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Cropping system effects on giant foxtail (*Setaria faberi*) demography: II. Retrospective perturbation analysis

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Cropping system characteristics affect weed management by altering key demographic rates of weeds, including recruitment, seedling survival, fecundity, and seed survival. To facilitate the design and improvement of cropping systems that limit weed population growth, analytical methods are needed to identify weed management “choke points” (weed life stages that vary in response to management and whose variation strongly affects weed population growth rate). The objectives of this study were to (1) determine whether wheat–red clover green manure can limit giant foxtail population growth rate (λ) in a wheat–corn–soybean crop sequence and (2) identify choke points in the giant foxtail life cycle with respect to the green manure treatment. Demographic data were used to construct a periodic matrix model of giant foxtail population growth in a wheat–corn–soybean crop sequence, with either a wheat sole crop (W) or a wheat–red clover intercrop (R) in the wheat phase. Identification of choke points was accomplished by adapting the life-table response experiment (LTRE) design for retrospective perturbation analysis of the periodic matrix model. The difference in λ ($\Delta\lambda$) between the two treatments was decomposed into contributions from each parameter in each rotation phase of the periodic model. Each LTRE contribution was equal to the product of the sensitivity of λ to changes in a given parameter by the treatment difference in that parameter. Those parameters making large contributions to $\Delta\lambda$ represented weed management choke points. Giant foxtail population growth rate in the simulation was more than twice as great in the W treatment ($\lambda = 2.54$) than in the R treatment ($\lambda = 1.16$). Retrospective perturbation analysis indicated that the proportion of seeds surviving predation in the wheat phase made the largest LTRE contribution (0.55) to $\Delta\lambda$, followed by seedling recruitment in the soybean (0.41) and corn (0.20) phases. By identifying weed management choke points within a given system, retrospective perturbation analysis can target research and management efforts for greater reductions in weed population growth.

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

Key words: Life-table response experiment, simulation model, integrated weed management, seed predation, crop rotation, legume green manure.

There is an increasing emphasis on weed prevention in agricultural systems in which herbicide use is minimized or eliminated (Bastiaans et al. 2000; Jordan 1996). 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). Cropping system characteristics that reduce weed population growth rates may provide a weed suppressive foundation upon which to layer complementary management tactics. Because cropping system characteristics can fundamentally alter the abiotic and biotic features of the agroecosystem in which weed populations exist, they may influence demographic rates throughout the entire weed life cycle. This introduces a level of complexity that is difficult to resolve without the analytical tools of demography. These tools make it possible to address complex environmental effects on weed populations with relatively simple models and to understand how changes in individual demographic rates contribute to overall weed population dynamics.

Demographic analyses can aid the use of cropping system characteristics in weed management systems in at least two

ways. First, population models integrate experimental results across the entire weed life cycle to predict management effects on weed population growth rates (Gonzalez-Andujar and Fernandez-Quintanilla 1991; Jordan et al. 1995). Models are especially useful for systems in which environmental changes affect different weed life stages in contrasting ways (e.g., a management practice that reduces germination but increases fecundity). Second, perturbation analyses (Caswell 2001) weigh the relative importance of management-induced variation in individual demographic parameters to overall changes in population growth rate. By identifying the life stage or stages that drive weed population dynamics under a given management scenario, perturbation analyses can focus efforts at improving the weed-suppressive qualities of a given management practice, as well as highlight other life stages to be targeted by complementary weed management tactics.

The demographic analyses described here comprise the second half of an empirical modeling study of cropping system effects on giant foxtail demography. The empirical work (Davis and Liebman 2003) measured giant foxtail demo-

graphic rates in response to green manure and tillage timing within a wheat–corn–soybean crop sequence in the central United States. In the current study, these demographic data were used to parameterize a matrix population model and conduct perturbation analyses. Our objectives were to (1) predict the effect of wheat–red clover green manure on giant foxtail population growth rate within a wheat–corn–soybean crop sequence and (2) identify weed management “choke points” in the giant foxtail life cycle (weed life stages that vary in response to management and whose variation strongly affects weed population growth rate). Demographic analyses were used to test two hypotheses. First, compared with a wheat sole crop, wheat underseeded with red clover will limit giant foxtail population growth rate within a wheat–corn–soybean crop sequence. Empirical studies have shown that wheat–red clover green manure can negatively affect weed recruitment, growth, and seed survival within a subsequent corn crop (Conklin et al. 2002; Davis and Liebman 2001, 2003). Second, differential survival of newly shed giant foxtail seed will be responsible for most of the difference in population growth rate between management systems (i.e., seed survival would be the primary weed management choke point). In a simulation analysis of crop rotation effects upon weed seedbanks, Jordan et al. (1995) found that overwinter survival of newly dispersed seed in the top 10 cm of the soil was of primary importance in determining population growth rate for velvetleaf (*Abutilon theophrasti*) and green foxtail (*Setaria viridis*).

