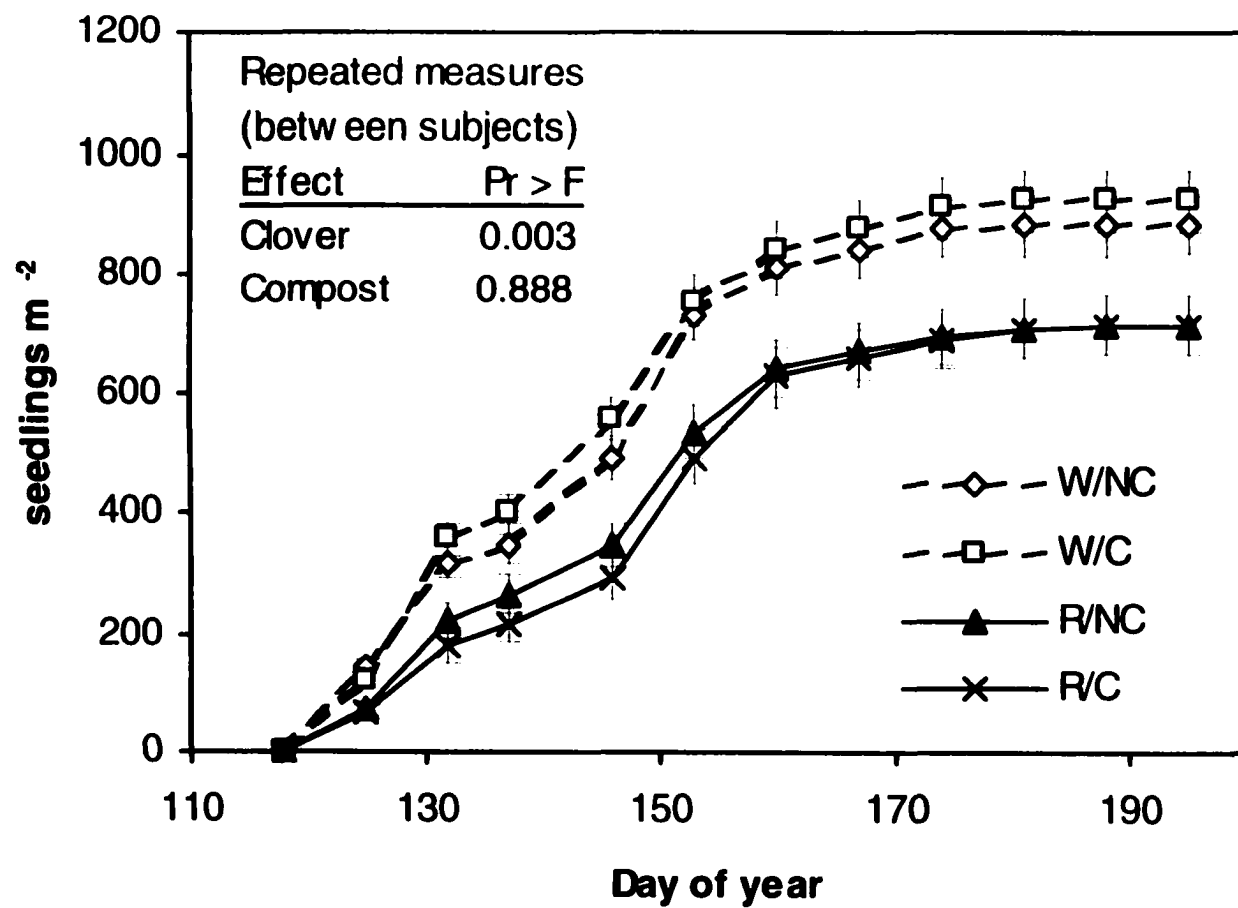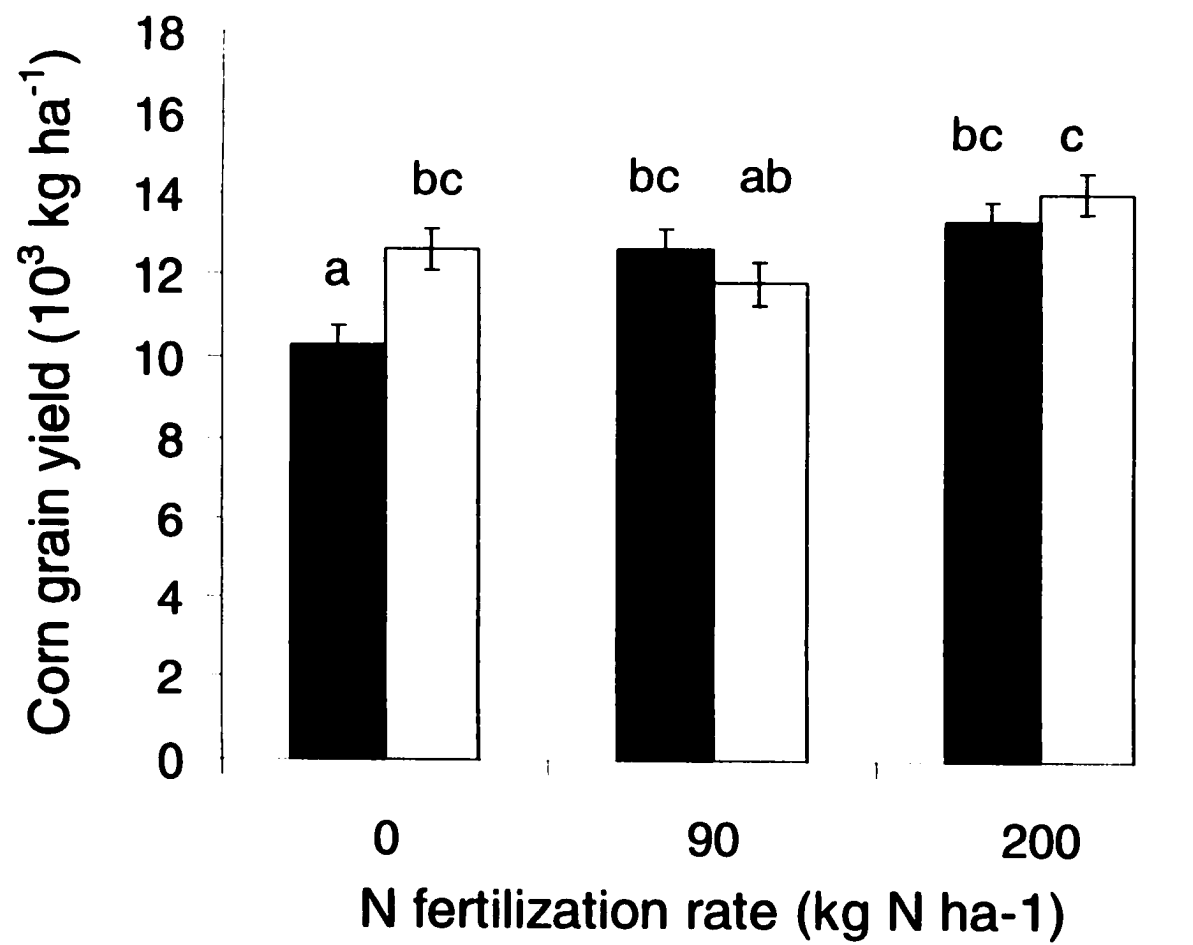
Fig. 2.1

Fig. 2.2

CHAPTER 4. CROPPING SYSTEM EFFECTS ON GIANT FOXTAIL DEMOGRAPHY: III. RETROSPECTIVE PERTURBATION ANALYSIS

Adam S. Davis. Philip M. Dixon and Matt Liebman

Abstract

Cropping system characteristics affect weed management by altering key demographic rates of weeds. We adapted the Life Table Response Experiment (LTRE) design to permit retrospective perturbation analysis of a periodic matrix model of cropping system effects on giant foxtail population growth rate (λ). Demographic data were collected for giant foxtail grown in a wheat-corn-soybean crop sequence in the central USA. with either a wheat sole-crop ('W') or wheat/red clover intercrop ('R') in the wheat phase. Demographic rates estimated from these data included seed survival from October to March ($\sigma_{s(o)}$) and March to October ($\sigma_{s(s)}$), seedling recruitment (γ), plant survival (σ_p), fecundity (ϕ) and survival of seeds exposed to predators ($\sigma_{s(pred)}$). More than a two-fold difference in λ ($\Delta\lambda$) existed between the W treatment ($\lambda = 2.54$) and the R treatment ($\lambda = 1.16$). We decomposed $\Delta\lambda$ into contributions (comprised of the product of the sensitivity of λ to changes in a given parameter by treatment differences in that parameter) from the six parameters in the three rotation phases of the periodic model for a total of 18 separate contributions. Five contributions accounted for 77% of $\Delta\lambda$: $\sigma_{s(pred)}$ (0.55), γ (-0.28) and $\sigma_{s(s)}$ (0.18) in the wheat phase, and γ in the corn (0.20) and soybean (0.41) phases. Retrospective perturbation analysis can help guide the design and improvement of future weed prevention systems.

Nomenclature: giant foxtail. *Setaria faberi* Herrm. SETFA; corn. 'Pioneer 3512'. *Zea mays* L.; red clover, 'Cherokee', *Trifolium pratense* L.; soybean, 'IA 2039', *Glycine max* L.; spring wheat. 'Sharp', *Triticum aestivum* L.

Keywords: LTRE. life table response experiment. simulation model. sensitivity, elasticity. integrated weed management, seed predation. crop rotation, legume green manure

Introduction

There is an increasing emphasis on weed prevention in agricultural systems in which herbicide use is minimized or eliminated (Jordan 1996; Bastiaans et al. 2000). Weed prevention systems seek to limit weed population growth, and are predicted to be most successful when they combine several management tactics (Liebman and Gallandt 1997). There has been much research on the efficacy of individual weed management tactics, but many fewer studies exist that examine what happens when several tactics are integrated into the same weed management system. The reason for this is clear: the factorial treatment design necessary to understand both main and interaction effects of the various management tactics requires experiments that are large, expensive, time-consuming, and difficult to interpret. This does not mean that those who would design integrated weed management systems must despair of rational approaches to doing so. Rather, they must augment the predictive power of existing empirical data with modeling techniques that allow for the integration and assessment of suites of management tactics.

Matrix models of weed population dynamics readily accommodate the many types of life histories observed among weed taxa and offer a straightforward way of accounting for management effects on weed life stage transitions (for an excellent overview of matrix

population models, see Caswell 2001). The basic equation for projecting population growth with a matrix model is:

$$\mathbf{n}_{t+1} = \mathbf{A}\mathbf{n}_t \qquad [1]$$

where **n** is a vector with i rows representing the numbers of individuals in each life stage at time t and $t+1$, and **A** represents the annual projection matrix with i rows and j (= i) columns containing all life stage transition probabilities for the weed species being modeled. Such models can be linear or non-linear in their parameters, and deterministic or stochastic with respect to parameter variability. Because the primary goal of preventative weed management is to keep weed populations low, density dependence in demographic parameters is unlikely to be a major factor in weed prevention models. For this reason, and for ease of analysis and interpretation, we are inclined to use linear, deterministic models to guide and assess preventative weed management strategies. For such models, population growth rate can be calculated as the dominant eigenvalue, λ_1, of **A** (for an example with complete MATLAB code, see appendix A).

In an agricultural setting, management operations often occur at some sub-annual time scale. To increase the capacity of matrix modeling methods to simulate the effects of multiple management tactics, it is necessary to use a periodic model. Periodic matrix models subdivide the annual projection matrix into two or more sub-matrices that describe the effect of different environments upon weed life stage transition probabilities. For a periodic model with m periods in a complete cycle, the projection equation for a projection interval starting at period h is:

$$\mathbf{n}_{t+1} = (\mathbf{B}_{(h-1)}...\mathbf{B}_{(1)}\mathbf{B}_{(m)}...\mathbf{B}_{(h+1)}\mathbf{B}_{(h)})\mathbf{n}_t \qquad h=1,...,m \qquad [2]$$

where **n** represents a weed population vector at time t and $t+1$, and each $\mathbf{B}_{(h)}$ represents a phase-specific projection matrix (Caswell 2001).

Perturbation analysis determines what happens to model output when projection matrix parameter values are changed. Perturbation analyses fall into two general categories. prospective and retrospective, each designed to ask different questions (Caswell 2000). Both types of analyses represent important tools for ecosystem managers, as they permit the identification of demographic processes and management interventions that are most likely to have strong regulatory control over λ.

Prospective perturbation analysis, which includes sensitivity and elasticity analysis, is by far the most common type of perturbation analysis in the applied ecology literature. Sensitivity analysis examines changes in λ in response to additive perturbations to each element of A ($S_A = \partial\lambda/\partial a_{ij}$), whereas elasticity analysis examines changes in λ in response to proportional perturbations to each a_{ij} ($E_A = (a_{ij}/\lambda)(\partial\lambda/\partial a_{ij})$) (Caswell 2001). The sensitivities of λ to changes in each a_{ij} can be calculated by varying one demographic parameter at a time and recording model output, but this technique is laborious, and does not allow the model user to take full advantage of computing power. A more direct method is to calculate eigenvalue sensitivities to perturbations of elements of the annual projection matrix (Caswell 2001). This procedure has been extended to permit the calculation of eigenvalue sensitivities of periodic projection matrices (Caswell and Trevisan 1994):

$$S_{B..} = D^T S_{A..}$$

$$= (B_{(h-1)}...B_{(1)}B_{(m)}...B_{(h+1)})^T S_{A..} \qquad [3]$$

where $S_{B..}$ represents the sensitivity of λ to changes in the elements of periodic projection matrix $B_{(h)}$, D^T represents the transpose of the product of the periodic projection matrices excluding $B_{(h)}$, and $S_{A..}$ represents the sensitivity of λ to changes in the elements of $A_{(h)}$ (the annual projection matrix for the interval beginning at time period h). Elasticities of λ to the elements, b_{hij}, of periodic projection matrices are then computed as:

$$E_{B_{i..}} = (b_{hij}/\lambda)S_{B_{i..}}$$ [4]

The periodic matrix modeling approach has been used previously to simulate weed population dynamics in crop rotations (Jordan et al. 1995; Ullrich 2000; Mertens et al. 2002), employing prospective perturbation analysis as a tool to describe the dynamics of the system. In a sensitivity analysis of crop rotation effects on weed population dynamics, Jordan et al. (1995) found that λ was most sensitive to changes in overwinter seedbank decline in the upper 10 cm of soil. By identifying overwinter seedbank decline as a parameter with the potential to greatly influence λ, this analysis suggested that overwinter seedbank decline represents a weed management "choke point" (i.e., a stage in the weed life cycle where management interventions may be applied with the greatest likelihood of reducing λ). But what if λ is found to be highly sensitive to a demographic process that also happens to be highly resistant to external manipulation? In such a case, what appears to be a promising weed management choke point with regard to sensitivity analysis may be virtually useless in practical terms. Retrospective perturbation analysis can help assess the utility of putative choke points by accounting for both sensitivity and observed variability in demographic parameters.

This article will focus on elaborations on one method of retrospective perturbation analysis, known as a Life Table Response Experiment (LTRE) (Caswell 2001). The LTRE approximation for an annual matrix model decomposes treatment effects on λ into the sum, over all a_{ij}, of the product of treatment differences in a_{ij} and sensitivity of λ to changes in each a_{ij}. For an LTRE model with a one-way treatment design, the relationship between λ for a treatment of interest (m) and λ for a reference treatment (r) may be described by

$$\lambda^{(m)} - \lambda^{(r)} \approx \sum_{ij}(a_{ij}^{(m)} - a_{ij}^{(r)})\frac{\partial \lambda}{\partial a_{ij}}\bigg|_{A^*} \qquad m = 1,...,N \quad [5]$$

where subscripts i and j refer to matrix rows and columns, respectively. a_{ij} refers to individual elements of the $\mathbf{A}^{(m)}$ and $\mathbf{A}^{(r)}$ projection matrices, and $\mathbf{A}^* = (\mathbf{A}^{(m)} + \mathbf{A}^{(r)})/2$. The first term on the right hand side of equation 5 denotes treatment differences in parameter values and the second term denotes the sensitivity of λ to changes in each a_{ij}, evaluated at $\mathbf{A}^*$. A parameter that differs only slightly between treatments m and r may still make a substantial contribution to treatment differences in population growth rate if λ is very sensitive to this parameter. Thus the LTRE provides a weighted measure, under a given set of conditions, of how demographic parameters contribute to treatment effects on λ.

Our objective was to extend the LTRE approximation for use in the retrospective perturbation analysis of lower-level demographic parameters (i.e., the individual life stage transitions comprising each of the elements of the projection matrix) in periodic matrix population models. Others have analyzed periodic models using the LTRE approach (Rydgren et al. 2001), but did not analyze contributions of lower-level demographic parameters to treatment differences in λ. We believe this step is essential to the precise identification of weed management choke points.

At least one alternative approach to the retrospective perturbation analysis of weed population dynamics simulation models appears in the weed science literature (Freckleton and Watkinson 1998). Our adaptation of the LTRE approach for use with periodic matrix models, however, offers some unique advantages for analyzing multitactic weed management systems. First, the modular design and multiple matrix dimensions of a periodic model allow the user to simulate complex population dynamics with a model that is not complicated. Second, the LTRE is specifically designed for the integration of empirical and modeling efforts; the basic LTRE design is analogous to analysis of variance, and may be modified to accommodate different experimental designs (Caswell 2001). Finally, LTRE analysis of

periodic models permits side-by-side comparisons of numerous system components. For periodic models where experimental data exist for a given management tactic. LTRE analysis is a powerful tool for assessing the weed prevention potential of choke points identified by prospective perturbation analysis.

By way of illustration, we include both elasticity and LTRE analyses of a periodic model parameterized with data from a field investigation of crop sequence effects on the population dynamics of giant foxtail, a warm-season annual grass species common to corn production systems in the central USA. We hypothesized that intercropping red clover with wheat in a wheat-corn-soybean crop sequence would alter the soil in ways that would affect giant foxtail seedling recruitment and seed survival, thus altering giant foxtail population dynamics.

Materials and methods

Field experiment, parameter estimation and model structure

During the 2000 and 2001 field seasons, giant foxtail demography was studied within the context of a wheat-corn-soybean crop sequence at the Iowa State University Agronomy Farm in Boone, IA (Davis and Liebman "SUBMITTED" a,b). In the wheat phase of the crop sequence, wheat was grown either as a sole crop ('W') or in an intercrop ('R') with red clover. The experiment was performed as a randomized complete block design with four replications. Procedures for measuring giant foxtail life stage transitions are described fully in Davis and Liebman ("SUBMITTED" a, b).

Six demographic parameters were estimated for giant foxtail using data from the 2000 field season: recruitment (γ), seed survival from March through October ($\sigma_{s(s)}$), plant survival to reproductive maturity (σ_p), seed production plant^{-1} (ϕ), seed survival of post-dispersal seed

predation prior to fall tillage ($\sigma_{s(pred)}$), and seed survival from October through March (σ_{ow}) (Table 3.1). The critical P-value for including factor level means for a given parameter (as opposed to averaging over treatments) in the model was set at $P < 0.15$. Choice of alpha level followed the Akaike Information Criterion (AIC) for model selection. Use of the AIC helps to optimize the tradeoff between bias and variance in model selection and suggests that a critical value of $P < 0.05$ is too conservative a basis for differentiating between models varying in one parameter (Burnham and Anderson 1998).

Recruitment, plant survival and fecundity were estimated as the mean of these parameters for the first two emergence cohorts, which accounted for over 90% of giant foxtail recruitment and reproductive output. Point estimates of $\sigma_{s(pred)}$ were converted into a season-long estimate of $\sigma_{s(pred)}$ by compounding the value of S measured in late September, when predation rates were at their peak, over 20 days. We considered compounding the daily rates of $\sigma_{s(pred)}$ over the entire predation period from August through October, but the resulting percentages of surviving seeds were too low to be realistic. With the exception of $\sigma_{s(pred)}$, which was measured in all three phases of the crop sequence, all other demographic parameters were measured in corn only. Applying parameter values from the corn phase to the soybean phase was probably a reasonable approximation of the actual values (Bussan et al. 2000), whereas applying them to the wheat phase probably overestimated giant foxtail recruitment and fecundity (Kegode et al. 1999). Work is currently underway to estimate all six demographic parameters for giant foxtail within each of the rotation phases.

Our model followed giant foxtail demography through four sub-annual periods in each of three phases in the wheat-corn-soybean crop sequence, for a total of 12 periods in one rotation cycle (Fig. 3.1). We did not define a depth-structured seedbank because seedbank decline is rapid for giant foxtail between 0 and 5 cm soil depth (Buhler and

Hartzler 2001), and is approximated well by compounding decay rates for an unstructured

seedbank across periods. We distinguished between newly-shed seed and the previous year's

seed so only the new seed experienced high rates of post-dispersal seed predation. In the

'Fecundity' projection matrix ($\mathbf{B}_{(3k)}$), newly shed seed were subjected to predation before

being combined with the previous year's seed fraction.

