Weed Technology 2013 27:475–487

Modeling the Evolution of Glyphosate Resistance in Barnyardgrass (*Echinochloa crus-galli*) in Cotton-Based Production Systems of the Midsouthern United States

Muthukumar V. Bagavathiannan, Jason K. Norsworthy, Kenneth L. Smith, and Paul Neve*

Glyphosate-resistant (GR) weeds have been a prime challenge to the sustainability of GR cotton-based production systems of the midsouthern United States. Barnyardgrass is known to be a high-risk species for evolving herbicide resistance, and a simulation model was developed for understanding the likelihood of glyphosate resistance evolution in this species in cotton-based systems. Under a worst-case scenario of five glyphosate applications in monoculture GR cotton, the model predicts resistance evolution in about 9 yr of continuous glyphosate use, with about 47% risk by year 15. A unique insight from this model is that management in response to GR Palmer amaranth in this system (a reactive response) provided a proactive means to greatly reduce the risks of glyphosate resistance evolution in barnyardgrass. Subsequent model analysis revealed that the risk of resistance is high in fields characterized by high barnyardgrass seedbank levels, seedling emergence, and seed production per square meter, whereas the risk is low in fields with high levels of postdispersal seed loss and annual seedbank loss. The initial frequency of resistance alleles was a high determinant of resistance evolution (e.g., 47% risk at year 15 at an initial frequency of $5e^{-8}$ vs. 4% risk at $5e^{-10}$). Monte Carlo simulations were performed to understand the influence of various glyphosate use patterns and production practices in reducing the rate and risk of glyphosate resistance evolution in barnyardgrass. Early planting and interrow cultivation are useful tools. Crop rotation is effective, but the diversity of weed management options practiced in the rotational crop is more important. Diversifying weed management options is the key, yet application timing and the choice of management option is critical. Model analyses illustrate the relative effectiveness of a number of diversified glyphosate use strategies in preventing resistance evolution and preserving the long-term utility of glyphosate in midsouthern U.S. cotton-based production systems.

Nomenclature: Glyphosate; barnyardgrass, *Echinochloa crus-galli* (L.) Beauv. ECHCG; cotton, *Gossypium hirsutum* L.
Key words: Glyphosate-resistant cotton, herbicide-resistant weed, simulation modeling, STELLA model, weed population dynamics, weed seedbank.

Las malezas resistentes a glyphosate (GR) han sido un reto primordial a la sostenibilidad de los sistemas de producción basados en algodón GR en el sur-medio de los Estados Unidos. *Echinochloa crus-galli* es reconocida como una maleza de alto riesgo de evolución de resistencia a herbicidas por lo que se desarrolló un modelo de simulación para entender la probabilidad de la evolución de resistencia a glyphosate en esta especie en sistemas basados en algodón. En el caso del peor escenario con cinco aplicaciones de glyphosate en monocultivo de algodón GR, el modelo predice la evolución de resistencia en aproximadamente 9 años de uso continuo de glyphosate, con cerca de 47% de riesgo en el año 15. Un detalle único de este modelo es que el manejo en respuesta a *Amaranthus palmeri* GR en este sistema (una respuesta reactiva) brindó los medios proactivos para reducir ampliamente el riesgo de la evolución de resistencia a glyphosate en *E. crus-galli*. El análisis siguiente del modelo reveló que el riesgo de resistencia es alto en campos caracterizados por tener niveles altos de bancos de semillas, emergencia de plántulas, y producción de semilla de *E. crus-galli* por metro cuadrado, mientras que el riesgo es bajo en campos con altos niveles de pérdida de semilla post-dispersión y pérdidas anuales del banco de semillas. La frecuencia inicial de alelos de resistencia fue un determinante importante en la evolución de resistencia (e.g., 47% de riesgo en el año 15 a una frecuencia inicial de $5e^{-8}$ vs. 4% de riesgo a $5e^{-10}$). Se realizaron simulaciones Monte Carlo para entender la influencia de varios patrones de uso de glyphosate y prácticas de producción en la reducción del riesgo y la tasa de evolución de resistencia a glyphosate en *E. crus-galli*. La siembra temprana y el cultivo entre hileras son herramientas útiles. La rotación de cultivos es efectiva, pero la diversidad en opciones de manejo de malezas en el cultivo de rotación es más importante. El diversificar las opciones de manejo de malezas es la clave, aunque el momento de aplicación y la escogencia de la opción de manejo son críticos. Análisis de modelos ilustran la efectividad relativa de utilizar un número variado de estrategias de uso de glyphosate en la prevención de la evolución de resistencia y la preservación de la utilidad de glyphosate en el largo plazo en los sistemas de producción basados en algodón en el sur-medio de los Estados Unidos.

Herbicide resistance in arable weed communities has been one of the major challenges to successful crop production in the midsouthern United States. Weed resistance to glyphosate has been particularly prevalent in this region in row crops such as cotton, corn (*Zea mays* L.), and soybean [*Glycine max* (L.) Merr.], which is partly attributed to the high adoption of GR cultivars in these production systems (Reddy and Norsworthy 2010). Crop rotation is limited and the rotational crops are often GR cultivars, resulting in high frequency of glyphosate applications. Heavy reliance on glyphosate as the prime weed management tool has favored the evolution of GR weeds. In Arkansas alone, glyphosate resistance has been reported in

---

DOI: 10.1614/WT-D-13-00013.1

* First, second, and third authors: Postdoctoral Research Associate, Professor, and Professor, respectively, Department of Crop, Soil, and Environmental Sciences, University of Arkansas, Fayetteville, AR 72701; fourth author: Assistant Professor, School of Life Sciences, University of Warwick, Wellesbourne, Warwick CV35 9EF, United Kingdom. Corresponding author's E-mail: muthu@uark.edu

horseweed [*Conyza canadensis* (L.) Cronq.] (McClelland et al. 2003), common ragweed (*Ambrosia artemisiifolia* L.) (Brewer and Oliver 2009), giant ragweed (*Ambrosia trifida* L.) (Norsworthy et al. 2011), Palmer amaranth (*Amaranthus palmeri* S. Wats.) (Norsworthy et al. 2008), johnsongrass (*Sorghum halepense*) (Riar et al. 2011), and Italian ryegrass [*Lolium perenne* L. subsp. *multiflorum* (Lam.) Husnot] (Dickson et al. 2011).

Cotton is an important row crop in the Mississippi Delta region of the midsouthern United States. In Arkansas in 2012, cotton was planted on 275,000 ha (NASS 2012), about 99% of which comprised herbicide-resistant cultivars, the vast majority of them being GR (J. K. Norsworthy, unpublished data). Some cotton growers have been practicing up to five solely glyphosate applications in a growing season in the Roundup Ready Flex® cotton (enhanced GR cotton that tolerates glyphosate application at advanced growth stages) (Norsworthy et al. 2007). The rise in glyphosate use has coincided with a reduction in the diversity of weed management practices in GR crops (Shaner 2000; Soteres 2012). As a result, there is a tremendous selection pressure for glyphosate resistance alleles in weed communities frequently found in GR cotton production fields. A Palmer amaranth population collected in fall 2004 was confirmed resistant to glyphosate in Georgia (Culpepper et al. 2006). Currently, GR Palmer amaranth has become widespread in the southern United States, particularly in cotton-based production systems of the Mississippi Delta region. According to a recent survey, about 87% of scouted cotton hectarage is infested with GR Palmer amaranth in Arkansas (J. K. Norsworthy, unpublished data).

Barnyardgrass is another important weed species commonly found in midsouthern U.S. cotton fields (Norsworthy et al. 2007). It is highly competitive with cotton and yield losses to the levels of 21, 59, 90, and 97% were reported when barnyardgrass competed for 6, 9, 12, and 25 wk after cotton emergence, respectively (Keeley and Thullen 1991). Barnyardgrass is a prolific species, producing up to 35,000 seeds plant^{-1} when emerging with cotton (Bagavathiannan et al. 2011b). It is likely that barnyardgrass populations have been subjected to high glyphosate exposure in the GR cotton-based production systems of the midsouthern United States. Barnyardgrass has long been known to be a high-risk species for evolving herbicide resistance (Osten et al. 2007; Walker et al. 2002). It is the sixth most important herbicide-resistant weed worldwide, with resistance to at least eight herbicide mechanisms of action (MOA) (Heap 2013). Barnyardgrass is the major herbicide-resistant weed in midsouthern U.S. rice (*Oryza sativa* L.) fields, with confirmed resistance to propanil (Baltazar and Smith 1994), quinclorac (Lovelace et al. 2000), clomazone (Norsworthy et al. 2009), and, lately, imazethapyr (Wilson et al. 2010). Junglerice [*Echinochloa colona* (L.) Link.], a species closely related to barnyardgrass, has been confirmed resistant to glyphosate in three Australian states (New South Wales, Queensland, and Western Australia) (Gaines et al. 2012; Heap 2013; Preston 2010) and in California (Alarcon-Reverte et al. 2011). Considering the exposure to glyphosate and the history of resistance elsewhere, it has been speculated that barnyardgrass is a potential candidate for glyphosate-resistance evolution in midsouthern U.S. cotton production systems.