Matrix models of weed population dynamics readily accommodate 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

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

where \mathbf{n} is a vector with i rows representing the number of individuals in each life stage at time t and $t + 1$, and \mathbf{A} represents the annual projection matrix with i rows and j ($= i$) columns containing all life-stage transition probabilities (a_{ij}) for the weed species being modeled. Such models can be linear or nonlinear in their parameters and deterministic or stochastic with respect to parameter variability. As a starting point, linear models were used because they simplified the analysis, but the methods described here can be applied to nonlinear models as well (Caswell 2001). For such models, population growth rate can be calculated as the dominant eigenvalue, λ_1 , of \mathbf{A} (for an example with complete MATLAB code, see Appendix A at <http://www.stat.iastate.edu/preprint/AppA.pdf>). Predictions of λ under different management treatments provide a measure of the relative effectiveness of the treatments in limiting weed population growth.

In an agricultural setting, management operations often occur at some subannual time scale or vary across years with the different phases of a crop rotation. To increase the capacity of matrix-modeling methods to simulate the effects of management at sub- or supra-annual time scales, it is necessary to use a periodic model. Periodic models account explicitly for variations in life-stage transition probabilities in a sequence of environments that repeats itself over time

(Caswell and Trevisan 1994). For a periodic model with m periods in a complete cycle, the projection equation for a projection interval starting at period h is

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

$$h = 1, \dots, m \quad [2]$$

where \mathbf{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 because 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 a_{ij} (i.e., each life-stage transition probability) of \mathbf{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):

$$S_{\mathbf{B}_{(h)}} = \mathbf{D}^T S_{\mathbf{A}_{(h)}}$$

$$= (\mathbf{B}_{(h-1)} \cdots \mathbf{B}_{(1)}\mathbf{B}_{(m)} \cdots \mathbf{B}_{(h+1)})^T S_{\mathbf{A}_{(h)}} \quad [3]$$

where $S_{\mathbf{B}_{(h)}}$ represents the sensitivity of λ 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 $S_{\mathbf{A}_{(h)}}$ represents the sensitivity of λ to changes in the elements of $\mathbf{A}_{(h)}$ (the annual projection matrix for the interval beginning at time period h). Elasticities of λ to the elements, b_{hij} (the life-stage transition probabilities for each period), of periodic projection matrices are then computed as

$$E_{\mathbf{B}_{(h)}} = (b_{hij}/\lambda) S_{\mathbf{B}_{(h)}} \quad [4]$$

The periodic matrix-modeling approach has been used previously to simulate weed population dynamics in crop rotations (Jordan et al. 1995; Mertens et al. 2002; Ullrich 2000), using 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 indicated 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.

One approach to retrospective perturbation analysis is the 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 the 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

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

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 .

As part of the second objective (identifying weed management choke points for giant foxtail), we extended the LTRE approximation for the analysis of individual life-stage transitions in periodic matrix population models. This extension was essential because it permitted us to use the analytical power of the LTRE to search for weed management choke points within each of the phases of the crop rotation. Others have analyzed periodic models using the LTRE approach (Rydgren et al. 2001) but did not analyze contributions of individual life-stage transitions to treatment differences in λ . We believe this step to be essential for the precise identification of weed management choke points.

The adaptation of the LTRE approach for use with periodic matrix models offers some unique advantages for analyzing integrated 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 systems where management effects on demographic rates are

known, LTRE analysis is a powerful tool for identifying weed life stages where management interventions may be targeted for greatest effect.

Materials and Methods

Field Experiment, Parameter Estimation, and Model Structure

Giant foxtail demography was studied in 2000 and 2001 within the wheat–corn transition of a wheat–corn–soybean crop sequence at the Iowa State University Agronomy Farm, Boone, IA. Experimental procedures are detailed in the study by Davis and Liebman (2003) and, thus, will be described only briefly here. In the wheat phase of the crop sequence, spring wheat was grown either as a sole crop (W) or underseeded with red clover (R) as a green manure for the following corn crop. In fall of the wheat phase, wheat and red clover residues were incorporated to a depth of 20 cm with a power takeoff-driven rototiller. Corn was planted into tilled residues from the wheat phase in late April in 0.76-m-wide rows at 64,500 seeds ha⁻¹ and received 90 kg ha⁻¹ N from urea banded in the corn row on June 5. Soybean was sown in 0.76-m-wide rows at 395,000 seeds ha⁻¹ in mid-May. The experiment was performed as a randomized complete block design with four replications.

