Dynamics of Weed Populations

spatial pattern formation

and

implications for control

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STELLINGEN

Er is niet één zin die zijn eigen betekenis adequaat weergeeft.
(A.N. Whitehead)

i De waarneming dat populaties van éénjarige onkruiden ruimtelijk heterogene patronen vormen, met clusters die vele jaren op vrijwel dezelfde plaats blijven, kan worden verklaard op basis van populatiedynamische processen alleen, zonder aan te nemen dat de abiotische omgeving heterogeen is.
(Dit proefschrift)

ii De zogenaamde 'inverse square law', die volgens bijvoorbeeld Begon *et al.* (1996) stelt dat een plantpopulatie zich ruimtelijk uitbreidt met een gesloten voortschrijdend front als de dispersiecurve sneller dan kwadratisch afneemt met afstand tot de moederplant, is onjuist.
(Dit proefschrift; Begon *et al.* 1996 *Ecology: individuals, populations and communities.* 3^{e} ed. Oxford: Blackwell, p 184)

iii Pleksgewijze onkruidbestrijding kan een zeer grote reductie in benodigde hoeveelheid herbiciden geven, en deze reductie kan worden gekwantificeerd door meting van de cumulatieve frequentie verdeling van afstanden tussen willekeurig gekozen punten in het veld en het dichtstbijzijnde onkruid voor elk punt.
(Dit proefschrift)

iv Als onkruid alleen bestreden wordt wanneer de dichtheid boven een drempelwaarde uitkomt, hangt de bestrijdingsfrequentie op de lange termijn niet of nauwelijks af van de hoogte van de bestrijdingsdrempel.
(Dit proefschrift)

v Bij toepassing van bestrijdingsdrempels neemt de relatieve fout in de voorspelde onkruiddichtheid lineair toe met de duur van het voorspellingsinterval.
(Dit proefschrift)

vi Een nulhypothese voor het ruimtelijke patroon van éénjarige onkruiden van een enkele soort op een akker is een patroon met een fractale dimensie van 1.19.
(Dit proefschrift)

vii De Rhônegletsjer zal over honderd jaar bijna verdwenen zijn door opwarming van het klimaat.
(J. Wallinga & R.S.W. van de Wal. 1998 Sensitivity of Rhonegletscher, Switzerland to climate change: experiments with a one-dimensional flowline model. *J. Glaciol.*, in druk)

viii De rol van wiskunde in de biologie is voornamelijk om gezond verstand consistent en precies te maken; dit garandeert niet dat de voorspellende waarde van de theorie beter wordt, maar het garandeert wel dat fouten in de theorie duidelijker naar voren komen.

ix Chemische reductie van het elektrodeoppervlak bij het maken van een zonnecel van amorf silicium kan leiden tot een daling in transparantie en geleidbaarheid van de elektrode en daardoor tot een vermindering van de energieopbrengst van de zonnecel.
(J. Wallinga *et al.* 1998 Reduction of tin oxide by hydrogen radicals. *J. Phys. Chem.* B 102, 6219-6224)

x In Nederland zijn socio-geografische clusters van niet-gevaccineerde personen te klein en te gefragmenteerd om de circulatie van het mazelenvirus onder de Nederlandse bevolking in stand te houden.

xi De wetenschappen zijn, na de kunsten, de meest verlichtende verdienste van de menselijke geest.
(Naar K. Popper)

xii Het wetenschappelijk streven naar eenvoudige verklaringen voor complexe fenomenen houdt geen vooronderstelling in dat complexe fenomenen van een nog onbegrepen eenvoud zijn.

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PROPOSITIONS

There is not a sentence which adequately states its own meaning.
(A.N. Whitehead)

i The observation that populations of annual weeds form spatially heterogeneous patterns, with clusters that remain on the same location for several years, can be explained solely on basis of population dynamical processes, without invoking assumptions about heterogeneity of the abiotic environment.
(This thesis)

ii The so-called 'inverse square law', which according to e.g. Begon *et al.* (1996) states that a plant population expands by a closed advancing front if the dispersion curve declines faster than quadratically with the distance to the mother plant, is incorrect.
(This thesis; Begon *et al.* 1996 *Ecology: individuals, populations and communities.* 3rd edn. Oxford: Blackwell, p 184)

iii Patch control can result in very large reductions in the required amount of herbicides, and this reduction can be quantified by measuring the cumulative frequency distribution of distances between randomly chosen points in the field and the nearest weed to each point.
(This thesis)

iv If weeds are controlled only when their density exceeds a threshold value, the frequency of control will, on the long term, not depend on the value of this threshold.
(This thesis)

v Threshold control leads to a relative error in predicted weed density that grows linearly with the duration of prediction interval.
(This thesis)

vi A null-hypothesis for the spatial pattern of annual weeds of any single species on an arable field is a pattern with a fractal dimension of 1.19.
(This thesis)

vii The Rhone Glacier will have almost disappeared within a hundred years due to climate warming.

(J. Wallinga & R.S.W. van de Wal. 1998 Sensitivity of Rhonegletscher, Switzerland to climate change: experiments with a one-dimensional flowline model. *J. Glaciol.*, in press)

viii The role of mathematics in biology is primarily to make common sense consistent and precise; this does not guarantee that predictions will improve, but it does guarantee that errors in the theory stand out more clearly.

ix Chemical reduction of the electrode surface in production of a solar cell of amorphous silicon may lead to a reduced transparency and conductivity of the electrode, causing a reduction in the energy yield of the solar cell.

(J. Wallinga *et al.* 1998 Reduction of tin oxide by hydrogen radicals. *J. Phys. Chem.* B 102, 6219-6224)

x The socio-geographical clusters of non-vaccinated persons in the Netherlands are too small and too fragmented to keep the measles virus circulating in the Dutch population.

xi The sciences are, next to the arts, the most enlightening achievement of the human spirit.

(After Karl Popper)

xii The scientific quest for simple explanation of complex phenomena does not imply a presupposition that complex phenomena are of a not yet understood simplicity.

J. Wallinga
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ABSTRACT

Modelling studies were carried out to analyse spatio-temporal dynamics of annual weed populations and to identify the key factors that determine the long-term herbicide use of weed control programmes. Three different weed control programmes were studied. In the first weed control programme, herbicides are applied to the whole field only if the weed density exceeds a threshold value, otherwise there is no control at all. The dynamics of a weed population subjected to such a 'threshold control programme' is characterized by aperiodic (quasi-periodic or chaotic) cycles, whereas the long-term herbicide use does not depend on the threshold value. In the second weed control programme, the optimum herbicide dosage is determined and applied to the whole field. In this case the density of the weed population will approach a low equilibrium value. The herbicide use of such an 'optimum dose control programme' is determined by the herbicide dose required to keep the weed population at a low density. In the third weed control programme, the spatial scale of weed control decision making is reduced such that only weed patches are sprayed. The herbicide use of such a 'patch control programme' is determined by the spatial pattern of weeds as well as the spatial resolution of the patch sprayer. The patch control programme is only of interest if weeds are heterogeneously distributed over space. It is shown that invading annual weed populations are capable of generating patches, even in an otherwise homogeneous habitat, if the forward tail of the projected seed dispersal curve declines slower than exponential. It is shown that annual weed populations are also capable of generating patches in an otherwise homogeneous habitat if they are held at a constant low density. In the latter case, the weed patch formation is a self-organized critical phenomenon.

PREFACE

Anyone who has seen the movie 'Invasion of the Body Snatchers' will realize that invasions by alien plants may pose a life-threatening danger to mankind. But what about the ordinary plants like chickweed and cleavers that grow in the farmers' fields? These ordinary plants also pose a considerable problem to mankind. If farmers leave the weeds uncontrolled, the weeds would cause considerable losses in crop yield and food production. If farmers control the weeds by chemical means, which is often considered to be the only economically feasible option for weed control in modern western agriculture, these chemicals may contaminate the surface water and thus impose a danger to public health.

One of the aims of this thesis is to highlight the impact that control has on the spatial dynamics and pattern formation in weed populations, and the opportunities this gives to design better weed control programmes that require less use of herbicides. It is not intended as a cookbook for applied ecologists to build decision support systems for weed management, nor is it intended as a guide for theoretical ecologists for designing abstract models of plant population dynamics. Rather, this thesis offers some new concepts and approaches that might appeal to both theoretical and applied ecologists.

This thesis would not have been possible without Jos Frantzen and Marcel van Oijen who encouraged me at an early stage to pursue the research on spatial pattern formation in weed populations, and who helped me to write down the results in such a way that somebody else might understand what had been achieved. No experimental results would have been obtained without the help of Roel Groeneveld who demonstrated that the value of fieldwork lies in doing it. I am glad to thank friends and colleagues for taking the time to read parts of this thesis as it developed, for providing stimulating discussions, and for pointing out the relevant literature. Particularly I would like to mention Michiel van Boven, Bert Bos, Frank van den Bosch, Jeroen Groot, Hans Heesterbeek, Gareth Hughes, Corné Kempenaar, Eddie Kremer, Shana Mertens, Dave Mortensen, André de Roos, Lisa Rew, Maurice Sabelis, Peter Schippers, Bert Schnieders, Leo Vleeshouwers, Rommie van der Weide and Wopke van der Werf. A special thanks goes to Bert Lotz for starting up the project on weed population dynamics at the DLO-Research Institute for Agrobiology and Soil Fertility at Wageningen. Of course, this thesis would not have been possible without Martin Kropff and Johan Grasman, whom I gratefully acknowledge. They encouraged my interests in weeds and in analysis of spatial dynamics, and they have been of great help to point out the most essential findings as they are reported here.

CONTENTS

GENERAL INTRODUCTION

Motivation for this study

The presence of weeds in a crop forms a threat to the crop yield. If no action is taken, weeds will reduce crop yield, reproduce, and form an even larger threat to future crops. Weed control is therefore a crucial element in cropping systems. At present, most cropping systems rely heavily on herbicides because they are a reliable and relatively cheap means for weed control. Because environmental side-effects of herbicide use have become apparent over the past decades, public concern has been aroused. For example, the Dutch government launched a multiple-year programme on crop protection that restricts the amount of agrochemicals used and that promotes agricultural practices that rely less on agrochemicals (Anonymous 1991). New weed control programmes have been developed that aim to avoid unnecessary use of herbicides as well as excessive yield losses.

It is in general very easy to develop new weed control programmes that reduce herbicide use over a short term. For instance, simply omitting weed control in cereal crops will give often acceptable yields in the current cropping season without the use of any herbicides. But this short-term benefit has its price on the long term: weeds are allowed to reproduce, and the weed population will increase in size and may cause considerable yield losses in subsequent years. Control programmes that give good results on a short term do not necessarily give good results in the long term. It is essential to evaluate newly developed weed control programmes for their long-term effectiveness and herbicide usage. However, it is almost impossible to set up field experiments for such an evaluation and, even if it were possible, the experimental results would come too late to be of any use. An alternative is to evaluate the effectiveness and herbicide usage of weed control programmes with models of weed population dynamics.

Models of weed population dynamics have been used for a few decades to evaluate weed control programmes (see, *e.g.*, Selman 1970; Mortimer *et al.* 1978). More recently, computer models have been used to simulate the dynamics of one particular weed species in response to a weed control programme. For instance, Doyle *et al.* (1986) simulated the dynamics of the grass weed *Alopecurus myosuroides* Hudson which was controlled whenever the weed density exceeded a threshold value; Pandey & Medd (1991) simulated the dynamics of the grass weed *Avena fatua* L. in response to annual applications of herbicide dosages optimized with respect to specific economic objectives; Day *et al.* (1996) simulated the dynamics of a theoretical grass weed in response to spatially selective weed control.

The above-mentioned list of studies shows that there are at least three different weed control programmes to avoid unnecessary herbicide usage and excessive yield losses:

- weed control programmes that apply herbicides only where needed, they will be referred to as 'patch control programmes';
- weed control programmes that apply herbicides over the whole field at the economic optimum dose, they will be referred to as 'optimum dose control programmes';
- weed control programmes that apply herbicides over the whole field only when the weed density exceeds a threshold value, they will be referred to as 'threshold control programmes'.

Alternatively, the herbicide use of weed control programmes can be reduced by relying on mechanical or biological weed control methods ('ecological weed control'). For such weed control programmes, it is also essential to evaluate the long-term effectiveness and to avoid unnecessary use of, for example, harrowing treatments or mycoherbicide applications. It is expected that at least some of the problems encountered in the evaluation of ecological weed control programmes will also be encountered in the evaluation of herbicide-based weed control programmes. Therefore, the evaluation of long-term effectiveness and long-term herbicide use of weed control programmes may be useful for the evaluation of weed control programmes that do not rely on chemical weed control.

Objectives of this study

The evaluation of weed control programmes usually requires a vast amount of quantitative data on herbicide efficacy, weed-crop interference and weed population dynamics, prices of crop and herbicide. In most cases, this data is not available. One possible way of circumventing the large data requirement is to identify the key factors involved in long-term herbicide use by a particular control program, and to estimate how the long-term herbicide use depends on these key factors.

In some cases, a better understanding of weed population dynamics is needed to evaluate the effects of a control programme. For example, consider the 'patch control programmes'. They only avoid unnecessary herbicide usage if the weed spatial pattern is aggregated. Many observations indicate that spatial pattern of annual weeds is indeed aggregated (*e.g.* Rew *et al.* 1996), a limited number of observations indicates that these patches remain at the same location over many years (*e.g.* Wilson & Brain 1991). It is not well understood why annual weeds form patches and how these patches persist despite years of uniform treatment, and, at present, it is not known what will happen if only weed patches are treated with herbicides (Rew & Cussans 1995). A better understanding of spatio-temporal dynamics of annual weed populations is required in order to evaluate the effects of patch control programmes.

The first objective of this thesis is to analyse spatio-temporal dynamics of annual weed populations in response to the control exerted by weed control programmes. The second objective is to identify the key factors that determine and control the long-term herbicide use for a weed control programme.

Methodology

Throughout this thesis, analysis of population dynamics will rely on the use of mathematical models that are based upon a very basic description of the life-history of annual weeds: seeds germinate in the beginning of the cropping season; they establish as plants; the plants are subjected to weed control; the surviving plants mature and produce seeds; the seeds are disseminated and added to the seedbank. If interest is in spatial pattern formation in populations, it is essential that a model also has discrete individuals, demographic stochasticity and local spatial interactions (Durrett & Levin 1994*a*,*b*; Bolker & Pacala 1997; Levin & Pacala 1997). If interest is in other aspects of population dynamics, more parsimonious models can be used, for instance models that use a continuous distribution of weed density over space (Allen *et al.* 1996*a*,*b*) or models that use a weed density that is averaged over a whole field (Firbank & Watkinson 1986).

Most of the data that is used for comparison with model assumptions and model results are obtained from previously conducted experiments (some of which have been reported by Wallinga 1995*a*). The analysis of weed population dynamics in response to weed control programmes is carried out analytically or by means of computer simulations.

Outline of this thesis

First, the spatio-temporal dynamics of annual weed populations are studied. What causes weeds to occur and persist in patches? Chapter 2 provides an answer to this question in case the weed population is kept at a constant, low density. Chapter 3 provides an answer to this question in the case of an expanding weed population.

Second, patch control programmes are evaluated. Chapter 4 suggests a method for estimation of the potential reduction in herbicide use by a patch spraying strategy, based on a description of the weed spatial pattern in a field.

Third, optimum dose control programmes are evaluated. The exact optimum herbicide dose may be calculated by available optimization algorithms that require large amounts of data which are often not available. Chapter 5 gives an approximation of the long-term herbicide usage when only limited data is available.

Fourth, the threshold control programmes are evaluated. Straightforward simulation methods result in a 'blurred' relation between threshold density and average herbicide use (see Cousens *et al.* 1986). Chapter 6 shows that it is possible to derive a better, unambiguous, relation between threshold density and long-term herbicide usage. Chapter

7 shows how the predicted weed density is affected by estimation errors of the initial weed density and the weed population growth rate.

Fifth, the results of the preceding chapters are integrated and used to indicate the key factors that determine and control the long-term herbicide use of the evaluated weed control programmes, and to formulate a conjecture about the spatio-temporal dynamics of annual weed populations (chapter 8).

THE ROLE OF SPACE IN PLANT POPULATION DYNAMICS: ANNUAL WEEDS AS AN EXAMPLE

Adapted from: Wallinga, J. 1995 *Oikos* 74, 377-383

Abstract

The dynamics and spatial pattern of a weed population are analysed with a model that takes explicit account of the spatial position of individual weeds. In this model weeds are held at a low density in an environment with homogeneous abiotic conditions. Maintaining low weed densities requires a weed removal rate close to the critical removal rate that marks the transition from possible survival to certain extinction of the population. At these low densities, the spatial pattern of weeds and the local population dynamics obey scaling laws. These scaling laws and the value of the scaling exponents are robust to changes in the model. Based on this analysis, weeds are expected to occur in scale-invariant spatial patterns. In a field observation, the spatial distribution of the weed *Galium aparine* L. is found to be scale-invariant.

Introduction

A plant population's establishment in an environment is determined by the population dynamic attributes of the plants that make up that population. Theoretical studies (*e.g.* Durrett & Levin 1994*b*; Sato *et al.* 1994) accounting for spatial position and dispersal of individuals and assuming an environment with homogeneous abiotic conditions, have shown that there is a marked threshold for mortality rate, below which the population can persist, but above which the population faces certain extinction. At mortality rates just below this threshold, the population may persist at low densities, while balancing between possible survival and certain extinction. In this situation, where conditions for survival are marginal, 'critical phenomena' are expected (see Grassberger 1983). These 'critical phenomena' imply that the dynamics and spatial pattern are pertinent to a nearby critical point (here the threshold value of mortality rate), and that the dynamics and spatial pattern are scale-invariant, with scaling exponents independent of many details of the system.

Weed populations are plant populations whose population growth is controlled by farmers, that is, their mortality rate is enhanced. The term 'weed' is used here to refer to annual plants that occur endemically in an arable field with homogeneous abiotic conditions. These plants are controlled to maintain them at a low density, without necessarily driving them to extinction (Pandey & Medd 1990). So, where a plant population with a high mortality rate (close to the threshold value) occurs at low densities, a weed population is subjected to a high mortality rate to maintain it at low densities. This evokes the question of whether critical phenomena might be expected for weed populations. If so, it would yield a very robust qualitative and quantitative hypothesis for dynamics and spatial pattern of weeds, which could prove useful for weed management (Mortensen *et al.* 1993*a*).

This paper examines whether such a robust hypothesis for dynamics and spatial pattern for weed populations might exist. A somewhat simple model of a weed population without spatial structure is presented as a preliminary to a more complicated stochastic model of weed population dynamics that explicitly accounts for the spatial position of weeds. It will be shown that the latter model generates dynamics and pattern that are typical for critical phenomena, and the 'typical' spatial pattern and dynamics of a weed population will be characterized. Finally, the expected spatial pattern is compared to a field observation.

A model of a weed population without spatial structure

Consider a population of plants as a spatially homogeneous mass. The individuals (annual weeds) reproduce in discrete generations of one year. The density of seeds is taken as the state variable, and the following transition rules are assumed:

- All seeds germinate and develop into plants.
- A fraction r is killed by weed control.

- The surviving plants reproduce and then die.
- The reproduction rate of the surviving plants depends on the plant density.

The fraction r is termed weed removal rate, the value of r is chosen such that the density of individuals does not change over time. This mimics the practice of removing plants when they are abundant, and not removing plants when they are rare. Time is denoted by t, the density of seeds is denoted as ρ. The maximum density is (arbitrarily) set to 1. At this maximum, each plant will yield on average 1 seed. The seed production per plant increases up to a maximum of a seeds per plant (with $a > 1$). This increase in seed production depends linearly on the difference between the actual and the maximum density.

In the absence of weed control, the growth of the population then obeys a simple logistic equation:

$$\rho_{t+1} = \rho_t + (a-1)\rho_t(1-\rho_t) \qquad (1a)$$

Weed control is introduced by substituting $(1-r)\rho_t$ for ρ_t. The fraction of plants that needs to be removed to keep the population at constant density is determined by solving the equation for r, after setting ρ_{t+1} equal to ρ_t:

$$r = 1 - \frac{a - \sqrt{a^2 - 4(a-1)\rho}}{2(a-1)\rho} \qquad (1b)$$

This relationship between weed removal rate r and weed density ρ is depicted graphically in figure 1. For weed control, we are interested in the fraction of weed plants that need to be removed in order to keep the population at a very low density. This rate of weed control is termed the critical removal rate r_c and is calculated as the limit $\rho \to 0$ of the right-hand side of equation 1b. For example, when the maximum growth rate a equals 5 seeds per

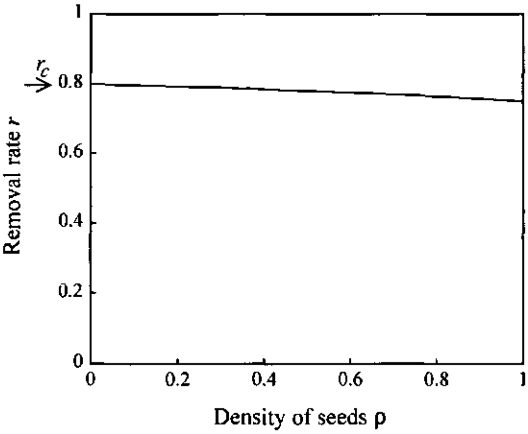

Figure 1. Removal rate r as a function of density of seeds ρ, according to the non-spatial model as in equation 1, with a maximum reproduction rate $a = 5$ seeds per plant.

plant, then four out of five weeds need to be removed to counterbalance this maximum growth rate, *i.e.* $r_c = 4/5$ (figure 1).

This system does not undergo dynamic changes, since density is held constant over time and is not allowed to vary over space.

A spatial model of weed population dynamics

The model

In a stochastic spatial analogue of the model described above, space is conceived as a collection of sites on a two-dimensional square lattice. The system is updated in discrete time steps corresponding to 1 year. Each site can be in one of two states: it can be either vacant or occupied by a single seed. The change in the state of a site at spatial position (x, y) at time t is determined by transition rules. The input for these rules consists of global and local information about the system at the preceding time. The global information is given as the density of occupied sites over the whole lattice (ρ). The local information is given as the states of the sites in the neighbourhood; this neighbourhood of the site (x, y) consists of the site itself and the four nearest neighbours $\{(x, y), (x+1, y), (x-1, y), (x, y+1), (x, y-1)\}$. From this information the new state of a site can be derived by applying the following transition rules:

- All seeds germinate and develop into plants.
- Plants die with probability r, where r is tuned so as to conserve the fraction of sites occupied by plants (ρ) on the whole lattice.
- If the plant survives, it will send a seed to each site in the neighbourhood (5 in total) and die.
- There can be at most one seed per site; if a particular site receives more than a single seed from its neighbourhood, one survivor is selected at random.

In this model there are no dynamics at a global level, but dynamic changes are allowed at a local level.

The pattern generated at low densities

To obtain a 'typical' spatial pattern of a weed population, Monte Carlo simulations were carried out with the model, using 1024 seeds distributed on a 512 × 512 lattice (these numbers are chosen as powers of 2 for computational convenience). When the model rendered a more or less stationary pattern, a snap-shot was taken of the two-dimensional spatial pattern. This pattern is shown in figure 2*a*, in which the sites occupied by weeds are marked as black dots. Clearly, the weeds appear in clusters. To find out how these clusters change over time, a transect across the lattice of figure 2*a* was selected. The spatial distribution of weeds on this transect was recorded for 512 consecutive time steps.

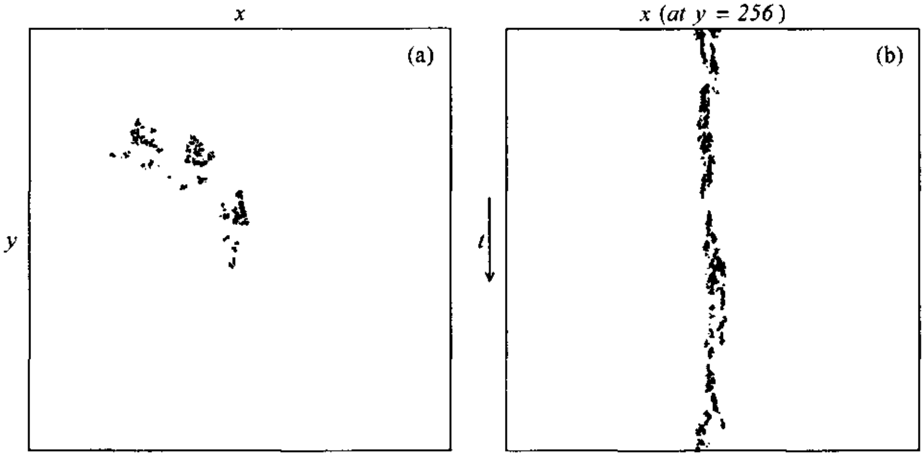

Figure 2. Results of Monte Carlo simulation with the spatial model on a 512 × 512 lattice. Lattice sites occupied by weeds are indicated as black dots. (*a*) A typical spatial distribution; (*b*) A typical temporal pattern for a transect through the spatial plane for 512 consecutive years. Spatial coordinates are denoted as x and y, time is indicated as t.

The resulting pattern is shown in figure 2*b*, where the sites occupied with weeds again appear as black dots and time increases from the top to the bottom. It illustrates that the clusters of weeds tend to remain on the same spot for a long time.