A glyphosate-resistance simulation model for Palmer amaranth developed by Neve et al. (2011a) predicted the evolution of resistance in some populations after 4 yr with five annual glyphosate applications in continuous GR cotton. Field observations corroborated with model predictions. Given this, it is not clear why glyphosate resistance has not yet been reported in barnyardgrass in the same system. Two interesting questions arise from this: (1) which biological, genetic, and management factors contribute to the difference in apparent resistance risks between Palmer amaranth and barnyardgrass and when may resistance evolve in the latter species and (2) what strategies could reduce the risks of GR barnyardgrass evolving in GR cotton-based production systems of the midsouthern United States. In the research reported here, a simulation model was used to answer these important questions.

Materials and Methods

Study Location and Experiment Details. The model simulates the evolution of GR barnyardgrass across 1,000 hypothetical cotton production fields. Barnyardgrass seedling emergence was predicted using historical (25 yr) weather data from three important cotton producing areas of eastern Arkansas. The locations include Blytheville (35.93°N, 89.91°W), West Memphis (35.15°N, 90.18°W), and Monticello (33.63°N, 91.79°W). The following experimental considerations were made in this model. Each cotton field was 60 ha in size. Cotton was planted on May 1 (normal planting date), but plantings on April 15 (early planting) or May 15 (delayed planting) were also considered. The crop was grown in 1-m-wide rows in an irrigated environment. Barnyardgrass emergence is influenced by the number of growing degree days (GDDs) accumulated. In the Mississippi Delta region, emergence usually commences during early to mid-April, depending on local environmental conditions (Bagavathiannan et al. 2011a).

Barnyardgrass emergence was categorized into seven cohorts, occurring at biweekly intervals: cohort 1 (prior to planting on May 1), cohort 2 (May 1 to May 14), cohort 3 (May 15 to May 31), cohort 4 (June 1 to June 14), cohort 5 (June 15 to June 30), cohort 6 (July 1 to July 14), and cohort 7 (emergence on or after July 15). Management interventions corresponding to each cohort were timed as follows: preplant (April 15), at-plant (PRE) (May 1), first POST (May 15), second POST (June 1), third POST (June 15), and lay-by (i.e., the final management intervention, July 1). In this region, cotton–corn is the predominant rotation practiced, followed by cotton–soybean, but model simulations only include cotton–corn rotations. Corn was planted on April 1 and barnyardgrass cohorts corresponding to the corn crop are as follows: cohort 1 (prior to planting corn on April 1), cohort 2 (April 1 to April 14), cohort 3 (April 15 to April 30), cohort 4 (May 1 to May 14), cohort 5 (May 15 to May 31), cohort 6 (June 1 to June 14), and cohort 7 (emergence on or after June 15). Barnyardgrass emergence is not likely to occur prior to planting corn most years. Because of dense crop canopy formation, weed management interventions in corn typically cease early in the season. The model assumes two management timings in corn: at-planting interventions on April 1 and first POST options on April 15.

Model Development. The simulation model was developed using the visual programming language STELLA (version 9.1; iSee systems, Lebanon, NH). The general framework and approach of the model follows the work of Neve et al. (2011a) on simulating glyphosate resistance evolution in Palmer amaranth. The model is stage-structured, representing the three distinct life-history stages of barnyardgrass: dormant seeds in the soil seedbank, emerged seedlings, and mature plants. In junglerice, a target-site mutation was found to confer glyphosate resistance (Alarcon-Reverte et al. 2011). The present model assumes that glyphosate resistance in barnyardgrass would be endowed by a single, completely dominant gene with a Mendelian pattern of inheritance. The evidence from previous cases suggests that glyphosate resistance is usually inherited as an incompletely dominant trait (e.g., Zelaya et al. 2004). However, complete dominance was assumed in order to simplify the model. The seedbank consists of different genotypes (homozygous susceptible [SS], heterozygous resistant [RS], and homozygous resistant [RR]) in a dormant state. In each cycle of simulation, the model estimates the transition from seed to seed of individual genotypes pertaining to each emergence cohort. A detailed description of the life-history stages and transition coefficients for barnyardgrass is given in the Appendix (see supplementary information). It is an open-system model, in which propagule immigration (Δ_I) and emigration (Δ_E) were allowed to occur at predetermined rates (see Table 1). The model is spatially implicit, and thus the population structure was assumed to be homogeneous across the field. For a detailed explanation of the model development, readers can consult Neve et al. (2011a).

Model Parameter Estimation. The majority of the data used for parameter estimation were obtained from field experiments in Arkansas. Relevant data were also obtained from published literature in comparable situations. When specific data were not available, assumptions were made based on expert opinions or based on information available in the literature. Tables 1, 2, and 3 summarize the parameter values used in the model, including parameter estimates for the various submodels. Some variables were judged to be associated with field-to-field or season-to-season variation (i.e., stochastic variables) and these include the initial frequency of resistance (R) alleles (δ), initial seedbank size (D_0), annual seedling emergence proportion (E_p), postdispersal seed loss (D_b), and annual seedbank loss (D_m). The parameter ranges for the stochastic variables were determined based on likely variations or range of parameter uncertainty: δ (5×10^{-10} to 5×10^{-7}), D_0 (50 to 2500), E_p (0.05 to 0.15), D_b (0.7 to 0.9), and D_m (0.6 to 0.8) (Table 1). For each stochastic variable, parameter values were drawn from a random distribution, except for δ, which was considered to be log-normally distributed (Neve et al. 2011a). Additionally, the model accounts for demographic stochasticity when the population size reaches low levels (< 10 plants for any genotype). Demographic stochasticity was included in the model by drawing an integer from a Poisson distribution with a mean equivalent to the predicted value (see Neve et al. 2011a for more details).

Table 1. Summary of the key parameters used in the model for glyphosate resistance simulation in barnyardgrass.

Parameter description	Symbol	Parameter value	Reference
Field size	α	60 ha	—
Mutation rate[a]	μ	5×10^{-9}	Assumption based on Neve et al. (2011a)
Initial frequency of resistance alleles[a]	δ	5×10^{-8} (5×10^{-10} to 5×10^{-7})	Assumption based on Neve et al. (2011a)
Proportion of cross-pollination	θ	0.03	Bagavathiannan et al. (2012c)
Inbreeding coefficient	F	0.94 (based on an outcrossing rate of 3%)	—
Initial seedbank size (m^{-2})[a]	D_0	1,000 (50–2,500)	Based on Bagavathiannan et al. (2011a)
Base temperature for barnyardgrass emergence	T_b	9.7 C	Wiese and Binning (1987)
Seedling emergence proportion (% of seedbank size)[a]	E_p	0.08 (0.05–0.15)	Derived from Ogg and Dawson (1984)
Seedling emergence proportion for the *i*th cohort (% of total emergence)	Se_i	Weibull function: $Y = 100 \{1 - \exp [-0.0034 (x - 23.27)^{1.493}]\}$	Bagavathiannan et al. (2011a)
Density-dependent seedling survival for the *i*th cohort	Ss_i	Exponential decay (modified single three-parameter): $Y = 22.8 \times \exp[1{,}239/(x + 826)]$	Bagavathiannan et al. (2011c)
Density-dependent fecundity for the *i*th cohort	Fd_i	Exponential decay (double five-parameter): $Y = 420 + 23{,}889 \times \exp(-0.195x) + 7{,}693 \times \exp(-0.014x)$	Bagavathiannan et al. (2011c)
Fecundity of the *i*th cohort relative to time of emergence in cotton	Fti	Exponential decay function: $Y = 64{,}800 \times \exp(-0.6x)$	Bagavathiannan et al. (2011b)
Maximum density of the weed reaching reproduction (plants m^{-2})	k	500	Assumption based on field observation
Maximum barnyardgrass seed production plant^{-1} in cotton	F_p	35,000	Bagavathiannan et al. (2011b)
Viability of freshly produced seeds	D_v	0.92	Bagavathiannan et al. (2011c)
Seed immigration (seeds m^{-2})	Δ_I	1	—
Seed emigration (% of fresh seeds)	Δ_E	1	—
Postdispersal seed loss[a,b]	D_b	0.85 (0.70–0.90)	Bagavathiannan et al. (2012 a,b)
Annual seedbank loss[a]	D_m	0.75 (0.60–0.80)	Derived from Egley and Chandler (1978)

[a] Indicates stochastic variables; parameter estimates followed by range given in parentheses.

[b] Includes seed loss through herbivory, microbial decay, and loss in viability.

