

## USING MATRIX MODELS TO DETERMINE CROPPING SYSTEM EFFECTS ON ANNUAL WEED DEMOGRAPHY

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**Abstract.** The design of most agricultural systems ignores the possibility that cropping system characteristics may affect weed population dynamics by altering key demographic rates of weeds. We examined legume green manure and tillage timing effects upon giant foxtail (*Setaria faberi*) demography with prospective and retrospective perturbation analyses 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. Wheat phase residues were incorporated either in fall (FT) or spring (ST) to form four cropping system treatments: FT/W, FT/R, ST/W, and ST/R. Demographic rates estimated from the field data included seed survival from October to March and March to October, seedling recruitment, plant survival, fecundity, and seed predation. The variable efficacy of post-emergence weed control was modeled by varying the proportion of seedlings surviving to reproductive maturity from 0.025 to 0.20. Deterministic simulations indicated that there was both interannual and management-induced variation in *S. faberi* population growth rate. Stochastic population growth rate depended upon an interaction between legume green manure and tillage-timing effects, such that stochastic population growth rate was lowest for fall-tilled wheat and red clover, greater for fall-tilled wheat, and greatest for both spring-tilled management regimes. Within the fall-tilled regime, the cropping system (wheat vs. wheat plus clover) had a greater influence on relative rates of stochastic population growth as plant survival increased. However, plant survival did not affect the stochastic population growth rates in the spring-tilled treatments. Elasticity analysis suggested that seed survival through the winter, fecundity, and the proportion of seeds escaping predation were important driving variables for this system. Retrospective perturbation analysis supported these results but also indicated that fecundity and predation levels varied more in response to changing management treatments than winter seed survival, leading to their having a greater influence on differences in population growth among the four management treatments. 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:** ecological weed management; elasticity analysis; giant foxtail; legume green manure; life table response experiment (LTRE); periodic matrix population model; *Setaria faberi*; stochastic simulation; tillage timing.

### 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 noncrop plant species, primarily arising from taxa with ruderal life histories, that are preadapted 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 McPeck 1992, Bierzychudek 1999, Emery et al. 1999, Rydgren et al. 2001, Pico et al. 2002) and conservation biology (Crouse et al. 1987, Crowder et al. 1994, Doak et al. 1994, Seamans et al. 1999), this approach has

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PLATE 1. Mature *Setaria faberi* (giant foxtail) panicles in corn in Boone, Iowa, USA, in September 2001. Photo credit: Adam Davis.

been applied less often to weed management questions (Jordan et al. 1995, Pino et al. 1998, Shea and Kelly 1998, McEvoy and Coombs 1999, 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 ( $\lambda$ ) under different conditions, matrix models may also be used to understand how perturbations to model parameters affect  $\lambda$ . Prospective perturbation analysis includes sensitivity and elasticity analysis to account for additive and proportional changes, respectively, to a given demographic rate (de Kroon et al. 2000). This approach may be used by ecosystem managers to identify demographic parameters whose variation has the potential to cause large changes in population growth rate. 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  $\lambda$  to a given demographic parameter tends to be inversely correlated with the variability of that parameter (de Kroon et al. 2000, Pico et al. 2002). That is, demographic parameters whose variation causes large changes in  $\lambda$  tend to resist change.

Because of the relative ease of performing replicated, small-scale experiments of management effects on weed demographic rates, it is practical to supplement prospective perturbation analysis with retrospective perturbation analysis of matrix simulation models. Such combined analyses will help to target life stage transitions whose disruption will have the greatest impact on weed population growth rate under a given set

of management conditions (McEvoy and Coombs 1999). The life table response experiment (LTRE) approach to retrospective perturbation analysis decomposes treatment effects on  $\lambda$  into contributions from each matrix element by weighting treatment differences in each matrix element by the sensitivity of  $\lambda$  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  $\lambda$ , even if  $\lambda$  is highly sensitive to potential changes in that parameter. We will refer to those life-stage transitions whose disruption not only has a large impact on  $\lambda$ , but who also exhibit a large degree of variability in response to a given management practice as “target transitions,” following the terminology of McEvoy and Coombs (1999).

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; see Plate 1). *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 amend-

TABLE 1. Abbreviations and estimators for *Setaria faberi* demographic parameters.

Parameter	Abbreviation	Units
Recruitment	$\gamma$	$N_{\text{plt(Jun)}}/N_{\text{sd(Mar)}}$
Plant survival	$\sigma_{\text{p}}$	$N_{\text{plt(Aug)}}/N_{\text{plt(Jun)}}$
Seed survival <sub>Mar-Oct</sub>	$\sigma_{\text{s(s)}}$	$(N_{\text{sd(Mar)}} - N_{\text{plt(Jun)}} - N_{\text{sd(Oct)}})/N_{\text{sd(Mar)}}$
Fecundity	$\phi$	Seeds/plant
Seed survival <sub>Predation</sub>	$\sigma_{\text{s(pred)}}$	$N_{\text{newsd(Oct)}}/N_{\text{newsd(Aug)}}$
Seed survival <sub>Oct-Mar</sub>	$\sigma_{\text{s(w)}}$	$N_{\text{sd(Mar)}}/N_{\text{sd(Oct)}}$

Notes:  $N_{\text{plt}}$  = number of plants,  $N_{\text{sd}}$  = number of seeds, and  $N_{\text{newsd}}$  = number of newly shed seeds.

ments 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 2003), 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. 2003) 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 (2003). 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 target transitions 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 com-

ponent of this research are explained fully in Davis and Liebman (2003) 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, Iowa, 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  $3.8 \times 12.2$  m main plots, each of which contained two  $3.8 \times 6.1$  m subplots.