Analysis of the population dynamics at low densities

The question remains how these 'typical' patterns can be described quantitatively, and how they relate to the local population dynamics. Here, this question is addressed from the perspective of an individual seed. A closer look at the expansion over time from such a single seed to a cluster of offspring might clarify how the local population dynamics generate and maintain the spatial patterns.

A population at low density was simulated by distributing 1024 seeds on a 8192 × 8192 lattice. When the model rendered a more or less stationary pattern, a seed from this population was selected at random. The number and positions of its offspring in the population were recorded over time, up to 1024 time steps. This procedure for tracking and recording the offspring of randomly chosen seeds was repeated 10 000 times. The result was a large ensemble of offspring. In this ensemble two quantities were measured: the mean number of offspring at time t, and the mean square radius of a cluster of offspring at time t originating from a single individual at $t = 0$ (means were taken over surviving offspring only, and the distance between two adjacent sites was arbitrarily set to 1). These quantities yield information about increase in the number of offspring, and the concomitant spreading over space of offspring. The results are shown in figure 3 (note the double logarithmic scales).

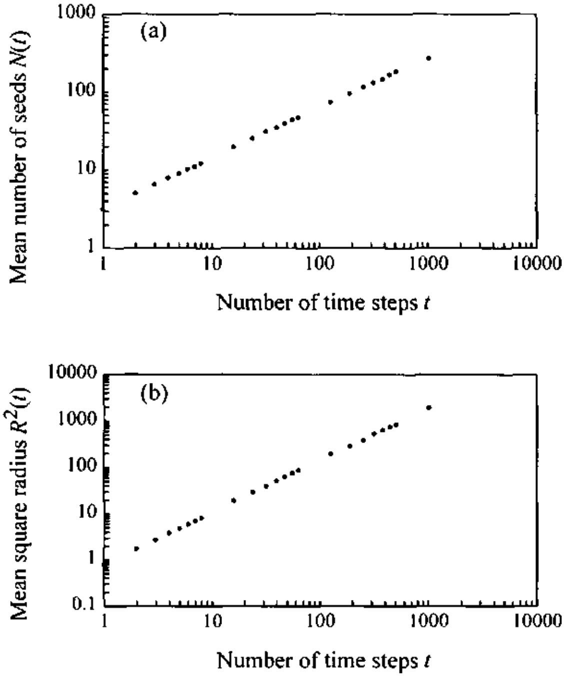

Figure 3. Results of Monte Carlo simulations, tracking all offspring of individual seeds. (*a*) The mean number of seeds stemming from a single parental individual $N(t)$ after t time steps. (*b*) The mean square radius of clusters of these seeds $R^2(t)$ after t time steps.

Figure 3*a* shows that the logarithm of number of offspring $N(t)$ increases linearly with the logarithm of time t. That is, the mean number of offspring present at time t, $N(t)$, increases with time according to a scaling law:

$$N(t) \sim t^{\varphi} \tag{2a}$$

where φ is the slope of the line in figure 3*a*. (Here, the sign ~ means either 'proportional to' or 'asymptotically proportional to'.) Figure 3*b* shows that the mean square radius of a cluster of offspring present at time t, $R^2(t)$, increases with time according to a similar scaling law

$$R^2(t) \sim t^{\chi} \tag{2b}$$

where χ is the slope of the line in figure 3*b*. The values of the exponents in these equations are estimated as $\varphi \approx 0.65$ and $\chi \approx 1.10$.

A static description of the resulting pattern of offspring can be inferred by combining these dynamic relationships (equations 2*a* and 2*b*) and eliminating t:

$$N(R) \sim R^{2\varphi/\chi} \tag{2c}$$

When the offspring of one seed are spread out over the lattice in a spatially uniform blob, the number of offspring should be proportional to the area occupied (*i.e.* $N \sim R^2$). So, a uniform distribution of offspring over space requires that the value of the exponent in equation 2*c* equals 2. However, the value of this exponent is found to be $2\varphi/\chi \approx 1.17$. This means that only few offspring disperse far from the centre of a cluster, while most offspring aggregate near the centre.

Conformation to a scaling relationship such as equation 2*c* means that the spatial pattern looks the same, no matter at which spatial scale the pattern is examined. This feature is termed 'scale invariance' and can be detected in the spatial distribution of weeds shown in figure 2*a*. Under magnification, each cluster consists of a set of clusters, each of which is in turn a set of clusters, giving rise to a nested hierarchy of self-similar clusters. Thus the same 'type' of cluster appears at a broad range of scales. This kind of pattern can be characterized by a fractal dimension D (*e.g.* Feder 1988; Sugihara & May 1990). Fractal dimensions can be determined in various ways; for example as the scaling exponent in the relationship between the number of occupied sites in a cluster and the cluster radius. This means that the scaling exponent in equation 2*c* is a bona-fide fractal dimension (*e.g.* Feder 1988). Thus, the local population dynamics can be related to the dimension of the pattern generated: $D = 2\varphi/\chi \approx 1.17$.

The relation between weed density and weed removal rate

The next point of interest in the study of the spatial model is the relation between the density of seeds on the lattice ρ, and the required removal rate r. Various densities were realized by simulating a population of 1024 and 2048 seeds distributed on lattices of 64 × 64, 128 × 128 and 256 × 256 sites. The removal rate r that was required to maintain the population at these densities was estimated by averaging over 250 time steps in a stationary situation. The results of these simulations are shown in figure 4. The removal rate approaches a critical value (r_c) for low densities. When the behaviour of removal rate near the critical point r_c was examined, it was found that the difference $r_c - r$ goes to zero according to a scaling law as density approaches zero (figure 4, inset):

$$(r_c - r) \sim \rho^{\omega} \qquad (3)$$

with critical removal rate $r_c \approx 0.64$ and exponent $\omega \approx 1.66$. The value of r_c is lower than the value obtained for the model without spatial structure (which resulted in $r_c = 4/5$) since weeds can now aggregate, even at low densities.

The relation between density and removal rate is comparable to the relation between density and mortality rate found for other models of spatially structured populations (Durrett & Levin 1994*b*; Sato *et al.* 1994). In those models, mortality rates below a critical value might result in equilibrium densities, and the equilibrium density approaches zero as the mortality rate approaches the critical value. Here, removal rates are below a critical

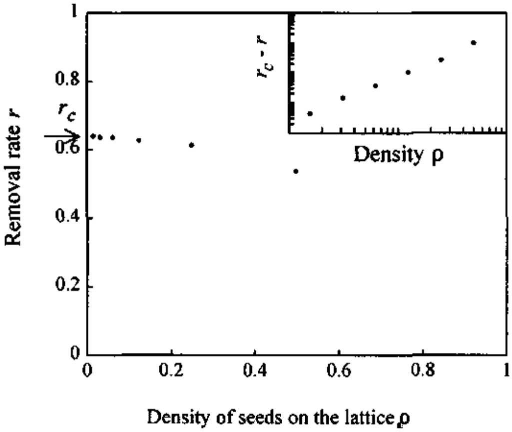

Figure 4. Removal rate r as a function of density ρ of seeds on the lattice. The inset shows the difference $r_c - r$ as a function of density ρ.

value when densities are held constant, and when the maintained density is close to zero, the removal rate approaches the critical value.

Robustness of the spatial model

If it is to serve as a simple prototype model for more complex models, the results of the spatial model must be robust to changes in the model's details. The abundance of scaling laws in the model results indicates critical phenomena and concomitant robustness (cf. Metz & De Roos 1992).

A more specific indicator of critical behaviour and concomitant robustness is the similarity between the spatial weed model and a model known as 'directed percolation'. Briefly, directed percolation in an epidemiological interpretation (see Grassberger 1986) deals with a population that inhabits a discrete lattice; each lattice site contains one individual. The population is susceptible to a disease, and the illness of an individual lasts one time step. Each individual has a probability p of infecting its neighbours. There is a critical point p_c where the epidemic barely survives. When $p \approx p_c$, directed percolation conforms to similar scaling laws as used here, with exponents corresponding to $\omega \approx 1.71$ (Brower *et al.* 1978), $\varphi \approx 0.67$, $\chi \approx 1.13$ (Grassberger 1989). The critical point corresponds to $r_c \approx 0.66$ (Grassberger 1989). These values are very close to those found for the spatial weed model, suggesting that the behaviour of the spatial weed model at low densities is consistent with the critical behaviour of directed percolation.

The critical behaviour of directed percolation near $p \approx p_c$ is 'universal' (*sensu* Grassberger 1983). This means that there is a wide variety of models (among which the 'basic contact process', Durrett & Levin 1994*b*) that differ in details but which, near the critical point, result in the same scaling laws with the same scaling exponents as those pertaining to directed percolation.

Drawing on the analogy between the spatial weed model and the directed percolation model, it can be conjectured that this 'universality' also applies to the behaviour of the spatial weed model at low densities (as in equations 2 and 3). This implies that the scaling laws and the value of the scaling exponents should still apply asymptotically when the following modifications are applied to the model:

- Replacing the square lattice by any other regular 2-dimensional lattice (see Grassberger 1983, 1989).
- Changing the population dynamic attributes of the weed, such as the dispersal range and length of the life cycle (provided finite characteristic scales are involved, *i.e.* probability distributions of dispersal distance and dormancy period should decline exponentially with distance or time, see Grassberger 1983, 1986).

Although these modifications do not influence the scaling laws and the value of the scaling exponents, they might influence the value of the critical removal rate as well as the spatial and temporal range, where the scaling laws represent a good approximation.

To demonstrate the effect of changing population dynamic attributes of the weed and the conjectured 'universality', the spatial model is modified by introducing a variable germination rate and a larger neighbourhood. To avoid confusion, the preceding spatial model will be referred to as spatial model I and the following modified spatial model will be referred to as spatial model II. In this spatial model II, the neighbourhood of the site (x, y) can consist of either 5 sites $\{(x, y), (x\pm1, y), (x, y\pm1)\}$ or 9 sites $\{(x, y), (x\pm1, y), (x, y\pm1), (x\pm1, y\pm1)\}$. The state of a site is set by the number of seeds on the site, so now more than one seed can exist on a single site. Spatial model II is based on the following rules:

- Seeds germinate with probability g, all non-germinated seeds remain dormant on the site.
- Of the germinated seeds on a site, only one can grow into a mature plant, and this one is selected randomly.
- Plants die with a probability r, the value of which is tuned so as to conserve the density of seeds over the whole lattice (ρ).
- If the plant survives it will send one seed to each site in the neighbourhood and die.
- Each site can receive at most one seed per time step, and if a particular site receives more than a single seed from its neighbourhood, one survivor is selected at random.

For germination rate $g = 1$ and a neighbourhood structure of 5 sites this modified model is equivalent to the spatial model I. The dynamics of the modified model are studied in the same way as before: the average fate of offspring of a single seed is determined, but now for germination rates $g = 1$ and $g = 1/5$ and for neighbourhood structures of 5 sites and 9 sites. The results of Monte Carlo simulations with the models are shown in figure 5. Although for small t the behaviour is influenced by germination rate and neighbourhood structure, at large t the scaling relationships as in equations 2*a* and 2*b* still apply. The scaling exponents in these equations (the slopes of the lines in figure 5 at large t) do not differ for various germination rates and neighbourhood structures.

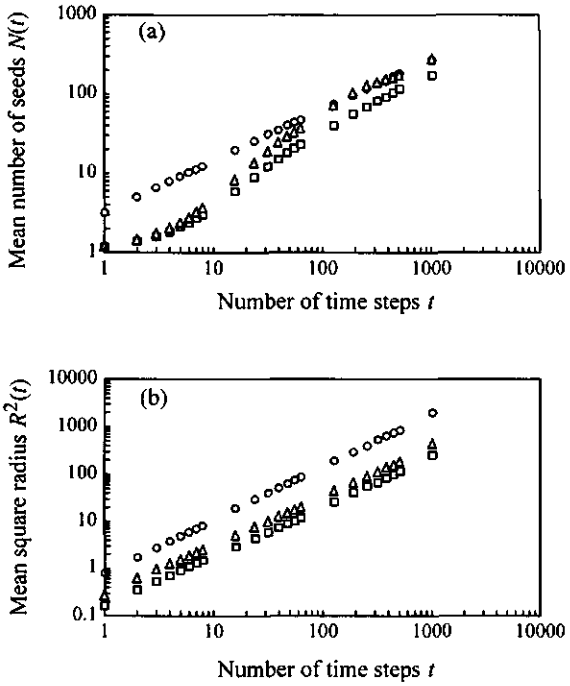

Figure 5. Results of Monte Carlo simulations with the spatial model II. (*a*) The mean number of seeds stemming from a single parental individual $N(t)$ after t time steps. (*b*) The average square radius of clusters of these seeds $R^2(t)$ after t time steps. The circles denote results for germination rate $g = 1$ and a neighbourhood structure of 5 sites; the squares denote results for $g = 1/5$ and a neighbourhood structure of 5 sites, the triangles denote results for $g = 1/5$ and a neighbourhood structure of 9 sites.

A field observation

The question is whether scale invariance in the spatial distribution of plants can be observed in real life, where numerous other factors act upon the population under study. Field observations have clearly shown that the spatial distribution of annual weeds tends to be clustered (*e.g.* Dessaint *et al.* 1991; Mortensen *et al.* 1993*a*). However, this clustering does not necessarily appear at many scales. In order to show scale invariance, the spatial distribution of weeds needs to be analysed at many scales.

The data for such an analysis were collected in May 1994 on an arable field cropped with winter wheat near Wageningen (the Netherlands). In a plot of 18.0 m × 32.4 m the spatial positions of seedlings of the weed *Galium aparine* L. were mapped by dividing the plot into small quadrats of 0.15 m × 0.27 m and counting the numbers of seedlings in each of these small quadrats.

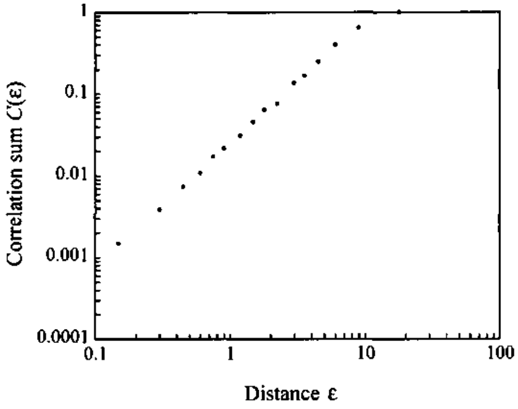

Figure 6. Scaling of the correlation sum $C(\varepsilon)$ with distance (grid spacing) ε for the observed spatial distribution of seedlings of the weed *Galium aparine* L. The slope of this log-log plot gives the fractal dimension.

For the spatial weed model the fractal dimension was derived as the scaling exponent in the relationship between number of occupied sites in a cluster and the cluster radius. There is however a more standard (and more convenient) way to infer this fractal dimension directly from an observed spatial pattern. This procedure is based on scaling of the correlation function with distance, yielding the so-called correlation dimension (Grassberger & Procaccia 1983). A grid with a spacing ε is superimposed on the observed pattern. The grid spacing ε is a multiple of the edge size of the small quadrats used in the observation. The number of grid cells required to cover the plot is termed $n(\varepsilon)$, the relative number of weeds in the i^{th} grid cell is denoted as p_i. Summing the squares of these relative numbers over all $n(\varepsilon)$ grid cells yields the correlation sum:

$$C(\varepsilon) = \sum_{i=1}^{n(\varepsilon)} p_i^{\,2} \tag{4a}$$

For a fractal set of points this correlation sum is expected to scale as

$$C(\varepsilon) \sim \varepsilon^{D} \tag{4b}$$

where D is the correlation dimension of the set.

From the observed spatial distribution the correlation sum $C(\varepsilon)$ is calculated for various grid spacings ε. The result is shown in figure 6 (note the double logarithmic scales). The scaling relationship does indeed hold for the observed pattern. Scaling extends from spatial scales of about 0.2 m, which is about the plant size, up to scales where the plot size becomes limiting. The correlation dimension of the spatial distribution pattern of weeds is estimated as the slope of the line in figure 6 resulting in $D \approx 1.51$, which is slightly higher than the value of 1.17 predicted by the model. The result shows that a scale-invariant spatial distribution of weeds is close to reality.

Discussion

The idea elaborated in this paper is that weed populations can be thought of as plant populations poised near the transition between possible survival and certain extinction, where critical phenomena are expected. In more detail, this idea encompasses the following steps. The removal rate required to keep weeds at a low density is very close to a critical removal rate, analogous to the critical mortality rate that marks the transition between possible survival and certain extinction. Near this critical point, critical phenomena are manifest as scale invariance in dynamics and spatial pattern. The accompanying scaling exponents are universal, that is, the exponents do not depend on model details such as the structure of the spatial lattice nor on modelled population dynamic attributes of the weed (provided finite scales are involved), and more specifically, the scaling exponents are identical to those obtained for directed percolation. This amounts to a very robust conjecture about annual weed populations in an arable field: the local population dynamics and the spatial pattern are expected to be scale-invariant, with scaling-exponents matching those of directed percolation.

The field observation of spatial pattern of weeds shows that scale invariance does indeed occur, although the observed and expected fractal dimensions do not match exactly. A possible explanation for this discrepancy is that the dispersal distribution of seeds does not decline exponentially with distance (cf. Mollison 1977) which might lead to scale-invariant patterns with other exponents, and thus to a different fractal dimension (Grassberger 1986).

Of course, the correspondence in scale invariance of the simulated and the observed pattern does not prove the validity of the model, nor the validity of the mechanisms involved in the model. The point is rather that there is no need to rely on external factors, such as soil properties, in order to explain the spatial pattern of a weed population in an arable field. The spatial pattern can be explained from the local reproduction and dispersal of these plants and the weed control that keeps them at a low density.

PATTERNS OF SPREAD OF ANNUAL PLANTS

Adapted from: Wallinga, J., Kropff, M.J. & Rew, L.J. submitted.

Abstract

The pattern of spread of plant populations is an important topic in the planning of control programmes of weeds. We consider the relationship between the dispersal distribution of seeds and the pattern of spread for an annual plant population in a homogeneous habitat. The so-called 'inverse square rule', which is often used in empirical studies, states that an invading population will display an advancing front if the slope of the seed dispersal curve declines according to the inverse square law or steeper. We show that this rule is incorrect and should be replaced by an 'exponential tail rule': if the tail of the projected seed dispersal curve declines slower than exponential, new colonies are established, otherwise a closed advancing front is formed.

Introduction

The pattern of spread of plants has been subject to scientific investigations for many decades (Salisbury 1961; Mack 1981; Cousens & Mortimer 1995). Mathematical models have been used to give *post hoc* explanations of the observed spread and to indicate implications for control of invading plants. Skellam (1951) characterized invading plant populations as a single expanding focus, and this characterization of the spatial spread has been used repeatedly (*e.g.* Allen *et al.* 1996*a*). Mollison (1977) and more recently Kot *et al.* (1996) and Lewis (1997) showed that, at least in theory, organisms may spread at accelerating rate or with occasional leaps. If plants display such a pattern of spread, it would be of fundamental importance to control programmes (Moody & Mack 1988; Levin 1989).

The rate and pattern of colonization of new sites by a plant's offspring is likely to be influenced by the shape of the seed dispersal curve around the parent plant. Dispersal curves are often empirically described by negative exponential curves or negative power law curves, which indicates that there are more propagules near the centre and in the tails than in a normal distribution. Portnoy & Willson (1993) examined tails of various seed dispersal curves and found that 35% could be described adequately by negative power law, 10% by a negative exponential, and 28% by both.

Harper (1977) conjectured that if the slope of the dispersal curve is less than that of the inverse square law, a population will display a spread-out pattern of isolated colonists. Otherwise, a population will spread into colonizable territory as a closed advancing front. This criterion for spread by isolated colonists will be referred to as 'the inverse square rule'. One of the assumptions underlying the inverse square rule is that a new colony can only establish at a particular location if an infinite amount of seeds has arrived at that location (cf. Van der Plank 1960). This very restrictive assumption provides a doubtful base for the inverse square rule. Despite this fact, the inverse square rule has been used repeatedly in analysis of seed dispersal data and is mentioned in ecological textbooks (Auld 1988; Willson 1993; Lonsdale 1993; Begon *et al.* 1996).

We are interested in the relationship between the seed dispersal distribution and the resulting pattern of spread for annual plant populations. Our objective is to show that the inverse square rule is too restrictive for characterizing seed dispersal distributions that lead to spread-out patterns of isolated colonists. We will present an alternative criterion for seed dispersal distributions in a homogeneous two-dimensional habitat. Finally we show by means of an example how this criterion can be applied in the planning of weed control programmes. We use a spatial stochastic model that is comparable to those used by Shaw (1995) and Wallinga (1995*b*), and we use a spatial deterministic model that is comparable to that used by Allen *et al.* (1996*a,b*). Dispersal of seeds of the *Alopecurus myosuroides* Hudson is used as an example because this is one of the most serious grass weeds of cereal crops in western Europe (Holms *et al.* 1997).

Stochastic simulation model

The inverse square rule is tested with a spatial stochastic model of plant population dynamics. In this model, space is discretized into a two-dimensional square lattice, consisting of 32768 × 32768 sites. Each site represents an area of 0.2 m × 0.2 m and is either empty or contains a discrete number of seeds. The system is updated in discrete time steps corresponding to one year according to the following rules:

- a seed germinates with probability g and emerges as a seedling;
- only one seedling per site establishes as a mature plant, other seedlings at the site are outcompeted and do not reproduce;
- a mature plant produces f seeds that will eventually emerge;
- a seed is dispersed over a distance $|\xi|$ drawn from a probability distribution $D(|\xi|)$, there is no preference for direction.

The pattern of plant spread was studied by following the offspring of a single seed in the centre of the lattice for up to twenty time steps (years). Spread was measured by recording the absolute distance from the centre of the lattice to the furthest individual. The number of colonies was measured at the spatial scale of $R = 1$ m, and two plants were associated with the same colony if they were within a distance R from each other or if both were within a distance R from other plants that belong to the same colony. The parameter values were set to $g = 0.7$ and $f = 5$. Three different probability distributions $D(|\xi|)$ were used,

distribution 1: $D(|\xi|) = 3.0\,e^{-3.0|\xi|}$;

distribution 2: $D(|\xi|) = 4.74(1 + 1.35|\xi|)^{-4.5}$;

distribution 3: $D(|\xi|) = 33.0(1 + 41.3|\xi|)^{-1.8}$.

These types of curves are frequently used for empirical description of seed dispersal curves (cf. Fitt *et al.* 1987; Portnoy & Willson 1993). All three distributions were parameterized such that only 5% of the seeds disperse beyond the distance of 1 m. These distributions are compared with the inverse square slope in figure 1.

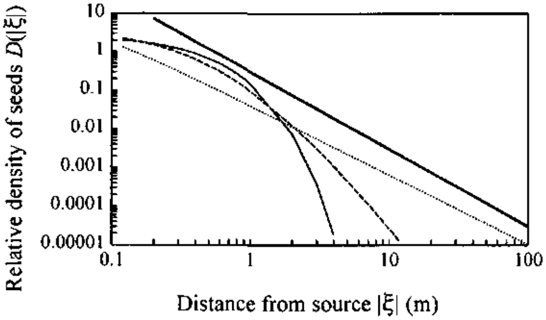

Figure 1. Distribution of dispersal distances used in the simulation model. The thick solid line indicates the inverse square slope; the solid line indicates distribution 1; broken line indicates distribution 2; dotted line indicates distribution 3.

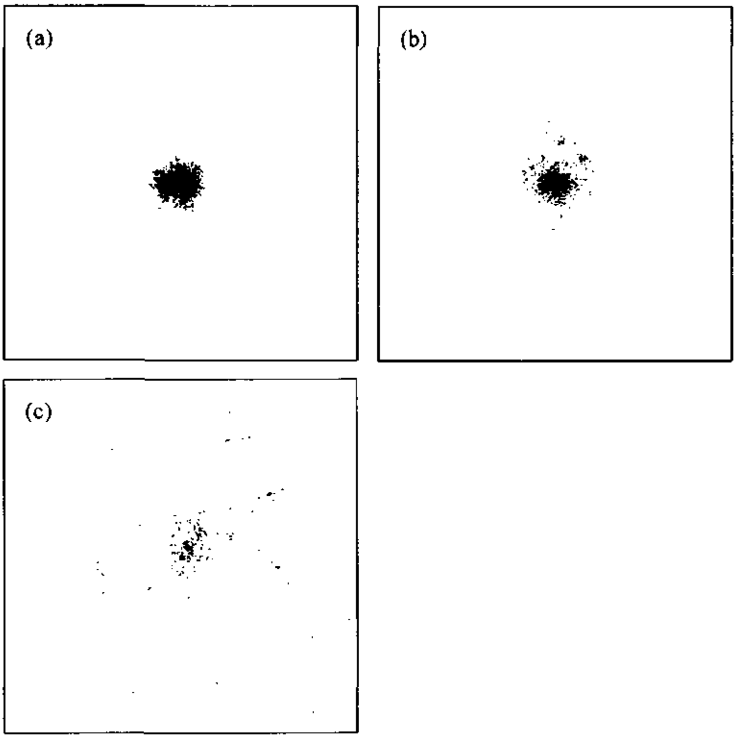

Figure 2. Simulated patterns of spread of an annual plant population for the various distributions of dispersal distance. (*a*) Dispersal of seeds according to distribution 1. (*b*) Dispersal of seeds according to distribution 2. (*c*) Dispersal of seeds according to distribution 3. Spatial pattern of seeds is shown at 10 time steps after introduction of the first seed in the centre of the lattice, the bounding box represents 51.2 m × 51.2 m.

