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Modeling Population Dynamics of Kochia (*Bassia scoparia*) in Response to Diverse Weed Control Options

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Abstract

Kochia [*Bassia scoparia* (L.) A. J. Scott] is a problematic weed species across the Great Plains, as it is spreading fast and has developed herbicide-resistant biotypes. It is imperative to understand key life-history stages that promote population expansion of *B. scoparia* and control strategies that would provide effective control of these key stages, thereby reducing population growth. Diversifying weed control strategies has been widely recommended for the management of herbicide-resistant weeds. Therefore, the objectives of this study were to develop a simulation model to assess the population dynamics of *B. scoparia* and to evaluate the effectiveness of diverse weed control strategies on long-term growth rates of *B. scoparia* populations. The model assumed the existence of a glyphosate-resistant (GR) biotype in the *B. scoparia* population, but at a very low proportion in a crop rotation that included glyphosate-tolerant corn (*Zea mays* L.) and soybean [*Glycine max* (L.) Merr.]. The parameter estimates used in the model were obtained from various ecological and management studies on *B. scoparia*. Model simulations indicated that seedling recruitment and survival to seed production were more important than seedbank persistence for *B. scoparia* population growth rate. Results showed that a diversified management program, including glyphosate, could provide excellent control of *B. scoparia* populations and potentially eliminate already evolved GR *B. scoparia* biotypes within a given location. The most successful scenario was a diverse control strategy that included one or two preplant tillage operations followed by preplant or PRE application of herbicides with residual activities and POST application of glyphosate; this strategy reduced seedling recruitment, survival, and seed production during the growing season, with tremendous negative impacts on long-term population growth and resistance risk in *B. scoparia*.

Introduction

Kochia [*Bassia scoparia* (L.) A. J. Scott] is one of the most problematic broadleaf weeds found in a very wide range of climatic regions throughout the world, but it is particularly adapted to arid and semiarid environments, such as the Great Plains region of the United States (Friesen et al. 2009). Its aggressive growth habit, prolific seed production, effective mechanism of seed dispersal, and resistance to important herbicides make the management of *B. scoparia* a great challenge. When this species occurs in cropland, it can grow up to 2 m in height with a woody stem more than 2 cm in diameter and a root system that can reach as deep as 4 m (Dille et al. 2017). An isolated *B. scoparia* plant can produce more than 100,000 seeds (Esser 2014; Osipitan 2016). The plant disperses its seeds through a tumbling mechanism after the stem dehisces at the base, dropping seeds as it bounces across the field in the direction of wind. This seed-dispersal mechanism promotes a rapid spread of *B. scoparia* to new ecological niches, making it one of the fastest-spreading weeds in the United States and Canada (Forcella 1985). *Bassia scoparia* seeds have very low to no dormancy, thus promoting a rapid seed germination from seedbanks under favorable conditions (Dille et al. 2017). The weed is often among the first species to emerge in the spring, as it has relatively low temperature requirements for germination compared with many other summer annual weeds (Dille et al. 2017; Kumar and Jha 2017); this early emergence provides *B. scoparia* a competitive growth advantage over later-emerging and neighboring summer annual weeds.

Tillage is an effective practice to control *B. scoparia*. Because *B. scoparia* germinates very early in the season, a tillage operation before crop planting can remove a significant proportion (20% to 50%) of the active seedbank reserves (Schwinghamer and Van Acker 2008).

With adoption of no-till cropping systems, however, chemical control has become the preferred method to control weeds, including *B. scoparia*. Several soil-applied herbicides sprayed before or at planting may effectively control *B. scoparia* (Kumar and Jha 2015; Tonks and Westra 1997). In many cropping systems, it is common to control the weed before crop planting by using foliar-applied herbicides (Kumar and Jha 2015; Wolf et al. 2000). Management of *B. scoparia* has become increasingly difficult with the widespread evolution of herbicide resistance in this species. *Bassia scoparia* populations have developed resistance to one or more of the following herbicide sites of action:5-enolpyruvylshikimate-3-phosphate synthase (EPSPS) inhibitor (glyphosate), photosystem II inhibitor (atrazine), synthetic auxins (dicamba/fluroxypyr), and acetolactate synthase inhibitors (Godar et al. 2015; Heap 2017; Osipitan and Dille 2017; Varanasi et al. 2015). Of these, resistance of *B. scoparia* to glyphosate is the most challenging. Glyphosate is widely used for *B. scoparia* control, especially in fallow lands, due to its high efficacy and low cost (Thompson 2013); and with the adoption of glyphosate as a selective herbicide in glyphosate-tolerant (GT) crops such as corn (*Zea mays* L.) and soybean [*Glycine max* (L.) Merr.], this has intensified its use for preplant and in-crop weed control within a growing season, leading to a widespread evolution of resistance to glyphosate.

In cropping systems, farmers are faced with the challenges of managing more than one weed species; thus, weed management decisions are based on the need to control all weeds that could interfere with a crop by using one broad-spectrum herbicide or herbicide tank mixes with multiple sites of action, especially in no-till systems where herbicides are the major weed management tools. This multifaceted weed management challenge often promotes the use of glyphosate by farmers (due to its broad-spectrum activity), despite the growing resistance challenges. Diversifying weed control inputs and reducing the use of glyphosate are expected to help in managing glyphosate-resistant (GR) weeds (Powles 2018). Studies have shown that cover cropping and other agronomic practices, when integrated with herbicides, can provide effective weed control, including the control of GR *B. scoparia* (Christenson 2015; Davis 2006; Petrosino et al. 2015).

Currently, information is lacking on the long-term impacts of weed control measures applied to *B. scoparia*. For a number of other weed species, population ecology data have been used to construct models to determine how best to manipulate population dynamics and to estimate the long-term effects of weed control strategies (Borger et al. 2009; Holst et al. 2007). These models can also be used to investigate both the importance of managing specific life-history stages, such as the seedbank or emerged plants, to control population growth (Borger et al. 2009; Davis 2006) and the risk for evolution of herbicide resistance (Bagavathiannan et al. 2013; Renton et al. 2014; Werle 2016). Models of population dynamics and weed control provide a means to understand interactions of weed management systems and impact on weeds without the need for expensive, long-term field studies. They also provide valuable insight on the gap between biological and ecological knowledge and research needs (Werle et al. 2014).