Sensitivities and elasticities of λ to lower level parameters

Equations 3 and 4 define the sensitivity and elasticity, respectively, of λ to

perturbations of elements of the $\mathbf{B}_{(h,)}$ making up the periodic model, where h refers to the

period and k refers to the rotation phase. At the core of these periodic sensitivity and

elasticity calculations is a sensitivity matrix of λ with respect to $\mathbf{A}_{(h,)}$. The elements of $\mathbf{A}_{,}$.

are determined by the product of the periodic matrices over all periods and rotation phases,

starting with period h in rotation phase k (at the right-hand side of the product matrix), such

that $\mathbf{A}_{,h,} = (\mathbf{B}_{(h-1)}...\mathbf{B}_{(1)}\mathbf{B}_{(m)}...\mathbf{B}_{(h+1)}\mathbf{B}_{(h)})_k$. For the simple system described in this study, all

$\mathbf{A}_{,}$, have only one non-zero element, a_{11}, which contains the product of all the demographic

parameters in each of the rotation phases: $[(\sigma_{s(w)})(\sigma_{s(s)})(1-\gamma) + (\sigma_{s(w)})(\phi)(\sigma_{s(pred)})(\sigma_p)(\gamma)]_k$. The

left-hand term describes the fate of dormant seeds, and the right-hand term describes new

inputs to the seedbank. Perturbations to a_{11} involve this entire string of parameters, yet for

management purposes, we want to know how λ responds to the perturbation of individual

demographic parameters, such as γ or ϕ. This problem is solved by applying the chain rule

for differentiation (Caswell 2001), so that for a given demographic parameter x

$$\frac{\partial \lambda}{\partial x^{(h_k)}} = \sum_{i,j} \frac{\partial \lambda}{\partial b_{ij}^{(h_k)}} \frac{\partial b_{ij}^{(h_k)}}{\partial x^{(h_k)}} \qquad [6]$$

and

$$\frac{x^{(h_k)}}{\lambda}\frac{\partial\lambda}{\partial x^{(h_k)}} = \frac{x^{(h_k)}}{\lambda}\sum_{i,j}\frac{\partial\lambda}{\partial b_{ij}^{(h_k)}}\frac{\partial b_{ij}^{(h_k)}}{\partial x^{(h_k)}} \qquad [7]$$

where equations 6 and 7 describe the sensitivity and elasticity, respectively, of λ with respect to x.

LTRE analysis of a periodic matrix population model

The LTRE equation was rewritten to decompose treatment effects on λ into the sum, over all periods and phases, of the product of treatment differences in each periodic matrix element b_{hijk} and sensitivity of λ to changes in each b_{hijk}. The equation used to describe the LTRE approximation for a periodic matrix model is

$$\lambda^{(m)} - \lambda^{(r)} \approx \sum_{hijk}(b_{hijk}^{(m)} - b_{hijk}^{(r)})\mathbf{D}^T S_{A^{(h_k)}}\Big|_{A^{(h_k)}}, \quad m = 1,....,N \quad [8]$$

where m is a treatment of interest, r is a reference treatment, h and k refer to period and rotation phase, respectively, i and j refer to matrix rows and columns, respectively, b_{hijk} refers to individual elements of the periodic projection matrices, $\mathbf{D}^T$ represents the transpose of the product of the phase-specific projection matrices excluding $\mathbf{B}_{(h_k)}$ (see equation 3). $S_{A(h_k)}$ represents the sensitivity of λ to changes in the elements of $\mathbf{A}_{(h_k)}^*$, and $\mathbf{A}_{(h_k)}^* = (\mathbf{A}_{(h_k)}^{(m)} + \mathbf{A}_{(h_k)}^{(r)})/2$. We calculated $\mathbf{A}_{(h_k)}^{(m)}$ and $\mathbf{A}_{(h_k)}^{(r)}$ as the products of treatment-specific $\mathbf{B}_{(h_k)}$, and then averaged over $\mathbf{A}_{(h_k)}^{(m)}$ and $\mathbf{A}_{(h_k)}^{(r)}$ to obtain $\mathbf{A}_{(h_k)}^*$.

To simplify the presentation of the LTRE results by making LTRE contributions positive, we chose to designate the R treatment as the reference treatment (r) and the W treatment as the treatment of interest (m). After the contribution of each b_{hijk} to treatment differences in λ was calculated, contributions were summed over all b_{hijk}. This sum was

compared to $\lambda^{(m)} - \lambda^{(r)}$ from the simulation model to obtain percentage error in the LTRE approximation, calculated as $(|\Delta\lambda_{LTRE} - \Delta\lambda_{Model}|)/\Delta\lambda_{Model}$.

Computational methods

Matrix calculations for the example included in this study were performed using MATLAB Version 5.0 (The Math Works, Inc. 1997). We used MATLAB to predict λ and calculate sensitivity of λ to changes in each b_{hijk} within each of the treatments (see Appendix A for MATLAB code). Parameter contributions to treatment differences in λ were calculated by multiplying treatment differences in b_{hij} by the sensitivity of λ to changes in each b_{hij} within a spreadsheet program.

Results and Discussion

Population growth

Projecting the initial weed population through six rotation cycles showed increases in giant foxtail population size for both the W and R treatments (Fig. 3.2). Population growth rate. however, was more than two times greater in the W treatment ($\lambda = 2.54$) than in the R treatment ($\lambda = 1.16$). These values of λ were calculated over the entire rotation cycle for use in the periodic LTRE, and thus were greater than the annual population growth rates in the W and R treatments ($\lambda^{1/3} = 1.36$ and $\lambda^{1/3} = 1.05$, respectively). Examination of Fig. 3.2 shows that. in both crop sequences, population size declined sharply in the wheat phase. declined moderately in the corn phase and increased rapidly in the soybean phase.

It was not surprising that model projections indicated that the giant foxtail population grew larger (i.e. $\lambda > 1$) in both the W and R treatments. No external forms of weed control were applied, therefore the only constraints on giant foxtail population growth were those

due to cropping system effects. What was surprising was that the rate of giant foxtail population growth was twice as great in the W treatment than in the R treatment. Analysis of the primary experimental results (Davis and Liebman "SUBMITTED" a. b) provided a detailed description of treatment effects on individual demographic processes. but yielded little insight into how such effects were integrated into the overall life cycle. Fortunately. perturbation analyses offer a method of recovering more information from the data. We compared what we learned using the method described in this article. LTRE analysis of periodic systems, to what we learned using elasticity analysis, the primary method of perturbation analysis that has been used in the weed science modeling literature (Gonzalez-Andujar and Fernandez- Quintanilla 1991; Jordan et al. 1995).

Elasticity analysis

Relative rankings of the elasticity of λ to giant foxtail demographic parameters were the same for the corn and soybean phases in both the W and R treatments (Table 3.2). Elasticity of λ to $\sigma_{s(w)}$ was ranked highest, σ_p, ϕ and $\sigma_{s(pred)}$ were ranked second. γ was ranked third and $\sigma_{s(s)}$ was ranked lowest.

Elasticity rankings for the wheat phase differed from those in the corn and soybean phases, and within the wheat phase, differed between the W and R treatments. In the W treatment, elasticity of λ to $\sigma_{s(w)}$ was ranked highest, $\sigma_{s(s)}$ was ranked second. γ was ranked third (with a negative elasticity value), and σ_p, ϕ and $\sigma_{s(pred)}$ were ranked lowest. In the R treatment, elasticity of λ to $\sigma_{s(w)}$ and $\sigma_{s(s)}$ were ranked first, γ was ranked second (with a negative elasticity value) and σ_p, ϕ and $\sigma_{s(pred)}$ were ranked third.

The high elasticity of λ to $\sigma_{s(w)}$ was to be expected for a seed bearing annual. where seed survival during the seed-only phase represents an annual bottleneck the entire

population must pass through. The pattern of elasticity rankings for the remaining parameters yielded more information about how the W and R treatments differed. Elasticity rankings were reversed in the wheat phase compared to the corn and soybean phases for the parameters other than $\sigma_{s(w)}$. These parameters could be divided into groups: 1) parameters important to seed production (γ, σ_p, ϕ and $\sigma_{s(pred)}$) and 2) parameters important to preservation of existing seeds ($\sigma_{s(s)}$ and γ). Recruitment (γ) appears in both groups because the recruitment of seedlings is necessary for seed production, yet $1-\gamma$ or dormancy, promotes the survival of existing seeds.

In the corn and soybean phases, seed production parameters were ranked higher than seed preservation parameters, whereas in the wheat phase, seed preservation parameters were ranked higher than seed production parameters. It makes sense that the seed production parameters should be important to the population growth of an annual seed bearing plant: this is the only way, besides immigration, that the population can grow. Why then, should the ranking have changed so that within-season seed preservation became more important than seed production in the wheat phase (especially within the R treatment)? The explanation can be found in the exact value of the elasticities of λ to each of the seed production-related parameters in the wheat phase: 4.6×10^{-6}. This is relatively close to the season-long probability (4.6×10^{-8}) of newly shed seed in the wheat/red clover intercrop surviving post-dispersal seed predation. The extremely low value of $\sigma_{s(pred)}$ reflected the nearly complete elimination of all inputs to the seedbank during the wheat phase in the R treatment, making the survival of those seeds that didn't germinate more important to long-term giant foxtail population growth (as seen in the large elasticity of λ to $\sigma_{s(w)}$ and in the negative elasticity of λ to γ.

LTRE analysis

Use of the AIC in our parameter estimation process resulted in four of the six demographic parameters (γ, $\sigma_{s(s)}$, $\sigma_{s(w)}$ and $\sigma_{s(pred)}$) differing between the W and R treatments (Fig. 3.3). Treatment differences in parameter values were greatest for γ (0.12), followed by $\sigma_{s(s)}$ (0.06), $\sigma_{s(w)}$ (0.04) and $\sigma_{s(pred)}$ (0.003). Survival of post-dispersal seed predation, $\sigma_{s(pred)}$, varied between the two crop sequences only in the wheat phase.

Sensitivity of λ to giant foxtail demographic parameters (Fig. 3.4) could be divided into three groups on the basis of magnitude: 1) sensitivity of λ to $\sigma_{s(pred)}$ in the corn ($S_{B(h)}$ =57) and wheat ($S_{B(h)}$ = 184) phases was at least an order of magnitude greater than all other sensitivities; 2) sensitivity of λ to γ, σ_p, $\sigma_{s(s)}$, $\sigma_{s(w)}$ and $\sigma_{s(pred)}$ (in soybean) was in an intermediate range ($S_{B(h)}$ varied from 0.66 to 4.9); and 3) sensitivity of λ to φ was at least an order of magnitude lower than the intermediate range ($S_{B(h)}$ varied from 0.005 to 0.03). Although the sensitivity of λ to γ in the wheat phase was intermediate in magnitude, it was distinct from the other sensitivity values in that its sign was negative.

Contributions of the b_{hijk} to treatment differences in λ (Fig. 3.5) were divided into two groups on the basis of sign: a negative contribution from γ in the wheat phase (-0.28), and positive contributions from the rest of the parameters, summing to 1.66. Among the positive contributions to λ, there were two distinct groups based on magnitude of the contribution: contributions of $\sigma_{s(pred)}$ in the wheat phase (0.55), γ in the corn (0.20) and soybean (0.41) phases, and $\sigma_{s(s)}$ in the wheat phase (0.18) were at least twice as large as all other contributions, which ranged from 0.01 to 0.09. Plant survival and fecundity did not contribute to treatment differences in λ. Three parameters, $\sigma_{s(pred)}$ in the wheat phase and γ in the corn and soybean phases, accounted for 84% of the total contributions to λ. The sum of

contributions to treatment differences in λ over all b_{hijk} was 1.38, in exact agreement with the difference in λ between the two crop sequences predicted by the simulation model.

The story told by the LTRE analysis of the periodic matrix model was much the same as that told by elasticity analysis: factors that influenced seed production were more important during the corn and soybean phases of the crop sequence, and factors that influenced seed preservation were more important during the wheat phase. What makes the use of the LTRE approach helpful here is the level of detail with which the story can be told. For each b_{hijk} the product of multiplying treatment differences in parameter value by the sensitivity of λ to that particular parameter represents the contribution of that parameter to treatment differences in λ. Thus it is possible, for the experimental system being studied, to understand the exact degree of importance of each of the demographic parameters to overall population growth rate.

In the elasticity analysis, we saw that factors affecting seed production were important in both corn and soybean phases of the crop sequence, with γ slightly less important than the other parameters. We discovered in the LTRE analysis, however, that of the four parameters influencing inputs to the seedbank in the corn and soybean phases, γ, σ_p, ϕ and $\sigma_{s(pred)}$, only γ showed any variation due to crop sequence in the system being studied, and therefore only γ contributed to differences in growth rate between the two crop sequences. Within the wheat phase, elasticity analysis told us that variation in parameters affecting inputs to the seedbank, including $\sigma_{s(pred)}$, would be less important than variation in parameters affecting seed preservation.

When the experimental data were taken into account, however, the extremely low value of $\sigma_{s(pred)}$ in the wheat rotation, combined with the strong regulatory role of seed survival in the annual plant habit, meant that additive perturbations to $\sigma_{s(pred)}$ would have a

large impact on λ. The high sensitivity of λ to $\sigma_{s(pred)}$ (at S_{Bih} = 184, the largest sensitivity value in the model) in the wheat phase, multiplied by modest differences in $\sigma_{s(pred)}$ between the R and W treatment, gave rise to the largest single LTRE contribution (0.55) to treatment differences in λ.

The large contribution made by $\sigma_{s(pred)}$ in the wheat phase is in contrast to the prediction made by elasticity analysis, and also helps explain the reversal in elasticity rankings for the wheat phase compared to the corn and soybean phases. The acute seed predation bottleneck in the wheat phase made seed preservation parameters more important than in the corn and soybean phases, where seed production proceeded relatively unimpeded. Both γ and $\sigma_{s(s)}$ contributed to treatment differences in λ within the wheat phase, although their contributions were made in opposite directions: variation in γ tended to increase λ in the R treatment compared to the W treatment (thus reducing $\Delta\lambda$), whereas variation in $\sigma_{s(s)}$ tended to decrease λ in the R treatment compared to the W treatment (thus increasing $\Delta\lambda$). The negative contribution made by γ was due to the seed preservation value of the increase in dormancy associated with a lower value of γ in the R treatment than in the W treatment (Fig3). Finally, although overwinter seed survival was identified by elasticity analysis as the single parameter whose variation would most affect λ, variation in $\sigma_{s(w)}$ between treatments was small, and it made only a small contribution to treatment differences in λ.

The periodic LTRE performed well for the experimental system being studied. It is likely that the exact agreement between the LTRE approximation and $\Delta\lambda$ predicted by the simulation model reflects the extreme simplicity of the life cycle of an annual plant with an unstructured seedbank. In such a case, the linear approximation of the LTRE modeled the data very precisely.

Both elasticity and LTRE analysis were useful in understanding the results of the experiment, but LTRE analysis gave much more specific information pertaining to the experimental system. This is not to question the importance of elasticity analysis, or prospective perturbation analysis in general, but rather to call attention to the suitability of retrospective perturbation analysis for analyzing experimental results in the hopes that it will be used more frequently in the future. Properly used, it can help to highlight management choke points (already identified through prospective perturbation analysis) that are indeed susceptible to management interventions in the field.

The modeling exercise presented here was intended to elucidate how cropping system design itself could affect weed population growth. The parameter values used in this model were therefore obtained in the absence of external weed control measures. Giant foxtail seedling survival rate in absence of weed control was very high (97%), whereas under production conditions, seedling survival rate would be likely to vary between 0 and 20%, depending upon the control tactics employed (Buhler et al., 1992; Mulder and Doll, 1993). We ran a second set of simulations (results not shown) to examine crop sequence effects on giant foxtail demography under a production scenario in which weed control with rotary hoeing and inter-row cultivation resulted in only 10% of giant foxtail seedlings surviving to reproductive maturity. Under the low seedling survival (LSS) scenario, the model projected rapid giant foxtail population declines under both treatments, with a slightly more rapid decline in the R treatment ($\lambda = 0.055$) than in the W treatment ($\lambda = 0.068$). Sensitivity analysis indicated that λ was most sensitive to $\sigma_{s(pred)}$ in the wheat and corn phases, similar to the high seedling survival (HSS) scenario. In contrast to the HSS scenario, λ was next most sensitive to σ_p in the corn and soybean phases, and $\sigma_{s(s)}$ in the corn and wheat phases, with lower sensitivity to γ and $\sigma_{s(w)}$.

The consistently high sensitivity of λ to $\sigma_{s(pred)}$ under both the HSS and LSS scenarios indicates that further research into cropping system effects on post-dispersal weed seed predation should be a high priority. It is especially important, for modeling purposes, to develop an improved understanding of 1) the proportion of weed seeds that is consumed by seed predators across the entire growing season, and 2) the effects of predator density and weed seed density on seed predation rate. Simple compounding of daily seed predation rate over the period of seed rain, the method used here to estimate season-long seed predation rates, probably results in unrealistically high values of seed predation. To understand what levels of seed predation would be necessary to maintain or reduce the giant foxtail population under the HSS and LSS scenarios, we plotted λ against the mean of $\sigma_{s(pred)}$ over the three phases of the crop rotation (Figure 6). The threshold values for the percentage of seeds surviving seed predation, below which the giant foxtail population would decrease, were approximately 3 and 4% for the W and R treatments, respectively, in the HSS scenario, and 27 and 37% for the W and R treatments, respectively, in the LSS scenario. It remains to be seen how closely these values correspond to season-long empirical measurements of giant foxtail seed predation.

Implications for agronomic management

Our results suggest that improved knowledge of agronomic management effects on post-dispersal seed predation would be useful to farmers. They also suggest that, wherever possible, farmers should consider taking steps to increase rates of post-dispersal seed predation, such as 1) postponing fall tillage to allow seed predators foraging on the soil surface sufficient time to find and consume newly dispersed seed, 2) diversifying crop rotations with legume-small grain intercrops to provide within-field habitat for seed predators

(Davis and Liebman "SUBMITTED" a), and 3) increasing landscape complexity of the farming operation to improve habitat for seed predators migrating from areas surrounding fields (Menalled et al. 2000).

Cropping system design tends to be driven by concerns other than weed prevention. Nevertheless, as more detailed information concerning cropping system effects on weed demography becomes available, producers may opt for more weed suppressive cropping systems when choosing between systems that are roughly equivalent in other important characteristics. Retrospective perturbation analysis of periodic matrix models offers one analytical method that should make such choices clearer in the future.

Acknowledgements

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the difference in parameter values between the two treatments (Fig. 3.3) and the sensitivity of λ to changes in that parameter (Fig. 3.4).

Fig. 3.6. The sensitivity of giant foxtail population growth rate (λ) to the mean percentage, over all rotation phases, of seeds not removed by seed predators ($\sigma_{s(pred)}$). Results are shown for contrasting weed management scenarios, in which either a) 97% or b) 10% of giant foxtail seedlings survived to reproductive maturity. The dotted horizontal line represents a situation where the population size remains the same ($\lambda = 1$). Note difference in x-axis scale.

Table 3.1. Estimated values for giant foxtail demographic parameters in two crop sequences in Boone, IA, USA.

Parameter	Abbreviation	Units[a]	Crop sequence	Parameter values in each crop phase[b]		
				Wheat	Corn	Soybean
Recruitment	γ	$N_{plt(Jun.)} N_{sd(Mar.)}^{-1}$	W-C-S	0.56	0.56	0.56
Plant survival	σ_p	$N_{plt(Aug.)} N_{plt(Jun.)}^{-1}$	W-C-S	0.97	0.97	0.97
Seed survival$_{Mar.-Oct.}$	$\sigma_{s(s)}$	$N_{sd(Oct.)} (N_{sd(Mar.)}-N_{plt(Jun.)})^{-1}$	W-C-S	.50	.50	.50
Fecundity	ϕ	seeds plant^{-1}	W-C-S	57	57	57
Seed survival$_{Predation}$	$\sigma_{s(Pred)}$	$N_{newsd(Oct.)} N_{newsd(Aug.)}^{-1}$	W-C-S	0.003	0.016	0.36
Seed survival$_{Oct.-Mar.}$	$\sigma_{s(w)}$	$N_{sd(Mar.)} N_{sd(Oct.)}^{-1}$	W-C-S	0.90	0.90	0.90
Recruitment	γ	$N_{plt(Jun.)} N_{sd(Mar.)}^{-1}$	R-C-S	0.44	0.44	0.44
Plant survival	σ_p	$N_{plt(Aug.)} N_{plt(Jun.)}^{-1}$	R-C-S	0.97	0.97	0.97
Seed survival$_{Mar.-Oct.}$	$\sigma_{s(s)}$	$N_{sd(Oct.)} (N_{sd(Mar.)}-N_{plt(Jun.)})^{-1}$	R-C-S	0.44	0.44	0.44
Fecundity	ϕ	seeds plant^{-1}	R-C-S	57	57	57
Seed survival$_{Predation}$	$\sigma_{s(Pred)}$	$N_{newsd(Oct.)} N_{newsd(Aug.)}^{-1}$	R-C-S	4.7×10^{-8}	0.016	0.36
Seed survival$_{Oct.-Mar.}$	$\sigma_{s(w)}$	$N_{sd(Mar.)} N_{sd(Oct.)}^{-1}$	R-C-S	0.86	0.86	0.86

[a] Abbreviations: N_{plt} = number of plants, N_{sd} = number of seeds, N_{newsd} = number of newly shed seeds; W = wheat, C = corn, S = soybean, R = wheat + red clover intercrop.

[b] Parameter estimates were based on data collected from a field study in Boone, IA, USA. All parameters were measured within the corn phase of each crop sequence, with the exception of $\sigma_{s(Pred)}$, which was measured within each phase of each crop sequence.

Table 3.2. Elasticity of population growth rate (λ) to demographic parameters of giant foxtail grown under contrasting crop sequences.

