

A spatio-temporal modelling framework for assessing the impact of weed management technologies on the spread of herbicide resistance

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Summary This paper presents a spatio-temporal modelling framework for predicting the spread of herbicide resistance. It includes a model of the population dynamics of weeds growing in competition with crops, a polygenic model of the development of herbicide resistance, and gene transfer by means of pollen and seed movement. The framework is used to predict the long-term spread of resistant weeds given different integrated weed management choices combining tillage and herbicide treatments, and seed capture at harvest. The model's predictions will be used to devise management options that minimise the spread of herbicide resistant weeds.

Keywords Herbicide resistance, modelling framework, spatial-temporal spread.

INTRODUCTION

Herbicide resistance is an increasing problem in Australian cropping systems, but little is known about how resistance spreads and how farmers can manage their paddocks to minimise its spread. The evolution of herbicide resistance depends on the intensity of selection, the frequency of resistance alleles in natural (unselected) populations, the mode of inheritance of resistance, fitness penalties associated with resistance and the spread of resistance by gene flow within and between populations. If there is no gene flow between adjacent populations, then population size is also an important factor affecting the rate of evolution of herbicide resistance. While initial gene frequencies (caused by underlying mutation rates) are beyond the control of management, weed population densities are not. Non-spatial simulation modelling has shown that maintaining low weed densities by means other than the herbicide in question decreases the rate of evolution of resistance to that herbicide (Diggle and Neve, 2001). However, geneflow does occur between neighbouring populations by pollen and seed movement. While farmers have little or no control over pollen movement, seed movement can be restricted by cleaning machinery between segregated areas and applying new technologies such as seed capture at harvest.

This paper presents a spatio-temporal modelling framework for predicting the spread of herbicide resistance.

DATA TYPES

The modelling framework is implemented as a *Mathematica* Version 6 package. The data types are designed to allow for efficient computer memory use. Described from the top-level to the bottom, a map is a sparse data representation composed of a list of cells, a background state and an underlying map showing areas that are managed differently. The list of cells includes only those that contain resistance. Each cell contains information about its current state and location. The state of a cell is composed of a community of species populations and information about the soil and any herbicide residues that are present in the soil at a particular time. Each population is separated into four components: the seed bank, plants, seed on plants and pollen. Each of these components comprises a set of cohorts. A cohort is identified by the time of its creation. For example, plant cohorts are identified by their germination time, seed on plant cohorts are identified by the time of seed set and seed cohorts are identified by the time of seed rain. At the lowest level, each cohort is composed of a set of genotypes. Genotypes are also stored in sparse sets. This allows any number of alleles to be included in the model. For example, consider the case where there are six alleles that may confer resistance. If the resistance alleles are rare, then many of the possible combinations of alleles will not be present in any cohort. The sparse set representation stores only a list of those combinations that are present in the cohort, and a count of the number of times it occurs.

THE DYNAMIC MODEL

The dynamic life-cycle model simulates the population biology of a crop and several weed species growing together. Its general structure (Figure 1) is similar to existing weed life-cycle models such as those used by Colbach *et al.* (2001) and Doyle (1991). Holst *et al.* (2007) provide a recent review of dynamic life-cycle models.

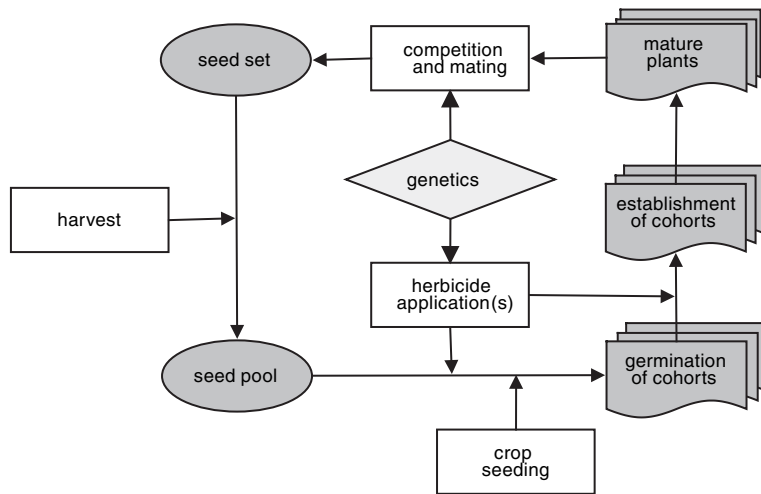


Figure 1. Overview of the dynamic life-cycle model.