**Parameter estimation.**—Six demographic parameters were estimated for *S. faberi* using data from the 2000 and 2001 field seasons: recruitment ( $\gamma$ ), seed survival from March through October ( $\sigma_{\text{s(s)}}$ ), plant survival to reproductive maturity ( $\sigma_{\text{p}}$ ), seed production per plant ( $\phi$ ), proportion of seeds not consumed due to postdispersal seed predation prior to fall tillage ( $\sigma_{\text{s(pred)}}$ ), and seed survival from October through March ( $\sigma_{\text{s(w)}}$ ). Rules for parameter estimation are given in Table 1, parameter values are given in Table 2, and the life history of *S. faberi* is summarized in Fig. 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 seed predation survival were converted into a season-long estimate of seed predation survival by compounding point estimates of seed predation sur-

TABLE 2. *Setaria faberi* demographic rates under four different cropping systems in 2000 and 2001 in Boone, Iowa.

Cropping system and rotation phase	Demographic parameter (mean $\pm$ 1 SE)					
	$\sigma_{s(w)}$	$\gamma$	$\sigma_p$	$\phi$	$\sigma_{s(s)}$	$\sigma_{s(pred)}$
Year 2000						
FT/W						
Corn	0.88 $\pm$ 0.01	0.54 $\pm$ 0.04	0.1	57 $\pm$ 9	0.54 $\pm$ 0.01	0.016 $\pm$ 0.007
Soybean	0.88 $\pm$ 0.01	0.54 $\pm$ 0.04	0.1	94 $\pm$ 15	0.54 $\pm$ 0.01	0.36 $\pm$ 0.067
Wheat	0.91 $\pm$ 0.01	0.54 $\pm$ 0.04	0.1	23 $\pm$ 4	0.54 $\pm$ 0.01	0.0003 $\pm$ 0.002
FT/R						
Corn	0.88 $\pm$ 0.01	0.54 $\pm$ 0.01	0.1	57 $\pm$ 9	0.54 $\pm$ 0.01	0.016 $\pm$ 0.007
Soybean	0.88 $\pm$ 0.01	0.54 $\pm$ 0.04	0.1	94 $\pm$ 16	0.54 $\pm$ 0.01	0.36 $\pm$ 0.067
Wheat	0.86 $\pm$ 0.01	0.54 $\pm$ 0.04	0.1	23 $\pm$ 4	0.54 $\pm$ 0.01	4.6 $\times 10^{-7} \pm 2.4 \times 10^{-7}$
ST/W						
Corn	0.88 $\pm$ 0.01	0.54 $\pm$ 0.04	0.1	278 $\pm$ 31	0.54 $\pm$ 0.01	0.016 $\pm$ 0.007
Soybean	0.88 $\pm$ 0.01	0.54 $\pm$ 0.04	0.1	459 $\pm$ 52	0.54 $\pm$ 0.01	0.36 $\pm$ 0.067
Wheat	0.86 $\pm$ 0.01	0.54 $\pm$ 0.04	0.1	111 $\pm$ 13	0.54 $\pm$ 0.01	0.0003 $\pm$ 0.002
ST/R						
Corn	0.88 $\pm$ 0.01	0.38 $\pm$ 0.01	0.1	1150 $\pm$ 210	0.54 $\pm$ 0.01	0.016 $\pm$ 0.007
Soybean	0.88 $\pm$ 0.01	0.54 $\pm$ 0.04	0.1	459 $\pm$ 52	0.54 $\pm$ 0.01	0.36 $\pm$ 0.067
Wheat	0.86 $\pm$ 0.01	0.54 $\pm$ 0.04	0.1	111 $\pm$ 13	0.54 $\pm$ 0.01	4.6 $\times 10^{-7} \pm 2.4 \times 10^{-7}$
Year 2001						
FT/W						
Corn	0.56 $\pm$ 0.02	0.80 $\pm$ 0.06	0.1	1080 $\pm$ 94	0.58 $\pm$ 0.04	0.016 $\pm$ 0.007
Soybean	0.56 $\pm$ 0.02	0.80 $\pm$ 0.06	0.1	1782 $\pm$ 155	0.58 $\pm$ 0.04	0.36 $\pm$ 0.067
Wheat	0.60 $\pm$ 0.01	0.80 $\pm$ 0.06	0.1	432 $\pm$ 38	0.58 $\pm$ 0.04	0.0003 $\pm$ 0.002
FT/R						
Corn	0.56 $\pm$ 0.02	0.80 $\pm$ 0.06	0.1	1080 $\pm$ 94	0.58 $\pm$ 0.04	0.016 $\pm$ 0.007
Soybean	0.56 $\pm$ 0.02	0.80 $\pm$ 0.06	0.1	1782 $\pm$ 155	0.58 $\pm$ 0.04	0.36 $\pm$ 0.067
Wheat	0.60 $\pm$ 0.01	0.80 $\pm$ 0.06	0.1	432 $\pm$ 38	0.58 $\pm$ 0.04	4.6 $\times 10^{-7} \pm 2.4 \times 10^{-7}$
ST/W						
Corn	0.56 $\pm$ 0.02	0.80 $\pm$ 0.06	0.1	1080 $\pm$ 94	0.70 $\pm$ 0.03	0.016 $\pm$ 0.007
Soybean	0.56 $\pm$ 0.02	0.80 $\pm$ 0.06	0.1	1782 $\pm$ 155	0.58 $\pm$ 0.04	0.36 $\pm$ 0.067
Wheat	0.51 $\pm$ 0.03	0.80 $\pm$ 0.06	0.1	432 $\pm$ 38	0.58 $\pm$ 0.04	0.0003 $\pm$ 0.002
ST/R						
Corn	0.56 $\pm$ 0.02	0.56 $\pm$ 0.06	0.1	1965 $\pm$ 165	0.70 $\pm$ 0.03	0.016 $\pm$ 0.007
Soybean	0.56 $\pm$ 0.02	0.80 $\pm$ 0.06	0.1	1782 $\pm$ 155	0.58 $\pm$ 0.04	0.36 $\pm$ 0.067
Wheat	0.51 $\pm$ 0.03	0.80 $\pm$ 0.06	0.1	432 $\pm$ 38	0.58 $\pm$ 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 1. No standard errors are given for  $\sigma_p$ , because this value was chosen rather than estimated.

