Does adding a spatial component to a herbicide resistance population model improve understanding and predictions of the build-up of herbicide resistance over time?

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Abstract: Weeds are patchy, and these patches can be dynamic. A model of weed population dynamics and herbicide resistance evolution that includes a spatial component can allow for more realistic modelling of important spatial heterogeneity. Local variability in genetic mutations and frequencies and density/yield interactions, and the stochastic nature of genetic drift and migration can be included. This can lead to new insights and understanding and an increase in grower and researcher confidence in model predictions.

One useful way to increase the transparency, accuracy and usefulness of an herbicide resistance model is through increasing the realism whereby biological processes are represented in the model. To model plant interactions occurring uniformly across a whole field of weeds is unrealistic; biological interactions and dispersal are typically local scale, likely causing the patches of weeds that occur in fields. The aim here was therefore to include a spatial component in an existing model by dividing a single homogeneous population into many individual sub-populations in areas defined as `sections'. This allowed us to incorporate both natural and anthropogenic pollen and seed spread within and between sections into the new SOMER model (Spatially Orientated Model of Evolutionary Resistance).

This new spatial model was developed by dividing a single homogenous population into many smaller sub-populations. These sub-populations were spread to cover the central area (1.1664 ha) of a larger homogeneous field. Pollen and seed spread between sub-populations (and pollen from further afield) was added each year to simulate realistic conditions. This new SOMER model was then compared with an identically parameterized non-spatial model of a single homogeneous population of the same size (1.1664 ha).

The spatial model has already provided new insights. For example, earlier non-spatial models predict that the number of resistant weeds in a field typically increases by a constant factor each year, at least until densities become high. However preliminary results from this spatial model indicate that resistance builds up more slowly when spatial factors are accounted for, due the need for the resistance genes to spread through the population. Additional studies evaluating the importance of pollen dispersal and the movement of seed by machinery are currently being examined.

Keywords: Herbicide resistance, spatial modelling, SOMER, agriculture

1. INTRODUCTION

Today's farming industry faces the serious issue of declining weed control due to evolved resistance to herbicides. Many methods have been proposed to delay the build-up of herbicide resistance, such as changing fertilizer rates or annual rotation strategies (Norsworthy et al., 2012), and new discoveries are extending farmers' options. However despite researchers' best efforts, farmers are often slow to adopt new strategies and many farmers are not using best practice (Walsh, Newman, & Powles, 2013). Difficulties in choosing strategies to implement on their farm are compounded by lack of situation-specific knowledge of the relative benefits of different strategies; the most effective combinations of strategies will most likely vary between different farming situations. Long-term multi-faceted field trials are slow, site-specific and expensive.

To compound these difficulties agriculturalists are sometimes reluctant to invest in new non-herbicide strategies. Many farmers are simply waiting for new herbicides to be developed, and in addition farmers have concerns that costly efforts to control herbicide resistance build-up within their farms may be thwarted by movement onto the farm of resistant seed and/or pollen from neighbouring farms, despite some evidence to the contrary (Malone, Boutsalis, Baker, & Preston, 2014). Patches of herbicide resistant weeds on individual farms can develop very quickly, and the specific source of resistant weeds is seldom known.

Spatial modelling is predicted to give timely, more realistic results. In addition these more realistic results will allow better visualization with an aim of increasing understanding by both non-modelling researchers and farmers of the importance of targeting best practices to minimize the build-up of herbicide resistance, and the accompanying increase in weed numbers.

2. MODEL DYNAMICS OVERVIEW

This study compares two simulations of the evolution of herbicide resistance in an annual weed growing in a typical winter cropping program in a Mediterranean-type climate. A new Spatially Oriented Model of Evolutionary Resistance (SOMER) model was compared to a simpler homogeneous model using identical population parameters. These two models both represent single gene resistance, while incorporating features from the existing "Polygenic Evolution of Resistance To Herbicides" (PERTH) model (Renton, 2009; Renton et al., 2011). The models are implemented in the 'R' language (R Core Team, 2014). Calculations of competition, seed production and seed genotype were conducted stochastically for each year of the simulations. These calculations were carried out for each genotype, with the equations used sourced from Renton et al. (2011).