The starting point for all simulations is the initial seed bank. Crop seeds are added to the seed bank. Seeds germinate and seedling cohorts become established. Herbicides may be applied at various times, affecting seedling germination and survival. Some seedlings survive to become mature plants that flower and set seed. The number of seed set is affected by the amount of competition from other plants. Crop seed is harvested and weed seed falls to replenish the seed bank. All annual plants die at the end of each year and the seed bank declines over time due to natural causes. The genetics of individual plants affect their response to herbicide applications, and are considered explicitly when plants mate to produce new seed. After the first year of simulation, the seed bank is also separated into cohorts. This allows the future inclusion of modifications to the model to allow seed viability to vary with age.

A model is specified by the number of years to be simulated and a given crop. For each crop, a sequence of events is specified that includes both life-cycle and management events. The life-cycle events (germination, pollen set, spread and pollination, seed rain, seed death and plant senescence) are the same for each crop, but the management events (tillage, herbicide applications, seeding and harvest method used) may differ. Events are specified to occur at particular times for each year with respect to an 'average' season. The parameters corresponding to different events depend on the species, herbicides applied and time of year.

The modelling framework is fully stochastic. Whereas a deterministic approach always gives the mean result, a stochastic approach gives different

values each time the model is run. By performing multiple simulations of the model, the stochastic approach enables the simulation of rare (and therefore important) events.

Competition, seedset and mating The numbers of seed set by each plant cohort is calculated using the age-structured hyperbolic competition model of Neve *et al.* (2003). Following Diggle *et al.* (2001), ovules and pollen are produced in direct proportion to predicted seed yields and all gamete haplotypes have an equal chance of reproductive success. The pollen and ovule haplotypes recombine at random to produce diploid zygotes that develop into mature seed.

THE SPATIAL MODEL

The spatial model includes two main causes of gene spread: pollen blown by the wind and seed moved by harvesting equipment. While pollen spread can not be easily controlled, seed movement can be minimised to reduce the chance that resistance will 'jump the fence' into new paddocks. The model includes an option to assess the use of a chaff cart to reduce the amount of seed that is spread.

Because of the importance of rare long-distance dispersal of both seed and pollen, dispersal models must be able to describe and predict these occurrences. The fat-tailed Cauchy distribution can be fully specified using the median dispersal distance, and it provides the best balance between goodness of fit and capacity for predicting long-distance dispersals (Evans *et al.* 2007).

The spread of pollen by wind is simulated using a product distribution of a circular uniform distribution for direction and a Cauchy distribution for dispersal distance. To allow for the effect of prevailing wind directions, a product distribution using a Von Mises distribution for wind direction is also implemented.

The spread of seed by harvesting equipment is modelled by first specifying the path of the harvester. As the harvester moves around a paddock, it collects seed. A proportion of the seed collected by the harvester is then spread along its path according to a Cauchy distribution. Seed can be moved long distances when 'caught' in machinery.

SPREAD OF GLYPHOSATE RESISTANT RYEGRASS

The spread of glyphosate resistant ryegrass when only pollen spread is considered has been modelled for a 1 km × 1 km area, under the following assumptions:

1. Map cells are 10 m × 10 m in size.
2. Continuous wheat-lupin crop rotations are applied. Susceptible weeds are controlled each year to a density of five plants per m².
3. Presence of a single allele of a dominant gene confers full resistance to glyphosate.
4. The background population contains resistance alleles at a rate of one in one million.
5. One cell is initialised to contain resistance alleles at a rate of one in 10.
6. The median distance for the spread of pollen is 0.3 m and the median distance for seed spread by harvester is 18 m.

Figure 2 shows a typical output from a single run of the model after five years. Local spread around the originating cell is considerable and weed densities in that area are increasing. In addition, several resistant satellite populations have formed. As the model allows different regions (e.g. paddocks) to be managed differently, future use of the model with additional movement of seed by harvesting equipment will consider the problem of whether resistance can 'jump the fence', and to devise management strategies farmers can use to minimise the impacts of herbicide resistance.

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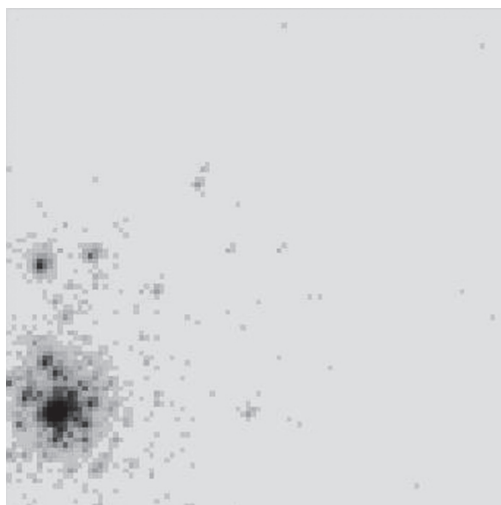


Figure 2. Output from a single run of the model for five years. Increasing weed density is shown in shades of grey and the log-scaled proportion of resistant seeds is overlaid in black.

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