

Mathematical modelling of a new weed incursion and its control in large area cropping systems

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Abstract

A mathematical model incorporating weed growth, dispersal and control is developed to represent the spread of a weed from a point source in cropping fields. This model allows the simulation of theoretical rates of weed spread and the examination of spatial distribution of a new weed infestation on a large regional scale. The model is cellular in structure, dividing space into discrete units. The starting point is with an initial population at a point source, such as might arise with the arrival of a newly invading species, an emerging sleeper weed or the first herbicide-resistant plants in an arable field. The location of this point source is set in the centre of the hypothetical grid field. From this starting point, the spread of weeds is modelled at annual intervals. Risk is a critical issue to this modelling; the weed spread functions being stochastic (with different probability distributions incorporating rare events in the dispersal process), and the weed control effort decision being probabilistic. Six case study weed spread simulations were undertaken to demonstrate the model's applicability to different weed incursions with differences in weed biology, rates of spread and to demonstrate the effects of weed search and control effort. The simulated model results are discussed in relation to a case study of awnless barnyard grass (*Echinochloa colona*) spread and its control in northern New South Wales, Australia.

Keywords: Weed population growth, weed dispersal, spread modelling.

Introduction

Invasions by non-indigenous plant species pose serious economic threats to Australian agricultural industries (Sinden *et al.* 2004). Effective quarantine strategies are the key to managing the risk of exotic invasive species. However, there is always a risk of new invasions due to international trade and travel by individuals. Moreover, there is also the threat of previously unidentified 'sleeper weeds' or herbicide resistant plants emerging in cropping areas. Consequently, it is important to have well developed strategies for dealing with

new incursions as they occur, rather than relying on a reactive approach to managing incursions. When a new invader is identified a rapid response is critical, particularly if the invasive species has the ability to spread rapidly. An early decision is required whether to eradicate or contain the infestation, or leave it to landholders to manage. The first step in developing these strategies is the realistic modelling of the spread of a weed. The ability of a weed to spread within a cropping area has significant implications for its management.

The current cost of weeds in Australian cropping systems is around \$1.5 billion per annum (Sinden *et al.* 2004) which represents 15% of the 2003–04 gross value of the Australian grains industry. This value ignores the potential future costs that may be imposed from new weed incursions. In general, early action on invasive plants can give significantly greater economic results than waiting for the weed problem to develop into one of significance before taking action. Once an infestation is well established the policy and management options may become limited, and the economic returns from strategies such as eradication may then be low or negative. Consequently, an efficient allocation of capital and scarce resources may be to deal quickly and decisively with new weed incursions in preference to managing existing large scale infestations.

Mathematical models of plant population dispersal from a point source have established that the rate of spread will depend on 1) the species potential for population increase in the habitats being invaded and 2) its dispersal characteristics (Okubo 1980). Seed production and probabilities of survival at different stages in the life cycle of several annual weeds have been thoroughly documented and their relative importance to population increase is understood (Cousens and Mortimer 1995). In contrast, dispersal of weeds in arable fields has seldom been studied and generalizations about dispersal are therefore rare (Woolcock and Cousens 2000).

Higgins and Richardson (1996) provided a comprehensive introduction to the topic, reviewing the potential modelling tools by categorizing models of plant

spread as either simple-demographic, spatial-phenomenological or spatial-mechanistic, based on the model's data inputs and outputs.

Demographic models aim to predict the future number of individuals in a population, making assumptions about the nature of population growth and by estimating demographic parameters regarded as being important in determining population dynamics. Such models include the exponential, logistic and logistic-difference models that assume constant environmental conditions and no variance in the behaviour of the population as well as stochastic models that account for variability by incorporating random variation into model parameters. In reviewing the demographic features of invasive organisms, Crawley (1986) concluded that simple demographic models are unlikely to be useful since there is no clear demographic profile of a successful invader. According to Higgins and Richardson (1996, p. 255), 'many modifications to demographic models can be found; these are usually applied when the underlying assumptions of the model are no longer satisfactory'.

Since invaded ecosystems have different attributes to uninvaded ecosystems, the area of land occupied and the rate of this occupation are said to be the key dimensions of an invasion. This observation has led to the development of a number of models aimed at the prediction of the area invaded. Higgins and Richardson (1996) referred these spatial models as phenomenological models because they invoke no ecological mechanism as a means to prediction. These models therefore assume that plant-environment interactions are best described by empirically derived constants. Spatial-phenomenological models include regression models, geometrical models as well as Markov models which use the tools of matrix algebra to formulate discrete-space and discrete-time variables. Since these models do not invoke any ecological mechanism in the prediction of plant invasive spread, they have the advantage that they can forecast future events without making any ecological assumptions. This is particularly useful when the ecological mechanisms are unknown and when the past can be confidently used to predict the future. As noted by Higgins and Richardson (1996, p. 257), 'The disadvantages of the phenomenological models are that one's understanding of ecological invasions and other ecological processes is not enhanced, the results cannot be applied to other invasion scenarios, and the techniques cannot be applied without historical spread records'.

Spatial-mechanistic models, in contrast to the phenomenological models, are based on independent estimates of ecological parameters. Since these ecological parameters represent some ecological

processes, the predictions are a function of ecological interactions and the model's assumptions. According to Higgins and Richardson (1996, p. 257), 'these mechanistic spread models thus invoke ecological knowledge of the nature and determinants of invasions in the prediction of plant spread'. Three sub-categories of spatial-mechanistic models have been discussed in this group namely; reaction-diffusion models, population dynamic metapopulation models and individual-based cellular automata models. The reaction-diffusion models use the formulation of partial differential equations which allows the modelling of population density in both space and time. Despite the moderate success of reaction-diffusion models in describing animal invasions, few plant invasion models have used the reaction-diffusion approach. Also, many criticisms have been levelled at the simplifying assumptions that reaction-diffusion models make (Higgins and Richardson 1996).