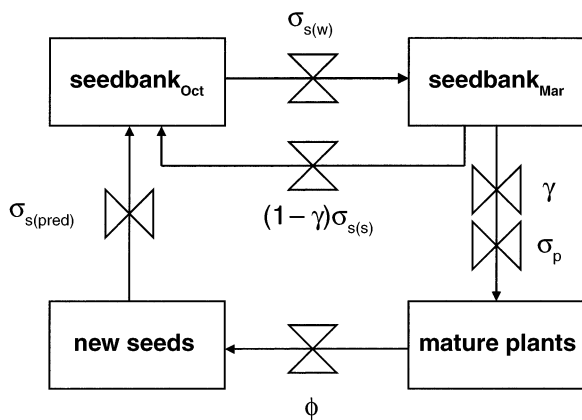


FIG. 1. Life cycle of *Setaria faberi*, including all demographic parameters measured in the field experiment. Parameter abbreviations are given in Table 1.

vival from late September, when predation rates were at their peak, over 20 d. We considered compounding the daily rates of seed-predation survival over the entire predation period from August through October, but the resulting percentages of surviving seeds were too low to be realistic. We measured recruitment, fecundity, and seed-predation survival in all three phases of the crop sequence, whereas we measured seed survival from October through March and March through October 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 postemergence weed control on weed seedling survival by setting seedling survival ( $\sigma_p$ ) at 10% for the deterministic simulation, and varying  $\sigma_p$  between 2.5% and 20% for the stochastic simulation. These values of  $\sigma_p$  fall within a range that is realistic for field crop production systems (Buhler et al. 1992, Mulder and Doll 1993).



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

$$\mathbf{n}_t = \begin{pmatrix} n_s \\ n_p \end{pmatrix} \quad \text{Recruitment} \quad \mathbf{B}_{(1k)} = \begin{pmatrix} 1 - \gamma & 0 \\ \gamma & 0 \end{pmatrix} \quad \text{Spring survival} \quad \mathbf{B}_{(2k)} = \begin{pmatrix} \sigma_{s(s)} & 0 \\ 0 & \sigma_p \end{pmatrix}$$

$$\mathbf{B}_{(3k)} = \begin{pmatrix} 1 & \phi \sigma_{s(\text{pred})} \\ 0 & 0 \end{pmatrix} \quad \text{Fecundity} \quad \text{Winter survival} \quad \mathbf{B}_{(4k)} = \begin{pmatrix} \sigma_{s(w)} & 0 \\ 0 & 0 \end{pmatrix}$$

FIG. 2. Subannual 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 1.

#### 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 subannual periods in each of the phases in the wheat–corn–soybean crop sequence, for a total of 12 periods in one rotation cycle (Fig. 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

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

$$= \mathbf{A}_{(h_k)} \mathbf{n}_t \quad (2)$$

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  $\mathbf{B}_{(h_k)}$  was a projection matrix for period  $h$  in phase  $k$  of the crop sequence,  $\mathbf{A}_{(h_k)}$  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 subannual periods (Fig. 2). The population growth rate of *S. faberi* over the rotation cycle ( $\lambda_{\text{cycle}}$ ) was calculated as the dominant eigenvalue of  $\mathbf{A}_{(h_k)}$  (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 nonzero element,  $a_{11}$ , in  $\mathbf{A}_{(h_k)}$ . 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 subannual 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  $\lambda_{\text{cycle}}$  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  $\ln(\lambda_{\text{cycle}})$ . The  $\log_e$  transformation of  $\lambda_{\text{cycle}}$  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). We treated year as a fixed effect, since we limited inferences about management effects to 2000 and 2001.

**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 ( $\ln(\lambda_{s(\text{cycle})})$ ) over the three-phase rotation cycle (Heyde and Cohen 1985, Caswell 2001). One-step estimates of  $\ln(\lambda_{s(\text{cycle})})$  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:

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

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

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

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

We examined the effects of variable postemergence weed control efficacy on  $\ln(\lambda_{\text{cycle}})$  by simulating population growth for values of  $\sigma_p$  ranging from 0.025 through 0.20 in increments of 0.025. At each level of  $\sigma_p$ , we took the mean of  $\ln(\lambda_{\text{cycle}})$  obtained through one realization of the stochastic simulation for each of the four experimental replications. We subjected values of  $\ln(\lambda_{\text{cycle}})$  at each level of  $\sigma_p$  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  $\ln(\lambda_{\text{cycle}})$  (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  $\lambda$ . Sensitivity analysis examines changes in  $\lambda$  in response to additive perturbations to each element of  $\mathbf{A}$  ( $\mathbf{S}_A = \partial\lambda/\partial a_{ij}$ ), whereas elasticity analysis examines changes in  $\lambda$  in response to proportional perturbations to each  $a_{ij}$  ( $\mathbf{E}_A = (a_{ij}/\lambda)(\partial\lambda/\partial a_{ij})$ ) (Caswell 2001). A direct method for obtaining  $\mathbf{S}_A$  is to calculate eigenvalue sensitivities to perturbations of elements of the annual projection matrix. The elements of  $\mathbf{S}_A$  are computed using the right ( $\mathbf{w}$ ) and left ( $\mathbf{v}$ ) eigenvectors:

$$\frac{\partial\lambda}{\partial a_{ij}} = \frac{v_i w_j}{\langle \mathbf{w}, \mathbf{v} \rangle} \quad (5)$$

where  $a_{ij}$  are the elements of  $\mathbf{A}$ , and  $\langle \mathbf{w}, \mathbf{v} \rangle$  is the scalar product of the right and left eigenvectors of  $\mathbf{A}$  (Caswell 2001).

