

Herbicide Resistance in Jointed Goatgrass (*Aegilops cylindrica*): Simulated Responses to Agronomic Practices¹

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Abstract: A population model was constructed to simulate the development of imazamox-resistant jointed goatgrass (AEGCY) in imazamox-resistant (Clearfield[®]) wheat. The model computed changes in the surface and in the buried AEGCY seed banks for both resistant and susceptible biotypes. Simulations started with an initial density of 1,000 susceptible and zero resistant seeds/m² in each seed bank. Simulation of continuous, no-till Clearfield wheat production resulted in rapid development of resistant AEGCY without hybridization with wheat and in extremely rapid resistance development with hybridization. In less than 10 yr, the resistant population was growing exponentially in both simulations. Adding a fallow year with tillage into the simulated rotation did not substantially slow down the appearance of resistance but did delay the rate of resistant population increase by several orders of magnitude over 10 yr. Alternating Clearfield and a nonresistant winter wheat in combination with fallowing prevented the establishment of a significant resistant AEGCY population and prevented the susceptible seed population from increasing exponentially. These projections suggest that imazamox-resistant wheat can be a tool for managing AEGCY populations especially if combined with rotations that include fallow and crops other than Clearfield winter wheat.

Nomenclature: Imazamox; jointed goatgrass, *Aegilops cylindrica* Host #³ AEGCY; winter wheat, *Triticum aestivum* L. Clearfield[®].

Additional index words: Crop rotation, pollen flow, population model, resistance management.

Abbreviations: ALS, acetolactate synthase; BSB, buried seed bank; DSP, local seed dispersal; EST, established plant; MAT, mature plant; PRD, seed production; SDL, seedling; SSB, surface seed bank.

INTRODUCTION

Jointed goatgrass (AEGCY) cannot be controlled selectively in winter wheat (Ball et al. 1999; Maxwell 1999). Only extended fallow periods or rotations that include summer annual crops can reduce its seed bank (Donald 1991). A herbicide-resistant wheat variety would provide selectivity that is otherwise unavailable (Ball et al. 1999). Repeatedly using herbicides with the same site of action, however, may lead to the rapid development of herbicide resistance in the target weed population (Jasieniuk et al. 1996).

Herbicides, such as imazamox, that inhibit the aceto-

lactate synthase (ALS) enzyme have an increased risk of selecting for resistant weed populations because several mutations of the enzyme produce resistant biotypes (Saari et al. 1994). In addition, gene flow can transfer herbicide resistance to susceptible plants, both within a species and among closely related species (Jasieniuk et al. 1996; Zemetra et al. 1998). For example, canola (*Brassica napus* L.), a crop resistant to glufosinate, has produced a herbicide-resistant hybrid with birdrape mustard (*Brassica rapa* L.) (Brown and Brown 1996). Multiple-resistant volunteer canola plants were produced in Canada under natural field conditions (Hall et al. 2000). The resistance was the result of cross-pollination among glufosinate-, glyphosate-, and imidazolinone-resistant canola volunteers. Subsequent crossing of the volunteers produced two plants that were resistant to all three herbicides. Transfer of ALS-herbicide resistance between two weed species, Palmer amaranth (*Amaranthus palmeri* S.Wats.) and common waterhemp (*Amaranthus rudis* Sauer), created resistant hybrids capable of backcrossing (Wetzel et al. 1999).

Wheat and AEGCY can form a low-frequency, fertile

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³ Letters following this symbol are a WSSA-approved computer code from *Composite List of Weeds*, Revised 1989. Available only on computer disk from WSSA, 810 East 10th Street, Lawrence, KS 66044-8897.