Table 2. Efficacy of various management options for barnyardgrass control in cotton.[a,b,c]

Management timing	Date	Management option	Emergence timing[d] C1	C2	C3	C4	C5	C6	C7
Preplant	April 15	Fomesafen	99	85	60	0	0	0	0
At-plant (PRE)	May 1	Glyphosate	99.99	0	0	0	0	0	0
		Paraquat	99.9	0	0	0	0	0	0
		Glufosinate	99.99	0	0	0	0	0	0
		Fluometuron	50	95	75	30	0	0	0
First POST	May 15	Glyphosate	99.5	99.9	0	0	0	0	0
		Glufosinate	50	99.99	0	0	0	0	0
		Clethodim	99	99.99	30	0	0	0	0
		S-metolachlor	0	0	99	90	60	0	0
Second POST	June 1	Glyphosate	99	99.5	99.9	0	0	0	0
		Glufosinate	0	50	99.99	0	0	0	0
		Clethodim	75	99	99.99	30	0	0	0
		S-metolachlor	0	0	0	99	90	60	0
		Cultivation	60	75	85	0	0	0	0
Third POST (OTT)	June 15	Glyphosate	95	99	99.5	99.9	0	0	0
		Glyphosate (Dir)	70	85	95	99	0	0	0
		Glufosinate	0	0	50	90	0	0	0
		Glufosinate (Dir)	0	0	30	80	0	0	0
		Prometryn (Dir)	0	5	15	50	95	60	0
		MSMA + prometryn (Dir)	0	0	60	99	70	30	0
		Cultivation	30	60	75	85	0	0	0
Lay-by (OTT)	July 1	Glyphosate	80	90	95	98	99	0	0
		Glufosinate	0	0	0	40	85	0	0
		MSMA (Dir)	0	0	0	50	95	0	0
		Flumioxazin	0	0	0	0	30	99	90
		Cultivation	20	20	20	50	90	0	0

[a] Abbreviations: OTT, over-the-top application above crop canopy; Dir, directed application towards weeds under the crop canopy; C1 to C7, cohort 1 to cohort 7.

[b] Efficacies remain the same for the susceptible (SS), heterozygous resistant (RS), and homozygous resistant (RR) genotypes, except for glyphosate applications where the chemical is assumed to be effective only on the SS genotype (the trait is assumed to be completely dominant).

[c] The cultivars represented in the simulations are tolerant to glyphosate or glyphosate+glufosinate.

[d] Barnyardgrass emergence timing: C1 (prior to May 1), C2 (May 1 to May 14), C3 (May 15 to May 30), C4 (June 1 to June 14), C5 (June 15 to June 30), C6 (July 1 to July 14), C7 (on or after July 15).

The initial frequencies of the different genotypes (SS, RS, and RR) were calculated assuming that the seedbank population was in Hardy-Weinberg equilibrium (Jasieniuk et al. 1996). A study conducted by Bagavathiannan et al. (2012c) estimated 3% average outcrossing among barnyardgrass plants occurring adjacent to each other. The model simulates the production of haploid (S or R) ova and pollen in proportion to the fecundity of the surviving plants in each genotype, and 3% of the ova were fertilized by foreign pollen (S or R type depending on the proportional abundance in the population). Specific gene functions can be altered as a result of random mutations that occur during gametogenesis, leading to the acquisition of or reversal from resistance. The model simulates random mutations among the gametes for the given allele at a rate equivalent to μ (i.e., 5×10^{-9}). The mode of inheritance of glyphosate resistance in barnyardgrass is not known because resistance is yet to be confirmed.

Table 3. Efficacy of various management options for barnyardgrass control in corn.[a,b]

Management timing	Date	Management option	Emergence timing[c] C1	C2	C3	C4	C5	C6	C7
At-plant (PRE)	April 1	Glyphosate	99.9	0	0	0	0	0	0
		S-metolachlor	0	99	90	30	0	0	0
		Atrazine	60	90	50	0	0	0	0
First POST	May 1	Glyphosate	99	99.9	99.9	0	0	0	0
		Glufosinate	85	99	99.9	0	0	0	0
		Atrazine	0	50	90	50	0	0	0

[a] Abbreviations: C1 to C7, cohort 1 to cohort 7.

[b] Efficacies remain the same for the susceptible (SS), heterozygous resistant (RS), and homozygous resistant (RR) genotypes, except for glyphosate applications where the chemical is assumed to be effective only on the SS genotype (the trait is assumed to be completely dominant).

[c] Barnyardgrass emergence timing: C1 (prior to May 1), C2 (May 1 to May 14), C3 (May 15 to May 30), C4 (June 1 to June 14), C5 (June 15 to June 30), C6 (July 1 to July 14), C7 (on or after July 15).

Table 4. Management options examined for barnyardgrass control in continuous cotton.[a,b,c]

Program	Short description	Preplant option	At-plant option	First POST option	Second POST option	Third POST option	Lay-by option
I	Glyphosate-only program	None	Glyphosate	Glyphosate	Glyphosate	Glyphosate	Glyphosate
II	Cultivation second POST	None	Glyphosate	Glyphosate	Cultivation	Glyphosate	Glyphosate
III	Cultivation third POST	None	Glyphosate	Glyphosate	Glyphosate	Cultivation	Glyphosate
IV	Cultivation second and third POST	None	Glyphosate	Glyphosate	Cultivation	Cultivation	Glyphosate
V	GL cotton I (two glufosinate applications)	None	Glyphosate	Glufosinate	Glyphosate	Glufosinate	Glyphosate
VI	GL cotton II (three glufosinate applications)	None	Glufosinate	Glyphosate	Glufosinate	Glyphosate	Glufosinate
VII	Clethodim first POST in a glyphosate-only program	None	Glyphosate	Glyphosate + clethodim	Glyphosate	Glyphosate	Glyphosate
VIII	Clethodim second POST in a glyphosate-only program	None	Glyphosate	Glyphosate	Glyphosate + clethodim	Glyphosate	Glyphosate
IX	Preplant residual herbicide in a glyphosate-only program	Fomesafen	Glyphosate	Glyphosate	Glyphosate	Glyphosate	Glyphosate
X	Early-season residuals	Fomesafen	Fluometuron	Glyphosate	Glyphosate	Glyphosate	Glyphosate
XI	POST-only residual herbicides	None	Glyphosate	Glyphosate + *S*-metolachlor	Glyphosate + *S*-metolachlor	Glyphosate + prometryn	MSMA + flumioxazin
XII	Diversified herbicide program	Fomesafen	Paraquat + fluometuron	Glyphosate + *S*-metolachlor	Glyphosate + *S*-metolachlor	Glyphosate + prometryn	MSMA + flumioxazin

[a] Abbreviation: GL, glyphosate and glufosinate tolerant.

[b] Application timing: preplant option, April 15; at-plant option, May 1; first POST option, May 15; second POST option, June 1; third POST option, June 15; lay-by option, July 1.

[c] The cultivars represented in the simulations are tolerant to glyphosate or glyphosate + glufosinate (GL cotton).

Efficacy values for various management options (Tables 2 and 3) were determined based on field observations in Arkansas cotton and corn production systems. Because resistance is assumed to be conferred by a completely dominant gene, it was considered that glyphosate application fails to impact RR and RS genotypes, whereas other management options will have equal efficacy on all three genotypes. In programs where interrow cultivation is practiced, it was assumed that the residual herbicides applied earlier lose activity following cultivation. The general assumption was that the residual herbicides were activated on time and there were no antagonistic or synergistic reactions among the various herbicide combinations used in each management program.

Model Analysis. Simulations were performed to understand the likelihood of glyphosate resistance evolution in barnyardgrass across the 1,000 hypothetical cotton fields (i.e., 1,000 model runs) over a 30-yr period. A population was considered resistant if at least 20% of the seedbank consisted of resistant (RR + RS) individuals. A Monte Carlo simulation approach was followed to understand the risk of resistance for a given management scenario across the 1,000 fields. An initial series of model runs were performed allowing the stochastic variables to vary within their likely parameter space. Following this, model sensitivity was tested for the chosen stochastic variables by varying individual parameter values across the predefined parameter space while keeping the rest of the parameters constant at their default value.

Initial model simulations were aimed at understanding the likelihood of glyphosate resistance evolution under various historical weed management scenarios. The adoption of GR cotton surpassed 50% of the total cotton production by 2001 (USDA-ERS 2012) and, as a result, the use of glyphosate increased tremendously in midsouthern U.S. cotton production. Because the first generation of GR cotton cultivars were sensitive to glyphosate at later growth stages, late-season applications were typically directed under the crop canopy, often mixed with residual herbicides (Givens et al. 2009). However, it was not until the availability of Roundup Ready Flex® cotton in 2006 that the sole use of glyphosate intensified (Norsworthy et al. 2007). By 2009, within only few years after the adoption of Roundup Ready Flex® cotton, glyphosate resistance had become prevalent in Palmer amaranth, forcing growers to adopt more diversified weed management programs to manage GR Palmer amaranth. Given this, the following scenarios were considered in the barnyardgrass model: (a) five annual glyphosate applications (i.e., glyphosate-only program) since 2001, a worst-case scenario (program I, Table 4), (b) glyphosate-only program until 2009, followed by a diversified herbicide rotation (program XII, Table 4), (c) glyphosate plus POST-directed residual herbicides from 2001 to 2005 (program XI, Table 4), then to a glyphosate-only program in the Roundup Ready Flex® cotton, and (d) scenario "c" from 2001 to 2009, followed by a diversified herbicide rotation.

Subsequent analyses were used to understand how various biological, genetic, and management factors influence the risk of resistance. General management approaches included (1) cultural and tillage practices, (2) crop/trait rotations, and (3) herbicide rotations. The model has been used to simulate various combinations of management options (i.e., programs) for (1) continuous monoculture GR cotton and (2) GR cotton rotated with other cotton and corn crops. The various management programs tested in the model, with individual management options and respective timing, are listed in Tables 4 and 5. Overall, 12 management programs (see Table 4 for details of specific management programs) along with two planting date scenarios were tested for monoculture cotton and one management program each for the five rotational crops (see Table 5).