Developing population dynamics and management models requires a wealth of research data on weed biology, ecology, and management. Population ecology of *B. scoparia* within the Great Plains agricultural system, including life cycle characteristics such as seed dormancy and seedbank longevity, germination potential, seed production under crop and non-crop situations, and fitness of the resistant biotype, has been the subject of recent studies (Dille et al. 2017; Esser 2014; Kumar and Jha 2017; Osipitan and Dille 2017). Information is also available on *B. scoparia* control (Brachtenbach 2015; Holman et al. 2015; Hulse 2012; Kumar and Jha 2015; Petrosino et al. 2015). Data from these studies and others, when integrated into a simulation model, provide valuable information to better explain and predict the long-term impact of control strategies on *B. scoparia*.

In designing population dynamic models, a structured model that recognizes biotypes possessing different demographic characteristics would provide a more realistic simulation (Caswell 2001). The evolution of glyphosate resistance has created biotypes in *B. scoparia* with individuals possessing different demographic characteristics (Osipitan 2016). For example, the germination, seed viability, and seed longevity varied between GR and glyphosate-susceptible (GS) biotypes of *B. scoparia* (Kumar and Jha 2017; Martin et al. 2017; Osipitan and Dille 2017). In terms of inheritance, the glyphosate-resistance trait appeared to be completely dominant, resulting in an unequal phenotypic ratio between the GR and GS biotypes after cross-pollination (Niehues 2014). It will be important to understand and predict how different weed control strategies that are suitable for and/or practiced in the Great Plains region could influence the dynamics of *B. scoparia* populations (including GR and GS biotypes) in a glyphosate-based cropping system. This cropping system uses GT crops but does not necessarily require glyphosate as the dominant weed control strategy.

In this study, a stage-structured matrix model of *B. scoparia* population dynamics and control was constructed using the available population ecology and control data to understand the major drivers of population growth. In this model, we assumed the existence of GR biotypes in the *B. scoparia* population, but at a very low frequency. We hypothesized that more diversified weed control strategies that control different biotypes and cohorts of *B. scoparia* during the growing season will reduce the population growth rate of *B. scoparia* and help manage an already evolved GR *B. scoparia* biotype. Thus, the objectives of this study were to (1) develop a stage-structured transition matrix model that assesses the population dynamics of *B. scoparia* and (2) evaluate the effectiveness of diverse weed control strategies potentially used in a glyphosate-based cropping system on *B. scoparia* population growth rate.

Materials and Methods

Model Description

The model was constructed with a stage-structured transition matrix to simulate population growth and dynamics of *B. scoparia* within 1 m^2 with a carrying capacity of 100,000 individuals. The model considers an annual life cycle of *B. scoparia* as described in Figure 1 and summarized into two demographic stages in Figure 2. The two demographic stages include the fate of seeds in the soil seedbank (SB) and the fate of reproductive plants (RP) to determine the long-term impact of the potential control scenarios on *B. scoparia*. Seeds that did not germinate continue to remain in the seedbank (SB → SB). The transition of seeds in the seedbank up to reproductive plants was given as SB → RP, and the transition of newly produced seed to the seedbank was given as RP → SB. The lower-level demographic probabilities that determine each transition are given in Table 1 and their applications in Equations 3 to 7. There are differential probabilities in seed

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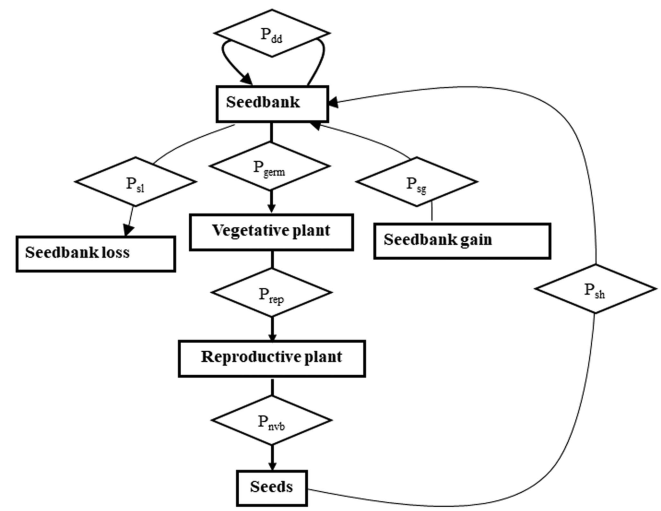

Figure 1. Diagrammatic annual life stages of *Bassia scoparia* with their respective probabilities. The rectangles represent life stages, such as seeds in the seedbank, vegetative and reproductive plants, and newly produced seeds. Seeds in the seedbank are naturally gained from another location (P_{sg}) or lost to another location or by predation (P_{sl}). The diamonds represent the survival probabilities of each life stage, including seed to vegetative plant (P_{germ}), vegetative to reproductive plant (P_{rep}), reproductive plant to newly produced seeds (P_{nvb}), newly produced seeds shed to the seedbank (P_{sh}), and dormant seed that will remain dormant (P_{dd}).

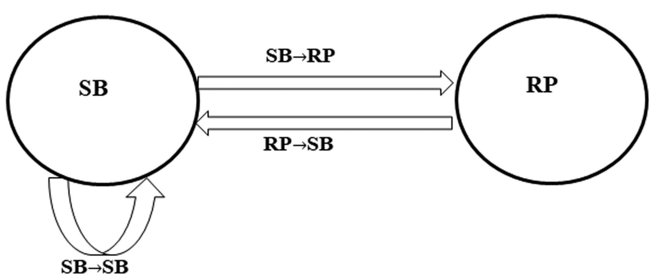

Figure 2. Summarized annual life cycle of *Bassia scoparia* from one fall to the next as used in the model. Each arrow represents transition from one stage (viable seeds in seedbank, SB) to the next (reproductive plants, RP). Transition of viable seeds in the seedbank to established plants includes all emerged plants that produced new seeds (SB → RP). Transition of newly produced viable seeds to the seedbank includes all seeds from shedding or dispersed seed from tumbling *Bassia scoparia* plants from another location (RP → SB). The cycling of viable seeds in the seedbank (i.e., persistent seeds) represents number of nongerminated viable seeds from the previous fall (SB → SB). See Table 1 for survival probabilities.

germination and viable seed longevity between the two biotypes (i.e., GR and GS) that made up the *B. scoparia* population. Thus, the combinations of stages and biotypes resulted in four classes: seedbank for GR and GS, that is, SB_R and SB_S, respectively, and established plants for GR and GS, that is, RP_R and RP_S, respectively.