Giant foxtail seeds were buried in mesh bags in the field from November through March to permit after-ripening. In early April, within the corn phase of the crop sequence, 50 giant foxtail seeds m⁻² were planted in a row parallel to, and offset 4 cm from, the crop row. Germinating seedlings were tagged with color-coded toothpicks to identify weekly emergence cohorts. Estimates of percent germination and seedling survival were obtained from a weekly census of newly emerged seedlings and dead seedlings. Before seed rain, 30 mature giant foxtail panicles per plot were enclosed in tightly woven, but highly permeable, bags made of woven vegetable row cover. Panicle length was regressed on seed production by the bagged panicles. This regression relationship was then used to convert measurements of giant foxtail panicle length in the rest of the plot into an estimate of seeds per plant. Two sets of synthetic seedbanks were used to measure seedbank survival in the top 5 cm of soil, one for the period of October through March and the other for the period from March through October. In October, after tillage, sections of polyvinyl chloride air-duct pipe 7.5 cm in length and 30.5 cm in diameter were driven flush with the soil surface. Four hundred giant foxtail seeds were then mixed into the top 5 cm of soil. Seeds from one set of synthetic seedbanks were recovered using a seedbank elutriator (Wiles et al. 1996) in March, and seeds from the remaining set of synthetic seedbanks were recovered the following October. Point estimates of daily rates of postdispersal seed predation were made within the wheat, corn, and soybean phases using the method of Menalled et al. (2000). At several dates after seed rain had begun in August, within each experimental unit, 200 giant foxtail seeds were placed on a 10- by 10-cm square of Bemis® humidifier filter flush with the soil surface. To determine the effects of wind and rain on seed losses from pads, a second set of seeds was placed within the experimental unit during the same time but was enclosed within a cage made of fine mesh to exclude predators. Seed pads were checked on a daily basis and re-

TABLE 1. Estimated values for giant foxtail demographic parameters in two crop sequences in Boone, IA.

Parameter	Abbreviation	Unit ^a	Crop sequence	Parameter values in each crop phase ^b		
				Wheat ^c	Corn	Soybean
Germination	γ	$N_{\text{plt}}(\text{Jun.}) N_{\text{sd}}(\text{Mar.})^{-1}$	W-C-S	0.56	0.56	0.56
Plant survival	σ_p	$N_{\text{plt}}(\text{Aug.}) N_{\text{plt}}(\text{Jun.})^{-1}$	W-C-S	0.97	0.97	0.97
Seed survival _{Mar.-Oct.}	$\sigma_{s(s)}$	$N_{\text{sd}}(\text{Oct.}) (N_{\text{sd}}(\text{Mar.}) - N_{\text{plt}}(\text{Jun.}))^{-1}$	W-C-S	0.50	0.50	0.50
Fecundity	ϕ	seeds plant ⁻¹	W-C-S	57	57	57
Seed survival _{Predation}	$\sigma_{s(\text{pred})}$	$N_{\text{newsd}}(\text{Oct.}) N_{\text{newsd}}(\text{Aug.})^{-1}$	W-C-S	0.003	0.016	0.36
Seed survival _{Oct.-Mar.}	$\sigma_{s(w)}$	$N_{\text{sd}}(\text{Mar.}) N_{\text{sd}}(\text{Oct.})^{-1}$	W-C-S	0.90	0.90	0.90
Germination	γ	$N_{\text{plt}}(\text{Jun.}) N_{\text{sd}}(\text{Mar.})^{-1}$	R-C-S	0.44	0.44	0.44
Plant survival	σ_p	$N_{\text{plt}}(\text{Aug.}) N_{\text{plt}}(\text{Jun.})^{-1}$	R-C-S	0.97	0.97	0.97
Seed survival _{Mar.-Oct.}	$\sigma_{s(s)}$	$N_{\text{sd}}(\text{Oct.}) (N_{\text{sd}}(\text{Mar.}) - N_{\text{plt}}(\text{Jun.}))^{-1}$	R-C-S	0.44	0.44	0.44
Fecundity	ϕ	seeds plant ⁻¹	R-C-S	57	57	57
Seed survival _{Predation}	$\sigma_{s(\text{pred})}$	$N_{\text{newsd}}(\text{Oct.}) N_{\text{newsd}}(\text{Aug.})^{-1}$	R-C-S	4.7×10^{-8}	0.016	0.36
Seed survival _{Oct.-Mar.}	$\sigma_{s(w)}$	$N_{\text{sd}}(\text{Mar.}) N_{\text{sd}}(\text{Oct.})^{-1}$	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 underseeded with red clover.