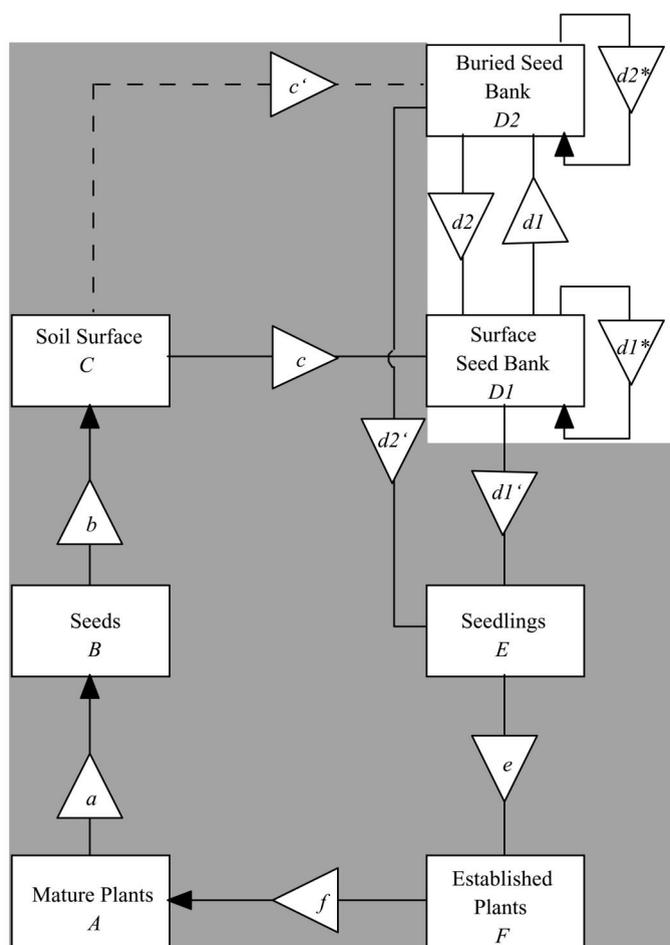


Figure 1. Conceptual model of population dynamics for jointed goatgrass. Stages are indicated in upper case italics (*X*); transition rates are indicated in lower case (*x*). The stages are as labeled, and transition rates are as follows: *a*: PRD, *b*: local dispersal, *c*: predation survival, *c'*: seed burial, *d1*: movement to BSB, *d1**: SSB survival, *d1'*: SSB germination, *d2*: movement to SSB, *d2**: BSB survival, *d2'*: BSB germination, *e*: SDL establishment, and *f*: maturation. Shaded areas indicate transitions that occur within a year; the unshaded portions indicate transitions occurring among years. Dashed lines indicate postulated transitions.

hybrid whose fertility increases when back-crossed with AEGCY (Zemetra et al. 1998). The potential for hybridization between herbicide-resistant winter wheat and AEGCY in the field needs critical evaluation because two naturally occurring herbicide-resistant hybrids have been found in a research plot (Seefeldt et al. 1998). Moreover, the effect of introducing herbicide-resistant winter wheat in combination with other weed control measures for management of herbicide-resistant AEGCY should be explored. Evaluating resistance evolution with field studies would take several years; however, model simulations offer an opportunity to estimate the likelihood of resistance development. Simulations provide the only timely method of assessing resistance

management strategies before field-scale problems develop.

Quantitative models have been used to predict the effects of management strategies on blackgrass (*Alopecurus myosuroides* Huds.) (Cavan et al. 2000) and wild oat (*Avena fatua* L.) (Cavan and Moss 2001). Population dynamics and genetic models have been linked to demonstrate that both fitness and gene flow were important in the evolution of herbicide resistance within a weed population (Maxwell et al. 1990). A bioeconomic model that evaluated wheat crop loss from AEGCY population and economic parameters predicted that crop rotation would maximize economic return while reducing the AEGCY seed bank. (Maxwell 1999).

This project was undertaken to assess the impact of agronomic practices on the development and persistence of ALS-herbicide resistance in AEGCY populations. We developed a quantitative model, based on management tactics for AEGCY population dynamics, and projected the growth of herbicide-resistant AEGCY populations under several crop management scenarios.

Data Underlying the Model. Information on AEGCY biology for use in model parameterization is available from the literature. The plant produces 3 to 12 spikelets per spike and up to 100 tillers per plant, depending on the competitive conditions (Donald and Ogg Jr. 1991). Averaged over two cropping seasons, AEGCY produced 139 spikelets per plant in a conventional winter wheat production system (Anderson 1997). Jointed goatgrass is more competitive than winter wheat under stressful conditions of drought, high temperature, or both (Fleming et al. 1988).

Freshly harvested AEGCY seeds are dormant (Gleichsner et al. 1987), but germination increases to between 52 and 75% 1 mo after harvest (Gealy 1988). Seeds emerged continuously for 10 wk after an August sowing with a bimodal distribution of emergence frequency (Anderson 1998). Germination of AEGCY seed on the soil surface can be as high as 96% (Donald and Ogg Jr. 1991). Surface seed viability drops to 10% or less after 2 yr, but seeds can remain viable in the buried seed bank (BSB) for up to 5 yr (Donald and Zimdahl 1987).