Crop sequence[a]	Crop phase	Demographic parameter					
		γ	$\sigma_{s(s)}$	σ_p	ϕ	$\sigma_{s(pred)}$	$\sigma_{s(w)}$
W-C-S		Elasticity of λ					
	wheat	-0.60	0.70	0.30	0.30	0.30	1.0
	corn	0.48	0.23	0.77	0.77	0.77	1.0
	soybean	0.96	0.02	0.98	0.98	0.98	1.0
R-C-S							
	wheat	-0.78	1.0	4.6×10^{-6}	4.6×10^{-6}	4.6×10^{-6}	1.0
	corn	0.47	0.30	0.70	0.70	0.70	1.0
	soybean	0.95	0.03	0.97	0.97	0.97	1.0

[a] Crop sequence and demographic parameter abbreviations are the same as described in Table 3.1.

$$n_{t+1} = (B_{(h-1)}...B_{(m)}B_{(1)}...B_{(h+1)}B_{(h)})_k n_t$$

$$n_t = \begin{bmatrix} n_s \\ n_p \end{bmatrix}$$

Recruitment

$$B_{(1_k)} = \begin{bmatrix} 1-\gamma & 0 \\ \gamma & 0 \end{bmatrix}$$

Spring survival

$$B_{(2_k)} = \begin{bmatrix} \sigma_{s(s)} & 0 \\ 0 & \sigma_p \end{bmatrix}$$

Fecundity

$$B_{(3_k)} = \begin{bmatrix} 1 & \phi\sigma_{s(pred)} \\ 0 & 0 \end{bmatrix}$$

Winter survival

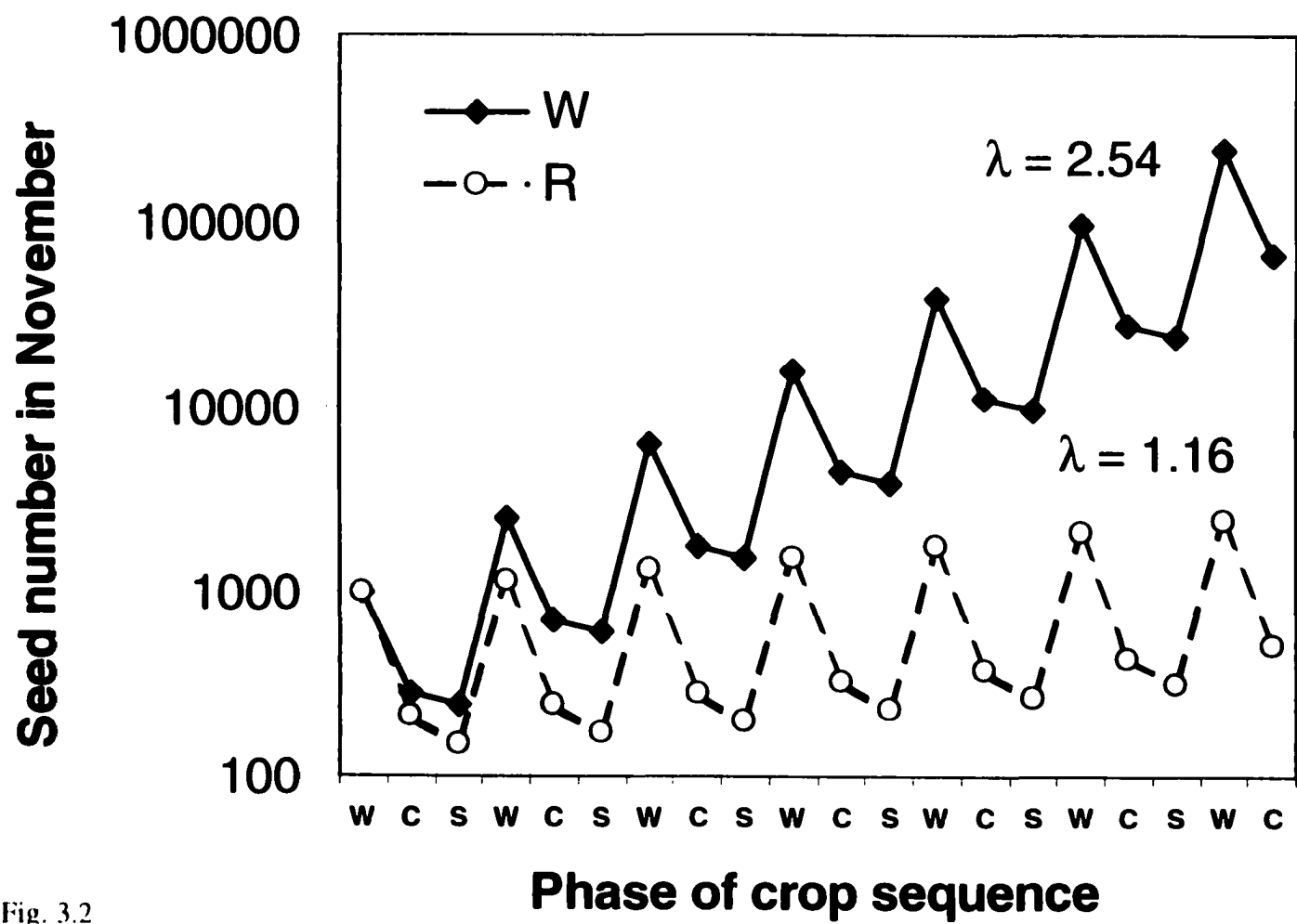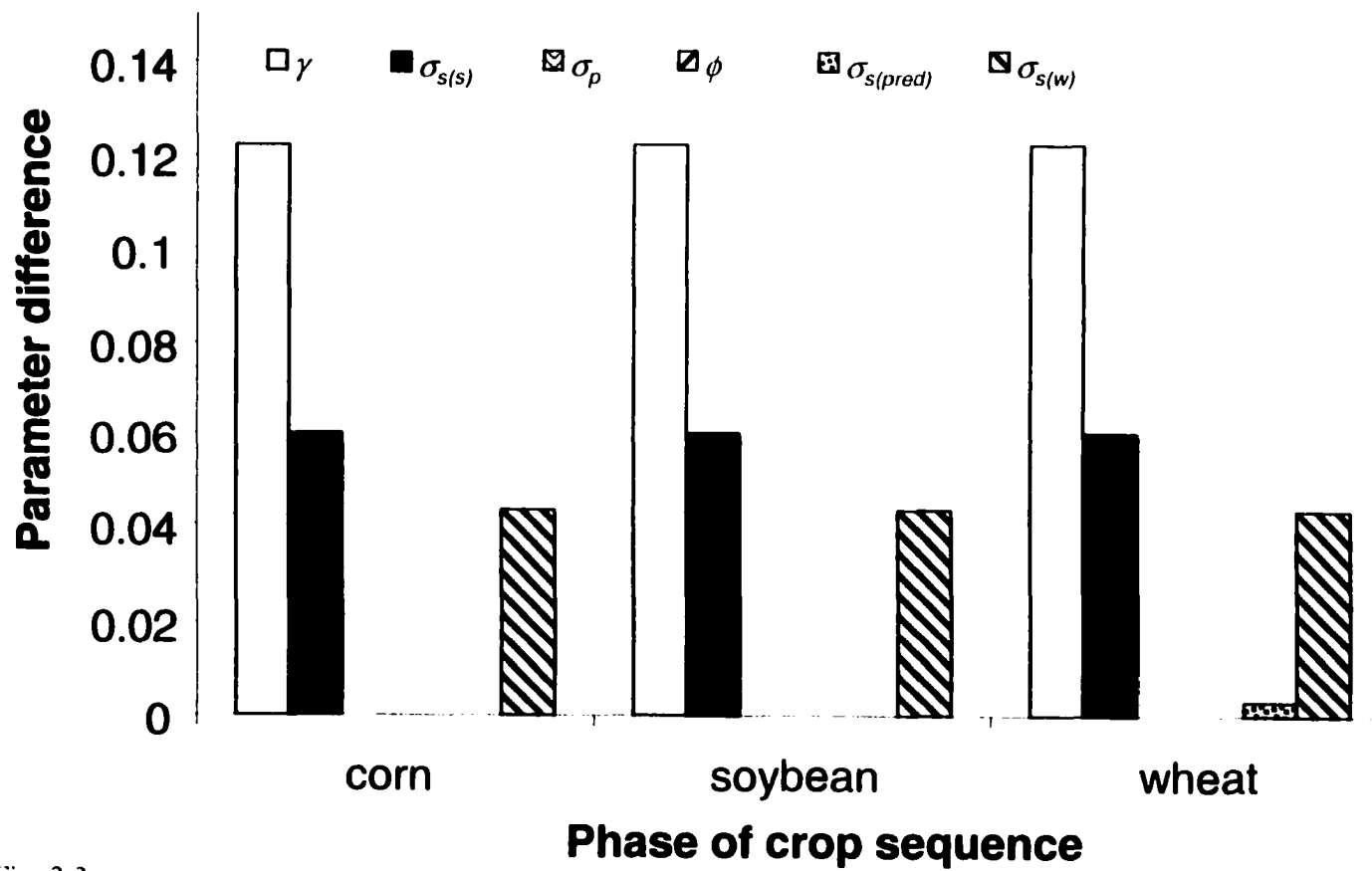$$B_{(4_k)} = \begin{bmatrix} \sigma_{s(w)} & 0 \\ 0 & 0 \end{bmatrix}$$
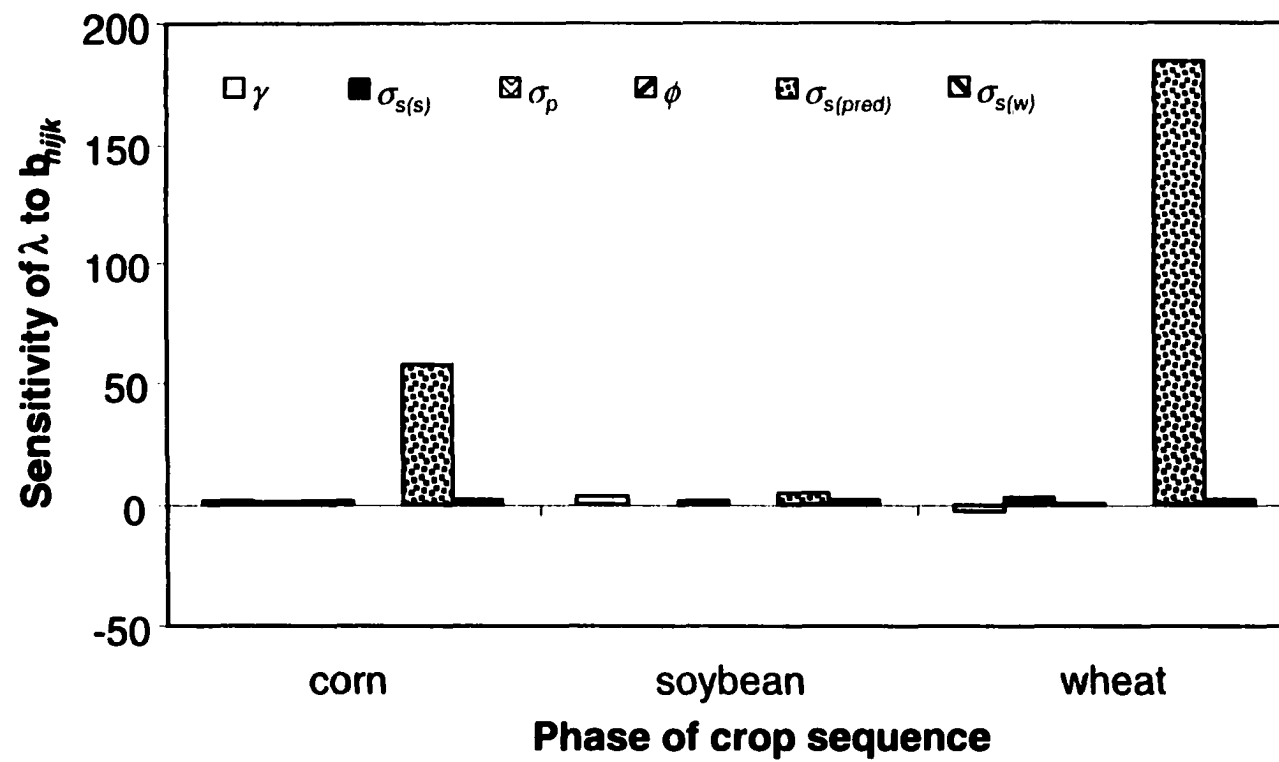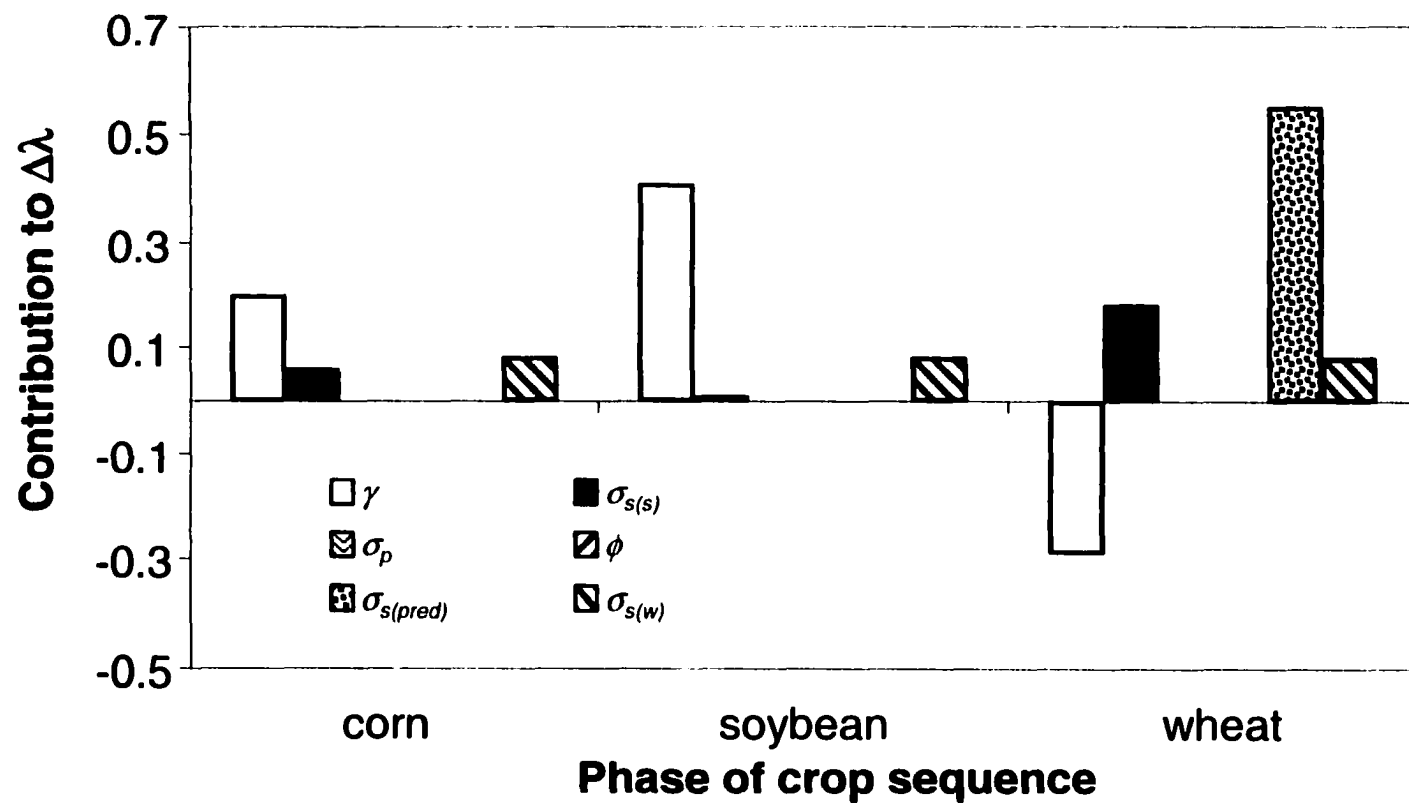
Fig. 3.1

Fig. 3.2

Fig. 3.3

Fig. 3.4

Fig. 3.5

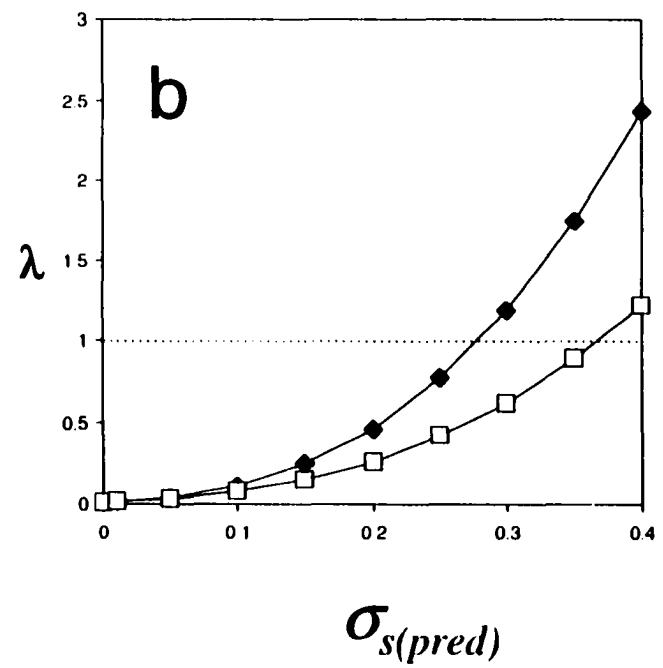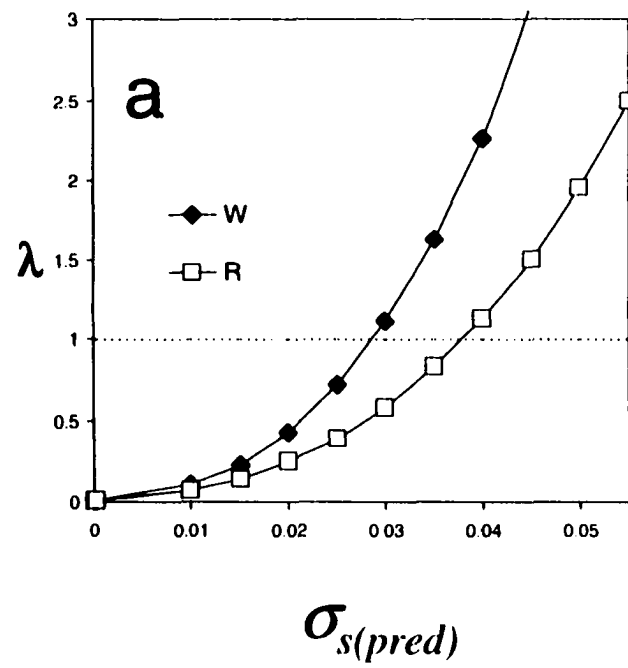Fig. 3.6

CHAPTER 5. PROSPECTIVE AND RETROSPECTIVE PERTURBATION ANALYSES OF CROPPING SYSTEM EFFECTS ON WEED DEMOGRAPHY

A paper for submission to Ecological Applications

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Abstract

Most agricultural systems are designed without regard to their intrinsic effects upon weed populations. Yet cropping system characteristics may affect weed population dynamics by altering key demographic rates of weeds. We examined the effects of legume green manure and tillage timing upon giant foxtail (*Setaria faberi*) demography using both prospective and retrospective perturbation analysis of a periodic matrix population model. Demographic data were collected for *S. faberi* grown in a wheat-corn-soybean crop sequence in the central USA in 2000 and 2001, with either a wheat sole-crop ('W') or wheat/red clover crop mixture ('R') in the wheat phase. Residues from the wheat phase were incorporated either in fall ('FT') or spring ('ST') for a factorial of four cropping system treatments: FT/W, FT/R, ST/W, ST/R. Demographic rates estimated from the field data included seed survival from October to March ($\sigma_{s(w)}$) and March to October ($\sigma_{s(s)}$), seedling recruitment (γ), plant survival (σ_p), fecundity (ϕ) and proportion of newly dispersed seeds not consumed by seed predators ($\sigma_{s(pred)}$). Variable efficacy of post-emergence weed control was simulated in the model by varying the proportion of seedlings surviving to reproductive maturity (σ_p) from 0.025 to 0.20. Deterministic simulations of *S. faberi* population growth indicated that there was both interannual and management-induced variation in *S. faberi* population growth rate (λ). Stochastic population growth rate (ln λ_s) was subject to an interaction between legume green manure and tillage timing effects, such that ln $\lambda_{s(FT/R)}$ < ln $\lambda_{s(FT/W)}$ < ln $\lambda_{s(ST/W)}$ = ln $\lambda_{s(ST/R)}$. Values of ln λ_s for the W and R levels of the FT treatment diverged as σ_p increased.

whereas the converse was true for the ST treatment. Elasticity analysis suggested that $\sigma_{s(w)}$, ϕ, and $\sigma_{s(pred)}$ were important driving variables for this system. Retrospective perturbation analysis supported these results, but also indicated that ϕ and $\sigma_{s(pred)}$ varied more in response to changing management treatments than $\sigma_{s(w)}$, leading to greater contributions from ϕ and $\sigma_{s(pred)}$ to differences in λ between the various management treatments than from $\sigma_{s(w)}$. Perturbation analyses of matrix population models will aid the development of integrated weed management systems by elucidating cropping system effects upon weed demography.

Key words: cropping system design; ecological weed management; legume green manure; tillage timing; *Setaria faberi*; giant foxtail; elasticity analysis; retrospective perturbation analysis; Life Table Response Experiment (LTRE); periodic matrix population model; stochastic simulation

INTRODUCTION

Agriculture is a form of ecosystem management that uses repeated disturbance, simplified trophic webs, and large pulses of plant macronutrients to promote vigorous crop growth (Altieri 1995). Most agricultural weeds are non-crop plant species, primarily arising from taxa with ruderal life histories, that are pre-adapted to exploit such conditions (Baker 1974). Although cropping system characteristics are usually chosen with little regard to their impacts upon weeds, they may affect weed population dynamics by altering key demographic rates of weeds (Mohler 2001; Mertens et al. 2002). We believe that this often overlooked facet of cropping system design may be of particular importance to farmers wishing to reduce their reliance upon herbicides for weed management (Liebman and Davis 2000). Our goal in the present study was to use some of the powerful tools developed for

demographic analysis, including matrix population models (Caswell 2001) and perturbation

methods (de Kroon et al 2000), to understand how cropping system characteristics might

contribute to weed management.