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

^c Wheat, *Triticum aestivum* L.; corn, *Zea mays* L.; soybean *Glycine max* L.; red clover, *Trifolium pratense* L.

covered before all seeds were removed. The daily probability of a seed surviving predation was calculated, assuming an exponential decline in seed number to be $C - R^{1/t}$, where C and R were the proportion of seeds remaining in the control and uncaged treatments, respectively, when the seed pads were recovered, and t was the number of days the seed pads were left in the field (Mittelbach and Gross 1984).

Six demographic parameters were estimated for giant foxtail, using data from the 2000 field season: recruitment (γ), seed survival in the soil from March through October ($\sigma_{s(s)}$), plant survival to reproductive maturity (σ_p), seed production per plant (ϕ), seed survival of postdispersal seed predation before fall tillage ($\sigma_{s(\text{pred})}$), and seed survival in the soil from October through March ($\sigma_{s(w)}$) (Table 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. Daily rates of weed seed removal were too high to allow for direct measurements of season-long probabilities of seeds surviving postdispersal seed predation ($\sigma_{s(\text{pred})}$). Instead, season-long estimates of the probability of newly shed seeds surviving postdispersal predation were obtained by compounding the daily probability of seed survival measured in late September, when predation rates were at their peak, over 20 d. We considered compounding the daily rates of $\sigma_{s(\text{pred})}$ over the entire predation period from August through October, but no seed survived in any of the treatments using this method. Even using the 20-d compounding period, estimated season-long values of $\sigma_{s(\text{pred})}$ (Table 1) were all lower than those given by Cromar et al. (1999), who reported 68 to 76% of barnyardgrass (*Echinochloa crus-galli*) and common lambsquart-

ers (*Chenopodium album*) seeds surviving postdispersal predation for the period of October 20 through January 5. The estimation method used here may therefore somewhat overemphasize the effect of seed predation on giant foxtail population growth.

With the exception of $\sigma_{s(\text{pred})}$, 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). The parameter values used in the wheat phase thus represent a worst-case scenario for giant foxtail population dynamics in wheat. Work is currently under way to estimate all six demographic parameters for giant foxtail within each rotation phase.

Our model followed giant foxtail demography through four subannual periods (recruitment, spring survival, fecundity, and winter survival) in each of three phases in the wheat-corn-soybean crop sequence, for a total of 12 periods in one rotation cycle (Figure 1). For species with highly persistent seedbanks, it is necessary to describe seedbank depth-structure to account for long-term effects of tillage on seed placement and recruitment probability. In our model, the seedbank was not defined as depth-structured 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. Newly shed seeds were distinguished from the previous year's seeds so only the new seed experienced high rates of postdispersal seed predation. In the fecundity projection matrix ($\mathbf{B}_{(3k)}$), newly shed seeds 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 $\mathbf{B}_{(h_k)}$

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

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

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

FIGURE 1. Periodic matrix model used to simulate giant foxtail population growth under contrasting crop sequences. Abbreviations: \mathbf{n}_t , a vector of the number of seeds (s) and plants (p) in the population at a given point in time (t); each $\mathbf{B}_{(h)}$ represents a subannual projection matrix accounting for a single life-stage transition (h) taking place in a given phase (k) of the crop sequence; lower-level demographic parameters in projection matrices are represented by Greek symbols, explained in Table 1.

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 $\mathbf{A}_{(h)}$ 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 $\mathbf{A}_{(h)} = (\mathbf{B}_{(h-1)} \dots \mathbf{B}_{(1)} \mathbf{B}_{(m)} \dots \mathbf{B}_{(h+1)} \mathbf{B}_{(h)})_k$. For the simple system described in this study, all $\mathbf{A}_{(h)}$ have only one nonzero 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 side term describes the fate of dormant seeds, and the right-hand side term describes new inputs to the seedbank. Perturbations to a_{11} involve this entire string of parameters, yet for management purposes, it is important to know how λ responds to the perturbation of lower-level demographic parameters (i.e., individual life-stage transitions), 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

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

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

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 the sensitivity of λ to changes in each b_{hijk} . The equation used to describe the LTRE approximation for a periodic matrix model is

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

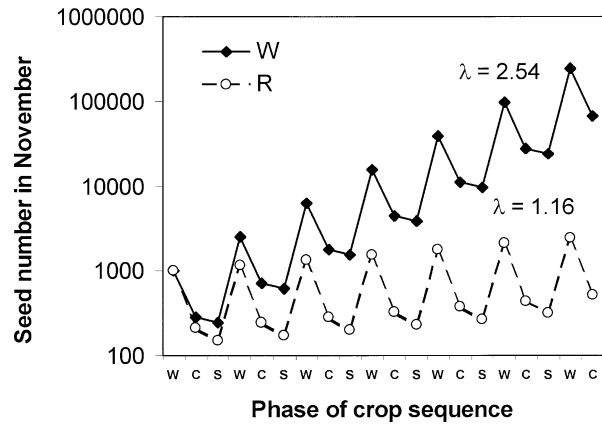


FIGURE 2. Projected growth of giant foxtail seedbank over six cycles of a wheat–corn–soybean (W) or wheat–red clover–corn–soybean (R) crop sequence. The symbol λ represents the population growth rate over the entire crop sequence rather than the annual population growth rate.

