Ecological Modelling 343 (2017) 131–141

Contents lists available at ScienceDirect

Ecological Modelling

journal homepage: www.elsevier.com/locate/ecolmodel

Modeling shattercane dynamics in herbicide-tolerant grain sorghum cropping systems

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ARTICLE INFO

Article history:
Received 29 March 2016
Received in revised form 23 October 2016
Accepted 30 October 2016
Available online 5 November 2016

Keywords:
Crop-to-weed gene flow
Weedy relative
Herbicide-tolerant grain sorghum
Herbicide-resistance

ABSTRACT

Traditional breeding technology is currently being used to develop grain sorghum [*Sorghum bicolor* (L.) Moench *ssp. bicolor*] germplasm that will be tolerant to acetolactate synthase (ALS)-inhibiting herbicides. This technology (Inzen™, DuPont™) has the potential to improve sorghum production by allowing for the postemergence control of traditionally hard-to-control grasses. However, grain sorghum and shattercane [weedy *Sorghum* species; *Sorghum bicolor* (L.) Moench *ssp. drummondii* (Nees ex Steud.) de Wet ex Davidse] can interbreed and introduced traits such as herbicide tolerance could increase the weediness of the weedy relative. Our objective was to develop a simulation model to assess management options to mitigate risks of ALS-resistance evolution in shattercane populations in US sorghum production areas. Assuming a single major gene confers resistance and gene frequencies change according to the Hardy-Weinberg ratios we constructed a stage-structured (seedbank, plants) matrix model with annual time steps. The model explicitly considered gene flow from Inzen plants to shattercane populations. The management strategies considered in the model were: a) continuous sorghum, b) sorghum followed by (*fb*) soybeans and c) sorghum *fb* fallow *fb* winter wheat, where postemergence ALS-inhibiting herbicides were only used in Inzen years. During sorghum years two options were tested: continuous Inzen and Inzen *fb* conventional sorghum, for a total of six management strategies. The parameter values used in the model were obtained from our research, the literature, and expert opinion. For each management strategy we ran deterministic and stochastic simulations (with stochastic levels of herbicide efficacy). The time for resistance evolution was predicted to decrease with increased cropping system complexity (more crop diversity than continuous production of Inzen). Evolution of resistance was predicted to occur rapidly if Inzen sorghum is planted continuously because of high selection pressure (ALS-inhibiting herbicide application) and crop-to-weed gene flow. Rotating Inzen with conventional sorghum did not assist with shattercane management. Rotating Inzen with non-sorghum crops where effective herbicide options are available assisted with keeping shattercane density at low levels while postponing resistance evolution to some extent. Crop and herbicide rotation will be key strategies for shattercane management in Inzen sorghum.

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1. Introduction

Grain sorghum is economically ranked as the fifth most important cereal crop in the world after wheat (*Triticum aestivum* L.), rice (*Oryza sativa* L.), corn (*Zea mays* L.), and barley (*Hordeum vulgare* L.), and is the third-most common cereal planted in the US, trailing corn and wheat (DeFelice, 2006; USDA-NASS, 2016). Sorghum is a warm season C4 grass species that is highly efficient in the conversion of solar energy and use of water. Sorghums are cultivated throughout the world for grain, fodder, syrup, and biofuel production. In the US, the crop is primarily used for livestock feed and is ranked second after corn for ethanol production (Paterson, 2008). In spite of the agronomic potential and food value of grain sorghum, the number of acres of sorghum production has declined in many parts of the US (USDA-NASS, 2016), in part because the number of herbicide options for weed management in sorghum is limited. Most post-emergence herbicides labeled for grain sorghum are effective on broadleaf weed species but have only limited activity on annual grasses. Consequently, soil applied herbicides are the primary option for annual grass control in grain sorghum (Hennigh et al., 2010). However, grain sorghum is often grown in dry environments and the absence of adequate soil moisture often reduces

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http://dx.doi.org/10.1016/j.ecolmodel.2016.10.023
0304-3800/Published by Elsevier B.V.

the activation and efficacy of soil applied herbicides (Hennigh et al., 2010).

Acetolactate synthase (ALS)-inhibiting herbicides, also known as acetohydroxyacid synthase (AHAS)-inhibitors, are commonly used to control grass weeds in certain broadleaf and grass crops (Hennigh et al., 2010). However, conventional grain sorghum is susceptible to ALS-inhibiting herbicides that have grass activity. In 2004, a shattercane population exhibiting resistance to ALS-inhibiting herbicides was identified in Kansas. Using conventional breeding, a project was then initiated by scientists at Kansas State University with the objective to introgress the ALS-resistant gene from the shattercane population into grain sorghum germplasm and ultimately commercialize grain sorghum varieties with tolerance to ALS-inhibiting herbicides (Tuinstra and Al-Khatib, 2008). DuPont® has acquired the license of the ALS-inhibiting herbicide tolerance trait from Kansas State University and has branded the technology as 'Inzen'. Nicosulfuron (Zest™; herbicide in the sulfonylurea family), an effective active ingredient for the control of weedy annual grasses, is the herbicide intended to be labeled for the technology. The ALS-tolerant grain sorghum varieties are expected to be on the market in 2017 (Saunders D. W. and K. L. Carlson, personal communication). This technology has the potential to improve weed control options in grain sorghum production by allowing for post-emergence control of grass weeds (Hennigh et al., 2010). Moreover, the technology has strong potential to increase the use of grain sorghum in crop rotations and expand its production in environments where grain sorghum is better adapted than corn, but where corn is typically cultivated because of the availability of more herbicide options.

Despite the potential of the Inzen technology, the co-existence of sympatric weedy relatives poses some threats to its adoption and potential lifespan. The main concerns are i) crop-to-weed gene flow that would increase the frequency of the ALS-resistance allele in sympatric weedy populations, ii) the difficulty of controlling weeds that are already ALS-resistant and iii) selection for additional resistant biotypes due to overreliance on the technology. Shattercane is a troublesome weedy sorghum in agronomic crops in the USA, especially in grain sorghum production (Hans and Johnson, 2002; Kegode and Pearce, 1998). Shattercane is a wild sorghum relative with many similarities to grain sorghum. Shattercane and grain sorghum are both diploid ($2n = 2x = 20$), sexually compatible, and may be cross-pollinated by wind, which can result in hybridization where flowering synchrony occurs (DeFelice, 2006; Sahoo et al., 2010; Schmidt et al., 2013). Thus, there is apparently no barrier to prevent the transfer of nuclear alleles from sorghum to shattercane (Sahoo et al., 2010; Schmidt et al., 2013). Sahoo et al. (2010) reported that shattercane x sorghum hybrids had similar ecological fitness to the wild-type parents with respect to several metrics (i.e., biomass and seed production). This indicates that any neutral or beneficial trait would likely persist in the weedy relative infesting agricultural fields, even in the absence of selection.

Due to the lack of new herbicide sites-of-action and increased reports of herbicide-resistant weeds, resistance management has become the most concerning topic in the field of Weed Science (Heap, 2016; Norsworthy et al., 2012). Simulation models of weed genetics and population dynamics have been developed to predict herbicide resistance evolution over time and have provided valuable insight on understanding the risks of resistance evolution and the importance of diversified strategies for delaying and managing herbicide-resistance (Bagavathiannan et al., 2013, 2014; Gressel and Segel, 1978; Jasieniuk and Maxwell, 1994; Maxwell et al., 1990; Neve et al., 2011a,b; Renton et al., 2011). These models have focused on genetics and dynamics of species that are not related to crops. To our knowledge, no risk assessment model has been developed to explore population genetics and dynamics in response to several management strategies where a weedy relative poses a threat to the adoption of a novel herbicide tolerant crop because of pollen-mediated gene flow, which may certainly expedite resistance evolution in the weedy relative.

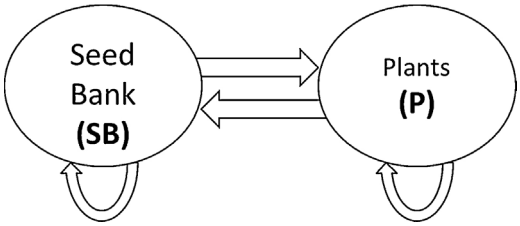

Fig. 1. Annual weed life cycle graph. The arrows indicate the transition rates between seedbank and plant stages.

Risk assessment models provide a means to compare management strategies without the need for long-term and often, impractical field studies (Neve, 2008). They also provide valuable insight in areas where genetic, biological, and ecological knowledge is lacking and indicate where future research efforts should be focused. In the era of genetically modified crops, whether developed by genetic engineering or conventional breeding, risk assessment models have become a valuable tool to support regulatory agencies with their decisions and policies, and industry with their stewardship programs.

We expect that continuous production of herbicide-tolerant sorghum will result in rapid fixation of the resistance allele in shattercane populations because crop-to-weed pollen-mediated gene flow and high selection pressure will favor individuals carrying the resistance trait. Since crop and herbicide rotation are claimed as important strategies to postpone evolution of resistance (Neve, 2008; Norsworthy et al., 2012), our working hypothesis is that more diversified management strategies will lead to more stable cropping systems where evolution of resistance will occur more slowly and population density of the weedy relative will remain at tolerable levels. Thus, our objective was to develop a simulation model to assess management options to mitigate risks of ALS-resistance evolution in shattercane populations in US sorghum production areas where the Inzen technology is likely to be adapted after its commercial deployment. We anticipate that our model will provide valuable insight on resistance management in Inzen sorghum technology and can also be used for risk assessment of novel traits in grain sorghum and other crops that have weedy relatives (e.g., rice [*Oryza sativa* L.], sunflowers [*Helianthus annuus* L.]).