Matrix population models offer a concise, analytically tractable way to simulate the

growth of age- or stage-structured populations over discrete time steps (Caswell 2001). In

contrast to the extensive use of matrix models in basic population ecology (Kalisz and

McPeek 1992, Bierzychudek 1999, Emery et al. 1999, Rydgren et al. 2001, Pico et al. in

press) and conservation biology (Crouse et al. 1987, Crowder et al. 1994, Doak et al. 1994,

Seamans et al. 1999), this approach has been applied only rarely to weed management

questions (Jordan et al. 1995, Pino et al. 1998, Shea and Kelly 1998, Mertens et al. 2002).

One of the clear benefits of applying matrix simulation models to problems in ecological

weed management is the ability of such models to integrate the effects of multiple

management tactics upon different life stage transitions so that weed population growth may

be observed as an emergent property of management practices.

In addition to providing information about weed population growth rate (λ) under

different conditions, matrix models may also be used to understand how perturbations to

model parameters affect λ. Prospective perturbation analysis, including sensitivity and

elasticity analysis (de Kroon et al, 2000), may be used by ecosystem managers to identify

potential management "choke points": demographic parameters whose variation causes large

changes in λ. Thus, management effort aimed at suppressing weed life stage transitions with

high elasticities has a good chance of limiting weed population size. One drawback of such

an approach, however, is that the elasticity of λ to a given demographic parameter tends to be

inversely correlated with the variability of that parameter (de Kroon et al. 2000, Pico et al. IN

PRESS). That is, demographic parameters whose variation causes large changes in λ tend to resist change.

Because of the relative ease of performing replicated, small scale experiments of management effects on weed demographic rates, we suggest that supplementing prospective perturbation analysis with retrospective perturbation analysis of matrix simulation models will help to verify putative weed management choke points for a given set of management conditions. The Life Table Response Experiment (LTRE) approach to retrospective perturbation analysis decomposes treatment effects on λ into contributions from each matrix element by weighting treatment differences in each matrix element by the sensitivity of λ to changes in each matrix element (Caswell 2001). Hence, a demographic parameter that is resistant to change across a wide range of experimental conditions will not make a substantial contribution to treatment differences in λ, even if λ is highly sensitive to potential changes in that parameter. The use of retrospective perturbation analysis to verify management choke points identified by elasticity analysis will help weed managers to understand which management choke points tend to be important under a given set of production conditions. Caswell (2001) points out that retrospective perturbation analysis describes the past performance of a system and may not accurately describe how demographic rates will vary in the future. Therefore, focusing solely on retrospective perturbation analysis will not yield an accurate description of the system, in the same way that blind adherence to elasticity methods may also ignore important information about the actual range of parameter variability.

Our specific modeling objectives were to understand how legume green manure and tillage timing affect the demography and management of *Setaria faberi* Herrm. (giant foxtail). *Setaria faberi* is a warm-season annual grass weed of economic importance throughout the midwest Corn Belt (Lindquist et al. 1999) that has been extensively

characterized at the genetic (Wang et al. 1995), morphological (Forcella et al. 2000) and

physiological (Dekker and Hargrove 2002) levels. We chose to examine legume green

manure and tillage timing effects on *S. faberi* demography because the management of

organic matter amendments to soil is of great importance to farmers wishing to reduce their

reliance upon external chemical inputs. Such amendments have historically been used for

their contributions to soil fertility and tilth, and have more recently been recognized to have

potential weed management benefits (Liebman and Davis 2000). Previous work has

demonstrated that weed growth and interference with corn may be limited in soils amended

with the residues of legume green manures (Dyck and Liebman 1994, Davis and Liebman

2001, Conklin et al. 2002). The strength of weed suppression by these residues was inversely

proportional to the amount of time elapsed following their incorporation into the soil

(Conklin et al. 2002), suggesting that tillage timing was a potentially important factor

affecting weed management in green manured systems. In a field experiment examining

legume green manure and tillage timing effects on *S. faberi* life stage transitions within the

context of a corn-soybean-wheat crop sequence (Davis and Liebman SUBMITTED), we

found that the two experimental factors interacted in their effects on *S. faberi* recruitment,

fecundity and overwinter seedbank decline. A preliminary modeling study (Davis et al.

SUBMITTED) showed that legume green manure residues had the potential to affect *S.

faberi* demography in the absence of external weed control practices, e.g., herbicide

application or cultivation.

In the present study, we wished to better understand the interaction between external

forms of weed control and the inherent effects of a particular set of management practices

upon weed demography and management. We used a periodic matrix population model

(Caswell 2001) to project *S. faberi* population growth in each the cropping system treatments

studied in Davis and Liebman (SUBMITTED). Our study focused on two primary research

questions: 1) could differential tillage timing and use of legume green manure influence the

population growth rate of *S. faberi* within an agricultural system subjected to some form of

external weed control?; and 2) could we identify, through prospective and retrospective

perturbation analysis, consistent weed management choke points in the *S. faberi* life cycle?

METHODS

Field study of S. faberi demography

Experimental design and field procedures. The materials and methods employed in

the empirical component of this research are explained fully in Davis and Liebman

(SUBMITTED) and will be described only in brief detail here. We studied the effects of

legume green manure and tillage timing on *S. faberi* demography within the context of a

corn-soybean-wheat crop sequence at the Iowa State University Agronomy Farm near Boone.

IA. in 2000 and 2001. The wheat phase of the crop sequence was grown either as a sole crop

('W') or was underseeded with red clover to form a wheat/red clover crop mixture ('R').

Residues from the wheat phase were incorporated into the soil with a power-takeoff driven

rototiller either in late fall ('FT') or early spring ('ST'). The two levels of the *Red clover* (W

and R) and *Tillage timing* (FT and ST) treatments were combined in a factorial treatment

design to give four cropping system treatments: FT/W, FT/R, ST/W and ST/R. These

treatments were arranged in a split plot experimental design with four replications, where

Tillage timing was the main plot factor. and *Red clover* was the subplot factor. Each

replication was composed of two adjacent 3.8 m by 12.2 m main plots, each of which

contained two 3.8 m by 6.1 m subplots.

Parameter estimation. Six demographic parameters were estimated for *S. faberi* using data from the 2000 and 2001 field seasons: recruitment (γ), seed survival from March through October ($\sigma_{s(s)}$), plant survival to reproductive maturity (σ_p), seed production per plant (Φ), proportion of seeds not consumed due to post-dispersal seed predation prior to fall tillage ($\sigma_{s(pred)}$), and seed survival from October through March ($\sigma_{s(w)}$). Rules for parameter estimation are given in Table 4.1, parameter values are given in Table 4.2, and the life history of *S. faberi* is summarized in Figure 4.1. Model selection using AIC (Akaike Information Criterion) was used to decide whether to use a separate parameter estimate for each factor or to average over factors. Use of AIC helps to optimize the tradeoff between variance (the average is more precise) and bias (the average is inappropriate when factor means are different) (Burnham and Anderson 1998).

Recruitment, plant survival and fecundity were estimated as the mean of these parameters for the first two emergence cohorts, which accounted for over 90% of *S. faberi* recruitment and reproductive output. Daily rates of $\sigma_{s(pred)}$ were converted into a season-long estimate of $\sigma_{s(pred)}$ by compounding point estimates of $\sigma_{s(pred)}$ from late September, when predation rates were at their peak, over 20 days. We considered compounding the daily rates of $\sigma_{s(pred)}$ over the entire predation period from August through October, but the resulting percentages of surviving seeds were too low to be realistic. We measured γ, Φ, and $\sigma_{s(pred)}$ in all three phases of the crop sequence, whereas we measured $\sigma_{s(w)}$ and $\sigma_{s(s)}$ in the corn phase only and applied these values to the soybean and wheat phases. Although the field experiment was performed with no form of external weed control, we accounted for the effects of post-emergence weed control on weed seedling survival by setting σ_p at 10% for the deterministic simulation, and varying σ_p between 2.5 and 20% for the stochastic

simulation. These values of σ_p fall within a range that is realistic for field crop production systems (Buhler et al. 1992, Mulder and Doll 1993).

Periodic matrix model

We simulated the effects of *Red clover* and *Tillage timing* on *S. faberi* population growth rate using linear deterministic and linear stochastic periodic matrix population models (Caswell 2001). Periodic models explicitly account for variations in life stage transition probabilities in a sequence of environments that repeats itself over time (Caswell and Trevisan 1994). Periodic matrix models have been used previously in the weed science literature to understand the effect of management within the sequence of environments arising from progression of crops within a crop rotation (Jordan et al. 1995, Mertens et al. 2002). Our model followed *S. faberi* demography through four sub-annual periods in each of the phases in the wheat-corn-soybean crop sequence, for a total of 12 periods in one rotation cycle (Fig. 4.2). We did not define a depth-structured seedbank because seedbank decline is rapid for *S. faberi* between 0 and 5 cm soil depth (Buhler and Hartzler 2001), and is approximated well by compounding decay rates for an unstructured seedbank across periods.

Deterministic simulation. Using the notation of Caswell (2001), the projection equation describing the dynamics of the population over an entire rotation cycle was

$$\mathbf{n}_{t+1} = (\mathbf{B}_{(h-1)}...\mathbf{B}_{(1)}\mathbf{B}_{(m)}...\mathbf{B}_{(h+1)}\mathbf{B}_{(h)})_k \mathbf{n}_t \qquad h=1,...,m \qquad [1]$$

$$= \mathbf{A}_{(h)}\mathbf{n}_t \qquad [2]$$

where $\mathbf{n}_t$ and $\mathbf{n}_{t+1}$ were vectors of the population size at the beginning and ends of the rotation cycle, respectively, each $\mathbf{B}_{(h)}$ was a projection matrix for period h in phase k of the crop sequence, $\mathbf{A}_{(h)}$ was a projection matrix for the entire rotation cycle starting at period h in

phase k of the crop sequence, and m was the number of sub-annual periods (Fig. 4.2). The population growth rate of *S. faberi* over the rotation cycle (λ_{cycle}) was calculated as the dominant eigenvalue of $A_{ih.}$ (Caswell 2001).

Because only the seeds of *S. faberi* survive over the winter, the projection over the entire rotation cycle starting in the winter describes changes in the number of seeds over time, with only one non-zero element. a_{11}, in $A^{(h_k)}$. We realize that it is unusual to use the matrix approach to simulate unstructured populations, but we felt justified in using matrix terminology for three reasons. First, including sub-annual transition matrices in the model helps clarify the life stage transitions included in the model for a more general audience. Second, we made use of the powerful prospective and retrospective perturbation analysis tools developed for matrix models (Caswell and Trevisan 1994, Caswell 2001), and wanted to highlight the utility of such techniques to those who might want to simulate the dynamics of weed species with structured populations or more complex life histories. Third, the periodic matrix model can be started at any phase, e.g., one with both plants and seeds, for which the transition matrix is not scalar.

The data set used to parameterize this model comprised four replications, allowing us to calculate λ_{cycle} for each replication within each year. We used this variation in the error terms of a split-plot analysis of variance of cropping system effects on ln λ_{cycle}. The log$_e$ transformation of λ_{cycle} was used to meet ANOVA assumptions (Neter et al. 1996). Our ANOVA model included terms for main effects of *Year*, *Tillage timing* and *Red clover*, and interaction effects between each of these factors (Wilkinson 1999).

Stochastic simulation. We simulated the effects of random environmental variation on *S. faberi* population projections under the four cropping system treatments using independent

identically distributed (*iid*) sequences of environments (Caswell 2001). Phase-specific annual

projection matrices were chosen in *iid* fashion from the 2000 and 2001 data sets. The *S.*

faberi population was projected forward from the fall of the wheat rotation phase, starting

with an initial population vector containing 1000 seeds. A numeric simulation was used to

calculate the stochastic population growth rate (ln $\lambda_{s(cycle)}$) over the three-phase rotation cycle

(Heyde and Cohen 1985, Caswell 2001). One-step estimates of ln $\lambda_{s(cycle)}$ from the wheat

phase in rotation cycle (*i*) to the wheat phase in rotation cycle (*i* + 1) were averaged over T

rotation cycles as follows

$$\ln \lambda_{s(cycle)}(i) = N(i+1) - \ln N(i) \qquad [3]$$

$$\ln \lambda_{s(cycle)} = \sum_i \ln \lambda_{s(cycle)}(i)/(T-1). \qquad [4]$$

We ran the simulation for 1500 iterations, and discarded the results for the first 500 iterations

to avoid the transient behavior of the model (Caswell 2001).

We examined the effects of variable post-emergence weed control efficacy on ln $\lambda_{s(cycle)}$

by simulating population growth for values of σ_p ranging from 0.025 through 0.20 in

increments of 0.025. At each level of σ_p, we took the mean of ln $\lambda_{s(cycle)}$ obtained through one

realization of the stochastic simulation for each of the four experimental replications. We

subjected values of ln $\lambda_{s(cycle)}$ at each level of σ_p to ANOVA, using models that included

terms for *Tillage timing*, *Red clover* and the interaction between these factors (Wilkinson,

1999). This was followed by a Tukey multiple comparison test to detect cropping system

treatment differences in ln $\lambda_{s(cycle)}$ (Neter et al., 1996).

Perturbation analysis of deterministic simulation model

Prospective. Prospective perturbation analysis, which includes sensitivity and

elasticity analysis, identifies model parameters whose variation has an important effect on λ.

Sensitivity analysis examines changes in λ in response to additive perturbations to each

element of A ($S_A = \partial\lambda/\partial a_{ij}$), whereas elasticity analysis examines changes in λ in response to

proportional perturbations to each a_{ij} ($E_A = (a_{ij}/\lambda)(\partial\lambda/\partial a_{ij})$) (Caswell 2001). A direct method

for obtaining S_A is to calculate eigenvalue sensitivities to perturbations of elements of the

annual projection matrix. The elements of S_A are computed using the right (w) and left (v)

eigenvectors

$$\frac{\partial\lambda}{\partial a_{ij}} = \frac{v_i w_j}{\langle w.v \rangle} \tag{3}$$

where a_{ij} are the elements of A, and $\langle w,v \rangle$ is the scalar product of the right and left

eigenvectors of A (Caswell 2001).

This procedure has been extended to permit the calculation of eigenvalue sensitivities

of periodic projection matrices (Caswell and Trevisan 1994):

$$S_{B..} = D^T S_{A..}$$

$$= (B_{(h-1)}...B_{(1)}B_{(m)}...B_{(h+1)})^T S_{A..} \tag{4}$$

where S_B represents the sensitivity of λ to changes in the elements of periodic projection

matrix $B_{(h)}$. D^T represents the transpose of the product of the periodic projection matrices

excluding $B_{(h)}$. and $S_{A..}$ represents the sensitivity of λ to changes in the elements of $A_{(h)}$ (the

annual projection matrix for the interval beginning at time period h). Elasticities of λ to the

elements, b_{hij}, of periodic projection matrices are then computed as:

$$E_{B..} = (b_{hij}/\lambda)S_{B..} \tag{5}$$

The periodic sensitivity and elasticity calculations shown above describe the response

of λ to perturbations of $A_{(h)}$. The elements of $A_{(h)}$ were determined by the product of the

periodic matrices over all periods and rotation phases, starting with period h in rotation phase

k (at the right-hand side of the product matrix), such that $\mathbf{A}_{(h_i)} = (\mathbf{B}_{(h-1)}...\mathbf{B}_{(1)}\mathbf{B}_{(m)}...\mathbf{B}_{(h+1)}\mathbf{B}_{(h)})_k$.

For the simple system described in this study, all $\mathbf{A}_{(h_i)}$ had only one non-zero element. a_{11}.

which contained the product of all the demographic parameters in each of the rotation phases:

$[(\sigma_{s(w_i)})(\sigma_{s(s_i)})(1-\gamma) + (\sigma_{s(w_i)})(\phi)(\sigma_{s(pred)})(\sigma_p)(\gamma)]_k$. The left-hand term described the fate of

dormant seeds, and the right-hand term described new inputs to the seedbank. Perturbations

to a_{11} involved this entire string of parameters, yet for management purposes, we wanted to

know how λ_{cycle} responded to the perturbation of individual demographic parameters, such as

γ or ϕ. This problem was solved by applying the chain rule for differentiation (Caswell

2001). so that for a given demographic parameter x

$$\frac{\partial \lambda}{\partial x^{(h_i)}} = \sum_{i,j} \frac{\partial \lambda}{\partial b_{ij}^{(h_i)}} \frac{\partial b_{ij}^{(h_i)}}{\partial x^{(h_i)}} \qquad [6]$$

and

$$\frac{x^{(h_i)}}{\lambda} \frac{\partial \lambda}{\partial x^{(h_i)}} = \frac{x^{(h_i)}}{\lambda} \sum_{i,j} \frac{\partial \lambda}{\partial b_{ij}^{(h_i)}} \frac{\partial b_{ij}^{(h_i)}}{\partial x^{(h_i)}} \qquad [7]$$

where equations 6 and 7 describe the sensitivity and elasticity, respectively, of λ with respect

to x.

Standard errors for the elasticity of λ to lower level demographic parameters were

obtained through a bootstrap procedure, using 100 bootstrap samples for each

parameter/treatment combination drawn from variability at the level of experimental

replication (Dixon 2001).

Retrospective. We modified the Life Table Response Experiment (LTRE) approach to

permit the retrospective perturbation analysis of a periodic matrix population model

(Rydgren et al. 2001, Davis et al. SUBMITTED). The LTRE equation was rewritten to

decompose treatment effects on λ into the sum, over all periods and phases, of the product of treatment differences for lower level demographic parameters x_{hijkl} comprising each periodic matrix element b_{hijk} and sensitivity of λ to changes in each x_{hijkl}. The equation used to describe the LTRE approximation for a periodic matrix model was

$$\lambda^{(m)} - \lambda^{(r)} \approx \sum_{hijkl} (x_{hijkl}^{(m)} - x_{hijkl}^{(r)}) \mathbf{D}^{T} S_{\mathbf{A}^{\cdot \cdot}} \Big|_{\mathbf{A}^{\cdot \cdot}}, \qquad m = 1, \ldots, N \quad [8]$$

where m is a treatment of interest, r is a reference treatment, h and k refer to period and rotation phase, respectively, i and j refer to matrix rows and columns, respectively, x_{hijkl} refers to individual lower level demographic parameters comprising elements within the periodic projection matrices, $\mathbf{D}^{T}$ represents the transpose of the product of the phase-specific projection matrices excluding $\mathbf{B}_{hk}$ (see equation 3). $S_{\mathbf{A}hk}$ represents the sensitivity of λ to changes in the lower level demographic parameters comprising the elements of $\mathbf{A}_{hk}*$, and $\mathbf{A}_{hk}* = (\mathbf{A}_{hk}^{(m)} + \mathbf{A}_{hk}^{(r)})/2$. We calculated $\mathbf{A}_{hk}^{(m)}$ and $\mathbf{A}_{hk}^{(r)}$ as the products of treatment-specific $\mathbf{B}_{hk}$, and then averaged over $\mathbf{A}_{hk}^{(m)}$ and $\mathbf{A}_{hk}^{(r)}$ to obtain $\mathbf{A}_{hk}*$.

Although the LTRE approximation can accommodate factorial experimental designs, including those with random experimental factors such as the split plot design (Caswell 2001), for clarity of interpretation and presentation of results, we chose to focus on simple effects of cropping system treatments on λ_{cycle}. For the decomposition of $\Delta\lambda_{cycle}$ into contributions from simple effects of Red clover on lower level S. faberi demographic parameters, we designated the W treatment as the reference treatment (r) and the R treatment as the treatment of interest (m). For the decomposition of $\Delta\lambda_{cycle}$ into contributions from simple effects of Tillage timing on lower level S. faberi demographic parameters, we designated the FT treatment as the reference treatment (r) and the ST treatment as the treatment of interest (m). After the contribution of each x_{hijkl} to treatment differences in λ was

calculated, contributions were summed over all x_{hijkl}. This sum was compared to $\lambda^{(m)} - \lambda^{(r)}$ from the simulation model to obtain percentage error in the LTRE approximation, calculated as $(|\Delta\lambda_{LTRE} - \Delta\lambda_{Model}|)/\Delta\lambda_{Model}$. Standard errors for LTRE contributions were computed using the same bootstrap procedure as described above for prospective perturbation analysis.

RESULTS

Cropping system effects on population growth rate

Deterministic simulation. The deterministic population growth rate of *S. faberi* over the rotation cycle (λ_{cycle}) showed considerable range among cropping systems and between growing seasons (Fig. 4.3, Table 4.3). Analysis of variance of ln λ_{cycle} (the intrinsic population growth rate over the rotation cycle) across growing seasons indicated several significant main and interaction effects of *Year, Tillage Timing* and *Red Clover* on ln λ_{cycle} (Table 4.3). There was a main effect of *Year* on ln λ_{cycle} (N = 16, s.e.m. = 0.18, $F_{1,16}$ = 9.32, P = 0.022), such that in 2000, the average of ln λ_{cycle} over all treatments was negative (-1.30), whereas in 2001, this average was positive (0.24). There was also a main effect of *Tillage timing* on ln λ_{cycle} (N = 16, s.e.m. = 0.18, $F_{1,16}$ = 30.45, P = 0.001). The average of ln λ_{cycle} across growing seasons was negative (-1.10) in the FT treatment, but positive (0.05) in the ST treatment.

