Proceedings of the 7th International Conference on Functional-Structural Plant Models, Saariselkä, Finland, 9 - 14 June 2013. Eds. Risto Sievänen, Eero Nikinmaa, Christophe Godin, Anna Lintunen & Pekka Nygren. http://www.metla.fi/fspm2013/proceedings. ISBN 978-951-651-408-9.

Weeds In Space – field-level epidemiology of herbicide resistance

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Highlights: Spatial epidemiology of herbicide resistance is insufficiently understood at present to allow us to provide quantified strategies for farmers attempting to contain or eradicate patches of resistance. SHeRA, a spatially-explicit model of herbicide-resistant weeds in patches, is a useful new tool for developing efficient strategies using a zonal management approach.

Keywords: Herbicide resistance, glyphosate, *Echinochloa colona*, patch dynamics, eradication, modelling

INTRODUCTION

Across the world, wherever industrialised production of food and fibre plants occurs, weeds have evolved to become resistant to commonly-used herbicides (Heap, 2013). At first, weeds became resistant to specialised, high-risk herbicides such as ACCase and ALS inhibitors, but changes in usage patterns over the last 20 years have seen the widespread development of populations resistant to even lower risk herbicides like glyphosate.

In Australian agriculture, the emphasis on dealing with resistance (to glyphosate in particular) is shifting from prevention to management. Enough farmers and land managers are now confronted with a population of resistant weeds that it makes sense to investigate and promote strategies for dealing with resistant biotypes that are present, rather than resistance as it evolves. Resistance management recommendations to date include useful tactics, but package them in non-quantified, generic ways, and are not aimed at eradication.

Through modelling, biochemistry and molecular biology, science has developed a good understanding of how, why, and when resistance occurs. This knowledge led to, underpins and validates current management recommendations. However, questions remain about the epidemiology of resistance: where it occurs in space, how patches grow, move, and spawn new patches, and at what rate these processes occur for different species. Understanding resistance epidemiology better at a field level could help us decide whether, and under what conditions, local eradication of resistant biotypes is a feasible goal, and to identify cost-effective zonal management approaches that could be used to achieve it.

MODEL DEVELOPMENT

In order to examine the spatial dynamics of herbicide resistance in an agricultural situation, we developed SHeRA, the **S**patial **He**rbicide **R**esistance **A**nalyser. SHeRA is a stochastic integer-based model of weed life cycles and gene flow, implemented in Python 3.2 and numpy 1.7. Sub-populations of weeds of 1 m^2 each, arranged in a grid, are subjected to a set of management tactics and, through flowering and seed set, communicate with each other through short- and long-distance movement of pollen and seeds.

Patch dynamics in an agricultural weed are a function of the pressure for expansion and propagation exhibited by the patch, and the manager's pressure for containment and eradication (see Cousens & Mortimer, 1995). In the case of resistance, patch expansion occurs both through seed dispersal and through pollen flow from resistant patches to the surrounding conspecific population. The presence of non-resistant conspecific plants causes a complex balance of competing non-resistant pollen (Baker & Preston, 2008) and the presence of potential seed parents for the creation of new, relatively distant heterozygous offspring. In the case of species that are self-fertile, like *E. colona*, questions remain over how important rare outcrossing events are in the propagation and expansion of resistance patches. Since successful outcrossing mainly occurs with close neighbours, and less frequently at longer distances that are limited by wind speed and pollen lifespan, SHeRA includes processes for both. Short-distance movement is simulated through sharing of pollen clouds and seeds proportionally with neighbours within a pre-defined distance. Long-distance movement is simplified as a random allocation of a random number of propagules with randomly-chosen distant cells.

SHeRA runs on a yearly timestep. The events in one step are as follows:

1. Germinate weed cohort one
2. Apply control measures to cohort one
3. Germinate cohort two
4. Apply control measures to cohort one survivors and cohort two
5. Germinate cohort three
6. Apply control measures to cohort one and two survivors and cohort three
7. Apply control measures to mature survivors of all cohorts
8. Determine potential seed production
9. Produce and move pollen between neighbouring cells and at long distance
10. Determine progeny genotypes
11. Move progeny (seed) between neighbouring cells
12. Process end-of-year mortality of new seeds prior to entering seed bank, and between-seasons mortality of old seeds in seed bank
13. Seed rain enters seed bank – return to start

Integer modelling is used in determining the survivorship of plants under self-thinning processes and simulated control tactics. As each cohort germinates, a number of plants (proportional to the cell's current seed bank density, rounded down) are entered into a Python list either as a 0 (no resistance alleles), 1 (one resistance allele, heterozygous) or 2 (homozygous resistant). Separate lists are maintained for each cohort. SHeRA simulates populations with a single-gene resistance mechanism, though that mechanism may be dominant, recessive, or in-between. For most currently-known glyphosate resistant populations, this is a reasonable simplification.

Cohort member lists are tested for survivorship against predetermined estimates of herbicide efficacy relative to genotype and plant age, with as many tests performed in series as necessary to determine the number and genotypes of individuals that survive a whole season of management tactics.

Seed production per plant is affected by plant density according to Cousens' hyperbolic yield penalty model (Cousens, 1985), potentially reduced to account for fitness penalties due to resistance. We developed parameters and mechanisms to test the patch dynamics of glyphosate-resistant awnless barnyard grass (*Echinochloa colona* L. Link) in a glyphosate-resistant cotton farming situation, using a variety of published and unpublished data. Key parameter estimates for the *E. colona* implementation of SHeRA are given in Table 1.