Cropping sequence affects the composition of weed species (Ball 1992). A 3-yr rotation of winter wheat, fallow, and spring crops reduced AEGCY infestations more effectively than a 2-yr rotation (Daugovish et al. 1999). The types of rotations used did not differ in their effect. Jointed goatgrass control of 95 to 100% can be

achieved by using herbicides in fallow (Westra 1989; Wiese et al. 1995).

Mechanical control of AEGCY can be substantial. In Colorado, tillage during fallow with a sweep or disk resulted in 75% control, and in 95% control with moldboard plowing. Moldboard plowing also reduced AEGCY spikelet production (Franetovich et al. 1998). This reduction likely resulted from moving seeds from the surface seed bank (SSB), where they readily germinate, and placing them deeper in the soil where there would be reduced germination (Donald and Ogg Jr. 1991; Maxwell 1999). Shallow disking leaves over 70% of the AEGCY spikes in the SSB (Donald and Zimdahl 1987; Maxwell 1999).

MATERIALS AND METHODS

We developed a quantitative model for AEGCY population dynamics. Stages in the initial model included buried seed bank (BSB), local seed dispersal (DSP), es-

tablished plants (EST), mature plants (MATs), seed production (PRD), seedlings (SDL), and SSB (Figure 1). The SSB was defined as seeds in the top 5 cm of soil, where emergence is greatest (Maxwell 1999; Morrow et al. 1982), and the BSB was defined as seeds at > 5 cm in depth. Because the time step for population change was 1 yr, the model was reduced to include only the stages where transitions occurred between years, i.e., the SSB and the BSB (Figure 2) (Hanson 2000). The revised model also contained explicit representation for both ALS-herbicide-resistant (*r*) and -susceptible (*s*) AEGCY biotypes in the population (Figure 2).

Population changes over the course of the cropping season were simulated with a transition matrix. Transition rates for this model were determined from the literature or estimated where no literature values were available (Table 1). Transition matrix (1) shows individual transition rates among all stages of the model in Figure 2.

	<i>SSB_{s+1}</i>	<i>BSB_{s+1}</i>	<i>SDL_{s+1}</i>	<i>EST_{s+1}</i>	<i>MAT_{s+1}</i>	<i>PRD_{s+1}</i>	<i>DSP_{s+1}</i>	<i>SSB_{r+1}</i>	<i>BSB_{r+1}</i>	<i>SDL_{r+1}</i>	<i>EST_{r+1}</i>	<i>MAT_{r+1}</i>	<i>PRD_{r+1}</i>	<i>DSP_{r+1}</i>
<i>SSB_s</i>	<i>d1_s*'</i>	<i>d2_s*'</i>	0	0	0	0	<i>c_s</i>	0	0	0	0	0	0	0
<i>BSB_s</i>	<i>d1_s</i>	<i>d2_s</i>	0	0	0	0	<i>c_s'</i>	0	0	0	0	0	0	0
<i>SDL_s</i>	<i>d_s</i>	<i>d_s'</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>EST_s</i>	0	0	<i>e_s</i>	0	0	0	0	0	0	0	0	0	0	0
<i>MAT_s</i>	0	0	0	<i>f_s</i>	0	0	0	0	0	0	0	0	0	0
<i>PRD_s</i>	0	0	0	0	<i>a_s</i>	0	0	0	0	0	0	<i>a_s'</i>	0	0
<i>DSP_s</i>	0	0	0	0	0	<i>b_s</i>	0	0	0	0	0	0	0	0
<i>SSB_r</i>	0	0	0	0	0	0	0	<i>d1_r*'</i>	<i>d2_r</i>	0	0	0	0	<i>c_r</i>
<i>BSB_r</i>	0	0	0	0	0	0	0	<i>d1_r</i>	<i>d2_r*'</i>	0	0	0	0	<i>c_r'</i>
<i>SDL_r</i>	0	0	0	0	0	0	0	<i>d_r</i>	<i>d_r'</i>	0	0	0	0	0
<i>EST_r</i>	0	0	0	0	0	0	0	0	0	<i>e_r</i>	0	0	0	0
<i>MAT_r</i>	0	0	0	0	0	0	0	0	0	0	<i>f_r</i>	0	0	0
<i>PRD_r</i>	0	0	0	0	<i>a_r'</i>	0	0	0	0	0	0	<i>a_r</i>	0	0
<i>DSP_r</i>	0	0	0	0	0	0	0	0	0	0	0	0	<i>b_r</i>	0

(1)

Although this transition matrix explicitly represents the interaction among the rates, it would not accurately simulate the population's development because some transitions occur within years, and others between them. Therefore, transitions that occurred within years were multiplied together in transition matrix (2). This final matrix thus included only the SSB and BSB stages for the susceptible and resistant biotypes but contained transition rates for all the stages in Figure 1.