Red clover interacted with *Year* in its effect on ln λ_{cycle} (N = 8, s.e.m. = 0.26, $F_{1,8}$ = 15.71, P = 0.002). In 2000, ln λ_{cycle} was lower in the W treatment (-1.42) than in the R treatment (-1.17), whereas in 2001, λ_{cycle} was greater in the W treatment (0.41) than in the R treatment (0.08). *Tillage timing* also interacted with *Year* in its effect on ln λ_{cycle} (N = 8, s.e.m. = 0.26, $F_{1,8}$ = 27.74, P = 0.002). In 2000, ln λ_{cycle} was much lower in the FT treatment (-2.42) than in the ST treatment (-0.17), but in 2001, ln λ_{cycle} was only slightly lower in the

FT treatment (0.22) than in the ST treatment (0.27). The cropping system treatment interactions with *Year* were due to drought conditions in 2000 (rainfall for the period from March through September was only 57% of the 30 year mean for this period) that limited *S. faberi* seed production in all cropping system treatments except for the ST/R treatment. High *S. faberi* fecundity in the ST/R treatment was due to phytotoxic inhibition of early corn growth by red clover residues that had been recently incorporated into the soil, which reduced the competitive effect of corn upon *S. faberi* growth and fecundity (Davis and Liebman SUBMITTED). Growing conditions in 2001 were favorable for *S. faberi*, leading to greater recruitment and fecundity in all treatments in 2001 than 2000 (Table 4.2). Despite treatment by *Year* interactions, there was a *Tillage timing* by *Red clover* interaction effect (N = 8, s.e.m. = 0.25, $F_{1,8}$ = 11.85, P = 0.005), across growing seasons, on ln λ_{cycle}. The natural log of λ_{cycle} was lower in the R level (-1.25) than in the W level (-0.95) of the FT treatment, whereas ln λ_{cycle} was greater in the R level (0.15) than in the W level (-0.06) of the ST treatment.

Stochastic simulation. At a level of post-emergence weed control resulting in 10% seedling survival, which was the value of σ_p assumed for the deterministic simulation, stochastic population growth rate of *S. faberi* over the rotation cycle (ln $\lambda_{s(cycle)}$) followed the pattern observed for the *Tillage timing* by *Red Clover* interaction effect on ln λ_{cycle} (Fig. 4.4).

The importance of cropping system effects on variation in *S. faberi* ln $\lambda_{s(cycle)}$ appeared to vary inversely with the success of post-emergent weed control within the FT treatment, but not within the ST treatment (Fig. 4.4). The W and R levels of the FT treatment were not different (P > 0.05) when post-emergent control resulted in ≤ 10% of seedlings surviving to reproductive maturity. When the percentage of seedlings surviving rose to

12.5%. however. and for all subsequent values. the two levels of the FT treatment were different. As percentage seedling survival increased. values of ln $\lambda_{s(cycle)}$ within the FT treatment continued to diverge (Fig. 4.4). In contrast. the values of ln $\lambda_{s(cycle)}$ for W and R levels of the ST treatment converged as seedling survival increased.

Perturbation analyses of cropping system effects on demography

Prospective. We analyzed the elasticity of λ_{cycle} to each of the lower level demographic parameters of *S. faberi* within each rotation phase. To streamline the presentation of results. the elasticity of λ_{cycle} to each parameter will be designated by the symbol '*e*' followed by the parameter abbreviation. For all cropping systems in all years. $e\sigma_{(n)}$ was 1.0 (Table 4.4). Values of *e*γ were strongly positive (0.74 to 0.99) for the soybean phase. and strongly negative (-1.03 to -4.0) for the wheat phase. in all treatments. In contrast. *e*γ for the corn phase was variable. with a wide range of negative values (-0.11 to -0.81) in the FT/W. FT/R and ST/W treatments in 2000. and a narrower range of positive values (0.48 to 0.61) in the remaining treatments for 2000 and 2001. The widest range in elasticity values across treatments and years was observed for $e\sigma_p$, $e\sigma_{s(s)}$ and $e\sigma_{s(pred)}$, which were identical and always positive within each treatment/year combination. The lowest values of $e\sigma_p$, $e\Phi$ and $e\sigma_{s(pred)}$ were consistently in the wheat phase of the crop sequence. with lower values for corresponding treatments in 2000 than in 2001. The largest values of $e\sigma_p$, $e\Phi$ and $e\sigma_{s(pred)}$ were consistently in the soybean phase of the crop sequence. with a narrow range of values (0.88 to 0.97) in 2000. and a single value for all treatments (1.0) in 2001. Values of $e\sigma_p$, $e\Phi$ and $e\sigma_{s(pred)}$ in the corn phase ranged from low to moderately high (0.17 to 0.68) in 2000. and were consistently high (0.85 to 0.92) in 2001. Values of $e\sigma_{s(s)}$ in the soybean phase were low (0.03 to 0.12) in 2000 and very low (0.002) in 2001. Values of $e\sigma_{s(s)}$ in the wheat phase were

very high (0.93 to 1.0) in 2000 and ranged from medium to very high (0.53 to 1.0) in 2001. Finally, values of $e\sigma_{s(s)}$ in the corn phase ranged from medium to high (0.32 to 0.83) in 2000 and were low (0.08 to 0.15) in 2001.

Retrospective. We used retrospective perturbation analysis to decompose the simple effects of *Red clover* and *Tillage timing*, within years, on λ_{cycle} into contributions made by simple treatment effects on lower level *S. faberi* demographic parameters. We will present the contributions to λ_{cycle} due to *Red clover* simple effects (Fig. 4.5), followed by those due to *Tillage timing* simple effects (Fig. 4.6).

There was only a very small difference ($\Delta\lambda_{cycle} = 0.006$) in λ_{cycle} between the R and W levels of the FT treatment in 2000. This difference was due to very small negative contributions from $\sigma_{s(w)}$ and $\sigma_{s(pred)}$ in the wheat phase (Fig. 4.5a). In 2001, there was a much larger difference between the R and W levels of the FT treatment ($\Delta\lambda_{cycle} = -1.50$), due solely to a large negative contribution from $\sigma_{s(pred)}$ in the wheat phase (Fig. 4.5b). Demographic parameter values for R level of the ST treatment in 2000 led to projections of a growing population ($\lambda_{cycle} = 1.57$), whereas the W level of the ST treatment in 2000 led to projections of a declining population ($\lambda_{cycle} = 0.79$). This difference in λ_{cycle} was due to small negative contributions from $\sigma_{s(pred)}$ in the wheat phase and γ in the corn phase, offset by a much larger positive contribution from ϕ in the corn phase (Fig. 4.5c). In 2001, both ST/R and ST/W had large positive values of λ_{cycle} (1.97 and 2.75, respectively), with a moderate-sized difference between their population growth rates ($\Delta\lambda_{cycle} = -0.78$). This difference resulted from a strong negative contribution from $\sigma_{s(pred)}$ in the wheat phase and strong positive contribution from ϕ in the corn phase that nearly canceled one another out, in addition to a small negative contribution from γ in the corn phase (Fig. 4.5d).

For both the W and R treatments in 2000, ϕ was the main demographic parameter affected by *Tillage timing* (Fig. 4.6a, c). In the W treatment in 2000, ϕ made contributions to $\Delta\lambda_{cycle}$ in all rotation phases, with successively larger contributions in the wheat, corn and soybean phases (Fig. 4.6a). There was also a small negative contribution from σ_{srw} in the wheat phase of the W treatment in 2000. In the R treatment in 2000, the contributions made by ϕ to $\Delta\lambda_{cycle}$ in the corn and soybean phases were large and nearly equal, but the contribution made by ϕ to $\Delta\lambda_{cycle}$ in the wheat phase was negligible (7.4×10^{-6}). In 2001, there was a *Tillage timing* by *Red clover* interaction effect on ϕ : there was no effect of *Tillage timing* on ϕ within the W treatment, but ϕ was greater in the ST level than the FT level of the R treatment (Table 4.2). This interaction was evident in the simple effects of *Tillage timing* on contributions to $\Delta\lambda_{cycle}$ in 2001. In the W treatment in 2001, $\Delta\lambda_{cycle}$ between the ST and FT treatments was due mainly to a strong negative contribution from σ_{srw} in the wheat phase, which was slightly offset by a small positive contribution from σ_{srs} in the corn phase (Fig. 4.6b). In contrast, in the R treatment in 2001, a strong positive contribution from ϕ in the corn phase accounted for most of $\Delta\lambda_{cycle}$, with only a small negative contribution from σ_{srw} in the wheat phase and γ in the corn phase (Fig. 4.6d).

For analyses of both *Red clover* and *Tillage timing*, percent errors were consistently less than 1%, indicating an almost exact agreement between the sum of parameter contributions to $\Delta\lambda_{cycle}$ and the actual value of $\Delta\lambda_{cycle}$ for each treatment pair.

DISCUSSION

Cropping system effects on population growth rate

The results of our simulations of *S. faberi* population growth demonstrate that cropping system characteristics can affect weed management outcomes even when some

form of weed control causes seedling mortality rates typical of commercial agricultural systems. The particular management factors studied, tillage timing and use of a legume green manure, interacted with one another such that spring tillage in combination with red clover green manure (the ST/R treatment) led to high values for *S. faberi* ϕ and λ_{cycle} (Fig. 4.3, Table 4.2). In contrast, the FT/R treatment achieved consistently low values for λ_{cycle} due to high predation rates in the R treatment without the risk of increased fecundity associated with the ST treatment (Fig. 4.3). Despite the large amount of inter-annual variation in demographic rates (Table 4.2), as seen in the strong main effect of *Year* on ln λ_{cycle} and cropping system treatment by *Year* interactions, stochastic simulations identified the FT/R treatment as the management system most likely to prevent *S. faberi* population increases under variable conditions.

At a level of post-emergent weed control that allowed $\geq$ 12.5% of seedlings to survive, stochastic simulations showed that the FT/R treatment aided weed prevention (Fig. 4.4). As the success of post-emergent weed control varied, ln $\lambda_{s(cycle)}$ for the FT/R treatment did not change in rank relative to the other cropping system treatments, but the separations between the treatments did change. Although it was clear that the FT treatment was superior to the ST treatment across the entire range of seedling survival studied, the benefit of using the FT/R treatment, relative to the FT/W treatment, diminished as post-emergent weed control became more and more successful. If percentage seedling survival was 10% or less, ln $\lambda_{s(cycle)}$ was equal for the FT/W and FT/R treatments. The threshold seedling survival level, above which ln $\lambda_{s(cycle)}$ became positive was approximately 10% for the both the ST/W and ST/R treatments, 17.5% for the FT/W treatment and 23% for the FT/R treatment. The FT/R treatment was thus somewhat buffered against weed control failures compared to the other treatments.

Perturbation analyses of cropping system effects on S. faberi demography

The stories told by the prospective and retrospective perturbation analyses were similar, differing mainly in the extra information on parameter variability in this particular set of experiments contained in the retrospective perturbation analysis. The results of both analyses are best understood in the context of the scalar expression for population growth that the product of the sub-annual matrices reduces to: $\sigma_{s(w)}\sigma_{s(s)}(1-\gamma) + \sigma_{s(w)}\sigma_{s(pred)}\phi\sigma_p\gamma$. The first term in this expression describes factors regulating the preservation of seeds remaining in the seedbank, whereas the second term describes factors responsible for regulating new inputs to the seedbank. Some parameters, such as $\sigma_{s(w)}$ and γ, affect both seed preservation and production, whereas other parameters affect either seed preservation or seed production. The changes in elasticity values from treatment to treatment (Table 4.4) resulted from trade-offs in the importance of seed preservation or seed production in a given environment.

It is unsurprising that $e\sigma_{s(w)}$ had a value of 1.0 for all treatment/year combinations: overwinter seed survival is a process that all individuals must pass through in a summer annual plant species. The elasticities of $\lambda_{(cycle)}$ to the remaining lower level demographic parameters revealed more about the effects of the cropping system treatments on *S. faberi* demography. In the two treatments with the lowest values of $\lambda_{(cycle)}$, the FT/W and FT/R treatments in 2000, ϕ was low (23 to 94 seeds plant^{-1}) and $\sigma_{s(pred)}$ was the same as for the other treatments. In this situation, seeds germinating in the corn and wheat phases did not produce enough seeds to replace themselves, whereas seeds germinating in the soybean phase did. Thus, $e\gamma$ was strongly negative in the corn and wheat phases, and strongly positive in the soybean phase. The values of $e\sigma_p$, $e\phi$ and $e\sigma_{s(pred)}$ were all positive in the corn, wheat and soybean phases, but the values were larger in the soybean phase, in which a larger proportion of newly dispersed seeds made it into the seedbank, than in the corn and wheat

phases, in which most of the newly dispersed seeds were eaten. Under this set of conditions, dormancy would have more of a positive effect on n_{t+1} in the corn and wheat phases, reflected in high values for $e\sigma_{s(s)}$ than in the soybean phase. Seeds remaining in the seedbank in the soybean phase not only would miss out on the opportunity to reproduce in the current season, but also would be subjected to unfavorable conditions for reproduction in the next phase of the crop sequence.

Elasticity values for the FT/W and FT/R treatments in 2001, when ϕ was much greater (432 to 1782 seeds plant^{-1}) in relation to $\sigma_{s(pred)}$, underscored the importance of the seedbank for allowing plant populations to avoid unfavorable conditions. Values of $e\gamma$, $e\sigma_p$, $e\phi$ and $e\sigma_{s(pred)}$ were all strongly positive for both the corn and soybean phases, indicating that seedlings in these phases would make a large contribution to n_{t+1}. In contrast, the value of $e\gamma$ was more negative in the wheat phase in 2001 than in 2000, in spite of increased positive values for $e\sigma_p$, $e\phi$ and $e\sigma_{s(pred)}$. Although seeds making the transition to become seedlings in the wheat phase of the FT/W and FT/R treatments in 2001 would make greater inputs to the seedbank than they would have in 2000, it would have been even more favorable to population growth for the seeds to have remained in the seedbank and emerged during the corn or soybean phases. The more strongly negative values of $e\gamma$ in the wheat phase in 2001 compared to the wheat phase in 2000 reflect the opportunity cost of seedling recruitment in a variable environment.

Because the elasticity of λ to $\sigma_{s(w)}$ was greater than its elasticity to all other variables, $\sigma_{s(w)}$ was an obvious management choke point. A comparison of elasticity values for the FT/W and FT/R treatments suggested that two other important variables in this system were fecundity and post-dispersal seed predation. Retrospective perturbation analysis of contributions from each of the lower level demographic parameters to treatment differences

in $\lambda_{(cycle)}$ supported this finding, and suggested that $\sigma_{s(w)}$ was also an important factor in this system. In five out of eight analyses of simple effects of *Tillage timing* or *Red clover* on $\lambda_{(cycle)}$, ϕ made large contributions to $\Delta\lambda_{(cycle)}$ (Figs. 5 and 6). In two out of eight analyses of simple effects of *Tillage timing* or *Red clover* on $\lambda_{(cycle)}$, $\sigma_{s(pred)}$ made large contributions to $\Delta\lambda_{(cycle)}$, and in two other analyses $\sigma_{s(pred)}$ made small contributions to $\Delta\lambda_{(cycle)}$. Next in importance was $\sigma_{s(w)}$, which made a contribution to $\Delta\lambda_{(cycle)}$ in four out of eight analyses, but only made a large contribution in one of these. Lastly, differences in γ showed up as negative contributions to $\Delta\lambda_{(cycle)}$ in four out of eight analyses, but in each of these the contribution made by γ was small relative to contributions from other parameters.

Following the example of Pico et al. (IN PRESS) we examined the relationship between the elasticity of λ to each demographic parameter and the coefficient of variation (c.v.) for each demographic parameter, across treatments and years. We found a negative correlation ($N = 109$, $r = -0.35$, $P < 0.001$, $F_{1,109} = 14.3$) between $\ln(e)$ and $\ln(c.v.)$ corroborating the results of Pico et al. (IN PRESS). This negative relationship echoed what we saw in the retrospective perturbation analysis: $e\sigma_{s(w)}$ was equal to 1 for all treatment/year combinations, but $\sigma_{s(w)}$ also had the lowest c.v. of any parameter, and the LTRE contributions to $\Delta\lambda$ were smaller for $\sigma_{s(w)}$ than for ϕ.

Taken together, the perturbation analyses suggest that fecundity and seed mortality factors, with an emphasis on seed predation, constitute important weed management choke points that may affect *S. faberi* population growth in a variety of treatments under variable growing conditions. This finding agrees with the conclusions of Bussan and Boerboom (2001), who modeled the effect of varying herbicide rates upon weed management outcomes for *S. faberi* in a corn-soybean crop rotation.

Implications for agronomic management

Although weed management considerations do not usually drive cropping system design, our results show that cropping system characteristics can have important effects on weed population growth in agricultural systems where weed control outcomes are variable. Cropping system characteristics may aid weed prevention efforts, as seen in the FT/R treatment, or they may hinder weed prevention efforts, as seen in the ST/R treatment. The difference between these two treatments lay in an interaction between the timing of tillage and *S. faberi* fecundity. In the ST/R treatment, the combined effects of red clover phytotoxicity and unfavorable soil physical properties due to spring tillage led to reduced early corn competition with *S. faberi* and increased *S. faberi* fecundity (Davis and Liebman SUBMITTED). If the choice between potential cropping systems does not carry other substantial costs, it should be beneficial for farmers to choose cropping systems with weed suppressive qualities. In Iowa, fall tillage is the preferred practice for corn and soybean production systems that utilize some form of tillage, therefore the choice between the FT/R and the ST/R treatments is simple in this case.

The choice between the two most promising cropping systems in this study, the FT/W and FT/R treatments, ultimately depends upon an economic trade-off: how does the number of years in which post-emergence weed control fails to keep percentage seedling survival at or below the 10% level balance against the extra cost of establishing a forage legume intercrop within the small grain phase of the crop rotation? This trade-off will most likely resolve itself in different ways in different systems. In intensively managed conventional systems, where *S. faberi* seedling mortality levels approaching 100% are not unusual, the FT/W treatment would probably be the most cost-effective cropping system, unless there is an additional need for the forage legume biomass in the system. In low-external-input (LEI)

farming systems, where minimizing or eliminating herbicide inputs and synthetic nitrogen fertilizer are important objectives, the level of seedling survival obtained through low herbicide rates combined with physical control tactics such as inter-row cultivation and rotary hoeing would be likely to vary more widely (Buhler 1992, Mulder and Doll 1993), with occasional serious weed control failures. Regular use of the FT/R cropping system in LEI systems would appear to be a favorable solution to the above trade-off.

For the system studied. it seems that additional emphasis in cropping system design should be placed upon regulation of inputs to the seedbank. Some of the factors affecting *Setaria* spp. fecundity include 1) successful recruitment of crop seedlings and vigorous early crop growth (Davis and Liebman SUBMITTED), 2) herbicide rate (Bussan et al. 2000). 3) crop planting date (Campbell et al. 1981), 4) effects of tillage regime on seedling recruitment (Schreiber 1992, Buhler 1995), 5) and post-harvest mowing or spraying of the stubble of small grain crops (Kegode et al. 1999). Although less is known about factors affecting post-dispersal weed seed predation, recent studies have suggested that increased landscape complexity (Menalled et al. 2000), crop diversification (Carmona and Landis 1999. Davis and Liebman SUBMITTED), and delayed fall tillage (Cardina et al. 1996) may lead to increases in post-dispersal weed seed predation rates.

Simulation analysis of matrix population models can highlight important issues in cropping system design by projecting the consequences of different management scenarios. It is important to remember, however, that the safest use of these models is for heuristic. as opposed to predictive, purposes. The large standard errors accompanying the largest contribution to $\Delta\lambda_{(cycle)}$ in many of the treatment/year combinations indicate the need for caution in applying our simulation results. The importance of controlling fecundity as part of preventing weed population growth seems obvious, especially for annual weed species.

Although these simulations suggest that post-dispersal seed predation may play an important role in weed prevention, the considerable variability attending our observations suggests that a more definitive answer will rely upon more precise estimates of seed predation. Our estimates of the proportion of newly dispersed seeds not consumed by seed predators were generated by a simple compounding of point estimates of the daily seed predation rate over time. For the R treatment, this clearly led to suspiciously high estimates of the total proportion of seeds consumed by predators. Further empirical and modeling work is needed to develop more realistic estimates of the proportion of seeds consumed by predators in an entire field season. Only then will we be able to confidently assess the relative importance of post-dispersal seed predation in preventing weed population growth.

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Figure Captions

Fig. 4.1. Life cycle of *S. faberi*, including all demographic parameters measured in field experiment. Parameter abbreviations are given in Table 4.1.

Fig. 4.2. Sub-annual projection matrices comprising the periodic matrix simulation of cropping system effects on *S. faberi* population dynamics for an unstructured system. Abbreviations for *S. faberi* demographic parameters are given in Table 4.1.

Fig. 4.3. Population growth rate of *S. faberi* grown in contrasting cropping systems in Boone, IA. in (a) 2000 and (b) 2001. Cropping system abbreviations are explained in Table 4.2.

Fig. 4.4. Stochastic population growth rate (ln $\lambda_{s(cycle)}$) of *S. faberi* grown in contrasting cropping systems, with simulated variation in post-emergence weed control. Cropping system abbreviations are explained in Table 4.2.

Fig. 4.5. Retrospective perturbation analysis of simple effects of *Red clover* on *S. faberi* population growth rate within a wheat-corn-soybean crop sequence with either a wheat sole crop (W) or wheat + red clover crop mixture (R) in the wheat phase. The difference in λ_{cycle} was computed by subtracting λ_{cycle} in the W treatment from λ_{cycle} in the R treatment. Analyses were conducted for projections based on experimental data from 2000 or 2001 within fall tillage (FT) or spring tillage (ST) treatments resulting in a factorial of four tillage/year combinations: a. FT/2000, b. FT/2001, c. ST/2000, d. ST/2001. Note variation in y-axis scale.

Fig. 4.6. Retrospective perturbation analysis of simple effects of *Tillage timing* on *S. faberi* population growth rate (λ_{cycle}) within a wheat-corn-soybean crop sequence subjected to either fall tillage (FT) or spring tillage (ST). The difference in λ_{cycle} was computed by subtracting λ_{cycle} in the FT treatment from λ_{cycle} in the ST treatment. Analyses were conducted for projections based on experimental data from 2000 or 2001 for treatments in which wheat was

grown either as a sole crop (W) or in a mixture with red clover (R), resulting in a factorial of

four *Year/Red clover* combinations: a. W/2000, b. W/2001, c. R/2000, d. R/2001. Note

variation in y-axis scale.

Table 4.1. Abbreviations and estimators for *S. faberi* demographic parameters.