Model Inputs

Annual Life Cycle Dynamics of Bassia scoparia

The life stages and their respective probabilities were illustrated in Figure 1; starting with viable seeds (S_v) in the seedbank from the previous fall with a probability that some of the seeds remain dormant (P_{dd}). *Bassia scoparia* seed longevity in the soil is 1 to 2 yr on average and is not affected by burial depth, but depth can be a physical barrier for seedling emergence (Dille et al. 2017). *Bassia scoparia* germinates and emerges with probability P_{germ} very early in the spring, as early as mid-March, and emergence continues until late summer in the Great Plains (Dille et al. 2017; Kumar and Jha 2017). By the end of the summer, it is expected that 80% to 95% of the viable seeds from the seedbank have germinated. Under high intraspecific density, self-thinning is typically expected among individual *B. scoparia* seedlings (Osipitan 2016). The probability that the seedling can survive and become reproductive was given as P_{rep}.

Bassia scoparia begins to flower from July to September (Esser 2014; OAO, personal observation). A biotic stress such as competition may encourage earlier flowering, thereby promoting early seed production (OAO, personal observation). An isolated *B. scoparia* plant with no competition or stress can produce more than 100,000 seeds (Esser 2014; Osipitan 2016). However, there is generally a reduction in the number of *B. scoparia* seeds produced (S_{fec}) within a crop due to intra- and interspecific competition (Esser 2014; Osipitan 2016). The probabilities that the seeds were viable and shed into the seedbank were given as P_{nvb} and P_{sh}, respectively.

As the plant matures, an abscission layer develops in the stem near the soil surface. In the presence of strong winds, this weakened area allows the dried plant to sever from the root system and tumble across the landscape, spreading viable seed wherever it rolls. The tumbling seed-dispersal mechanism means that the *B. scoparia* seeds were either lost to or gained from another location. The probability that the seedbank gained new seeds from another location was given as P_{sg}, while the probability of seed loss from seedbank was given as P_{sl}.

By late fall, a *B. scoparia* plant will stop producing seed, senesce, and die. This marks the last stage of the life cycle. By fall of the subsequent year (year 2), a proportion of these seeds from the previous year's seed rain have grown up to become reproductive plants, while some seeds have remained dormant or have died in the seedbank. By the fall of the third year, most of the dormant seed (≥95%) would have germinated to produce another generation of plants or died (Dille et al. 2017). The reproductive plant produces subsequent seed rain events to continue the cycle.

Outcrossing among Bassia scoparia Biotypes

Bassia scoparia bears protogynous flowers, necessitating seed production through outcrossing among individuals in a population. In this study, inheritance probability (P_i) of the glyphosate resistance versus susceptible trait at phenotypic level was incorporated into the model. We assumed that glyphosate resistance in *B. scoparia* was associated with duplications of a single *EPSPS* gene (monogenic) with nuclear inheritance (Jugulam et al. 2014; Niehues 2014). The phenotypic ratio of seeds produced from selfed heterozygous *B. scoparia* plants was 3:1 (GR:GS), suggesting that glyphosate resistance is a completely dominant trait (Niehues 2014).

We assumed a stable genotype (and phenotype) proportion over time (Hardy-Weinberg proportion) (Bagavathiannan et al. 2013; Werle 2016). We classified *B. scoparia* individuals into three genotypes: homozygous GR (RR), heterozygous GR (RS), and homozygous GS (SS). We expected six possible mating outcomes from these three genotypes: RR × RR, RR × RS, RR × SS, RS × RS, RS × SS, and SS × SS, using the Mendelian model of four offspring from each mating. We calculated our phenotypic probabilities as follows:

$$\text{Phenotypic probability for GR } (P_{iR}) = \frac{\text{number of RR} + \text{number of RS}}{\text{total number of offspring}}$$

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Table 1. Mean and standard deviation of each parameter value used in the model simulating the population dynamics of *Bassia scoparia*.[a]

Parameter[b]	Definition	Mean values[c]	SD	References
S_{vR}	Viable seed in the seedbank for GR biotype (no. m^{-2})	1	0.1	Assumption
S_{vS}	Viable seed in the seedbank for GS biotype (no. m^{-2})	9	0.3	Assumption
P_{germR}	Probability of viable seeds in the seedbank that germinate to become seedlings of GR biotype	0.77*	0.14	Dille et al. 2017; Osipitan and Dille 2017
P_{germS}	Probability of viable seeds in the seedbank that germinate to become seedling of GS biotype	0.81*	0.17	Dille et al. 2017; Osipitan and Dille 2017
P_{rep}	Probability that surviving seedling will become a reproductive plant	0.94	0.21	OAO, unpublished data
S_{fec}	Fecundity in the presence of crop (no. m^{-2})	23,580*	10,004	Esser 2014; Osipitan 2016
P_{nvbR}	Probability that newly produced seed will be viable for GR biotype	0.85	0.18	OAO, unpublished data
P_{nvbS}	Probability that newly produced seed will be viable for GS biotype	0.90	0.25	OAO, unpublished data
P_{sh}	Probability that newly produced seed will be shed within 1 m^2	0.15	0.10	Borger et al. 2009
P_{vpsR}	Probability that ungerminated viable seed at the beginning of the just concluded growing season is still viable in the seedbank for GR biotype	0.01*	0.001	Dille et al. 2017; OAO, unpublished data
P_{vpsS}	Probability that ungerminated viable seed at the beginning of the just concluded growing season is still viable in the seedbank for GS biotype	0.02*	0.001	Dille et al. 2017; OAO, unpublished data
P_{iR}	Probability that seeds produced from cross-pollination are GR	0.75	0.26	Niehues 2014
P_{iS}	Probability that seeds produced from cross-pollination are GS	0.25	0.14	Niehues 2014
P_{sl}	Probability of natural seed loss	1		Borger et al. 2009
P_{sg}	Probability of natural seed gain	1		Borger et al. 2009
P_{dd}	Probability that dormant seed will remain dormant after 2 yr	0.03	0.01	Dille et al. 2017

[a]Field size was 1 m^2.
[b]A parameter that ends with R or S subscript was specific for glyphosate-resistant (GR) or glyphosate-susceptible (GS) biotype, respectively.
[c]An asterisk (*) indicates values were averaged across studies.

Table 2. Weed control strategies, components and their respective mean P_{1-ctr} values.