2. Methods

2.1. Model description

We constructed a density dependent, stage-structured matrix model with annual time steps (Caswell, 2001). We assumed weed plants to be at pre-flowering stage at population census (pre-breeding census) and seed production and shattering to take place afterwards. The core structure of our model was based on: i) weed demography, ii) genetics and inheritance of the resistance trait, and iii) crop and weed management strategies. The model accounted for two stage classes: viable weed seeds in the seedbank (SB) and established weed plants (P). In our model, surviving seeds that did not germinate remained seeds in SB (SB → SB), and surviving seeds that germinated became P (SB → P). Surviving plants (P) produced seeds. The newly produced seeds that did not germinate before the next population census were added to SB (P → SB), and those that did geminate were added to P (P → P, Fig. 1).

Table 1
Life-history parameters of shattercane (*Sorghum bicolor* L. Moench ssp. *bicolor*). Base value for demographic parameters in our model were determined by using the midpoint of the reported range (maximum–minimum) from published data in the literature.

Parameters	Symbol	Base	Range	Reference
Proportion of newly produced (fresh) seeds that are viable	s_{viab}	0.91	0.83–1.00	Burnside (1965)
Proportion of fresh seeds that are predated	s_{pred}	0.70	0.60–0.80	Bagavathiannan and Norsworthy (2013)[a]
Proportion of viable seeds that survive in the seed bank over the winter	s_{survW}	0.15	0.10–0.21	Teo-Sherrell and Mortensen (2000) Teo-Sherrell et al. (1996)
Proportion of viable seeds that germinate	s_{germ}	0.35	0.15–0.55	Teo-Sherrell et al. (1996)
Proportion of viable seeds that survive in the seed bank during the season	s_{survS}	0.30	0.14–0.45	Teo-Sherrell and Mortensen (2000)
Theoretical maximum seed production (seeds m^{-2})	s_{max}	80510	62293–108488[b]	R. Werle (unpublished data)
Weed competitiveness	k_w	0.1277	0.0525–0.6199[b]	R. Werle (unpublished data)

[a] Adapted from johnsongrass (*Sorghum halepense* L. Pers).
[b] Represent the 95% confidence intervals around the parameter estimate.

2.1.1. Weed demography

We assumed that new seeds produced at the end of the season are viable with probability s_{viab}, survive predation with probability s_{pred}, and survive the winter with probability s_{survW}. We assumed predation to impact only new seeds. Surviving seeds either germinate with probability s_{germ} and become young plants during early season, or stay viable in the seedbank with probability (1- s_{germ}), survive microbial seed decay during the season with probability s_{survS}, and represent the seedbank at next census. Young plants survive herbicide treatment with probability (1-p_{ctrl}) and become established plants at next census. Plants at census produce p_{fec} number of new seeds. At next census new seeds contribute to SB if they do not germinate and remain viable or contribute to P if they germinate and become established plants. When compared to other 22 summer annual weed species, shattercane seedlings emerged in a relative short period of time (Werle et al., 2014a). The model has annual time steps, so the mortality due to herbicide application can be considered the average for the shattercane cohort. This average considers that at herbicide application the smaller seedlings have a slightly higher mortality than the larger seedlings. Most parameter estimates used in our model are based on research conducted in Nebraska. When not available, we used parameter estimates from published data on similar species, extension bulletins, unpublished data, or based on expert opinion (Tables 1 and 2).

2.1.1.1. Density-dependent seed production. Plant fecundity (p_{fec}; seeds $plant^{-1}$) in weed population models has been estimated using the hyperbolic competition function, which uses the weed and crop density as explanatory variables and assumes seed production to achieve an asymptote at high weed densities (Firbank and Watkinson, 1985; Renton et al., 2011). We modeled p_{fec} as follows:

$$p_{fec} = \frac{s_{\max} k_w d_w}{d_w(1 + k_w d_w + k_c d_c)} \quad (1)$$

where s_{max} is the maximum seed production (seeds m^{-2}), k_w represents weed competitiveness, k_c represents crop competitiveness, d_w is the weed density (plants m^{-2}), and d_c is the crop density (plants m^{-2}).

Since no data on density-dependent seed production were available for shattercane, we visited sorghum, soybean, and fallow fields infested with shattercane in the eastern part of Nebraska in the fall of 2014 (R. Werle, unpublished data). Briefly, we determined shattercane density using a counting quadrat (0.3 by 0.3 m) and harvested, processed and counted seeds within the demarked area. Crop density (plants m^{-2}) at each site was also recorded. According to our data, shattercane plants have the ability to produce more seeds under fallow than cropped conditions and similar amount of seeds were produced in sorghum and soybean fields (Fig. 2).

Since no difference was detected in shattercane seed production in sorghum and soybean fields, we accounted k_c and d_c as one parameter (kd_c; Table 1 and Fig. 2). We used the parameter values estimated for the hyperbolic competition function (Eq. (1)) for the density-dependent seed production function in the model. p_{fec} was the only density-dependent mechanism included in our model. Using the p_{fec} estimated from our field data (Eq. (1)), we assumed that all shattercane plants produced the same amount of seeds given a certain density. The model has annual time steps, so p_{fec} can be considered the average for the shattercane cohort. This average considers that early emerging individuals have a slightly higher p_{fec} than the later emerging individuals.

2.1.2. Genetics and inheritance of the resistance trait

2.1.2.1. Inheritance of ALS-resistance. We modeled ALS-resistance as a single completely dominant gene with two alleles (i.e., homozygous and heterozygous resistant individuals equally tolerant to ALS-inhibiting herbicide at field application rate). Resistance to ALS-inhibiting herbicides is typically conferred by a single, nuclear-encoded gene that is either dominant or partially dominant, resulting in a dominant inheritance pattern (Preston and Mallory-Smith, 2001). Therefore, dominant homozygous and heterozygous plants are likely to survive ALS-inhibiting herbicide treatment. ALS-tolerant sorghum (hereafter referred to as "Inzen") carries the Trp574Leu mutation in the ALS gene (Tuinstra and Al-Khatib, 2008), which confers high levels of resistance to herbicides in the sulfonylurea and imidazolinone families (Tuinstra and Al-Khatib, 2008; Werle et al., 2013, 2016). Under field and greenhouse conditions, shattercane × Inzen F1 hybrids were tolerant to ALS-inhibiting herbicides and herbicide application did not reduce F1 hybrid growth (Werle et al., 2013, 2014b).

For our model, we assumed the mutation present in Inzen sorghum to be the only type of resistance allele conferring resistance to ALS-inhibiting herbicides in shattercane. However, there are eight confirmed sites of ALS gene mutation in different weed species that confer resistance to ALS-inhibiting herbicides (Ala_{122}, Pro_{197}, Ala_{205}, Asp_{376}, Arg_{377}, Trp_{574}, Ser_{653}, and Gly_{654}) (Tranel et al., 2016). At each site, multiple amino acid substitutions are possible. The specific amino acid substitution at each site may confer different types and levels of resistance to different ALS herbicide families (Tranel et al., 2016). The ALS-resistance alleles only confer resistance to ALS-inhibiting herbicides and not to other herbicide sites of action such as EPSPs- and/or ACCase-inhibiting herbicides (glyphosate and clethodim, respectively), which are commonly used herbicides in non-sorghum years. Monogenic target site mutation has also been reported to confer resistance to other herbicide modes of action (i.e., resistance to EPSPs inhibitors, resistance to ACCase-inhibitors). Therefore, our modeling framework could also be used to predict resistance evolution to other herbicide modes-of-action in case grain sorghum with novel herbicide tolerance traits conferred by single genes become available in the future. Moreover, our modeling framework could also be adapted for other crops that have weedy relatives (i.e., rice, sunflowers).

2.1.2.2. Genotypic distribution. We classified shattercane seeds and plants into genetically differing biotypes: ALS-homozygous resistant (RR), ALS-heterozygous resistant (RS), and ALS-homozygous susceptible (SS). We assumed gene frequencies across generations to change according to the Hardy-Weinberg ratios (Roughgarden, 1998). We calculated the total frequency of the resistance allele in the population (p_i) at census (considering SB and P) as an indicator of resistance evolution over time (Roughgarden, 1998):

$$p_i = \frac{SB_{RRi} + \frac{1}{2}SB_{RSi} + P_{RRi} + \frac{1}{2}P_{RSi}}{SB_{RRi} + SB_{RSi} + SB_{SSi} + P_{RRi} + P_{RSi} + P_{SSi}} \quad (2)$$

where i represents the year, SB_{RR}, SB_{RS}, SB_{SS}, represent the number of RR, RS, and SS seeds, and P_{RR}, P_{RS}, P_{SS}, represent the number of RR, RS, and SS plants at census, respectively.