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 $\mathbf{B}_{(h)}$ (see Equation 3), $\mathbf{S}_{\mathbf{A}_{(h_k)}}$ represents the sensitivity of λ to changes in the elements of $\mathbf{A}_{(h_k)}^*$, and $\mathbf{A}_{(h_k)}^* = (\mathbf{A}_{(h_k)}^m + \mathbf{A}_{(h_k)}^r)/2$. The matrices $\mathbf{A}_{(h_k)}^m$ and $\mathbf{A}_{(h_k)}^r$ were calculated as the products of treatment-specific $\mathbf{B}_{(h)}$ 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, the R treatment was designated as the reference treatment (r), and the W treatment was designated 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 with $\lambda^{(m)} - \lambda^{(r)}$ from the simulation model to obtain percentage error in the LTRE approximation, calculated as $(|\Delta \lambda_{\text{LTRE}} - \Delta \lambda_{\text{Model}}|)/\Delta \lambda_{\text{Model}}$.

Computational Methods

Matrix calculations for the example included in this study were performed using MATLAB Version 5.0 (MathWorks 1997). MATLAB was used to predict λ and calculate sensitivity of λ to changes in each b_{hijk} within each treatment (see Appendix B, at <http://www.stat.iastate.edu/preprint/AppB.pdf>, 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} .

Results and Discussion

Population Growth

Projecting the initial giant foxtail seedbank through six rotation cycles showed population increases for the W (wheat sole crop in the wheat phase) and R (wheat underseeded with red clover in the wheat phase) treatments (Figure 2). Population growth rate, however, was more than two times greater in the W treatment ($\lambda = 2.54$) than in the R treatment ($\lambda = 1.16$), supporting Hypothesis 1 (the R treat-

TABLE 2. Elasticity of population growth rate (λ) to demographic parameters of giant foxtail grown under contrasting crop sequences.

Crop sequence ^a	Crop phase ^b	Demographic parameter					
		γ	$\sigma_{s(s)}$	σ_p	ϕ	$\sigma_{s(pred)}$	$\sigma_{s(w)}$
		— elasticity of λ —					
W–C–S	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 described in Table 1.

^b Wheat, *Triticum aestivum* L.; corn, *Zea mays* L.; soybean *Glycine max* L.; red clover, *Trifolium pratense* L.

ment should limit giant foxtail population growth in a wheat–corn–soybean crop sequence). 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). Figure 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. As noted earlier, recruitment and fecundity of giant foxtail were probably overestimated in the wheat phase. The sharp population decline in the wheat phase is therefore primarily due to the low probability of seeds surviving predation in this phase in either the W or the R treatment.

It was not surprising that model projections indicated that the giant foxtail population grew larger (i.e., $\lambda > 1$) in 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 as in the R treatment. Analysis of the primary experimental results (Davis and Liebman 2003) provided a detailed description of treatment effects on individual demographic processes but did not integrate such effects into the overall life cycle. This latter step is necessary for identifying weed management choke points (i.e., determining the relative importance of treatment effects on individual life-stage transitions to changes in λ). Fortunately, perturbation analysis offers a method for recovering more information from the data. To highlight the relative merits of prospective and retrospective perturbation analyses for identifying weed management choke points, results for elasticity analysis and the modified LTRE analysis were compared. Elasticity analysis has been the primary method of perturbation analysis used in the earlier studies of weed population dynamics (Gonzalez-Andujar and Fernandez-Quintanilla 1991; Jordan et al. 1995; Mertens et al. 2002).

Elasticity Analysis

Relative rankings of the elasticity of λ to giant foxtail demographic parameters were the same for the corn and soybean phases in the W and R treatments (Table 2). Elasticity of λ to $\sigma_{s(w)}$ was ranked first, σ_p , ϕ , and $\sigma_{s(pred)}$ were ranked second, γ was ranked third, and $\sigma_{s(s)}$ was ranked fourth.