		Weed control component (from spring to crop harvest)		P_{1-ctr}[a] (SD)		
Options	Control name	Preplant/PRE option(s)	In-crop option(s)	GR	GS	References
1	No-till1	Glyphosate	Glyphosate	0.98 (0.18)	0.002 (0.001)	Kumar and Jha 2015; Osipitan and Dille 2017
2	No-till2	Tank mix of residual herbicides with glyphosate	Glyphosate	0.15 (0.09)	0.002 (0.001)	Kumar and Jha 2015; Osipitan and Dille 2017; Hulse 2012
3	No-till3	Termination of the cover crop with a herbicide and subsequent PRE herbicides with residual activities	Glyphosate with cover crop residue	0.04 (0.02)	0.002 (0.001)	Petrosino et al. 2015; Kumar and Jha 2015; Osipitan and Dille 2017
4	Reduced-till	One tillage operation and subsequent PRE herbicides with residual activities	Tank mix of POST herbicides including glyphosate	0.002 (0.001)	0.0001 (0.000)	Brachtenbach 2015; Kumar and Jha 2015; Osipitan and Dille 2017
5	Conventional-till	Two tillage operations and subsequent PRE herbicides with residual activities	No in-crop weed control	0.001 (0.001)	0.01 (0.001)	Brachtenbach 2015

[a]P_{1-ctr} is probability that emerged *Bassia scoparia* plant will survive weed control. P_{1-ctr} was estimated from mean proportion of plant control (P_{ctr}); $P_{1-ctr} = 1 - P_{ctr}$. Efficacy values were averaged from preplant to in-crop weed control on different cohorts of *B. scoparia*.

$$\text{Phenotypic probability for GS}\,(P_{iS}) = \frac{\text{number of SS}}{\text{total number of offspring}}$$

Bassia scoparia Control Strategies

The model assumed an annual cropping cycle in a glyphosate-based cropping system such as GT corn and soybean, as this is a common system in which GR biotypes have evolved due to repeated use of glyphosate. We considered a crop-rotation system between corn and soybean with five weed control strategies that farmers currently or could practice, and a no-control scenario. The no-control scenario simulates how *B. scoparia* population dynamics could change when left uncontrolled. Each weed control strategy has two components: preplanting/PRE and in-crop weed control. The probability that *B. scoparia* will survive a weed control strategy was given by P_{1-ctr} (Table 2). The P_{1-ctr} is the proportion of *B. scoparia* that survived weed control by late fall, at the time of census during the crop-growing season. The P_{1-ctr} was averaged across the two components (preplant/PRE and in-crop) for each weed control strategy. Specific *B. scoparia* control

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Table 3. Weed control inputs used for *Bassia scoparia* control.

Timing	Active ingredient	Herbicides (corn or soybean) Application rate (kg ae/ai ha^{-1})	Trade name	Manufacturer
Preplant	Glyphosate	1.3	Roundup WeatherMax®	Monsanto Company, 800 North Lindberg Avenue, St Louis, MO 63167
PRE	Acetochlor + atrazine	2.6 + 2.1	HarnessXtra®	Monsanto Company
PRE	Metribuzin + linuron	0.4 + 0.8	Sencor® + Linex®	Bayer Crop Science, Research Triangle Park, NC 27709; and DuPont Crop Protection, Wilmington, DE
PRE	Pyroxasulfone + atrazine	0.1 + 0.6	Zidua® + AAtrex®	BASF Corporation, 26 Davis Drive, Research Triangle Park, NC 27709; and Syngenta Crop Protection, Inc., Greensboro, NC 27409
PRE	*S*-metolachlor + atrazine + mesotrione	0.9 + 0.3 + 0.1	Lumax®	Syngenta Crop Protection
In-crop	Glyphosate	0.8	Roundup WeatherMax®	Monsanto Company
	Saflufenacil + linuron	0.03 + 0.8	Sharpen® + Linex®	BASF Corporation + DuPont Crop Protection
	S-metolachlor + mesotrione	1.9 + 0.2	Dual Magnum® + Callisto®	Syngenta Crop Protection
	Tembotrione + atrazine	0.1 + 0.6	Laudis® + AAtrex®	Bayer Crop Science and Syngenta Crop Protection
		Cover crops		
Species		Seeding rate (kg ha^{-1})		Comments
Winter triticale [× Tritisecale Wittm. ex A. Camus (Secale × Triticum)]		71		Cover crops were sown in fall and terminated 1 to 2 wk before planting of main crops.
Hairy vetch (*Vicia villosa* Roth)		28		
Triticale + hairy vetch		53 + 21		
Triticale + Austrian winter pea (*Pisum sativum* L.)		53 + 81		
		Tillage		
Tillage type	Equipment	Tillage depth (cm)	Frequency of tillage	Comments
Reduced	V-blade undercutter	8 to 10	1	Tillage was conducted in spring, 4 to 5 wk before planting.
Conventional	Undercutter	8 to 10	2	Tillage was conducted in spring, up to the week of planting.
	Field cultivator	8 to 9		

inputs are shown in Table 3. For instance, within a growing season, use of effective herbicides can provide P_{1-ctr} of 0.98 to 0.0001 depending on the sensitivity of the *B. scoparia* biotype (Brachtenbach 2015; Kumar and Jha 2015; Petrosino et al. 2015; Osipitan and Dille 2017). Cover crop (winter triticale [× *Tritisecale* Wittm. ex A. Camus (*Secale* × *Triticum*]) and reduced-tillage (V-blade undercutter) for *B. scoparia* control provided an average P_{1-ctr} of 0.10 and 0.001, respectively (Brachtenbach 2015; Hulse 2012; Petrosino et al. 2015). In general, the smaller the P_{1-ctr}, the better the control strategy. The P_{1-ctr} was incorporated into the model as a lower-level parameter (Equation 3). The control strategies were ranked based on the growth rate of the entire population or based on the size of SB and RP for GR and GS biotypes at census year 10. The lower the growth rate, SB, and RP, the better the *B. scoparia* control strategy. In the Great Plains, weed control programs are usually associated with the type of tillage system; thus, the control strategies were termed no-till1, no-till2, no-till3, reduced-till, and conventional-till:

1. No-till1 relied solely on glyphosate for both preplant and in-crop *B. scoparia* control.
2. No-till2 used diverse herbicide sites of action for preplant control but relied solely on glyphosate for in-crop control.
3. No-till3 used a cover crop for preplant *B. scoparia* control; the cover crop was terminated using burndown herbicides and tank mixes with residual herbicides applied late spring or early summer, followed by in-crop application of herbicides (including glyphosate) with diverse sites of action in the presence of cover crop residue.
4. Reduced-till used one preplant tillage operation approximately 1 to 2 wk before planting in the summer, followed by PRE herbicides with residual activity and in-crop application of herbicides (including glyphosate) with diverse sites of action.
5. Conventional-till used two preplant tillage operations, followed by PRE herbicides with residual activity and no in-crop *B. scoparia* control.