Table 5. Simulated management options for barnyardgrass control in the rotational crop.[a]

Rotational crop	Preplant option	At-planting option	First POST option	Second POST option	Third POST option	Lay-by option
Glufosinate-resistant cotton (Glufosinate-only program)	None	Glufosinate	Glufosinate	Glufosinate	Glufosinate	Glufosinate
Glufosinate-resistant cotton (diversified program)	Fomesafen	Fluometuron	Glufosinate + *S*-metolachlor	Glufosinate	Glufosinate	MSMA + flumioxazin
Conventional cotton	Fomesafen	Fluometuron	*S*-metolachlor	*S*-metolachlor + cultivation	Prometryn + MSMA	Cultivation + flumioxazin
Glyphosate-resistant corn	None	Glyphosate + *S*-metolachlor + atrazine	Glyphosate + atrazine	—	—	—
Glufosinate-resistant corn	None	Glyphosate + *S*-metolachlor + atrazine	Glufosinate+ atrazine	—	—	—

[a] Application timing for cotton: preplant option, April 15; at-plant option, May 1; first POST option, May 15; second POST option, June 1; third POST option, June 15; lay-by option, July 1. Application timing for corn: at-plant option, April 1; first POST option, April 15.

Results and Discussion

Risk of Glyphosate Resistance under Historical Weed Management Scenarios. Under the worst-case scenario of five glyphosate applications annually, the model predicts resistance evolution in 9 yr and about 20% risk in 11 yr (Figure 1Aa). The risk of resistance evolution is minimal after 15 yr because the seedbank size would have been driven to very low levels in fields where resistance did not evolve by that time, due to the high efficacy of glyphosate on barnyardgrass. The low seedbank size greatly reduces the likelihood for a resistant mutant occurring in these fields, further reducing resistance risk. In Australian GR cotton production system, Werth et al. (2008) predicted the evolution of GR barnyardgrass in 8 yr (assuming resistance has evolved when R alleles exceed 20% of the total population) in a glyphosate-only system consisting of four glyphosate applications annually. In junglerice, Thornby and Walker (2009) predicted the evolution of glyphosate resistance in about 13 yr of sole glyphosate use (three applications per year) in Australian grains (wheat–sorghum) cropping systems. Our model predictions are largely comparable to previous reports elsewhere. However, there were few farmers who were adopting the glyphosate-only program in the first generation of Roundup Ready® cotton because applications after the four-leaf stage were typically directed; directed herbicide applications require additional efforts and, as a result, growers preferred to tank-mix residual herbicides to avoid frequent applications. Tank-mixing glyphosate with alternative herbicide MOA, albeit only for POST-directed applications, could have slowed the selection for R alleles.

The situation has changed since the commercialization of the Roundup Ready Flex® cotton in 2006, which favored season-long over-the-top applications of glyphosate. With this scenario, there is about 10% risk by year 15 (Figure 1Ac). Given that GR cotton witnessed widespread adoption by 2001, we may anticipate GR barnyardgrass within a few years of this publication in fields characterized by the above weed management scenario. It is important, however, to recognize that weed management programs again changed in most midsouthern U.S. cotton fields within a few years after the adoption of Roundup Ready Flex cotton. By 2008, GR Palmer amaranth was a serious issue in this region, forcing growers to adopt diversified herbicide programs (Nichols et al. 2009). The herbicide options included in the diversified program recommended for glyphosate resistance management in Palmer amaranth (Program XII, Table 4) have sufficient efficacy on barnyardgrass (R. Scott, personal communication). Considering a situation in which a grower adopted the glyphosate-only program until GR Palmer amaranth became a serious issue, the subsequent risks of GR barnyardgrass in that system could have been brought to minimal by shifting to the diversified program (Figure 1Ab). The model also predicts that the risks of resistance are nil for the commonplace scenario in which growers tank-mixed residual herbicides until the availability of Roundup Ready Flex cotton, abandoned residual herbicides in the Flex cotton, and then shifted to the diversified program upon resistance evolution in Palmer amaranth (Figure 1Ad). This perhaps explains why GR barnyardgrass has not evolved in midsouthern U.S. cotton and suggests that this strategy greatly minimizes risks of GR evolution in barnyardgrass. Nevertheless, the risk of resistance still holds true in specific fields where glyphosate use is still continued without diversification (see Figure 1Ac), albeit these fields are extremely rare now (J. K. Norsworthy, unpublished data).

Comparisons between Barnyardgrass and Palmer Amaranth Models. Neve et al. (2011a) predicted the evolution of GR Palmer amaranth in 4 yr of sole glyphosate use in midsouthern U.S. cotton, whereas in barnyardgrass, resistance is expected to be delayed substantially (Figure 1A). When comparing these two models (keeping crop production and management factors similar), it is evident that the differences in the rapidity of resistance evolution is primarily attributable to differences in fecundity levels between these two species. Palmer amaranth is a profuse seed producer with $> 500{,}000$ seeds produced plant^{-1} (e.g., Massinga et al. 2001), whereas barnyardgrass produces $>$ 20-fold less seed plant^{-1} (Bagavathiannan et al. 2011b). High fecundity favors resistance evolution in two ways. The frequency with which novel R alleles arise via mutation is proportional to population size. High fecundity also facilitates rapid enrichment of the seedbank with a resistant population. Alleles conferring resistance to glyphosate are known to be relatively rare in plant populations (Duke and Powles 2009); however, high fecundity levels may compensate for low mutation rates in weed populations. Typically, the number of resistant mutants in a population is directly proportional to the seedbank size (Jasieniuk et al. 1996). The sensitivities of both the models were similar in that the risks of resistance were greater with high seedbank density, high initial frequency of R alleles, and high annual recruitment proportion and lesser with annual seed mortality (results not shown, see figure 3 in Neve et al. 2011a). As such, the likelihood of resistance was greater in Palmer amaranth compared to barnyardgrass.

Scenarios of High Resistance Risk. The resistance risks shown in Figure 1 represent a wide range of demographic, genetic, and management scenarios for barnyardgrass. The risks could be different in production fields with specific population characteristics. Model analysis illustrated that resistance risks are greater under higher seedbank population, seedling emergence, and fecundity, whereas the risks are lower in fields with greater postdispersal seed loss and annual seedbank loss (Figure 1B). The processes increasing the risk of resistance typically favor rapid seedbank enrichment of the resistant population and vice versa. This insight is useful for guiding resistance management.

At very low seedbank levels, the likelihood for resistance evolution is very low because the chances for the appearance of the R alleles are low (Jasieniuk et al. 1996). A focus on preventing seed production in weed escapes is elemental to maintaining low seedbank levels (Hartzler 1996). A strong emphasis on seedbank management, particularly encouraging postdispersal weed seed herbivory and microbial seed decay, is also vital (Cardina et al. 1996; Liebman et al. 2001). Several approaches have been suggested for managing weed seedbanks (Davis 2006; Gallandt 2006). Additionally, harvest weed seed control strategies such as use of the Harrington Seed Destructor has been shown to be very effective in minimizing weed seedbank size under certain situations (Walsh et al. 2012). Resistance risks increase with high levels of seedling recruitment because high recruitment increases the likelihood that resistant individuals germinate and reproduce, instead of being lost due to seedbank mortality (Neve et al. 2011a). Seedling recruitment could be manipulated by practices such as deep tillage (Blackshaw 1990; Davis and Renner 2006; DeVore et al. 2012a,b), planting cover crops (DeVore et al. 2012a,b), or establishing plant residue cover (Teasdale and Mohler 1993).

The initial frequency of R alleles was the most important determinant of resistance risk in this model (Figure 1C). Higher initial frequency levels not only increase the risks of resistance, but also advance the evolution of resistance. These findings are in agreement with previous research (e.g., Neve et al. 2011a; Thornby and Walker 2009; Werth et al. 2008). Initial frequency of R alleles is a very difficult parameter to accurately estimate and is known to be governed by the mutation rate and the selective advantage or disadvantage of the resistant mutant in the absence of the selective agent (Jasieniuk et al. 1996). These factors are difficult to control, but a feasible way of reducing the frequency of R alleles in a population is to reduce the seedbank size. The model assumes complete dominance of the trait, but the predictions could have been a degree of overestimation of the rate and risk of resistance evolution in the event that resistance is conferred by an incompletely dominant trait. Under incomplete dominance, the typical glyphosate use rates could cause greater seedling mortality and greater reduction in fecundity in RS genotypes compared to RR genotypes, thus delaying resistance evolution.

Relative Effectiveness of Management Options. The management options tested in the model use the glyphosate-only program (Table 4, program I) as the baseline for comparison. Individual glyphosate applications in the glyphosate-only program were then replaced with alternative options, depending on the management program tested (see Table 4).