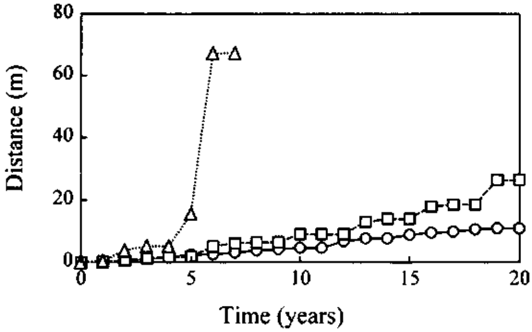

Figure 3. Simulated increase with time of distance from centre of the lattice to the furthest individual within an annual plant population. Circles and solid line indicate results for distribution 1; squares and broken line indicate results for distribution 2; triangles and dotted line indicate results for distribution 3.

If the inverse square rule is correct, distributions 1 and 2 should lead to spread with a closed front because the curve declines faster than the inverse square, and distribution 3 should lead to formation of new colonies because the curve declines slower than the inverse square (figure 1).

The simulation results are shown in figures 2 and 3. The spatial pattern resulting from distribution 1 displays a single colony with a front that is blurred at a small scale (figure 2*a*). The distance to the furthest seed increases gradually with time, there is an almost constant speed of population expansion (figure 3, solid line). This simulation result is in agreement with the inverse square rule. The spatial pattern resulting from distribution 2 (figure 2*b*) displays 10 colonies, one central colony surrounded by a few satellite colonies, there is no distinct closed front. The distance to the furthest seed increases with periods of steady progress alternated with occasional leaps forward, there is no constant speed of population expansion (figure 3, broken line). This simulation result does not agree with the inverse square rule. The spatial pattern resulting from distribution 3 (figure 2*c*) shows a spread-out pattern of 33 colonies, most of which consist of only a few seeds. The distance to the furthest seed increases very rapidly with seeds dispersing beyond the lattice edge after 20 time steps (figure 3, dotted line). This simulation result is in agreement with the inverse square rule.

In summary, the simulation results show that the inverse square rule does not hold for distribution 2.

Deterministic model

A deterministic model is formulated for plant population dynamics in a homogeneous two-dimensional habitat to assess, in an analytical manner, what types of seed dispersal curve can never cause spread-out patterns of isolated colonists. For each year, the fate of annual plants is described by the following rules:

- a seed germinates with probability g and establishes as a mature plant;
- a mature plant produces f seeds that will eventually establish;
- the probability of a seed to disperse to position (ξ_1,ξ_2) from a parent plant at position (0,0) is given by the dispersal distribution $D(\xi_1,\xi_2)$.

We denote the density of plants at a particular location and time by $s(x_1,x_2,t)$. The population is introduced at one location with an initial density $s(0,0,0)=s_0$. We are interested in spread in the direction of the x_1-axis. For notational convenience we introduce the germination distribution $G(\tau)$, which gives the probability distribution of a seed to remain inactive in the soil for τ years (such that each year a proportion g of all seeds germinates). The projected plant density

$$\tilde{s}(x_1,t)=\int_{-\infty}^{\infty} s(x_1,x_2,t)\,\mathrm{d}x_2$$

integrates all plant densities at a particular value of x_1. The projected dispersal curve

$$\widetilde{D}(\xi_1) = \int_{-\infty}^{\infty} D(\xi_1, \xi_2)\,\mathrm{d}\,\xi_2$$

gives the probability for a seed to be displaced over a distance ξ_1 along the x_1-axis.

The corresponding model for spread of annual plants along the direction of the x_1-axis is then derived as:

$$\widetilde{s}(x_1,t) = \sum_{\tau=1}^{\tau=t} \int_{-\infty}^{\infty} G(\tau)\widetilde{D}(\xi_1) f \widetilde{s}(x_1 - \xi_1, t-\tau)\,\mathrm{d}\,\xi_1 \qquad (1)$$

(see appendix 1). Analysis of this model shows that the annual plant population spreads by a closed front if the type of dispersal distribution $\widetilde{D}(\xi_1)$ is such that

$$c_1 = \int_{-\infty}^{\infty} \mathrm{e}^{c_2 \xi_1}\, \widetilde{D}(\xi_1)\,\mathrm{d}\,\xi_1 \qquad (2)$$

where c_1 and c_2 are finite positive constants (see appendix 1). If the forward tail of the projected dispersal distribution declines exponentially or faster, the condition described in equation 2 is fulfilled. We refer to this condition as the 'exponential tail rule'. It distinguishes two cases:

- the forward tail of the projected dispersal distribution $\widetilde{D}(\xi_1)$ declines exponentially or faster and, therefore, the plant population starting out from a point source will spread by a closed front of exponential shape that advances with a constant speed;
- the forward tail of the projected dispersal distribution $\widetilde{D}(\xi_1)$ declines slower than exponentially and. Therefore, the plant population starting out from a point source may result in spread-out pattern of isolated colonists.

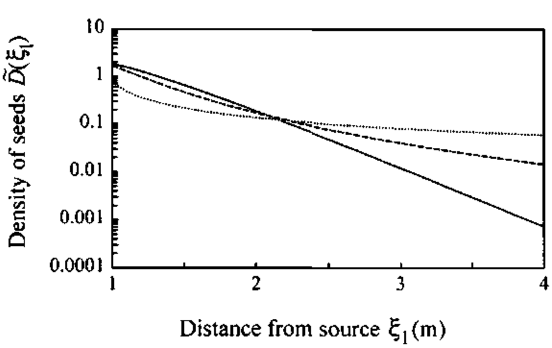

Figure 4. The forward tail of projected seed dispersal distributions that correspond to distribution of dispersal distances used in the simulation model. Solid line indicates distribution 1; broken line indicates distribution 2; dotted line indicates distribution 3.

The exponential tail rule is applied to the three dispersal distributions listed in the previous section. The corresponding projected seed dispersal distributions are calculated numerically and shown in figure 4. Distribution 1 results in a forward tail that declines exponentially, distributions 2 and 3 result in forward tails that decline slower than exponentially. Therefore, seed dispersal according to distribution 1 leads to plant population spread by a closed advancing front, and seed dispersal according to distribution 2 and 3 may result in plant population spread by a spread-out pattern of isolated colonists. This is in agreement with the simulation results presented in the previous section.

Empirical example

The pattern of spread is of fundamental importance for the planning of weed control programmes since we need to understand how weed populations disperse if we are to control current infestations and predict future ones. Currently, emphasis in weed control is changing towards weed control practices at finer spatial resolutions. Weed control is applied only to the parts of the field that are infested with weeds and to a small 'buffer zone' around these parts (Rew *et al.* 1996). If the weed population will spread with a closed advancing front, a map of weed infestations created at an earlier date may be used for a number of years, even when the control measures are insufficient to prevent the weed population from expanding. If the weed population is capable of generating new patches, a map of weed infestations created at an earlier data cannot be used for a number of years, and the weed control programme should include an extensive monitoring programme to detect and control new emerging weed patches. We consider the outbreeding annual grass

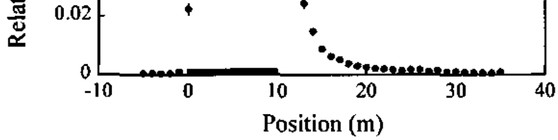

Figure 5. Distribution of *A. myosuroides* seeds that have dispersed from a 10 m wide source. Markers indicate observations (mean ± standard error), the black bar indicates the source. The inset shows the tail shape of the observed curve, the solid line indicates the seedling distribution that results when the projected dispersal curve declines as a negative exponential, the broken line indicates the seedling distribution that results when the projected dispersal curve declines as a negative power law.

weed *Alopecurus myosuroides* Hudson in a cereal field, and we assume that there is a sufficient number of *A. myosuroides* plants in nearby fields to ensure pollination of all solitary plants in the cereal field. We are interested in the question whether a control programme for this weed at a fine spatial resolution should include an extensive monitoring programme.

Rew & Cussans (1995) examined the dispersal distribution of viable *A. myosuroides* seeds. A homogeneous population of *A. myosuroides* plants was allowed to produce seeds in 10 m × 10 m plots in an otherwise weed-free crop of winter wheat. The crop was combine harvested, and the field was tine cultivated twice and sown to a second crop of winter wheat, with all operations in the same direction. The number of seedlings that emerged the following spring were counted in 0.1 m^2 quadrats at 1 m intervals along a 40 m length in the direction of the machinery passes (figure 5). The dispersal in directions perpendicular to the direction of machine passes was limited and independent of dispersal along the direction of machine passes.

The observed tail shape of the seedling density is shown more clearly in figure 5, inset. For comparison, we indicated the distribution of seedlings that results from dispersal from a 10 m wide source according to a projected dispersal curve with a tail that declines as a negative exponential curve (figure 5, inset, solid line) and as a negative power law (figure 5, inset, broken line). This comparison shows that it is hard, if not impossible, to determine whether the tail of the observed projected seed dispersal curve of *A. myosuroides* declines exponentially or slower than exponentially over this range of observed distances.

The immediate implication is that at these small scales we cannot predict the pattern of spread. Hence we cannot be sure that *A. myosuroides* does not escape control, so a weed control programme of *A. myosuroides* at a fine spatial scale should include a monitoring programme to detect and control new emerging weed patches.

Discussion

Harper (1977) conjectured that a plant population will display a spread-out pattern of isolated colonists if the slope of the seed dispersal curve is less than that of the inverse square law. Several studies have used this conjecture to interpret empirical seed dispersal curves (*e.g.* Willson 1993). The simulation study in the present paper shows that the inverse square rule is too restrictive since some curves that decline faster than the inverse square law can result in a spread-out pattern of plants. In this paper we derived theoretically that a plant population may display a spread-out pattern if the forward tail of the projected seed dispersal curve declines slower than exponential. We refer to this criterion as the 'exponential tail rule'.

The exponential tail rule is derived from a deterministic model of spatial plant population dynamics. This deterministic model is, to our knowledge, the first deterministic model that addresses the spread of an annual plant population that reproduces in discrete time, in a two-dimensional habitat. It is closely related to models that are used to calculate the velocity of spatial population expansion (Van den Bosch *et al.* 1990; Allen *et al.* 1996*a*,*b*; Kot *et al.* 1996; Lewis 1997). The deterministic model rests on the following assumptions: (i) the effects of demographic stochasticity at very low densities are negligible; (ii) the effects of intraspecific competition at high densities are negligible; (iii) individuals do not benefit from the presence of other individuals; (iv) the uninvaded environment is homogeneous; (v) the number of individuals increases with time. Below, we will argue that only the latter three model assumptions are also restrictions of the exponential tail rule.

The exponential tail rule is based on a condition for the existence of closed fronts that move with a constant velocity. The velocity and shape of the fronts are determined by the plants at the leading edge where plant density is low, therefore effects of competition on reproductive output can be neglected. The density at the leading edge increases rapidly, due to reproduction and dispersal, and this wipes out effects of demographic stochasticity (see the simulation results). The deterministic model does show that there are no closed fronts that move with a constant velocity when the projected dispersal curve declines slower than exponential. So, the exponential tail rule does not depend on the assumptions about continuous density and absence of competitive effects. However, the deterministic model does not capture the inherently stochastic effects of jump dispersal with concomitant cluster formation as seen in simulations when the projected dispersal curve declines slower than exponential (figure 2; cf. Shaw 1995). In order to incorporate some of these effects the model should include terms that account for spatial correlation (Bolker & Pacala 1997; Lewis 1997).

An annual plant may benefit from the proximity of another plant if it is an outbreeder, e.g. *A. myosuroides*. Observations show that grass pollen dispersal curves decline rapidly but level off with distance such that, if there are sufficient populations around, there is a low background level of pollen (Fitt *et al.* 1987; Rew & Cussans 1995), in which case outbreeders may show similar population behaviour as self-pollinators. If the environment is heterogeneous, the reproductive output of plants will vary and the pattern of population spread may reflect the environments suitability for establishment rather than the intrinsic pattern of spread. If the number of plants remains constant, for instance as a result of weed control practices, annual plant populations do not form a closed front but they aggregate, even when the seed dispersal curve declines faster than exponential with distance (Wallinga 1995*b*). In summary, the exponential tail rule does not hold when the annuals invade a heterogeneous environment, when the number of plants does not increase with time and may not hold when the annuals are obligate outbreeders.

The exponential tail rule may provide a useful tool to predict the spatial population structure that corresponds to the observed seed dispersal curve. However, the empirical example showed that it is hard to obtain conclusive evidence about the actual tail shape. The observed tail shape may not correctly reflect the actual shape because of the stochastic effects that are inherent to the tail, and there is a practical limit to the range of dispersal distances that can be observed. If the observation of tail shape is to predict pattern of population spread, the prediction should remain restricted to those scales that match the observations. The predictive power of the exponential tail rule is thus limited to relatively small scales. At continental scales, the exponential tail rule can provide, at most, a plausible post-hoc explanation of the observed pattern of spread (Skellam 1951; Clark *et al.* 1998).

Accepting the restrictions that have been outlined, the exponential tail rule could be usefully applied to the design of weed control strategies within an arable field and indicate whether there is a need for an ongoing monitoring programme to detect and control new emerging weed patches. The exponential tail rule may thus provide a dual benefit: it is an instrument to adapt weed control strategies to anticipated patterns of population spread, and it provides a crucial understanding of the role that seed dispersal has in shaping the spatial structure of an expanding population of self-pollinating annual plants in a homogeneous habitat.

Appendix 1

The deterministic model is derived from the three rules that describe the life history of annual plants. The first rule states that a seed germinates and emerges as a seedling with probability g. Thus, the probability to germinate and emerge in year τ is $G(\tau) = g(1-g)^{\tau-1}$. The density of plants at a particular position in a particular year t, $s(\cdot)$, depends on the density of seeds arrived at this position in earlier years, $n(\cdot)$:

$$s(x_1-\xi_1, x_2-\xi_2, t) = \sum_{\tau=1}^{\tau=t} G(\tau) n(x_1-\xi_1, x_2-\xi_2, t-\tau) . \qquad \text{(A1)}$$

The second rule states that a mature plant produces f seeds that will eventually establish as a mature plant. The density of seeds produced, $p(\cdot)$, is the density of plants times f:

$$p(x_1-\xi_1, x_2-\xi_2, t-\tau) = f \cdot s(x_1-\xi_1, x_2-\xi_2, t-\tau) . \qquad \text{(A2)}$$

The third rule states that the seeds that are produced at the position $(x_1-\xi_1, x_2-\xi_2)$ and dispersed to position (x_1,x_2) have a density $D(\xi_1,\xi_2)$. The total density of seeds that arrived at location (x_1,x_2) at year $t-\tau$ is

$$n(x_1, x_2, t-\tau) = \int_{-\infty}^{\infty}\int_{-\infty}^{\infty} D(\xi_1,\xi_2) p(x_1-\xi_1, x_2-\xi_2, t-\tau)\, \mathrm{d}\xi_1\, \mathrm{d}\xi_2 . \qquad \text{(A3)}$$

Substitution of equations A2 into equation A3, and substitution of the result in equation A1 with $\xi_1 = \xi_2 = 0$ gives:

$$s(x_1, x_2, t) = \sum_{\tau=1}^{\tau=t} \int_{-\infty}^{\infty}\int_{-\infty}^{\infty} G(\tau) D(\xi_1,\xi_2) f s(x_1-\xi_1, x_2-\xi_2, t-\tau)\, \mathrm{d}\xi_1\, \mathrm{d}\xi_2 . \qquad \text{(A4)}$$

Integration over x_2 gives the deterministic model:

$$\tilde{s}(x_1, t) = \sum_{\tau=1}^{\tau=t} \int_{-\infty}^{\infty} G(\tau) \tilde{D}(\xi_1) f \tilde{s}(x_1-\xi_1, t-\tau)\, \mathrm{d}\xi_1 . \qquad \text{(A5)}$$

If the population would spread with a closed front and at a constant velocity v along the x_1-axis, the density would increase exponentially at the leading edge of the front:

$$\tilde{s}(x_1, t) = a\, \mathrm{e}^{q(vt-x_1)} \qquad \text{(A6)}$$

where a is a constant and q indicates the steepness of the front (this is a so-called travelling wave solution (Van den Bosch *et al.* 1991; Allen *et al.* 1996*a*; Kot *et al.* 1996). Substitution of equation A6 into equation A5 gives

$$c_1\, \mathrm{e}^{q(vt-x_1)} = \sum_{\tau=1}^{\tau=t} \int_{-\infty}^{\infty} G(\tau) \tilde{D}(\xi_1)(1-r) f c_1\, \mathrm{e}^{q(v(t-\tau)-(x_1-\xi_1))}\, \mathrm{d}\xi_1 \qquad \text{(A7)}$$

which yields after some rearranging

$$1 = f\sum_{\tau=1}^{\tau=t} \mathrm{e}^{-qv\tau}\, G(\tau) \int_{-\infty}^{\infty} \mathrm{e}^{q\xi_1}\, \tilde{D}(\xi_1)\,\mathrm{d}\,\xi_1 . \tag{A8}$$

Using $G(\tau) = g(1-g)^{\tau-1}$ gives

$$1 = f\frac{g}{\mathrm{e}^{qv} - (1-g)} \int_{-\infty}^{\infty} \mathrm{e}^{q\xi_1}\, \tilde{D}(\xi_1)\,\mathrm{d}\,\xi_1 \ , \tag{A9}$$

rearranging yields

$$v = \frac{1}{q}\ln\left[(1-g) + fg\int_{-\infty}^{\infty} \mathrm{e}^{q\xi}\, D(\xi)\,\mathrm{d}\,\xi\right]. \tag{A10}$$

The velocity of the closed front v evaluates to a constant only if the integral in this equation exists, which is the case if there are positive finite constants c_1 and c_2 such that

$$c_1 = \int_{-\infty}^{\infty} \mathrm{e}^{c_2\xi_1}\, \tilde{D}(\xi_1)\,\mathrm{d}\,\xi_1 . \tag{A11}$$

That is, if the forward tail of the projected seed dispersal distribution declines exponentially or faster than exponential.

MEASURES THAT DESCRIBE WEED SPATIAL PATTERNS AT DIFFERENT LEVELS OF RESOLUTION, AND THEIR APPLICATIONS FOR PATCH SPRAYING OF WEEDS

Adapted from: Wallinga, J., Groeneveld, R.M.W. & Lotz, L.A.P. 1998
Weed Research **38**, 351-359.

Abstract

If weeds occur in aggregated spatial patterns, it is possible to reduce herbicide use by spraying only weed patches. The reduction in herbicide use will then depend on the spatial resolution of the patch sprayer and the weed-free area at that level of resolution. Three distance measures are presented that describe the weed spatial pattern at different levels of resolution. They give information on aspects of pattern that are relevant to patch spraying. The distance measures were applied to a spatial pattern of *Galium aparine* L. seedlings recorded in an area of 18.0 m × 32.4 m. In this area, the herbicide use of an idealized patch sprayer that detects and sprays all weeds with a spatial resolution of 1.0 m would be 41% of the amount required for a whole-field application. Spraying with a finer spatial resolution of 0.5 m would give a further 26% reduction in herbicide use.

Introduction

The spatial pattern of weeds is typically aggregated (Marshall 1988; Wilson & Brain 1991; Wiles *et al.* 1992; Johnson *et al.* 1995). By spraying only the weed patches, the applied amount of herbicide can be reduced compared to a whole-field application. The use of a patch spraying machine reduced herbicide use by 9% up to 60% in a fallow season, and 50% to 80% in a post-harvest application on the Canadian prairies (Blackshaw 1996). The weed-free area can be used to estimate the potential reduction in herbicide use by patch spraying (Johnson *et al.* 1995). However, as in any study of spatial pattern analysis, the appropriate scale for analysis must be chosen (Rew *et al.* 1997). If an arable field is divided into sections of 10 m × 10 m, and the presence of weeds is assessed for each section, then a very small part of the area will appear weed-free. If, however, every square millimetre of the field is scrutinized, then a very large proportion of the area will almost certainly appear weed-free. If the weed-free area is used to estimate the potential reduction in herbicide use by patch spraying, the appropriate scale for estimation of weed free area is determined by the spatial resolution of the patch sprayer. When there is no a priori interest in one particular level of resolution, spatial pattern should be studied at different levels of resolution.

Many observations of weed spatial pattern rely on the use of a quadrat, which is defined as a study area of fixed size and shape (Upton & Fingleton 1985). The most current spatial statistics are indices that describe the weed spatial pattern at one scale only, such as Lloyd's index of patchiness (Nordbo *et al.* 1995) and the negative binomial *k* (Wilson & Brain 1991; Wiles *et al.* 1992; Johnson *et al.* 1995). The semivariance statistic has been used to describe the variation in weed spatial pattern at levels of resolution that are larger than the quadrat size (Donald 1994; Cardina *et al.* 1995, 1996; Johnson *et al.* 1996). Navas & Goulard (1991) and Rew *et al.* (1996, 1997) used contiguous quadrats to record weed spatial pattern at one particular level of resolution, the weed spatial pattern at coarser levels of resolution was retrieved by combining quadrats into larger quadrats. In all cases, the weed spatial pattern could be analysed only at scales equal to or larger than the quadrat size. Distance measures do not make use of a quadrat and they describe spatial pattern over a wide, continuous range of scales. As summaries of spatial point pattern, the distance measures offer a vast improvement over the previously mentioned indices for quadrat data and the semivariance statistic for geostatistical data (Pielou 1969; Upton & Fingleton 1985; Ripley 1981; Cressie 1991).

This paper presents three distance measures that describe weed spatial pattern. These three distance measures are based on: (i) the distance between a randomly selected point and the nearest weed; (ii) the distance between a randomly selected weed and the nearest weed; (iii) the distance between a randomly selected weed and another randomly selected weed. It will be shown that these measures give some information about the aspects of the pattern that are relevant to patch spraying: (i) the amount of herbicide that a patch sprayer will use relative to a whole-field application; (ii) the probability that a patch sprayer leaves an undetected weed uncontrolled; (iii) the spatial prediction of weed positions. The distance measures will be illustrated for a spatial pattern of seedlings of the weed *Galium aparine* L. as observed in a field cropped with winter wheat.

Methods

Observation

The spatial pattern of individual seedlings of the weed species *Galium aparine* L. (cleavers) was recorded on a field with loamy sand soil, cropped with winter wheat, and located in the vicinity of Wageningen, the Netherlands. The data were collected in May 1994, just before post-emergence herbicides were applied. The spatial positions of 1851 seedlings of *G. aparine* in a plot of 18.0 m × 32.4 m were recorded. The pattern of seedling locations in this plot is shown in figure 1.

Definition of distance measures

A 'point – nearest weed distance' is defined as the distance between a randomly selected point and its nearest weed. $F(R)$ is the cumulative probability distribution function of point – nearest weed distances:

$$F(R) = \Pr(\text{point} - \text{nearest weed distance} \leq R)\,. \tag{1}$$

$F(R)$ is a quantitative measure of incidence of weeds. R indicates distance. $F(R)$ is 0 for all values of R when there are no weeds at all and 1 for all values of R when the field is

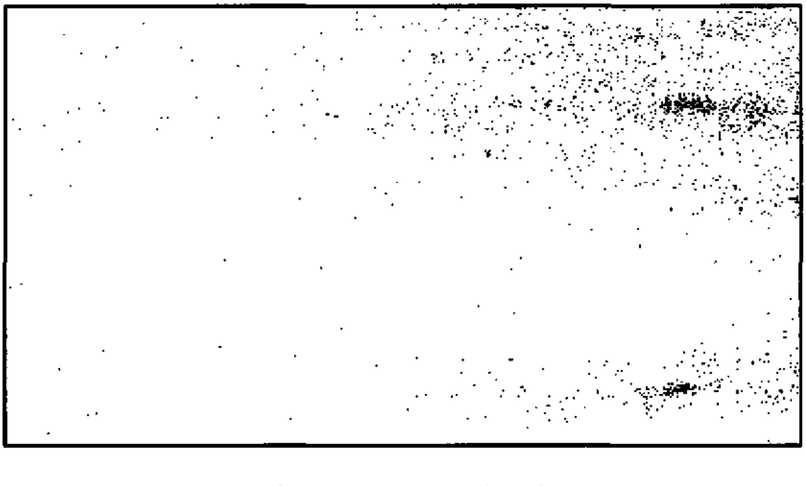

Figure 1. An observed pattern of *G. aparine* seedlings in a plot (32.4 m × 18.0 m) cropped with winter wheat. Direction of cultivation is from left to right and vice versa.

infested homogeneously with an infinite number of weeds. Similar distance measures for spatial point patterns are the cumulative distribution function of point – nearest neighbour distances as discussed by Upton & Fingleton (1985) and the cumulative distribution function of point – nearest event distances as discussed by Cressie (1991).

A 'weed – nearest weed distance' is defined as the distance between a randomly selected weed and its nearest weed. $G(R)$ is the cumulative probability distribution function of the weed – nearest weed distances:

$$G(R) = \Pr(\text{weed} - \text{nearest weed distance} \leq R). \tag{2}$$

Similar distance measures for spatial point patterns are the cumulative distribution function of plant – nearest neighbour distances as discussed by Upton & Fingleton (1985) and the cumulative probability distribution function of event – nearest event distances as discussed by Cressie (1991).