2.1.2.3. Mating and crop-to-weed gene flow. According to Hardy-Weinberg, the frequency of the resistance allele among recruits (new individuals) produced after census (year $i+1$) equals the frequency of the resistance allele in established plants at census (year i). However, pollen-mediated gene flow (g) from crop to weed will influence the allele frequency in recruits and thus, needs to be accounted for. Our model explicitly considered gene flow from conventional sorghum plants (hereafter referred to as "sorghum") and Inzen plants to shattercane populations. The ALS-resistance allele is fixed in Inzen sorghum, absent in conventional sorghum, and is assumed to be rare in shattercane populations prior to Inzen adoption and in the absence of selection by ALS-inhibiting herbicides in other crops (i.e., corn and soybeans) (Preston and Powles, 2002). Crop to weed gene flow (g) was estimated from Schmidt et al. (2013), who quantified *in situ* shattercane × sorghum hybridization. According to Schmidt et al. (2013) *in situ* hybridization of neighboring plants varied from 0.02 to 0.25 with a mean proportion of 0.16. In hybrid lines half of the ancestry is from shattercane and half from sorghum; therefore, g was estimated by dividing the hybridization rate reported by Schmidt et al. (2013) by two (Table 1). Gene flow from adjacent fields during non-grain sorghum years was not considered in this version of the model. Hence, our model provides a conservative estimate of the speed of resistance evolution.

Following Hedrick (2011), we used Wright's "Continent-Island" model (1969) to account for pollen-mediated crop-to-weed gene flow and estimated the frequency of the resistance allele in shattercane recruits (p^*_{i+1}) as follows:

$$p^*_{i+1} = \left(\frac{P_{RRi} + \frac{1}{2}P_{RSi}}{P_{RRi} + P_{RSi} + P_{SSi}}\right)(1-g) + g(p_{crop}) \quad (3)$$

where p_{crop} represents the frequency of the resistance allele in the crop planted at year i (p_{crop} = 1 during Inzen [homozygous resistant] and p_{crop} = 0 during sorghum [homozygous susceptible] years). p^*_{i+1} is increased after planting Inzen and is decreased after planting sorghum because of g. Differing from p_i estimated by Eq. (2), p^*_{i+1} is estimated using exclusively the number of plants within each genotypic category at time i and g. The p in seeds at time i will not influence p^*_{i+1} because seeds will not produce new seeds nor change their genotype.

2.1.3. Crop and weed management strategies

2.1.3.1. Management strategies. One of our objectives was to evaluate how different management strategies or herbicide-crop rotation programs could assist growers in postponing the evolution of ALS-inhibiting herbicide resistance in shattercane populations as well as keeping shattercane population density at low levels. For that, we conducted a survey with University Extension experts across the US sorghum production areas (Illinois, Indiana, Kansas, Missouri, and Nebraska) to assess the most common crop rotation strategies where sorghum is included and shattercane is a problematic weed species. According to expert opinion, the following are commonly used crop rotation schemes in these regions:

a) Continuous sorghum.
b) Sorghum followed by (*fb*) soybeans (areas where water is not a major limiting factor).
c) Sorghum *fb* fallow *fb* winter wheat (hereafter referred to as "wheat"; areas where water availability is limited).

Since the Inzen technology will soon become available to grain sorghum growers, we decided to exploit two options during grain sorghum years: continuous Inzen and Inzen *fb* sorghum. Thus, the following six management strategies (strat-) were considered in our model:

strat-1) continuous Inzen.
strat-2) Inzen *fb* sorghum.
strat-3) Inzen *fb* soybean.
strat-4) Inzen *fb* soybean *fb* sorghum *fb* soybean.
strat-5) Inzen *fb* fallow *fb* wheat.

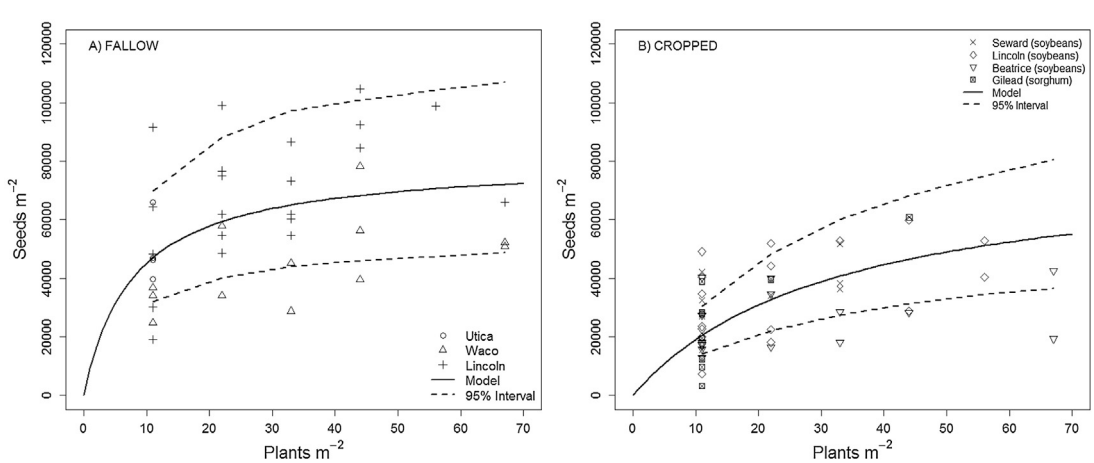

Fig. 2. Density-dependent shattercane seed production under fallow (A) and cropped conditions (B; soybeans and grain sorghum). Names represent the closest cities in Nebraska from each field where shattercane samples were collected from. y = (80510*0.1277*x)/(1 + 0.1277*x + dk_c), where dk_c = 0 and 3.1052 for fallow and crop, respectively. The "95% Interval" (dashed lines) represents the 95% prediction interval estimated using a lognormal sampling distribution (ln[seeds]~N(μ,σ)) around the hyperbolic competition function (Eq. (1)) with a standard deviation set to 0.2.

strat-6) Inzen *fb* fallow *fb* wheat *fb* sorghum *fb* fallow *fb* wheat.

2.1.3.2. Weed control parameters. Shattercane plant survival (1-p_{ctrl}) at time *i* within the model depended on the genotype of the established plants, the crop planted, and whether and which herbicides were applied before crop emergence (PRE) and/or after crop emergence (POST). We assumed PRE plant control with glyphosate to be used in Inzen and sorghum years. Proportion of shattercane seedlings that can be controlled prior to sorghum planting largely varies from year to year and is dependent on early-season weather conditions, time of shattercane emergence, and crop planting date. According to expert opinion, 40–80% of total shattercane emergence may occur prior to crop planting, which represents the proportion of plants likely to be controlled with a PRE plant ($p_{ctrlPRE}$) herbicide. POST herbicides ($p_{ctrlPOST}$) were used in soybeans (glyphosate + clethodim) and Inzen (nicosulfuron; only effective on SS plants). In fallow-wheat systems, glyphosate applied PRE was used in the fallow period before wheat planting (which takes place in September) and POST harvest glyphosate application was used after wheat harvest (which takes place in June). Thus, in season shattercane survival (1-p_{ctrl}) = (1-$p_{ctrlPRE}$)(1-$p_{ctrlPOST}$). We obtained weed control data for each crop-herbicide program from extension publications and expert opinion (Table 2; Knezevic et al., 2016; Roeth et al., 1994; Thompson et al., 2016).

2.1.3.3. Management strategy ranking. We evaluated the frequency of the resistance allele (p_i; Eq. (2)), and the total shattercane plant ($P = P_{RR} + P_{RS} + P_{SS}$) and seed ($SB = SB_{RR} + SB_{RS} + SB_{SS}$) densities in year 13 because all six management strategies included Inzen in that year. Based on p_{13}, P_{13}, and SB_{13}, strategies were ranked from best to worst. The best strategy had the lowest p_{13}, P_{13}, and/or SB_{13}.

2.2. Development of matrix model structure

We constructed a stage-structured model that considered three different genotype categories (RR, RS, and SS) for each life history stage (P and SB) resulting in six stages/categories (Fig. 3). The population structure can be represented as a vector n_i specifying the number of individuals in the different stages and genotypes at time *i*. The model predicts the evolution of n_i over time using the following steps: first, the model kept track of the number of seeds produced by each genotype (fecundity matrix, F), then the resulting seeds were distributed into the different genotype categories according to the Hardy–Weinberg ratios (mating matrix, H), and lastly the fate of the seeds of the different genotypes was determined (recruitment matrix, R). So,

$$n_{i+1} = \mathbf{R}_{i+1}\mathbf{H}_{i+1}\mathbf{F}_{i+1}\mathrm{n}_i \tag{4}$$

The *n* vector and F, H and R matrices are displayed in Fig. 3.

2.2.1. Programing language

The programming language used for model construction was R version 2.15.1 (R Foundation for Statistical Computing, Wien, Austria).