Metapopulation biology is concerned with the dynamic consequences of migration among local populations and therefore, metapopulation models have been referred as a system of models that can be used to predict the movement patterns of individuals, the dynamics of species, and the distribution patterns in multispecies communities in real fragmented landscapes (Hanski 1998). Auld and Coote (1980, 1990) developed a metapopulation model of plant spread to consider the spread of a wind-dispersed annual or perennial species in a two-dimensional landscape in Australia. The landscape is divided into a grid of neighbouring sites, each of which supports exponential population growth. A proportion of each local population was set to disperse to neighbouring sites, with sites differing in their susceptibility to colonization. The model was successfully applied in the prediction of the spread of *Nassella trichotoma* (Auld and Coote 1981) and *Avena fatua* in eastern Australia (Auld and Coote 1990). Metapopulation models view landscapes as networks of idealized habitat patches (fragments) in which species occur as discrete local populations connected by migration. When this patch structure does not correspond to patterns of environmental heterogeneity experienced by the modelled population, as commented by Higgins and Richardson (1996, p. 259), 'it follows that individual-based cellular automata models are appropriate in situations where no ecological motivation for the delineation of local populations exists, when the environmental conditions experienced by each individual plant is important, or when the presence of a single plant can influence invasion patterns'. Recently, there has been weed process-based spatio-temporal modelling work done for the Australian landscapes (Diggle *et al.* 2002, 2003,

Monjardino *et al.* 2004). These studies have simulated the spread of organisms including the movement of seed in Australian cropping systems.

Careful consideration of the ecology of the invasion, and a proper understanding of the processes which determine the dynamics of the invasion are important in selecting which plant spread modelling approach is appropriate for a given invasion. As reported by Higgins *et al.* (2001), parameterization of process-based spatially explicit models is often challenging and time consuming. Also, these models are seldom validated which makes their predictive value in applied contexts uncertain. As Higgins *et al.* (2001, p. 572) commented, 'Few contemporary invasion scenarios have been validated; Auld and Coote's (1990) INVADE model is the only spread model that we are aware of that has been validated using data on contemporary invasions'. Moreover, process-based spatially explicit demographic modelling on a large regional scale can be computationally very intensive.

The aim of this paper is to present a flexible modelling approach that can incorporate the key processes that determine the spatial population dynamics of an invading plant species in a large area cropping system. The approach falls into the spatial-mechanistic categorization, as it is based on independent estimates of ecological parameters and neither the invader nor the environmental and ecological mechanisms of the receiving environment is known in this large area system. A framework such as described in this paper has considerable value to the development of more effective alien plant management strategies as it is amenable for inclusion in an economic framework to assess the benefits and costs of alternative actions to a new invasion.

Materials and methods

A spatially explicit framework was developed for regional-level modelling of alien plant spread in arable fields. A raster-based approach was used to represent a large region as a grid of neighbouring cells. The model uses an annual time step and a two-dimensional grid of sites representing space. The mathematical model follows three stages; population growth, dispersal processes to represent spread of a weed from a point source and the weed control effort.

The space (the region at risk of invasion) is divided into an $n \times m$ array (grid) of rectangular cells of equal size. The grid size can be readily changed to suit the representation of a particular case study region. The starting point is with an initial population at a point source, such as might arise with the arrival of a newly invading species, a re-emerging sleeper weed or the first herbicide-resistant plants in the

arable field. The location of this point source is set in the centre of the hypothetical grid field. A model was developed to simulate weed population density for each cell of the grid field at annual intervals.

Population growth

The first part of the model comprises a population growth sub-model which describes the weed population growth based on the logistic equation:

$$\frac{dX}{dt} = rX \left(1 - \frac{X}{K} \right) \quad (1)$$

where r is the intrinsic growth rate, $X = X(t)$ denotes the size of the weed population at time t , and K is the environmental carrying capacity or saturation level. Such models have had wide application in a variety of biological resource stock problems (Clark 1990). This equation is modified to obtain the following discrete version of the logistic growth relationship:

$$X(t+1) = X(t) + rX(t) \left(1 - \frac{X(t)}{100} \right) \quad (2)$$

where $X(t)$ and $X(t+1)$ are the weed populations expressed in percentage infestations (corresponds to the percentage of a grid cell occupied by the weed) at time t and $t+1$ respectively and $K = 100$ denotes the maximum carrying capacity (100% infestation). Here, and in the following determinations of weed populations within a cell $X(t)$ at time t is restricted to the range $[0, 100]$. That is, $X(t)$ set equal $\min\{100, \max\{0, X(t)\}\}$.

Using Equation (2), weed population size $X(t)$ can be computed for different values of the intrinsic growth rate parameter r and $X(0)$. Conversely, this equation can be used to determine an r value for a particular case study weed spread scenario in the field. Depending on the initial size of the invasion and number of years a weed may take to reach a 95% spread level in one grid cell, the model is set to compute the corresponding r parameter value. It is expected that the required information 'how many years it takes to reach 95% infestation level in one grid cell' can be obtained for a particular case study weed spread scenario. This percentage level is considered as more plausible at field practitioner level.

