



Modeling the evolution of herbicide resistance in weeds: Current knowledge and future directions

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Received: 18 March 2016; Revised: 4 May 2016

ABSTRACT

Simulation models have been instrumental in understanding the evolutionary dynamics of herbicide resistance in weeds and making informed management decisions for preventing/delaying resistance. Continued improvements in model development and analysis will be critical to address the complex interactions involved in herbicide resistance evolution. Here we review current knowledge on the development of herbicide resistance simulation models using published examples and also discuss future directions.

Key words: Herbicide resistance, Simulation modeling, Population dynamics, Selection pressure, resistance best management practices

Simulation models have long been employed to understand weed population dynamics and changes to vital rates in response to crop and weed management practices (Holst *et al.* 2007). Their utility has been further extended to gain a deeper understanding of herbicide resistance evolution in weed communities and devise effective resistance management strategies (*e.g.*, Maxwell *et al.* 1990, Maxwell and Mortimer 1994, Diggle *et al.* 2003, Neve *et al.* 2011). Simulation models save tremendous amount of time and resources, which would otherwise be spent on conducting long-term field experiments, which are often impracticable. A prime benefit of using simulation models is that they allow for the comparison of various management options and evaluate the relative benefits of different management combinations in reducing the risk of resistance (Jasienski *et al.* 1996, Cavan *et al.* 2000). For instance, Bagavathiannan *et al.* (2013) used a model to compare the relative benefits of altered planting dates, cultivation, crop/trait rotations, and herbicide rotations in proactive herbicide resistance management in barnyardgrass (*Echinochloa crus-galli* (L.) Beauv.). Thus, models can serve as excellent decision-support tools for growers and weed managers for making informed management decisions.

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This article was presented at the Symposium on "Herbicide Resistance: Current Status and Future Challenges Globally" held as part of the 25th APWSS Conference, Hyderabad, India during 13-16 October, 2015.

Model components

The evolution of herbicide resistance is influenced by three key factors: (1) factors related to the ecology and biology of the weed species, (2) genetic factors governing the rate of resistance evolution, and (3) management factors. Therefore, models that simulate herbicide resistance evolution are comprised of three integral components - ecology and biology, population genetics, and management (Diggle *et al.* 2003, Roux and Reboud 2007). A general framework of a herbicide resistance simulation model for an annual weed species is presented in (Figure 1). The processes on ecology and biology is usually represented by a demographic sub-model, which accounts for initial seedbank size, annual germination proportion, seedling recruitment pattern, density-dependent survival and fecundity, post-dispersal seed loss, and seed immigration/emigration. The genetic processes include initial frequency of resistance alleles, mode of inheritance of resistance, mating system, dominance, and fitness. Management is a critical factor determining resistance evolution, particularly the combinations of management options used and efficacies of different options.

Roux and Reboud (2007) suggested that genetic factors are important for a highly outcrossing species, whereas management is important for a predominantly selfing species in influencing resistance dynamics. Further, the intrinsic population dynamics, particularly seedbank persistence

(Mortimer *et al.* 1992) and fitness (Vila-Aiub *et al.* 2009) can greatly influence resistance. The significance of ecological fitness and gene flow in governing the evolution and dynamics of herbicide resistance was demonstrated by Maxwell *et al.* (1990). Model sensitivity analysis is used to identify the prime parameters that influence model dynamics. Some notable ones for which the models were found to be highly sensitive include initial seedbank density, initial frequency of resistance alleles, proportion of seedling recruitment, post-dispersal seed loss, and annual seedbank loss (Neve *et al.* 2011, Bagavathiannan *et al.* 2013). Model analysis revealed that the likelihood for resistance evolution is low under low initial seedbank size, low initial frequency of resistance alleles, low levels of seedling recruitment, high post-dispersal seed loss, and high annual seedbank loss (Fig. 2). Stochasticity is often included in the models to account for likely spatial and temporal variations in parameter values across different production fields and years. Diggle and Neve (2001) outlined the specifics of herbicide resistance simulation modeling and the applications and limitations of various methodologies used in model development.