This procedure has been extended to permit the calculation of eigenvalue sensitivities of periodic projection matrices (Caswell and Trevisan 1994):

$$\begin{aligned} \mathbf{S}_{\mathbf{B}(h)} &= \mathbf{D}^T \mathbf{S}_{\mathbf{A}(h)} \\ &= [\mathbf{B}_{(h-1)} \cdots \mathbf{B}_{(1)} \mathbf{B}_{(m)} \cdots \mathbf{B}_{(h+1)}]^T \mathbf{S}_{\mathbf{A}(h)} \end{aligned} \quad (6)$$

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

$$\mathbf{E}_{\mathbf{B}(h)} = (b_{hij}/\lambda) \mathbf{S}_{\mathbf{B}(h)}. \quad (7)$$

The periodic sensitivity and elasticity calculations shown above describe the response of  $\lambda$  to perturbations of  $\mathbf{A}(h_k)$ . The elements of  $\mathbf{A}(h_k)$  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  $\mathbf{A}(h_k) = (\mathbf{B}_{(h-1)} \cdots \mathbf{B}_{(1)} \mathbf{B}_{(m)} \cdots \mathbf{B}_{(h+1)} \mathbf{B}_{(h)})_k$ . For the simple system described in this study, all  $\mathbf{A}(h_k)$  had only one nonzero element,  $a_{11}$ , which contained the product of all the demographic parameters in each of the rotation phases:  $([\sigma_{s(w)}][\phi][\sigma_{s(s)}][1 - \gamma] + [\sigma_{s(w)}][\phi][\sigma_{s(pred)}][\sigma_p][\gamma])_k$ . 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  $\lambda_{\text{cycle}}$  responded to the perturbation of individual demographic parameters, such as recruitment ( $\gamma$ ) or fecundity ( $\phi$ ). This problem was solved by applying the chain rule for differentiation (Caswell 2001), so that for a given demographic parameter  $x$ ,

$$\frac{\partial\lambda}{\partial x^{(h_k)}} = \sum_{i,j} \frac{\partial\lambda}{\partial b_{ij}^{(h_k)}} \frac{\partial b_{ij}^{(h_k)}}{\partial x^{(h_k)}} \quad (8)$$

$$\frac{x^{(h_k)}}{\lambda} \frac{\partial\lambda}{\partial x^{(h_k)}} = \frac{x^{(h_k)}}{\lambda} \sum_{i,j} \frac{\partial\lambda}{\partial b_{ij}^{(h_k)}} \frac{\partial b_{ij}^{(h_k)}}{\partial x^{(h_k)}} \quad (9)$$

where Eqs. 8 and 9 describe the sensitivity and elasticity, respectively, of  $\lambda$  with respect to  $x$ .

Standard errors for the elasticity of  $\lambda$  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. 2003). The LTRE equation was rewritten to decompose treatment effects on  $\lambda$  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  $\lambda$  to changes in each  $x_{hijkl}$ . The equation used to describe the LTRE approximation for a periodic matrix model was

$$\begin{aligned} \lambda^{(m)} - \lambda^{(r)} &\approx \sum_{hijkl} (x_{hijkl}^{(m)} - x_{hijkl}^{(r)}) \mathbf{D}^T \mathbf{S}_{\mathbf{A}(h_k)} |_{\mathbf{A}(h_k)^*} \\ m &= 1, \dots, N \end{aligned} \quad (10)$$

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  $\mathbf{B}(h_k)$  (see Eq. 6),  $\mathbf{S}_{\mathbf{A}(h_k)}$  represents the sensitivity of  $\lambda$  to changes in the lower level demographic parameters comprising 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 treat-

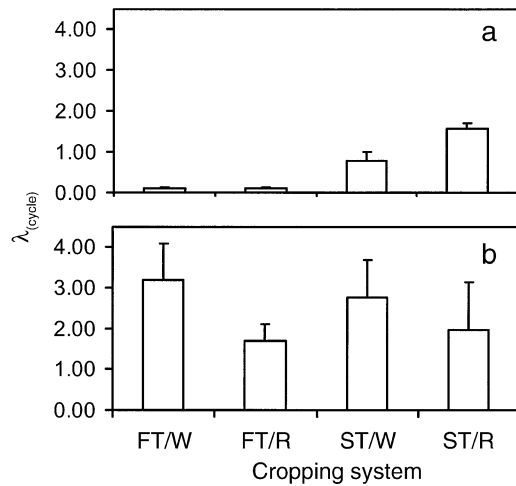


FIG. 3. Population growth rate ( $\lambda$ ) of *Setaria faberi* grown in contrasting cropping systems in Boone, Iowa, in (a) 2000 and (b) 2001. Cropping system abbreviations are explained in Table 2. Error bars represent 1 SE.

ment-specific  $\mathbf{B}(h_k)$ , and then averaged over  $\mathbf{A}(h_k)^{(m)}$  and  $\mathbf{A}(h_k)^{(r)}$  to obtain  $\mathbf{A}(h_k)^*$ .