To denote the infestation level post growth but prior to dispersal, for each cell across the $n \times m$ array Equation (2) can be written as:

$$X_{ij}^{pd}(t+1) = X_{ij}(t) + r_{ij}(t)X_{ij}(t) \left(1 - \frac{X_{ij}(t)}{100} \right) \quad (3)$$

where ij denotes the cell at i^{th} row and j^{th} column of the hypothetical grid field with the constraint that $X_{ij}^{pd}(t) \in [0, 100]$. Here

$r_{ij}(t)$ is set up to allow dependence on both cell and time. Replacing $r_{ij}(t)$ with r would have the growth parameter independent of both space and time. The superscript pd denotes 'prior to dispersal'.

When modelling $X_{ij}^{pd}(t)$ above we restrict percentage intensity to the nearest decimal place. Hence the unit of infestation is 0.1% and each cell can be considered to have an integer number of infestation units between 0 and 1000 inclusive.

Dispersal

The second part of the model comprises a dispersal process sub-model. In addition to growth within each time interval, weed dispersal takes place with a proportion P_{ij}^{ij} of the weed intensity in the $(i, j)^{\text{th}}$ cell dispersed to the $(i', j')^{\text{th}}$ cell. Hence, after growth and dispersal the weed intensity in the $(i, j)^{\text{th}}$ cell is given by:

$$X_{ij}^{pc}(t+1) = \sum_{i'j'} P_{i'j'}^{ij} X_{i'j'}^{pd}(t+1) \quad (4)$$

where superscript pc denotes 'prior to control'. As already noted, the $X_{ij}^{pc}(t)$ values are restricted to $[0, 100]$. Incorporating Equation (3) we get:

$$X_{ij}^{pc}(t+1) = \sum_{i'j'} P_{i'j'}^{ij} \left\{ X_{i'j'}(t) + r_{i'j'}(t) X_{i'j'}(t) \left(1 - \frac{X_{i'j'}(t)}{100} \right) \right\} \quad (5)$$

Here we see that the model for weed intensity at time $t+1$ relates to the growth since time t and then dispersal.

When modelling dispersal, particular focus is given to the term $P_{i'j'}^{ij} X_{i'j'}^{pd}(t)$, this being the infestation in the $(i', j')^{\text{th}}$ cell dispersed to the $(i, j)^{\text{th}}$ cell. In modelling this, it is essential that the model captures the possibility of long distance dispersal. This represents rare events in the dispersal process, often less than 0.1% of the total infestation, whereby units are moved unusually long distances, e.g. by vehicle. One approach to modelling such dispersal is to use a radial Cauchy distribution. A related approach has been used in Diggle *et al.* (2002), to model dispersal of Anthracnose spores. The problem with this approach is the high computational effort required when undertaking simulations. Hence, in this paper we use an alternative dispersal mechanism which retains the possibility of rare long distance dispersal.

We first assume that each infestation unit is independently distributed of each other, and decompose dispersal from each cell into two components, being short and long distance dispersal components. The probability that a unit is dispersed short or long distance is denoted by p_{sd} and $p_{ld} = (1 - p_{sd})$, respectively.

For modelling short distance dispersal we use the approach of Auld and Coote (1990). They define distribution of new plants as determined by the proportion of

these that can move into pre-determined grid units away from the spreading source on a rectangular grid. In line with this approach, we set up the short distance conditional probability distribution, letting each unit dispersed locally to have a probability equal to p_0, p_1, \dots, p_w , of being dispersed to a 'ring' 0, 1, ..., w cells away respectively from the dispersing cell. Within a ring each cell is equally likely to be selected. For this purpose a matrix (DM) of short distance dispersal probabilities is established. Based on this matrix, we simulate the contribution from the dispersing cell to infestation into the neighbouring cells, that is, the sub-grid of cells receiving short distance dispersed units. Here the simulation is based on the multinomial distribution with parameters nsd_{ij} (the number of infestation units in the cell dispersed short distance) and probabilities as given in DM . The variable nsd_{ij} itself is a binomial variate, $Binomial(10X_{ij}^{pd}(t), p_{sd})$. It is assumed that units dispersed short distance and falling outside the full $n \times m$ grid are lost to the system.

The remaining units, $(10X_{ij}^{pd}(t) - nsd_{ij})$, are distributed long distance. Each long distance dispersed unit is then assigned at random to one of the 'long distance' cells of the grid, these being those cells of the grid that are the complement to the short distance cells. The probability of a unit being assigned to any particular long distance cell is set inversely proportional to the squared distance the cell is from the dispersing cell. These probabilities approximate the probabilities for a Cauchy distribution in the tails and hence the long distance dispersal approximates a radial Cauchy distribution.

In the example to be considered later, DM , the matrix of short distance conditional probabilities is established with a maximum number of rings equal to four so that a maximum of 81 cells (9×9 sub grid) receive, from any cell, weed units dispersed short distance. It is also assumed that, on average, of the units dispersed short distance;

- 95% of infestation units remain within the dispersing cell itself,
- 2% move to the eight neighbouring cells,
- 1.5% move to the next 16 neighbouring cells,
- 1% move to the next 24 neighbouring cells, and
- 0.5% move to the last 32 neighbouring cells away from the dispersing middle cell.