Elasticity rankings for the wheat phase differed from those

in the corn and soybean phases. Within the wheat phase, elasticity rankings differed between the W and R treatments. In the W treatment, elasticity of λ to $\sigma_{s(w)}$ was ranked first; $\sigma_{s(s)}$ was ranked second; γ was ranked third (with a negative elasticity value); and σ_p , ϕ , and $\sigma_{s(pred)}$ were ranked fourth. In the R treatment, elasticity of λ to $\sigma_{s(w)}$ and $\sigma_{s(s)}$ was ranked first; γ was ranked second (with a negative elasticity value); and σ_p , ϕ , and $\sigma_{s(pred)}$ were ranked third. The negative elasticity of λ to γ in the wheat phase described a situation where seeds that gave rise to new plants actually reduced the population growth rate because these seeds were lost from the seedbank, but almost all seeds produced by the new plants were consumed by predators.

The high elasticity of λ to $\sigma_{s(w)}$ was to be expected for an annual plant, for which seed survival during the seed-only phase represents a bottleneck that the entire population must pass through each year. 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 with the corn and soybean phases for the parameters other than $\sigma_{s(w)}$. These parameters could be divided into groups: (1) parameters affecting inputs to the seedbank (γ , σ_p , ϕ , and $\sigma_{s(pred)}$) and (2) parameters important to the 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, elasticities for seed input parameters were ranked higher than those for seed preservation parameters, whereas in the wheat phase, elasticities for seed preservation parameters were ranked higher than those for seed input parameters. It makes sense that the seed input parameters should be important to the population growth of an annual seed-bearing plant; this is the only way, besides immigration, in which the population can grow. Why then should the ranking have changed so that within-season seed preservation became more important than seed inputs 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 input–related parameters in the wheat phase: 4.6×10^{-6} . This is relatively similar to the season-long probability (4.6×10^{-8}) of newly shed seeds 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 did not germinate more

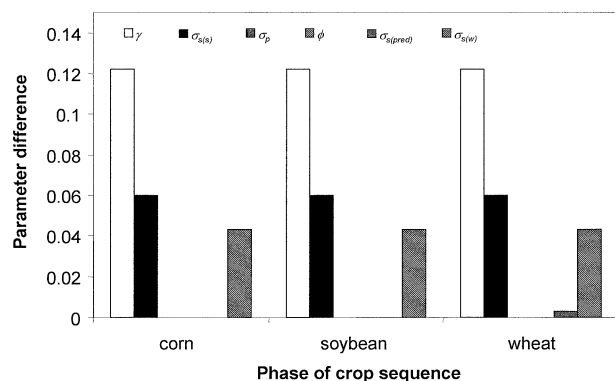


FIGURE 3. Difference in values for giant foxtail demographic parameters in the W and R treatments (see Figure 2 for explanation of abbreviations), where R was designated as the reference treatment (from which values of demographic parameters in the W treatment were subtracted).

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 Akaike's Information Criterion (Burnham and Anderson 1998) 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 (Figure 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 postdispersal seed predation, $\sigma_{s(pred)}$, varied between the two crop sequences only in the wheat phase.

Sensitivity of λ to giant foxtail demographic parameters (Figure 4) could be divided into three groups on the basis of magnitude: (1) sensitivity of λ to $\sigma_{s(pred)}$ in the corn ($S_{B(h_b)} = 57$) and wheat ($S_{B(h_b)} = 184$) 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 ($S_{B(h_b)}$ 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 ($S_{B(h_b)}$ 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.

The sum of contributions to treatment differences in λ over all b_{hijk} was 1.38, equal to the difference in λ between the two crop sequences predicted by the simulation model (Figure 2). Contributions of the b_{hijk} to treatment differences in λ (Figure 5) were divided into two groups based on 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 contribution to λ . The primary importance of $\sigma_{s(pred)}$ as a weed management choke point

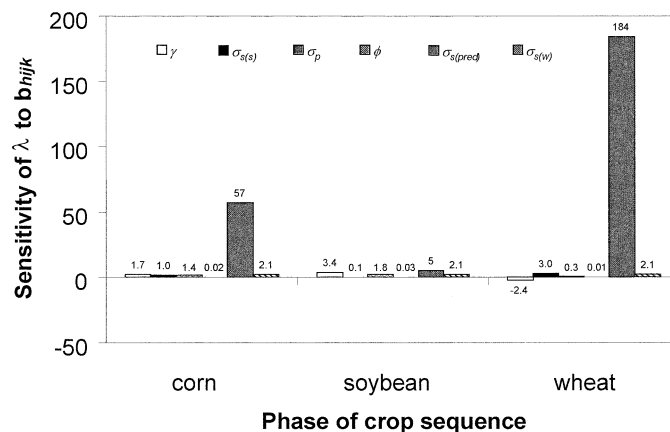


FIGURE 4. Sensitivity of λ to changes in lower-level giant foxtail demographic parameters in corn, wheat, and soybean. The sensitivities were evaluated for a projection matrix taken as the average of the W and R treatments.

