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On Weed Competition and Population Dynamics

considerations for

crop rotations & organic farming

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Shana K. Mertens

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Propositions

I am very little inclined on any occasion to say anything
unless I hope to produce some good by it. –Abraham Lincoln

1. The diversity of crops is not the only explanation for the effects of crop rotations on weed populations. Different sequences of the same set of crops can result in different weed population growth rates and patterns of sensitivity to changes in underlying biological processes.
   (This thesis.)

2. Organic farmers who aim to reduce weed population densities in the long term by minimising weed seed production require less labour for hand weed control.
   (This thesis.)

3. Policies aimed at increasing on-farm plant species diversity, including weed diversity, will lead to increases in weed densities, and costs of weed control.
   (This thesis.)

4. Even though a wide crop row-spacing combined with mechanical hoeing in cereal crops will result in lower weed densities, weed seed production will be the same as or higher than in a narrowly spaced cereal crop where weed mortality due to mechanical weed control is lower.
   (This thesis.)

5. More effective weed management strategies can be developed if increased attention is given to the perspective and role of individual weed plants in the population.
   (This thesis.)

6. A mathematical model [of a biological population] is neither a hypothesis nor a theory. Unlike scientific hypotheses, a model is not verifiable directly by an experiment. For all models are both true and false… The validation of a model is not that it is "true" but that it generates good testable hypotheses relevant to important problems.
   Levins, R. 1966. The strategy of model building in population biology. *American Scientist* **54**:421-31.

7. Though the general public may consider demography to be a dry science, it is the life-blood of long-term policy development and so gives bounds to our uncertainty of the future.

8. The Global Environment Facility, in being answerable for global benefits, must ensure its projects have local benefits. Only then will a sense of collective responsibility for the environment be created and sustained global benefits be achieved.
   Mertens, S.K. 1994. Towards accountability in the restructured Global Environment Facility. *Review of European Community and International Environmental Law* **3**:105-110.

9. Nothing is truer than Pasteur's famous statement that only 'the prepared mind' makes discoveries. But little thought has been given up to now to the process by which the mind is prepared.
   Mayr, E. 1982. *The Growth of Biological Thought. Diversity, Evolution, and Inheritance.* Belknap Press. Cambridge. USA.

10. … how difficult it is for one to become a Human Being where one is not born a Citizen.
    From the dedication of George Anastaplo to his parents, as Immigrants from Greece, in his book *Human Being and Citizen. Essays on Virtue, Freedom and the Common Good.* (1975) Swallow Press. Chicago. USA.

Shana K. Mertens
On Weed Competition and Population Dynamics
Wageningen University, 14 October 2002

Abstract

Experiments, monitoring studies and modelling of weed population dynamics were carried out to investigate potential methods for reducing weed populations in farming systems where herbicides are not applied (organic farming). Six years of monitoring weed populations on five organic farms showed that farmers who took a long-term approach to weed management had lower weed populations. Farms with low weed densities also had a lower diversity of weed species. An experiment was carried out to investigate whether using the combination of a wide row spacing and aggressive weed control (mechanical hoeing) or a narrow row spacing and less aggressive weed control (harrowing) would decrease weed populations more. Using weed seed production as the criterion for comparing the row spacing/weed control combinations, it was concluded that a narrow row spacing with less aggressive control resulted in fewer weed seeds being produced. Because the experiment involved marking individual plants of the species *Polygonum convolvulus*, *Polygonum persicaria*, and *Stellaria media*, it was possible to investigate how individual plant biomass and survival are related to descriptors of the local environment. In this case the descriptors were distance to the nearest crop plant and the local row width. For all three species it was shown that the same form of predictor gave the best fit and included distance to the nearest crop plant and the crop row spacing where the plant is located. Survival in the wide spacing could be predicted using the distance to the nearest crop row, while in the other row spacings all plants had an equal chance of survival. Predictors of individual plant biomass and survival can be used in modelling the spatial dynamics of weed populations. Finally the effect of crop sequence on weed population dynamics was investigated. Using a periodic matrix model, it was shown that the order of crops in a crop rotation will affect the weed population growth rate and its sensitivity to changes in underlying parameter values. It is stressed that research on weed ecology and non-herbicide management would benefit from long-term experiments and monitoring studies and a closer integration of modelling of weed population dynamics and long-term data.