In the SOMER model the central 1.17 ha area was split into one-metre square sections, each containing a separate sub-population. These sub-populations were modelled separately each year, except at pollination and seed-fall, when mixing of genetic material through seed and pollen dispersal occurred between sub-populations. Squares were chosen as the best section shape as they align with activities such as seeding and harvest. The movement of pollen and seed between these sub-populations in the SOMER model is illustrated by the dotted lines in Figure 1, whereas the simpler homogenous model it is compared to does not include this interaction.
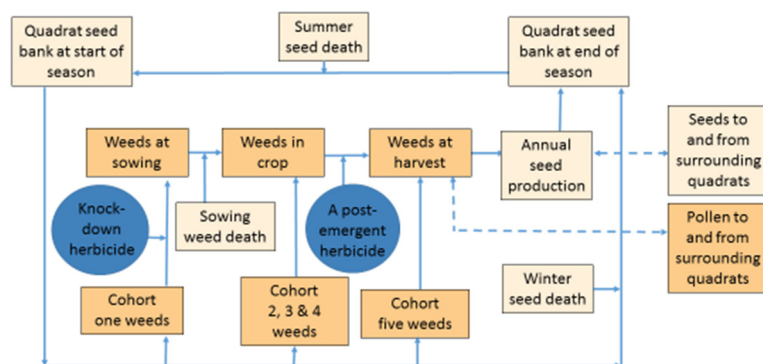

Figure 1. Representation of the lifecycle of managed *L. rigidum* weeds growing in a Western Australian wheat crop and modelled in both the non-spatial and SOMER models.

3. PARAMETRIZATION

The simulations in this study were based on a single well-studied weed species, annual ryegrass (*Lolium rigidum*), within a wheat crop (*Tritium* spp). Annual ryegrass (*L. rigidum*) is a widespread obligate-outcrossing and genetically diverse species, with the majority of populations in Western Australia containing some level of herbicide resistance to many ACCase- and AHAS-inhibiting herbicides (Boutsalis, Gill, & Preston, 2012; Llewellyn, D'Emden, Owen, & Powles, 2009; Owen, Martinez, & Powles, 2014). Parameters used are based on RIM (Lacoste & Powles, 2014) and PERTH (Renton, 2011) (Table 1). Unverified parameters were calibrated by adjusting within biologically reasonable limits (Lacoste & Powles, 2014; Renton, 2011) to give realistic annual weed numbers at harvest over time, in the absence of resistance. The density and species of crop, and the type of weed will affect the distance of weed seed spread (Humston, Mortensen, & Bjornstad, 2005), making the specific estimations used here both weed and crop specific. However, we expect the general conclusions should be more far-reaching.

Table 1. Parameter values used in the model runs in this study

Parameter	Explanation	Value (s)	Source
area	Simulated population area	1.1664 ha	*a*
den0	Initial ryegrass seedbank density	125 m^{-2}	*a, d*
iaf	Initial resistance allele frequency	5.00e-5	*a*
dom	Dominance for resistance	1	*c*
ng	Number of genes for resistance	1	*c*
u	Probability of mutation causing gain in resistance	1.00e-7	*c*
v	Probability of mutation causing loss of resistance	1.00e-7	*c*
sowing death	Probability of weeds killed by mechanics of crop sowing.	0.05	*b*
winter death	Probability of growing season death of ungerminated seeds	0.10	*b*
summer death	Probability of between-season seed death	0.25	*b*
germination	Probability of annual seed germination from seedbank	0.80	*b*
kr[1]	Probability of kill for knockdown on cohort 1	0.99	*b*
kr[2]	Probability of kill for pre-emergent on cohorts 2 and 3	0.95	*b*
kr[3]	Probability of kill for post-emergent on cohorts 1, 2, 3 and 4	0.95	*b*
dc	Wheat sowing density	150 m^{-2}	*a*
kc	Crop size/competitiveness parameter	0.09	*b*
kw	Weed size/competitiveness parameter for cohort 1	0.03	*b*
kw	Weed size/competitiveness decreased for later cohorts	0.03 x (0.45-0.02)	*b*
SSmax	Maximum weed seed production per metre	35,000 m^{-2}	*d*
Imported seeds	Seeds joining the seedbank	0.1/m/yr	*a*