in wheat offers some support for Hypothesis 2 (that differential survival of newly shed seed would account for most of the treatment difference in λ). A strict interpretation of elasticity values implies that overwinter seed survival (with an elasticity of 1 in all rotation phases) should always be an important weed management choke point. However, when actual parameter variability in response to management was factored in, using the LTRE, it became apparent that Hypothesis 2 oversimplified matters because γ was an important choke point in both the corn and the soybean phases.

The LTRE analysis of the periodic matrix model shared general features with the 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. Low values for $\sigma_{s(pred)}$ in the wheat phase meant that seeds would contribute more to population growth by remaining in the soil than by being recruited into the aboveground population, where their offspring were likely to be consumed. What distinguished the LTRE approach was the level of detail it provided. For each b_{hijk} , the product of multiplying treatment differences in parameter value by the sensitivity of λ to that particular parameter gave the contribution of that parameter to treatment differences in λ . Thus, it was possible to understand the exact degree

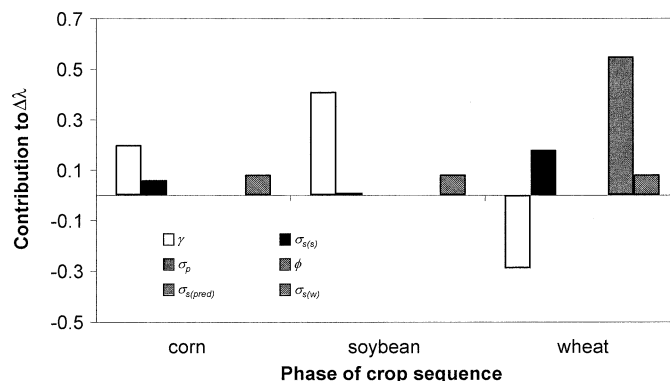


FIGURE 5. The contributions of lower-level giant foxtail demographic parameters to the difference in λ between the W and R treatments. Each contribution represents the product of the difference in parameter values between the two treatments (Figure 3) and the sensitivity of λ to changes in that parameter (Figure 4).

of importance of each of the demographic parameters to overall population growth rate. This only holds for systems where detailed demographic data exist.

In the elasticity analysis, factors affecting seed inputs were important in corn and soybean phases of the crop sequence, with γ being slightly less important than the other parameters. In the LTRE analysis, however, it became apparent that of the four parameters influencing inputs to the seedbank in the corn and soybean phases, γ , σ_p , ϕ , and $\sigma_{s(\text{pred})}$, 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 revealed that variation in parameters affecting inputs to the seedbank, including $\sigma_{s(\text{pred})}$, would be less important than variation in parameters affecting preservation of seeds already in the seedbank.

When the experimental data were taken into account, however, the extremely low value of $\sigma_{s(\text{pred})}$ in the wheat rotation, combined with the strong regulatory role of seed survival in the annual plant habit, meant that additive perturbations to $\sigma_{s(\text{pred})}$ would have a large impact on λ . The high sensitivity of λ to $\sigma_{s(\text{pred})}$ (at $S_{B(h)} = 184$, the largest sensitivity value in the model) in the wheat phase, multiplied by modest differences in $\sigma_{s(\text{pred})}$ between the R and W treatments, gave rise to the largest single LTRE contribution (0.55) to treatment differences in λ .

The large contribution made by $\sigma_{s(\text{pred})}$ in the wheat phase is in contrast to the prediction made by elasticity analysis and also helps in explaining the reversal in elasticity rankings for the wheat phase compared with the corn and soybean phases. The acute seed predation bottleneck in the wheat phase made seed preservation parameters more important than those 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 with the W treatment (thus reducing $\Delta\lambda$), whereas variation in $\sigma_{s(s)}$ tended to decrease λ in the R treatment compared with 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 being associated with a lower value of γ in the R treatment than in the W treatment (Figure 3). 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 close agreement between the LTRE approximation and $\Delta\lambda$ predicted by the simulation model reflects the lack of age or stage structure in our model. In such a case, the linear approximation of the LTRE modeled the data very precisely. For plants with more complex life histories, as for annuals with structured seedbanks or perennials, greater error should be expected in the LTRE approximation.