Preface

Having attended my father's lectures on human population growth and worked by my mother in the garden, it was unexpected, though perhaps inevitable, that I should end up studying aspects of weed demography and ecology. The last four years have been the start of setting out my ideas in the terrain of plant ecology and this thesis represents a distillation of those ideas. Setting out one's own ideas, forming them into answerable and relevant questions, and finding the means –intellectual and practical– of answering them is often arduous, lonely, and to a certain extent selfish. Along the way, I have been fortunate to have had much company from people who have helped to lighten the load through direct contributions in this process of distillation, through patience and support during the hard times, and through sharing of the joyful moments.

My adopted supervisors, Hans Heesterbeek and Frank van den Bosch showed me how I could find answers to my questions on weed population dynamics and have given me the confidence and necessary feedback to work through the other ideas. Discussions with Jacco Wallinga at all stages of this work have been instrumental in clarifying my ideas and in finding methods for answering the questions. Leo Vleeshouwers and Jacob Weiner have provided instructive comments on several of my manuscripts, and Hans de Kroon pointed out a critical reference. In analysing the data of my experiments, I have benefited from discussions, corrections, and over-the-shoulder lessons from Wies Akkermans, Hans Jansen, Remy van de Ven, and Jacques Withagen. There would have been no data to analyse were it not for the logistical assistance and hours of back-breaking and tedious labour from a number of people, including Andries Siepel, Marco Siepel, Henk Pepping, Henk de Rein, Piet de Man, Adrie Kooijman, Herman Peeters, Nettie van Dijk, Roel Groeneveld, Wim van der Slikke, Henk van Roekel, Elisabeth Oosterhuis, Evert Walraven, and John van der Lippe. In my pursuit of understanding weed populations on farms, Sjaak Twisk, Henk Leenstra, Sialto Eskes, Henk Oosterhuis, and Digny van den Dries, have let me walk through their crops and shared their knowledge and philosophy of weed management and farming with me.

Athina Amanatidou, Eric Esveld, Andreas Karatzas, Sophie Margulien, Vasiliki Palli, Hector Planella, Maria Vasquez-Perez, Bjørn Dirks, Jacco Wallinga, and others, all guests at the 2000 Greek Easter Party, took time from eating, drinking and dancing to help with labelling stakes. Corrie and Lieuwe Wallinga provided me with company and shelter during my stays in the NoordOostPolder, lightening the days of heavy fieldwork. I am grateful to Martin Kropff for initiating the project and allowing me the freedom to follow my own ideas and to the programme leaders Remmie Booij, Bert Lotz, and Jaap Schröder for making space in their budgets. Marijn de Visser saved me much time with her excellent translation for the Dutch summary.

Completing a PhD thesis often depends on a critical discussion, a quick introduction to a new method, the cutting of bureaucratic snarls, or small acts of kindness, all of which help to remove obstacles from the path, or provide a step over them. Lammert Bastiaans, Daniel Baumann, Gijs-Bertje Berkhout, Astrid Bon, Ton Claassen, Dirk Creybolder, Jacques Davies, Ries de Visser, Tom Dueck, Els Geurts, Eltje Groendijk, Anton Haverkort, Lia Hemerik, Bert Jansen, Corné Kempenaar, Peter Leffelaar, Carin Lombaers-van der Plas, Ellis Meekes, Frank Nieuwenhuijsen, Elma Schoenmaker, Mira Teofanovic, Marcel van Oijen, Wolter van de Zweerde, Linda van Duijn, Wopke van de Werf, Gon van Laar, and Ronald Visser, perhaps without their realising, have made a difference when it was needed.