Model Analysis

Deterministic Model

A deterministic model simulated the growth rate (λ) and population size (SB and RP) for all control strategies projected for a period of 15 yr and assumed that the model parameter values remained constant over time using a stage-structured transition matrix. The λ represents the highest eigenvalue of the transition matrix (Caswell 2001). We envisioned a scenario wherein *B. scoparia* seeds were present in the seedbank at a relatively low density with 18% GR and 82% GS biotype densities (Table 1). At the initiation of the simulation (during fall at census, year 0), the location was assumed to have 11 viable seeds m^{-2} from the previous fall in the seedbank and no established plants. Equations 3 to 7 show how the matrix model was constructed from the summarized life cycle of *B. scoparia* in Figure 2. The transition matrix in Equation 7 was used to project overall population λ and SB and RP of GR and GS over time (years).

Below are the transition parameters and their respective lower-level probabilities or parameters:

$$SB \rightarrow RP = P_{germ} \times S_{v} \times P_{rep} \times P_{1\text{-}ctr} \quad [3]$$

$$RP = S_{fec} \times P_{nvb} \times P_{vps} \times P_{sh} \times P_{i} \times P_{sl} \times P_{sg} \quad [4]$$

$$SB \rightarrow SB = P_{dd} \quad [5]$$

Construction of the matrix for the overall stage transition (without any specific reference to the biotypes) is given below:

$$\begin{bmatrix} SB \\ RP \end{bmatrix} = \begin{bmatrix} SB \rightarrow SB & RP \rightarrow SB \\ SB \rightarrow RP & 0 \end{bmatrix} \quad [6]$$

The constructed matrix with biotypes:

$$\begin{bmatrix} SB_R \\ SB_S \\ RP_R \\ RP_S \end{bmatrix} = \begin{bmatrix} SB_R \rightarrow SB_R & 0 & RP_R \rightarrow SB_R & 0 \\ 0 & SB_S \rightarrow SB_S & 0 & RP_S \rightarrow SB_S \\ SB_R \rightarrow RP_R & 0 & 0 & 0 \\ 0 & SB_S \rightarrow RP_S & 0 & 0 \end{bmatrix}$$

Structured transition matrix from time (t) to $t+1$, which was used to project population λ over time:

$$\begin{bmatrix} SB_R \\ SB_S \\ RP_R \\ RP_S \end{bmatrix}_{t+1} = \begin{bmatrix} SB_R \rightarrow SB_R & 0 & RP_R \rightarrow SB_R & 0 \\ 0 & SB_S \rightarrow SB_S & 0 & RP_S \rightarrow SB_S \\ SB_R \rightarrow RP_R & 0 & 0 & 0 \\ 0 & SB_S \rightarrow RP_S & 0 & 0 \end{bmatrix} \times \begin{bmatrix} SB_R \\ SB_S \\ RP_R \\ RP_S \end{bmatrix}_{t} \quad [7]$$

Parameters with R and S subscripts represent GR and GS biotypes, respectively.

Stochastic Model

Stochasticity was incorporated into the model because of possible effects of environmental and demographic changes on population projection and was done according to the methods described by Caswell (2001) and Borger et al. (2009). The consideration of stochasticity also ensured that initial conditions in the deterministic model did not solely determine the population projection. Probabilities for seed production, germination, viability, and dormancy were considered as stochastic variables, which were more likely to be influenced by environmental changes or uncertainties relating to inheritance. The model assumed a positive autocorrelation between *B. scoparia* plant survival probabilities and seed production (OAO, personal observation). For each simulation, the values of the lower-level parameters that estimated transition parameters were calculated as:

$$A = B + (C \times D) \quad [8]$$

where A is the parameter value for a given year in a given simulation, B and C are the mean and standard deviation, respectively, of each parameter shown in Table 1, and D is the hypothesized normal standard deviation randomly assigned for each simulation. Each simulation has four matrices characterized by different values of these stochastic variables. For each weed control strategy, 500 independent simulations were carried out for a period of 15 yr. All initial conditions set for the deterministic model were also used in the stochastic model. The stochastic model was used to estimate the probability of population size becoming insignificant over time, and this was measured using the quasi-extinction probability threshold of 0.1 for total *B. scoparia* individuals for each biotypes (Holmes et al. 2007).

Sensitivity and Elasticity Analyses

Sensitivity (*SI*) and elasticity (*E*) analyses were conducted on the transition parameters to determine the impacts of each parameter on λ in an absolute or relative term, respectively. The sensitivity and elasticity analyses were performed based on the procedure described by Caswell (2001).

$$SI = \frac{\partial \lambda}{\partial a_{ij}} \quad [9]$$

$$E = \frac{\partial \log \lambda}{\partial \log a_{ij}} \quad [10]$$

where a_{ij} represents a transition parameter in row i, column j of the matrix. Sensitivity measures the absolute change in λ resulting from an additive change in a_{ij}, whereas elasticity measures the relative change in λ resulting from a proportional change in a_{ij}.

Model analyses were conducted with the 'popbio' statistical package of R v. 3.4.1 (R Core Team 2017).

Results and Discussion

Bassia scoparia Population Dynamics

The uncontrolled *B. scoparia* population in this study represents a naturally growing population with no agronomic or management influence on its annual life cycle. The model indicates that the population growth rate (λ) was 6.94 for an uncontrolled *B. scoparia* population (Figure 3). Estimated λ values indicated that *B. scoparia* populations can rapidly expand if left uncontrolled. The model shows that the elasticity of growth rate to transition parameters was consistently greatest for the transition from seedbank to established plants (SB → RP) and from established plants to seedbank (RP → SB), whereas seedbank persistence (P_{dd}; SB → SB) consistently had very low elasticity, suggesting that the *B. scoparia* dormant seedbank was less important to population growth rate (Table 4). For example, increasing P_{dd} from 3% to 50% did not increase growth rate