Cultural and Tillage Practices. Advancing cotton planting to April 15 (instead of usual planting on May 1) delayed the evolution of resistance by 3 yr, with about 10% less risk over the 30-yr period (Figure 2A). Conversely, delayed planting (May 15) slightly increased the risks. Early planting of cotton favors crop canopy formation prior to the peak emergence of barnyardgrass in this region; dense crop canopy formation can greatly reduce the reproductive potential of weed escapes (Anderson 2005; Rushing and Oliver 1998). Delayed planting can be beneficial if planting can be delayed beyond peak emergence and the emerged seedlings can be effectively controlled using nonglyphosate options. However, delaying cotton planting beyond a certain period may not be feasible for certain growers due to local soil or climate restrictions. Altering planting dates should consider the emergence pattern of the given weed species and a thorough understanding of weed emergence pattern is therefore essential for effective management (Buhler et al. 1997). Replacing glyphosate application with cultivation at the second POST (program II) or third POST (program III) application timing delayed the onset of resistance by 5 to 7 yr, with about 25 to 30% lower risk of resistance, whereas cultivation at both the second and third POST application timings (program IV) delayed resistance by 12 yr, with a 40% reduction in risk. Interrow cultivation, where possible, is a useful strategy because cultivation can eliminate weed escapes that are not controlled by herbicide options. Thus, cultivation can be a valuable tool in integrated resistance management (Cavan et al. 2000; Norsworthy et al. 2012).

Crop/Trait Rotations. Rotating GR cotton with other cotton or corn cultivars was effective in reducing the rate and risk of glyphosate resistance evolution (Figure 2B). By rotating GR cotton with GR or glufosinate-resistant (LL) corn, resistance could be delayed for up to 6 yr, with about 25% reduction in risk. Rotating GR cotton with other cotton options such as LL cotton with a glufosinate-only program, LL cotton with a diversified herbicide program, or conventional, nontransgenic cotton with a standard herbicide program (see Table 5) provided similar benefits in reducing the rate of glyphosate resistance evolution as growing GR or LL corn in rotation. However, adopting a diversified herbicide program in the rotational LL cotton or growing a nontransgenic cotton crop in rotation that eliminate glyphosate use has greatly reduced the risks of glyphosate resistance compared to the herbicide options used in the corn crop (Figure 2B). Moreover, adoption of LL cotton with a glufosinate-only program or a similar program with minimal diversity might lead to

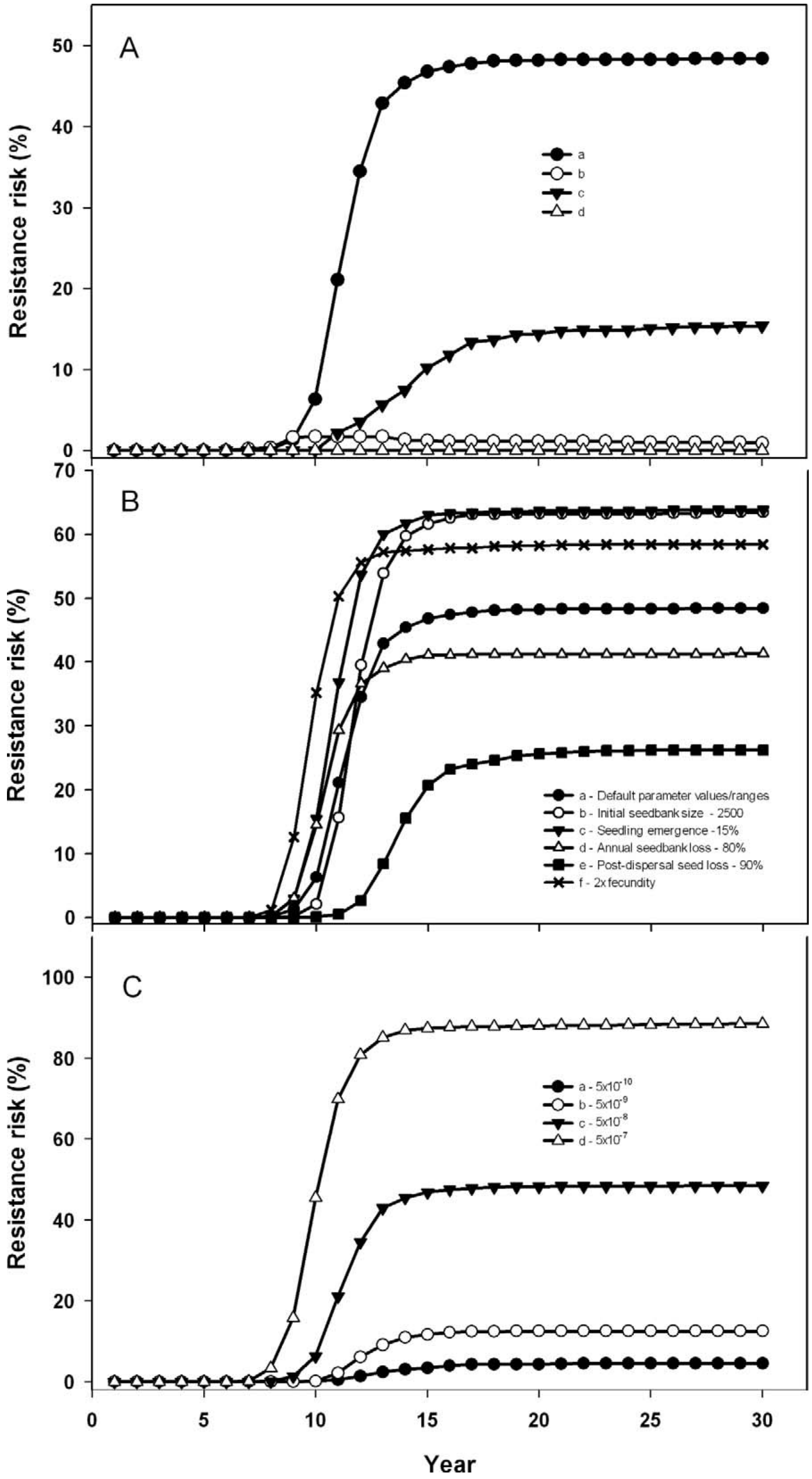

Figure 1. Risks of barnyardgrass evolving resistance to glyphosate in monoculture glyphosate-resistant cotton. (A) Under various historical weed management scenarios: (a) five annual applications of glyphosate alone (glyphosate-only program) from 2001 onward, a worst-case scenario; (b) scenario "a" from 2001 to 2009, then shifted to a diversified herbicide rotation (fomesafen applied prior to planting, paraquat tank-mixed with fluometuron applied at planting, glyphosate tank-mixed with *S*-metolachlor applied at first and second POST application timings, glyphosate tank-mixed with prometryn applied at third POST application timing, followed by MSMA tank-mixed with flumioxazin at lay-by application); (c) glyphosate-dominant herbicide program that consisted of POST-directed residual herbicides from 2001 to 2005

glufosinate resistance and adoption of more diversified management programs are vital to prevent this from happening.

Crop rotation is an effective strategy, which in addition to weed management benefits provides a number of other ecosystem benefits (Cardina et al. 2002; Liebman and Dyck 1993). Strictly viewed in the context of herbicide resistance management, the diversity of weed management options in the rotational crop is more important than the rotation per se. As shown above, rotating GR cotton with nontransgenic cotton or with LL cotton consisting of a diversified management program was more effective in reducing the risks of resistance than rotating with GR or LL corn (Figure 2B). Although corn typically provides crop canopy benefits (Teasdale 1995) greater than those of cotton, the weed management options used in GR or LL corn consisted of at least one glyphosate application (common practice in this region) and the additional options do not provide effective control of GR barnyardgrass (see Table 3). The key is to reduce the selection pressure for any single management tool across the production system as a whole rather than focusing merely on a single crop, thereby providing opportunities for the elimination of the R alleles in the rotational crop (or crops). This in fact warrants an evolutionary thinking in weed management (Neve et al. 2009).

Herbicide Rotations. Increasing MOA diversity by including alternative herbicides largely delayed the evolution of resistance with a substantial reduction in risks (Figure 2C). Increasing herbicide diversity reduces selection pressure for a given herbicide; the greater the diversity of options, the lesser the risk of resistance evolution for any given option (Beckie 2006). The degree of benefit, however, depends on three important factors: the number of glyphosate applications being replaced with alternative herbicides, time of application, and the choice of alternative herbicide (i.e., efficacy). Replacing three glyphosate applications with glufosinate in a continuous cotton cultivar resistant to both glyphosate and glufosinate (Table 4, program VI,) was more effective than replacing two glyphosate applications (program V) (Figure 2C). The importance of increasing alternative MOAs in reducing the risks of glyphosate resistance has also been illustrated by other similar studies (e.g., Neve et al. 2003, 2011b). Simply increasing MOA diversity is not sufficient, as some application timings are more critical than others. Tank-mixing glyphosate with clethodim applied at the second POST application timing (program VIII) was more effective in reducing the risks than glyphosate plus clethodim applied at the first POST application timing (program VII). A closer inspection revealed that the application of clethodim at the second POST timing provided excellent control of barnyardgrass cohorts 3 and 4 (largest cohorts) compared to application at the first POST timing (Table 2), thereby reducing total seed production.