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  $\lambda_{\text{cycle}}$ . For the decomposition of  $\Delta\lambda_{\text{cycle}}$  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  $\Delta\lambda_{\text{cycle}}$  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  $\lambda$  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  $(|\Delta\lambda[\text{LTRE}] - \Delta\lambda[\text{model}]|)/\Delta\lambda[\text{model}]$ . 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 ( $\lambda_{\text{cycle}}$ ) showed considerable range among cropping systems and between growing seasons (Fig. 3, Table 3). There was a main effect of year on  $\ln(\lambda_{\text{cycle}})$  ( $N = 16$ ,  $1 \text{ SE} = 0.18$ ,  $F_{1,16} = 9.32$ ,  $P = 0.022$ ), such that in 2000, the average of  $\ln(\lambda_{\text{cycle}})$  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  $\ln(\lambda_{\text{cycle}})$  ( $N = 16$ ,  $1 \text{ SE} = 0.18$ ,  $F_{1,16} = 30.45$ ,  $P = 0.001$ ). The average of  $\ln(\lambda_{\text{cycle}})$  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  $\ln(\lambda_{\text{cycle}})$  ( $N = 8$ ,  $1 \text{ SE} = 0.26$ ,  $F_{1,8} = 15.71$ ,  $P = 0.002$ ). In 2000,  $\ln(\lambda_{\text{cycle}})$  was lower in the W treatment ( $-1.42$ ) than in the R treatment ( $-1.17$ ), whereas in 2001,  $\lambda_{\text{cycle}}$  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  $\ln(\lambda_{\text{cycle}})$  ( $N = 8$ ,  $1 \text{ SE} = 0.26$ ,  $F_{1,8} = 27.74$ ,  $P = 0.002$ ). In 2000,  $\ln(\lambda_{\text{cycle}})$  was much lower in the FT treatment ( $-2.42$ ) than in the ST treatment ( $-0.17$ ), but in 2001,  $\ln(\lambda_{\text{cycle}})$  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-yr 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

TABLE 3. Analysis of variance of log<sub>e</sub>-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 $\times$ tillage timing	1	9.62	27.74	0.002
Error B	6	2.08		
Red clover	1	0.016	0.038	0.549
Year $\times$ red clover	1	0.67	15.71	0.002
Tillage timing $\times$ red clover	1	0.50	11.85	0.005
Year $\times$ tillage timing $\times$ red clover	1	0.029	0.69	0.422
Error C	12	0.508		

Notes: The experimental design was a split plot with four replications of four treatments over two years ( $n = 32$ ). Tillage timing was the main plot factor, and red clover was the split-plot factor. See Table 2 for an explanation of tillage-timing and red-clover treatments.

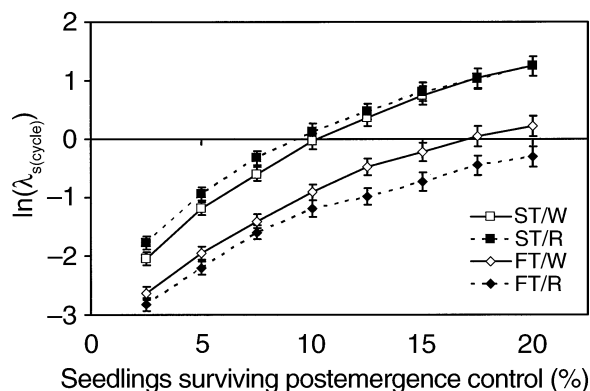


FIG. 4. Stochastic population growth rate [ $\ln(\lambda_{s(cycle)})$ ] of *S. faberi* grown in contrasting cropping systems, with simulated variation in postemergence weed control. Cropping-system abbreviations are explained in Table 2. Error bars represent  $\pm 1$  SE.

that had been recently incorporated into the soil, which reduced the competitive effect of corn upon *S. faberi* growth and fecundity (Davis and Liebman 2003). Growing conditions in 2001 were favorable for *S. faberi*, leading to greater recruitment and fecundity in all treatments in 2001 than 2000 (Table 2). Despite treatment  $\times$  year interactions, there was a tillage timing  $\times$  red clover interaction effect ( $N = 8$ ,  $1 \text{ SE} = 0.25$ ,  $F_{1,8} = 11.85$ ,  $P = 0.005$ ), across growing seasons, on  $\ln(\lambda_{cycle})$ . The natural log of  $\lambda_{cycle}$  was lower in the R level ( $-1.25$ ) than in the W level ( $-0.95$ ) of the FT treatment, whereas  $\ln(\lambda_{cycle})$  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 postemergence weed control resulting in 10% seedling survival, which was the value of seedling survival 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  $\times$  red clover interaction effect on  $\ln(\lambda_{cycle})$ .