Parameter	Abbreviation	Units[a]
Recruitment	γ	$N_{plt(Jun.)}\, N_{sd(Mar.)}^{-1}$
Plant survival	σ_p	$N_{plt(Aug.)}\, N_{plt(Jun.)}^{-1}$
Seed survival$_{Mar.-Oct.}$	$\sigma_{s(s)}$	$N_{sd(Oct.)}\, (N_{sd(Mar.)}-N_{plt(Jun.)})^{-1}$
Fecundity	ϕ	seeds plant^{-1}
Seed survival$_{Predation}$	$\sigma_{s(Pred)}$	$N_{newsd(Oct.)}\, N_{newsd(Aug.)}^{-1}$
Seed survival$_{Oct.-Mar.}$	$\sigma_{s(w)}$	$N_{sd(Mar.)}\, N_{sd(Oct.)}^{-1}$

[a] Abbreviations: N_{plt} = number of plants, N_{sd} = number of seeds, N_{newsd} = number of newly shed seeds

Table 4.2. *Setaria faberi* demographic rates under four different cropping systems in 2000 and 2001 in Boone, IA.

Year	Cropping system	Rotation phase	Demographic parameter ($\pm$ s.e.)					
			$\sigma_{v(n)}$	γ	σ_p	ϕ	$\sigma_{s(s)}$	$\sigma_{s(pred)}$
2000	FT/W	Corn	0.88 ± 0.01	0.54 ± 0.04	0.1	57 ± 9	0.54 ± 0.01	0.016 ± 0.007
		Soybean	0.88 ± 0.01	0.54 ± 0.04	0.1	94 ± 15	0.54 ± 0.01	0.36 ± 0.067
		Wheat	0.91 ± 0.01	0.54 ± 0.04	0.1	23 ± 4	0.54 ± 0.01	0.0003 ± 0.002
	FT/R	Corn	0.88 ± 0.01	0.54 ± 0.01	0.1	57 ± 9	0.54 ± 0.01	0.016 ± 0.007
		Soybean	0.88 ± 0.01	0.54 ± 0.04	0.1	94 ± 16	0.54 ± 0.01	0.36 ± 0.067
		Wheat	0.86 ± 0.01	0.54 ± 0.04	0.1	23 ± 4	0.54 ± 0.01	$4.6 \times 10^{-7} \pm 2.4 \times 10^{-7}$
	ST/W	Corn	0.88 ± 0.01	0.54 ± 0.04	0.1	278 ± 31	0.54 ± 0.01	0.016 ± 0.007
		Soybean	0.88 ± 0.01	0.54 ± 0.04	0.1	459 ± 52	0.54 ± 0.01	0.36 ± 0.067
		Wheat	0.86 ± 0.01	0.54 ± 0.04	0.1	111 ± 13	0.54 ± 0.01	0.0003 ± 0.002
	ST/R	Corn	0.88 ± 0.01	0.38 ± 0.01	0.1	1150 ± 210	0.54 ± 0.01	0.016 ± 0.007
		Soybean	0.88 ± 0.01	0.54 ± 0.04	0.1	459 ± 52	0.54 ± 0.01	0.36 ± 0.067
		Wheat	0.86 ± 0.01	0.54 ± 0.04	0.1	111 ± 13	0.54 ± 0.01	$4.6 \times 10^{-7} \pm 2.4 \times 10^{-7}$
2001	FT/W	Corn	0.56 ± 0.02	0.80 ± 0.06	0.1	1080 ± 94	0.58 ± 0.04	0.016 ± 0.007
		Soybean	0.56 ± 0.02	0.80 ± 0.06	0.1	1782 ± 155	0.58 ± 0.04	0.36 ± 0.067
		Wheat	0.60 ± 0.01	0.80 ± 0.06	0.1	432 ± 38	0.58 ± 0.04	0.0003 ± 0.002
	FT/R	Corn	0.56 ± 0.02	0.80 ± 0.06	0.1	1080 ± 94	0.58 ± 0.04	0.016 ± 0.007
		Soybean	0.56 ± 0.02	0.80 ± 0.06	0.1	1782 ± 155	0.58 ± 0.04	0.36 ± 0.067
		Wheat	0.60 ± 0.01	0.80 ± 0.06	0.1	432 ± 38	0.58 ± 0.04	$4.6 \times 10^{-7} \pm 2.4 \times 10^{-7}$
	ST/W	Corn	0.56 ± 0.02	0.80 ± 0.06	0.1	1080 ± 94	0.70 ± 0.03	0.016 ± 0.007
		Soybean	0.56 ± 0.02	0.80 ± 0.06	0.1	1782 ± 155	0.58 ± 0.04	0.36 ± 0.067
		Wheat	0.51 ± 0.03	0.80 ± 0.06	0.1	432 ± 38	0.58 ± 0.04	0.0003 ± 0.002
	ST/R	Corn	0.56 ± 0.02	0.56 ± 0.06	0.1	1965 ± 165	0.70 ± 0.03	0.016 ± 0.007
		Soybean	0.56 ± 0.02	0.80 ± 0.06	0.1	1782 ± 155	0.58 ± 0.04	0.36 ± 0.067
		Wheat	0.51 ± 0.03	0.80 ± 0.06	0.1	432 ± 38	0.58 ± 0.04	$4.6 \times 10^{-7} \pm 2.4 \times 10^{-7}$

Notes: Explanation of cropping system abbreviations: FT = fall tillage; ST = spring tillage; W = wheat sole crop in the wheat phase of the crop sequence; R = wheat + red clover intercrop in the wheat phase of the crop sequence. Explanation of abbreviations for demographic parameters is given in Table 4.1. No standard errors are given for σ_p because this value was chosen rather than estimated.

Table 4.3. Analysis of variance of log_e-transformed *S. faberi* population growth rate (for the entire rotation cycle) under four cropping system treatments.

Source	df	SS	F	P
Year	1	18.93	9.32	0.022
Error A	6	12.19		
Tillage timing	1	10.56	30.45	0.001
Year x Tillage timing	1	9.62	27.74	0.002
Error B	6	2.08		
Red Clover	1	0.016	0.038	0.549
Year x Red clover	1	0.67	15.71	0.002
Tillage timing x Red Clover	1	0.50	11.85	0.005
Year x Tillage timing x Red clover	1	0.029	0.69	0.422
Error C	12	0.508		

Notes: The experimental design was a split plot with 4 replications of 4 treatments over two years (n = 32). Tillage timing was the main plot factor and Red clover was the split-plot factor. See Table 4.2 for explanation of Tillage timing and Red clover treatments.

Table 4.4. Elasticity of *Setaria faberi* population growth rate (over the entire rotation cycle) to lower level demographic parameters under four different cropping systems.

Year	Cropping system	Rotation phase	$\sigma_{s(w)}$	γ	σ_p	ϕ	$\sigma_{s(s)}$	$\sigma_{s(pred)}$
			Elasticities of $\lambda_{(cycle)}$ to *S. faberi* demographic parameters					
2000	FT/W	Corn	1.0	-0.81	0.17	0.17	0.83	0.17
		Soybean	1.0	0.74	0.88	0.88	0.12	0.88
		Wheat	1.0	-1.14	1.48×10^{-2}	1.48×10^{-2}	0.99	1.48×10^{-2}
	FT/R	Corn	1.0	-0.81	0.17	0.17	0.83	0.17
		Soybean	1.0	0.74	0.88	0.88	0.12	0.88
		Wheat	1.0	-1.17	2.30×10^{-6}	2.30×10^{-6}	1.00	2.30×10^{-6}
	ST/W	Corn	1.0	-0.11	0.49	0.49	0.51	0.49
		Soybean	1.0	0.94	0.97	0.97	0.03	0.97
		Wheat	1.0	-1.03	0.07	0.07	0.93	0.07
	ST/R	Corn	1.0	0.48	0.68	0.68	0.32	0.68
		Soybean	1.0	0.94	0.97	0.97	0.03	0.97
		Wheat	1.0	-1.17	1.11×10^{-5}	1.11×10^{-5}	1.00	1.11×10^{-5}
2001	FT/W	Corn	1.0	0.61	0.92	0.92	0.08	0.92
		Soybean	1.0	0.99	1.00	1.00	0.002	1.00
		Wheat	1.0	-1.64	0.47	0.47	0.53	0.47
	FT/R	Corn	1.0	0.61	0.92	0.92	0.08	0.92
		Soybean	1.0	0.99	1.00	1.00	0.002	1.00
		Wheat	1.0	-4.00	1.37×10^{-4}	1.37×10^{-4}	1.00	1.37×10^{-4}
	ST/W	Corn	1.0	0.54	0.91	0.91	0.09	0.91
		Soybean	1.0	0.99	1.00	1.00	0.002	1.00
		Wheat	1.0	-1.64	0.47	0.47	0.53	0.47
	ST/R	Corn	1.0	0.66	0.85	0.85	0.15	0.85
		Soybean	1.0	0.99	1.00	1.00	0.002	1.00
		Wheat	1.0	-4.00	1.37×10^{-4}	1.37×10^{-4}	1.00	1.37×10^{-4}

Notes: See Tables 4.1 and 4.2 for explanation of abbreviations of *S. faberi* demographic parameters and cropping system treatments, respectively.
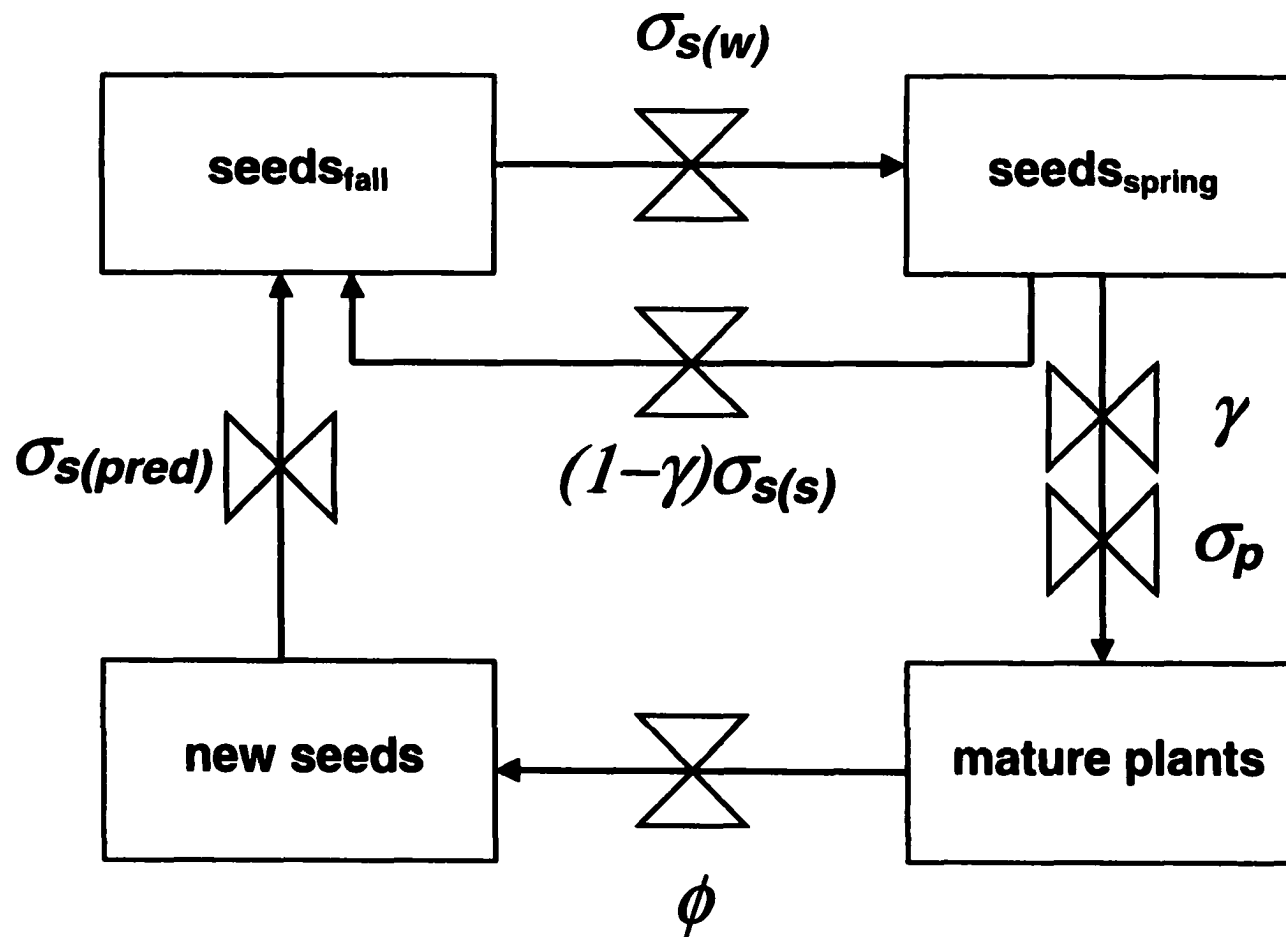
Fig. 4.1

$$\mathbf{n}_{t+1} = (\mathbf{B}_{(h-1)} \dots \mathbf{B}_{(m)} \mathbf{B}_{(1)} \dots \mathbf{B}_{(h+1)} \mathbf{B}_{(h)})_k \mathbf{n}_t$$

$$\mathbf{n}_t = \begin{pmatrix} n_s \\ n_p \end{pmatrix}$$

Recruitment

$$\mathbf{B}_{(1_k)} = \begin{pmatrix} 1-\gamma & 0 \\ \gamma & 0 \end{pmatrix}$$

Spring survival

$$\mathbf{B}_{(2_k)} = \begin{pmatrix} \sigma_{s(s)} & 0 \\ 0 & \sigma_p \end{pmatrix}$$

Fecundity

$$\mathbf{B}_{(3_k)} = \begin{pmatrix} 1 & \phi\sigma_{s(pred)} \\ 0 & 0 \end{pmatrix}$$

Winter survival

$$\mathbf{B}_{(4_k)} = \begin{pmatrix} \sigma_{s(w)} & 0 \\ 0 & 0 \end{pmatrix}$$