2.3. Deterministic model

The deterministic model simulated resistance evolution and population density for all management strategies proposed for a period of 20 years assuming parameter values remained constant over time (Tables 1 and 2). We envisioned a scenario where shattercane seeds were present in the seedbank at a relative low density and the frequency of the resistance alleles in the source population to be low because Inzen had not been previously used and reliance on ALS-inhibiting herbicides had been low. As our initial conditions (census at year 0), fields were in fallow and we assumed 20 seeds m^{-2} to be present in the seedbank with no established plants ($SB_{RR} = 0$, $SB_{RS} = 0.0004$, and $SB_{SS} = 19.9996$; $SB_{RR} + SB_{RS} + SB_{SS} = 20$ seeds m^{-2} and $P_{RR} + P_{RS} + P_{SS} = 0$ plants m^{-2}), whereas the initial frequency of the resistance allele in the seedbank was set to 1×10^{-5} (Preston and Powles, 2002).

Next we conducted a perturbation analysis by changing each model parameter by ±10% while keeping all other parameter values constant to evaluate to what extent demographic parameter uncertainty influenced model outcome. Then we explored if the ranking of the management strategies changed at year 13 (p_{13}, P_{13}, and SB_{13}).

$$n_i^{\mathrm{T}} = \begin{vmatrix} SB_{RR}, & SB_{RS}, & SB_{SS}, & P_{RR}, & P_{RS}, & P_{SS} \end{vmatrix}$$

$$\mathrm{F}_{i+1} = \begin{vmatrix} 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & p_{fec}\, s_{viab}\, s_{pred} & p_{fec}\, s_{viab}\, s_{pred} & p_{fec}\, s_{viab}\, s_{pred} \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \end{vmatrix}$$

$$\mathrm{H}_{i+1} = \begin{vmatrix} 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & (p^*_{i+1})^2 & 0 & 0 \\ 0 & 0 & 0 & 2(p^*_{i+1})(1-p^*_{i+1}) & 0 & 0 \\ 0 & 0 & 0 & (1-p^*_{i+1})^2 & 0 & 0 \end{vmatrix}$$

$$\mathrm{R}_{i+1} = \begin{vmatrix} s_{survW}(1-s_{germ})\, s_{survS} & 0 & 0 & s_{survW}(1-s_{germ})\, s_{survS} & 0 & 0 \\ 0 & s_{survW}(1-s_{germ})\, s_{survS} & 0 & 0 & s_{survW}(1-s_{germ})\, s_{survS} & 0 \\ 0 & 0 & s_{survW}(1-s_{germ})\, s_{survS} & 0 & 0 & s_{survW}(1-s_{germ})\, s_{survS} \\ s_{survW}\, s_{germ}(1-p_{crtl}) & 0 & 0 & s_{survW}\, s_{germ}(1-p_{crtl}) & 0 & 0 \\ 0 & s_{survW}\, s_{germ}(1-p_{crtl}) & 0 & 0 & s_{survW}\, s_{germ}(1-p_{crtl}) & 0 \\ 0 & 0 & s_{survW}\, s_{germ}(1-p_{crtl}) & 0 & 0 & s_{survW}\, s_{germ}(1-p_{crtl}) \end{vmatrix}$$

Fig. 3. Matrix model structure. The population vector (n_t^{T}) specifies the number of individuals in the different stages at time *i* where T indicates transpose; *Fecundity matrix (F)* keeps track of the number of seeds produced by individual plants within each genotype category; *Hardy-Weinberg or mating Matrix (H)* distributes new seeds into the different genotype categories according to the Hardy–Weinberg ratios; *Recruitment matrix (R)* determines the fate of all individuals in the model. Model parameters are described in Tables 1 and 2.

Table 2
Crop and weed genotype-related parameters[a].

Parameters	Symbol	Inzen	Sorghum	Soybeans	Fallow	Wheat
PRE planting burndown herbicide program		*Glyphosate*	*Glyphosate*	–	–	*Glyphosate*
Proportion of plants controlled PRE planting	$p_{ctrlPRE}$	0.60 (0.40–0.80)[b]	0.60 (0.40–0.80)	–	–	0.995 (0.99–1.0)
POST planting herbicide program		*Nicosulfuron*	–	*Glyphosate + Clethodim*	*Glyphosate*	–
Proportion of resistant (RR and RS) plants controlled POST planting	$p_{ctrlPOST}$	0	–	0.99 (0.98–1.0)	0.995 (0.99–1.0)	–
Proportion of susceptible (SS) plants controlled POST planting	$p_{ctrlPOST}$	0.975 (0.96–0.99)	–	0.99 (0.98–1.0)	0.995 (0.99–1.0)	–
Pollen-mediated crop to weed gene flow	g	0.08 (0.01–0.16)[c]		–		–
Frequency of the resistance allele (p) in the crop	p_{crop}	1	0	–	–	–
Crop density and competitiveness	dk_c	3.1052 (2.3096–4.1466)[d]			0	

[a] Control estimates were obtained from extension guides and expert opinion (Knezevic et al., 2016; Roeth et al., 1994; Thompson et al., 2016).
[b] Shattercane plants controlled before planting with effective non-ALS herbicides.
[c] g values estimated by Schmidt et al. (2013).
[d] Estimated from R. Werle (unpublished data) for fallow, grain sorghum and soybeans (Fig. 2).

2.4. Stochastic model

Quality (proper weed coverage) and timing (weed size) of herbicide application, and environmental conditions (i.e., temperature, humidity, soil moisture, period between herbicide application and first rainfall) are all factors that may directly impact weed control (p_{ctrl}). To mimic the variability in weed response to herbicide application from year to year we treated p_{ctrl} as a stochastic parameter. During Inzen years, PRE and POST emergence control varied simultaneously (keeping in mind that POST control was genotype dependent), while during the other years (sorghum, soybean, wheat, and fallow) we only varied the effect of a single herbicide application.

For each herbicide application we drew random p_{ctrl} values from a beta distribution (proportion of plants killed by the herbicide), which is commonly used to model mortality (Tenhumberg et al., 2008, 2009). We determined the shape parameters of the beta distribution (α and β) using the estimates of the mean (μ) and variance (σ^2) of the herbicide efficacy:

$$\alpha = -\frac{\mu(\sigma^2 + \mu^2 - \mu)}{\sigma^2} \tag{5}$$

$$\beta = \frac{(\sigma^2 + \mu^2 - \mu)(\mu - 1)}{\sigma^2} \tag{6}$$

For all management strategies we assumed that the standard deviation (σ) for p_{ctrl} is 0.05 because it resulted in a range of p_{ctrl} values that were in close agreement with the range (maximum and minimum) reported in extension publications and expert opinion (Knezevic et al., 2016; Roeth et al., 1994; Thompson et al., 2016). Response to herbicide treatments is typically reported on a visual basis or biomass reduction, but actual plant mortality in response to herbicides is rarely reported. Thus, there is a lack of reported variance around demographic weed response to herbicides (weed mortality) in the weed science literature. We ran the model 500 times for a period of 20 years for each management strategy and recorded the median, which is less sensitive to extreme values than the mean, for p_i, SB_i, and P_i. The 2.5th and 97.5th quantiles for p_i, P_i, and SB_i were recorded and interpreted as the 95% confidence intervals. Our initial conditions for the stochastic simulations were the same as in the deterministic simulations.

3. Results

3.1. Deterministic model

According to our deterministic model, crop and herbicide rotation will play a major role in postponing ALS-resistance evolution while maintaining shattercane population density at low levels over time (Fig. 4). Management strategy ranking at year 13 varied according to the response variable evaluated: p, P, or SB (Table 3). For p_{13}, strat-6 resulted in the lowest frequency of the resistance allele in the population *fb* strat-4, 2, 5, 3, and 1. For P_{13}, strat-6 resulted in the lowest number of plants *fb* strat-5, 4, 3, 2 and 1. For SB_{13}, strat-5 resulted in the lowest number of seeds *fb* strat-6, 3, 4, 2, and 1. According to our results, the continuous use of Inzen (strat-1) represents the worst-case scenario, where the highest value of p and number of P and SB are expected over time. Rotating Inzen with sorghum (strat-2) resulted in the 2nd highest number of P and SB, and quickly led to unacceptable shattercane density. Because sorghum is incorporated every other year in this rotation strategy, flow of the susceptible allele from conventional sorghum plants assists with "delaying" resistance evolution, explaining why p is not as high as in strat-1, 3, and 5, where sorghum is not included. Therefore, rotating Inzen with conventional sorghum also does not seem a very promising strategy after the implementation of the Inzen technology. Overall, the more diverse the system, the lower the frequency of the resistance allele and the population density (SB and P). Strat-6 was our most diverse strategy and resulted in the lowest P_{13} and p_{13} and second lowest SB_{13}. This supports our working hypothesis that more diversified management strategies will lead to more stable cropping systems where evolution of resistance will occur more slowly and population density of shattercane will remain at tolerable levels for a longer period of time. Rotating Inzen to non-sorghum crops (strat-3 through 6) was not a solution to avoid resistance evolution, but was an effective way of keeping shattercane population density at low level while postponing resistance evolution to some extent because effective herbicide options are available to manage this weed during those years (Table 2). There was value in including conventional sorghum as part of the rotation because that takes selection pressure away; however, sorghum should not be planted after Inzen because that will not allow for the control of ALS-resistant plants originated from new individuals produced by resistant plants and individuals produced by plants that received the resistance allele from Inzen sorghum in the previous year.