Examples of model applications

Herbicide resistance simulation models are broadly grouped into simplified major-gene based models, models simulating polygenic resistance evolution, models accounting for spatial heterogeneity in resistance evolution and spread (*i.e.* spatially explicit models), and models used as education and extension tools.

Simplified major-gene-based models: In a pioneering research, Gressel and Segel (1978) used a simple population model in an attempt to identify important factors that influence the evolution of herbicide resistance. They used the model to illustrate the evolution of resistance under conditions of monoculture and/or single herbicide usage. In subsequent research, Gressel and Segel (1990) modeled the effectiveness of herbicide rotations and mixtures for managing resistance. Maxwell *et al.* (1990) used a population model to predict the evolution, spread, and dynamics of resistant and susceptible weed genotypes and found that resistance could evolve rapidly under repeated herbicide applications in the absence of a nearby susceptible source population. Gorddard *et al.* 1995 adopted the resistance simulation model developed by Maxwell *et al.* (1990) and developed an optimal control model for weed management under herbicide resistance, with a

goal of finding an economic balance between ongoing control of susceptible weeds and future likelihood for resistance evolution.

Mortimer *et al.* (1992) assessed the fitness of susceptible and resistant biotypes of blackgrass (*Alopecurus myosuroides* Huds.) under different herbicide selection regimes and tested their impacts on resistance. They emphasized that the interaction between density-dependent and density-independent regulations was a critical factor in controlling the frequency of resistance alleles. Using a simple model, Jasieniuk *et al.* (1996) compared the rates of resistance evolution under various mutation rates, management efficacies, and levels of outcrossing. Cavan *et al.* (2000) investigated the effect of cultivation regimes, herbicide factors (rotations and kill rate), initial frequency of resistance alleles, and initial seedbank density on the number of years taken for the evolution of target-site resistance for aryloxyphenoxypropionate (AOPP) and cyclohexanedione (CHD) herbicides in blackgrass. The authors developed a subsequent model (Cavan *et al.* 2001) for predicting and managing the risks of resistance evolution for AOPP and CHD herbicides in wild oat (*Avena fatua* L.). Hanson *et al.* (2002) developed a quantitative model to simulate the evolution of imazamox resistance in jointed goatgrass (*Aegilops cylindrica* Host) in imazamox-resistant wheat (*Triticum aestivum* L.) production in the Pacific Northwest, specifically assessing the impacts of different agronomic practices on the evolution and persistence of resistance in this species.

Gustafson (2008) developed a herbicide resistance modeling system (HERMES) to explore the sustainability of glyphosate in glyphosate-resistant cropping systems. Results suggested that prudent use of additional herbicides are necessary to sustain the utility of glyphosate in North American cropping systems. Werth *et al.* (2008) used a simulation model for guiding the development of a robust crop management plan for minimizing the risk of glyphosate-resistance evolution in some of the major weeds present in Australian glyphosate-resistant cotton production systems. Thornby and Walker (2009) developed a model for predicting the evolution of glyphosate resistance in awnless barnyardgrass/junglerice (*Echinochloa colona* (L.) Link) in Northern Australian sub-tropical grains farming region and examined the rate of resistance evolution under a range of key model parameters and under conditions expected to result in high selection pressure.

Jacquemin *et al.* (2009) modeled the effect of herbicide mixtures on the evolutionary dynamics of a weed population in which resistance has already occurred for one of the modes of action (MOAs) used in the mixture. Their findings illustrated that use of herbicide mixtures as a resistance management strategy is inadequate if resistance has already been detected in that population. Neve *et al.* (2011) investigated various herbicide use strategies (herbicide mixtures and rotations) applied at various timings to identify effective management options for mitigating the risk of glyphosate resistance evolution in Palmer amaranth (*Amaranthus palmeri* S. Wats) in the midsouthern US cotton production system. Richter *et al.* (2012) developed an evolutionary genetic model, using the joint evolutionary dynamics model of Huillet and Martinez (2011), for understanding the evolution and dynamics of metabolic (monogenic) resistance under field conditions.