A 'weed – weed distance' is defined as the distance between a randomly selected weed and another randomly selected weed. $C(R)$ is the cumulative probability distribution function of weed – weed distances:

$$C(R) = \Pr(\text{weed} - \text{weed distance} \leq R). \tag{3}$$

$C(R)$ is the expected number of other weeds within radius R from an arbitrary weed, relative to the total number of weeds. This distance measure was introduced by Grassberger & Procaccia (1983). A closely related distance measure is the K-function, which is described by Ripley (1981), Upton & Fingleton (1985) and Cressie (1991).

Estimation procedures

Estimation of distance measures is not as straightforward as one would suppose because of the necessity to correct for edge effects. For instance, edge effects may arise in the estimation of $F(R)$ because points near the boundary of the plot are denied the possibility of having a nearest weed outside the plot. As a consequence, the expected distance to the nearest weed will be greater for a point near the boundary of the plot than for a point well inside the plot. There are several approaches to correcting for edge effects. One of them is to restrict attention to the inner region of the plot and to treat the outer region of the study area as a guard area (see, for instance, Upton & Fingleton 1985). In the present analysis a guard area of variable width R is used, that is, attention is restricted to the point – nearest weed distances, weed – nearest weed distances and weed – weed distances where the distance between the point or weed and the plot boundary is larger than R.

$F(R)$ was estimated by the following approach. Points were regularly spaced at 0.09 m distance parallel to the direction of cultivation and 0.075 m perpendicular to the direction of cultivation. For each point the distance to the nearest weed was measured. This resulted in a set of 86 400 point – nearest weed distances. The distance R was increased from 0.00 m to 3.96 m with step size of 0.09 m. For each value of R the set of distances was evaluated. Whenever a point – nearest weed distance was based on a point within distance R from the border of the plot, it was disregarded. For the remaining set of distances, the relative frequency of weed distances smaller than or equal to R was calculated. This relative frequency of a point having a nearest weed within distance R was used as an estimate of $F(R)$. This estimate is indicated by $\hat{F}(R)$.

$G(R)$ was estimated by the following approach. For each weed the distance to the nearest weed was measured. This resulted in a set of 1 851 weed – nearest weed distances. The distance R was increased from 0.00 m to 3.96 m with step size of 0.09 m. For each value of R the set of distances was evaluated. Whenever the weed – nearest weed distance was based on a weed within distance R from the border of the plot, it was disregarded. For the remaining set of distances, the relative frequency of weed – nearest weed distances smaller than or equal to R was calculated. This relative frequency of a weed having its nearest neighbour within distance R was used as an estimate for $G(R)$. The estimate is indicated by $\hat{G}(R)$.

$C(R)$ was estimated by the following approach. For each weed the distance to other weeds was measured. This resulted in a set of 1 712 175 weed – weed distances. The distance R was increased from 0.00 m to 3.96 m with step size of 0.09 m. For each value of R the set of distances was evaluated. Whenever a weed – weed distance was based on a pair of weeds with both weeds within distance R from the border of the plot, it was disregarded. For the remaining set of distances, the relative frequency of weed – weed distances smaller than or equal to R was calculated. The relative frequency was used as an estimate of $C(R)$. This estimate is indicated as $\hat{C}(R)$.

Description of the shape of F(R) and C(R)

If the spatial weed pattern is a random pattern, the shape of the cumulative distribution functions for distances are known exactly: $F(R) = G(R) = 1 - \exp\left(-N\pi R^2/A\right)$ and $C(R) = \pi R^2/A$, where A is the area of the plot and N is the number of weeds in the plot (cf. Upton & Fingleton 1985; Cressie 1991). However, from a biological point of view there is no reason to suppose that the weed spatial pattern is a random pattern. An alternative statistical description of a weed spatial pattern is:

$$C(R) \sim R^D \qquad (4a)$$

(Wallinga 1995*b*). Here, the exponent D is a positive constant smaller than 2 and the '~' sign means 'asymptotically proportional to'. To test whether equation 4*a* gives a good description of the estimated distance measure $\hat{C}(R)$, $\log\hat{C}(R)$ was plotted against log R. The range where the relation conformed to a straight line was determined by eye. The slope of the line, as determined by linear regression, was used as an estimate of D.

If equation 4*a* holds exactly over a number of scales, the shape of $F(R)$ should conform to the following equation:

$$F(R) \sim R^{2-D}. \qquad (4b)$$

The relation between equation 4*a* and equation 4*b* holds in theory (cf. Hentschel & Procaccia 1983; Hastings & Sugihara 1993) and is demonstrated in computer simulations (Wallinga 1995*c*). To test whether equation 4*b* gives a good description of the estimated distance measure $\hat{F}(R)$, log $\hat{F}(R)$ was plotted against log R. The range where the relation conformed to a straight line was determined by eye.

Estimation of aspects of pattern that are relevant to patch spraying

Distance measures can be used to give quantitative estimates of the amount of herbicide that a patch sprayer will use relative to a whole field application, and the probability that a patch sprayer leaves an undetected weed uncontrolled. The estimates are exact in an idealized situation where the patch sprayer detects all weeds and applies herbicide to each detected weed and to a zone around it. The width of this zone is called R, and it indicates the level of spatial resolution at which a patch sprayer operates. The motivation for spraying all detected weeds is that it will minimize herbicide use over the long term (Wallinga 1995*c*; Day *et al.* 1996). The motivation for applying herbicides to a zone around each weed is that there is a minimum area to which herbicides can be applied (*e.g.* the area covered by a single nozzle) and that there is an additional area that needs to be sprayed to allow for delays in sprayer response time and for mapping and navigation errors (cf. Rew *et al.* 1996).

The amount of herbicides that is applied to the field may be estimated by placing small cups randomly over the field and recording the fraction of cups that catch herbicide. All cups will receive some herbicide if herbicides are applied to the whole field. Some cups may remain empty if herbicides are applied to weed patches only. When herbicides are applied to a zone of radius R around each weed, a randomly placed cup will catch herbicides when it is within distance R of the nearest weed. The fraction of cups that catch herbicides is thus estimated by $F(R)$, the frequency of point – nearest weed distances smaller than R. Therefore, $F(R)$ estimates the herbicide use by an idealized patch sprayer with spatial resolution as determined by R, relative to a whole-field application.

An undetected weed is sprayed with herbicides when it is sufficiently close to another weed that is detected and sprayed. When herbicides are applied to a zone of radius R around each detected weed, the probability that an undetected weed is controlled is estimated by the probability that a randomly selected weed is within distance R from the nearest weed. This probability is given by $G(R)$. Therefore, $G(R)$ estimates the probability that an undetected weed is controlled when the weeds are sprayed by a patch sprayer with spatial resolution as determined by R.

Spatial prediction of weed positions may obviate some of the problems with inaccurate weed detection (Heisel *et al.* 1996). The derivative $\mathrm{d}C(R)/\mathrm{d}R$ gives the correlation function, which can be used for optimal spatial interpolation in a more-or-less similar way as the semivariance statistic (Cressie 1991). A simple example of spatial prediction is the calculation of the expected number and density of weeds near a distance R from an 'average' weed. The total number of weeds on the field is indicated by N. The number of weeds within a distance R from an 'average' weed is estimated by $N \cdot C(R)$, and likewise the number of weeds within a distance $R+d$ from an 'average' weed is estimated by $N \cdot C(R+d)$. The expected number of weeds near a distance R from an 'average' weed is estimated by $N \cdot C(R+d) - N \cdot C(R)$ when d is small. The expected density of weeds near a distance R from an 'average' weed is estimated as

$[N \cdot C(R+d) - N \cdot C(R)]/[\pi(R+d)^2 - \pi R^2]$.

So, $C(R)$ can be used to estimate the expected number and density of weeds surrounding an 'average' weed.

Results

Description of the observed weed spatial pattern

$\hat{F}(R)$ increased monotonically with R at a decreasing rate (figure 2). Starting out from a randomly selected point, the probability of finding at least one weed within 0.5 m from a randomly selected point was 0.24, the probability of finding at least one weed within 1.0 m was 0.41, the probability of finding at least one weed within 2.0 m was 0.62, the probability of finding at least one weed within 4.0 m was 0.85.

$\hat{G}(R)$ increased with R at a decreasing rate (figure 3). Starting out from a randomly selected weed, the probability of finding at least one weed within 0.5 m was 0.81, the probability of finding at least one weed within 1.0 m was 0.93, the probability of finding at least one weed within 2.0 m was 0.98, the probability of finding a weed within 4 m was 0.99.

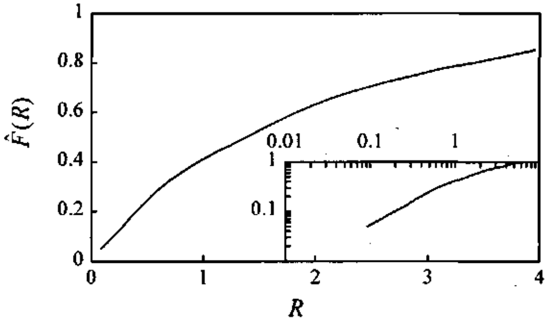

Figure 2. The relation between $\hat{F}(R)$ and R (in metres) for the observed weed pattern. The inset shows the same data on double logarithmic axes.

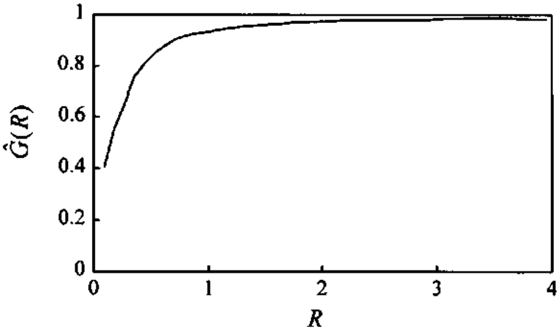

Figure 3. The relation between $\hat{G}(R)$ and R (in metres) for observed weed pattern.

$\hat{C}(R)$ increased at an increasing rate up to a value of 0.26 at $R = 3.8$ m, thereafter the estimated values decreased (figure 4). Starting out from a randomly selected weed, the probability of finding another randomly selected weed within a distance of 0.5 m was 0.01, the probability of finding another randomly selected weed within a distance of 1.0 m was 0.04, the probability of finding another randomly selected weed within a distance of 2.0 m was 0.11, the probability of finding another randomly selected weed within a distance of 4.0 m was 0.25.

Description of the observed shape of F(R) and C(R)

The observed relation between $\hat{F}(R)$ and R was plotted with double logarithmic axes (figure 2, inset). The relation appeared slightly curved over the range of scales that was examined. The observed relation between $\hat{C}(R)$ and R was also plotted with double logarithmic axes (figure 4, inset). The relation appeared straight over the range from 0.36 m to 3.51 m, the slope of the line over this range was estimated to be 1.5. The observed shape was well described by equation 4*a*, with exponent $D \approx 1.5$.

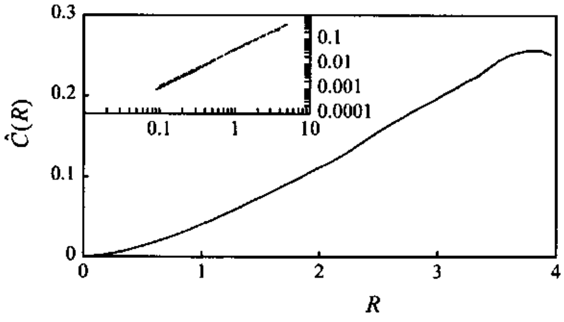

Figure 4. The relation between $\hat{C}(R)$ and R (in metres) for the observed weed pattern. The inset shows the same data on double logarithmic axes, the broken line indicates the relation $\hat{C}(R) \sim R^{1.5}$.

Aspects of pattern that are of interest for patch spraying

$\hat{F}(R)$ is used to estimate the herbicide use of an idealized patch sprayer that detects and sprays all weeds. The herbicide use of such a patch sprayer operating at a spatial resolution of 4.0 m is 85% of the amount required for a whole-field application, and the herbicide use of an idealized patch sprayer operating at a spatial resolution of 2.0 m is 74% of the amount required by the patch sprayer with a spatial resolution of 4.0 m. Changing spatial resolution from 4.0 m to 2.0 m gives a 26% reduction in herbicide use. The herbicide use of an idealized patch sprayer that operates at a spatial resolution of 1.0 m is 41% of the amount required for a whole-field application, and the herbicide use of an idealized patch sprayer operating at a spatial resolution of 0.5 m is 54% of the amount required by the patch sprayer with a spatial resolution of 1.0 m. Changing spatial resolution from 1.0 m to 0.5 m gives a 46% reduction in herbicide use.

$\hat{G}(R)$ is used to estimate the probability that an idealized patch sprayer controls an undetected weed. The probability that a patch sprayer operates at a spatial resolution of 4.0 m controls an undetected weed is 0.99. Spraying at a spatial resolution of 1.0 m will result in a probability for control of undetected weeds of 0.93.

$\hat{C}(R)$ is used to estimate the number of weeds at a certain distance from an 'average' weed. There are 5.6 weeds at a distance between 0.5 m and 0.55 m from an average weed, and 31.5 weeds at a distance between 2.0 m and 2.2 m from an average weed. These numbers correspond to a density of 34 weeds m^{-2} near 0.5 m distance from an average weed, and 12 weeds m^{-2} near 2.0 m distance from an average weed.

Discussion

Methodological aspects

In this paper, it is shown that distance measures can be used to describe weed spatial pattern at different levels of resolution. In practice, however, the usefulness of distance measures in practice does not only depend on these descriptive merits but also on the time needed for data acquisition. Point – nearest weed distances can be measured rapidly by going out in the field, selecting random points and recording the distance from each point to the nearest weed (see *e.g.* Upton & Fingleton 1985). This estimation procedure of $\hat{F}(R)$ by sampling point – nearest weed distances is more suited for use in the field than counting all the weeds in a sample plot, as described in the methods section. The measurement of weed – nearest weed distances and weed – weed distances requires selection of random weeds, which presupposes knowledge on the number and positions of all weeds in the field. Counting all the weeds in a sample plot, as described in the material and methods section, may well be the most rapid procedure for estimation of $\hat{G}(R)$ and $\hat{C}(R)$.

Regardless of the procedure for estimating distance measures, some care is needed to avoid bias due to edge effects. In the present study, bias due to edge effects was avoided by restricting attention to the inner region of the observed plot. The advantage of this method is that it does not require any assumption about the weed spatial pattern outside the observed plot. The disadvantage is that it throws away a lot of information about the spatial pattern at the coarser levels of resolution. As a consequence the estimated shape of the cumulative distribution functions is less accurate for large distances R. This is most apparent in the observed shape of $\hat{C}(R)$ for values of R larger than 3.8 m: the estimated values decrease with increasing R whereas the actual values should increase monotonically with increasing R. Omission of edge-corrections will in general have little effect on the outcome of $\hat{F}(R)$ and $\hat{G}(R)$ when the number of weeds is large. This is a result of using distance to nearest neighbours, which focuses on local characterization of the pattern (Cressie 1991).

Assumptions

The cumulative distribution functions $F(R)$, $G(R)$ and $C(R)$ allow a more tangible and practical interpretation than most other spatial statistics. It is shown that the distance measure $\hat{F}(R)$ can be interpreted as the amount of herbicide used by an idealized patch sprayer, relative to a whole-field application, and that the distance measure $\hat{G}(R)$ can be interpreted as the probability that an undetected weed is controlled by an idealized patch sprayer. It is not possible to test the accuracy of predictions based on distance measures in practice, since there are as yet no patch sprayers that are capable of spraying at different levels of resolution. It is possible to show that in theory the predictions are exact if the patch sprayer conforms to an idealized patch sprayer that detects and sprays all weeds. The intention of this theoretical argument is to show that the aspects of pattern described by distance measures are closely related to those aspects of pattern that determine the performance of a patch sprayer; it is not suggested that currently used patch sprayers meet the description of an idealized patch sprayer, nor is it suggested that predictions of herbicide use based on distance measures are exact.

The derivative of $\hat{C}(R)$ versus R gives the spatial auto-correlation function, *i.e.* information about the probability that there is a weed at distance R from an average weed. If the shape of the cumulative distribution function $C(R)$ is known, the shape of the spatial auto-correlation function is also known. The spatial auto-correlation function can be used for spatial prediction of weed positions, assuming that correlation does not depend on the spatial position (cf. Cressie 1991).

The observed shape of cumulative distribution functions

The relation between $\hat{C}(R)$ and R could be described accurately by equation 4*a*. Patterns for which such a relation holds are called 'scale-invariant' (Hastings & Sugihara 1993).

According to theory, one would suppose that the relation between $\hat{F}(R)$ and R would be described by equation 4*b*, but this is not confirmed by the observation. A possible explanation for the discrepancy between theory and observation is that almost all weeds conform to a scale-invariant pattern and that a few weeds are scattered. The measure $\hat{C}(R)$ contains information about the pattern around the average weed, which is the more dense part of the pattern where effects of scattering are hardly detectable. Therefore $\hat{C}(R)$ will reflect the scale-invariance and not the scattering. The measure $\hat{F}(R)$ contains information about the pattern near a randomly chosen point, which is on average the less dense part of the pattern where effects of scattering are easily detected. Therefore $\hat{F}(R)$ will reflect the scattering and not the scale-invariance.

Other observations of weed incidence at different levels of resolution

If weed incidence is defined as proportion of quadrats that contain at least one weed (cf. Christensen *et al.* 1996), the distance measure $F(R)$ is a quantitative measure of incidence of weeds at different levels of resolution. Assessments of spatial pattern of weed incidence at different levels of resolution have been reported by Navas & Goulard (1991) and by Rew *et al.* (1996, 1997). Both used contiguous quadrats and mapped weed infestations by recording presence or absence of weeds. Different levels of resolution were obtained by joining quadrat counts in one direction. Navas & Goulard (1991) mapped patterns of *Rubia peregrina* L. using a quadrat width of 1.9 m. A halving of quadrat length, from 5.2 m to 2.6 m, caused a reduction in incidence from 0.6 to 0.5 in one of the patterns they studied. Rew *et al.* (1996) mapped patterns of *Elymus repens* (L.) Gould using a quadrat width of 2 m. A reduction of the quadrat length, from 5 m to 3 m, caused a reduction in incidence from 0.38 to 0.33 for one of the fields in their study. Rew *et al.* (1997) also mapped patterns of *Alopecurus myosuroides* Huds. using a quadrat width of 2 m. A reduction of the quadrat length, from 9 m to 5 m, caused a reduction in incidence from 0.73 to 0.66 for one of the fields in their study.

The reported values for incidence may be interpreted as a rough estimate of $F(R)$, where quadrat length is a rough estimate of R. In this interpretation, the observations shows that $F(R)$ continues to increase with R even at scales larger than those used in the present study. However, it is impossible to make a more exact comparison between the observations reported here and the observations by Navas & Goulard (1991) and Rew *et al.* (1996, 1997) because of differences in methodology and differences in scale of observation.

Opportunities for patch spraying

Distance measures give information about aspects of pattern that are of interest for patch spraying: the distribution of weed – weed distances gives information about the spatial auto-correlation which can be used for spatial prediction of weed positions; the distribution of weed – nearest weed distances gives information about the risk of undetected weeds escaping control; the distribution of point – nearest weed distances gives information about the herbicide use. Application of the distance measures to the observed pattern reveals that: the distribution of weed – weed distances can be described accurately by equation 4*a*; the risk that undetected weeds escape control by an idealized patch sprayer is high only at relatively high spatial resolution; changing the spatial resolution of an idealized patch sprayers from 4.0 m to 2.0 m will give a 26% reduction in herbicide use, and changing the spatial resolution of an idealized patch sprayers from 1.0 m to 0.5 m will give a 46% reduction in herbicide use.

The quantitative estimates of herbicide use are exact if the patch sprayer detects and sprays all weeds. Of course, the present patch sprayers do not conform exactly to this idealized patch sprayer and therefore the presented methodology is not a finalised technique for accurate estimation of herbicide usage by all patch sprayers in all practical situations. Instead, the presented methodology is best regarded as a first step towards quantitative assessment of the potential for patch spraying at different levels of spatial resolution. The application of this methodology to a spatial pattern of *G. aparine* shows that increasing the spatial resolution of patch spraying appears to be a promising way to reduce herbicide use.

ANALYSIS OF THE RATIONAL LONG-TERM HERBICIDE USE: EVIDENCE FOR HERBICIDE EFFICACY AND CRITICAL WEED KILL RATE AS KEY FACTORS

Adapted from: Wallinga, J. 1998 *Agricultural Systems* **56**, 323-340

Abstract

The aim of this paper is to identify the key factors that determine the herbicide use of rational weed control strategies on the long term. A system is considered that includes a crop, a weed, and a herbicide. Of all the bioeconomic factors that are taken into account, only the herbicide efficacy and the critical kill rate are major determinants of the rational long-term herbicide use; the critical kill rate is here defined as the kill rate that compensates for the growth rate of the weed population at low densities. Rational long-term herbicide use can be estimated with information on only these key factors. Implications for the reduction of future herbicide use are discussed.

Introduction

Over the last 50 years herbicide application has been the mainstay of weed control in intensive agricultural systems. However, health and environmental problems as well as the economic costs of routine herbicide application have become increasingly apparent. Various weed control strategies have been suggested that avoid unnecessary herbicide use and that base management decisions on available knowledge of the weed and control methods (Cousens 1987). The knowledge whereupon weed control strategies can be based involves weed population dynamics (*e.g.* Firbank & Watkinson 1986; Cousens & Mortimer 1995), herbicide efficacy (*e.g.* Streibig 1988), weed-crop interference (*e.g.* Cousens 1985; Kropff & Van Laar 1993), and economics of weed control (*e.g.* Auld & Tisdell 1987; Swinton & King 1994).

The term 'rational herbicide use' refers to herbicide use that is adapted to the economic objective of the manager (Tait 1987). It is useful to distinguish between two different meanings of rational herbicide use. First, it may indicate the amount of herbicides that is to be applied on rational grounds in a particular year for a particular situation. This is of interest when alternative weed control options for the current year are evaluated by farmers (*e.g.* Swinton & King 1994). Second, it may indicate the annual herbicide use by rational weed control strategies, averaged over many years. This is of interest when alternative weed control strategies are evaluated (*e.g.* Pandey *et al.* 1991). The latter meaning is indicated as 'rational long-term herbicide use' throughout the rest of this paper.

The evaluation of rational long-term herbicide use by rational weed control strategies requires a vast amount of quantitative data on herbicide efficacy, weed-crop interference and weed population dynamics, prices of crop and herbicide. In most cases, this data is not available. Therefore evaluation of herbicide use by rational weed control strategies has been limited to a few well-documented cases with one particular weed, one herbicide and one or two crops (Pandey & Medd 1990; Gorddard *et al.* 1996). If these evaluations are to find a wider application, the large data requirement should be circumvented.

The objectives of this paper are i) to identify the key factors involved in rational long-term herbicide use, ii) to provide an estimate of the rational long-term herbicide use that uses only these key factors, and iii) to indicate perspectives for lowering the rational long-term herbicide use. Attention is restricted to systems with one crop, one weed and one herbicide. These systems are relatively simple and provide a useful starting point for more complex systems. The analysis of these systems is carried out in four steps. First, a model is presented that includes weed population dynamics, weed-crop interference, herbicide efficacy, and economics of weed control. Second, the dynamic behaviour of this model will be demonstrated with computer simulations. Third, long-term solutions of this model will be investigated analytically. Fourth, heuristic arguments will be given to generalize the obtained results to a wider range of crops, weeds and herbicides. The implications for reduction in herbicide use will be discussed.

Components of rational herbicide use

Consider a farm field where every year the same crop is sown and that is infested by an annual weed with a seed bank. The manager controls the weed by an annual application of a post-emergent herbicide, and the weed will cause crop yield loss if it is not controlled. The herbicide dose is adapted to the manager's economic objective, so the manager uses a rational weed control strategy (*sensu* Tait 1987). The processes involved in rational herbicide use are categorized into five components: herbicide efficacy, weed population dynamics, weed-crop interference, economics and decision making (figure 1).

Herbicide efficacy

The manager controls the weed population by killing weed seedlings with a single post-emergent herbicide application. The fraction of emerged seedlings that is killed by weed control in year t is termed the kill rate r_t, and this kill rate is determined by the efficacy of the applied herbicide. The efficacy of herbicides is frequently assessed as a relation between herbicide dose and weed biomass after application of that dose. This relation can be described by a logistic response of biomass to the logarithm of herbicide dose (Streibig 1988). By interpreting relative reduction in biomass as kill rate, and after rearrangement (see appendix 1) this relation between herbicide dose h_t and kill rate r_t is:

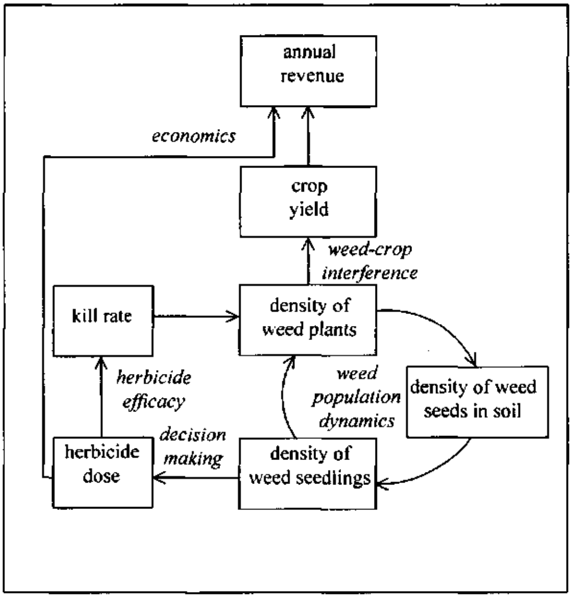

Figure 1. A schematic representation of rational weed control with one crop, one weed and one herbicide.

$$r_t = \frac{r_{\max}}{1+\left(e/h_t\right)^c} \tag{1}$$

where $r_{\max}$ is the maximum kill rate, e is the dose that results in half the maximum kill rate, c is a measure of efficacy of the herbicide. This relation between kill rate and herbicide dose is depicted in figure 2.