These parameters can be readily changed to suit for the requirements of a particular case study weed. However, it should be noted that dispersal of weeds in arable fields has rarely been studied. A rule of thumb developed in a summary of dispersal data by Cousens and Mortimer (1995) and later adopted by Woolcock

and Cousens (2000) is that in species without clear dispersal adaptations, half the seeds are distributed within a distance of half the height of the parent plant. While most seeds are likely to be dispersed short distances by passive means, it is possible for a small proportion of seeds to disperse considerable distances due to rare events such as gale force winds, birds, farm machinery, etc. Some evidence of these rare events is presented in field experiments by Auld (1988) in which he found a single *Avena fatua* plant established at 14 m from the nearest source in the second year. *Mimosa pigra* spread at 76 m y^{-1} in northern Australia (Lonsdale 1993). *Parthenium hysterophorus* (parthenium weed) long distance spread is mostly by produce, vehicles and farm machinery but it can also be spread by flooding and by animals. This was first discovered in Queensland in 1955. In a short time it spread from isolated outbreaks to establish core infestations across the Central Highlands of Queensland and into New South Wales and the Northern Territory (CRC for Australian Weed Management 2003).

Rare long-distance dispersal events are critically important in invasions and plant migration (Higgins *et al.* 1996, Higgins and Richardson 1999). The conclusions drawn by Higgins and Richardson (1999) are that data on rare long-distance dispersal will remain (by definition) hard to come by, and that the rare long-distance dispersal component of the mixture model can, if sufficiently rare, be estimated independently of the local dispersal components. In their analysis, they suggest that relatively large errors in estimating the long distance dispersal component are unlikely to strongly influence the predicted spread rate. Hence, it may be that accurate characterization of the long distance dispersal component is not as important as its identification. Accordingly, the spread modelling as discussed in this paper has incorporated both short and long distance weed spread. As shown in Figure 1, the new weed infestation starts in the middle of the grid field and spreads along the two dimensional fields (both length and breadth). Much of the spread takes place from the short distance dispersal while a much lower level of spread occurs from the rare long distance dispersal of this mixed distribution spread model.

Figure 2 illustrates the movement of the spreading weed populations on the grid space for a possible set of parameters. The spreading population moves along two dimensional fields as a 'wave' of population density. The weed 'search and control effort' is incorporated into this model as described in the next section.

Control

Cacho *et al.* (2006) modelled detection curves representing the proportion of

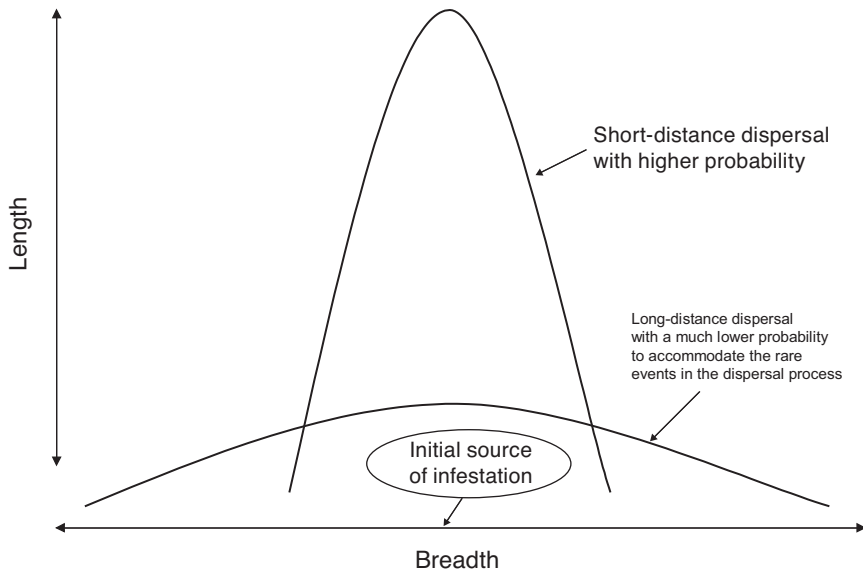


Figure 1. Representation of the mixed distribution of weed dispersal adopted in the model. Note: Bivariate distribution over a rectangular field having specified length and breadth

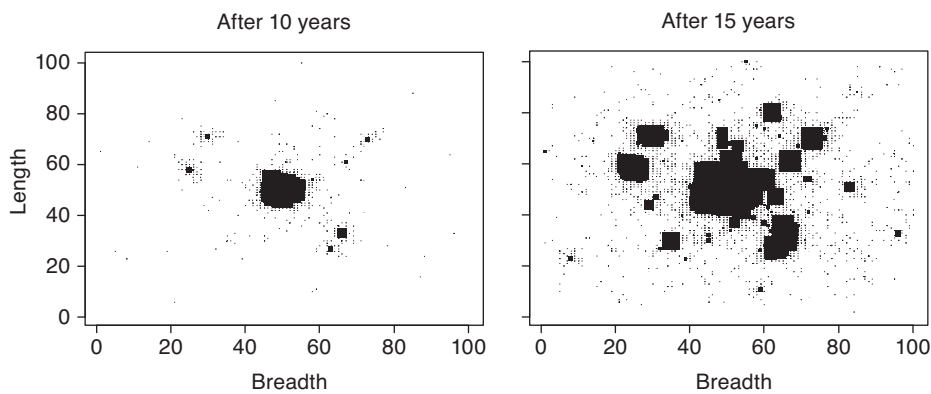


Figure 2. Spreading weed populations on the grid space. Note: Parameterization given in Table 1 with r value taken as 1.35.

targets detected (p_{detect}), or equivalently the probability of detecting a single target, as a function of coverage (c) defined as the ratio of the area actually searched over the total area of the invasion:

$$c = \frac{S \times T \times R}{A} \quad (6)$$

where A is the total area (km^2) at risk of invasion, S is the speed of search (km h^{-1}), T is time spent searching (hours) and R is the effective sweep width (km). T is the product of two components namely; the number of man days employed on search and control (0 to 400 man days y^{-1}) and the number of hours of search time spent per man day (7 h day^{-1}). R is a measure of the detection capability of the searchers, taking into account target characteristics and environmental conditions and is referred to as the detectability of the weed. The numerator of equation represents the area searched (km^2) as the product of search

effort in terms of distance traversed ($S \times T$) times the detectability of the weed (R).