The importance of cropping system effects on variation in *S. faberi*  $\ln(\lambda_{s(cycle)})$  appeared to vary inversely with the success of postemergent weed control within the FT treatment, but not within the ST treatment (Fig. 4). The W and R levels of the FT treatment were not different ( $P > 0.05$ ) when postemergent control resulted in  $\leq 10\%$  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). 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  $\lambda_{cycle}$  to each of the lower level demographic parameters of *S.*

*faberi* within each rotation phase. To streamline the presentation of results, the elasticity of  $\lambda_{cycle}$  to each parameter will be designated by the symbol  $e$  followed by the parameter abbreviation given in the methods section and in Table 1. For all cropping systems in all years,  $e\sigma_{s(w)}$  (the elasticity of  $\lambda$  to seed survival from October through March) was 1.0 (Table 4). Values of  $e\gamma$  (the elasticity of  $\lambda$  to recruitment) 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,  $e\gamma$  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  $e\sigma_{s(pred)}$  (seedling survival, seed survival from March through October and seed predation survival, respectively), 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 (0.17–0.68) in 2000, and were consistently high (0.85–0.92) in 2001. Values of  $e\sigma_{s(s)}$  in the soybean phase were low (0.03–0.12) in 2000 and very low (0.002) in 2001. Values of  $e\sigma_{s(s)}$  in the wheat phase were very high (0.93–1.0) in 2000 and ranged from medium to very high (0.53–1.0) in 2001. Finally, values of  $e\sigma_{s(s)}$  in the corn phase ranged from medium to high (0.32–0.83) in 2000 and were low (0.08–0.15) in 2001.

**Retrospective.**—We used retrospective perturbation analysis to decompose the simple effects of red clover and tillage timing, within years, on  $\lambda_{cycle}$  into contributions made by simple treatment effects on lower level *S. faberi* demographic parameters. We will present the contributions to  $\lambda_{cycle}$  due to red clover simple effects (Fig. 5), followed by those due to tillage timing simple effects (Fig. 6).

There was only a very small difference ( $\Delta\lambda_{cycle} = 0.006$ ) in  $\lambda_{cycle}$  between the R and W levels of the FT treatment in 2000. This difference was due to very small negative contributions from seed survival from October through March ( $\sigma_{s(w)}$ ) and seed predation survival ( $\sigma_{s(pred)}$ ) in the wheat phase (Fig. 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 seed predation survival in the wheat phase (Fig. 5b). Demographic parameter values for R level of the ST treatment in 2000 led to projections of a growing population



TABLE 4. Elasticity of *Setaria faberi* population growth rate (over the entire rotation cycle) to lower-level demographic parameters under four different cropping systems.

Cropping system and rotation phase	Elasticities of $\lambda_{\text{cycle}}$ to <i>S. faberi</i> demographic parameters					
	$\sigma_{s(w)}$	$\gamma$	$\sigma_p$	$\phi$	$\sigma_{s(s)}$	$\sigma_{s(\text{pred})}$
Year 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	$1.48 \times 10^{-2}$	$1.48 \times 10^{-2}$	0.99	$1.48 \times 10^{-2}$
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	$2.30 \times 10^{-6}$	$2.30 \times 10^{-6}$	1.00	$2.30 \times 10^{-6}$
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	$1.11 \times 10^{-5}$	$1.11 \times 10^{-5}$	1.00	$1.11 \times 10^{-5}$
Year 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	$1.37 \times 10^{-4}$	$1.37 \times 10^{-4}$	1.00	$1.37 \times 10^{-4}$
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	$1.37 \times 10^{-4}$	$1.37 \times 10^{-4}$	1.00	$1.37 \times 10^{-4}$

Notes: See Tables 1 and 2 for explanation of abbreviations of *S. faberi* demographic parameters and cropping-system treatments, respectively.

( $\lambda_{\text{cycle}} = 1.57$ ), whereas the W level of the ST treatment in 2000 led to projections of a declining population ( $\lambda_{\text{cycle}} = 0.79$ ). This difference in  $\lambda_{\text{cycle}}$  was due to small negative contributions from seed predation survival in the wheat phase and recruitment ( $\gamma$ ) in the corn phase, offset by a much larger positive contribution from fecundity ( $\phi$ ) in the corn phase (Fig. 5c). In 2001, both ST/R and ST/W had large positive values of  $\lambda_{\text{cycle}}$  (1.97 and 2.75, respectively), with a moderate-sized difference between their population growth rates ( $\Delta\lambda_{\text{cycle}} = -0.78$ ). This difference resulted from a strong negative contribution from seed predation survival in the wheat phase and strong positive contribution from fecundity in the corn phase that nearly canceled one another out, in addition to a small negative contribution from recruitment in the corn phase (Fig. 5d).

For both the W and R treatments in 2000, fecundity was the demographic rate most affected by tillage timing (Fig. 6a, c). In the W treatment in 2000, fecundity

made contributions to  $\Delta\lambda_{\text{cycle}}$  in all rotation phases, with successively larger contributions in the wheat, corn and soybean phases (Fig. 6a). There was also a small negative contribution from seed survival from October through March in the wheat phase of the W treatment in 2000. In the R treatment in 2000, the contributions made by fecundity to  $\Delta\lambda_{\text{cycle}}$  in the corn and soybean phases were large and nearly equal, but the contribution made by fecundity to  $\Delta\lambda_{\text{cycle}}$  in the wheat phase was negligible ( $7.4 \times 10^{-6}$ ). In 2001, there was a tillage timing  $\times$  red clover interaction effect on fecundity: there was no effect of tillage timing on fecundity within the W treatment, but fecundity was greater in the ST level than the FT level of the R treatment (Table 2). This interaction was evident in the simple effects of tillage timing on contributions to  $\Delta\lambda_{\text{cycle}}$  in 2001. In the W treatment in 2001,  $\Delta\lambda_{\text{cycle}}$  between the ST and FT treatments was due mainly to a strong negative contribution from seed survival from October through