	<i>SSB_{s+1}</i>	<i>BSB_{s+1}</i>	<i>SSB_{r+1}</i>	<i>BSB_{r+1}</i>
<i>SSB_s</i>	<i>d1_s*' + d1_s' · e_s · f_s · a_s · b_s · c_s</i>	<i>d2_s + d2_s' · e_s · f_s · a_s · b_s · c_s</i>	<i>d1_r' · e_r · f_r · a_r · b_r · c_r</i>	<i>d2_r' · e_r · f_r · a_r' · b_r · c_s</i>
<i>BSB_s</i>	<i>d1_s + d1_s' · e_s · f_s · a_s · b_s · c_s'</i>	<i>d2_s*' + d2_s' · e_s · f_s · a_s · b_s · c_s'</i>	<i>d1_r*' · e_r · f_r · a_s' · b_s · c_s'</i>	<i>d2_r' · e_r · f_r · a_s' · b_s · c_s'</i>
<i>SSB_r</i>	<i>d1_s' · e_s · f_s · a_r' · b_r · c_r</i>	<i>d2_s' · e_s · f_s · a_r' · b_r · c_r</i>	<i>d1_r*' + d1_r' · e_r · f_r · a_r · b_r · c_r</i>	<i>d2_r + d2_r' · e_r · f_r · a_r · b_r · c_r</i>
<i>BSB_r</i>	<i>d1_s' · e_s · f_s · a_r' · b_r · c_r'</i>	<i>d2_s' · e_s · f_s · a_r' · b_r · c_r'</i>	<i>d1_r + d1_r' · e_r · f_r · a_r · b_r · c_r'</i>	<i>d2_r*' + d2_r' · e_r · f_r · a_r · b_r · c_r'</i>

(2)