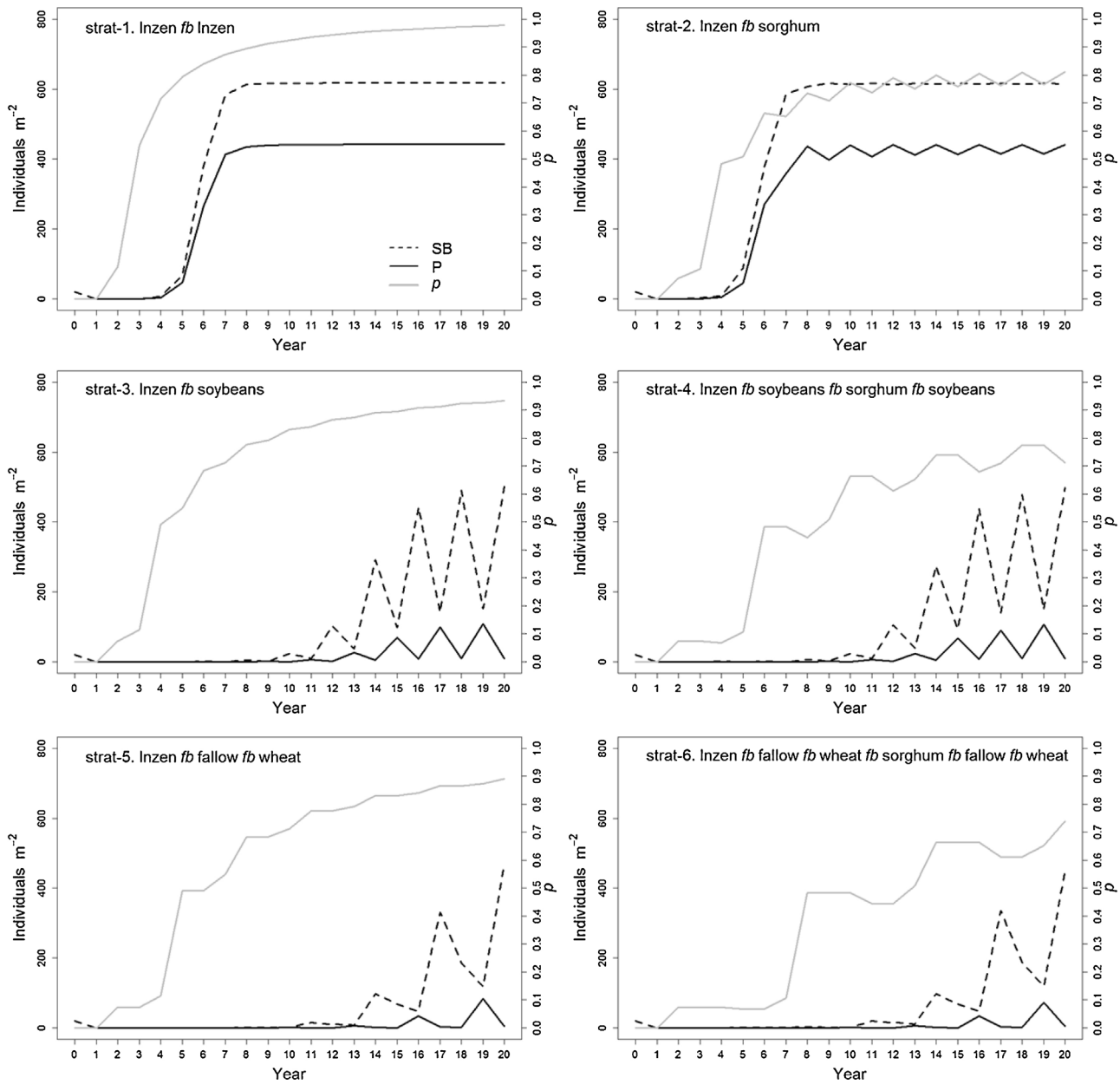

Fig. 4. Total number of established shattercane plants m^{-2} (P) and viable seeds in the seedbank m^{-2} (SB), and frequency of the resistance allele (p) in the population at census over time estimated by our deterministic model for each management strategy (strat-) considered.

3.1.1. Perturbation analysis

According to our perturbation analysis, parameter uncertainty did not change the strategy ranking for p_{13}, P_{13}, and SB_{13} when compared to the deterministic results (Supplementary Tables 1, 2, and 3). This indicates that our model predictions are robust and strategy ranking is not likely to be influenced by parameter uncertainty. Varying parameter values did not have a major impact on p_{13} values over time; however, it did have an impact on P_{13} and SB_{13} values, with s_{pred} being the most sensitive parameter (Supplementary Tables 2 and 3). We assumed predation to be high and one of the first demographic parameters to influence the dynamics of shattercane recruits in our model; therefore, we expected that perturbation around this parameter would have a major impact on model outcome.

3.2. Stochastic model

Corroborating our deterministic outputs, crop and herbicide rotation played a major role in postponing ALS-resistance evolution while maintaining shattercane population density at low levels over time under stochastic conditions (Fig. 5). Strategy ranking also differed for p_{13}, P_{13}, and SB_{13} in our stochastic simulations (Table 3). For p_{13}, strat-6 resulted in the lowest frequency of the resistance allele in the population *fb* strat-4, 2, 5, 3, and 1. For P_{13} and SB_{13}, strat-5 resulted in the lowest number of plants and seeds *fb* strat-6, 4, 3, 2 and 1. Corroborating our deterministic outputs, the continuous use of Inzen (strat-1) will be the worst-case scenario, where the highest value of p number of P and SB are expected. Strat-2 also does not seem very promising under stochastic conditions in terms of P and SB over time. For the remaining strategies (strat-3 through 6), p increased over time on a similar trend observed in the deter-

Table 3
Strategy ranking according to our deterministic predictions, and stochastic median and 95% confidence interval of the frequency of the resistance allele (p), number of established plants m-2 (P), and number of viable seeds in the seedbank m-2 (SB) at census of year 13 for each management strategy (strat-)[a].

	Deterministic		Stochastic	
		p_{13}		
Strategy[b]	Value	2.5th	Median	97.5th
strat-6	0.509	0.183	0.513	0.566
strat-4	0.652	0.546	0.651	0.677
strat-2	0.751	0.736	0.751	0.758
strat-5	0.793	0.74	0.803	0.838
strat-3	0.873	0.851	0.876	0.89
strat-1	0.95	0.944	0.951	0.956
		P_{13}		
Strategy	Value	2.5th	Median	97.5th
strat-6	5.75	1.40×10^{-13}	1.72×10^{-11}	1.22×10^{-7}
strat-5	5.78	1.23×10^{-13}	9.12×10^{-12}	6.53×10^{-8}
strat-4	23.76	3.65×10^{-8}	1.12×10^{-5}	3.87×10^{-2}
strat-3	26.48	3.70×10^{-8}	1.39×10^{-5}	1.59×10^{-1}
strat-2	441.26	315.51	409.88	513.42
strat-1	442.1	329.89	438.5	557.59
		SB_{13}		
Strategy	Value	2.5th	Median	97.5th
strat-5	8.47	1.73×10^{-13}	1.27×10^{-11}	1.05×10^{-7}
strat-6	11.44	3.34×10^{-13}	3.28×10^{-11}	3.04×10^{-7}
strat-3	37.53	5.65×10^{-8}	2.02×10^{-5}	2.47×10^{-1}
strat-4	38.81	6.13×10^{-8}	1.89×10^{-5}	6.99×10^{-2}
strat-2	617.14	604.19	617.1	624.96
strat-1	617.33	605.32	617.15	626.62

[a] We ran the stochastic model 500 times for each management strategy and recorded the median and the 2.5th and 97.5th quantiles for p_{13}, SB_{13}, and P_{13}. The 2.5th and 97.5th quantiles can be interpreted as the 95% confidence interval. Year 13 is used for comparison because all six management strategies included Inzen in that year.
[b] strat-1 = continuous Inzen; strat-2 = Inzen followed by (*fb*) sorghum; strat-3 = Inzen *fb* soybeans; strat-4 = Inzen *fb* soybeans *fb* sorghum *fb* soybeans; strat-5 = Inzen *fb* fallow *fb* wheat; and strat-6 = Inzen *fb* fallow *fb* wheat *fb* sorghum *fb* fallow *fb* wheat.

ministic outcomes; however, SB and P were kept at very low and promising levels over time when compared to strat-1 and 2 (Fig. 5).

3.3. Deterministic versus stochastic outputs

Predictions over time and strategy ranking for *p* were very similar between the deterministic and stochastic outputs (Table 3; Figs. 4 and 5). However, for strat-3 through 6, predictions for P and SB were much lower by the stochastic model when compared to the deterministic model. Under our stochastic simulations, 100% plant control was a possibility; thus, production of new recruits was less likely in a stochastic system, leading to a scenario where if good crop and herbicide rotations are implemented, population density can be kept at low levels, despite the resistance level in the population. For our deterministic simulations, 100% control was never an option and plants would always produce at least a few seeds each generation, which led population density to build up over time. Demographic stochasticity leading to lower population prevalence/density or resulting in higher extinction risk when compared to deterministic models has been commonly reported in the ecological literature (Lloyd et al., 2007; Gotelli and Ellison 2006; Grenfell et al., 1995; Pelosse et al., 2013).