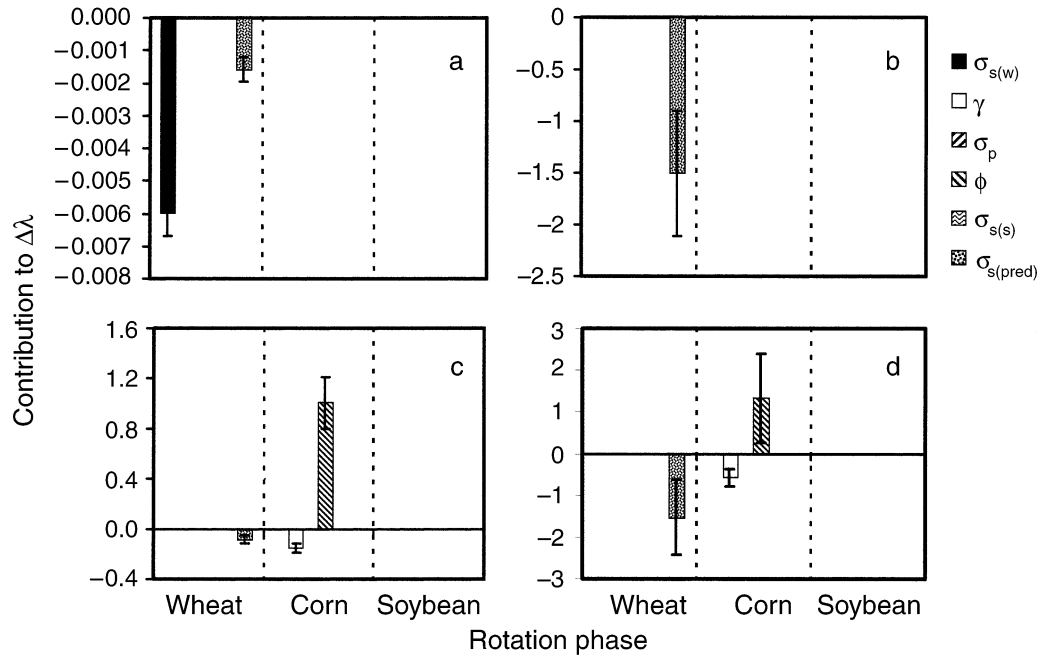


FIG. 5. Retrospective perturbation analysis of simple effects of red clover on *S. faberi* population growth rate within a wheat–corn–soybean crop sequence with either a wheat sole crop (W) or wheat + red clover crop mixture (R) in the wheat phase. The difference in  $\lambda_{\text{cycle}}$  was computed by subtracting  $\lambda_{\text{cycle}}$  in the W treatment from  $\lambda_{\text{cycle}}$  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, and (d) ST 2001. Note the variation in y-axis scales. Error bars represent  $\pm 1$  SE.

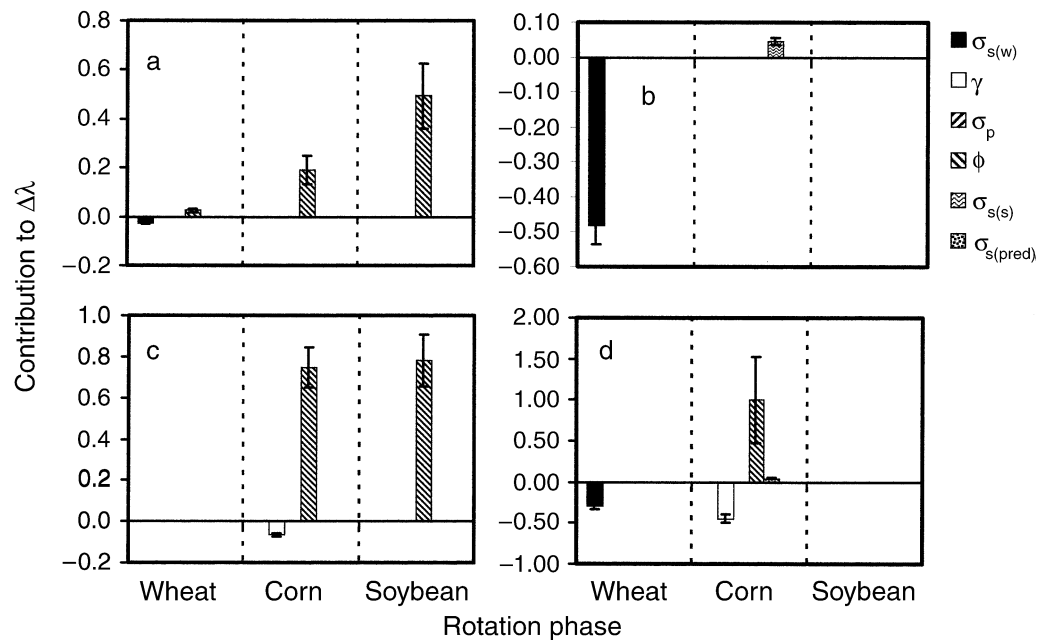


FIG. 6. Retrospective perturbation analysis of simple effects of tillage timing on *S. faberi* population growth rate ( $\lambda_{\text{cycle}}$ ) within a wheat–corn–soybean crop sequence subjected to either fall tillage (FT) or spring tillage (ST). The difference in  $\lambda_{\text{cycle}}$  was computed by subtracting  $\lambda_{\text{cycle}}$  in the FT treatment from  $\lambda_{\text{cycle}}$  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, and (d) R 2001. Note the variation in y-axis scales. Error bars represent  $\pm 1$  SE.

March in the wheat phase, which was slightly offset by a small positive contribution from seed survival from March through October in the corn phase (Fig. 6b). In contrast, in the R treatment in 2001, a strong positive contribution from fecundity in the corn phase accounted for most of  $\Delta\lambda_{\text{cycle}}$ , with only a small negative contribution from seed survival from October through March in the wheat phase and recruitment in the corn phase (Fig. 6d).