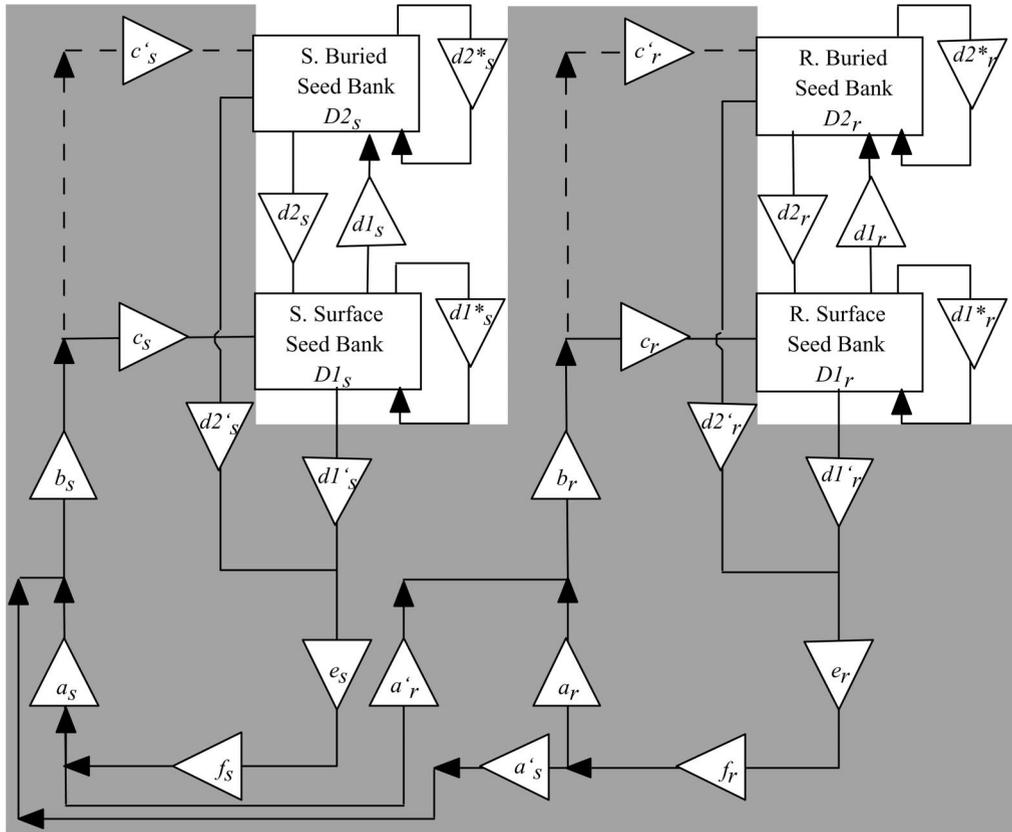


Figure 2. Conceptual model of population dynamics for jointed goatgrass susceptible (*s*) and resistant (*r*) biotypes. Stages are indicated in upper case italics (*X*); transition rates are indicated in lower case (*x*). The stages are as labeled, and transition rates are as follows: *a*: PRD, *b*: local dispersal, *c*: predation survival, *c'*: seed burial, *d1*: movement to BSB, *d1**: SSB survival, *d1'*: SSB germination, *d2*: movement to SSB, *d2**: BSB survival, *d2'*: BSB germination, *e*: SDL establishment, *f*: maturation. Shaded areas indicate transitions that occur within a year, whereas the unshaded portions indicate transitions occurring among years. Dashed lines indicate postulated transitions.

In some cases, the transition rates used in transition matrices (1) and (2) are determined by equations. The SSB survival in resistant and susceptible populations, $d1_{(x)}^*$, is the difference between the total SSB, its losses from germination, and movement to the BSB. It is represented by the equation

$$d1_{(x)}^* = 1 - d1_{(x)} - d1'_{(x)}, \quad (3)$$

where *x* is either the *s* or the *r* population. Similarly, BSB survival, $d2_{(x)}^*$, is expressed by the equation

$$d2_{(x)}^* = 1 - d2_{(x)} - d2'_{(x)} - 0.25, \quad (4)$$

where the final value (0.25) is an assumed annual seed mortality rate. The transition rate for SDL establishment, $e_{(x)}$, is given by the equation

$$e_{(x)} = \alpha e_{(x)} \times \beta e_{(x)} \times \gamma e_{(x)}, \quad (5)$$

where the values of $\alpha e_{(x)}$, $\beta e_{(x)}$, and $\gamma e_{(x)}$ are taken from Table 1. This equation accounts for the multiplicative

effect of natural mortality (α), herbicide-induced mortality (β), and crop competition (γ) on SDL establishment. Individual transition rates could vary in this model with different agronomic practices. For example, the rate of seed movement from SSB to BSB was greatest with moldboard plowing, intermediate with chisel plowing, and negligible with no-till (Table 1).

Four management scenarios were simulated to determine how the proportions of AEGCY biotypes in the herbicide-resistant and -susceptible seed banks were affected (Table 2). All the scenarios had some common characteristics. First, the initial susceptible population was 1,000 seeds/m² in both SSB and BSB, which is in the same order of magnitude (ca. 4,800 seeds/m²) as the population estimated by Donald and Zimdahl (1987). There were no ALS-resistant seeds in the initial population. Second, herbicide resistance was assumed to be a dominant trait controlled by a single gene mutation that occurred 1:1,000,000 times (C.A.M.-S., personal communication). Third, it was assumed that susceptible and

Table 1. Effects of agronomic practices on jointed goatgrass transition rates.

Agronomic operation	Tactic ^a	Transition ^b name	Rate	Citation ^c	
Tillage	Plow	<i>d</i>	0.28	Maxwell 1999	
	Chisel	<i>d1</i>	0.14	Maxwell 1999	
	No-till	<i>d1</i>	0.34–0.00	<i>Est.</i>	
	N/A	<i>d1</i> *	0.06	<i>Est.</i>	
	Plow	<i>d1'</i>	0.67	Maxwell 1999	
	Chisel	<i>d1'</i>	0.67	Maxwell 1999	
	No-till	<i>d1'</i>	0.67	Maxwell 1999	
	Plow	<i>d2</i>	0.09	Maxwell 1999	
	Chisel	<i>d2</i>	0.00	<i>Est.</i>	
	No-till	<i>d2</i>	0.00	<i>Est.</i>	
	N/A	<i>d2</i> *	0.67–0.59	<i>Est.</i>	
	Plow	<i>d2'</i>	0.08	Maxwell 1999	
	Chisel	<i>d2'</i>	0.08	Maxwell 1999	
	No-till	<i>d2'</i>	0.08	Maxwell 1999	
Weed control	ALS herbicide	βe_s	0.05	<i>Est.</i>	
	Other herbicide	βe_s	1.00	<i>Est.</i>	
	Crop condition (excellent)	γe_s	0.75	<i>Est.</i>	
	Crop condition (good)	γe_s	1.00	<i>Est.</i>	
	Crop condition (poor)	γe_s	1.50	<i>Est.</i>	
	None	αe_s	0.48	Maxwell 1999	
	ALS herbicide	βe_r	1.00	<i>Est.</i>	
	Other herbicide	βe_r	1.00	<i>Est.</i>	
	Crop condition (excellent)	γe_r	0.75	<i>Est.</i>	
	Crop condition (good)	γe_r	1.00	<i>Est.</i>	
	Crop condition (poor)	γe_r	1.50	<i>Est.</i>	
	None	αe_r	0.48	Maxwell 1999	
	Self thinning	Crop competition	<i>f_s</i>	0.9	<i>Est.</i>
		None	<i>f_s</i>	0.95	<i>Est.</i>
Crop competition		<i>f_r</i>	0.9	<i>Est.</i>	
None		<i>f_r</i>	0.95	<i>Est.</i>	
Seed production	N/A	<i>a_s</i>	140	Anderson 1997	
	N/A	<i>a'_s</i>	140	Anderson 1997	
	N/A	<i>a_r</i>	140	Anderson 1997	
	N/A	<i>a'_r</i>	140	Anderson 1997	
Local dispersal	N/A	<i>b</i>	1.00	<i>Est.</i>	
Seed survival (mortality)	N/A	<i>c</i>	0.25	<i>Est.</i>	
Seed burial	N/A	<i>c'</i>	0.00	<i>Est.</i>	