Weed population dynamics

The weed population dynamics are modelled according to Spitters (1990) and Kropff *et al.* (1996). In the model, the density of weed seeds in the soil is indicated as S_t. Each year a fraction m of the seeds is removed by natural mortality of seeds, and a fraction g germinates and emerges. The density of plants that survived weed control is indicated as P_t, each surviving plant will produce on average z viable seeds that return to the seed reserve. The dynamics are then described by

$$S_{t+1} = (1-g-m)S_t + zP_t \tag{2a}$$

The effect of weed plant density on average reproduction per plant z is introduced by

$$z = \frac{a}{1+aP_t/b} \tag{2b}$$

where a is the production of viable seeds per plant at low weed densities, and b is the maximum seed production per unit area at high weed densities.

A fraction r_t of emerged seedlings is killed by weed control, this fraction is termed the kill rate. The density of plants that survived or escaped weed control is

$$P_t = (1-r_t)gS_t \tag{2c}$$

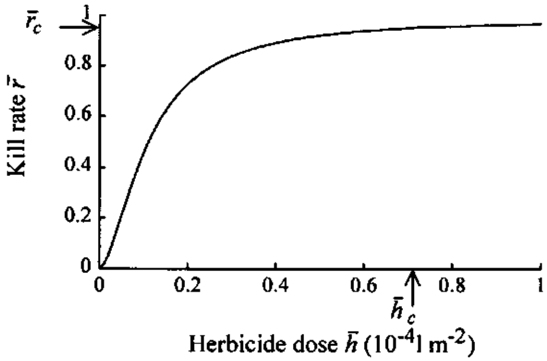

Figure 2. The relation between herbicide dose and kill rate, which corresponds to equation 1 based on Streibig (1988). The critical herbicide dose is indicated as $\bar{h}_c$, the critical kill rate is indicated as $\bar{r}_c$, parameter values are as in appendix 2.

The equations 2*a*, 2*b* and 2*c* are combined to give the weed population dynamics:

$$S_{t+1} = (1-g-m)S_t + \frac{a(1-r_t)gS_t}{1+a(1-r_t)gS_t/b}. \qquad (2d)$$

Weed-crop interference

Crop yield decreases with increasing density of weed plants that survived or escaped herbicide application. The relation between weed plant density and crop yield is frequently described by a hyperbolic relationship (Cousens 1985):

$$Y_t = \frac{Y_{\max}}{1+iP_t} \qquad (3)$$

where Y_t is the crop yield, $Y_{\max}$ is the weed-free crop yield and i is a measure of competitiveness of the weed versus the crop, and P_t is the density of plants that survived weed control. This relation is depicted in figure 3.

Economics

The annual revenue of cropping R_t is calculated from crop yield and herbicide use:

$$R_t = pY_t - qh_t - f \qquad (4a)$$

where p is the price of the crop, Y_t is the crop yield in year t, q is the price of the herbicide, h_t is the herbicide dose applied in year t, and f is the fixed costs of cropping (including the fixed costs of herbicide application, as well as fertilizer costs, seeding costs, and costs of other crop protection measures). Usually a manager is not only concerned about the current year's revenue, but also about revenue in the years to come. The number of years

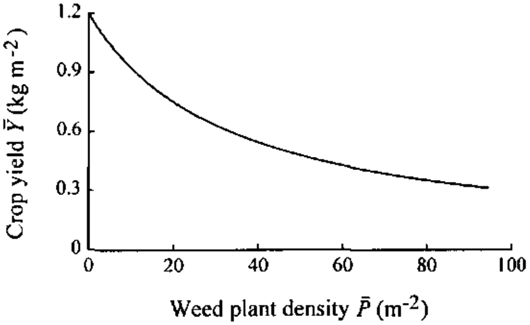

Figure 3. The relation between weed plant density and crop yield, which corresponds to equation 3 after Cousens (1985), parameter values are as in appendix 2.

of interest to the manager is called the planning horizon. Since revenue in a next year is usually valued less then revenue in a current year, the expected revenues in future yearsare discounted. The sum of discounted revenues over the years that are of interest to the manager is termed the present value V_t:

$$V_t = R_t + \sum_{j=1}^{j=H-1} \alpha^j R_{t+j} \tag{4b}$$

where H is the planning horizon and α is the discount factor.

Decision making

In economical terms, the weed management problem is to find the herbicide dose for the current year that maximizes present value. A necessary condition for a maximum is that neither increase nor decrease in herbicide dose in the current year t results in a higher present value:

$$\frac{\mathrm{d}V_t}{\mathrm{d}h_t} = \frac{\mathrm{d}R_t}{\mathrm{d}h_t} + \frac{\mathrm{d}\sum_{j=1}^{j=H-1} \alpha^j R_{t+j}}{\mathrm{d}S_{t+1}} \frac{\mathrm{d}S_{t+1}}{\mathrm{d}h_t} = 0 \tag{5}$$

where V_t is present value in year t, h_t is the herbicide dose applied in year t, R_t is annual revenue in year t, H is the planning horizon and α is the discount factor, and S_{t+1} is the density of weed seeds in the soil in the next year.

Calculation of long-term herbicide use

Simulation results

The rational long-term herbicide use is calculated with a computer model that includes the equations 1 - 5 and uses parameter values as listed in appendix 2, which resemble the cropping of winter wheat and control of the weed *Galium aparine* L. with the herbicide fluroxypyr. The results of the two simulation runs are depicted in figure 4*a*,*b*. One run simulated the herbicide use by a strategy with short-term objectives (present value is calculated according to equation 4*b* with $H = 1$, $\alpha = 0$), the other simulated the herbicide use by a strategy with long-term objectives (present value is calculated according to equation 4*b* with $H = 5$, $\alpha = 0.8$).

The results show that the weed density rapidly settles down into a steady state (figure 4*a*). There are no suitable long-term observations of *G. aparine* population dynamics to

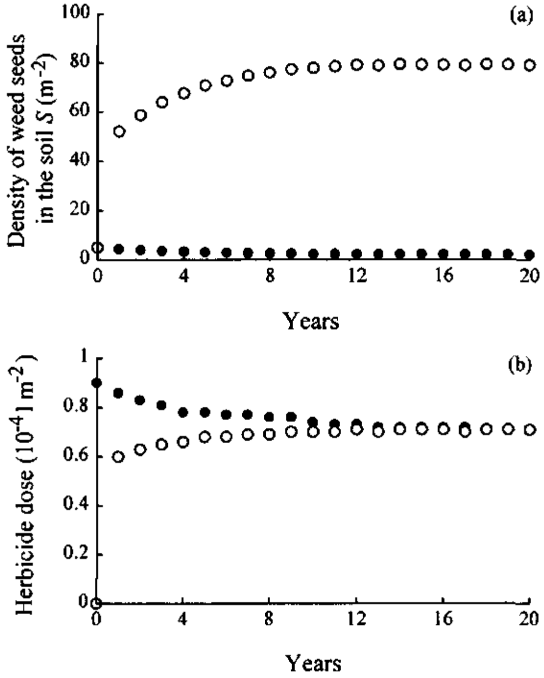

Figure 4. Simulation of rational weed control using a computer model that incorporates equations 1 - 5 and parameter values according to appendix 2. (*a*) Simulated course of density of weed seeds in the soil, measured before emergence and weed control. (*b*) Simulated course of annual herbicide use. Closed markers indicate a management strategy with short-term objectives (present value is calculated using $H = 1$, $\alpha = 0$), open markers indicate a management strategy with long-term objectives (present value is calculated using $H = 5$, $\alpha = 0.8$).

confirm or oppose these simulations. For comparison, long-term observations showed that the weed *Alopecurus myosuroides* Hudson persisted at low levels on a conventionally managed farm throughout a 10-year monitoring period (Wilson & Brain 1991). The simulations show that in the long term herbicide use hardly differs between the strategies with long-term and short-term objectives (figure 4*b*).

Analytical results

The same model is studied analytically to find out why the long-term herbicide use hardly differs between strategies with long-term and short-term objectives. The analytical results that are presented in this section show that the rational long-term herbicide use is largely determined by herbicide efficacy and population dynamics and hardly by weed-crop interference and economics or objectives.

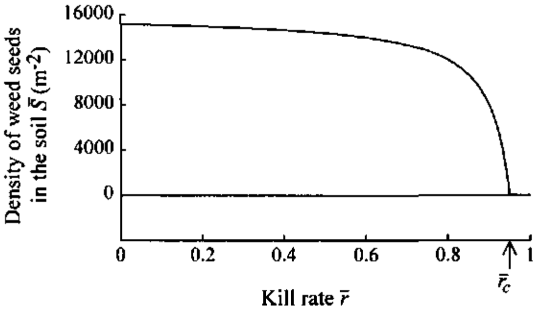

Figure 5. The steady states for weed seed density and kill rate. The critical kill rate is indicated as $\bar{r}_c$. The relation corresponds to equation 6*a* with parameter values as in appendix 2.

In a steady state, the density of weed seeds in the soil can be inferred from equation 2b by putting $S_t = S_{t+1} = S$, which gives the following solutions:

$$\begin{cases} \bar{S} = 0 & \text{for} \quad 0 \le \bar{r} \le 1 \\ \bar{S} = \dfrac{b}{g+m} - \dfrac{b}{ag(1-\bar{r})} & \text{for} \quad 0 \le \bar{r} \le \bar{r}_c \end{cases} \tag{6a}$$

where

$$\bar{r}_c = 1 - \frac{g+m}{ag}. \tag{6b}$$

$\bar{r}_c$ is the smallest kill rate that prevents population increase (see figure 5), it is termed the 'critical kill rate' (Wallinga 1995*b*; Kropff *et al.* 1996). The value of $\bar{r}_c$ is 0.95 for the parameter values in appendix 2. The herbicide dose that results in the critical kill rate is termed the critical herbicide dose h_c. It can be found through equation 1:

$$\bar{h}_c = e(1 - r_{\max}/\bar{r}_c)^{-1/c} \tag{6c}$$

The value of h_c is 0.709 10^{-4} l m^{-2} for the parameter values of appendix 2.

The solutions with $\bar{S} = 0$ in equation 6*a* reflect situations of weed control without weeds, which are clearly no rational situations, and a situation without weeds and weed control, which is only relevant when import of weeds is categorically excluded. Further analysis is therefore restricted to the part of the steady-state solutions that is relevant for weed control, *i.e.* the solutions of equation 6*a* where $\bar{S} \neq 0$. The relevant steady-state weed plant densities are then given by:

$$\bar{P} = \frac{bg(1-\bar{r})}{g+m} - \frac{b}{a} \quad \text{for} \quad 0 \le \bar{r} < \bar{r}_c \,. \tag{6d}$$

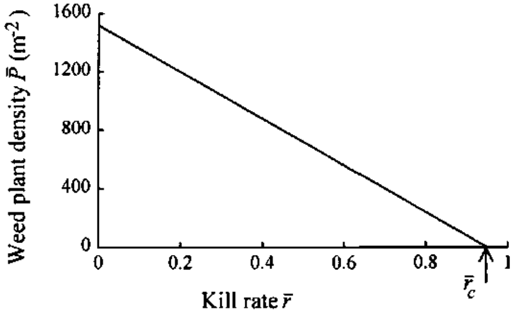

Figure 6. The steady states for weed plant density and kill rate. The relation corresponds to equation 6d with parameter values as in appendix 2. The critical kill rate is indicated as $\overline{r}_c$.

This relation is depicted in figure 6, it shows which combinations of weed plant density and kill rate are sustainable on the long term.

The combinations of annual revenue and herbicide dose that are sustainable on the long term are obtained by substitution of equation 1 in equation 6*d*, and the result in equation 3, and that result in equation 4*a*:

$$\overline{R}(\overline{h}) = p\cdot\overline{Y}(\overline{P}(\overline{r}(\overline{h}))) - q\overline{h} - f \quad \text{for} \quad 0<\overline{h}<\overline{h}_c . \tag{6e}$$

This relation is depicted in figure 7. The equation 6e clearly shows that the critical herbicide dose, which is $0.709\ 10^{-4}\ \mathrm{l\ m^{-2}}$, sets an upper bound to long-term rational herbicide doses:

$$\overline{h} < 0.709\,10^{-4}\,\mathrm{l\,m^{-2}} . \tag{6f}$$

A rational herbicide dose should maximize the present value, that is, it should meet the demands laid down in equation 5. A closer inspection of equation 5 reveals that a herbicide dose h_t that maximizes the present value should meet the following condition:

$$\frac{\mathrm{d}R_t}{\mathrm{d}h_t} \leq 0 . \tag{7a}$$

This can be seen as follows. In case the rational manager has short-term objectives, the revenues in future years are not taken into account, i.e. $\alpha = 0$, so the last term in equation 5 equals zero and the term $\mathrm{d}R_t/\mathrm{d}h_t$ should therefore also equal zero. In case the manager has long-term objectives, the revenues in future years are taken into account, i.e. $\alpha > 0$ and $H > 1$, so the last term in equation 5 is positive and the term $\mathrm{d}R_t/\mathrm{d}h_t$ should therefore be negative. As a consequence, $\mathrm{d}R_t/\mathrm{d}h_t$ should be equal to or smaller than zero.

After a little rewriting the economic constraint for rational herbicide doses, equation 7*a*, becomes:

$$p\cdot\frac{\mathrm{d}Y_t}{\mathrm{d}P_t}\cdot\frac{\partial P_t}{\partial r_t}\cdot\frac{\mathrm{d}r_t}{\mathrm{d}h_t} - q \leq 0 . \tag{7b}$$

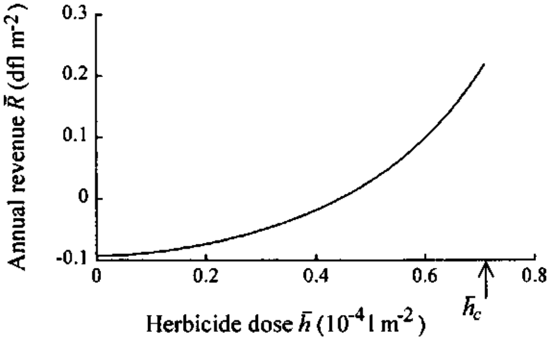

Figure 7. The steady states for herbicide dose and annual revenue of cropping. The relation corresponds to equation 6*e*, parameter values are as in appendix 2. The rational long-term herbicide doses are within a very small range from 0.706 up to 0.709 10^{-4} l m^{-2}, adjacent to the critical herbicide dose which is indicated as $\bar{h}_c$.

The derivatives can be written out, and variables can be expressed in terms of herbicide dose $\bar{h}$. Using parameter values of appendix 2, equation 7*b* than shows that herbicide doses maximizing the present value should be larger than 0.706 10^{-4} l m^{-2}, which gives a lower bound for the rational long-term herbicide dose:

$$0.706\ 10^{-4}\ \mathrm{l\,m^{-2}} < \bar{h}\,. \qquad (7c)$$

Combining the upper and lower bound (equations 6*f* and 7*c*) gives the following constraint for rational long-term herbicide doses:

$$0.706 10^{-4}\ \mathrm{l\,m^{-2}} < \bar{h} < 0.709 10^{-4}\ \mathrm{l\,m^{-2}}\,. \qquad (8a)$$

For all practical purposes the difference between upper and lower bound is negligible. Therefore it is legitimate to say that all long-term rational doses are very close to the critical herbicide dose, as defined in equation 6*c*:

$$\bar{h} \approx \bar{h}_c = e\left(1 - r_{\max}/\bar{r}_c\right)^{-1/c}. \qquad (8b)$$

This means that herbicide efficacy and critical kill rate determine in coarse lines the value of long-term rational herbicide dose, and that the other components only determine the small differences from this coarse value.

A heuristic approach

Herbicide efficacy and critical kill rate appear to be the key factors that determine long-term herbicide use in the specific case of controlling *G. aparine* with fluroxypyr in continuously grown winter wheat. In this section it is argued that a similar situation arises whenever weeds are 'noxious' and the herbicide is 'adequate', in a sense to be made precise below.

Consider a system with one crop, one weed and one herbicide (as depicted in figure 1), and consider a class of weed control strategies that avoid obvious spilling of herbicide and that avoid excessive yield losses. This class includes rational weed control strategies. Each weed control strategy is characterized by its long-term herbicide use and long-term crop yield. These are interrelated because crop yield depends on weed plant density, weed plant density depends on the kill rate, and the kill rate depends on herbicide dose.

Consider the case where weed density is low and long-term crop yield is highly sensitive to the long-term annual herbicide dose. Such a case arises if i) changing herbicide dose has an effect on the kill rate, *i.e.* the herbicide is 'adequate'; ii) changing the steady-state kill rate has a large effect on the steady-state weed density and changing weed density has a large effect on crop yield, *i.e.* the weed is 'noxious'. Furthermore, suppose that costs of control are small compared to economic crop yield, so that long-term annual revenue is, just like crop yield, highly sensitive on long-term annual herbicide dose.

In the above mentioned case, avoidance of excessive yield losses and obvious spilling of herbicides will place severe restrictions on the long-term herbicide use. The demands are met for a long-term herbicide use that is slightly higher than the critical herbicide dose, because weed density is contained at a low level and no herbicides are spilled. However, only a slight decrease in long-term herbicide dose (say, a few percent) will suffice to evoke a large decrease in long-term yield (say, over ten percent, which will be unacceptable in most cases). And a slight increase of long-term herbicide use beyond the critical dose would eradicate the weed population if immigration of weeds was excluded. When there is immigration of weeds, an increase in herbicide use is not counterbalanced by a significant decrease in weed density and yield loss. Summarizing, avoidance of excessive yield losses and obvious spilling of herbicides places restricts the long-term herbicide use to values close to the critical dose.

The main difference with the previous section is that the result is now derived in a more general context. Long-term herbicide use is close to the critical dose for all situations with one crop, one 'noxious' weed and one 'adequate' herbicide, even when managers do not maximize revenue, but are satisfied with a 'acceptable' crop yield.

Discussion

Key factors that determine the rational herbicide use

This paper shows that the rational long-term herbicide dose approximates the critical herbicide dose, and that the calculation of the critical herbicide dose only requires knowledge about the herbicide efficacy and critical kill rate. A few common-sense arguments hide behind this result: i) a sensible weed control strategy should avoid unacceptable yield losses, therefore weed control should prevent weed populations to grow to high densities; ii) the fraction of weeds that needs to be killed in order to contain the weed population at low densities is close to the critical kill rate; iii) the herbicide dose that suffices to kill this fraction of weeds is determined by the herbicide efficacy. The present paper makes this common sense more precise, and points out how this common sense can be used to estimate the long-term herbicide use by rational weed control strategies.

The identification of herbicide efficacy and critical kill rate as the key factors is very suggestive in indicating ways to lower the rational long-term herbicide dose: the herbicide should be made more effective, or the critical kill rate should be lowered, *e.g.* by decreasing weed seed production. More surprising, however, is the identification of the less important processes and parameters: weed-crop interference, the manager's planning horizon, and prices of crop and herbicide. Changing these factors will have little impact on herbicide use in the long run.

As an example of the implications of these findings, interference between weeds and crop is considered. Weed interference with crop growth (or crop tolerance, Jordan 1993) has little effect on the rational long-term herbicide use other than to meet the requirement of a 'noxious' weed, whereas crop interference with weed growth reduces the critical kill rate and thus affects the rational long-term herbicide use. So, if studies on interference between weed and crop have the objective to reduce herbicide use, they should address the effect of crops on weeds and not vice versa. Moreover, the effects of increased crop interference on long-term herbicide use can be evaluated quantitatively with only data on herbicide efficacy and data on the effect of crop interference on critical kill rate.

Relations to other work

In several studies it was implicitly supposed that rational decisions result in a small range of steady-state kill rates. For instance, Wilson & Wright (1991) calculated a 0.97 - 0.99 kill rate required to maintain a steady-state density of the weed *Galium aparine*, and Moss (1990) calculated a 0.87 kill rate to maintain a steady-state density of the weed *Alopecurus myosuroides* Hudson in winter wheat with ploughing and baling of straw. The authors presented a small range or a single value, and gave no indication of a wide range of kill rates that would contain a population at reasonable densities. The values they presented can be regarded as estimates for the critical kill rate of the weeds.

The small difference in kill rates that result from rational decision rules for different planning horizons results was already implicit in an independent case-study by Pandey and Medd (1990, 1991) who constructed a bioeconomic model of *Avena fatua* L. in continuously grown wheat, controlled with the herbicide diclofop-methyl. From this model they derived a rational short-term decision rule and a rational long-term decision rule. Application of those decision rules to the model showed that weed densities soon settled down into an approximate steady state. The steady-state weed density corresponding to short-term decision rule was around 40 plants m^{-2}, the steady-state weed density corresponding to long-term decision rule was around 3 plants m^{-2}. The kill rates required to maintain these densities, as estimated with the model of Cousens *et al.* (1986), differed only by 8%.

The relation between dynamic optimization problems, as in equation 5, and the resulting steady states, as in equations 6*a* - 6*e*, is often used in biological resource management (Getz 1987). The relation was for instance used by Pandey *et al.* (1993) to evaluate the long-term economic benefits of research into innovative weed control techniques, under the assumptions that managers maximize current profits. Their paper clearly illustrates the usefulness a steady-state approach as an aid in planning weed control policies. A steady-state approach has also been used to derive near-optimal decision rules for weed control (Taylor & Burt 1984).

Limitations of this study

The novel element in the calculation of rational long-term herbicide use is the avoidance of optimization procedures that necessitate the use of extensive data sets. Instead, a requirement is derived that should be met by all rational strategies (equation 8*a*). As has been shown throughout this paper, this requirement suffices to approximate the long-term herbicide use (equation 8*b*). The approximation requires relatively few data, and reveals the key factors that determine the rational long-term herbicide use. However, simplifying assumptions have been made in a number of areas. It is assumed that the same crop is grown each year, while farmers do often rotate crops and rotation is very important in determining the level of weed control. Only one weed control option is examined, while farmers usually have several options. Furthermore, it is assumed that there is no effect of weed density on herbicide performance and that herbicides have no direct effect on crops. Effects of variation in responses and effects of risk aversion are not dealt with, although herbicide activity can be highly variable and variability may increase when herbicide dosage is reduced.

The simplifications made here facilitated analysis, but they are not indicative of essential limitations. When crop rotations are introduced, additional information is needed to determine the level of control for each crop in the rotation (cf. Fisher & Lee 1981). When several weed control options are introduced, additional information is required to determine the optimal combination of available options (cf. Gorddard *et al.* 1996). Effects of year-to-year variation and effects of risk aversion can be studied by considering stochastic systems (cf. Pandey & Medd 1991; Pannell 1995), but even then a rational control strategy is tied to the kill rates and herbicide doses that prevent a serious population increase in the long run. All these effects add new elements and make analysis more complicated, but they do not alter the essence of rational weed management.

Concluding remarks

The rational weed management problem is a complex problem even with one crop, one weed and one herbicide. Under the assumption that the weed is noxious and the herbicide is adequate, rational long-term herbicide use is determined by two key factors: critical kill rate and the herbicide efficacy. Less important are the exact objectives of the manager (*i.e.* his planning horizon and the discount rate), the response of crop yield to weed density and the prices of crop and herbicide. These results show that it is possible to estimate the rational long-term herbicide use without excessive demands of quantitative data. The results are also suggestive of ways to decrease long-term herbicide use: increase herbicide efficacy and interfere with the weed population processes as to lower the critical kill rate.

Appendix 1

The relation between herbicide dose and weed biomass is often described as a logistic response of biomass to the logarithm of dose. The relation is written in the notation as used by Streibig (1988):

$$U = C + \frac{D - C}{1 + \exp(2b(\log ED50 - \log dose))}.$$

When the relative reduction in biomass is identified with kill rate of weeds, and when the notation is changed by substituting

$$b = -\frac{1}{2} c \ln 10\,;\ U/D = 1 - r;\ C/D = 1 - r_{max};\ ED50 = e;\ dose = h,$$

the above equation can be written as:

$$r = \frac{r_{\max}}{1 + (e/h)^c}. \qquad \text{(A1)}$$

Appendix 2

Explanation of the various symbols used. The figures were made with the indicated values which are representative for cropping winter wheat in the Netherlands where the weed *Galium aparine* L. is controlled with the herbicide fluroxypyr.