a Renton, Diggle, Manalil, and Powles (2011)

b Lacoste and Powles (2014)

c Powles and Yu (2010)

d Lacoste (2014)

3.1. Maximum *L. rigidum* density

The maximum density of *L. rigidum* per section was set at 3000 full size equivalent adult plants per metre square. Density in subsequent generations was limited when weed numbers exceeded 3000m^{-2} by lowering the fitness of weeds in the later emerging cohorts to one percent of its initial value. Due to the stochastic nature of seed production (Renton, 2009) this insured that stochastic population numbers per section were maintained.

4. SPATIAL COMPONENTS

The 1.1664 hectare area and its simulated population were divided into sub-populations contained within sections, with each sub-population assigned to a specific section. The calculations of weed and crop competition, seed production and seed genotype were carried out for each sub-population in the SOMER model; for each genotype, identically to in the non-spatial model.

The spatial model also included weed pollen and seed spread sub-models, enable us to address our specific research question on the effects of adding spatial realism to an evolutionary weed resistance population model. In the SOMER simulation model, pollen and seed spread rates declined with distance from the source. A larger environment, outside the spatially modelled 1.17 hectare area, but still part of the wheat field, was included

into the SOMER pollen spread sub-model by extending the area available to source pollen beyond the defined 1.17 ha area. The aim was to ensure that every sub-population (including those near the edge of the 1.17 ha study area) had access to similar pollen levels. This larger area was incorporated into the spatial sub-model of pollen flow based on distance from the home section, with the assumption that weeds in the un-modelled areas were homozygous susceptible and occurred in similar densities (to the investigated area) across a wider (un-modelled) area of field.

4.1. Spatial pollen spread sub-model

The decline in pollination probability due to distance from the source was based on data from Knowles and Ghosh (1968). An analysis was conducted on their data of the seed percentages and the location of each of the local and external plants in the two neighbouring plots (1440 plants in a 45 by 16 yd. area). A Weibull model gave the best fit to the data (error =0.002), and yielded the followed equation.

$$average\ percent\ locally\ fertilised\ seeds = \frac{\sum_{i=1}^{720} A - D\ e^{-e^l\ distance_i^p}}{\sum_{i=1}^{1439} A - D\ e^{-e^l\ distance_i^p}} \tag{1}$$

After the data in Knowles and Ghosh (1968) was adjusted to remove 8% self fertilised seeds, the parameters were: Asymptote (A=0), Drop (D=-1), Natural logarithm (l=1.9304) and Power (p=0.2294). These parameters were then used to yield the pollination probabilities for each plant, based on the distance between each home section and the pollen source sections.

$$pollen\ proportion\ per\ plant = \frac{e^{-e^l\ (\frac{distance}{0.9136})_i^p}}{\sum_{i=1}^{11664} e^{-e^l\ (\frac{distance}{0.9136})_i^p}} \tag{2}$$

These results are explained graphically in Figure 2.