^a Transition rates with only one value are indicated as N/A. ALS, acetolactate synthase.

^b Transition rate names correspond to those in Figure 1.

^c Estimated transition rates are indicated *Est.*

resistant biotypes did not differ in fitness; therefore, all the characteristics of the two were the same except for ALS-herbicide tolerance. Fourth, imazamox was presumed to provide 95% AEGCY control and to have no adverse effects on resistant winter wheat (Ball et al. 1999).

In scenario 1, continuous no-till Clearfield winter wheat was the sole cropping practice. Hybridization be-

tween AEGCY and wheat was not allowed in this scenario. In scenario 2, AEGCY and wheat hybridized at a rate of 0.10%, with all other aspects and transition rates remaining the same as in scenario 1. Hybridization was assumed to occur in all subsequent scenarios as well. The model does not take into account that there may be reduced PRD on the hybrids and subsequent generations (Zemetra et al. 1998). Additionally, the stability of the herbicide-resistant gene in backcross generations is not known at this time.

A wheat-fallow-wheat rotation was used in scenario 3. In this scenario, Clearfield winter wheat was planted and sprayed with imazamox for weed control each crop year. Chisel plow-based tillage operations and application of non-ALS herbicides were simulated for AEGCY management in the fallow year. Control of AEGCY from fallow operations was assumed to be 100%.

Table 2. A summary of crop rotation and tillage conditions, and jointed goatgrass hybridization effects used in model simulation scenarios.

Scenario	Tillage	Crop rotation	Hybridization
1	No-till	Clearfield–Clearfield	No
2	No-till	Clearfield–Clearfield	Yes
3	Chisel plow	Clearfield–fallow–Clearfield–fallow	Yes
4	Chisel plow	Clearfield–fallow–standard wheat–fallow	Yes