Symbol	Interpretation	Value	Units
N	density of weed seeds in the soil		m^{-2}
P	density of weed plants after herbicide application		m^{-2}
Y	actual crop yield		$\mathrm{kg\ m}^{-2}$
R	annual return on cropping		$\mathrm{dfl\ m}^{-2}$
V	present value		$\mathrm{dfl\ m}^{-2}$
z	production of viable seeds per weed plant		m^{-2}
r	kill rate of weed seedlings caused by herbicide		-
h	herbicide dose		$\mathrm{l\ m}^{-2}$
$Y_{\max}$	maximum crop yield	1.2	$\mathrm{kg\ m}^{-2}$
$r_{\max}$	maximum kill rate of weeds	0.99	
r_c	critical kill rate of weeds		-
h_c	critical herbicide dose		$\mathrm{l\ m}^{-2}$
a	maximum production of viable seeds per weed plant	100	-
b	maximum production of viable seeds per unit area	8000	m^{-2}
g	fraction of seeds that germinate and emerge	0.1	-
m	fraction of seeds died due to natural mortality	0.4	-
i	measure of competitiveness of weed versus crop	0.03	m^{-2}
c	measure of sensitivity of kill rate to herbicide dose	1.7	-
e	herbicide dose that effects half the possible response	$0.11\ 10^{-4}$	$\mathrm{l\ m}^{-2}$
p	price of crop	0.27	$\mathrm{dfl\ kg}^{-1}$
q	price of herbicide	70.5	$\mathrm{dfl\ l}^{-1}$
f	fixed costs of cropping	0.1	$\mathrm{dfl\ m}^{-2}$
H	planning horizon		years
α	discount factor		-

LEVEL OF THRESHOLD WEED DENSITY DOES NOT AFFECT THE LONG-TERM FREQUENCY OF WEED CONTROL

Adapted from: Wallinga, J. & Van Oijen, M. 1997 *Crop Protection* **16**, 273-278.

Abstract

Weed control thresholds are often presented as a means to reduce unnecessary control measures, thereby increasing the effectiveness of weed management. While the threshold is a useful tool for cost-effective application of control on a single year base, its role over a longer term is more complicated. It is shown that long-term application of thresholds results in a control frequency that is independent of threshold level, and in aperiodic dynamics of the weed population which may cause uncertainty about what control frequency and hence what costs of control are expected over a given period. We conclude that the economic underpinning of the threshold concept is deceptive and does not provide a base for rational use of weed control in the long term.

Introduction

In management of pests, diseases and weeds there is an ongoing need for methods and concepts that allow less costly control with less environmental impact. Different concepts of pest and disease management have evolved, including control thresholds. The essence of the threshold concept is that control is applied only when the density of a pest, disease or weed exceeds a threshold density. The threshold concept provides a tool to decide whether or not to apply control measures, by accounting for costs and benefits of control in the current crop. The threshold itself is the density of pest or disease at which the benefit of control just exceeds the costs of control. To stress the economic underpinning of this concept, this threshold is often referred to as the 'economic threshold' (Auld *et al.*1987; Cousens 1987).

The threshold concept has proven appropriate for controlling fungal epidemics like mildew and rusts in cereal crops (Zadoks 1985; Drenth *et al.* 1989). There is little correlation in size of such epidemics in successive years, since only a few fungal propagules will overwinter in the field. This is very convenient, since it implies that decisions on long-term control (concerning several years) can easily be broken down into a series of short-term control decisions (concerning single years). In other words: when threshold control is appropriate for controlling epidemics within one cropping season and there is hardly any carry-over effect, threshold control is also appropriate for several years.

For weed infestations, the situation is somewhat different. If only economic effects in the current crop are considered, the threshold concept may still serve its purpose (*e.g.* Auld *et al.* 1987; Gerowitt & Heitefuss 1990; Zanin *et al.* 1993). However, weed infestations and control decisions do provide carry-over effects from the current year to the following year. Omitting weed control in the current period not only reduces the current crop yield, it also leads to weed seed production, which can result in future reduction of crop yields. Consequently, decisions on weed control over a period of several years cannot be broken down easily into a number of decisions concerning a single year. Long-term weed management requires that future effects of current decisions are taken into account, which complicates evaluation of costs and benefits of control.

A straightforward way of dealing with thresholds in long-term weed management is to use a mathematical model and simulate the economic effects of applying threshold control over several years. Then it is possible to identify the threshold that gives the maximum profitability (to stress the difference with the single-year 'economic threshold', this long-term threshold is termed 'economic optimum threshold' by Cousens 1987). In case studies this approach is used to calculate the economic effect of applying thresholds in various crop-weed combinations over periods of 10 to 40 years (Cousens *et al.* 1986; Doyle *et al.* 1986; Lapham 1987; Murdoch 1988; Bauer & Mortensen 1992; Mortensen *et al.* 1993*b*). The results of these case studies show little difference in financial benefit for the thresholds in the range between the economic threshold and the economic optimum threshold. Over this range weed densities typically vary over an order of magnitude. For some weed species, the number of years controlled could hardly be reduced compared to prophylaxis (always control). This, among more pragmatic arguments, led Cousens (1987) to the conclusion that "there is little importance in being exact in the calculation and application of thresholds". Clearly, this remark is about the use of thresholds, not about the concept in itself.

A further aspect of these studies was that in some cases the control frequency, defined as number of years controlled over a given period, did not alter for a wide range of thresholds. When the control frequency appears insensitive to threshold level, this evokes the question whether thresholds do provide a rational economic underpinning of the required control frequency - which is the role for which thresholds were intended. This question does address the very concept of thresholds. Are case studies with a constant control frequency exceptional, or is the intuitive appeal of thresholds misplaced?

Here, we attempt to provide an answer to this question by exploring the effects of long-term use of threshold on control frequency. Since these effects pertain to thresholds in a general sense, we have not considered more case studies. Instead, our aim has been to identify the basic response of weed population dynamics, where the weeds were subjected to threshold control.

Weed population growth resembles exponential growth

In order to address the question how control frequency is affected by use of thresholds, the essentials of weed population dynamics and threshold control are formally described. The natural system under study is an arable field, where a single crop is sown every year and where an annual weed species persists. The state of the system can be characterized by the weed density (as number of plants and seeds per unit area, over the whole field). This state variable is not directly accessible but can be measured by sampling seedling densities. In the context of this paper, only the population dynamics over the years is of interest. Therefore, only one census of the weed density for a particular time in a year is required. Such a census can take place for instance at the beginning of the year, before any weed control is applied. The weed density next year is assumed to depend on the weed density and weed control in the current year. When the observed weed density in the next year is termed N_{t+1}, and the observed weed density in the current year is termed N_t, the weed population dynamics can be formulated as $N_{t+1} = f\ (N_t)$. The function f differs for situations with and without control.

The biological question what the weed population dynamics looks like now is simplified to the identification of the function f. One way to find out is to look at field observations. Selman (1970) presented observations that are appropriate to this context. In a 10 year experiment with continuously grown barley, the weed *Avena fatua* L. was not controlled for the first 5 years and properly controlled for the next 5 years. In figure 1 the weed counts are plotted as the density observed in one year (N_t) versus the density observed in the next year (N_{t+1}). In most years, the simplest description of these observations is that N_{t+1} varies approximately proportionally to N_t. That is, the population density increased or decreased in an exponential fashion (*cf.* Harper 1977; Cousens *et al.* 1987). Observations for *Avena fatua* L. and *Alopecurus myosuroides* Huds. were presented by Mortimer (1987) in a similar setting. The observations for *A. myosuroides* showed that N_{t+1} changed proportionally with N_t, with and without control. The observations for *A. fatua* showed deviations from such a proportional relationship, probably due to density dependent reduction of growth rates. Other experimental observations that lend support to this thesis are seed bank depletion experiments, which can be regarded as population dynamics of a weed population under complete control. The seed bank depletion rate is reported to be proportional to the seed bank size, and therefore the weed population density will decline exponentially (Roberts & Dawkins 1967; Wilson & Lawson 1992).

Summarizing, over the range of weed densities that is of interest for weed management, the weed population dynamics can be approximated by:

$$N_{t+1} = \begin{cases} aN_t & \text{when not controlled} \\ bN_t & \text{when controlled} \end{cases} \qquad (1)$$

where N is the weed density, the subscripts t and t+1 denote the year, and a is the *per capita* growth rate of the uncontrolled population, b is the *per capita* growth rate of the controlled population (with $a > 1$ and $0 < b < 1$). This model is a simple combination of exponential growth and exponential decline, which appears as an appropriate approximation of what goes on in reality.

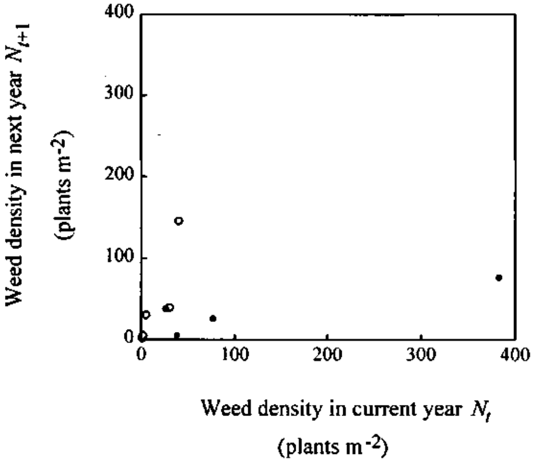

Figure 1. Observed changes in weed density of *Avena fatua* L. over several generations in a field with repeated crops of barley. Open markers indicate generations growing without weed control, closed markers indicate generations exposed to weed control. (From data in Selman 1970.)

Threshold control involves a discontinuity

The essence of the threshold concept is that control is applied only when the weed density exceeds a threshold. Below this threshold weeds are not controlled. The model obtained in the previous section (equation 1) can now be modified to account for threshold control:

$$N_{t+1} = \begin{cases} aN_t & \text{when } N_t \leq K \\ bN_t & \text{when } N_t > K \end{cases} \tag{2}$$

where K is the threshold. In order to exclude eradication of weeds as a special form of threshold control it is assumed that $K > 0$. Since threshold control is only applied when there are weeds it is assumed that $N > 0$. The resulting relationship between N_{t+1} and N_t is plotted in figure 2. The relation is discontinuous, and this discontinuity is the direct consequence of the threshold concept. Although equation 2 is a very simple model, the resulting population dynamics are quite complicated.

The discontinuity causes aperiodic dynamics

The weed population dynamics can be obtained directly from figure 2 by a method called 'graphical iteration': pick an arbitrary weed density N_0, put it on the x-axis and read the resulting next years' weed density N_1 from the y-axis. Put this value on the x-axis, read the corresponding N_2 and so on (see figure 3a). From any starting point N_0 the population density will home in towards the threshold. Near the threshold the densities are trapped in a region where they are bounced back and forth around the threshold, but remain bounded

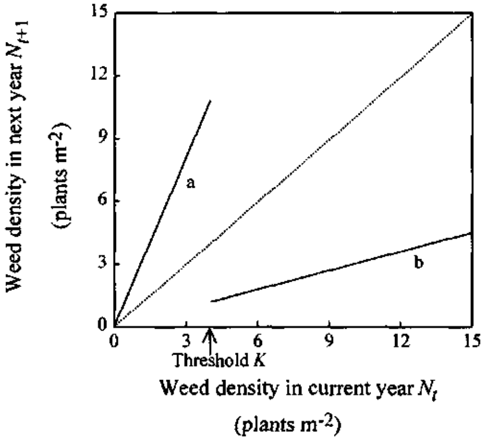

Figure 2. Idealized changes in weed density of a weed population subjected to threshold control. K indicates the threshold density, slope a indicates the *per capita* growth rate of the population when not controlled, b indicates the *per capita* growth rate when controlled, the broken line is of unit slope ($N_t = N_{t+1}$).

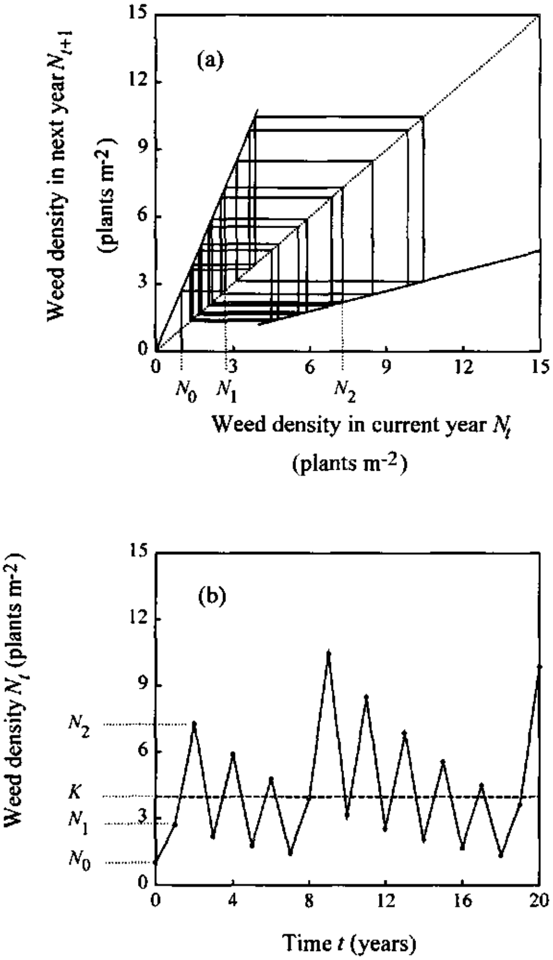

Figure 3. Dynamics of a weed population subjected to threshold control. (*a*) Derivation of subsequent weed densities by graphical iteration. (*b*) The course of weed density with time. The initial weed density is indicated by N_0, the weed density in the first year by N_1, in the second year by N_2.

above and below. Even for a large number of iterations, this bouncing pattern will never repeat itself, that is, the course of weed density with time is aperiodic (figure 3*b*).

In the literature the model of equation 2 is reported as capable of generating 'chaotic' dynamics (May & Oster 1976). More precisely, the model only produces cycles of finite period in the unlikely case that the ratio of logarithm of the *per capita* growth rates ($\log a / \log b$) is a rational number, for all other ratios of the growth rates the dynamics are aperiodic (Felsenstein 1979; Bélair & Milton 1988). In line with the terminology employed in May & Oster (1976) and Felsenstein (1979) we will call this behaviour 'chaotic', where this term does not refer to disorder or indeterminacy but to the fact that itineraries are aperiodic (hence not stationary nor periodic) and remain bounded. It implies that prediction of weed density over the first few years is possible but accurate prediction of the itinerary over several years is not possible when there is some uncertainty about the exact initial conditions or parameter values.

However, for long-term management purposes there is no specific interest in accurate prediction of the actual density of weeds in a particular year. What is needed, is a set of densities that can be expected over the period that one is interested in. To obtain such a set of densities, we make use of the observation that the aperiodic itinerary remains bounded and can get arbitrarily close to any point within the bounds (Felsenstein 1979). Thus, a kind of probability distribution for weed densities can be extracted from the dynamics (see *e.g.* Devaney 1986). This probability distribution may serve as an approximation to the set of densities that can be expected over any period of interest. Such a probability distribution is better suited for analysis of the long-term population dynamics of weeds subjected to threshold control than a single outcome of all possible itineraries.

Control frequency does not depend on threshold level when growth is exponential

Since our aim was to study long-term effects pertaining to the threshold concept, the properties of the population dynamics resulting from equation 2 are now further examined in order to obtain the probability distribution of population density N. The initial transient towards this region is disregarded since it depends on the initial conditions and is of limited interest for long-term effects. This examination is confined to the region around the threshold that is within the bounds of the itineraries. For this purpose the results of previous studies of these type of models (Felsenstein 1979; Bélair & Milton 1988) are interpreted in the setting of weed control.

The lower bound of weed density is achieved when in the previous year the weed density was just above the threshold K and weeds were controlled: lower bound = bK. The upper bound of the attracting region is achieved when in the previous year the weed density equalled the threshold K and weeds were not controlled: upper bound = aK. All other weed densities that can be achieved are within these bounds, and therefore fall in the range $\langle bK, aK]$. Felsenstein (1979) found that on a logarithmic scale the itinerary fills this range uniformly, which means in the present context that the logarithm of weed densities, $\log N$, is uniformly distributed over $\langle \log bK, \log aK]$.

The expected ratio of years with control to years without control can be derived from this distribution. The number of years with weed control within a given period (y_b) is determined by the probability that the weed density exceeds the threshold K. Since the distribution of $\log N$ is uniform, this probability is proportional to the difference $\log aK - \log K$. The number of years without weed control in the same period (y_a) is determined by the probability that the weed density is below the threshold. This probability is then proportional to the difference log K – log bK. Therefore, the average control frequency which is defined as the ratio of years with control to total number of years is

$$\frac{y_b}{y_b + y_a} = \frac{\log aK - \log K}{\log aK - \log bK} = \frac{\log a}{\log a - \log b}. \tag{3}$$

Equation 3 implies that the control frequency is completely determined by the population dynamics of the weed and by the effectiveness of control, as implemented in the *per capita* growth rates a and b. Most importantly, the control frequency is not at all influenced by the value of threshold K.

The insensitivity of control frequency to the threshold level is illustrated by simulations with the model of equation 2. The control frequency for a weed population subjected to threshold control was simulated for three different threshold levels (figure 4*a*).

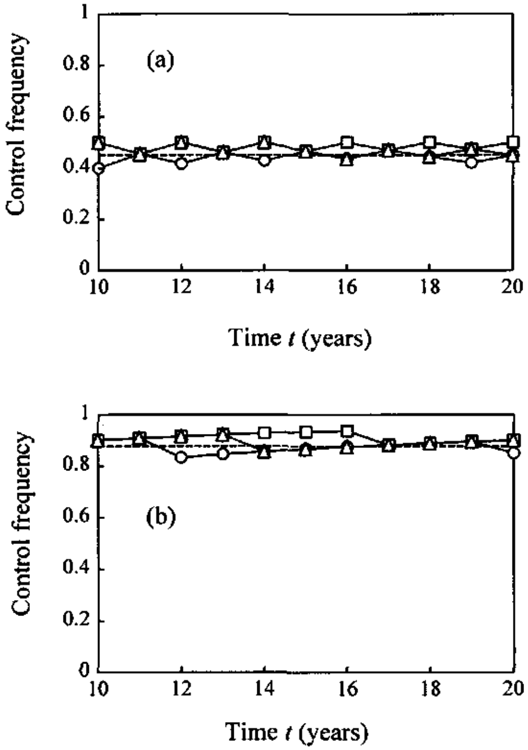

Figure 4. Influence of the threshold level on the control frequency. The simulated populations have the same initial density and are subjected to a threshold level of 1 plant m^{-2} (circles), 2 plants m^{-2} (squares), and 4 plants m^{-2} (triangles). The broken line indicates the control frequency according to equation 3. (*a*) Population where the *per capita* growth rate is 2.7 when controlled and 0.3 when not controlled. (*b*) Population where *per capita* growth rate is 5 when controlled and 0.8 when not controlled.

The control frequency, calculated as the number of years controlled divided by the total number of years elapsed since start of the simulation, does not depend on the exact threshold level and approximates the average long-term value as determined by equation 3. The simulations were repeated with increased *per capita* growth rates of the weed population, resembling a situation where the weed fecundity is high and control is poor (figure 4*b*). The densities are above the thresholds more often than below and the control frequency is higher as compared to the situation of lower fecundity and better control. The control frequency does not depend on the threshold level.

A note on robustness

In the preceding sections, the weed population dynamics subjected to threshold control were described by a simple model (equation 2), which was characterized by chaotic population dynamics and a fixed control frequency. These characteristics only bear meaning when they do not result from oversimplifications present in the exact mathematical formulation of the model. Therefore we checked whether these characteristics hinge on particular aspects of the model formulation by using heuristic reasoning, and by using a comparison with the more complicated formulations used in case studies on long-term application of weed control thresholds.

The simple model (equation 2) says that *per capita* growth rates of the weed population can attain only two values. At the threshold density there is a discontinuous transition between the two growth rates caused by the binary decision making ('control' or 'no control'). The two options we choose from ('control' or 'no control') must link to 'decline' and 'increase' of the population, otherwise the decision making lacks sense. So, the discontinuous transition between decline and increase in equation 2 reflects the essence of the threshold concept. A direct effect of this discontinuous transition between decline and increase is that stable constant densities (neither decline nor increase) are very unlikely to result, hence cycles of any period in population density are expected. Cycles of infinite period (chaos) may arise in many cases, for instance when growth rates are constant. Constant growth rates are an obviously crude simplification: the growth rates must decrease with higher densities, and they do depend on environmental conditions and change from year to year. However, these effects are limited since we are interested in a rather small range of densities, approximately from the economic optimum to economic threshold, and added noise will not stabilize the system. So in spite of its crudeness, the simplification made by assuming constant growth rates has little effect on the resulting dynamics. Nearly constant growth rates will result in cycles of large period, if not infinite period (chaos). So heuristic arguments lend support to the generality of the behaviour of the mapping in a more extended form, that is we expect long (perhaps chaotic) cycles in population density and insensitive (perhaps constant) control frequency.

When the characteristics of the simple mapping are indeed preserved in more elaborate models, a comparison with independent case studies with those more elaborate models should reveal similar results. We should observe the control frequency (after eliminating direct effects of the initial transient) to be insensitive to threshold level. We should also expect long cycles in population density, which cast some uncertainty on the number of years controlled over a given period and thus impose some non-smooth 'surprising' changes on the further insensitive relation between control frequency and threshold level. Cousens *et al.* (1986) and Lapham (1987) provided useful sensitivity analyses of their models, where the relation between control frequency and threshold level was calculated for various initial densities. Direct effects of the initial density can be eliminated by only including the number of years controlled when initial density was close to the threshold. By doing so, the simulated number of years controlled out of 10 seasons by Lapham (1987) is 9 - 10 years. The simulated number of years controlled out of 10 years by Cousens *et al.* (1986) is either 7 - 9 or 5 - 8 years, depending on tillage. Thus the control frequency appears rather insensitive to threshold, but does vary somewhat. The threshold level where the frequency changes appears 'surprising'. For instance, Cousens *et al.* (1986) found for a 'serious' infestation of *Avena fatua* in winter wheat with ploughing that the number of years controlled changed from 6 years control to 5, to 6, to 5, to 4 and back to 5 again when the threshold level was gradually increased from 5 to 20 seedlings m^{-2}. Similar sudden jumps back and forth appeared also in other figures where benefit is plotted against threshold level (Doyle *et al.* 1986; Murdoch 1988; Bauer & Mortensen 1992; Mortensen *et al.* 1993*b*). These jumps are characteristic of cycles with long, perhaps infinite, period in the underlying dynamics.

Summarizing, the properties of the simple model (equation 2) - long (perhaps chaotic) cycles and insensitivity (perhaps independence) of control frequency to threshold level - are expected to be robust and are preserved in the more elaborate models. Thus, equation 2 can be regarded as a 'prototype' model for such behaviour: it is a simple model that lends easily to analysis of behaviour, and it already demonstrates the 'typical' dynamics of more elaborate models.

Implications for the use of thresholds on the long term

With the results of the preceding section the question whether thresholds are an appropriate tool to implement economic weed control is discussed. We have shown that, apart from the direct effects of the initial infestation level, control frequency is insensitive to threshold level. As equation 3 shows, the frequency does not depend on economic evaluation but is instead based on the balance of decline and increase of the population density in order to contain the density within broad bounds. The threshold concept provides no clue why containment of a population is economical - containment is tacitly declared to be economical. And if containment would be economical, the threshold concept provides no clue why it is economical to use binary decisions ('control' or 'no control'). The foregoing shows that the binary decisions may bring undesirable properties such as unpredictability into the decision making. Replacing binary decisions by continuous decisions (varying the degree of control, by adjusting herbicide dose) would overcome this problem. Therefore, the apparent value of threshold control on the long-term as a strategy to implement economic weed control is deceptive.

These undesirable properties pertain to the long-term application of thresholds in weed control, they are not relevant when only the current crop is considered. Hence, the results presented here do not contradict the studies on use of thresholds for some fungal epidemics (Zadoks 1985; Drenth *et al.* 1989) and on single-year economic thresholds (*e.g.* Gerowitt & Heitefuss 1990; Zanin *et al.* 1993), but it is emphasized that their results are rational and economic on a single year base only. By adopting a single-year time horizon it is possible to profit without any problem from eliminating control measures that are not cost-effective in that year. But when the time horizon is extended and the threshold concept is still used, it leads to a very specific containment policy that is not necessarily economic in the long term.

The statement that threshold level does not affect frequency of control does not imply that the economic net revenue of cropping is not effected by threshold level, but it means that from the viewpoint of minimization of weed control there is no preference at all for any particular threshold level. Other approaches, *e.g.* increasing herbicide efficacy, might have more perspective for decreasing herbicide use. Although we have raised questions about the rationality of the long-term application of thresholds, this does not imply that containment policy should be abandoned and prophylactic or eradication strategies are the way to proceed. Long-term use of thresholds must be understood as a particular form of containment, and there are other containment policies, *e.g.* adjusting the herbicide dose, that might be more preferable. There is no indication that thresholds are the best option for containment and there is even no firmly established indication that containment is the best policy.

In summary, the present study shows that the weed control threshold as a tool to base control frequency on economic considerations loses meaning when it is applied to the long term. Thresholds are certainly not the tool *par excellence* to implement the desired rational use of weed control.

PREDICTION OF WEED DENSITY: THE INCREASE OF ERROR WITH PREDICTION INTERVAL, AND THE USE OF LONG-TERM PREDICTION FOR WEED MANAGEMENT

Adapted from: Wallinga, J., Grasman, J., Groeneveld, R.M.W., Kropff, M.J. & Lotz, L.A.P. submitted.

Abstract

This paper addresses the errors that are associated with long-term prediction of weed densities, and the effect of these errors on the performance of weed management decisions based on those long-term predictions. A model of weed population dynamics was constructed. It was based on experimental observations of population dynamics of the weed species *Stellaria media* in a crop rotation. The observations showed that estimates of weed population growth rate differed between two locations. The model was used to analyse error propagation for predicted weed densities in an enlarged prediction interval. It is concluded that errors due to an uncertain population growth rate pose an upper limit to the horizon for long-term predictions. It is shown that model-based decisions can give near-optimum results even when the model's predictions are poor. A limited ability to predict weed densities does not impair the practical use of weed population dynamic models in planning for long-term weed control programmes.