A larger environment, outside the spatially modelled 1.1664 hectare area, but still part of the wheat field, was included into the SOMER pollen spread sub-model by extending the area available to source pollen beyond the defined 1.17 ha area. The aim was to ensure that every section (including those near the edge of the 1.1664 ha study area) had access to similar pollen levels. This larger area was incorporated into the spatial sub-model of pollen flow based on distance from the home section, with the assumption that weeds in the un-modelled areas were homozygous susceptible and occurred in similar densities (to the investigated area) across a wider (un-modelled) area of field.
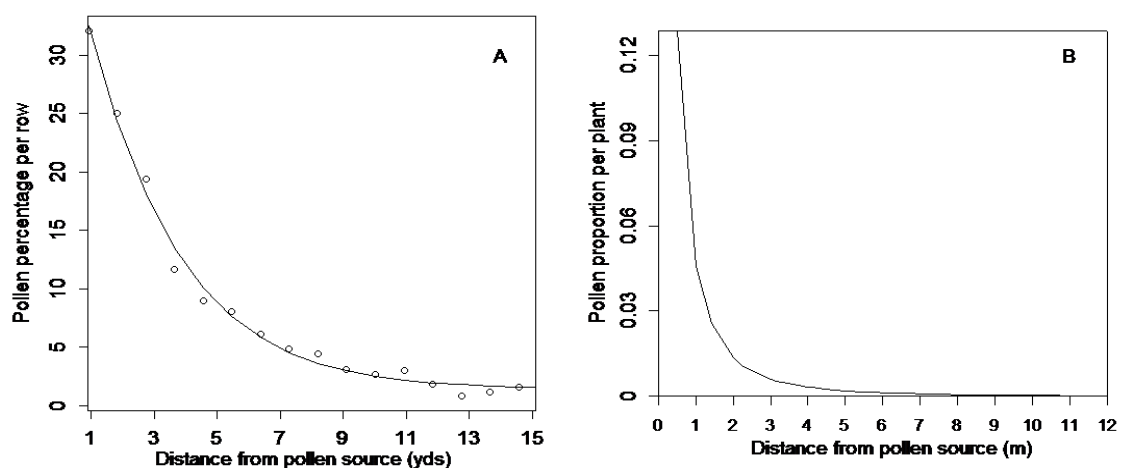

Figure 2. Fitting a fat-tailed Weibull curve to individual plant pollen spread data in Knowles and Ghosh (1968). The Weibull curve in figure A is constructed using a best-fit parameter estimation for the distances to each pollen producing plant in the test area (Equation1). The parameters calculated in figure 2A are then used to calculate the pollen proportion for individual plants in figure 2B.

4.2. Seed dispersal into adjoining sections

Wind, insects and farming activities were assumed to spread weed seeds radially from each sub-population into sub-populations in surrounding sections. The dispersal calculations therefore reflected inter-section seed spread by all methods; from spring weed seed shed until autumn germination. This type of seed spread is assumed to be small due to trash left by commonly used conservative harvest methods, (Aguiar & Sala, 1997; Fenner, 1985) and is therefore confined to the eight sections immediately surrounding the source sub-population (Blanco-Moreno, Chamorro, Masalles, Recasens, & Sans, 2004; Petit et al., 2013).

The proportion of a seed dispersing outside the source sub-population's home section was trailed at both 4% and 10% of annual seed production, with 2% of this seed-loss directed into each corner section, and the remaining 92% into the four immediately adjacent sections. Header seed spread is assumed not to occur (Table 2).

5. EVOLUTION OF RESISTANCE

The model was run-in for 10 years prior to adding a single herbicide resistant allele to a weed plant in the sub-population in the central section of the SOMER model. This run-in was used to establish a realistically variable population distribution across the 1.17 hectare test area (Blanco-Moreno, Chamorro, & Sans, 2006). The average weed density for the entire area was maintained at 125 weeds m^{-2}, however [by] year 10 there was a density range from 1:1000 m^{-2} with weak development of patches (Figure 3). A single resistant allele was also added to the non-spatially modelled population at year 11.
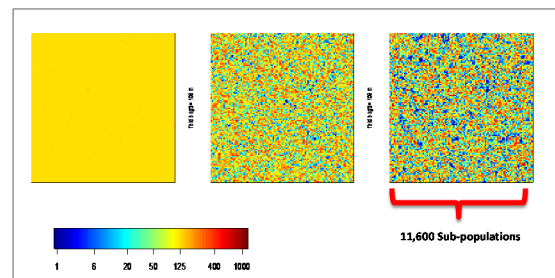

Figure 3. Changes in weed numbers per section during the run in period.