My family and friends all require a much more personal thanks than I can give here. Suffice it to say that they have been an indispensable support, even in the face of neglect on my part, and I only hope their patience does not run out before my thanks arrive.

Contents

CHAPTER 1

Introduction and Overview

MOTIVATION FOR THE STUDY

In his painting, 'Weeding flax in Flanders', Emile Claus has succeeded in depicting the drudgery of weeding by hand. Recently, the possibility of observing such labour again in Western Europe has increased with the increasing favour of farming methods which do not use synthetic pesticides. The forces acting to reduce synthetic pesticide inputs range from concerns on impacts of runoff on the environment, and health and safety concerns, to fears concerning the power of multinational chemical corporations and to more undefined spiritual reasons that farming without synthetic inputs is somehow morally better. In Europe the societal demand and perception of a need for less intensive farming methods (coupled with the need for reform the agricultural sector in general) has lead to various national and EU wide policies to increase the proportion of land that is farmed without synthetic inputs (Lucas and Pau Vall 1999, LNV 2000).

A question of major importance, in the face of imposed and voluntary reductions in pesticide use, is how to manage non-crop plants growing in a field with a crop – in other words, how to manage weeds. Such questions are of particular importance for farmers who choose to eschew any use of pesticides and artificial fertilisers, and instead use what are called organic farming methods, or for farmers who do not have any choice but to use hand, animal or mechanical methods of weed control. While weeds can have beneficial uses (Vieyra-Odilon and Vibrans 2001), they can also reduce crop yield and the quality of the harvested product, e.g., due to poisonous seeds. Organic farmers rely mainly on mechanical and hand control, as well as using ecological knowledge to manipulate the agroecosystem so that weed populations are reduced. For example organic farmers may have a more diverse crop rotation and use wide variety of implements such as hoes, harrows, fingerweeders, and flame weeders (Lampkin 1990, Mohler 2001).

Hand-weeding and mechanical control (in the broad sense), however, carry their own costs and risks. While mechanical weed control is more efficient than hand-weeding, its effectiveness depends on the weather, it can damage the crop, cause erosion or damage soil structure, or just may not be possible, such as on steep slopes. Flame weeding, whereby weeds are burned prior to crop emergence requires heavy use of fossil fuels. With regard to hand weeding, finding sufficient labour for hand weed control is more and more difficult, notwithstanding the growth in the world population. In Europe and North America enough more attractive jobs than weeding exist, while in many parts of Africa, for example, migration to urban areas and the HIV/AIDS epidemic is severely reducing the able-bodied population in rural areas (FAO 1995, Mwenya 2000).

As with herbicides, mechanical and hand weed-control both rely on the fact that germinating or emerged weed plants are killed. Weed plants, like any other organism, do not exist independently of their environment, whether biotic or abiotic. Therefore knowledge of an organism's interactions with its environment, i.e. its ecology, and the resulting effects on life-cycle processes such as reproduction, survival and dispersal, can give insights which lead to other means of management and thus lessen the efforts needed for killing plants. Many examples already exist of how knowledge of plant ecology has contributed to weed management. For example, it has long been known that weed plants have windows of germination and emergence (Roberts and Neilson 1980). The sowing date of some crops can be delayed so that seedlings of early germinating weed species can be removed through regular cultivation prior to sowing. Another example is use of the knowledge that when individual plants are crowded by other plants, they do not grow as large and produce fewer seeds. By adjusting crop row spacing or planting another species (e.g., clover) around the crop, weed seed production may be lowered and crop yield increased (Teasdale 1998). If it is known how weed seeds are dispersed, then implements (e.g., harvesters, hoes) can be designed to prevent the seeds from being returned to the soil. Corncockle (*Agrostemma githago*), for example, has disappeared from the European weed flora due to improved crop seed-cleaning techniques, which prevented the weed seeds from being sown again with the crop (Salisbury 1961).