Introduction

Weed ecologists have put much effort in quantifying life-history characteristics of weeds and incorporating this knowledge into models of population dynamics (*e.g.* Doyle *et al.* 1986; Cousens *et al.* 1987; Mortimer *et al.* 1989). One of the main objectives of this effort was to predict weed densities over a long period, and to use the predictions for the selection of weed control measures that have some desired effect. However, most measured ecological characteristics are highly variable, and it is not known to what extent uncertainties in a weed's life-cycle affect the reliability of the predicted densities and the reliability of decisions based on these predictions. Cousens & Mortimer (1995) conclude that it is not at all evident that reliable long-term predictions can be made and that these predictions can be used to plan for long-term weed control programmes.

Only a few studies have compared model predictions of weed densities with field observations, and their outcome showed that predictions were not very accurate (Firbank 1991; Cousens & Mortimer 1995). Based on these studies, it is not possible to separate effects of poor understanding of a weed's life-cycle from effects of external influences like the weather. Sensitivity analysis is an approach to gain some idea of the confidence that should be put into the predictions. In a sensitivity analysis the effect of a change in the value of a model variable on the predicted weed density is quantified (cf. Cousens & Mortimer 1995). Sensitive dependence of predicted density on uncertain variables may indicate to what extent prediction is fundamentally limited at the current level of knowledge.

The objective of this paper is to derive a simple, but not unrealistic, model of weed population dynamics from experimental data and to analyse the error in predicted density for the most likely sources of uncertainty. The model is used to examine the change of error in predicted weed density when the prediction interval is enlarged, and to examine how errors in long-term prediction affect the performance of weed control decisions that are based on those predictions. The error in predicted weed density as studied here applies to the deviation between a prediction based on 'correct' values of variables and a prediction based on 'incorrect' estimates.

First, an experiment is described that examines the population dynamics of the weed *Stellaria media* L. in a crop rotation of winter wheat and sugar beet. The experimental results are used to construct a model of population dynamics of *S. media*. The effect of small changes in uncertain model variables on predicted density is determined. Subsequently, the effect of small changes in uncertain model variables on the control decisions are analysed. Finally, it is indicated what the implications are for the practical use of weed population dynamic models in planning for long-term weed management.

Material and methods

Experiments

Two similar experiments were conducted at two research stations in the Netherlands, one near Wageningen, henceforth indicated as experiment 1, and another near Nagele, henceforth indicated as experiment 2. Both experiments were carried out over the period 1990 - 1993, during which time the experimental plots were cropped in successive years with winter wheat, sugar beet and winter wheat. The most dominant weed at both sites was *S. media.* Two weed management regimes were imposed in both experiments: (i) weeds were left uncontrolled in winter wheat, but weeds were controlled in sugar beet; (ii) weeds were controlled in both winter wheat and sugar beet. Each management regime was carried out on 10 plots at each site. Full experimental details are given in table 1. The number of *S. media* plants in each plot was assessed in the winter wheat crop in March 1991 and March 1993. Crop yield of winter wheat was measured in each plot in 1993. Weed control in the sugar beet crop sufficed to eliminate weed plants.

Table 1. Experimental setting in which population density of *Stellaria media* L. was observed over three years. Half of the plots were treated with herbicides when winter wheat was cropped, in the other half of the plots weed control was omitted when winter wheat was cropped.

		Experiment 1	Experiment 2
	location	Wageningen, the Netherlands	Nagele, the Netherlands
	soil type	loamy sand soil	sandy loam soil
	plot size	18 m × 10 m	21 m × 10 m
1991	crop	winter wheat	winter wheat
	observation	20 March 1991, for each plot the number of weeds was counted in 3 quadrats of 0.25 m^2	21 March 1991, for each plot the number of weeds was counted in 3 quadrats of 1 m^2
	weed control	fluroxypyr / none	mecoprop, 2,4D, fluroxypyr / none
	fertilizer	189 kg N or 148.5 kg N 1)	122 kg N or 92 kg N 1)
1992	crop	sugar beet	sugar beet
	weed control	ethofumesate, fenmedifam 2), metamitron with additional hoeing	ethofumesate, fenmedifam 2), metamitron with additional hoeing
1993	crop	winter wheat	winter wheat
	observation	25 March 1993, for each plot the number of weeds was counted in 8 quadrats of 0.25 m^2	22 March 1993, for each plot the number of weeds was counted in 8 quadrats of 0.25 m^2
	weed control	fluroxypyr / none	fluroxypyr, MCPA / none
	fertilizer	171 kg N or 141 kg N 1)	180 kg N or 150 kg N 1)
	observation	6 August 1993, for each plot the kernel dry weight was measured	14 August 1993, for each plot the kernel dry weight was measured

1) one half of the replications received slightly more fertilizer than the other half.

2) fenmedifam is used as common name for 3-methoxycarbonylaminofenyl 3-methylfenylcarbamate.

Model

The dynamics of *S. media* over a 2 year crop rotation of winter wheat - sugar beet were described by

$$N(t)=\begin{cases} aN(t-1) & \text{if} \quad r(t-1)=0 \\ bN(t-1) & \text{if} \quad r(t-1)=1 \end{cases} \tag{1a}$$

where N is the *S. media* density in winter wheat, t denotes time (with 2-year time steps), a is the relative growth rate of the weed population when weeds are left uncontrolled, b is the relative growth rate of the weed population when weeds are controlled, and r is a binary control variable (r = 1 when weeds are controlled in winter wheat, r = 0 when weeds are left uncontrolled in winter wheat). The resulting winter wheat yields are described by:

$$Y(t)=\begin{cases} Y_{\max}-cN(t) & \text{if} \quad r(t)=0 \\ Y_{\max} & \text{if} \quad r(t)=1 \end{cases} \tag{1b}$$

where Y is winter wheat yield (kg m^{-2} kernel dry wt), $Y_{\max}$ represents the crop yield when weeds are controlled (kg m^{-2} kernel dry wt), and the parameter c indicates the yield loss per weed plant when weeds are left uncontrolled (kg^{-1} kernel dry wt).

The annual revenue of cropping winter wheat is described by the following equation:

$$R(t)=\begin{cases} pY(t) & \text{if} \quad r(t)=0 \\ pY(t)-h & \text{if} \quad r(t)=1 \end{cases} \tag{1c}$$

where R is annual revenue (Dfl yr^{-1}), p is the wheat price (Dfl kg^{-1} kernel dry wt), and h is the costs of weed control (Dfl m^{-2}).

Parameter estimation

Relative growth rate of the weed population when weeds are left uncontrolled, a, was estimated for both experiments by linear regression of weed density observed in 1993 against weed density observed in 1991 in plots where weeds were left uncontrolled. Relative growth rate of the weed population when weeds are controlled, b, was estimated for both experiments by linear regression of weed density observed in 1993 against weed density observed in 1991 in plots where weeds were controlled. The average yield loss per weed plant, c, was estimated for both experiments by linear regression of winter wheat yield against weed density observed in 1993 in plots where weeds were left uncontrolled. The economic parameters were estimated as p = 0.40 Dfl kg^{-1} kernel dry wt, and h = 0.01 Dfl m^{-2}.

Prediction of weed densities

It is assumed that each year a weed control decision is made that gives the best expected economic results. For a specific *S. media* density this decision is derived by a computer program that applies the following rules:

- consider all possible combinations of weed control decisions (either control or no control) in winter wheat crops in the following years;
- calculate for each combination of decisions the effects of decisions on the annual weed densities, crop yields and economic returns with the model;
- calculate for each combination of decisions on the sum of discounted revenues;
- select the weed control decision that leads to the highest sum of discounted revenues.

It is assumed that the planning horizon is 6 years and that the discount rate is 0.8, which means that the sum of discounted revenues is calculated by adding the expected revenue of the current winter wheat crop weighed with a factors 0.8^0, the subsequent winter wheat crop weighed with a factor 0.8^2, and the following winter wheat crop weighed with a factor 0.8^4.

Prediction of density of a weed population that is controlled according to optimum control decisions proceeds as follows. For an initial weed density $N(0)$ the corresponding weed control decision $r(0)$ is derived using the above mentioned rules. Both $N(0)$ and $r(0)$ are substituted into equation 1*a* to calculate the expected weed density in the following winter wheat crop $N(1)$. For this weed density, the corresponding weed control decision $r(1)$ is derived. Both $N(1)$ and $r(1)$ are substituted into equation 1*a* to derive the expected weed density in the subsequent winter wheat crop $N(2)$. And so on.

Results

Experiments

The average density of *S. media* plants was 26.8 m^{-2} in experiment 1 in 1991. For each management regime the densities observed in 1991 were approximately linearly related to the densities as observed in 1993 (figure *1a*), densities increased on average by a factor 2.0 when weeds were not controlled and densities decreased on average by a factor 0.8 when weeds were controlled (table 2). The kernel dry weight of winter wheat in 1993 declined approximately linearly with increasing density of *S. media* (figure 1*b*).

The average density of *S. media* plants was 1.1 m^{-2} in experiment 2 in 1991. For each management regime the densities as observed in 1991 were approximately linearly related to the densities as observed in 1993 (figure 2*a*). Density increased on average by a factor 43.5 when weeds were not controlled and densities decreased on average by a factor of 0.7 when weeds were controlled (table 2). The kernel dry weight of winter wheat in 1993 declined approximately linearly with increasing density of *S. media* (figure 2*b*).

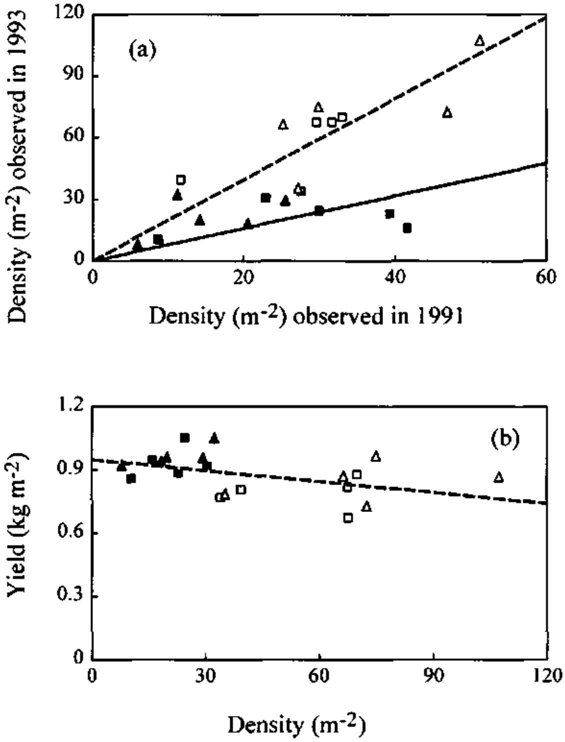

Figure 1. Results of experiment 1, at site Wageningen. (*a*) The density of *Stellaria media* per plot as observed in spring 1991 and in spring 1993 in winter wheat crops. (*b*) The relation between density of *Stellaria media* observed in spring 1993 and kernel dry weight of winter wheat in that year. The plots were either sprayed with a herbicide after observation of density in 1991 and 1993 (filled markers, linear regression on this data is indicated by the drawn line) or weed control was omitted in 1991 and 1993 (open markers, linear regression on this data is indicated by the broken line). Some plots received slightly more fertilizer (squares) than others (triangles). In 1992, all plots were cropped with sugar beet, weeds were controlled on all plots.

Table 2. Results of experiment 1, conducted at site Wageningen, and experiment 2, conducted at site Nagele. Data are presented as mean (± standard error of the mean) and winter wheat yield is given as kernel dry weight.

		Experiment 1	Experiment 2
initial density of *S. media* plants (m^{-2})	$N(0)$	26.8 (± 2.8)	1.1 (± 0.2)
rate of increase without weed control	a	2.0 (± 0.1)	43.5 (± 4.6)
rate of increase with weed control	b	0.8 (± 0.1)	0.7 (± 0.4)
crop yield in absence of weeds (kg m^{-2})	Y_{max}	0.95 (± 0.02)	0.85 (± 0.01)
reduction of crop yield per weed plant (kg)	c	1.7 (± 0.5) 10^{-3}	2.4 (± 0.3) 10^{-3}

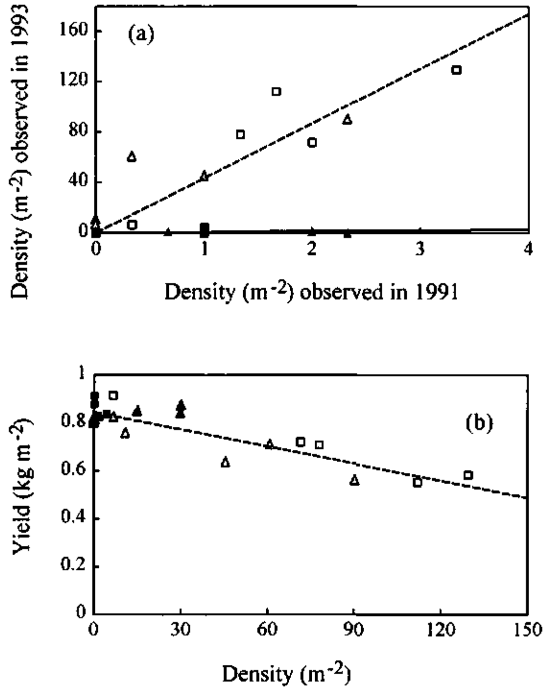

Figure 2. Results of experiment 2, at site Nagele. (*a*) The density of *Stellaria media* per plot as observed in spring 1991 and in spring 1993 in winter wheat crops. (*b*) The relation between density of *Stellaria media* observed in spring 1993 and kernel dry weight of winter wheat in that year. The plots were sprayed with a herbicide after observation of density in 1991 and 1993 (filled markers, linear regression on this data is indicated by the drawn line) or weed control was omitted in 1991 and 1993 (open markers, linear regression on this data is indicated by the broken line). Some plots received slightly more fertilizer (squares) than others (triangles). In 1992, sugar beet was grown on all plots and weeds were controlled.

Population dynamics when weeds are controlled according to optimum decisions

For a wide range of *S. media* densities the weed control decision that leads to the highest sum of discounted future revenues is calculated. When model parameters are estimated from experiment 1, the best decision is to control in the current year when the weed density exceeds 10.85 plants m^{-2}, otherwise the best decision is to skip control in the current year. When model parameters are estimated from experiment 2, the best decision is to control in the current year when the weed density exceeds 6.80 plants m^{-2}, otherwise the best decision is to skip control. This means that the dynamics of a *S. media* population, subjected to optimum control decision, are thus effectively described by:

$$N(t) = \begin{cases} aN(t-1) & \text{if} \quad N(t-1) \leq K \\ bN(t-1) & \text{if} \quad N(t-1) > K \end{cases} \tag{2}$$

where N is the density of *S. media* in winter wheat, t denotes time (with 2-year time steps), a is the relative growth rate of the weed population when weeds are left uncontrolled, b is the relative growth rate of the weed population when weeds are controlled, and K is the density threshold for applying weed control. When model parameters are estimated from experiment 1, $a = 2.0$, $b = 0.8$, and $K = 10.85$ plants m^{-2}. When model parameters are estimated from experiment 2, $a = 43.5$, $b = 0.7$, and $K = 6.80$ plants m^{-2}.

Effect of error in estimates of initial density on predicted density

It is derived in appendix 1 that, on the long term, the relation between a small error in the estimate of initial density $N(0)$ and the resulting error in predicted density $N(t)$ is:

$$\frac{\mathrm{d}\,N(t)}{\mathrm{d}\,N(0)} = 1. \qquad (3)$$

This means that an error in the estimate of initial density is preserved over the long term, and that the magnitude of the resulting error in predicted density does not depend on the length of the prediction interval.

Effect of error in estimates of population growth rate on predicted density

In appendix 2 it is derived that, on the long term, the relation between a small error in the estimate of growth rate a and the resulting error on predicted density $N(t)$ is:

$$\frac{\mathrm{d}\,N(t)}{\mathrm{d}\,a} \approx \alpha N_E t\,, \qquad (4)$$

where α is the relative frequency of years in which weeds are left uncontrolled and N_E is the expected weed density when weeds are not controlled. This means that the absolute error in predicted densities increases linearly with the length of the prediction interval if there is an error in the estimate of growth rate. When model parameters are estimated from experiment 1, the value of the term αN_E is estimated as 2.4 plants m^{-2} per time step. When model parameters are derived from experiment 2, the value of this term is estimated as 0.5 plants m^{-2} per time step (see appendix 2).

Effect of an error in control decisions on crop yield

The relation between an error in the estimated density threshold for weed control K and the expected annual crop yield, denoted by Y_A, is (see appendix 3):

$$\frac{\mathrm{d}\,Y_A}{\mathrm{d}\,K} = \frac{-c(1-b)}{\ln a - \ln b}. \qquad (5)$$

When model parameters are estimated from experiment 1, an overestimate of 1 plant m^{-2} in the density threshold would cause a decrease in average crop yield of 0.37 10^{-3} kg m^{-2}. When model parameters are estimated from experiment 2, an overestimate of 1 plant m^{-2} in the density threshold would cause a decrease in average crop yield of 0.17 10^{-3} kg m^{-2}.

Discussion

The purpose of the present paper was to examine the change of error in predicted weed density when the prediction interval is enlarged, and to examine how errors in long-term prediction affect the performance of control decisions based on those predictions. To this purpose, a simple prediction model was used. The model's dynamics, as described by equation 2, have been studied before (Felsenstein 1979; Hughes & González-Andújar 1997; Wallinga & Van Oijen 1997). Up to now, there has been no analysis of the effects of a change in initial condition or in parameter values on the projected trajectories.

As any prediction model, the model rests on a number of assumptions. Some assumptions have been made about the economic objectives of weed control and about the prices of the crop and weed control. They were necessary to derive a rational weed control strategy, but, since the assumed parameter values do not affect the existence of a density threshold for weed control and do not enter the derived equations, they do not have a direct impact on the outcome. It is assumed that the model parameters remain constant and do not depend on weed density. This assumption made it possible to estimate the parameter values by linear regression. Over the range of densities that is of practical interest, and over the range of densities that is attained in the experiment, this assumption holds quite well (see figures 1 and 2). However, over a wider range of weed densities that includes very large densities such an assumption is unlikely to hold. So, with the restriction that weed densities are limited to the range of values that is of practical interest, the model can be applied to analyse the error in predicted densities.

Table 2 shows a more than 20-fold difference in observed values for the initial weed density $N(0)$ between experiment 1 and experiment 2. In principle, the weed density can be measured exactly for any location, but in practical situations such an exact measurement will be too labour intensive and as a result the estimated weed density will have some measurement error. Equation 3 shows that an error in estimate of initial weed density results in an error in predicted weed density, and that the absolute error is preserved and does not, on average, increase or decrease.

Table 2 also shows a more than 20-fold difference in relative population growth rate a between experiment 1 and 2. In practical situations it is impossible to estimate weed population growth rate since this requires to leave weeds uncontrolled. Hence, the uncertainty associated with the growth rate a is very large. Equation 4 shows that an error in the estimate of relative weed population growth rate results in an error in predicted density, and that the absolute error increases with increasing prediction interval. The relative error will increase with prediction interval and eventually the magnitude of error will exceed the predicted weed density, rendering predictions meaningless.

Equation 4 makes explicit the rate at which error in prediction increases, and on which variables the increase in error depends:

- the error increases linearly with length of the prediction interval;
- the growth of error is positively related to the density that weeds achieve, on average, in the years when weeds are left uncontrolled (that is, if higher weed densities are tolerated, the prediction errors will increase more rapidly);
- the growth of error is positively related to the frequency of years in which the weeds are left uncontrolled (that is, if the weed population requires less intensive control, the prediction errors will increase more rapidly).

It follows that the prediction error increases more slowly for the most noxious weeds because these weeds can be tolerated only at very low densities, rarely allowing non-use of control measures.

The error that is made in long-term prediction of weed density will cause an error in estimated optimum density threshold for weed control. For example, consider a prediction made with estimates for *a* and *b* that differ as much from the actual values as the observed parameter values for experiment 1 differ from those for experiment 2; the resulting error in predicted weed densities in the subsequent winter wheat crops will then be very large. In this case, the resulting estimated density threshold for weed control will differ as much from its actual optimum value as the estimated threshold for experiment 1 differs from that for experiment 2, that is, the threshold will be overestimated by 4.05 plants m^{-2}. The long-term consequence of this overestimation for average crop yield can be calculated by equation 5: overestimation of the threshold as estimated for experiment 2 by 4.05 plants m^{-2} causes a reduction in average crop yield by 0.69 10^{-3} kg m^{-2} (0.08% of the weed-free crop yield). This is a negligible small amount. This example shows that the model, even when its predictions are poor, can still be able to recommend long-term control decisions that would result in near-optimum crop yields; the variability in ecological variables does not mean that models of weed population dynamics are useless in evaluating long-term weed management options.

Conclusion

Relative errors in predicted weed density increase linearly with the length of the prediction interval. This sets a limit to the period over which density can be predicted. Model-based decisions can give near-optimum results even when the model's predictions are very inaccurate; a limited ability to predict weed density over a long term does not impair the use of models in planning for long-term weed control programmes.

Appendix 1

Effect of error in initial density on predicted density

The weed population is controlled when the density of weeds exceeds a density threshold. The resulting dynamics are given by:

$$N(t) = \begin{cases} aN(t-1) & \text{if} \quad N(t-1) \leq K \\ bN(t-1) & \text{if} \quad N(t-1) > K \end{cases} \tag{A1.1}$$

where K is the density threshold for weed control, a is the relative growth rate of the uncontrolled population (such that $a > 1$), b is the relative growth rate of the controlled population (such that $0 < b < 1$).

The relative frequency of years in which density does not exceed the threshold value is denoted by α, and the relative frequency of years in which density exceeds the threshold value is denoted by β. Both relative frequencies can be expressed in terms of population growth rates (Wallinga & Van Oijen 1997):

$$\begin{cases} \alpha = \dfrac{-\ln b}{\ln a - \ln b} \\ \beta = \dfrac{\ln a}{\ln a - \ln b} \end{cases} \tag{A1.2}$$

The error in predicted population density $N(t)$ due to an error in the initial density $N(0)$ is obtained by taking the derivative of prediction density with respect to initial density. On the long term, this derivative is:

$$\frac{\mathrm{d}\,N(t)}{\mathrm{d}\,N(0)} = \frac{\mathrm{d}\,N(t)}{\mathrm{d}\,N(t-1)} \frac{\mathrm{d}\,N(t-1)}{\mathrm{d}\,N(t-2)} \cdots \frac{\mathrm{d}\,N(1)}{\mathrm{d}\,N(0)} = \prod_{n=1}^{n=t} \frac{\mathrm{d}\,N(n)}{\mathrm{d}\,N(n-1)} = a^{\alpha t} b^{\beta t} = 1. \tag{A1.3}$$

So, for large t,

$$\frac{\mathrm{d}\,N(t)}{\mathrm{d}\,N(0)} = 1. \tag{A1.4}$$

Appendix 2

Effect of error in population growth rate on predicted density

The error in predicted population density $N(t)$ due to error in to the relative growth rate a is obtained by taking the derivative of predicted density with respect to relative population growth rate a. This derivative is:

$$\frac{\mathrm{d}\,N(t)}{\mathrm{d}\,a}=\frac{\partial N(t)}{\partial N(t-1)}\frac{\mathrm{d}\,N(t-1)}{\mathrm{d}\,a}+\frac{\partial N(t)}{\partial a}. \tag{A2.1}$$

For convenience, the following notations are introduced:

$$u(t)=\frac{\mathrm{d}\,N(t)}{\mathrm{d}\,a}, \tag{A2.2a}$$

$$p(t)=\frac{\partial N(t+1)}{\partial N(t)}=\begin{cases} a & \text{if} \quad N(t)\le K \\ b & \text{if} \quad N(t)>K \end{cases}, \tag{A2.2b}$$

$$q(t)=\frac{\partial N(t+1)}{\partial a}=\begin{cases} N(t) & \text{if} \quad N(t)\le K \\ 0 & \text{if} \quad N(t)>K \end{cases}. \tag{A2.2c}$$

In this notation, equation A2.1 becomes
$u(t)=p(t-1)u(t-1)+q(t-1)$, which can be expanded as
$u(t)=p(t-1)[p(t-2)u(t-2)+q(t-2)]+q(t-1)$, and so on, until it finally yields
$u(t)=\prod_{\tau=0}^{t-1}p(\tau)u(0)+\sum_{s=1}^{t-1}q(s-1)\prod_{\tau=s}^{t-1}p(\tau)+q(t-1)$.
Since $u(0)=\dfrac{\partial N(0)}{\partial a}=0$ the above equation reduces to

$$u(t)=q(t-1)+\sum_{s=1}^{t-1}q(s-1)\prod_{\tau=s}^{t-1}p(\tau). \tag{A2.3}$$

Equation A2.3 can be decomposed into three terms

$$\begin{cases} u(t)=x(t)+y(t)+z(t) \\ x(t)=\sum_{s=1}^{t}q(s-1)\prod_{\tau=1}^{t-1}p(\tau) \\ y(t)=q(t-1)\left[1-\prod_{\tau=1}^{t-1}p(\tau)\right] \\ z(t)=\sum_{s=1}^{t-1}q(s-1)\left[\prod_{\tau=s}^{t-1}p(\tau)-\prod_{\tau=1}^{t-1}p(\tau)\right] \end{cases} \tag{A2.4}$$

and for each of these terms the behaviour with increasing t is studied.