Achieving MOA diversity using herbicides that provide extended barnyardgrass control through soil residual activity are particularly helpful in preventing or delaying resistance. For instance, inclusion of fomesafen (program IX), a preplant residual herbicide, can delay resistance for up to 9 yr, with about 40% less risk (Figure 2C). The value of residual herbicides in weed management (Grichar et al. 2004; Porterfield et al. 2002), particularly herbicide resistance management (Neve et al. 2011b), has been demonstrated in GR cotton. Beckie (2011) recommended that supplementing glyphosate with soil-residual herbicides is a valuable herbicide strategy for proactively or reactively managing GR weeds. Nevertheless, timing of residual herbicide application is an important consideration. Tank-mixing glyphosate with residual herbicides at all POST applications (i.e., POST-only residuals, program XI) failed to delay resistance, whereas application of fomesafen prior to planting followed by fluometuron applied at planting (i.e., early-season residuals, program X) was effective in preventing resistance (Figure 2C). Early-season residual herbicides are particularly valuable because they provide effective control of the individuals that possess high seed production potential, severely impacting population sizes. Even though POST-only residual herbicides are very effective in controlling mid- to late-season escapes, such programs allow for substantial escapes among early recruits (Faircloth et al. 2001). As emphasized by Neve et al. (2011a), alternative management options that effectively help maintain low population sizes, particularly through appropriate timing and choice of intervention, are imperative for effective resistance management.

A diversified herbicide rotation has been widely implemented for GR Palmer amaranth control in GR cotton in the midsouthern United States (Table 4, program XII). The model shows that this program can prevent the occurrence of glyphosate resistance in barnyardgrass (Figure 2C). The diversified herbicide rotation was so effective in managing a wide spectrum of weeds in cotton that in a recent survey conducted across the midsouthern U.S. region, some cotton consultants questioned the need for integrating nonchemical options in weed management (J. K. Norsworthy, unpublished data). Diversified herbicide rotations may be effective for the short term, but they are neither sufficient to sustainably prevent herbicide resistance evolution nor always preferable. The importance of integrating nonchemical weed management tools in herbicide resistance management should not be overlooked for two key reasons: firstly, a strategy that is solely based on rotating herbicide MOAs does not address metabolism-based polygenic resistance in weed populations (Shaner 2013). For instance, cytochrome P450 monooxygen-

---

←

(glyphosate [at planting], glyphosate tank-mixed with *S*-metolachlor applied at first and second POST application timings, glyphosate tank-mixed with prometryn applied at third POST application timing, followed by MSMA tank-mixed with flumioxazin at lay-by application), then shifted to a glyphosate-only program from 2006 onward upon the availability of Roundup Ready Flex® cotton; and (d) option "c" from 2001 to 2009, followed by a diversified herbicide rotation as described in "b." (B) Under different scenarios of barnyardgrass population biology in a glyphosate-only system: (a) at default parameter values and ranges used to generate Figure 1A, (b) at an initial seedbank size of 2,500 seeds m^{-2}, (c) at 15% annual seedling recruitment level, (d) at 80% annual seedbank loss, (e) at 90% loss of freshly produced seeds through postdispersal herbivory, decay, and loss in viability, and (f) at double the rate of fecundity. (C) Under different initial frequency levels of resistance alleles in a glyphosate-only system: (a) 5×10^{-10}, (b) 5×10^{-9}, (c) 5×10^{-8}, and (d) 5×10^{-7}.

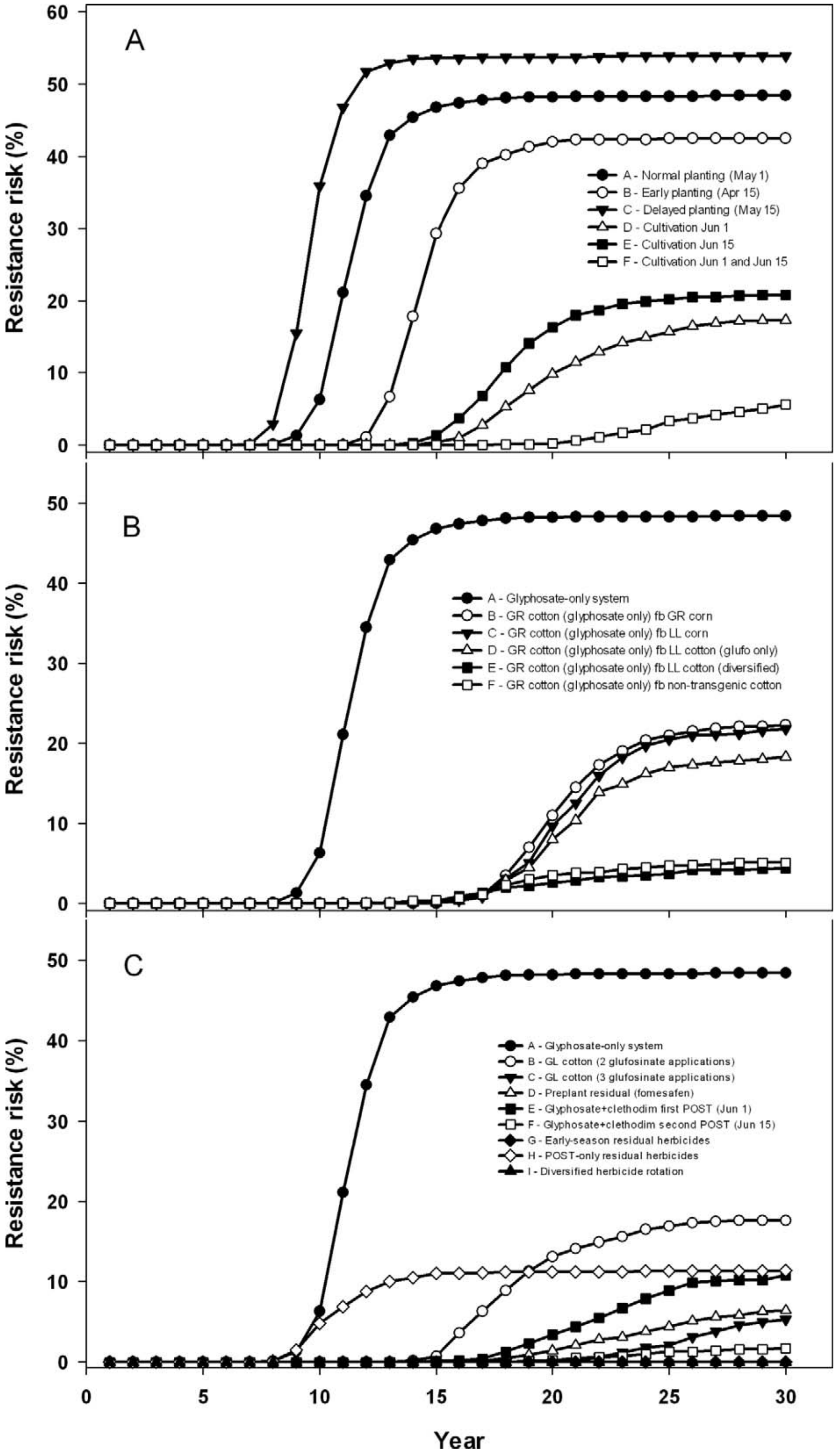

Figure 2. Impact of various management practices on the rate and risk of barnyardgrass evolving resistance to glyphosate. (A) Impact of altered planting dates and interrow cultivation: it is assumed that cotton is cultivated as a monoculture crop year after year and is treated with five glyphosate applications each year. (A) Cotton is planted during usual planting time (May 1); (B) cotton is planted a 2 wk earlier (April 15); (C) cotton is planted 2 wk later (May 15); (D) a glyphosate application is replaced with cultivation on June 1 (second POST timing); (E) a glyphosate application is replaced with cultivation on June 15 (third POST timing); (F) glyphosate applications at both the second and third POST timings are replaced with cultivation. (B) Impact of crop/trait rotations: (A) glyphosate-only system where glyphosate-

ases or glutathione *S*-transferases can endow enhanced rates of herbicide metabolism (Yuan et al. 2007). In rigid ryegrass (*Lolium rigidum* Gaudin), Neve and Powles (2005) demonstrated that resistance might evolve as a result of stacking of several genes of minor effect among the survivors. Yu et al. (2013) further confirmed that an enhanced rate of herbicide metabolism was responsible for resistance in the population studied by Neve and Powles (2005).The present model assumes a single gene trait and, as such, does not account for the possibilities of polygenic resistance evolution under the various herbicide rotation strategies tested using the model. Secondly, a weed management strategy that is based on intensive herbicide use can be economically and environmentally detrimental (Pimental et al. 1992).

An important insight from this model is that the diversified weed management programs currently implemented in response to GR Palmer amaranth in midsouthern U.S. cotton (a reactive response) provides a proactive means to greatly reduce the risks of glyphosate resistance in barnyardgrass. This phenomenon can also be true for other weed species in this system, but the selection pressure typically depends on how effective the alternative (i.e., nonglyphosate) strategies are on the given species. In the present case, the residual herbicides used for controlling Palmer amaranth are also effective on barnyardgrass, thus providing alternative MOAs for controlling resistant individuals. Nevertheless, the risk of GR barnyardgrass remains high in fields where glyphosate continues to be used with limited or no diversity.

It was difficult to generalize a best management program that integrates various nonchemical weed management options and that is applicable across a wide region, due to geographical and practical limitations. However, the model outputs illustrate the value of a number of nonchemical strategies in reducing the risk of resistance. Growers should aim at integrating every possible option in their weed management programs. The key to preventing and managing herbicide resistance in a sustainable manner is to maintain seedbank size at low levels using a diversified approach that utilizes all possible weed management tools.

Acknowledgments

Financial support for this work was provided by BASF, Monsanto, Valent, Dow AgroSciences, Syngenta Crop Protection, Bayer Crop Sciences, and Cotton Incorporated.