4. Discussion

Crop and herbicide rotation have long been claimed as important tools to postpone the occurrence of resistant weeds (Norsworthy et al., 2012). To be a valuable tool, crop rotation needs to be accompanied by effective herbicide rotation(s) (Neve et al., 2011b). Rotating crops but using the same herbicide will still favor resistant individuals and no benefits will be detected from crop rotation in regards to herbicide-resistance management. Therefore, ALS-inhibiting herbicides should be avoided during non-Inzen years to reduce selection pressure for individuals carrying the resistance trait. Empirical work conducted by Evans et al. (2016) demonstrated the importance of diversity in delaying occurrence of herbicide-resistance in long-term weed management programs. According to these authors, rotation and combination of multiple effective herbicide modes-of action (MOA) should be considered in order to reduce the likelihood of selecting for and favoring resistant weeds. During Inzen and sorghum years, multiple effective MOA for shattercane management after crop planting will not be a possibility; however, multiple MOA should be considered by growers when managing shattercane prior to planting Inzen and conventional sorghum, and during non-sorghum years.

Alternative strategies such as inter-row cultivation, spot treatment, rope wick herbicide application (using non-ALS herbicides), and/or manually eliminating surviving resistant or escape plants before flowering may play an important role in management of ALS-resistance in shattercane during Inzen and sorghum years. Even though these strategies were not considered in our model, they can reduce the likelihood of pollen-mediated gene flow from Inzen to shattercane and reduce seedbank replenishment with resistance alleles (Goulart et al., 2012; Roeth et al., 1994). Shattercane seeds have short longevity in the seedbank (Teo-Sherrell and Mortensen, 2000; Teo-Sherrell et al., 1996) and any effort to manage seedbank replenishment will assist with herbicide-resistance management (Norsworthy et al., 2012).

Our strat-1 through 4 are likely to be adopted in areas where enough water is available for crop production throughout the season (Illinois, Indiana, eastern Kansas, Missouri, and eastern Nebraska). In areas where water becomes a limiting factor for crop production (e.g., western Nebraska and Kansas), strat-1, 2, 5 and 6 will be more common. Thus strat-3 or 4 are not likely to be adopted where strat-5 or 6 will be. According to our simulations, Inzen should be rotated with a non-sorghum crop to postpone ALS-resistance evolution while providing an opportunity to keep shattercane density at low levels, regardless of the geographic region (soybean or wheat production areas). By adopting a diversified approach, growers are also likely to improve management and reduce the occurrence of ALS-resistance in other grasses not related to sorghum (i.e., *Setaria* spp., *Digitaria* spp., *Echinochloa* spp., *Pan-*

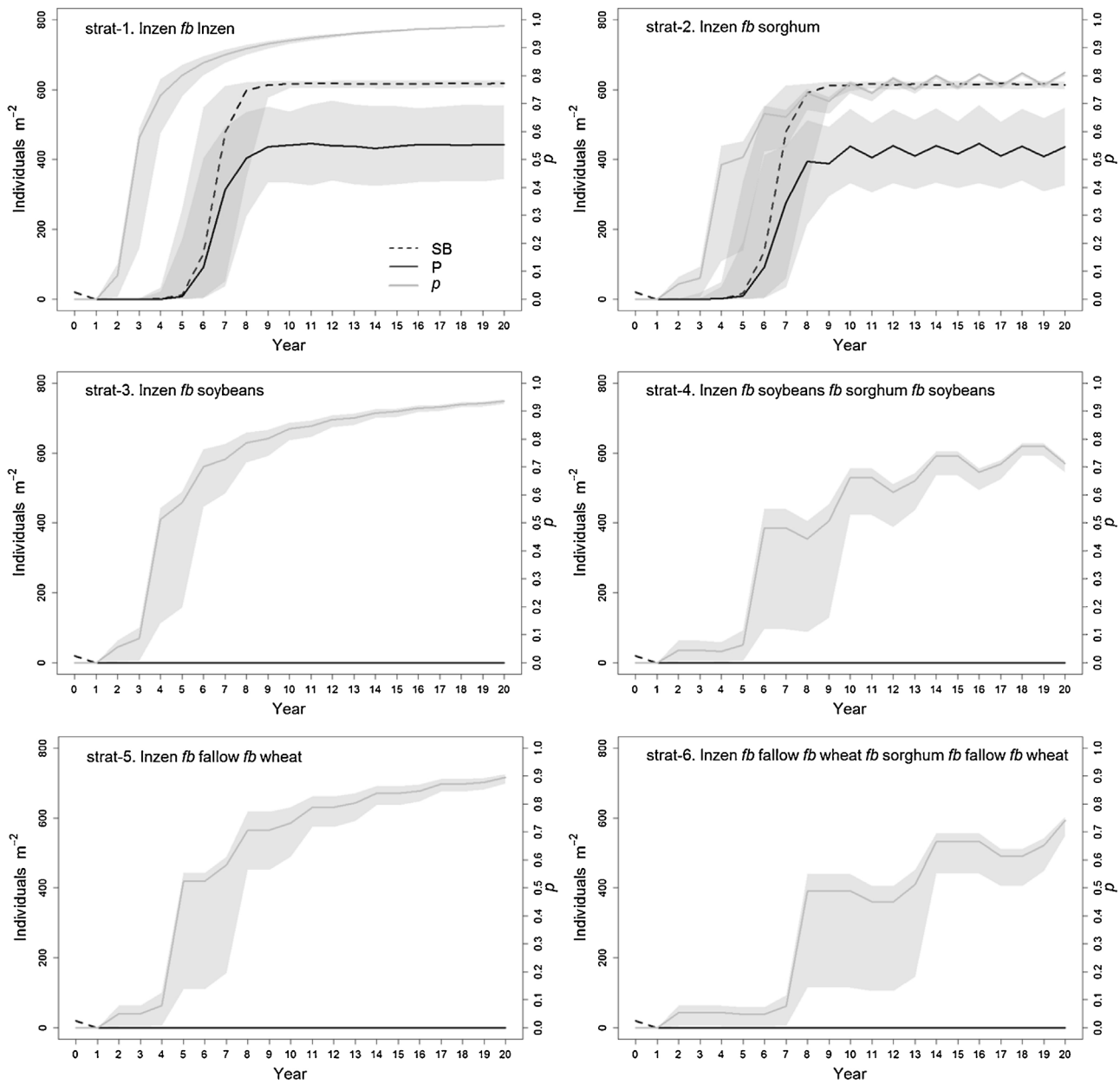

Fig. 5. Total number of established shattercane plants m^{-2} (P) and viable seeds in the seedbank m (SB), and frequency of the resistance allele (p) in the population at census over time estimated by our stochastic model for each management strategy (strat-) considered. Solid lines represent the median of 500 runs and shaded areas represent the 95% confidence interval.

icum spp.), which are the major focus of the technology (Saunders D. W. and K. L. Carlson, personal communication). Glyphosate and clethodim are the alternative herbicides used during non-sorghum years in our model and we don't consider the likelihood of resistance evolution to these herbicides. Shattercane resistance to these herbicide MOA has not been reported in the US yet (Heap, 2016); however, under continuous use of these chemicals, selection for resistance becomes likely.

In our model, we assumed the initial frequency of the ALS-resistance allele (p_0) in the population to be 1×10^{-5} because Inzen had not been previously used and reliance on ALS-inhibiting herbicides had been low. Neve et al. (2011a) assumed the initial frequency of the resistance allele to range from 1×10^{-7} to 5×10^{-6} for their modeling efforts looking at glyphosate resistance evolution. Since ALS-resistance is generally more likely than glyphosate-resistance (Heap, 2016; Tranel et al., 2016), we assume p_0 to be greater than the one used by Neve et al. (2011a). Preston and Powles (2002) evaluated the initial frequency of individuals resistant to ALS herbicides in *Lolium rigidum* populations that were not previously exposed to these herbicides and found it ranging from 1.2×10^{-4} to 5.8×10^{-5}. Anderson et al. (1998) and Dweikat (2012) screened 11,200 and 30,000 shattercane plants from fields previously exposed to ALS-inhibiting herbicides and detected 1 and 4 ALS-resistant plants, respectively. Therefore, ALS-resistant alleles are commonly present in weed populations, even in the absence of selection pressure, suggesting the rapid evolution of resistance when ALS-inhibiting herbicides are adopted (Heap, 2016; Preston and Powles, 2002).

Changing our initial conditions (p_0, P_0 or SB_0) changed the model outcomes; however, management strategy ranking remained the same (data not shown). By having a higher p_0, and P_0 or SB_0, evolution of resistance occurred faster and population density built up

quicker, respectively. Werle et al. (2016) conducted a survey and reported that ALS-resistance persists in corn-soybean production areas where resistance was reported in the early 1990s (Lee et al., 1999), even though ALS-inhibitors have not been widely used to control shattercane for over 15 years. This indicates the lack of a strong fitness cost associated with ALS-resistance, corroborating observations of Davis et al. (2009), Park et al. (2004), and Sibony and Rubin (2003). Thus, Inzen sorghum should probably be avoided in fields with high shattercane infestations and where ALS-resistant weeds have been detected at a high frequency in the past and are still present.