First, it is determined how $x(t)$ increases with increasing t. Note that equation A1.3 rewritten in the notation of equation A2.2*b* means that $\prod_{\tau=1}^{t-1} p(\tau)$ approaches unity on the long term. Therefore, on the long term,

$$x(t)=\sum_{s=1}^{s=t} q(s-1)\prod_{\tau=1}^{t-1} p(\tau)=\sum_{s=1}^{t} q(s-1).$$

Recalling that $q(t)$ is defined by equation A2.2*c* as weed density if weeds are left uncontrolled and zero if weeds are controlled, the resulting sum can be written as the product of prediction interval t, the frequency that weeds are left uncontrolled α, and the expected weed density when weeds are left uncontrolled N_E:

$$x(t)=\sum_{s=1}^{t} q(s-1)=\alpha N_E t.$$

Second, it is determined whether $y(t)$ increases with increasing t, and again use is made of the fact that $\prod_{\tau=1}^{t-1} p(\tau)$ approaches unity on the long term:

$$y(t)=q(t-1)\left[1-\prod_{\tau=1}^{t-1} p(\tau)\right]=0. \tag{A2.6}$$

Third, it is determined how $z(t)$ increases with increasing t. For this purpose, $z(t)$ is split up into two parts:

$$z(t)=z_1(t)+z_2(t)$$

$$z_1(t)=\sum_{s=1}^{r-1} q(s-1)\left[\prod_{\tau=s}^{t-1} p(\tau)-\prod_{\tau=1}^{t-1} p(\tau)\right]$$

$$z_2(t)=\sum_{s=r}^{t-1} q(s-1)\left[\prod_{\tau=s}^{t-1} p(\tau)-\prod_{\tau=1}^{t-1} p(\tau)\right]$$

where $r=t-1-\rho(t)$, and $\rho(t)$ increases with t such that when $t\rightarrow\infty$, $\rho(t)\rightarrow\infty$ and $\rho(t)/t\rightarrow 0$ (these requirements are met when, for instance, $\rho(t)$ is taken as $\frac{1}{2}{}^{a}\log t$, truncated to the nearest integer). $z_1(t)$ approaches zero because $\prod_{\tau=1}^{t-1} p(\tau)$ approaches unity on the long term. For increase of $z_2(t)$ with t an upper limit is derived by using the facts that $q(s-1)\le K$, $\prod_{\tau=s}^{t-1} p(\tau)\le a^{\rho(t)}$, and $\prod_{\tau=1}^{t-1} p(\tau)\ge 0$ (these restrictions follow in a straightforward manner from the definitions of q and p in equation A2.2*b* and equation A2.2*c*):

$$z(t)=\sum_{s=1}^{t-1} q(s-1)\left[\prod_{\tau=s}^{t-1} p(\tau)-\prod_{\tau=1}^{t-1} p(\tau)\right]\le\sum_{s=r}^{t-1} Ka^{\rho(t)}$$

writing out the last term gives then:

$$z(t)=\sum_{s=1}^{t-1} q(s-1)\left[\prod_{\tau=s}^{t-1} p(\tau)-\prod_{\tau=1}^{t-1} p(\tau)\right]\le\rho(t)a^{\rho(t)}K \tag{A2.7}$$

This increase of the upper limit to $z(t)$ with t is on the long term negligible as compared to the increase of $x(t)$ with t. For instance, take $\rho(t) = \frac{1}{2}{}^{a}\log t$:

$$\lim_{t\to\infty} \frac{\rho(t)a^{\rho(t)}}{\alpha N_E t} = \lim_{t\to\infty} \frac{{}^{a}\log t}{2\alpha N_E \sqrt{t}} = 0.$$

In summary, $u(t)$ is decomposed into three terms $x(t)$, $y(t)$ and $z(t)$ of which $y(t)$ is zero and $z(t)$ is negligible compared to $x(t)$ when t is large:

$u(t) \approx x(t)$.

Substituting equation A2.2*a* and equation A2.5 into the above equation gives

$$\frac{dN(t)}{da} \approx \alpha N_E t, \tag{A2.8}$$

The term αN_E can be expressed in terms of a, b and K, the variables that are used to describe the weed population dynamics. If the weed population follows the dynamics of equation 2, the logarithm of weed density is distributed uniformly over the interval $(\ln bK, \ln K]$ (see Felsenstein 1979 for a derivation of thes result in a slightly different context). The probability density function for weed densities that do not exceed the threshold value K is then $P(N_t | N_t < K) = \frac{1}{-\ln b}\frac{1}{N}$. The expected weed density, given that the density does not exceed density threshold K, is $N_E = \int_{bK}^{K} N \frac{1}{-\ln b}\frac{1}{N} dN = \frac{K(1-b)}{-\ln b}$. The frequency of years in which density does not exceed the threshold value K is given by equation A1.2: $\alpha = \frac{-\ln b}{\ln a - \ln b}$. Combining the expressions for N_E and α gives

$$\alpha N_E = \frac{K(1-b)}{\ln a - \ln b}. \tag{A2.9}$$

Appendix 3

Effect of an error in control decisions on crop yield

The expected weed density, given that density does not exceed the threshold, is denoted by N_E. The expected crop yield, given that density does not exceed the threshold is denoted by Y_E:

$$Y_E = Y_{\max} - cN_E \tag{A3.1}$$

The expected yield, given that density exceeds the threshold, is the maximum yield $Y_{\max}$. Furthermore, α is the frequency of years in which density does not exceed the threshold. It follows then that the average yield over all years, denoted by Y_A, is given by:

$$Y_A = Y_{\max} - c\alpha N_E \tag{A3.2}$$

Substitution of equation A2.9 into equation A3.2 gives:

$$Y_A = Y_{\max} - c\frac{K(1-b)}{\ln a - \ln b}. \tag{A3.3}$$

Taking the derivative with respect to K gives

$$\frac{\mathrm{d}Y_A}{\mathrm{d}K} = \frac{-c(1-b)}{\ln a - \ln b}. \tag{A3.4}$$

Herbicide use decreases as the spatial scale of weed control decreases. If the current state of technology would allow to detect and spray weeds at a scale much smaller than the plant size, the area that needs to be sprayed is approximately the total leaf area of the weeds, which is usually much smaller than the area of the whole field, and this would allow an enormous reduction in herbicide use. Of course, the current state of technology does not yet allow application of weed control at such small scales. Therefore, the herbicide use of patch control programmes is determined by the spatial scale of weed control, which is set by the current state of affordable technology.

Spatio-temporal dynamics of weed populations

The other objective of this thesis is to analyse spatio-temporal dynamics of weed populations. The dynamics of average weed density obviously depends on the weed control programme. If the weed population is subjected to threshold control, the average density will fluctuate around the threshold value with aperiodic cycles. These aperiodic cycles are either quasi-periodic or chaotic (chapters 6 and 7). If the weed population is subjected to optimum dose control, the average density will approach a low equilibrium density (chapter 5). Although at this equilibrium the overall weed density in a field will remain constant, the local dynamics are rather complicated.

Chapter 2 gives a probabilistic explanation for emergence and persistence of weed patches in an otherwise homogeneous habitat when the size of the weed population is held at a low overall density. The explanation invokes only a few basic principles of plant population biology and weed control. In loose terms this explanation runs as follows. Most seeds are shed close to the mother plants, and therefore the seed density in the centre of a patch is much higher than at the edge. When the weed population is subjected to high kill rates, such that the population density does not increase, the probability of local population extinction due to stochastic fluctuations in density is very high at the edge of a patch where the seed density is low, whereas the probability of local population persistence in spite of stochastic fluctuations in density is high in the centre of the patch where the seed density is high. As a consequence, the patch tends to persist. This probabilistic explanation leads to an exact, testable prediction about weed spatial patterns: standing on a randomly selected weed, the expected number of other weeds, N, within a neighbourhood of radius R will increase with R as $N \sim R^{1.17}$. This result may be regarded as a plausible null-hypothesis for weed spatial pattern.

Analysis of an observed weed spatial pattern (chapters 2, 4) shows that there is a power-law relation between number of weeds and radius with a non-trivial exponent, but the observed value of the exponent does not equal the predicted value; the hypothesis about the weed spatial pattern is partly confirmed. Other aspects of patch formation must have played a role as well. Chapter 3 provides an alternative probabilistic explanation for emergence of patches in an otherwise homogeneous habitat if the weed population size has increased in the years prior to the observation. This alternative explanation leads to a testable hypothesis: if the population originates from a single seed, it could only have formed irregular spread-out patterns if the forward tail of the projected seed dispersal curve declines slower than exponentially with distance. It is very well possible that dispersal curves for weed seeds have this property, but it will be rather difficult to make a decisive observation of the tail shape of the seed dispersal curve (chapter 3).

In conclusion, weed patch formation and weed patch persistence are expected even in an otherwise homogeneous environment. Testable hypotheses have been derived to determine whether patches were formed by processes that are inherent to life-cycle processes alone.

Self-organized criticality in a model of weed population dynamics

Perhaps surprisingly, the above mentioned 'plausible null-hypothesis for weed spatial pattern', $N \sim R^{1.17}$, does not depend on the specific model details (see chapter 2). A similar result (namely, $N \sim R^{1.19}$) is also reported for a process called 'directed percolation', which may be regarded as the most simple stochastic spatial model of population dynamics (Grassberger 1989).

Directed percolation can be explained in terms of annual plant population dynamics in a constant homogeneous environment. Directed percolation then describes a process where plants are distributed onto a two-dimensional lattice. At each time step a new plant will grow on every lattice site which has at least one seed. This plant is killed with a probability r. If the plant survives it disperses seeds to the neighbouring lattice sites and dies. There is a critical kill rate ($r = r_c$) at which the population barely persists at a very low density. When the population is subjected to this critical kill rate r_c, the system shows so-called 'critical phenomena' and some quantities of interest can be described by power laws. Adding more complex details to this simple model does not affect the existence of the power laws nor does it affect the values of the exponents of the power laws.

It is conjectured that directed-percolation-like critical phenomena are expected if the model has the following six features, expressed in terms of plant population dynamics (cf. Grassberger 1997):

- space is two dimensional;
- seed dispersal is local;
- the number of seeds per unit area is discrete;
- the seed production per unit area is limited;
- the kill rate is independent of spatial position;
- the kill rate is near a critical value.

Almost all explicit spatial stochastic models of plant population dynamics in a homogeneous habitat have the first five features. However, there is no reason to assume that for a plant population in a natural environment without management the plant kill rate approximates the critical value.

As pointed out by Bak *et al.* (1989), there exist models which show critical behaviour without possessing any obvious analogue of a constant critical kill rate. This phenomenon, called 'self-organized criticality', has been intensively studied in the last ten years. It is possible to construct a self-organized critical analogue of the plant population dynamics model described above by keeping the overall density of plants on the lattice constant at low values, and leaving the kill rate variable. The kill rate is then implicitly driven to its critical value. One of the above mentioned requirements for a model to exhibit directed-percolation-like critical phenomena, 'the kill rate is near a critical value', can then be replaced by 'the overall plant density is at a very low value'. If the plants are weeds, there is a good reason to hold the plant density at low values, since it will maximize the economic returns to the farmer (chapters 5, 6 and 7). Therefore, a model of annual weed population dynamics will show directed-percolation-like critical behaviour for almost all feasible weed control programmes, if the model assumes a homogeneous habitat and local seed dispersal, and if the model acknowledges the fact that annual weeds are discrete individuals in a two dimensional space that have a limited seed production per unit area. Indeed, the simple stochastic spatial model of weed population dynamics as presented and analysed in chapter 2 displays self-organized critical behaviour that is very closely related to directed percolation (Bröker & Grassberger, preprint).

As a consequence it is possible to make specific quantitative statements about the dynamics and pattern formation in weed population models that assume a homogeneous habitat, even without explicit knowledge of the exact model details.

Relations to other research

Several studies have focused on the evaluation of threshold control programmes (see Cousens & Mortimer 1995 for a review). Here, some results of those case studies are generalized and it is shown that the discrete-choice threshold may be an inappropriate basis for weed-control decision making when the objective is to limit the frequency of herbicide use in the long term (chapters 6 and 7, see also Hughes & Gonzalez Andujar 1995). Some studies have considered optimum herbicide dose control programmes (*e.g.* Pandey & Medd 1990, 1991). Here, it is shown that the long-term herbicide use by such control programmes will be determined by critical weed kill rate and herbicide use. Hardly any studies have been published that evaluate patch control programmes over a long term (but see Day *et al.* 1996). Some of the difficulties in the evaluation of patch control programmes are discussed by Cousens & Woolcock (1997). They state that "...all of the modelling has been concerned with spread from a new focus of invasion. If we are to model the effects of patch spraying on existing populations, we need to model weeds that have already had the opportunity to occupy all parts of a field (*i.e.* closer to equilibrium)." Chapter 2 deals with such an existing population that is 'close to equilibrium', and it may give new perspectives for the design and evaluation of patch control programmes.

The weed population dynamics model of chapter 2 has been further analysed by Bröker & Grassberger (preprint) who formulated and tested the scaling laws of this model in much more detail. They verified most of the results of chapter 2, including the non-trivial claim that the growth of surviving labelled clusters inside a large critical population obeys exactly the same scaling laws as the growth of surviving isolated clusters. They also noted that the centre of a surviving cluster of weeds makes essentially a random walk in space. But since this is a very slow process, weed patches will appear to persist on the time scales that are of interest for weed control.

The probabilistic explanations for weed patch formation lead to testable hypotheses about the spatial weed pattern and weed seed dispersal curve (chapters 2 and 3). If these hypotheses are rejected, other processes than population biology alone may have played a role in weed spatial pattern formation. For example, weeds may remain in patches because these are situated at sites that have more favourable conditions than other parts of the field, or a weed might help neighbouring weeds to survive and reproduce because it catches herbicides and shields neighbouring weeds (Rew & Cussans 1995; Mortensen & Dieleman 1997). These explanations of pattern formation are equally plausible as the ones that are elaborated in this thesis but it will be harder to derive testable hypotheses since interactions between weeds and their abiotic environment are involved.

Perspectives for future reductions of herbicide use

If one is interested in the question 'how to further reduce herbicide use', the results reported here suggest that applying weed control measures at finer spatial resolution has a very large potential for reducing herbicide use. The advent of precision agriculture will provide a technological impetus for weed control at ever finer precision. The following types of observations are needed to design an effective patch control programme.

- Observations of spatial patterns of weeds. To assess the optimum scale of weed control, weed spatial patterns need to be mapped at different scales (cf. Rew *et al.* 1997). The methodology presented in chapter 4 may be helpful to obtain this information for spatial point patterns.
- Observations of spatial pattern of herbicide resistant weeds. Since savings in herbicide use will decrease rapidly if herbicide resistant weeds spread, it is essential to recognise herbicide resistance as soon as possible. The spatial structure of a weed patch may give an indication whether the weeds are herbicide resistant or not (cf. Davidson *et al.* 1996).
- Observations of tail shapes of weed seed dispersal curves are required to estimate the potential of weed seeds to disperse from a patch into the untreated area (cf. chapter 3; Portnoy & Willson 1993).

Perspectives for future research on weed population biology

From a biologist's viewpoint, self-organized critical phenomena in biological systems should be of interest because they make it possible to characterize the system by a condensed general description of spatio-temporal dynamics, and because they allow a simple correlation between spatial pattern and the dynamic processes that are involved in the pattern formation. There are several biological processes that may exhibit self-organized criticality: evolution of species and mass extinction (Bak & Sneppen 1993), epidemics in isolated populations (Rhodes *et al.* 1997) and the growth in tropical rain forests (Solé & Manrubia 1995). For those processes it is practically impossible to find out whether self-organized criticality is as evident in real life as it is in the modelled behaviour of these systems. A weed population in an arable field may form an excellent study object for self-organized criticality in biological systems, since it is relatively easy to observe and is expected to show critical behaviour. The following types of observations on pattern formation in weed populations can be used to test whether the expected self-organized critical phenomena also occur in real life.

- Observations of spatial patterns of weeds. If the population is in a critical state, the spatial pattern should be fractal. The correlation sum, which is presented in chapters 2 and 4, may be a helpful statistic to summarize the observed pattern and to see if the patterns are fractal (see also Avnir *et al.* 1998).
- Observations of spatial patterns of weeds with specified genetic markers. If the population is in a critical state, the spatial distribution of plants with identical genetic markers should be fractal, and the frequency distribution of the periods that a genetic marker is present in the population should decline with time according to a power law relationship (chapter 2; Bröker & Grassberger, preprint).
- Observations of tail shapes of weed seed dispersal distributions. The description of the system as a self-organized analogon of direction percolation requires that seed dispersal is a local process. To find out whether seed dispersal can be considered as a local process or not, it is necessary to know the typical tail shape of the actual distribution of seed dispersal distances (cf. chapter 3; Portnoy & Willson 1993).

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SAMENVATTING

Inleiding

Onkruidbeheersing is een essentieel element in de teelt van gewassen. In Nederland wordt meestal gebruik gemaakt van herbiciden, omdat chemische onkruidbestrijding een relatief goedkope en betrouwbare onkruidbeheersingsmethode is. Afgelopen decennia is men in toenemende mate bewust geworden van nadelige effecten van herbicidengebruik op het milieu, en daarom zijn er onkruidbeheersingsprogramma's ontwikkeld die het onnodig gebruik van herbiciden tegengaan. In dit proefschrift worden drie verschillende typen onkruidbeheersingsprogramma's geanalyseerd:

- alleen herbiciden toepassen waar dat nodig is (pleksgewijze beheersing);
- alleen herbiciden toepassen met optimale herbicide dosis (optimum dosering beheersing);
- alleen herbiciden toepassen als de onkruiddichtheid hoger is dan een bepaalde drempelwaarde (drempel beheersing).

Het is noodzakelijk om de effectiviteit en het herbicidengebruik van deze programma's te testen over een termijn van enkele jaren, maar het is bijna onmogelijk om een veldexperiment op te zetten voor zo'n test en bovendien zouden de experimentele resultaten te laat beschikbaar komen. Het is wel mogelijk om de effectiviteit en het herbicidengebruik van onkruidbeheersingsprogramma's over een lange termijn te evalueren met een model van de dynamica van onkruidpopulaties.

Een doel van dit proefschrift is het aangeven van de essentiële factoren die het herbicidengebruik van onkruidbeheersingsprogramma's bepalen over de lange termijn. Een ander doel van dit proefschrift is het analyseren van ruimtelijke dynamica van onkruidpopulaties. Kennis is hiervan vereist om pleksgewijze beheersing te evalueren. In dit proefschrift worden alleen ééjarige onkruiden besproken, en er wordt aangenomen dat één van de doelen van onkruidbestrijding is om economisch rendabele teelt van gewassen mogelijk te maken.

Ruimtelijke dynamica van ééjarige onkruiden

Allereerst wordt een mogelijke verklaring gegeven voor het ontstaan en de persistentie van clusters onkruiden in velden die uniform behandeld worden. Deze verklaring verloopt als volgt: de meeste zaden vallen vlak bij de moederplant, de dichtheid van zaden is in het midden van de cluster hoger dan aan de rand van de cluster. Als elk jaar veel onkruiden worden verwijderd, zodat de totale populatiedichtheid over het hele veld op een laag niveau wordt gehouden, is de kans op lokale uitsterving van de onkruiden aan de rand van de cluster zeer groot terwijl de kans op lokale overleving in het midden van de cluster relatief hoog is. Daarom blijft een cluster onkruiden lang op dezelfde plek zonder zich uit te breiden. Deze uitleg leidt tot een exacte hypothese over het ruimtelijke patroon van onkruiden: als je op een willekeurig onkruid gaat staan neemt het aantal andere onkruiden N dat je kan tellen in de directe omgeving binnen straal R toe volgens $N = cR^{1.17}$, waarbij c een willekeurige constante is. Met andere woorden, de verdeling is fractaal; of je het ruimtelijk patroon van onkruiden op een kleine schaal bekijkt of op een grote schaal, het patroon blijft in grote trekken gelijk.

Het voorspelde patroon is vergeleken met een waargenomen ruimtelijk patroon van onkruiden in een veld wintertarwe. De onkruidsoort was hier kleefkruid (*Galium aparine* L.). De waargenomen verdeling liet zich goed beschrijven volgens de vergelijking $N = cR^{1.5}$. Het type van de relatie is dus goed voorspeld, maar de waarde van de exponent niet; de hypothese houdt in deze voorlopige test gedeeltelijk stand. Het is mogelijk dat ook andere factoren een rol hebben gespeeld in vorming van het waargenomen patroon. Als het aantal kleefkruidplanten in de voorgaande jaren is toegenomen, is het patroon mede bepaald door de verspreiding van zaden rond een moederplant. Er is een algemene relatie tussen de vorm van de zaadverspreidingscurve en het ruimtelijk patroon van populatie uitbreiding: als de staart van de zaadverspreidingcurve langzamer afneemt dan een exponentiële curve, breidt de populatie zich uit door vorming van nieuwe clusters, anders breidt de populatie zich uit door groei van een enkele cluster. Analyse van de waargenomen verspreiding van zaden van de soort duist (*Alopecurus myosuroides* Huds.) laat zien dat een dergelijke vorm van de zaadverspreidingscurve mogelijk is.

Evaluatie van onkruidbeheersingsprogramma's

Als onkruiden voorkomen in clusters is het mogelijk herbicidengebruik te reduceren door pleksgewijze beheersing toe te passen. Als een extreem geval van pleksgewijze beheersing kunnen we herbiciden toedienen op elke vierkante millimeter van het veld waar onkruid voorkomt, het behandelde oppervlak is dan ongeveer gelijk aan het bladoppervlak van onkruiden. Het bladoppervlak van onkruiden is meestal zeer klein vergeleken met de totale oppervlakte van een veld, en dus is de benodigde hoeveelheid herbiciden zeer klein vergeleken met de benodigde hoeveelheid herbiciden voor een behandeling van het gehele veld. De besparing in herbicidengebruik kan dus zeer groot zijn, maar met de huidige stand van technologie is het nog niet mogelijk op zo'n kleine schaal te werken.

Voor een waargenomen ruimtelijke patroon van kleefkruidplanten in een veld wintertarwe werd de reductie in herbicidengebruik ten opzichte van een behandeling van het gehele veld geschat met behulp van de frequentieverdeling van afstanden tussen willekeurig gekozen punten en de dichtstbijzijnde onkruidplant. Het herbicidengebuik zou kunnen worden teruggedrongen tot 41% vergeleken met behandeling van het gehele veld indien pleksgewijze bestrijding zou gebeuren op een schaal van 1 m. Indien pleksgewijze bestrijding zou gebeuren op een schaal van 0.5 m zou het herbicide gebruik verder teruggebracht kunnen worden tot 24% vergeleken met behandeling van het gehele veld.

Bij optimum-dosering-beheersingsprogramma's gaat de dichtheid van de onkruidpopulatie naar een evenwicht bij een lage dichtheid. De fractie van het aantal planten dat verwijderd moet worden om de populatie op lage dichtheid te handhaven wordt de kritische fractie genoemd. Het herbicidengebruik over lange termijn wordt bepaald door deze kritische fractie en de herbicide-effectiviteit.

Bij toepassing van drempel-beheersingsprogramma's schommelt de onkruidpopulatie dichtheid rondom de drempelwaarde volgens een onregelmatig, aperiodiek, patroon (de dynamica is quasi-periodiek of chaotisch). Het herbicidengebruik over lange termijn wordt bepaald door de fractie van het aantal jaren waarin bestreden moet worden, f. Dit hangt af van de relatieve toename van aantal zaden in de zaadbank zonder bestrijding, a, en met bestrijding, b, volgens de formule $f = \log a / (\log a - \log b)$. De exacte hoogte van de drempelwaarde heeft dus geen invloed op het herbicidengebruik over de lange termijn als deze formule opgaat. Voorspelling van onkruiddichtheden in toekomstige jaren is bij dit type beheersingsprogramma niet zo eenvoudig. Vaak is er een schattingsfout in de vermeerderingsfactor van onkruiden, en indien dit het geval is, neemt de fout in de voorspelling toe, evenredig met het aantal jaren dat vooruit voorspeld wordt.

Conclusies

Eénjarige onkruiden worden verwacht persistente clusters te vormen, zelfs in een omgeving waar alle andere omstandigheden homogeen zijn. Het herbicidengebruik van de geëvalueerde onkruidbeheersingsprogramma's wordt bepaald door de reproductiefactor van onkruidplanten, herbicide-effectiviteit en ruimtelijke schaal van onkruidbeheersing.

CURRICULUM VITAE

The author, Jacob (Jacco) Wallinga, was born in 1968 in the Noordoostpolder. He started his studies in Agronomy at Wageningen Agricultural University in 1986 and obtained his 'ingenieurs' degree (comparable to M.Sc.) in 1992 with majors in Theoretical Production Ecology, Mathematics and Ecophysiology. In 1992, he took a position as a researcher at the Research Institute for Agrobiology and Soil Fertility (AB-DLO) where he did research on the population dynamics of weeds. A part of this research is reported in this thesis. In 1997, he started working as a post-doc researcher at the National Institute for Public Health and Environment (RIVM). There he is doing research on the population dynamics of infectious disease agents.