Literature Cited

Alarcon-Reverte, R., A. Garcia, M. Jasieniuk, T. Lanini, B. D. Hanson, A. J. Fischer. 2011. Glyphosate Driven Selection Strikes Again: Investigating the Mechanism of Resistance in *Echinochloa colona* from California. http://ucanr.org/blogs/UCDWeedScience/ blogfiles/6198.pdf. Accessed July 12, 2012.

Anderson, R. L. 2005. A multi-tactic approach to manage weed population dynamics in crop rotations. Agron. J. 97:1579–1583.

Bagavathiannan, M. V., J. K. Norsworthy, and K. L. Smith. 2012a. Post-dispersal herbivory of selected weed seeds as affected by residue cover. Abstract 350 *in* Proceedings of the Weed Science Society of America Meeting. Waikoloa, HI: Weed Science Society of America.

Bagavathiannan, M. V., J. K. Norsworthy, and K. L. Smith. 2012b. Weed seed decay as affected by depth and duration of seed burial. *In* Proceedings of the Weed Science Society of America Meeting. Waikoloa, HI: Weed Science Society of America.

Bagavathiannan, M. V., J. K. Norsworthy, K. L. Smith, and N. Burgos. 2011a. Seedbank size and emergence pattern of barnyardgrass (*Echinochloa crus-galli*) in Arkansas. Weed Sci. 59:359–365.

Bagavathiannan, M. V., J. K. Norsworthy, K. L. Smith, and P. Neve. 2011b. Seed production of barnyardgrass (*Echinochloa crus-galli*) in response to time of emergence in cotton and rice. J. Agric. Sci.. 150:717–724.

Bagavathiannan, M. V., J. K. Norsworthy, K. L. Smith, and P. Neve. 2011c. Density dependent growth and reproduction in barnyardgrass (*Echinochloa crus-galli*). Page 131 *in* Proceedings of the Southern Weed Science Society Meeting. San Juan, PR: Southern Weed Science Society.

Bagavathiannan, M. V., J. K. Norsworthy, K. L. Smith, and P. Neve. 2012c. Pollen-mediated gene flow in barnyardgrass. Page 166 *in* Proceedings of the Southern Weed Science Society Meeting. Charleston, SC: Southern Weed Science Society.

Baltazar, A. and R. J. Smith, Jr. 1994. Propanil-resistant barnyardgrass (*Echinochloa crus-galli*) control in rice (*Oryza sativa*). Weed Technol. 8:576–581.

Beckie, H. J. 2006. Herbicide-resistant weeds: management tactics and practices. Weed Technol. 20:793–814.

Beckie, H. J. 2011. Herbicide-resistant weed management: focus on glyphosate. Pest Manag. Sci. 67:1037–1048.

Blackshaw, R. E. 1990. Influence of soil temperature, soil moisture, and seed burial depth on the emergence of round-leaved mallow (*Malva pusilla*). Weed Sci. 38:518–521.

Brewer, C. E. and L. R. Oliver. 2009. Confirmation and resistance mechanisms in glyphosate-resistant common ragweed (*Ambrosia artemisiifolia*) in Arkansas. Weed Sci. 57:567–573.

Buhler, D. D., R. G. Hartzler, and F. Forcella. 1997. Implications of weed seedbank dynamics to weed management. Weed Sci. 45:329–336.

Cardina, J., C. P. Herms, and D. J. Doohan. 2002. Crop rotation and tillage system effects on weed seedbanks. Weed Sci. 50:448–460.

Cardina, J., H. M. Norquay, B. R. Stinner, and D. A. McCartney. 1996. Postdispersal predation of velvetleaf (*Abutilon theophrasti*) seeds. Weed Sci. 44:534–539.

Cavan, G., J. Cussans, and S. R. Moss. 2000. Modelling different cultivation and herbicide strategies for their effect on herbicide resistance in *Alopecurus myosuroides*. Weed Res. 40:561–568.

Culpepper, A. S., T. L. Grey, W. K. Vencill, J. M. Kichler, T. M. Webster, S. M. Brown, A. C. York, J. W. Davis, and W. W. Hanna. 2006. Glyphosate-resistant Palmer amaranth (*Amaranthus palmeri*) confirmed in Georgia. Weed Sci. 54:620–626.

←

resistant (GR) cotton monoculture is treated with five glyphosate applications each year; (B) GR cotton with glyphosate-only herbicide program is rotated with GR corn at each cycle; (C) GR cotton is rotated with glufosinate-resistant (LL) corn; (D) GR cotton is rotated with LL cotton, where LL cotton is treated with a glufosinate-only herbicide program; (E) GR cotton is rotated with LL cotton, where LL cotton is treated with a diversified herbicide program; (F) GR cotton is rotated with conventional (nontransgenic) cotton, where a standard nonglyphosate herbicide program is used. (C) Impact of herbicide rotations: (A) glyphosate-only system where monoculture GR cotton is treated with five glyphosate applications each year; (B) cotton tolerant to glyphosate and glufosinate (GL) with two glufosinate and three glyphosate applications each year; (C) GL cotton with three glufosinate and two glyphosate applications each year; (D) preplant residual: preplant application of fomesafen, followed by five glyphosate applications; (E) glyphosate-only system (option A) with clethodim tank-mixed with glyphosate at first POST application; (F) glyphosate-only system (option A) with clethodim tank-mixed with glyphosate at second POST application; (G) early-season residual herbicides: fomesafen applied prior to planting and fluometuron applied at planting, followed by four glyphosate applications; (H) POST-only residual herbicides: glyphosate (at planting), glyphosate tank-mixed with *S*-metolachlor at first and second POST applications, glyphosate tank-mixed with prometryn at third POST application, followed by MSMA tank-mixed with flumioxazin at lay-by application; (I) diversified herbicide rotation: fomesafen applied prior to planting, paraquat tank-mixed with fluometuron applied at planting, glyphosate tank-mixed with *S*-metolachlor at first and second POST applications, glyphosate tank-mixed with prometryn at third POST application, followed by MSMA tank-mixed with flumioxazin at lay-by application.

Davis, A. S. 2006. When does it make sense to target the weed seed bank? Weed Sci. 54:558–565.

Davis, A. S. and K. A. Renner. 2006. Influence of seed depth and pathogens on fatal germination of velvetleaf (*Abutilon theophrasti*) and giant foxtail (*Setaria faberi*). Weed Sci. 55:30–35.

DeVore, J. D., J. K. Norsworthy, and K. R. Brye. 2012a. Influence of deep tillage and a rye cover crop on glyphosate-resistant Palmer amaranth emergence in cotton. Weed Technol. 26:832–838.

DeVore, J. D., J. K. Norsworthy, and K. R. Brye. 2012b. Influence of deep tillage, a rye cover crop, and various soybean production systems on Palmer amaranth emergence in soybean. Weed Technol. In press.

Dickson, J. W., R. C. Scott, N. R. Burgos, R. A. Salas, and K. L. Smith. 2011. Confirmation of glyphosate-resistant Italian ryegrass (*Lolium perenne* ssp. *multiflorum*) in Arkansas. Weed Technol. 25:674–679.

Duke, S.O. and S. B. Powles. 2009. Glyphosate-resistant crops and weeds: now and in the future. AgBioForum 12:346–357.

Egley, G. H. and J. M. Chandler. 1978. Germination and viability of weed seeds after 2.5 years in a 50-year buried seed study. Weed Sci. 26:230–239.

Faircloth, W. H., M. G. Patterson, C. D. Monks, and W. R. Goodman. 2001. Weed management programs for glyphosate-tolerant cotton (*Gossypium hirsutum*). Weed Technol. 15:544–551.

Gaines, T.A., A. Cripps, and S.B. Powles. 2012. Evolved resistance to glyphosate in junglerice (*Echinochloa colona*) from the tropical Ord River region in Australia. Weed Technol. 26:480–484.

Gallandt, E. R. 2006. How can we target the weed seedbank? Weed Sci. 54:588–596.

Givens, W. A., D. R. Shaw, W. G. Johnson, S. C. Weller, B. G. Young, R. G. Wilson, M.D.K. Owen, and D. Jordan. 2009. A grower survey of herbicide use patterns in glyphosate-resistant cropping systems. Weed Technol. 23:156–161.

Grichar, W. J., B. A. Besler, K. D. Brewer, and B. W. Minton. 2004. Using soil-applied herbicides in combination with glyphosate in a glyphosate-resistant cotton herbicide program. Crop Prot. 23:1007–1010.

Hartzler, R. G. 1996. Velvetleaf (*Abutilon theophrasti*) population dynamics following a single year's seed rain. Weed Technol. 10:581–586.

Heap, I. 2013. The International Survey of Herbicide Resistant Weeds. http://www.weedscience. com. Accessed January 7, 2013.

Jasieniuk, M., A. L. Brule-Babel, and I. N. Morrison. 1996. The evolution and genetics of herbicide resistance in weeds. Weed Sci. 44:176–193.

Keeley, P. E. and R. J. Thullen. 1991. Growth and interaction of barnyard grass (*Echinochloa crus-galli*) with cotton (*Gossypium hirsutum*). Weed Sci. 39:369–375.

Liebman, M. and E. Dyck. 1993. Crop rotation and intercropping strategies for weed management. Ecol. Appl. 3:92–122.