Since no data was available on predation of shattercane seeds under Midwest US conditions, we obtained an estimate for s_{pred} from Bagavathiannan and Norsworthy (2013), who evaluated seed predation of johnsongrass (*Sorghum halepense* L. Pers.; sorghum weedy species that produces seeds that are slightly smaller than shattercane seeds), in the southern part of US. In our model we assumed predation to only impact newly produced seeds. According to Bagavathiannan and Norsworthy (2013), predation by insects and small rodents was more likely to occur after seed dispersal in the fall. During the winter and spring, remaining seeds were mostly incorporated in the soil, probably due to natural soil swelling and shrinking. After incorporation in the soil, predation was significantly reduced and seeds became prone to winter kill and decay due to microbial activity during the season (Bagavathiannan and Norsworthy, 2013). Our simulations have indicated the importance of s_{pred} on shattercane demographics and further research needs to be conducted to quantify this demographic parameter in the US Midwest. Davis et al. (2004) modeling population demographics of giant foxtail (*Setaria faberi* Herrm) under different cropping systems also reported predation as an important parameter influencing weed population growth.

Simulation models have indicated the importance of diversified systems (i.e., crop rotation, herbicide mode of action rotation), and timely application of proper herbicide rates on management of herbicide-resistance (Bagavathiannan et al., 2014; Neve et al., 2011b; Renton et al., 2011). The uniqueness of our model is the incorporation of pollen-mediated crop-to-weed gene flow, which expedited resistance evolution, along with comparison of multiple crop management strategies and their effect on resistance evolution and weed population density over time. Our modeling framework could be used to predict resistance evolution in case grain sorghum with novel herbicide tolerance trait conferred by single gene becomes available in the future. Moreover, our modeling framework could also be adapted for other crops that have weedy relatives (i.e., rice, sunflowers); however, modifications to the current model would be necessary for different systems (i.e., incomplete dominance in case homozygous and heterozygous resistant individuals are not equally tolerant to the herbicide).

ALS-tolerant rice (Clearfield® technology) became commercially available in the US in 2002 (Tan et al., 2005). Clearfield rice allows growers to spray ALS-inhibiting herbicides in the imidazolinone family for management of hard-to-control grasses and some broadleaf weeds in rice. One of the major concerns regarding the introduction of this technology was the likelihood of gene escape to weedy relatives. Red rice (*Oryza sativa* L.) is in the same genus and species as cultivated rice, and outcrossing rate ranging from 0.109 to 0.434% have been reported under field conditions (Burgos et al., 2007). The likelihood of outcrossing in the rice-red rice complex is lower than in the sorghum-shattercane (2–25%; Schmidt et al., 2013), but still significantly higher than naturally occurring mutations conferring resistance (Goulart et al., 2012). The continuous use of Clearfield rice in the US and in other parts of the World has led to an increase in the occurrence and frequency of resistance alleles in red rice populations (Burgos et al., 2008; Roso et al., 2010; Scarabel et al., 2012). Crop and herbicide rotation have been reported by scientists and growers as the most effective way to manage and slow resistance evolution in red rice populations where Clearfield rice has been adopted (Burgos et al., 2008; Roso et al., 2010; Scarabel et al., 2012). ALS-resistant red rice is detected in fields where Clearfield rice has been grown; however, if diversified crop and herbicide rotation strategies have been adopted, resistant individuals are detected at low densities during Clearfield rice years (Burgos et al., 2008; Zhang et al., 2006).

The current recommendations for Clearfield rice are the utilization of certified weed-free seeds, control of weedy rice escapes, and most importantly, crop and herbicide rotation. The BASF (BASF Corporation, Florham Park, NJ) stewardship program recommends planting Clearfield rice only once in three years or not planting Clearfield rice consecutively in two years. These recommendations corroborate our results, where Inzen should not be planted continuously nor rotated only to conventional sorghum, and, most importantly, it must be rotated to non-sorghum crops that allow the use of non-ALS herbicides to keep weed density at low levels. Despite the risks of gene escape to weedy relatives, Clearfield rice has been widely adopted in the US rice belt. For instance, after a decade of its introduction, Clearfeld rice was adopted in 57% of the rice area in Arkansas (J. Hardke, personal communication, 2013). The lessons learned from Clearfield rice growers alongside with our modeling efforts indicate that the Inzen technology is going to last only if sorghum growers adopt a proactive and diversified management approach. In case this technology succeeds at a commercial level, industry interest in grain sorghum may increase and new traits likely become available in the future, making sorghum a more attractive crop throughout the US grain belt. Moreover, if this technology succeeds in the US, it may be considered in other places around the globe where sorghum is a major crop and tools to assist growers with weed management to increase yields are needed (Adenle, 2011).

Acknowledgments

We would like to thank Drs. Kevin Bradley from University of Missouri, William Johnson from Purdue University, and Curtis Thompson from Kansas State University for sharing their expertise on sorghum production and shattercane biology and management. David Saunders, Jeffrey Krumm, and Kenneth Carlson from DuPont® provided valuable information to this research. This project was funded by the United Sorghum Checkoff Program (USCP: CI008-13).

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolmodel.2016.10.023.

References

Adenle, A.A., 2011. Global capture of crop biotechnology in developing world over a decade. J. Genet. Eng. Biotechnol. 9, 83–89.

Anderson, D.D., Roeth, F.W., Martin, A.R., 1998. Discovery of a primisulfuron-resistant shattercane (*Sorghum bicolor*) biotype. Weed Technol. 12, 74–77.

Bagavathiannan, M.V., Norsworthy, J.K., 2013. Postdispersal loss of important arable weed seeds in the midsouthern United States. Weed Sci. 61, 570–579.

Bagavathiannan, M.V., Norsworthy, J.L., Smith, K.L., Neve, P., 2013. Modeling the evolution of glyphosate resistance in barnyardgrass (*Echinochloa crus-galli*) in cotton-based production systems of the midsouthern United States. Weed Technol. 27, 475–487.

Bagavathiannan, M.V., Norsworthy, J.K., Smith, K.L., Neve, P., 2014. Modeling the simultaneous evolution of resistance to ALS- and ACCase-inhibiting herbicides in barnyardgrass (*Echinochloa crus-galli*) in Clearfield® rice. Weed Technol. 28, 89–103.