Under random searching there is no pattern to the search process, some areas will be searched repeatedly while others may not be searched at all. This provides a conservative estimate of search effectiveness. As commented by Cacho *et al.* (2006), random searching would be expected to produce the least detections unless there were systematic biases in the search process. The proportion of targets detected (p_{detect}) for random sweeping is given by:

$$p_{\text{detect}} = 1 - e^{-c} \quad (7)$$

Cacho *et al.* (2006) reported a p_{detect} value of approximately 0.63 under the random detection function at $c = 1.0$ coverage. They illustrated how search time affects coverage considering a plant/environment combination with $S = 1000 \text{ m h}^{-1}$ and $R = 20 \text{ m}$; thus $S \cdot R = 20\,000 \text{ m}^2 \text{ h}^{-1}$,

implying that 2 ha can be searched in one hour, or that a coverage of 2.0 can be achieved with a search time of 1 h on an one hectare plot.

Once detection is made, it is assumed that an attempt is made to kill the weeds found, subject to the effectiveness of the control method used. The mortality caused by the search and control effort (D) is:

$$D = p_{\text{detect}} p_{\text{kill}} \quad (8)$$

where p_{kill} is the probability that a target organism will die each time a control is applied.

Search effort When a large area cropping system is considered, localized search for a new invader would begin when a certain threshold level is reached in terms of visible detection of weed densities in those locations. While it is not rational to equally distribute the search and control effort across the large region, the modelling becomes complex when smaller sized sub grids (the number and their sizes etc.) have to be defined to focus this control effort. Previously Jayasuriya and Jones (2008) and Jayasuriya *et al.* (2008a) adopted a method to allocate search and control effort into one sub grid in the full grid space assuming a new invasion is discovered in a particular locality of a very large region. Consistent with Jayasuriya *et al.* (2008b), in this paper we have adopted a method to allocate search and control effort proportionately into each grid cell based on the weed density in those cells each year. This approach implicitly assumes that individual farmers in the large region are accurate in observing the weed densities and thus focus their search and control effort on those locations. Therefore T_{ij} for each (i, j)th cell across the $n \times m$ array at time t , is set proportional to $X_{ij}^{pc}(t)$ so that:

$$\sum_j T_{ij}(t) = T.$$

Re-infestation from the soil seed bank Although a visible infestation can be killed after applying 'search and control effort' as shown in Equation (8), there is always the possibility of re-infestation occurring from the soil seed bank. Process-based demographic modelling such as Woolcock and Cousens (2000) has incorporated effective germination rates separately for new and old seeds in the seed bank. Literature citations on the seed germination rates vary for different weeds ranging from 25–50% for new and old seeds respectively in the case of *Raphanus raphanistrum* (wild radish), while just 2% of *Orobancha ramosa* (branched broomrape) seeds may germinate in field conditions due to the requirement of host plants to be present. Due to the existing complexity of the spatial modelling framework, weed demography was not included into the regional level

spread model as it would add considerably to the computational burden. Instead, a more simplistic approach of incorporating weed re-infestation from the seed bank was used where the mortality caused by the search and control effort (D) was adjusted to accommodate the re-infestation of weeds from the soil seed bank:

$$M = D(1-\theta) \tag{9}$$

where M is mortality caused by the search and control effort after adjusting for the seed bank re-infestation rate (θ) where $\theta \in [0, 1]$.

To include dependence of M on cell (i, j) across the $n \times m$ array and on time t , Equation (9) can be written as:

$$M_{ij}(t) = D_{ij}(t) [1-\theta_{ij}(t)] \tag{10}$$

Here $\theta_{ij}(t)$ is set up to allow dependence on both cell and time. Replacing $\theta_{ij}(t)$ with $\theta(t)$ would have the re-infestation parameter independent of space. In resembling the overall weed control effort in the arable field, this $M_{ij}(t)$ is then applied to the Equation (5) to obtain:

$$X_{ij}(t+1) = X_{ij}^{pc}(t+1) [1- M_{ij}(t)] \tag{11}$$

Parameterization for case study simulations

As explained previously, Equation (2) is used to determine different values of the intrinsic growth rate parameter r . This value was computed for six hypothetical weed spread scenarios, being 4, 7, 10, 15, 20 and 25 years to reach a 95% infestation level, starting with a 0.1% infestation in a 1 km² area (individual cell size in the grid).

The dispersal probabilities considered in the example simulation are $p_{sd} = 0.999$ and $p_{ld} = 0.001$, with the conditional short distance dispersal probabilities to neighbouring ‘rings’, up to the fourth ring, i.e. $p_{0r}, p_{1r}, \dots, p_{4r}$, set equal 0.95, 0.02, 0.015, 0.01 and 0.005 respectively. These have already been mentioned. For the remaining parameters in the model we include a stochastic component to capture temporal and possible spatial variation. In each case, the sampling distribution for the parameter is taken as a triangular distribution having mode at the most likely value for the parameter and the minimum and maximum of the distribution corresponding to the parameter’s possible range. In each case the corresponding distribution is denoted by Tri(min, mode, max).