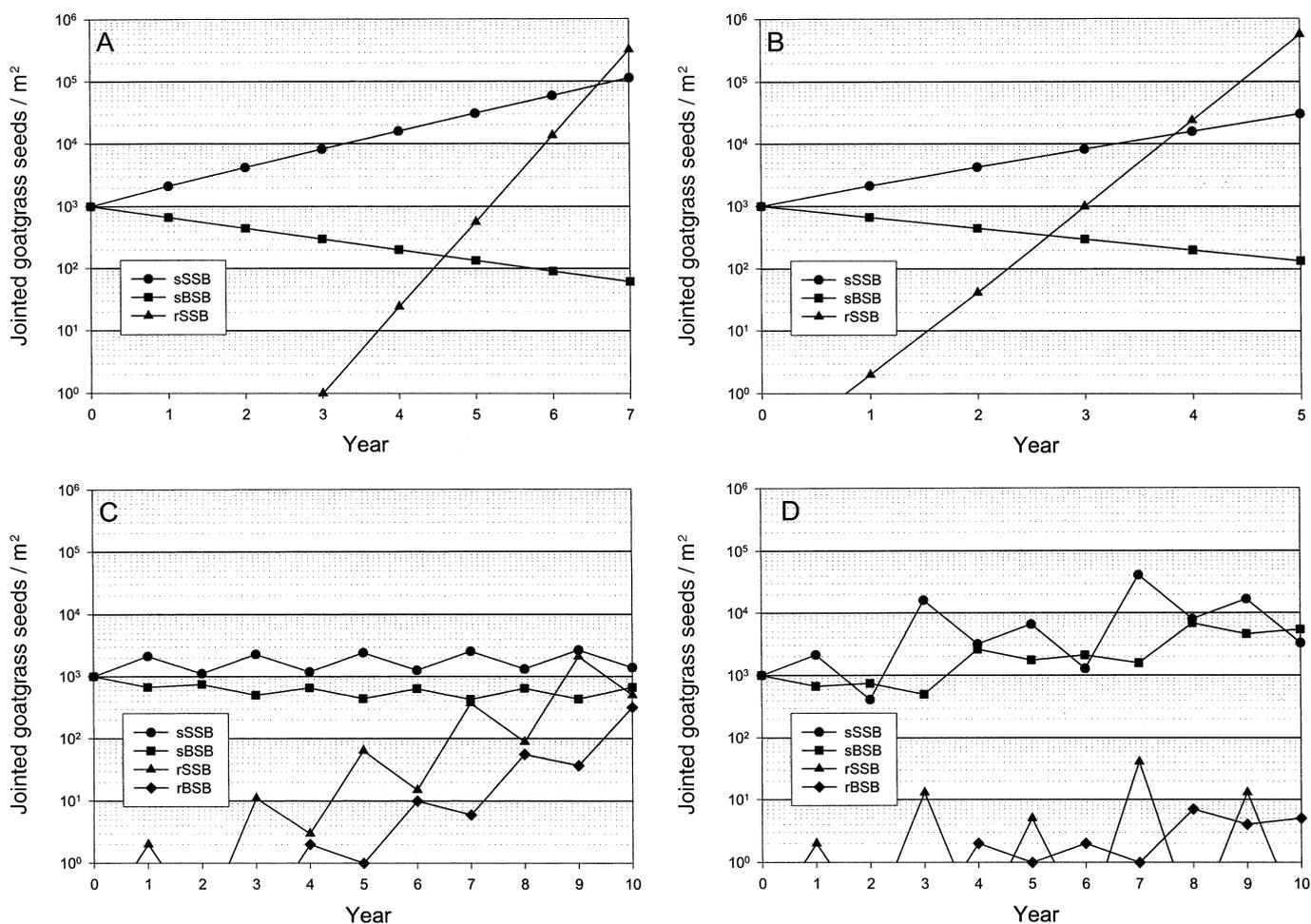


Figure 3. Simulated population change in jointed goatgrass seed over (A) 7 yr with the scenario 1 cropping pattern, (B) 5 yr with the scenario 2 cropping pattern and hybridization between AEGCY and wheat, (C) 10 yr with the scenario 3 cropping pattern, and (D) 10 yr with the scenario 4 cropping pattern. Scenarios are described in Table 2. Abbreviations: sSSB, susceptible surface seed bank; sBSB, susceptible buried seed bank; rSSB, resistant, surface seed bank; rBSB, resistant, buried seed bank.

In scenario 4, which tested the effectiveness of a resistance management strategy, Clearfield and susceptible winter wheat varieties were alternated in a wheat–fallow rotation. Clearfield winter wheat was planted in year 1, the land was fallowed in year 2, and imazamox-susceptible wheat was planted in year 3, followed by another fallow year. This pattern was repeated for a total of 10 yr. Imazamox was applied to the Clearfield variety, and non-ALS herbicides were applied to the fallow and non-herbicide resistant winter wheat. Chisel plowing during the fallow period with 100% control of AEGCY was used in this simulation as well.

RESULTS AND DISCUSSION

The model, as described, is primarily designed to simulate the time of resistance development, and not the absolute magnitude of AEGCY populations. No attempt

was made to account for population-limiting factors such as intra- and interspecific plant competition. Refinement of the model to include improved AEGCY population-limiting factors is necessary to predict more accurately the changes in the densities of susceptible AEGCY populations. However, the amount of time required for the development of a resistant AEGCY population is the primary information obtained from the model simulations.