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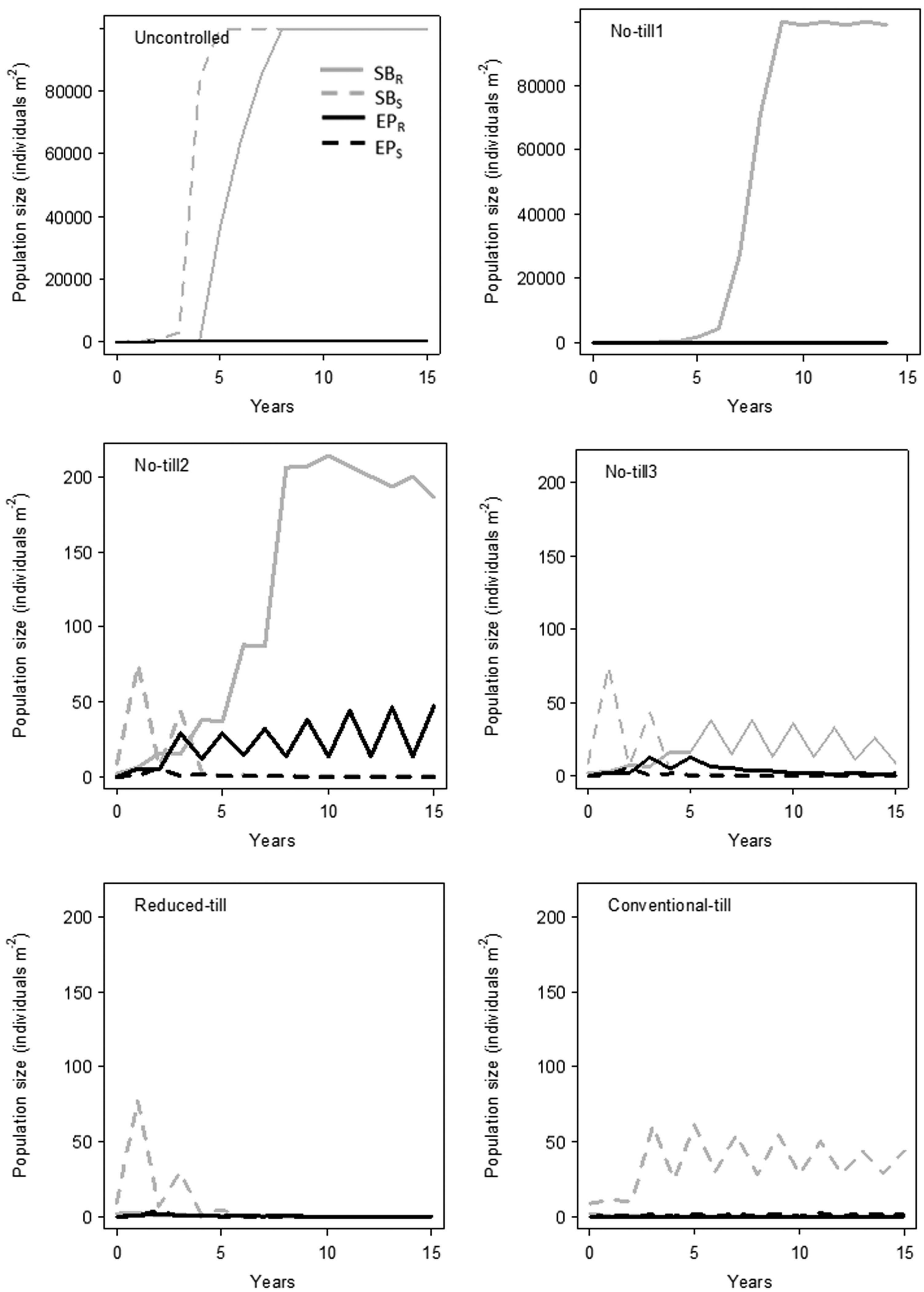

Figure 3. Population size (total number of established *Bassia scoparia* per square meter and viable seeds in the seedbank per square meter) in the population over time, estimated by the stage-structured transition model for each control strategy.

(6.94). When P_{dd} was increased to 95%, which is much higher than likely to happen ecologically (Dille et al. 2017), then growth rate increased to 6.96. Instead of relying on a dormant seedbank for future generations, *B. scoparia* relies on prolific seed production (Esser 2014) and high viability and abundant seedling recruitment (Kumar and Jha 2017), suggesting that any management effort that prevents seed production, seedbank replenishment, and emergence (or survival) of seedlings will assist in reducing the population growth of *B. scoparia*.

Our analysis further showed that population growth rate was consistently most sensitive to transition from RP → SB than SB → SB and SB → RP (Table 4), confirming that preventing *B. scoparia* seed production could have the greatest impact on the population growth irrespective of the biotype. The GR *B. scoparia* biotype has previously been found to have lower seed viability and seedling emergence than the GS biotype (Kumar and Jha 2017; Martin et al. 2017; Osipitan and Dille 2017); however, these differences did not change the importance of each life stage or transition on *B. scoparia* population growth in this model. In addition, the glyphosate-resistance trait appears not to have an impact on seed production, which is the most important stage to the population growth (Kumar and Jha 2015; Osipitan and Dille 2017), indicating that survival of a GS or GR seedling to seed production will equally contribute to population growth rate.

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Table 4. Sensitivity and elasticity of population growth to transition parameters for each control strategy.[a]

Management	$SB \rightarrow SB_R$	$SB \rightarrow SB_S$	$SB \rightarrow RP_R$	$SB \rightarrow RP_S$	$RP \rightarrow SB_R$	$RP \rightarrow SB_S$
			Sensitivity[b]			
Uncontrolled	0.502	0.501	0.082	0.349	3.020	0.714
No-till 1	0.502	0.516	1.982	21.199	0.126	0.012
No-till 2	0.504	0.513	5.243	21.199	0.048	0.012
No-till 3	0.506	0.516	6.762	21.199	0.039	0.012
Reduced-till	0.509	0.529	9.573	23.801	0.026	0.010
Conventional-till	0.519	0.508	21.399	7.535	0.011	0.033
			Elasticity[b]			
Uncontrolled	0.003	0.001	0.498	0.499	0.497	0.499
No-till 1	0.003	0.004	0.499	0.498	0.499	0.498
No-till 2	0.002	0.004	0.499	0.498	0.499	0.498
No-till 3	0.009	0.004	0.495	0.498	0.495	0.498
Reduced-till	0.019	0.055	0.490	0.472	0.491	0.472
Conventional-till	0.038	0.017	0.481	0.491	0.481	0.499

[a]Subscript R and S represent transition for glyphosate-resistant (GR) and glyphosate-susceptible (GS) biotypes, respectively.
[b]Sensitivity and elasticity values determined the impacts of each parameter on population growth rate (λ) in an absolute and relative term, respectively.