For parameters p_{kill} and θ , these are assumed constant across the grid within each year but across years are assumed independently sampled from Tri(0.9, 0.95, 0.97) and Tri(0.2, 0.25, 0.3) respectively. Here the variation in these parameters aims to capture seasonal variation. For parameters S (km h⁻¹) and R (km) it is expected that these will vary spatially as well as

temporally. Hence these parameters are sampled for each grid cell at each time independently from Tri(0.95, 1.0, 1.05) and Tri(0.018, 0.02, 0.021) respectively. These settings are summarized in Table 1. Time spent searching, as denoted by T in Equation (6), was the decision variable on the weed control strategy and is expressed in ‘man days’ assuming seven hours of search and control time spent per man day in the field.

A case study of awnless barnyard grass spread in Northern New South Wales

Awnless barnyard grass (*Echinochloa colona*), an annual species, grows rapidly during spring to autumn period. Flowering occurs during summer and autumn, particularly in response to rain. Emergence occurs mainly during October to January

in southern Queensland. The weed germinates in a number of cohorts in response to rain of at least 90 mm. Three major flushes of emergence have been identified during late spring and early summer. Although *E. colona* is an annual, it may be vegetatively propagated by production of new roots and shoots at the nodes when it is in a stage of prostrate growth (Holm *et al.* 1977).

The production of a large number of easily dispersed seeds and the ability to flower under a wide range of photoperiods contributes to the success of barnyard grass. The ability to grow in flooded fields, in waterways, and on levees has enabled several species of barnyard grass to spread over much of the older rice cropping areas in the Murrumbidgee and Murray Valleys of New South Wales. On older cropping land, the weed density is

Table 1. Parameters used in the model.

Variable	Parameter	Value
Total area at risk of invasion (km ²)	A	grid of 100 × 100 cells = 10 000
Intrinsic growth rate when Y years taken to reach 95% infestation in 1 km ² grid cell:	r	
$Y = 25$		0.44
$Y = 20$		0.57
$Y = 15$		0.80
$Y = 10$		1.35
$Y = 7$		2.38
$Y = 4$		9.19
Probability of long distance dispersal	p_{ld}	0.001
Conditional short distance dispersal probabilities: probability of dispersal:		
within the dispersing cell itself		0.950
among the 8 cells lying around one cell away		0.020
among the 16 cells lying around two cells away		0.015
among the 24 cells lying around three cells away		0.010
among the 32 cells lying around four cells away		0.005
Speed of search (km h ⁻¹)	S	
minimum value		0.95
mode value		1.00
maximum value		1.05
Effective sweep width (km)	R	
minimum value		0.018
mode value		0.020
maximum value		0.021
Probability of kill each time control is applied	p_{kill}	
minimum value		0.90
mode value		0.95
maximum value		0.97
Re-infestation rate from the soil seed bank	θ	
minimum value		0.20
mode value		0.25
maximum value		0.30
Threshold level of infestation (%)		1.0

generally increased by cultivation, possibly because buried seed is brought close to the soil surface. *E. colona* hosts a number of diseases, being an alternate host for the viruses which produce mosaic diseases in rice and sugarcane (Holm *et al.* 1977). Barnyard grass interferes with harvesting of row crops and increases labour costs; the crop must be separated from the weed clumps.

One plant may produce up to 42 000 seeds. The seeds are readily spread by irrigation or river water and often enter rice fields with crop seeds or transplants. Because it resembles rice in the seedling stage, it is sometimes transplanted by accident into the fields with the rice crop. Seeds may also be transferred between fields on farm machinery and on mud on the feet, fur, feathers and skin of rodents, birds and larger animals including humans (Holm *et al.* 1977). In Australia it is suspected that wild ducks may have been important in the initial distribution of the weed (CRC for Australian Weed Management 2006). Cultivation buries the seed which will survive for many years and stock help spread seeds from infested paddocks. Wu *et al.* (2004) indicate that seeds buried deep in the soil are able to persist, providing a potential seed source of further infestation.

Herbicides are the major means of controlling *E. colona* in crops, but few chemicals are available for its economic control during fallow periods. Glyphosate is used for fallow weed control in the north-east grain region and elsewhere as it has broad spectrum of weed control, is non-residual, and non-toxic to animals. Despite repeated warnings of the threat of glyphosate resistance developing in several significant weed species, the herbicide has been unwisely relied upon as the only weed control in fallow. The recent discovery of glyphosate resistance in *E. colona* in New South Wales has left growers with few options as there is already resistance to herbicide mode-of-action groups A, B and C overseas and one population in northern New South Wales resistant to atrazine – group C (NSW DPI 2007). Implementing control options other than glyphosate is seen as an insurance policy that will delay or prevent the onset of glyphosate resistance. As the weed has a long-lived seedbank, one season of poor control can set paddocks up for many years of high weed numbers and difficult control, so it is important to prevent the seed-set. Spraying with a high rate of paraquat or Spray Seed (a mixture of paraquat and diquat) – a second application might be needed if the plants are large – and controlling new germinations until the end of the season is recommended. A new control regime will be required the following summer in all paddocks to prevent resistance developing. To obtain total control a minimum of

two control tactics must be used on each flush of awnless barnyard grass (NSW DPI 2007). In the USA, rotations with rice, soybeans, and/or oats have been effective in reducing the levels of infestation (Holm *et al.* 1977).