Burgos, N.R., Scott, R.C., Guice, J.B., 2007. Detectable gene flow in commercial rice fields and impact of Clearfield technology on red rice infestation. In: Proceedings of the 2007 Annual Meeting of the Weed Science Society of America, Champaign, IL: WSSA (Accessed 16 January 2016) http://wssa.net/meeting/meeting-abstracts/.
Burgos, N.R., Norsworthy, J.K., Scott, R.C., Smith, K.L., 2008. Red rice (*Oryza sativa*) status after 5 years of imidazolinone-resistant rice technology in arkansas. Weed Technol. 22, 200–208.
Burnside, O.C., 1965. Seed and Phenological Studies with Shattercane, vol. 220. University of Nebraska Agricultural Experiment Station Bull, Lincoln NE (36 p).
Caswell, H., 2001. Matrix Population Models, 2nd ed. Sinauer Associates Inc., Sunderland, MA.
Davis, A.S., Dixon, P.M., Liebman, M., 2004. Using matrix models to determine cropping systems effects on annual weed demography. Ecol. Appl. 14, 655–668.
Davis, V.M., Kruger, G.R., Stachler, J.M., Loux, M.M., Johnson, W.G., 2009. Growth and seed production of horseweed (*Conyza canadensis*) populations resistant to glyphosate, ALS-inhibiting, and multiple (glyphosate + ALS-inhibiting) herbicides. Weed Sci. 57, 494–504.
DeFelice, M.S., 2006. Shattercane, *Sorghum bicolor* (L.) Moench ssp. *drummondii* (Nees ex steud.) de wet ex davidse-black sheep of the family. Weed Technol. 20, 1076–1083.
Dweikat, I., 2012. ALS mutants sequence in shattercane (*Sorghum bicolor*). In: Proceedings of the 2012 Plant & Animal Genome Conference, San Diego, CA, p. P0099 (Accessed 2 February 2016) https://pag.confex.com/pag/xx/webprogram/Paper3831.html.
Evans, J.A., Tranel, P.J., Hager, A.G., Schutte, B., Wu, C., Chatham, L.A., Davis, A.S., 2016. Managing the evolution of herbicide resistance. Pest Manage. Sci. 72, 74–80.
Firbank, L.G., Watkinson, A.R., 1985. On the analysis of competition within two-species mixtures of plants. J. Appl. Ecol. 22, 503–517.
Gotelli, N.J., Ellison, A.M., 2006. Forecasting extinction risk with nonstationary matrix models. Ecol. Appl. 16, 51–61.
Goulart, I.C.G.R., Pacheco, M.T., Nunes, A.L., Merotto Jr, A., 2012. Identification of origin and analysis of population structure of field-selected imidazolinone-herbicide resistant red rice (*Oryza sativa*). Euphytica 3, 437–447.
Grenfell, B.T., Bolker, B.M., Kleczkowski, A., 1995. Seasonality and extinction in chaotic metapopulations. Proc. R. Soc. B 259, 97–103.
Gressel, J., Segel, L.A., 1978. The paucity of plants evolving genetic resistance to herbicides: possible reasons and implications. J. Theor. Biol. 75, 349–371.
Hans, S.R., Johnson, W.G., 2002. Influence of shattercane (*Sorghum bicolor* (L.) Moench.) interference on corn (*Zea mays* L.) yield and nitrogen accumulation. Weed Technol. 16, 787–791.
Heap, I.M. 2016. The international survey of herbicide resistant weeds. http://weedscience.org/. (Accessed 2 February 2016).
Hedrick, P.W., 2011. Genetics of Populations, fourth ed. Jones & Bartlett (675 p).
Hennigh, D.S., Al-Khatib, K., Tuinstra, M.R., 2010. Postemergence weed control in acetolactate synthase-resistant grain sorghum. Weed Technol. 24, 219–225.
Jasieniuk, M., Maxwell, B.D., 1994. Population genetics and the evolution of herbicide resistance in weeds. Phytoprotection 75, 25–35.
Knezevic, S.Z., Creech, C.F., Jhala, A.J., Klein, R.N., Kruger, G.R., Proctor, C.A., Shea, P.J., Ogg, C.L., 2016. Guide for Weed, Disease, and Insect Management in Nebraska. University of Nebraska-Lincoln Extension, pp. EC130.
Lee, C.D., Martin, A.R., Roeth, F.W., Johnson, B.E., Lee, D.J., 1999. Comparison of ALS inhibitor resistance and allelic interactions in shattercane accessions. Weed Sci. 47, 275–281.
Lloyd, A.L., Zhang, J., Root, A.M., 2007. Stochasticity and heterogeneity in host-vector models. J. R. Soc. Interface 4, 851–863.
Maxwell, B.D., Roush, M.L., Radosevich, S.R., 1990. Predicting the evolution and dynamics of herbicide resistance in weed populations. Weed Technol. 4, 2–13.
Neve, P., Norsworthy, J.K., Smith, K.L., Zelaya, I.A., 2011a. Modelling evolution and management of glyphosate resistance in *Amaranthus palmeri*. Weed Res. 51, 99–112.
Neve, P., Norsworthy, J.K., Smith, K.L., Zelaya, I.A., 2011b. Modeling glyphosate resistance management strategies for Palmer amaranth (*Amaranthus palmeri*) in cotton. Weed Technol. 25, 335–343.
Neve, P., 2008. Simulation modelling to understand the evolution and management of glyphosate resistance in weeds. Pest Manage. Sci. 64, 392–401.
Norsworthy, J., Ward, S., Shaw, D., Llewellyn, R., Nichols, R., Webster, T., Bradley, K., Frisvold, G., Powles, S., Burgos, N., Witt, W., Barrett, M., 2012. Reducing the risks of herbicide resistance: best management practices and recommendations. Weed Sci., 31–62, Special Issue.
Paterson, A.H., 2008. Genomics of sorghum. Int. J. Plant Genom., 362451.
Park, K.W., Mallory-Smith, C.A., Ball, D.A., Muellar-Warrant, G.W., 2004. Ecological fitness of acetolactate synthase inhibitor-resistant and -susceptible downy brome (*Bromus tectorum*) biotypes. Weed Sci. 52, 768–773.
Pelosse, P., Kribs-Zaleta, C.M., Ginoux, M., Rabinovich, J.E., Gourbiere, S., Menu, F., 2013. Influence of vectors' risk-spreading strategies and environmental stochasticity on the epidemiology and evolution of vector-borne diseases: the example of Chagas' disease. PLoS One 8 (8), e70830.
Preston, C., Mallory-Smith, C.A., 2001. Biochemical mechanisms, inheritance, and molecular genetics of herbicide resistance in weeds. In: Powles, S.B., Shaner, D.L. (Eds.), Herbicide Resistance in World Grains. CRC Press, Boca Raton, Florida, USA, pp. 23–60.
Preston, C., Powles, S.B., 2002. Evolution of herbicide resistance in weeds: initial frequency of target site-based resistance to acetolactate synthase-inhibiting herbicides in *Lolium rigidum*. Heredity 88, 8–13.
Renton, M., Diggle, A., Manalil, S., Powles, S., 2011. Does cutting herbicide rates threaten the sustainability of weed management in cropping systems? J. Theor. Biol. 283, 14–27.
Roeth, F., Martin, A., Klein, R.N., 1994. Shattercane and Its Control. University of Nebraska-Lincoln Extension (G94-1205) http://digitalcommons.unl.edu/extensionhist/1503.
Roso, A.C., Merotto Jr, A., Delatorre, C.A., Menezes, V.G., 2010. Regional scale distribution of imidazolinone herbicide-resistant alleles in red rice (Oryza sative L.) determined through SNP markers. Field Crops Res. 119, 175–182.
Roughgarden, J., 1998. Primer of Ecological Theory. Prentice Hall, Upper Saddle River, New Jersey.
Sahoo, L., Schmidt, J.J., Pedersen, J.F., Lee, D.J., Lindquist, J.L., 2010. Growth and fitness components of wild × cultivated *Sorghum bicolor* (Poaceae) hybrids in Nebraska. Am. J. Bot. 97, 1610–1617.
Scarabel, L., Cenghialta, C., Manuello, D., Sattin, M., 2012. Monitoring and management of imidazolinone-resistant red rice (*Oryza sativa* L. var. *sylvatica*) in Clearfield® Italian Paddy Rice. Agronomy 2, 371–383.
Schmidt, J.J., Pedersen, J.F., Bernards, M.L., Lindquist, J.L., 2013. Rate of shattercane × sorghum hybridization in situ. Crop Sci. 53, 1677–1685.
Sibony, M., Rubin, B., 2003. The ecological fitness of ALS-resistant *Amaranthus retroflexus* and multiple-resistant *Amaranthus blitoides*. Weed Res. 43, 40–47.
Tan, S., Evans, R.R., Dahmer, M.L., Singh, B.K., Shaner, D.L., 2005. Imidazolinone-tolerant crops: history: current status and future. Pest Manage. Sci. 61, 246–257.
Tenhumberg, B., Louda, S.M., Eckberg, J.O., Takahashi, M., 2008. Monte Carlo analysis of parameter uncertainty in matrix models for the weed *Cirsium vulgare*. J. Appl. Ecol. 45, 438–447.
Tenhumberg, B., Tyre, A., Rebarber, R., 2009. Model complexity affects transient population dynamics following a dispersal event: a case study with pea aphids. Ecology 90, 1878–1890.
Teo-Sherrell, C.P.A., Mortensen, D.A., 2000. Fates of buried *Sorghum bicolor* ssp. *drummondii* seed. Weed Sci. 48, 540–554.
Teo-Sherrell, C.P.A., Mortensen, D.A., Keaton, M.E., 1996. Fates of weed seeds in soil: a seeded core method of study. J. Appl. Ecol. 33, 1107–1113.
Thompson, C.R., Peterson, D.E., Fick, W.H., Stahlman, P.W., Slocombe, J.W., 2016. Chemical Weed Control for Field Crops, Pastures, Rangeland, and Noncropland. Kansas State University Agricultural Experiment Station and Cooperative Extension Service, pp. 1126.
Tranel, P.J., Wright, T.R., Heap I.M., 2016. Mutations in herbicide-resistant weeds to ALS inhibitors. http://www.weedscience.com. (Accessed 2 February 2016).
Tuinstra M.R., Al-Khatib K., 2008. Acetolactate synthase herbicide resistant sorghum. U.S patent application 20080216187. Alexandria, VA : U.S. patent and trademark office.
USDA-NASS, 2016. United States Department of Agriculture-National Agricultural Statistics Service. http://www.nass.usda.gov/. (Accessed 3 February 2016).
Werle, R., Bernards, M.L., Sattler, S.E., Lindquist, J.L., 2013. Susceptibility of shattercane x ALS-resistant sorghum hybrids and their parents to rimsulfuron and nicosulfuron. Baltimore, BD In: Proceedings of the Weed Science Society of America Annual Meetings, 53, p. 331.
Werle, R., Jhala, A., Yerka, M.K., Dille, J.A., Lindquist, J.L., 2016. Distribution of herbicide-resistant shattercane and johnsongrass populations in sorghum production areas of Nebraska and northern Kansas. Agron. J. 108, 321–328.
Werle, R., Sandell, L.D., Buhler, D.D., Hartzler, R.G., Lindquist, J.L., 2014a. Predicting emergence of 23 summer annual weed species. Weed Sci. 62, 267–279.
Werle, R., Schmidt, J.J., Laborde, J., Tran, A., Creech, C., Lindquist, J.L., 2014b. Shattercane X ALS-resistant sorghum F1 hybrid and shattercane interference in ALS-resistant sorghum. J. Agric. Sci. 6, 159–165.
Wright, S., 1969. Evolution and the Genetics of Populations, vol. II. University of Chicago Press, Chicago, IL (520 p).
Zhang, W., Linscombe, S.D., Webster, E., Tan, S., Oard, J., 2006. Risk assessment of the transfer of imazethapyr herbicide tolerance from Clearfield rice to red rice (*Oryza sativa*). Euphytica 152, 75–86.