Models have also evaluated the risk of multiple herbicide resistance evolution conferred by more than one unlinked major gene. Diggle *et al.* (2003) modeled the risk of multiple resistance evolution conferred by two discrete, unlinked nuclear genes in a finite weed population. They compared the effectiveness of herbicide mixtures and annual herbicide rotations and concluded that herbicide mixtures (or combinations) rather than annual rotations can greatly delay resistance evolution. Bagavathiannan *et al.* (2014a) predicted the risk of simultaneous and independent evolution of resistance to more than one resistance trait (resistance to the acetolactate synthase (ALS) and acetyl-CoA carboxylase (ACCase) inhibitors) in barnyardgrass in mid Southern US rice production. Results illustrated the value of combining multiple effective MOAs (three or more) in minimizing the risk of resistance in this species.

Single-gene based models were also used for risk assessment of transgenic herbicide-resistant crop lines. For instance, Madsen *et al.* (2002) employed a simulation model to understand the risk of glufosinate resistance evolution in weedy rice (*Oryza sativa* L.) in glufosinate-resistant rice production in Latin America.

Models concerned with polygenic resistance: The majority of the existing models are concerned with single major genes, but polygenic resistance is also likely to occur depending on the nature of management regime followed. Gardner *et al.* (1998) modeled strategies for preventing both single-gene based and polygenic resistance and recommended

that a revolving dose strategy (*i.e.*, dosage rotation) can be effective in delaying resistance evolution to both modes compared to successive applications of constant doses. Renton (2009) developed the PERTH model (Polygenic Evolution of Resistance To Herbicides), an individual-based simulation model for demonstrating the polygenic basis of resistance evolution in annual ryegrass (*Lolium rigidum* Gaud.) under low herbicide doses. Manalil *et al.* (2012) utilized the PERTH model along with data collected from field study for identification of the resistance mechanism in a ryegrass population selected under low-dose applications and found that resistance was polygenic.

Spatially explicit models: Most models developed so far predict resistance under homogeneous environments. However, production fields are typically heterogeneous and resistance evolution and spread largely occurs at spatially heterogeneous patterns. A small number of models have been developed by accounting for the movement of propagules (*i.e.*, gene flow) in a heterogenous spatial scale. Using a spatio-temporal model, Richter *et al.* (2002) modeled the spread of herbicide resistance in a hypothetical grass weed and suggested that spatial spread of resistance could be minimized by maintaining untreated strips between adjacent production fields. Roux and Reboud (2007) used a model to understand herbicide resistance dynamics in a spatially heterogeneous environment by accounting for the presence of favorable and unfavorable areas across a cultivated landscape. The model outputs indicated that resistance dynamics is governed by interactions among various factors, some of which are not controlled by human and are spatially variable. Liu *et al.* (2010) modeled the spatial spread of glyphosate-resistant common waterhemp (*Amaranthus rudis* Sauer.) in the US Midwest. With maximum wind speeds of 10 m/s, the model predicts resistance movement for less than 20 km in four years. When comparing model outputs with field observations, the authors concluded that factors other than wind (such as movement of farm equipment) may play an important role in the long-distance spread of resistance. Rummland *et al.* (2012) predicted the spatial distribution of resistant loose silkybent (*Apera spica-venti* (L.) P. Beauv.) plants spreading across a production field, by simulating random seed distribution and gene flow using a cellular automation process.