Elasticity and LTRE analyses were useful in understanding the results of the experiment, but LTRE analysis gave much more specific information pertaining to the experi-

mental system. The LTRE identified $\sigma_{s(\text{pred})}$ and γ as weed management choke points, whereas elasticity analysis only indicated whether factors affecting seed inputs or seed preservation were important in a given rotation phase. 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 hope that it will be used more frequently in the future. Through the identification of weed management choke points for a given system, LTRE analysis can focus research and weed management efforts on weed life stages that not only vary in response to management but whose variation also results in substantial changes in population growth rate. Because the results obtained from detailed demographic investigations are very system-specific, choke points identified for one cropping system should be treated as hypothetical when extrapolating to other systems.

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 the 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 on the control tactics used (Buhler et al. 1992; Mulder and Doll 1993). A second set of simulations (results not shown) was performed to examine crop sequence effects on giant foxtail demography under a production scenario in which weed control with rotary hoeing and interrow 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 in the LSS scenario was most sensitive to variation in $\sigma_{s(\text{pred})}$ in the wheat and corn phases, as was observed for the high-seedling survival (HSS) scenario.

The consistently high sensitivity of λ to $\sigma_{s(\text{pred})}$ under both the HSS and the LSS scenarios indicates that further research into cropping system effects on postdispersal 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 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, λ was plotted against the mean of $\sigma_{s(\text{pred})}$ 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

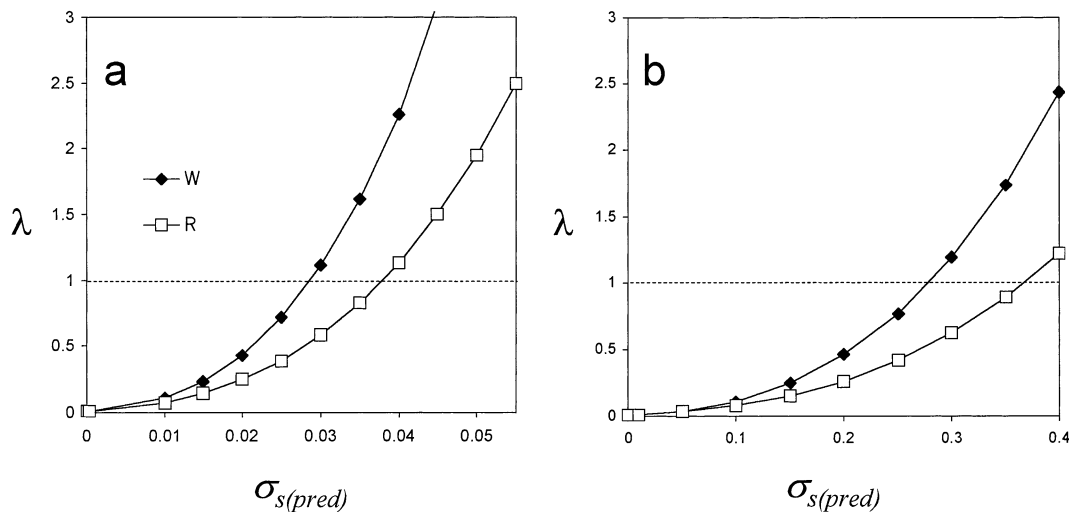


FIGURE 6. The sensitivity of giant foxtail population growth rate (λ) to the mean percentage, over all rotation phases, of seeds surviving postdispersal seed predation ($\sigma_{s(pred)}$). Results are shown for contrasting weed management scenarios, in which either (a) 97% (HSS, high seed survival) or (b) 10% (LSS, low seed survival) of giant foxtail seedlings survived to reproductive maturity. The dotted horizontal line represents constant population size over time ($\lambda = 1$). Note different x-axis scales in (a) and (b).

correspond to season-long empirical measurements of giant foxtail seed predation.

Future Directions

Our results indicate that improved knowledge of agonomic management effects on postdispersal seed predation would be useful to farmers. They also indicate that, wherever possible, farmers should consider taking steps to increase rates of postdispersal 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 2003), and (3) increasing landscape complexity of the farming operation to improve habitat for seed predators migrating from areas surrounding fields (Menalled et al. 2000).

Much weed management and research effort has been directed at killing weed seedlings. In many respects this has been a successful strategy, but its very success has had the unintended consequence of obscuring other opportunities for management interventions within the weed life cycle. Demographic analyses can open up new research avenues in the development of integrated weed management systems by (1) assessing the impact of cropping system characteristics upon weed population growth, (2) identifying weed management choke points with respect to specific management practices, and (3) predicting the weed management outcomes of combining complementary tactics that target different points in the weed life cycle. By focusing attention on combinations of practices most likely to lead to improvements in weed management, demographic analyses will help set the research agenda for the next generation of integrated weed management systems.

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