



How do spatial heterogeneity and dispersal in weed population models affect predictions of herbicide resistance evolution?



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ABSTRACT

Weed population simulations can be useful to predict the effects of alternative management practices on herbicide resistance (HR) evolution. Almost all previous simulations have ignored the possibility of within-field spatial structure in a weed population, instead making the implicit assumption of perfect dispersal and spatial homogeneity in population density and genetics. The effects of this simplifying assumption have not been examined, despite the fact that dispersal limitations and spatial structure within the population are likely to occur and to affect the evolution of resistance. Therefore, we developed a new spatially-explicit model called SOMER, and examined how changing the following factors affected the predicted evolution of resistance: the degree of spatial resolution used in the model; whether resistance was semi-dominant or fully-dominant; distances of pollen and natural seed dispersal; and inadvertent collection and grain harvester weed seed dispersal (GHWS). Simulations showed that spatial resolution is important when modelling HR evolution, with the size of sub-population divisions, the pollen dispersal parameter, the level of dominance, and GHWS all being important factors in predicting the rate and type of HR evolution. Our results show that accounting for spatial structure and dispersal does affect predictions of HR evolution, with the non-spatial model generally predicting faster resistance evolution compared to the more realistic equivalent spatial model. Most importantly, GHWS increased the speed of HR evolution. Our spatial model also allowed us to investigate the dynamics of density and genetic structure within patches of herbicide resistant weeds, and we found that resistance genes were spread several times wider than the visible patch, and that homozygous mutations were commonly found in more centrally located weeds. We conclude that an 'integrated spatial modelling' approach that accounts for spatial structure should be considered when modelling HR evolution, and the evolution of resistance in general.

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1. Introduction

Herbicide resistance (HR) in agricultural weeds has evolved in many countries as a consequence of the widespread and persistent use of herbicides (Heap 2017). Adoption of no-till farming systems increased grower reliance on herbicides, resulting in an increase in herbicide resistance. One common farmer response to herbicide resistant weeds is to use alternative herbicides to regain weed control. However, increasing demands for alternative herbicides have not been matched by a satisfactory rate of new herbicide discovery and registration. In addition, once HR is established within weed populations, it may be difficult to remove. The paucity of usable her-

bicides to control weeds has led to a higher priority for responsible stewardship of herbicides, which is now being globally advocated (Norsworthy et al., 2012).

While several farming practices are commonly acknowledged as slowing the speed of resistance evolution (Norsworthy et al., 2012), new populations of herbicide resistant weeds are still appearing (Heap 2017). More work is needed to identify and quantify the role of specific practices in delaying the evolution of herbicide resistant populations. Typically, early in the evolution of a resistant population, there is a 'latent' stage where weed numbers are low whilst the frequency of resistance genes in the population is being enriched. This stage is largely invisible in the field, thus it is difficult to track early resistance evolution through field observations alone. However, once the resistant weeds are at high frequency in the population, herbicide failure can rapidly follow, illustrating the importance of the early latent stage. By allowing us to focus on and understand this stage, simulation modelling can aid in the early

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identification of farming practices more likely to delay resistance evolution and keep weed numbers low.

Previous modelling of the evolution of HR had largely assumed, at least implicitly that there is spatial homogeneity of both weed seeds and resistance genes (reviewed in [Renton et al., 2014](#); [Bagavathiannan and Norsworthy 2016](#)). For example, weeds in a field are often represented as a single population, with equal competition, and random mating (of cross-pollinating species) equally possible between all individuals across the field. In reality, weeds are often patchy in their distribution. Spatial distinction within a crop field means there can be local variations in resistance gene frequency or weed density, and growth reduction due to localised competition within weed patches. Localised variations in gene frequency can lead to localised genetic drift, which in turn can result in local gene extinctions, or concentrations of particular genes within cross-pollinated plants. In particular, allowing all weeds within any simulated large agricultural field to freely interbreed each year appears to be an unreasonable assumption (reviewed in [Renton et al., 2014](#)). Predictions and recommendations generated using models that account for spatial heterogeneity are thus likely to be more accurate. However, the effect of spatial heterogeneity in weed populations on resistance evolution has not been explored.

There are examples of spatially-explicit models of HR evolution, but these studies have generally not investigated whether the specific spatial location of individual plants makes a difference to modelled predictions. Previous spatial modelling of HR often focussed on how variation in the landscape can influence the spread of resistance evolution, but still represented populations within a field (or environment) as homogeneous ([Roux and Reboud 2007](#); [Richter 2008](#); [Roux et al., 2008](#)). Some spatial modelling of HR has recognised that weed populations within a field are not homogeneous, and examined the spread of specific genes ([Richter et al., 2002](#); [Richter and Seppelt 2004](#); [Rummland et al., 2012](#)). However, no study has clearly investigated to what extent and in what ways spatial heterogeneity will affect simulated predictions of HR evolution.