Models as educational tools: Besides their use as research tools, models can also serve as excellent educational tools in transferring research knowledge

to growers. These models do not necessarily simulate or predict resistance, but test various combinations of strategies on long-term weed seedbanks and economics, with direct relevance to herbicide resistance management. They tremendously help the extension personnel demonstrate to the clients the benefits of adopting or the penalties of not adopting a given resistance management practice. In fact, growers and crop consultants can themselves use such models to evaluate and compare various weed management strategies on the long-term sustainability and profitability of farming operations. Rainbolt *et al.* (2004) modified a general life cycle model into an extension teaching tool to demonstrate the effects of weed biology factors and crop rotation on resistance evolution in a number of major weed species in the Pacific Northwest dryland wheat-based cropping systems. Stanton *et al.* (2008) developed a risk calculator to enable farmers and crop advisors assess the risk of glyphosate resistance evolution in annual ryegrass in Australia. Another notable example is the ryegrass integrated management (RIM) model, widely adopted in the Australian Southern grainbelt (Pannell *et al.* 2004, Lacoste and Powles 2014). The original RIM model was adapted to other weed species, notably RIMPhil for barnyardgrass (Beltran *et al.* 2011), RIM for wild radish (*Raphanus raphanistrum* L.) (Monjardino *et al.* 2003), PIM for poppy (*Papaver rhoeas* L.) (Torra *et al.* 2010), and PAM for Palmer amaranth (Bagavathiannan *et al.* 2014b). The RIM model has also served as the basis for ‘weed seed wizard’, a more advanced user-oriented software model for guiding Best Management Practices for herbicide resistance management in Australia (Renton *et al.* 2007).

Challenges and limitations

Simulation models as both research and educational tools have been greatly assisting the development and transfer of valuable knowledge, but there are some limitations and challenges to the development and application of models for resistance management. A prime limitation is the lack of specific data for parameter estimation. Rapid progress has been made over this past decade in collecting necessary biological and management data for supporting model developments, but there is still a long way to go in amassing a comprehensive knowledge base. Specifically, details on mutation rates, initial frequency of resistance alleles, genetic basis of resistance, fitness costs associated with resistance alleles, seedbank dynamics, patterns of gene flow, and metapopulation dynamics within

agricultural landscapes is yet to be accumulated. The current models rely heavily on simplifying assumptions and expert opinions in generating predictions. Furthermore, most of the existing resistance simulation models are deterministic (do not account for environmental and demographic stochasticity) and spatially implicit (assume that the production fields are homogeneous). As a result, there are uncertainties on the accuracy of model predictions. Yet, models remain valuable as the best available tool in understanding system behavior, given the limited inherent knowledge of the system. The models will gradually become more robust as more relevant data are continued to be collected.

A model requires validation in order to secure trust among users. Validation can be replicative, predictive or structural (Zeigler 1985, Troitzsch 2004). Replicative and predictive validation deals with match between model predictions and data already acquired or to be acquired from the real system, respectively. Structural validation, however, deals with reproducing real system behavior in a way that the system functions to produce the behavior. Model validation typically presents practical challenges due to the hidden weed population and farming system variables (Rykiel 1996, Thornby and Walker 2009). Moreover, timely validation is critical to make useful decisions for preventing resistance before it is too late. Direct empirical validation from field evidence has been used as a convenient way for model validation in some situations (Neve *et al.* 2011, Bagavathiannan *et al.* 2014a). Even then required information from such field evidences are extremely difficult to obtain because details are recorded only after resistance is noticed, but the field management history over the life of the system is rarely documented (Thornby and Walker 2009). Thus, empirical field validations may be useful, but not adequate.

A number of alternative approaches have been proposed to validate the models. Barlas (1996) suggested that model validations should be based on verification of model structure and output patterns rather than its predictive accuracy. Balci (1995) outlined 15 principles for model validation, emphasizing that it is unreasonable to expect perfect representation of the system since models are only an abstraction of the system in question. Balci (1995) further argued that validation is not a binary variable (correct or incorrect), but is a test of the degree of model credibility and judgment on the model

sufficiency for specific applications. Expert knowledge test of model structure was also suggested as a way of validating the model throughout the course of its development (Thornby *et al.* 2009). Although some of the validation approaches noted above may not be ideal, the shortfall should be weighed against the value of the model as a decision-support tool in making timely management decisions.

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