Table 1. Parameter values for SHeRA simulating patches of glyphosate resistance in *Echinochloa colona*

Parameter	Value
Cohort 1 germination proportion (of total seed bank)	0.05
Cohort 2 germination proportion	0.05
Cohort 3 germination proportion	0.01
Carrying capacity	3000 plants/m^2
Initial seed bank density	400 seeds/m^2
Initial resistance patch size	4 m^2
Proportion of pollen shared with nearby cells	0.4
Pollen spread distance	2 cells
Chance of long distance pollination, per cell	0.01
Proportion of pollen spread at long distance	0.001
Mortality of seeds prior to entering seed bank	0.1
Annual seed mortality	0.5
Proportion of seed shared with nearby cells	0.2
Seed spread distance	1 cell
Self-fertilisation proportion	0.95
Maximum seed production	15 000 per plant

RESULTS

SHeRA provides outputs for total and per-cell values of seed bank density (separated by genotype) and resistance proportion, per step. This output can be used to analyse the rate of expansion of resistance patches and the success of any given strategy at controlling weed numbers across the whole field.

A simple test of patch dynamics is shown in Figs 1-3. We simulated three scenarios: glyphosate used alone after the emergence of every cohort (Fig 1); the glyphosate strategy plus paraquat applied to every cell in a containment zone 15m^2 in diameter around the original resistance patch (Fig 2); and the glyphosate strategy plus paraquat applied only to cells in the original patch zone (Fig 3). As expected, glyphosate alone allows the patch to spread. The addition of paraquat was only successful at severely limiting spread when applied in a zone outside the original patch; applications to the patch area alone were soon overtaken by survivors spreading seed and pollen outside the original patch zone.

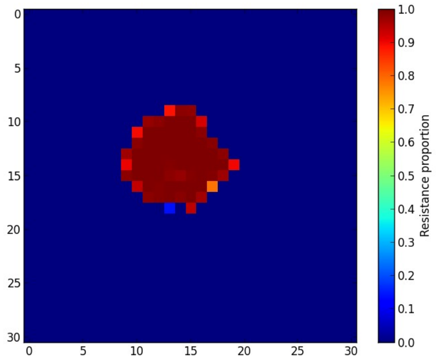

Fig 1. Resistance proportion in each cell of a test field after five years of glyphosate applied after emergence of every cohort

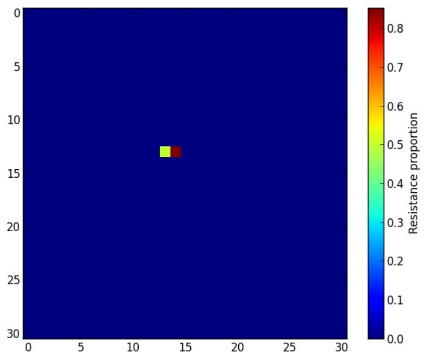

Fig 2. Resistance proportion in each cell of a test field after five years of glyphosate applied to every cohort plus paraquat applied to every cohort in a zone 12m^2 in diameter around the original resistance patch

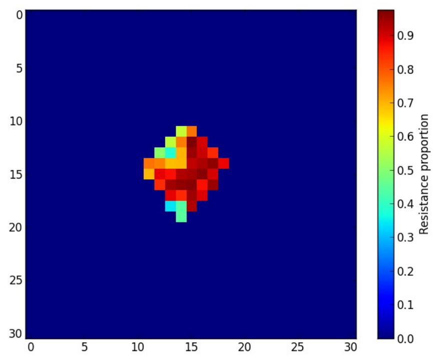

Fig 3. Resistance proportion in each cell of a test field after five years of glyphosate applied to every cohort plus paraquat applied to every cohort in the 4m^2 diameter of the original resistance patch

FURTHER WORK: ZONAL MANAGEMENT AND PATCH ERADICATION

When a patch of herbicide-resistant plants is identified, the manager of the land in which the patch occurs could choose to either manage the whole area as if it were herbicide-resistant, or to isolate the patch and perhaps some surrounding zone, and treat them differently from the rest of the area. In SHeRA, we nominate the original patch as the eradication zone, an area immediately outside the patch as the containment zone, and the rest of the field as the background zone. The eradication zone should receive highly intensive management aimed at preventing all seed set on all emerged plants, for as long as necessary to exhaust the supply of resistant seeds. The containment zone should receive sufficiently robust management to ensure that recruits from short-distance gene flow are likely to be controlled. The background zone receives some version of ‘business as usual’ management, which in a best-management-practice case would consist of glyphosate plus a range of options used in rotation, which would be of use in preventing the successful establishment of satellite patches of resistance.

We intend to use SHeRA to investigate the potential for eradicating glyphosate-resistant patches of *E. colona* in Australian non-irrigated cotton farming, and to optimise management tactics used in each zone such that the least intensive, effective strategies can be identified. This will require the development of a set of scenarios for weed management in glyphosate-tolerant cotton crops. We hope to develop quantified strategy recommendations for on-farm use where early identification of glyphosate-resistant *E. colona* occurs. The development and implementation of such strategies will be critical in determining the medium- to long-term sustainability of glyphosate-tolerant cotton farming in Australia.

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