Impact of Control Strategies on B. Scoparia Population Dynamics

Overall, *B. scoparia* population growth rate was reduced by all control strategies, as λ decreased from 6.94 in an uncontrolled scenario to a range of 5.36 to 0.81, depending on the control strategy. A λ less than 1 suggests a decline in population growth rate. *Bassia scoparia* population controlled with reduced-till exhibited the lowest growth rate (0.81), followed by no-till3 (0.96), conventional-till (1.06), no-till2 (2.44), and no-till1 (5.36) (Figure 3). This indicates that the whole *B. scoparia* population was declining to negligible size with the reduced-till, and this was likely within 15 yr (Figure 4). Reduced-till in this case was a weed control strategy that used one preplant tillage operation a few weeks before planting in the summer, followed by an application of a PRE herbicide and POST application of tank-mixed herbicides, including glyphosate, in a GT crop such as corn or soybean (Table 2). This diverse weed control strategy uses mechanical and chemical methods sequentially to ensure removal of different cohorts of *B. scoparia* at multiple times during the growing season. The tillage (i.e. mechanical) component was reported to be a very effective input for the control of all emerged *B. scoparia* biotypes, with an average percentage control of 99.9% (Brachtenbach 2015). During the tillage operation, *B. scoparia* seeds are buried in the soil, preventing them from germinating and emerging during the growing season, with a high (95%) chance of losing their viability in the following season (Dille et al. 2017). There was also a possibility that the tillage operation placed *B. scoparia* seeds from previous growing seasons on the soil surface or at a shallow depth (Brachtenbach 2015; Kumar et al. 2018); however, few of these seeds are expected to be viable, and any emerging seedling could be effectively controlled by subsequent application of PRE as well as POST herbicides tank mixed with glyphosate (Dille et al. 2017; Kumar and Jha 2015).

The no-till3 weed control strategy, which included cover crops terminated using herbicides with residual activity at spring or early summer, followed by POST application of tank-mixed herbicides, including glyphosate, in the presence of cover crop residues, led to a slight decline of *B. scoparia* populations toward negligible size (λ = 0.96). In principle, this control strategy ensured that B. *scoparia* removal occurred at multiple times, with the cover crop suppressing the growth of *B. scoparia*, and the effect of cover crop was complemented with herbicides (including glyphosate) during the growing season. There is increasing adoption of cover crops by farmers, as they have been shown to provide satisfactory weed suppression at termination that lasts up to 7 wk after planting of main crops (Dille et al. 2017; Osipitan et al. 2018). Petrosino et al. (2015) reported that a fall-sown triticale cover crop provided 94% control of *B. scoparia* density. Termination of the cover crop with herbicide at early summer provided an average of 99.9% control of *B. scoparia* density (Petrosino et al. 2015). This coincided with planting dates for GT corn or soybean. Application of residual herbicides and POST application of herbicides together with cover crop residues will provide effective control of later-emerging *B. scoparia* cohorts during the growing season.

Bassia scoparia controlled with conventional-till allowed for a marginal increase in population growth rate (λ = 1.06). Conventional-till used two preplant tillage operations, followed by PRE herbicides with residual activity and no POST weed control. Conventional-till operates on the same principle as reduced-till, but with an increased frequency and depth of tillage operation. In this case, the repeated tillage operation impacted the *B. scoparia* seedbank more and successfully removed all emerged plants (Brachtenbach 2015). The greater depth of seed burial by tillage operations reduced the chances of seedling emergence. At a shallow seed burial depth of 2 mm, *B. scoparia* emergence was reduced by approximately 50%, and at a depth of 40 mm, emergence declined to 10% (Schwinghamer and Van Acker 2008). Use of PRE herbicides will remove subsequent cohorts of *B. scoparia*; however, with no in-crop weed control, there was a 10% increase in survival probabilities of *B. scoparia* plants (Table 2). This caused a marginal increase in population growth rate. There was a 5% to 20% chance that *B. scoparia* could still emerge in mid- to

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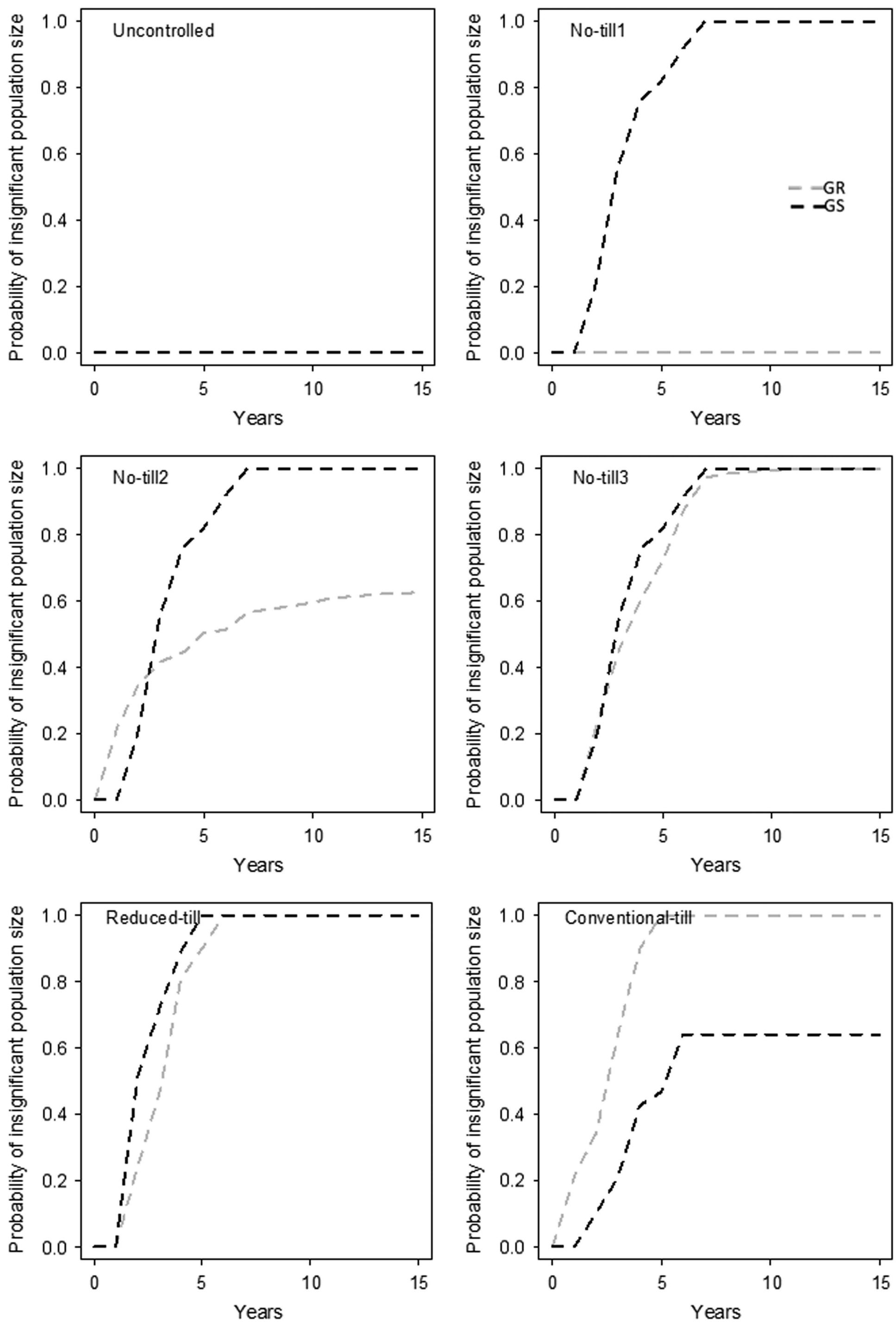