Spatial structure within weed populations will influence resistance evolution due to the movement of genetic material within the simulated area. Pollen and seed are dispersed within the field both by natural effects and by human activities, with weed seed dispersal by harvest machinery possibly one of the most important factors in moving herbicide resistant weeds throughout a crop field ([Barroso et al., 2006](#)). Many of the weed species that are problematic in crops retain their seeds at maturity at a height that ensures collection by the grain harvester ([Walsh and Powles, 2014](#)). This 'harvested' weed seed is immediately fanned out behind the grain harvester and thus dispersed across the field ([Blanco-Moreno et al., 2004](#)).

Gene flow within a simulated area will also be affected by the specific characteristics of the resistance genes. Herbicide resistance can be conferred by genes encoding traits with varying levels of dominance, which will interact with spatial structure in the population. Spatial modelling allows us to account for natural and human-mediated gene flow and its interaction with different levels of dominance in predicting HR evolution, which is simply not possible with non-spatial models. In addition, none of the previous spatially-explicit field-scale modelling of HR ([Richter et al., 2002](#); [Richter and Seppelt 2004](#); [Rummland et al., 2012](#)) has examined how the parameterisation of the pollen and natural seed dispersal functions will affect predictions of HR evolution at the field scale.

The first aim here is to; (1) develop a spatially-explicit weed model of HR evolution, and then use this model to test whether a spatially-explicit model gives different predictions to a non-spatially-explicit model; (2) test how the predictions of a spatially-explicit model were affected by semi-dominant vs fully-dominant resistance; (3) investigate alternative parameterisations

of dispersal functions mimicking the natural spread of pollen and seeds; (4) investigate the effects of inadvertent grain harvester weed seed dispersal (GHWS) during crop harvest.

2. Methods

2.1. Model structure

2.1.1. Model overview

To address the aims of this study, a new spatially-explicit individual-based stochastic model, the Spatially Orientated Model of Evolutionary Resistance (SOMER), has been developed to simulate the evolution of resistance in weeds infesting a crop field. Essentially, aspects related to spatial structure and the dispersal of pollen and seeds within a field have been added to our earlier non-spatial model ([Somerville et al., 2017](#)). In the new SOMER model, the simulated crop field area is evenly subdivided into square sectors, similar to a checkerboard, each with an associated sub-population of weeds. The term 'integrated spatial modelling' has been chosen to describe this type of model, where every plant and weed seed within the field area is accounted for, along with their individual age, location and resistance genetics. Squares have been chosen as the best sector shape as they align with activities such as crop seeding and harvest. The weed seeds are assumed to germinate and emerge throughout the growing season, modelled as discrete sequential weed cohorts ([Fig. 1](#)), in the same way as our previous non-spatial model. The earliest emerging weeds (prior to crop seeding) are classified as cohort one, with subsequent subdivisions between weed cohorts based on sequential annual activities such as herbicide application dates. The new model tracks the number of weeds of each genotype, in each cohort, in each sector of the simulated area, in each year, as well as the seeds of each genotype within the soil seedbank, within each sector.

Competition between weed cohorts and crop plants is modelled in the same way as in our non-spatial model ([Somerville et al., 2017](#)), using a hyperbolic competition function ([Firbank and Watkinson 1986](#); [Somerville et al., 2017](#)) to predict the number of weeds/m² and their subsequent seed production, except that competition is modelled separately within each sub-population (i.e. within each sector). Weed numbers are capped at a maximum density of 100 plants/m² via a non-selective cull, and model calibration was used to give realistic results ([Somerville et al., 2017](#)). Interactions between sub-populations by dispersed pollen and seed occur after determination of the amount of weed seed produced by each sub-population. To maintain consistent language it is written that 'seed dispersal' is the spread of weed seeds between sectors, whereas pollen travels within and between sub-populations, which are growing within sectors. Sector size is invariant within each simulation, whereas the size of each sub-population is dynamic, and influenced by annual processes such as herbicide application, competition, seed dispersal, and the evolution of resistance. The model is implemented in the 'R' language ([R Core Team, 2014](#)), and the model code is available on request from the authors.

2.1.2. Genetics

While our model can simulate the inheritance of up to six resistance genes using independent assortment, here we modelled resistance conferred by a single gene. The weed is assumed to be obligate cross-pollinating and diploid, with individuals possessing three possible genotypes: homozygous susceptible (SS), heterozygous resistant (RS) or homozygous resistant (RR). The genotype of each new seed is determined stochastically from a hereditary transition matrix ([Richter et al., 2016](#)). Mating is random, with restrictions imposed by cohort-based fitness and a sector-based pollen dispersal function. The cohort-based fitness weightings are based on the premise that plants emerging earlier will be bigger

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