After discussions with the Technical Specialist (weeds) and the Technical Officer (weeds) at the Tamworth Agricultural Institute of New South Wales Department of Primary Industries, we concurred that the first two hypothetical case study spread scenarios in Table 1, being 25 and 20 years to reach a 95% infestation level, starting with a 0.1% infestation in a 1 km² area (individual cell size in the grid), would resemble the case of *E. colona* spread in the northern New South Wales. It was also suggested that this varies depending on: type of cultivation, time taken for cultivation (to prepare wheat crop), slope of ground, fertility of the paddock, occurrence of heavy rainfall events, whether the area is grazed (seeds will move on mud and in the gut of the animals) and presence of ants etc.

Results and discussion

Dividing space into discrete units (grid of 100 × 100 cells equivalent to 10 000 km²), the spread model was run for 50 years starting with a 10% infestation (100 units of 0.1% infestations) dispersing from the central cell of the grid space. Six case study weed spread scenarios were run by varying the intrinsic growth rate parameter *r*. The model counts the number of grid cells that have weed infestations above a threshold level of 1% and reports the proportion of grid cells infested beyond this threshold for every year of the model runs. This is termed the 'infestation level' and is presented in Figure 3 for the initial decision of no search and control effort.

Figure 3 shows the weed spread (under the four highest *r* parameter values in Table 1) in the entire cropping region of 10 000 km² defined as the area at risk from a new invasion. With a *r* parameter of 0.80 (where it takes 15 years to reach 95% infestation level in a 1 km² area starting with a 0.1% infestation), the whole region reaches 100% infestation by year 34 without any search and control effort. With higher values for the *r* parameter the region reaches full infestation level rapidly, indicating that this would occur by the year 26, 20 and 12 for the *r* parameter values of 1.35, 2.38 and 9.19 respectively. The variability of each curve is shown in marked lines indicating the 5th and 95th percentiles from 100 simulation runs. This variability entails the stochastic nature of the spread functions with different probability distributions incorporating rare events in the dispersal process.

The six simulations shown in Figure 4 (a) to (f) indicate the relationship between the weed intrinsic growth rate *r*, its spread

in the field and the search and control effort required in the total cropping region of 10 000 km² defined as the area at risk of a new invasion. In the first case study simulation (Figure 4a) with an *r* parameter of 0.44 (where it takes 25 years to reach 95% infestation level in a 1 km² area starting with a 0.1% infestation), the region reaches 30% infestation by year 50 without any search and control effort. With 100 man days per annum input in search and control effort it seems possible to maintain near zero infestation level in the region for the full 50 year period (coincides with horizontal axis of the graph).

In the second case study simulation (Figure 4b) with an *r* parameter of 0.57 (where it takes 20 years to reach 95% infestation level in a 1 km² area starting with a 0.1% infestation), the whole region reaches 100% infestation by year 43 without any search and control effort. With increasing control effort, the infestation curves are pushed to the right thus slowing the weed population spread rate in the region. A 100 man days per annum input in search and control effort would not be adequate as the infestation level starts increasing after 30 years. With around 400 man days per annum input in search and control effort it seems possible to maintain near zero infestation level in the region for the full 50 year period (coincides with horizontal axis of the graph). These results suggest that a control effort in the range of 200 to 400 man days per annum would be required to keep the barnyard grass invasion under control in this region.

In the third case study simulation (Figure 4c) with an *r* parameter of 0.80 (where it takes 15 years to reach 95% infestation level in a 1 km² area starting with a 0.1% infestation), the whole region reaches 100% infestation by year 34 without any search and control effort. With control effort, the infestation curves are pushed to the right thus slowing the weed population spread rate in the region. With around 400 man days per annum input in search and control effort it seems possible to maintain near zero infestation level in the region for the full 50 year period (coincides with horizontal axis of the graph).

The fourth case study simulation (Figure 4d) shows that with the *r* parameter increasing to 1.35, the time taken to reach 100% infestation in the region gets shortened for both with and without control scenarios. As shown in the fifth simulation (Figure 4e), with an *r* parameter of 2.38, the full infestation is reached by year 20 without a search and control effort. None of the search and control scenarios evaluated would be adequate in suppressing weed spread, thus requiring a much higher level of search and control effort. Finally as shown in Figure 4f, with a very high *r* value of 9.19 (where it takes only 4 years to reach 95% infestation level in a 1 km² area),

it takes only 12–13 years for the particular weed to spread into the entire region of 10000 km², regardless of the search and control scenarios evaluated.

Conclusion

We described a spatially explicit large regional scale spread modelling approach and presented an application of the model to awnless barnyard grass spread in northern New South Wales. This model could be applied to large area cropping systems when a single grid cell can be equivalent to the size of an individual farm and where

long distance weed spread can occur due to vehicles, farm machinery, weather and animals. The model has modest data requirements (for a spatial simulation model) in that it concentrates on simulating population growth, dispersal processes and mortality (including search and control) and ignores the environmental and biotic heterogeneity of the receiving environment. We have incorporated this into a broader bioeconomic framework to evaluate optimal policy responses to new weed incursions from an economic perspective (Jayasuriya and Jones 2008, Jayasuriya *et*

al. 2008a). This bioeconomic application clearly shows that there are significant benefits to be achieved by controlling highly invasive weeds when initial infestations are at a low level. The cost of weed control also increases with invasiveness, but the magnitude of this is smaller compared to the increased benefits received. As a result the increase in the benefit-cost ratio is large under a highly invasive weed infestation control scenario. Even when an invasion cannot be eradicated due to its high invasiveness or budget constraints, it still pays to maintain invasions at lower level. This is in line with the work by Sharov and Liebhold (1998) and Cacho (2004) which showed that slowing population spread is a viable strategy of invasion control while the optimal strategy changes from eradication to slowing the spread to finally doing nothing.