For analyses of both red clover and tillage timing, percent errors were consistently less than 1%, indicating a very close agreement between the sum of parameter contributions to  $\Delta\lambda_{\text{cycle}}$  and the actual value of  $\Delta\lambda_{\text{cycle}}$  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* fecundity and  $\lambda_{\text{cycle}}$  (Fig. 3, Table 2). In contrast, the FT/R treatment achieved consistently low values for  $\lambda_{\text{cycle}}$  due to high predation rates in the R treatment without the risk of increased fecundity associated with the ST treatment (Fig. 3). Despite the large amount of interannual variation in demographic rates (Table 2), as seen in the strong main effect of year on  $\ln(\lambda_{\text{cycle}})$  and cropping system treatment  $\times$  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 postemergent weed control that allowed  $\geq 12.5\%$  of seedlings to survive, stochastic simulations showed that the FT/R treatment helped prevent increases in weed population size (Fig. 4). As the success of postemergent weed control varied,  $\ln(\lambda_{\text{s(cycle)}}$ ) 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 postemergent weed control became more and more successful. If percentage seedling survival was 10% or less,  $\ln(\lambda_{\text{s(cycle)}}$ ) was equal for the FT/W and FT/R treatments. The threshold seedling survival level, above which  $\ln(\lambda_{\text{s(cycle)}}$ ) became positive was  $\sim 10\%$  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 treat-

ment 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 subannual 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 seed survival from October through March ( $\sigma_{s(w)}$ ) and recruitment ( $\gamma$ ), 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) resulted from trade-offs in the importance of seed preservation or seed production in a given environment.

It is unsurprising that the elasticity of  $\lambda$  to seed survival from October through March ( $e\sigma_{s(w)}$ ) 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  $\lambda_{\text{(cycle)}}$  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  $\lambda_{\text{(cycle)}}$ , the FT/W and FT/R treatments in 2000, fecundity was low (23 to 94 seeds per plant) and seed predation survival 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, the elasticity of  $\lambda$  to recruitment ( $e\gamma$ ) was strongly negative in the corn and wheat phases, and strongly positive in the soybean phase. The elasticity values of  $\lambda$  to seedling survival ( $e\sigma_p$ ), fecundity ( $e\phi$ ), and seed predation survival ( $e\sigma_{s(pred)}$ ) 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 the elasticity of  $\lambda$  to seed survival from March through October ( $e\sigma_{s(s)}$ ), 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 fecundity was much greater (432 to 1782 seeds per plant) in relation to seed predation survival, underscored the importance of the seedbank for allowing plant populations to avoid unfavorable conditions. The elasticities of  $\lambda$  to recruitment ( $e\gamma$ ), seedling survival ( $e\sigma_p$ ), fecundity ( $e\phi$ ), and seed predation survival ( $e\sigma_{s(pred)}$ ) 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 elasticity of  $\lambda$  to recruitment ( $e\gamma$ ) was more negative in the wheat phase in 2001 than in 2000, in spite of increased positive elasticities of  $\lambda$  to seedling survival ( $e\sigma_p$ ), fecundity ( $e\phi$ ), and seed predation survival ( $e\sigma_{s(pred)}$ ). 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 elasticity of  $\lambda$  to recruitment ( $e\gamma$ ) in the wheat phase in 2001 compared to the wheat phase in 2000 reflects the opportunity cost of seedling recruitment in a variable environment.

Because the elasticity of  $\lambda$  to overwinter seed survival was greater than its elasticity to all other variables, overwinter seed survival was an obvious target transition for weed management. 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 postdispersal 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 confirmed that overwinter seed survival was also an important factor in this system. In five out of eight analyses of simple effects of tillage timing or red clover on  $\lambda_{(cycle)}$ , fecundity 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  $\lambda_{(cycle)}$ , seed predation survival made large contributions to  $\Delta\lambda_{(cycle)}$ , and in two other analyses seed predation survival made small contributions to  $\Delta\lambda_{(cycle)}$ . Next in importance was overwinter seed survival, 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 recruitment showed up as negative contributions to  $\Delta\lambda_{(cycle)}$  in four out of eight analyses, but in each of these the contribution made by recruitment was small relative to contributions from other parameters.

Following the example of Pico et al. (2002) we examined the relationship between the elasticity of  $\lambda(e)$  to each demographic parameter and the coefficient of variation (CV) for each demographic parameter, across

treatments and years. We found a negative correlation ( $N = 109$ ,  $r = -0.35$ ,  $F_{1, 109} = 14.3$ ,  $P < 0.001$ ) between  $\ln(e)$  and  $\ln(CV)$ , corroborating the results of Pico et al. (2002). This negative relationship echoed what we saw in the retrospective perturbation analysis: the elasticity of  $\lambda$  to overwinter seed survival ( $e\sigma_{s(w)}$ ) was equal to 1 for all treatment/year combinations, but overwinter seed survival also had the lowest CV of any parameter, and the LTRE contributions to  $\Delta\lambda$  were smaller for overwinter seed survival than for fecundity.

Taken together, the perturbation analyses suggest that fecundity and seed mortality factors, with an emphasis on seed predation, constitute important target transitions 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 2003). 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 preferred over spring tillage by most corn and soybean producers, 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 postemergence 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 interrow 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 2003), (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 postdispersal weed seed predation, recent studies have suggested that increased landscape complexity (Menalled et al. 2000), crop diversification (Carmona and Landis 1999, Davis and Liebman 2003), and delayed fall tillage (Cardina et al. 1996) may lead to increases in postdispersal 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  $\Delta\lambda_{\text{(cycle)}}$  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 postdispersal 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 accurate 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. 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 postdispersal seed predation in preventing weed population growth.

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