Although herbicide resistance occurred in all the four tested scenarios, the rates of development of imazamox resistance in the AEGCY populations differed greatly. In scenario 1, herbicide resistance (one or more *r* seeds/m²) developed by year 4, and by year 7 the resistant portion of the SSB was greater than the susceptible component (Figure 3A). In this simulation, the seed number of both biotypes in the SSB continued to increase with time. Population-limiting factors, such as intraspecific competition, and herbicide injury to the surviving AEGCY

plants would have a greater negative impact on the susceptible AEGCY populations than is shown in this scenario. However, the rate of increase in the resistant AEGCY population is the key point to be considered in this simulated scenario. In addition, a resistant BSB did not develop in scenario 1 because the no-till management system did not bury the AEGCY seeds.

In scenario 2, the same agronomic regime of continuous Clearfield winter wheat was used, but hybridization between Clearfield winter wheat and the AEGCY was factored into the model. In this simulation, a resistant population developed in the SSB by the end of year 1 (Figure 3B), and the resistant portion of the AEGCY population was greater than the susceptible one by year 4. Again, because there was no tillage, the BSB did not develop a resistant component, and because limited AEGCY population mortality factors were used in the model, the absolute values of the susceptible AEGCY population became very large.

Adding fallow and tillage to the management plan changed the development of herbicide-resistant AEGCY greatly. In the third simulation scenario, a wheat–fallow–wheat system was modeled using Clearfield wheat and treating with imazamox each crop year of the rotation. A chisel plow tillage operation was also simulated during the fallow period, and hybridization between wheat and AEGCY was assumed to occur. Fallowing and tillage slowed the rate of increase in the resistant AEGCY population compared with the continuous wheat scenarios (Figure 3C). Unlike the two scenarios with continuous wheat, the resistant portion of the population did not exceed the susceptible one until year 9. However, a permanent herbicide-resistant population did develop by year 4 (Figure 3C). Because the soil was tilled during the fallow year, resistant seeds were moved into the BSB. Nevertheless, the total projected AEGCY population was almost two orders of magnitude less than for the previous scenarios because of fallowing and tillage.

A final model scenario (scenario 4) was run using a rotation of imazamox-susceptible and -resistant wheat varieties in a wheat–fallow–wheat crop rotation. Chisel plowing during fallow periods and rotating herbicide classes were also employed in an effort to slow down the development of a herbicide-resistant AEGCY population. Although a resistant population did develop in this simulation as well, it never exceeded the susceptible SSB during the 10-yr simulation (Figure 3D). The risk of creating a permanent resistant population, therefore, was not considered to be serious. Moreover, this simulated rotation did not cause an exponential increase in the AEGCY seed bank over the 10-yr simulation period.

These simulations suggest that the effect of agricultural practices on herbicide resistance in AEGCY is both substantial and variable, with results ranging from an explosion of the population and rapid development of resistance to no population increase and a negligible incidence of resistance.

The model was useful for evaluating the risks and benefits of several management tactics on both herbicide resistance and AEGCY management. The model requires two primary areas of improvement: parameterization and increased generality. The current model is well parameterized for seed bank and weed control transitions, but it assumes that tillage does not affect seed longevity in SSB and BSB. Other work has shown that shallow tillage does not affect AEGCY emergence (Anderson 1998); therefore, it was assumed that AEGCY seed longevity was not affected. In addition, there are few published data on factors such as inter- and intraspecific competition effects on self-thinning and PRD in AEGCY populations. Information on DSP, seed predation, natural seed mortality, and seed burial transition rates are also limited. A PRD–weed density relationship would provide an initial step toward density dependence in the model (Maxwell 1999). The simulation results reported from this study show an unlimited, exponential growth in AEGCY populations under several of the simulation scenarios because population-limiting factors were not included in the model.

The model is limited by the agronomic practices and the environmental conditions that it can simulate. Although scenarios involving continuous wheat and wheat–fallow rotations may meet the needs of many growers, potential crop rotations are available that are not readily simulated with this model. Barley (*Hordeum vulgare* L.), pea (*Pisum sativum* L.), canola, spring wheat, sunflower (*Helianthus annuus* L.), and millet (*Panicum miliaceum* L.) are all crop options for which simulations could be developed. Moreover, transition rates can vary within a crop. Winter wheat yield loss from AEGCY was found to be more variable among sites than within years at a site, in a comparison of results from several western states (Jasieniuk et al. 1999). Additionally, the demographic data for AEGCY yield loss used in a population model varied between years (Maxwell 1999). The site-to-site and year-to-year variation in AEGCY suggests that the model should be made stochastic to account for climatic variation and regional differences. Therefore, the model could be revised to provide data-based transition rates where estimates are currently used and simulation capability for a wider range of crop rotation op-

tions across a range of conditions. The goal for a model of this type is to develop an easy to use decision aid for the introduction of Clearfield wheat.

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