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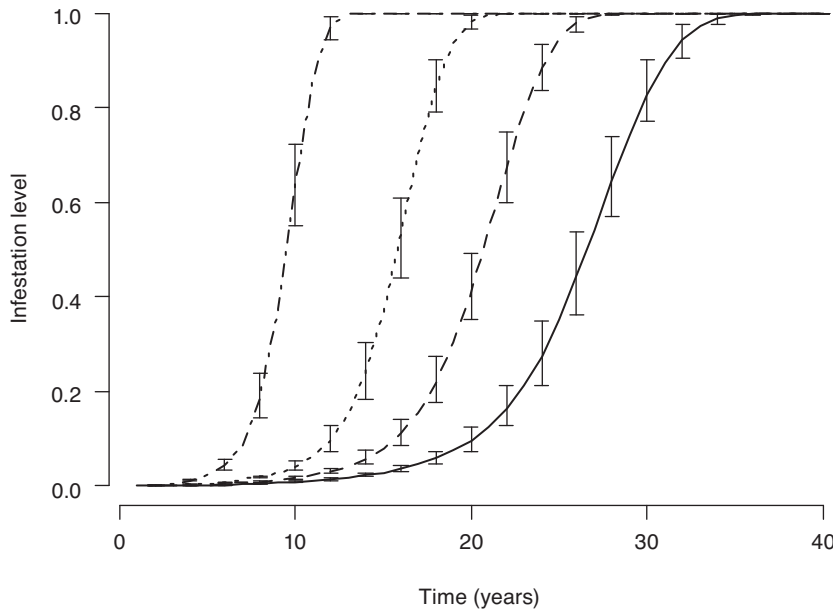


Figure 3. Weed spread without any control under different *r* values (—) 0.80, (---) 1.35, (· · ·) 2.38, (- · - ·) 9.19.

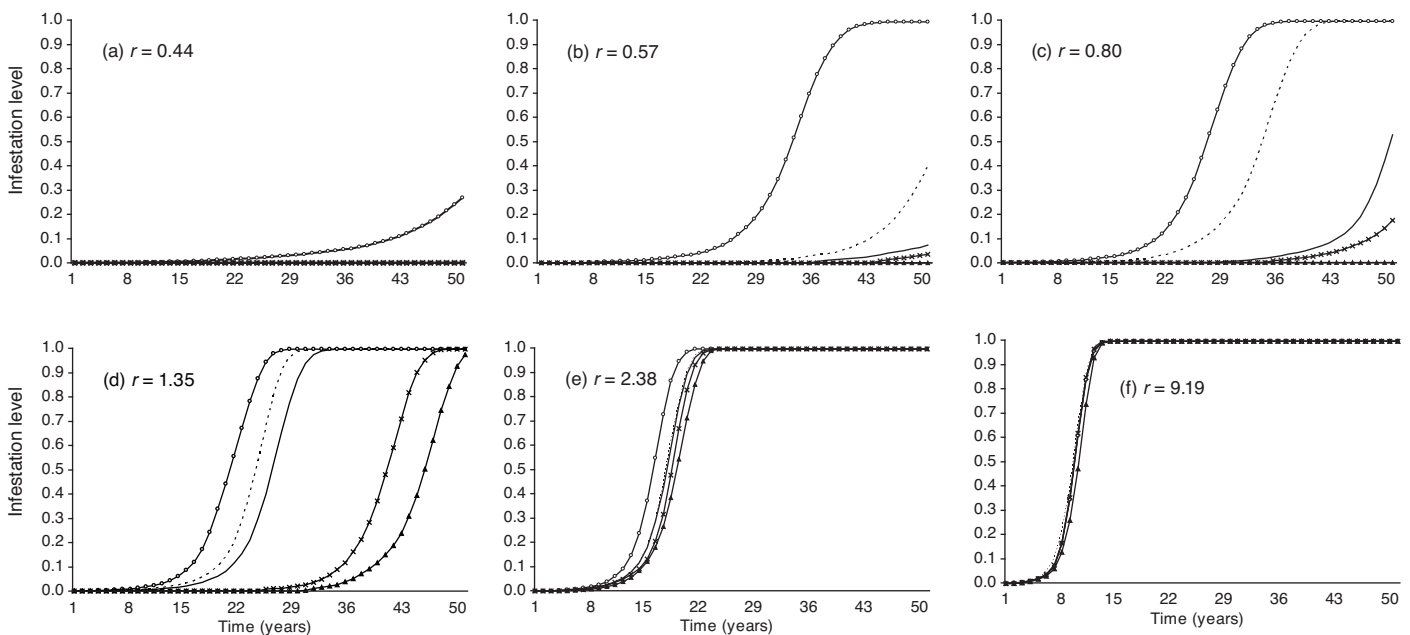


Figure 4. Weed spread under different *r* values and with different levels of control (—○—) no control, (- · - ·) 100 man days y⁻¹, (—) 200 man days y⁻¹, (—×—) 300 man days y⁻¹, (—▲—) 400 man days y⁻¹.

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Footnote

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