Fig. 4.2

Fig. 4.3

Cropping system

Fig. 4.4

Fig. 4.5

Fig. 4.6

CHAPTER 6. GENERAL CONCLUSION

The primary goal of my dissertation research was to understand how cropping system characteristics typical of low-external-input farming systems influence the population dynamics of giant foxtail. an important weed in Midwestern corn-soybean production systems. Each of the articles in this dissertation examined a sub-component of this central research question. Articles 1 and 2 reported the results of field experiments examining the effects of tillage timing and green manure. and c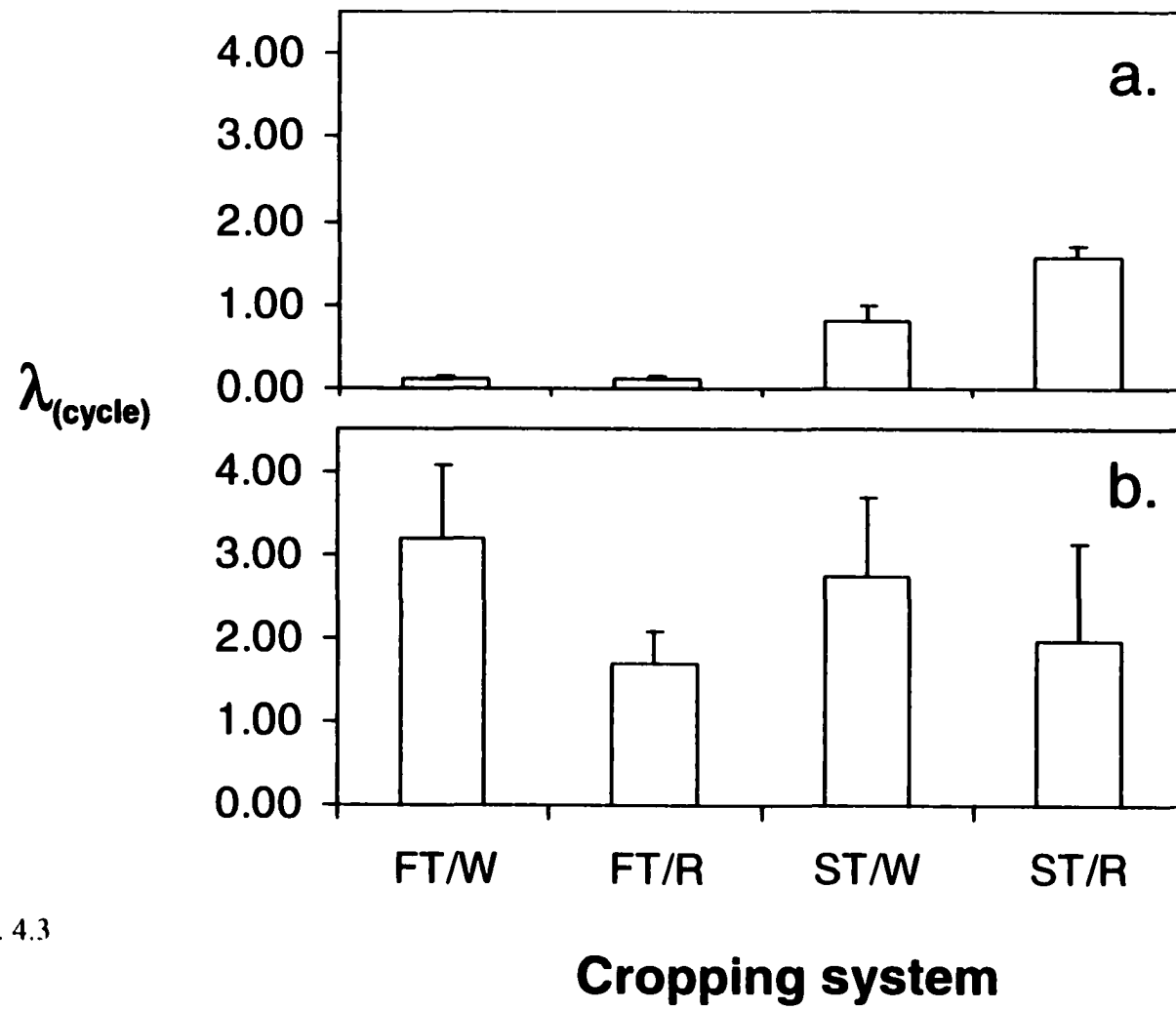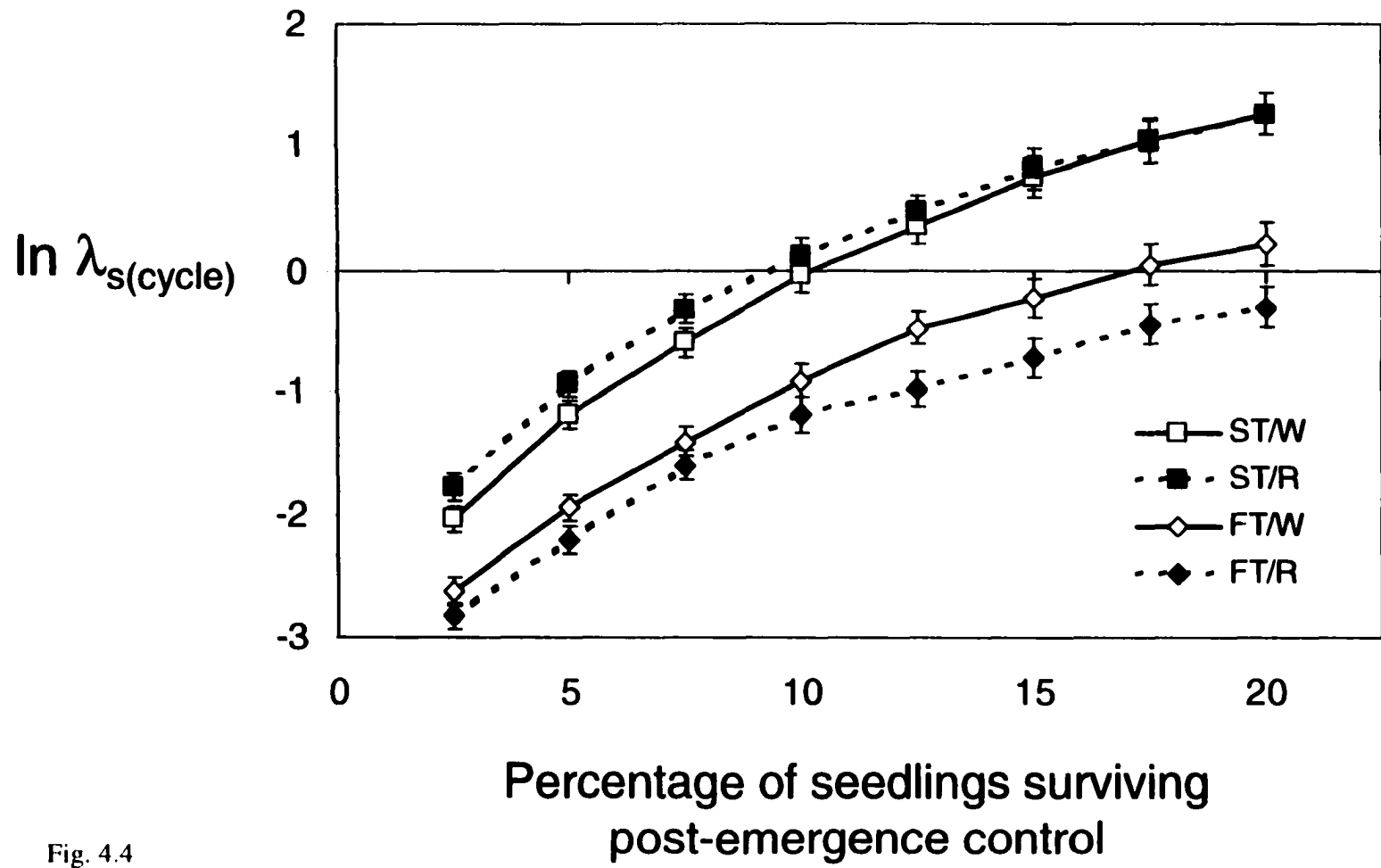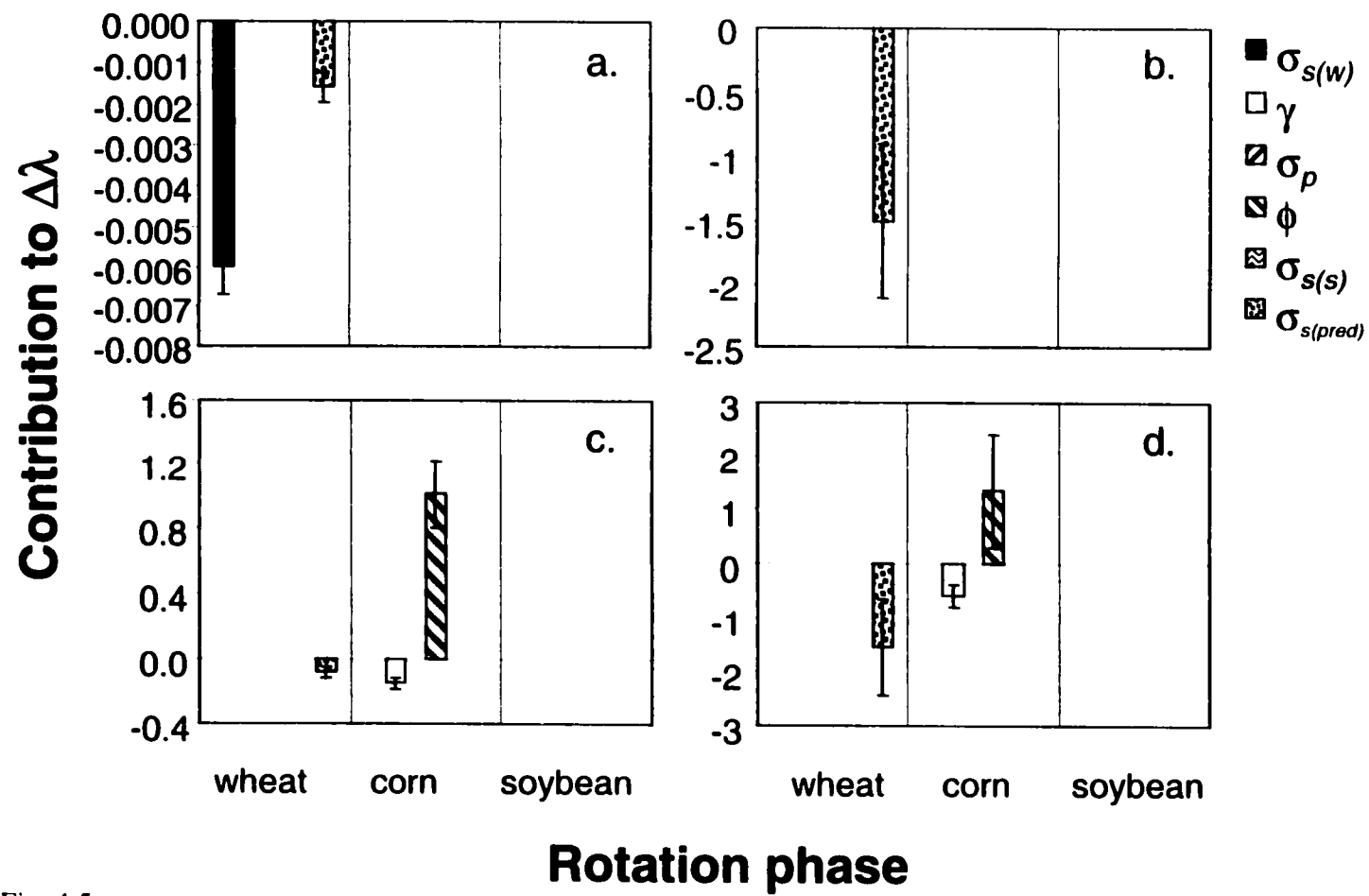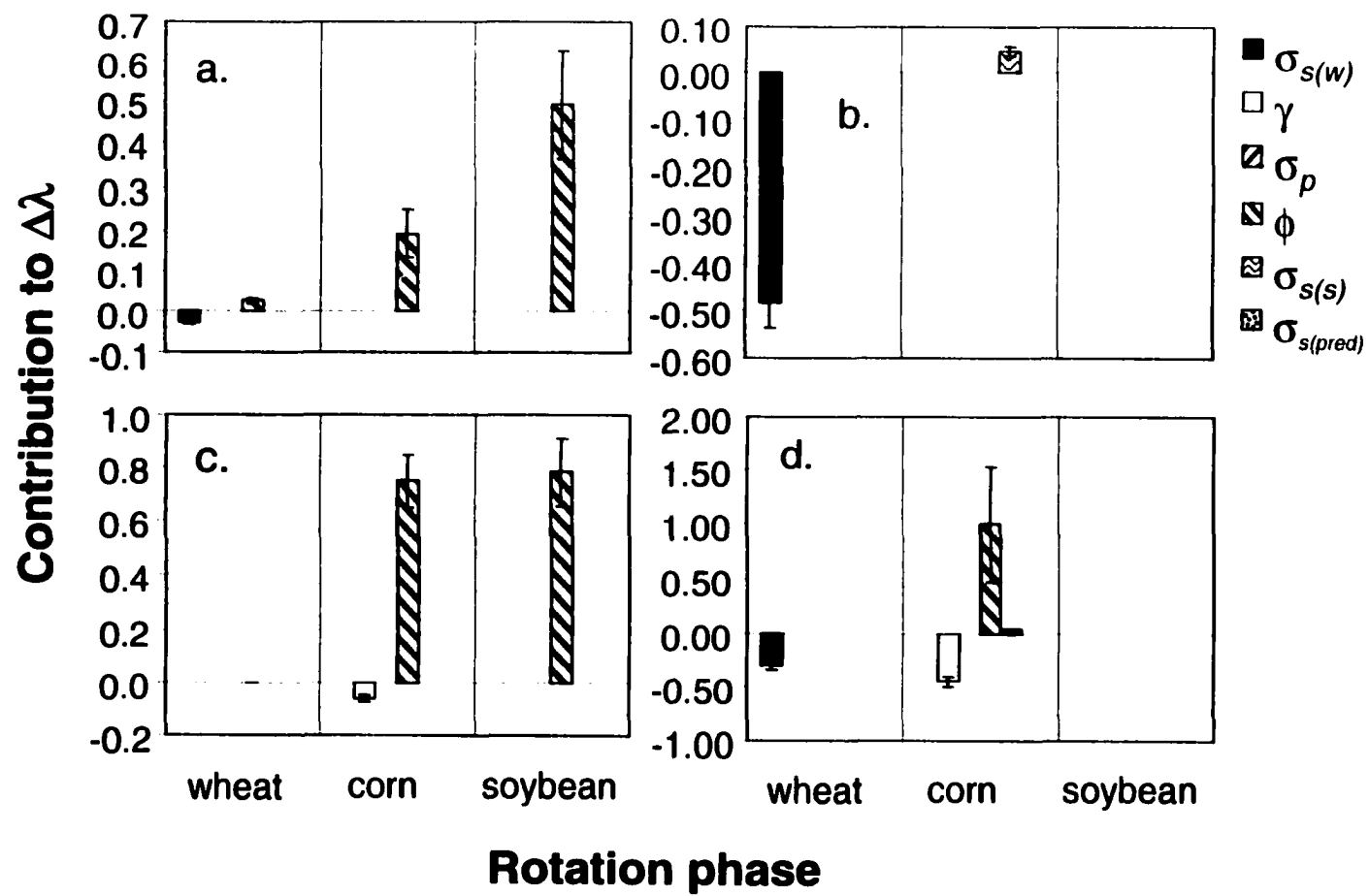ompost. respectively. on giant foxtail demography within a corn-soybean-wheat crop sequence. Articles 3 and 4 reported the results of modeling studies of giant foxtail population dynamics in cropping systems featuring green manure without external weed control. and tillage timing by green manure interactions with external weed control. respectively. The results from these articles suggest that cropping system effects on weed demography should be taken into consideration as a design factor for agroecosystems. especially in low-external-input production systems.

Of the three cropping system characteristics studied. tillage timing and green manure had the greatest effects on giant foxtail demography. Spring tillage was associated with lower overwinter seedbank persistence. but greater fecundity (due to poor corn recruitment and early growth). of giant foxtail. Red clover green manure effects on giant foxtail demography were subject to interactions with tillage timing. When red clover residues were incorporated in the fall, they were associated with lower overwinter seedbank persistence of giant foxtail. When red clover residues were incorporated in the spring, they were associated with lower giant foxtail recruitment. but were also associated with greater giant foxtail fecundity (due to phytotoxic suppression of early corn recruitment and growth. which released giant foxtail from the competitive effects of corn). Regardless of tillage regime. the presence of standing red clover residues in the fall was associated with large increases in post-dispersal seed

predation. compared to residues of wheat. corn or soybean. Compost supported corn growth.

but did not substantially alter giant foxtail demography.

Management implications and recommendations for future research

When the effects of tillage timing and red clover residues on giant foxtail demography

were integrated with a simulation model of giant foxtail population dynamics. the

management implications were clear. First. if red clover green manure is to be included

in the wheat phase of a corn-soybean-wheat crop sequence in Iowa. the green manure

residues should be incorporated in late fall. This practice will decrease giant foxtail

population growth rates (relative to a system with no green manure) by extending the period

for post-dispersal weed seed predation in the red clover residues. while avoiding the increase

in giant foxtail fecundity brought on by phytotoxic suppression of early corn growth by

spring-tilled red clover residues. Second. tillage timing and green manure affected giant

foxtail demography primarily by altering inputs to the weed seedbank. with smaller

contributions from changes in seedling recruitment. This was especially apparent when

seedling recruitment was kept low through some form of external weed control. Cropping

system characteristics that reduce inputs to the weed seedbank may thus be used to augment

weed management in production systems where most of the weed control effort is aimed at

minimizing seedling recruitment. Third. the importance of cropping system effects on giant

foxtail population growth rate varied with the level of weed control efficacy. If post-

emergence weed control efficacy fell below 90% in simulations. then the cropping system

featuring fall-tilled green manure resulted in lower giant foxtail population growth rates than

the other cropping systems studied. This suggests that cropping system characteristics may

be especially important to producers in low-external-input systems, in which weed control

efficacy tends to be more variable than in conventional systems. Finally, given the potential importance of post-dispersal weed seed predation to weed population growth and management, we need improved information about how to measure and manage seed predation in agricultural systems.

The empirical and modeling studies comprising this dissertation complemented one another, leading to conclusions that would not have been reached had only one of the approaches been taken. Future investigations in integrated weed management will benefit from a combined empirical-modeling approach, in which empirical data lead to management insights derived from modeling studies that, in turn, suggest new areas for empirical exploration.

APPENDIX A. MATLAB CODE

Population growth rate

```
% Giant foxtail population dynamics simulation

% Treatment: Fall/RC- (see below for Fall/RC+)
% Draft date: 3/4 02

%Years in simulation
Y=20;

% Population at beginning of simulation
n=[0;0];
n(1)=1000;    % Newly shed seeds entering the seedbank in Nov
Seed_Start=1000;


% Variable declarations

% Seed survival probabilities
b3s1=.004;    % seed predation survival for year 1 seed in corn
b4s1=.9;      % overwinter survival for year 1 seed
c1s1=.44;     % year 1 seed left after germination
b2s1=.5;      % spring-summer survival for year 1 seed

% Germination probabilities
c1g1=.56;     % cohort 1&2 germination as percent of viable seed

% Seedling cohort 1&2 survival probabilities (germ. through repro. maturity)
c1p1=.97;

% Fecundity of cohort 1&2
c1f1=57;

% Post-Dispersal Seed Predation Survival in Wheat Phase
b6s1=.003;

% Post-Dispersal Seed Predation Survival in Soybean Phase
b7s1=.36;

% Matrix declarations

CB3=zeros(2,2);
CB3(1,1)=1;
CB3(1,2)=b3s1*b3f1;
CB3;
% The matrix B3 applies to the period Sept. through Nov. and accounts for
% seed rain and predation of newly shed seed in the corn phase.

CB4=zeros(2,2);
CB4(1,1)=b4s1;
CB4;

% The matrix B4 applies to the period Nov. through Mar. and accounts for
% overwinter seedbank decline.

CB1=zeros(2,2);
CB1(2,1)=b1g1;
CB1(1,1)=b1s1;
```

```
CB1;
% The matrix B1 applies to the period Mar. through June and accounts for
% seedling germination and seedbank depletion due to seedling germination.

CB2=zeros(2,2);
CB2(1,1)=b2s1;
CB2(2,2)=b2p1;
CB2;
% The matrix B2 applies to the period June through August and accounts for
% seedling survival to reproductive maturity and seed survival during this time.

WB3=zeros(2,2);
WB3(1,1)=1;
WB3(1,2)=b6s1*b3f1;
WB3;
WB2=CB2;
WB1=CB1;
WB4=CB4;
% The matrix WB3 applies to the period Sept. through Nov. and accounts for
% predation of newly shed seed in the wheat phase. All the rest of wheat
% matrices are the same as the corn matrices

SB3=zeros(2,2);
SB3(1,1)=1;
SB3(1,2)=b7s1*b3f1;
SB3;
SB2=CB2;
SB1=CB1;
SB4=CB4;
% The matrix SB3 applies to the period Sept. through Nov. and accounts
% for predation of newly shed seed in the soybean phase. All the rest of
% bean matrices are the same as the corn matrices

Yr=[1:Y];
Years=Yr';
S=[1:Y];
SdsNoRC=S';   % Creates a storage vector for seed simulation data.
c=1;

% Begin model

for y=1:Y
        if y==1
                SdsNoRC(y)=n(1);
                Years(y)=y;
        else
                if c==1
                        nnov=n;                    % seeds in Nov. sdbk. before wheat
phase
                        nmar=SB4*nnov;
                        njun=WB1*nmar;
                        naug=WB2*njun;
                        nnov=WB3*naug;
                        n=nnov;
                        SdsNoRC(y)=nnov(1);
                        Years(y)
                        c=c+1
                elseif c==2           % seeds in Nov. sdbk. before corn phase
                        nnov=n;
                        nmar=WB4*nnov;
                        njun=CB1*nmar;
```

```
                    naug=CB2*njun;
                    nnov=CB3*naug;
                    n=nnov;
                    SdsNoRC(y)=nnov(1);
                    Years(y)
                    c=c+1
            elseif c==3          % seeds in Nov. sdbk. before bean phase
                    nnov=n;
                    nmar=CB4*nnov;
                    njun=SB1*nmar;
                    naug=SB2*njun;
                    nnov=SB3*naug;
                    n=nnov;
                    SdsNoRC(y)=nnov(1);
                    Years(y)
                    c=1
            end
        end
end


%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%

% Treatment: Fall/RC+
% Draft date: 3/4/02
% Emergence data: rows

% Population vector at beginning of simulation
n=[0;0];
n(1)=1000;    % Newly shed (year 1) seeds entering the seedbank in Nov
Seed_Start=1000;


% Variable declarations

% Seed survival probabilities
d3s1=.024;    % seed predation survival for year 1 seed in corn
d4s1=.857;    % overwinter survival for year 1 seed
d1s1=.562;    % year 1 seed left after germination
d2s1=.44;     % spring-summer survival for year 1 seed

% Germination probabilities
d1g1=.438;    % cohort 1&2 germination as percent of viable seed

% Seedling cohort survival probabilities (germ. through repro. maturity)
d2p1=.97;

% Fecundity by cohort
d3f1=57;


% Post-Dispersal Seed Predation Survival in Wheat Phase
d6s1=.000000047;

% Post-Dispersal Seed Predation Survival in Soybean Phase
d7s1=.36;

% Matrix declarations

CD3=zeros(2,2);
CD3(1,1)=1;
CD3(1,2)=d3s1*d3f1;
```

```
CD3;
% The matrix D3 applies to the period Sept. through Nov. and accounts
% for seed rain and predation of newly shed seed in the corn phase.

CD4=zeros(2,2);
CD4(1,1)=d4s1;
CD4;

% The matrix D4 applies to the period Nov. through Mar. and accounts for
% overwinter seedbank decline.

CD1=zeros(2,2);
CD1(2,1)=d1g1;
CD1(1,1)=d1s1;
CD1;
% The matrix D1 applies to the period Mar. through June and accounts for
% seedling germination and seedbank depletion due to seedling
% germination.

CD2=zeros(2,2);
CD2(1,1)=d2s1;
CD2(2,2)=d2p1;
CD2;
% The matrix D2 applies to the period June through August and accounts
% for seedling survival to reproductive maturity and seed survival
% during this time.

WD3=zeros(2,2);
WD3(1,1)=1;
WD3(1,2)=d6s1*d3f1;
WD3;
WD2=CD2;
WD1=CD1;
WD4=CD4;
% The matrix WD3 applies to the period Sept. through Nov. and accounts
% for predation of newly shed seed in the wheat phase. All the rest of
% wheat matrices are the same as the corn matrices


SD3=zeros(2,2);
SD3(1,1)=1;
SD3(1,2)=d7s1*d3f1;
SD3;
SD2=CD2;
SD1=CD1;
SD4=CD4;
% The matrix SD3 applies to the period Sept. through Nov. and accounts
% for predation of newly shed seed in the soybean phase. All the rest of % bean
matrices are the same as the corn matrices

Yr=[1:Y];
Years=Yr';
S=[1:Y];
SdsRC=S';     % Creates a storage vector for seed simulation data.
c=1;

% Begin model

for y=1:Y
        if y==1
                SdsRC(y)=n(1);
```

```
                    Years(y)=y;
          else
                    if c==1
                              nnov=n;                              % seeds in Nov. sdbk. before wheat
phase
                              nmar=SD4*nnov;
                              njun=WD1*nmar;
                              naug=WD2*njun;
                              nnov=WD3*naug;
                              n=nnov;
                              SdsRC(y)=nnov(1);
                              Years(y);
                              c=c+1;
                    elseif c==2            % seeds in Nov. sdbk. before corn phase
                              nnov=n;
                              nmar=WD4*nnov;
                              njun=CD1*nmar;
                              naug=CD2*njun;
                              nnov=CD3*naug;
                              n=nnov;
                              SdsRC(y)=nnov(1);
                              Years(y);
                              c=c+1;
                    elseif c==3            % seeds in Nov. sdbk. before bean phase
                              nnov=n;
                              nmar=CD4*nnov;
                              njun=SD1*nmar;
                              naug=SD2*njun;
                              nnov=SD3*naug;
                              n=nnov;
                              SdsRC(y)=nnov(1);
                              Years(y);
                              c=1;
                    end
          end
end

% Calculate lambda
format short e;
A1=WB3*WB2*WB1*SB4*SB3*SB2*SB1*CB4*CB3*CB2*CB1*WB4;  % compute overall A beginning
[W,D]=eig(A1);                                        % at Nov.of wheat phase for RC-
d=diag(D);
imax=find(d==max(d));
lambdaNoRC=d(imax)

A2=WD3*WD2*WD1*SD4*SD3*SD2*SD1*CD4*CD3*CD2*CD1*WD4;  % compute overall A beginning
[W,D]=eig(A2);                                        % at Nov.of wheat phase for RC+
d=diag(D);
imax=find(d==max(d));
lambdaRC=d(imax)


% Tabulate simulation data
format short e
disp('Weed Population Dynamics')
disp(' ')
disp(['Simulation length (years) = ' num2str(Y)])
disp(['Initial seedbank size = ' num2str(Seed_Start)])
disp(' ')
disp('    Years        Seeds RC-     Seeds RC+')
```

```
disp([(1:Y)' SdsNoRC SdsRC])


Seeds = [SdsNoRC;SdsRC];

% Graph simulation data
subplot(2,1,1)
plot(Years,SdsNoRC,'ko:', Years, SdsRC, 'k*-')
xlabel('Simulation year')
ylabel('Seeds in Nov')
legend('Seeds RC-', 'Seeds RC+')
title('Giant foxtail population dynamics in corn, soybeans and wheat (+ - RC)')

subplot(2,1,2)
semilogy(Years,SdsNoRC,'ko:', Years, SdsRC, 'k*-')
xlabel('Simulation year')
ylabel('Seeds in Nov')
legend('Seeds RC-', 'Seeds RC+')
title('Giant foxtail population dynamics in corn, soybeans and wheat (+/- RC)')
```