Liebman, M., C. L. Mohler, and C. P. Staver. 2001. Ecological Management of Agricultural Weeds. New York: Cambridge University Press. 548p.

Lovelace, M. L., R. E. Talbert, R. E. Schmidt, E. F. Scherder, and J. R. Reaper. 2000. Multiple resistance of propanil-resistant barnyardgrass (*Echinochloa crus-galli*) to quinclorac. 44n Proceedings of the Rice Technical Working Group Meeting. Biloxi, MS: Rice Technical Working Group.

Massinga, R. A., R. S. Currie, M. J. Horak, and J. Boyer, Jr. 2001. Interference of Palmer amaranth in corn. Weed Sci. 49:202–208.

McClelland, M. R., R. E. Talbert, K. L. Smith, J. L. Barrentine, S. Matthews, and O. C. Sparks. 2003. Update on Glyphosate-Resistant Horseweed in Arkansas Cotton. Summaries of Arkansas Cotton Research. http://arkansasagnews.uark.edu/521-24.pdf. Accessed January 4, 2013.

[NASS] National Agricultural Statistics Service. 2012. Acreage (June 2012). http://usda01.library.cornell.edu/usda/nass/Acre//2010s/2012/Acre-06-29-2012.pdf. Accessed January 4, 2013.

Neve, P., A. J. Diggle, F. P. Smith, and S. B. Powles. 2003. Simulating evolution of glyphosate resistance in *Lolium rigidum* II: past, present and future glyphosate use in Australian cropping. Weed Res. 43:418–427.

Neve, P., J. K. Norsworthy, K. L. Smith, and I. A. Zelaya. 2011a. Modelling evolution and management of glyphosate resistance in *Amaranthus palmeri*. Weed Res. 51:99–112.

Neve, P., J. K. Norsworthy, K. L. Smith, and I. A. Zelaya. 2011b. Modeling glyphosate resistance management strategies for Palmer amaranth (*Amaranthus palmeri*) in cotton. Weed Technol. 25:335–343.

Neve, P. and S. B. Powles. 2005. Recurrent selection with reduced herbicide rates results in the rapid evolution of herbicide resistance in *Lolium rigidum*. Theor. Appl. Genet. 110:1154–1166.

Neve, P., M. Vila-Aiub, and F. Roux. 2009. Evolutionary-thinking in agricultural weed management. New Phytol. 184:783–793.

Nichols, R. L., J. Bond, A. S. Culpepper, D. Dodds, V. Nandula, C. L. Main, M. W. Marshall, T. C. Mueller, J. K. Norsworthy, A. Price, M. Patterson, R. C. Scott, K. L. Smith, L. E. Steckel, D. Stephenson, D. Wright, and A. C. York. 2009. Glyphosate-resistant Palmer amaranth (*Amaranthus palmeri*) spreads in the southern United States. Resistant Pest Manag. Newsl. 18:8–10.

Norsworthy, J.K., G. M. Griffith, R. C. Scott, K. L. Smith, and L. R. Oliver. 2008. Confirmation and control of glyphosate-resistant Palmer amaranth (*Amaranthus palmeri*) in Arkansas. Weed Technol. 22:108–113.

Norsworthy, J. K., D. Riar, P. Jha, and R. C. Scott. 2011. Confirmation, control, and physiology of glyphosate-resistant giant ragweed (*Ambrosia trifida*) in Arkansas. Weed Technol. 25:430–435.

Norsworthy, J. K., R. Scott, K. Smith, J. Still, L. Estorninos, Jr., and S. Bangarwa. 2009. Confirmation and management of clomazone-resistant barnyardgrass in rice. Page 211 *in* Proceedings of the Southern Weed Science Society Meeting. Orlando, FL: Southern Weed Science Society.

Norsworthy, J. K., K. L. Smith, R. C. Scott, and E. E. Gbur. 2007. Consultant perspectives on weed management needs in Arkansas cotton. Weed Technol. 21:825–831.

Norsworthy, J. K., S. Ward, D. Shaw, R. Llewellyn, R. Nichols, T. M. Webster, K. Bradley, G. Frisvold, S. Powles, N. Burgos, W. Witt, and M. Barrett. 2012. Reducing the risks of herbicide resistance: best management practices and recommendations. Weed Sci. 60 (Special Issue):31–62.

Ogg, A. G., Jr. and J. H. Dawson. 1984. Time of emergence of 8 weed species. Weed Sci. 32:327–335.

Osten, V. A., S. R. Walker, A. Storrie, M. Widderick, P. Moylan, G. R. Robinson, and K. Galea. 2007. Survey of weed flora and management relative to cropping practices in the north-eastern grain region of Australia. Aus. J. Exp. Agric. 47:57–70.

Pimental, D., H. Acquay, M. Biltonen, P. Rice, M. Silva, J. Nelson, V. Lipner, S. Giordano, A. Horowitz, and M. D'Amore. 1992. Environmental and human costs of pesticide use. Bioscience 42:750–760.

Porterfield, D., J. W. Wilcut, and S. D. Askew. 2002. Weed management with CGA-362622, fluometuron, and prometryn in cotton. Weed Sci. 50:642–647.

Preston, C. 2010. Australian Glyphosate Resistance Register. Australian Glyphosate Sustainability Working Group. www.glyphosateresistance.org.au. Accessed January 6, 2013.

Reddy, K. N. and J. K. Norsworthy. 2010. Glyphosate-resistant crop production systems: impact on weed species shifts. Pages 165–184 *in* V. K. Nandula, ed. Glyphosate Resistance in Crops and Weeds: History, Development, and Management. New York: J. Wiley.

Riar, D. S., J. K. Norsworthy, D. B. Johnson, R. C. Scott, and M. Bagavathiannan. 2011. Glyphosate resistance in a johnsongrass (*Sorghum halepense*) biotype from Arkansas. Weed Sci. 59:299–304.

Rushing, G. S. and L. R. Oliver. 1998. Influence of planting date on common cocklebur interference in early maturing soybean. Weed Sci. 46:99–104.

Shaner, D. L. 2000. The impact of glyphosate-tolerant crops on the use of other herbicides and on resistance management. Pest Manag. Sci. 56:320–326.

Shaner, D. 2013. My View. Herbicide Resistance Action Committee. http://www.hracglobal.com/ Publications/MyView.aspx. Accessed January 7, 2013.

Soteres, J. K. 2012. The Roundup Ready revolution in agriculture. Abstract 309 *in* Proceedings of the Weed Science Society of America Meeting. Waikoloa, HI: Weed Science Society of America.

Teasdale, J. R. 1995. Influence of narrow row/high population corn (*Zea mays*) on weed control and light transmittance. Weed Technol. 9:113–118.

Teasdale, J. R. and C. L. Mohler. 1993. Light transmittance, soil temperature, and soil moisture under residue of hairy vetch and rye. Agron. J. 85:673–680.

Thornby, D. F. and S. R. Walker. 2009. Simulating the evolution of glyphosate resistance in grains farming in northern Australia. Ann. Bot. 104:747–756.

[USDA-ERS] U.S. Department of Agriculture–Economic Research Service. 2012. Adoption of Genetically Engineered Crops in the U.S.: Recent Trends in GE Adoption. http://www.ers.usda.gov/data-products/adoption-of-genetically-engineered-crops-in-the-us/recent-trends-in-ge-adoption.aspx#.UXGDIGfy3z4. Accessed April 19, 2013.

Walker, S., V. Osten, A. Storrie, G. Robinson, T. Cook, and K. Galea. 2002. Weeds at risk of developing herbicide resistance in the different cropping systems of the northern region. Pages 620–621*in* Proceedings of the 13th Australian Weeds Conference. Perth, WA: Plant Protection Society of Western Australia.

Walsh, M. J., R. B. Harrington, and S. B. Powles. 2012. Harrington Seed Destructor: a new nonchemical weed control tool for global grain crops. Crop Sci. 52:1343–1347.

Werth, J. A., C. Preston, I. N. Taylor, G. W. Charles, G. N. Roberts, and J. Baker. 2008. Managing the risk of glyphosate resistance in Australian glyphosate-resistant cotton production systems. Pest Manag. Sci. 64:417–421.

Wiese, A. M. and L. K. Binning. 1987. Calculating the threshold temperature of development for weeds. Weed Sci. 35:177–179.

Wilson, M. J., J. K. Norsworthy, D. B. Johnson, E. K. McCallister, J. D. DeVore, J. M. Griffith, and S. K. Bangarwa. 2010. Herbicide programs for controlling ALS-resistant barnyardgrass in Clearfield rice. *In* Proceedings of the Rice Technical Working Group Meeting. Biloxi, MS: Rice Technical Working Group.

Yu, Q., H. Han, G. R. Cawthray, S. F. Wang, and S. B. Powles. 2013. Enhanced rates of herbicide metabolism in low herbicide-dose selected resistant *Lolium rigidum*. Plant Cell Environ. 36:818–827.

Yuan, J. S., P. J. Tranel, and C. N. Stewart. 2007. Non–target-site herbicide resistance: a family business. Trends Plant Sci. 12:6–13.

Zelaya, I. A., M. D. Owen, and M. J. VanGessel. 2004. Inheritance of evolved glyphosate resistance in *Conyza canadensis* (L.) Cronq. Theor. Appl. Genet. 110:58–70.

Received January 15, 2013, and approved April 27, 2013.