A field size of 1.17 hectare (108m by 108m) was selected as large enough to incorporate the significant annual spread of *L. rigidum* pollen and seeds. An area slightly larger than one hectare was chosen to allow a header width of 12m to be incorporated into later simulations.

6. RESULTS

Incorporating a spatial constraint into resistance modelling slowed the build-up of herbicide resistance. In the non-spatial model numbers of resistant weeds increased from 10 per hectare to 100 per hectare in just one year. In comparison the SOMER spatial model with 10% annual seed dispersal took 3 years to increase average weed numbers from 10 per hectare to 100 per hectare (Figure 4). A drop in seed dispersal rates from 10% to 4% resulted in a further delay in resistance evolution, when it took four years for average weed numbers to increase from 10 per hectare to 100 per hectare.

Realistic depictions of resistance spread across a field were also generated (Figure 5).
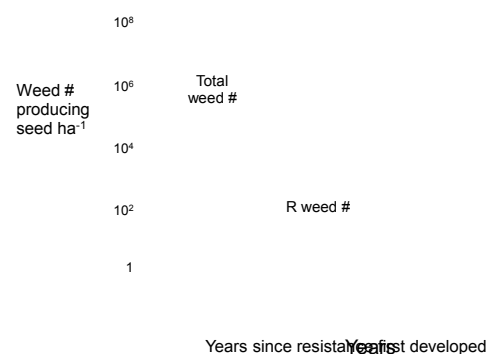

Figure 4. The solid lines in this diagram show the total number of weeds /ha estimated by each of three models on a log scale. The dashed lines show the number of herbicide resistant weeds in each simulation.

7. DISCUSSION

All three models started with the same level of herbicide resistance, in the same sized field. Numbers of weeds increased much more rapidly in the non-spatial model where numbers of resistant weeds followed an exponential growth curve (linear on the log scale). This meant that one extra year of herbicide control was gained for every one tenth reduction in the initial frequency of resistant genes, a result which seems unrealistic for some herbicides (Powles & Yu, 2010). In contrast in the SOMER spatial model the increase in numbers of resistant weeds was much more gradual (Figure 4), due the earl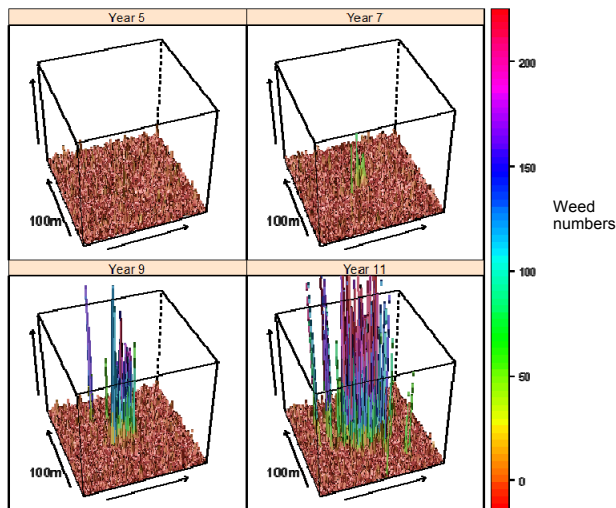ier spatial constraints on density reducing the more rapid increase in weed numbers in the non-spatial model. In addition, the graphical representations possible with this system of modelling produced informative graphs; showing growth in resistance, as well and changes in weed numbers, and visually realistic images of increases in weed numbers in the field. This may help address the short-term management focus of some growers (Norsworthy et al., 2012).

Further research could incorporate the use of harvest weed seed control, although adding the seed spreading actions of a harvester may require the modelling of a larger area, possibly incorporating larger sub-population sizes. In addition as one of the two years of data from Knowles and Ghosh (1968) contained directional wind mediated pollen spread it should be possible to incorporate this effect into the pollen spread calculations.

Figure 5. Weeds per m^2 in each of the sections of the wheat field.

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