Figure 4. Probabilities for glyphosate-resistant (GR) and glyphosate-susceptible (GS) biotypes to decline to insignificant population size, estimated with quasi-extinction probability threshold of 0.1 as total *Bassia scoparia* individuals for each control strategy.

late July (Anderson and Nielsen 1996; OAO, personal observation); thus, application of PRE herbicides in mid- or late May (as commonly practiced) may not provide season-long in-crop weed control for the later-emerging cohorts in July (Sbatella and Wilson 2010). Our model showed that when conventional-till was complemented with an in-crop weed control using POST herbicides, the survival probability of established plants was reduced by 10%, and the population growth rate (λ) was 0.67, indicating a decline to negligible population size. This suggests the importance of multiple timings of weed removal to ensure control of later-emerging *B. scoparia* cohorts. Conventional-till was the most effective control strategy against the already evolved GR biotype, as it caused the least abundance of GR at the 10th year of census (Figure 3). In addition, the estimated probability of obtaining an insignificant population size of the GR biotype within 15 yr was 100% with conventional-till (Figure 4).

The no-till1 control strategy, which relied solely on glyphosate for preplant and in-crop weed control, caused the greatest

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expansion of the *B. scoparia* population among all control strategies, which was expected. The model indicated that the GR biotype was the major contributor to the increased population growth rate recorded for no-till1 (Figure 3). This implies that the sole reliance on glyphosate for *B. scoparia* control promoted selection of the GR biotype. *Bassia scoparia* plants are known to have prolific seed production irrespective of being GR or GS (Osipitan and Dille 2017). Survival of one GR *B. scoparia* plant resulted in production of thousands of new *B. scoparia* individuals, and thus influenced the population growth rate (Figure 3). The probability that the size of the already evolved GR biotype will be negligible within 15 yr was zero (Figure 4). Repeated and exclusive use of single-herbicide site of action has been widely discouraged, as this weed control tactic increases selection pressure on weed species for herbicide-resistance evolution (Beckie and Harker 2017; Lamichhane et al. 2017; Powles 2018). The selected herbicide-resistance trait may spread quickly if the resistance trait is dominant and biotypes undergo outcrossing, as in the case of the *EPSPS* gene for glyphosate resistance in *B. scoparia* (Nieuhues 2014).

The no-till2 control strategy, which used diverse herbicide sites of action for preplant and PRE *B. scoparia* control, did not reduce the population growth rate (λ) to less than 1.0, below which the *B. scoparia* population is in decline. As with the no-till1 control strategy, the GR biotype was the major contributor to the increased population growth rate for no-till2, suggesting that the diverse herbicide options did not guarantee a long-term decline in the already evolved GR *B. scoparia* biotype. The first cohort of *B. scoparia* is usually very dense in the Great Plains. A mix of effective herbicides with glyphosate applied at preplanting and at planting may control a majority of the *B. scoparia* plants, resulting in a much lower density (Dille et al. 2017). However, a POST herbicide program that relies on glyphosate (as in the case of no-till2) will only provide effective control of the GS *B. scoparia*, while the GR biotype will be left uncontrolled. This suggests the reason for the increased population growth rate recorded for no-till2. In a scenario with an application of a tank mix of POST herbicides with different sites of action and with glyphosate in the GT crops, the survival probability of the established GR plant was reduced to 2%, resulting in a population growth rate of 0.88 (i.e., population declining to negligible size). Such diverse POST options for *B. scoparia* control are available in GT corn more than in soybean. However, multiple herbicide resistance has been reported in *B. scoparia* (Varanasi et al. 2015), which further reduces the number of herbicide options available for effective control of GR *B. scoparia* in GT crops.

The stage-structured simulation model developed in this study provides a means for quick comparison of sustainable control strategies for GS and already evolved GR *B. scoparia* biotypes without the need for very long-term studies that are often very labor and capital intensive. This model can also be adopted or modified to understand how weed control practices will promote or mitigate already evolved herbicide-resistant weed populations in a specific cropping system.

The model confirmed our hypothesis that diversified weed control strategies that control different biotypes and cohorts of *B. scoparia* during the growing season in a glyphosate-based cropping system will reduce the expanding growth rate of *B. scoparia* and significantly reduce an already evolved GR biotype. The model indicated that seedling emergence, seedling survival, and prolific seed production were important demographic stages that promoted *B. scoparia* population growth, while seed dormancy had little, if any, impact on the population growth. This highlighted that control strategies should focus on preventing seedling emergence, seedling survival, and seed production. The use of glyphosate remains a key component of effective weed control programs among farmers in the Great Plains. Glyphosate is commonly used because it provides broad-spectrum control of weed species, it is easy and relatively cheap to use, and provides effective weed control in important crops such as GT corn and soybean. Our model indicated that glyphosate could be used together with other effective weed control methods to provide excellent control of *B. scoparia* populations and potentially eliminate an already evolved GR *B. scoparia* biotype within a given location. It should be noted that the efficacy values for the control inputs used in this simulation study might be variable under different field conditions. A diverse control strategy that includes one or two preplant tillage operation (s), followed by preplant or PRE application of herbicides with residual activity and POST application of glyphosate will reduce seed germination, minimize seedling survival, and reduce seed production during the growing season, which in the long term will potentially significantly reduce *B. scoparia* biotypes within a given location. Similarly, a diverse weed control strategy that uses a biological competitor such as a fall-sown cover crop to suppress early spring flushes of *B. scoparia*, coupled with an application of a herbicide with residual activity during cover crop termination, with subsequent physical impediments provided by cover crop and application of glyphosate, will provide effective long-term control of *B. scoparia* in a given location.

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