Sensitivity Calculations

```
% Giant foxtail population dynamics sensitivity calculations.

% Treatment: Fall/RC- (see below for Fall/RC+)
% Draft date: 3/4/02

% Variable declarations

% Seed survival probabilities
b3s1=.024;    % seed predation survival for year 1 seed in corn
b4s1=.9;      % overwinter survival for year 1 seed
b1s1=.44;     % year 1 seed left after germination
b2s1=.5;      % spring-summer survival for year 1 seed

% Germination probabilities
b1g1=.56;     % cohort 1&2 germination as percent of viable seed

% Seedling cohort 1&2 survival probabilities (germ. through repro. maturity)
b2p1=.97;

% Fecundity of cohort 1&2
b3f1=57;

% Post-Dispersal Seed Predation Survival in Wheat Phase
b6s1=.003;

% Post-Dispersal Seed Predation Survival in Soybean Phase
b7s1=.36;

% Matrix declarations

CB3=zeros(2,2);
CB3(1,1)=1;
CB3(1,2)=b3s1*b3f1;
CB3;
% The matrix B3 applies to the period Sept. through Nov. and accounts
% for seed rain and predation of newly shed seed in the corn phase.
```

```
CB4=zeros(2,2);
CB4(1,1)=b4s1;
CB4;

% The matrix B4 applies to the period Nov. through Mar. and accounts for
% overwinter seedbank decline.

CB1=zeros(2,2);
CB1(2,1)=b1g1;
CB1(1,1)=b1s1;
CB1;
% The matrix B1 applies to the period Mar. through June and accounts for
% seedling germination and seedbank depletion due to seedling
% germination.

CB2=zeros(2,2);
CB2(1,1)=b2s1;
CB2(2,2)=b2p1;
CB2;
% The matrix B2 applies to the period June through August and accounts
% for seedling survival to reproductive maturity and seed survival
% during this time.

WB3=zeros(2,2);
WB3(1,1)=1;
WB3(1,2)=b6s1*b3f1;
WB3;
WB2=CB2;
WB1=CB1;
WB4=CB4;
% The matrix WB3 applies to the period Sept. through Nov. and accounts
% for predation of newly shed seed in the wheat phase. All the rest of
% wheat matrices are the same as the corn matrices

SB3=zeros(2,2);
SB3(1,1)=1;
SB3(1,2)=b7s1*b3f1;
SB3;
SB2=CB2;
SB1=CB1;
SB4=CB4;
% The matrix SB3 applies to the period Sept. through Nov. and accounts
% for predation of newly shed seed in the soybean phase. All the rest of % bean
matrices are the same as the corn matrices


%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%
% Treatment: Fall/RC+

% Variable declarations

% Seed survival probabilities
d3s1=.024;    % seed predation survival for year 1 seed in corn
d4s1=.857;    % overwinter survival for year 1 seed
d1s1=.562;    % year 1 seed left after germination
d2s1=.44;     % spring-summer survival for year 1 seed

% Germination probabilities
d1g1=.438;    % cohort 1&2 germination as percent of viable seed
```

```
% Seedling cohort survival probabilities (germ. through repro. maturity)
d2p1=.97;

% Fecundity by cohort
d3f1=57;


% Post-Dispersal Seed Predation Survival in Wheat Phase
d6s1=.000000047;

% Post-Dispersal Seed Predation Survival in Soybean Phase
d7s1=.36;

% Matrix declarations

CD3=zeros(2,2);
CD3(1,1)=1;
CD3(1,2)=d3s1*d3f1;
CD3;
% The matrix D3 applies to the period Sept. through Nov. and accounts
% for seed rain and predation of newly shed seed in the corn phase.

CD4=zeros(2,2);
CD4(1,1)=d4s1;
CD4;

% The matrix D4 applies to the period Nov. through Mar. and accounts for
% overwinter seedbank decline.

CD1=zeros(2,2);
CD1(1,1)=d1g1;
CD1(1,1)=d1s1;
CD1;
% The matrix D1 applies to the period Mar. through June and accounts for
% seedling germination and seedbank depletion due to seedling
% germination.

CD2=zeros(2,2);
CD2(1,1)=d2s1;
CD2(1,1)=d2p1;
CD2;
% The matrix D2 applies to the period June through August and accounts
% for seedling survival to reproductive maturity and seed survival
% during this time.

WD3=zeros(2,2);
WD3(1,1)=1;
WD3(1,2)=d6s1*d3f1;
WD3;
WD2=CD2;
WD1=CD1;
WD4=CD4;
% The matrix WD3 applies to the period Sept. through Nov. and accounts
% for predation of newly shed seed in the wheat phase. All the rest of
% wheat matrices are the same as the corn matrices

SD3=zeros(2,2);
SD3(1,1)=1;
SD3(1,2)=d7s1*d3f1;
SD3;
SD2=CD2;
```

```
SD1=CD1;
SD4=CD4;
% The matrix SD3 applies to the period Sept. through Nov. and accounts
% for predation of newly shed seed in the soybean phase. All the rest of % bean
matrices are the same as the corn matrices


%%%%%%%%%%%%%%%%%%%%%%%%%%%
% Calculate sensitivities

%%%%%%%%%%%%%%%%%%%%%%%%%%%%

% h=1   Sensitivity analysis with respect to time period 1
format short e;
A1=WB4*WB3*WB2*WB1*SB4*SB3*SB2*SB1*CB4*CB3*CB2*CB1;
% compute A from Mar corn, RC-


C1=WD4*WD3*WD2*WD1*SD4*SD3*SD2*SD1*CD4*CD3*CD2*CD1;
% compute A from Mar corn, RC+


A=(A1+C1)/2;


Dmin=WB4*WB3*WB2*WB1*SB4*SB3*SB2*SB1*CB4*CB3*CB2;
Dplus=WD4*WD3*WD2*WD1*SD4*SD3*SD2*SD1*CD4*CD3*CD2;
Davg=(Dmin + Dplus)/2;


[W,D]=eig(A);        % compute eigenvalues and right eigenvector of A (see Caswell
d=diag(D);                       % (2000), section 9.1.1
imax=find(d==max(d));  % finds index of largest positive eigenvalue
V=conj(inv(W));        % scalar product of V and W will scale to 1
w=W(:,imax);
v=real(V(imax,:)).';   % gets rid of complex part of any complex numbers
lambda=d(imax);


SensA=(v*w'); % multiply v*w' to get full matrix of A sensitivity values
SensCB1=Davg'*SensA;   % get sensitivity with respect to period CB1


%%%%%%%%%%%%%%%%%%%%%%%%%%%%%
% h=2   Sensitivity and elasticity analysis with respect to time period 2
format short e;
A2=CB1*WB4*WB3*WB2*WB1*SB4*SB3*SB2*SB1*CB4*CB3*CB2; % RC-
C2=CD1*WD4*WD3*WD2*WD1*SD4*SD3*SD2*SD1*CD4*CD3*CD2; % RC+
A=(A2+C2)/2;


Dmin=CB1*WB4*WB3*WB2*WB1*SB4*SB3*SB2*SB1*CB4*CB3;
Dplus=CD1*WD4*WD3*WD2*WD1*SD4*SD3*SD2*SD1*CD4*CD3;
Davg=(Dmin + Dplus)/2;


[W,D]=eig(A);        % compute eigenvalues and right eigenvector of A (see Caswell
d=diag(D);                       % (2000), section 9.1.1
imax=find(d==max(d));  % finds index of largest positive eigenvalue
V=conj(inv(W));        % scalar product of V and W will scale to 1
w=W(:,imax);
v=real(V(imax,:)).';   % gets rid of complex part of any complex numbers
lambda=d(imax);


SensA=(v*w'); % multiply v*w' to get full matrix of A sensitivity values
SensCB2=Davg'*SensA;   % get sensitivity with respect to period CB2


%%%%%%%%%%%%%%%%%%%%%%%%%%%%%
% h=3
format short e;
```

```
A3=CB2*CB1*WB4*WB3*WB2*WB1*SB4*SB3*SB2*SB1*CB4*CB3;  % RC-
C3=CD2*CD1*WD4*WD3*WD2*WD1*SD4*SD3*SD2*SD1*CD4*CD3;  % RC+
A=(A3+C3)/2;


Dmin=CB2*CB1*WB4*WB3*WB2*WB1*SB4*SB3*SB2*SB1*CB4;
Dplus=CD2*CD1*WD4*WD3*WD2*WD1*SD4*SD3*SD2*SD1*CD4;
Davg=(Dmin + Dplus)/2;


[W,D]=eig(A);          % compute eigenvalues and right eigenvector of A (see Caswell
d=diag(D);                        % (2000), section 9.1.1
imax=find(d==max(d));  % finds index of largest positive eigenvalue
V=conj(inv(W));        % scalar product of V and W will scale to 1
w=W(:,imax);
v=real(V(imax,:)).';   % gets rid of complex part of any complex numbers
lambda=d(imax);


SensA=(v*w');  % multiply v*w' to get full matrix of A sensitivity values
SensCB3=Davg'*SensA;   % get sensitivity with respect to period CB3
SensCB3fec=SensCB3.*((b3s1+d3s1)/2);
%gives sens to lower level param by chain rule
SensCB3pred=SensCB3.*((b3f1+d3f1)/2);


%%%%%%%%%%%%%%%%%%%%%%%%%%%%
% h=4
format short e;
A4=CB3*CB2*CB1*WB4*WB3*WB2*WB1*SB4*SB3*SB2*SB1*CB4;  % RC-
C4=CD3*CD2*CD1*WD4*WD3*WD2*WD1*SD4*SD3*SD2*SD1*CD4;% RC+
A=(A4+C4)/2;


Dmin=CB3*CB2*CB1*WB4*WB3*WB2*WB1*SB4*SB3*SB2*SB1;
Dplus=CD3*CD2*CD1*WD4*WD3*WD2*WD1*SD4*SD3*SD2*SD1;
Davg=(Dmin + Dplus)/2;


[W,D]=eig(A);          % compute eigenvalues and right eigenvector of A (see Caswell
d=diag(D);                        % (2000), section 9.1.1
imax=find(d==max(d));  % finds index of largest positive eigenvalue
V=conj(inv(W));        % scalar product of V and W will scale to 1
w=W(:,imax);
v=real(V(imax,:)).';   % gets rid of complex part of any complex numbers
lambda=d(imax);


SensA=(v*w');  % multiply v*w' to get full matrix of A sensitivity values
SensCB4=Davg'*SensA;   % get sensitivity with respect to period CB4


%%%%%%%%%%%%%%%%%%%%%%%%%%%%
% h=5
format short e;
A5=CB4*CB3*CB2*CB1*WB4*WB3*WB2*WB1*SB4*SB3*SB2*SB1;  % RC-
C5=CD4*CD3*CD2*CD1*WD4*WD3*WD2*WD1*SD4*SD3*SD2*SD1;  % RC+
A=(A5+C5)/2;


Dmin=CB4*CB3*CB2*CB1*WB4*WB3*WB2*WB1*SB4*SB3*SB2;
Dplus=CD4*CD3*CD2*CD1*WD4*WD3*WD2*WD1*SD4*SD3*SD2;
Davg=(Dmin + Dplus)/2;


[W,D]=eig(A);          % compute eigenvalues and right eigenvector of A (see Caswell
d=diag(D);                        % (2000), section 9.1.1
imax=find(d==max(d));  % finds index of largest positive eigenvalue
V=conj(inv(W));        % scalar product of V and W will scale to 1
w=W(:,imax);
v=real(V(imax,:)).';   % gets rid of complex part of any complex numbers
```

```
lambda=d(imax);

SensA=(v*w'); % multiply v*w' to get full matrix of A sensitivity values
SensSB1=Davg'*SensA; % get sensitivity with respect to period SB1

%%%%%%%%%%%%%%%%%%%%%%%%%%
% h=6
format short e;
A6=SB1*CB4*CB3*CB2*CB1*WB4*WB3*WB2*WB1*SB4*SB3*SB2; % RC-
C6=SD1*CD4*CD3*CD2*CD1*WD4*WD3*WD2*WD1*SD4*SD3*SD2; % RC+
A=(A6+C6)/2;

Dmin=SB1*CB4*CB3*CB2*CB1*WB4*WB3*WB2*WB1*SB4*SB3;
Dplus=SD1*CD4*CD3*CD2*CD1*WD4*WD3*WD2*WD1*SD4*SD3;
Davg=(Dmin + Dplus)/2;

[W,D]=eig(A);          % compute eigenvalues and right eigenvector of A (see Caswell
d=diag(D);                      % (2000), section 9.1.1
imax=find(d==max(d));  % finds index of largest positive eigenvalue
V=conj(inv(W));         % scalar product of V and W will scale to 1
w=W(:,imax);
v=real(V(imax,:)).';  % gets rid of complex part of any complex numbers
lambda=d(imax);

SensA=(v*w'); % multiply v*w' to get full matrix of A sensitivity values
SensSB2=Davg'*SensA; % get sensitivity with respect to period SB2;

%%%%%%%%%%%%%%%%%%%%%%%%%%
% h=7
format short e;
A7=SB2*SB1*CB4*CB3*CB2*CB1*WB4*WB3*WB2*WB1*SB4*SB3; % RC-
C7=SD2*SD1*CD4*CD3*CD2*CD1*WD4*WD3*WD2*WD1*SD4*SD3; % RC+
A=(A7+C7)/2;

Dmin=SB2*SB1*CB4*CB3*CB2*CB1*WB4*WB3*WB2*WB1*SB4;
Dplus=SD2*SD1*CD4*CD3*CD2*CD1*WD4*WD3*WD2*WD1*SD4;
Davg=(Dmin + Dplus)/2;

[W,D]=eig(A);          % compute eigenvalues and right eigenvector of A (see Caswell
d=diag(D);                      % (2000), section 9.1.1
imax=find(d==max(d));  % finds index of largest positive eigenvalue
V=conj(inv(W));         % scalar product of V and W will scale to 1
w=W(:,imax);
v=real(V(imax,:)).';  % gets rid of complex part of any complex numbers
lambda=d(imax);

SensA=(v*w'); % multiply v*w' to get full matrix of A sensitivity values
SensSB3=Davg'*SensA; % get sensitivity with respect to period CB1
SensSB3fec=SensSB3.*((b7s1+d7s1)/2);
%gives sens to lower level param by chain rule
SensSB3pred=SensSB3.*((b3f1+d3f1)/2);

%%%%%%%%%%%%%%%%%%%%%%%%%%
% h=8
format short e;
A8=SB3*SB2*SB1*CB4*CB3*CB2*CB1*WB4*WB3*WB2*WB1*SB4; % RC-
C8=SD3*SD2*SD1*CD4*CD3*CD2*CD1*WD4*WD3*WD2*WD1*SD4; % RC+
A=(A8+C8)/2;

Dmin=SB3*SB2*SB1*CB4*CB3*CB2*CB1*WB4*WB3*WB2*WB1;
Dplus=SD3*SD2*SD1*CD4*CD3*CD2*CD1*WD4*WD3*WD2*WD1;
```

```
Davg=(Dmin - Dplus)/2;

[W,D]=eig(A);           % compute eigenvalues and right eigenvector of A (see Caswell
d=diag(D);                        % (2000), section 9.1.1
imax=find(d==max(d));   % finds index of largest positive eigenvalue
V=conj(inv(W));            % scalar product of V and W will scale to 1
w=W(:,imax);
v=real(V(imax,:)).';    % gets rid of complex part of any complex numbers
lambda=d(imax);

SensA=(v*w'); % multiply v*w' to get full matrix of A sensitivity values
SensSB4=Davg'*SensA;  % get sensitivity with respect to period SB1

%%%%%%%%%%%%%%%%%%%%%%%%%%
% h=9
format short e;
A9=SB4*SB3*SB2*SB1*CB4*CB3*CB2*CB1*WB4*WB3*WB2*WB1; % RC-
C9=SD4*SD3*SD2*SD1*CD4*CD3*CD2*CD1*WD4*WD3*WD2*WD1; % RC+
A=(A9+C9)/2;

Dmin=SB4*SB3*SB2*SB1*CB4*CB3*CB2*CB1*WB4*WB3*WB2;
Dplus=SD4*SD3*SD2*SD1*CD4*CD3*CD2*CD1*WD4*WD3*WD2;
Davg=(Dmin - Dplus)/2;

[W,D]=eig(A);           % compute eigenvalues and right eigenvector of A (see Caswell
d=diag(D);                        % (2000), section 9.1.1
imax=find(d==max(d));   % finds index of largest positive eigenvalue
V=conj(inv(W));            % scalar product of V and W will scale to 1
w=W(:,imax);
v=real(V(imax,:)).';    % gets rid of complex part of any complex numbers
lambda=d(imax);

SensA=(v*w'); % multiply v*w' to get full matrix of A sensitivity values
SensWB1=Davg'*SensA;  % get sensitivity with respect to period SB1

%%%%%%%%%%%%%%%%%%%%%%%%%%
% h=10
format short e;
A10=WB1*SB4*SB3*SB2*SB1*CB4*CB3*CB2*CB1*WB4*WB3*WB2; % RC-
C10=WD1*SD4*SD3*SD2*SD1*CD4*CD3*CD2*CD1*WD4*WD3*WD2; % RC+
A=(A10+C10)/2;

Dmin=WB1*SB4*SB3*SB2*SB1*CB4*CB3*CB2*CB1*WB4*WB3;
Dplus=WD1*SD4*SD3*SD2*SD1*CD4*CD3*CD2*CD1*WD4*WD3;
Davg=(Dmin + Dplus)/2;

[W,D]=eig(A);           % compute eigenvalues and right eigenvector of A (see Caswell
d=diag(D);                        % (2000), section 9.1.1
imax=find(d==max(d));   % finds index of largest positive eigenvalue
V=conj(inv(W));            % scalar product of V and W will scale to 1
w=W(:,imax);
v=real(V(imax,:)).';    % gets rid of complex part of any complex numbers
lambda=d(imax);

SensA=(v*w'); % multiply v*w' to get full matrix of A sensitivity values
SensWB2=Davg'*SensA;  % get sensitivity with respect to period SB1

%%%%%%%%%%%%%%%%%%%%%%%%%%
% h=11
format short e;
A11=WB2*WB1*SB4*SB3*SB2*SB1*CB4*CB3*CB2*CB1*WB4*WB3; % RC-
```
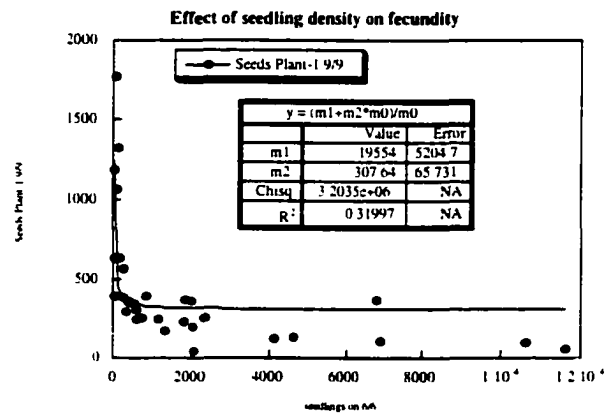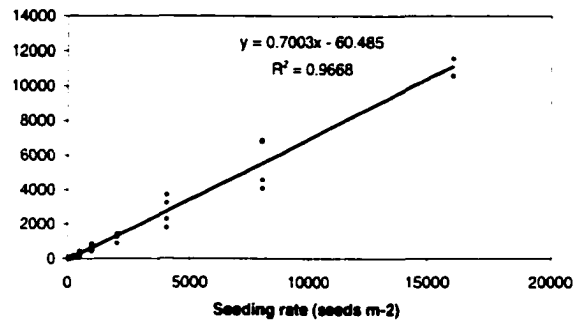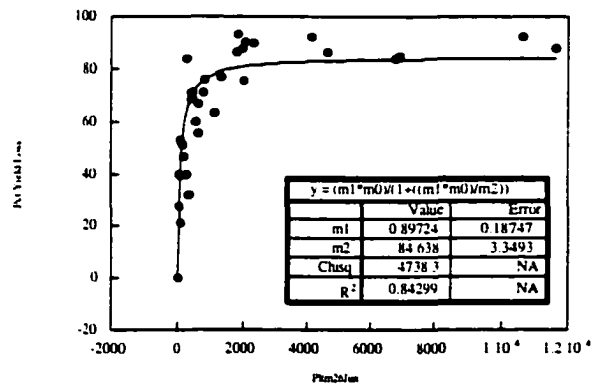
```
C11=WD2*WD1*SD4*SD3*SD2*SD1*CD4*CD3*CD2*CD1*WD4*WD3;  % RC+
A=(A11-C11) 2;


Dmin=WB2*WB1*SB4*SB3*SB2*SB1*CB4*CB3*CB2*CB1*WB4;
Dplus=WD2*WD1*SD4*SD3*SD2*SD1*CD4*CD3*CD2*CD1*WD4;
Davg=(Dmin + Dplus)/2;


[W,D]=eig(A);       % compute eigenvalues and right eigenvector of A (see Caswell
d=diag(D);                        % (2000), section 9.1.1
imax=find(d==max(d));  % finds index of largest positive eigenvalue
V=conj(inv(W));         % scalar product of V and W will scale to 1
w=W(:,imax);
v=real(V(imax,:)).';  % gets rid of complex part of any complex numbers
lambda=d(imax);


SensA=(v*w');  % multiply v*w' to get full matrix of A sensitivity values
SensWB3=Davg'*SensA;   % get sensitivity with respect to period CB1
SensWB3fec=SensWB3.*((b6s1+d6s1)/2);
%gives sens to lower level param by chain rule
SensWB3pred=SensWB3.*((b3f1+d3f1) 2);


%%%%%%%%%%%%%%%%%%%%%%%%%%
% h=10
format short e;
A12=WB3*WB2*WB1*SB4*SB3*SB2*SB1*CB4*CB3*CB2*CB1*WB4;  % RC-
C12=WD3*WD2*WD1*SD4*SD3*SD2*SD1*CD4*CD3*CD2*CD1*WD4;  % RC+
A=(A12-C12) 2;


Dmin=WB3*WB2*WB1*SB4*SB3*SB2*SB1*CB4*CB3*CB2*CB1;
Dplus=WD3*WD2*WD1*SD4*SD3*SD2*SD1*CD4*CD3*CD2*CD1;
Davg=(Dmin + Dplus)/2;


[W,D]=eig(A);       % compute eigenvalues and right eigenvector of A (see Caswell
d=diag(D);                        % (2000), section 9.1.1
imax=find(d==max(d));  % finds index of largest positive eigenvalue
V=conj(inv(W));         % scalar product of V and W will scale to 1
w=W(:,imax);
v=real(V(imax,:)).';  % gets rid of complex part of any complex numbers
lambda=d(imax);


SensA=(v*w');  % multiply v*w' to get full matrix of A sensitivity values
SensWB4=Davg'*SensA;   % get sensitivity with respect to period WB4


%%%%%%%%%%%%%%%%%%%%%%%%
% Print sensitivity matrices

SensCB1
SensCB2
SensCB3fec
SensCB3pred
SensCB4
SensSB1
SensSB2
SensSB3fec
SensSB3pred
SensSB4
SensWB1
SensWB2
SensWB3fec
SensWB3pred
SensWB4
```

APPENDIX B. DENSITY DEPENDENCE OF GIANT FOXTAIL VITAL RATES

Effect of seedling density on fecundity

Effect of giant foxtail seedling recruitment (Jun 6) on % corn yield loss

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