While much has been achieved in weed management through formal and informal knowledge of plant ecology, there is still much to learn, both about the ecology of specific weed species, and about more general principles of how weeds interact with their environment and farmer decisions. On the one hand, detailed knowledge about the ecology of specific weed species may be more likely to lead to direct applications, but is very time consuming to acquire, particularly when one begins to consider the variation that exists within a species. General principles, on the other hand, may be less likely to lead to direct application. The insight they provide, however, can open previously un-thought of avenues for exploration.

OBJECTIVES

Two important research strands in weed ecology are weed-crop competition and weed population dynamics. The former deals with how crowding of weed plants by the crop plant affects weed growth and reproduction, and also reduces negative effects on crop yield. The latter strand is concerned with how the number of weeds changes over time and the factors that influence the changes. A basic measure in examining population dynamics is the population growth rate, i.e., the magnitude of the weed population change (as a fraction or multiple) of the population that was present a year ago. Competition and population dynamics are joined by the fact that competition can affect the weed population growth rate and also the qualitative pattern of the population dynamics, for example whether or not the population shows cyclic behaviour in time. Aspects that have not received sufficient attention within weed ecology are the roles of weed control and farmer strategies regarding crop and weed management. The choices that a farmer makes will affect weed population dynamics, and he or she may also use weed-crop competition deliberately.

Through following and linking these two strands, this thesis seeks to expand the set of weed management options available to practitioners, the set of concepts and methods used by weed ecologists, and to raise questions that should be answered by policymakers. Not every chapter addresses each of these aspects equally – one chapter may address more practical questions, while another is more theoretical in nature. Furthermore, while the immediate motivation for this thesis are the problems faced by Dutch organic farmers, it is hoped that at least parts of this work will be of use to farmers and weed scientists in general, and indeed for managers and researchers concerned with invasive or endangered plant species.

Competition, population dynamics and weed control are broad topics and must necessarily be focused. The three specific objectives of this thesis are therefore to increase understanding of weed population dynamics in crop rotations, particularly with regard to the effect of crop order, to investigate how weed populations may be influenced by competition from the crop and the trade-offs that may occur due to constraints of weed control, and lastly to study factors affecting weed populations on organic farms.

CONTEXT AND APPROACHES: AN OVERVIEW OF THIS THESIS

Within each of the objectives of this thesis exist a multitude of questions and approaches to answering them. Below is an overview of the questions that are posed in Chapters 2 through 5, the context from which they arose, the methods used to answer them, and the resulting conclusions and extensions. In Chapter 6, based on the experience gained in carrying out the studies presented in Chapters 2 to 5, broad perspectives for future research in weed ecology are offered.

The questions treated in Chapters 2 to 5 range from the applied to the theoretical, and consequently the methods range from observational and experimental to the mathematical. And, while the questions may differ substantially, a unifying theme behind them is that a long-term perspective to weed management is imperative. This is because, unlike many crop pests and diseases, weed seeds can remain viable in the soil for substantial amounts of time and therefore seeds produced one year will contribute to future weed populations. One can only make a fair evaluation of weed management strategies by considering the longer-term effects, at the minimum considering what are the consequences for the following growing season. Taking a long-term perspective, however, does not mean that the weed population dynamics are observed or modelled in every chapter. For example in Chapter 3, the goal of the experiment was to minimise weed seed production, but the motivation for the experiment was to reduce weed populations in the long term.

Discovering the problem

In order to be able to start to find strategies and methods for managing weeds on organic farms, it is important first to know what the problem is, whether a problem exists at all, and what are the possible causes of the problem. At least an initial, if only partial understanding, can be achieved by surveying and monitoring weed populations on organic farms, using statistical analysis to investigate whether there is any relationship between the weed population, and various controllable or uncontrollable factors, and lastly by discussing with farmers what their approach to management is. Such is the primary aim of the study presented in Chapter 2. Weeds were monitored on five organic farms for a total of six years (1995, and 1997 to 2001), in every field and the farmers recorded information on weed and crop management.

The analysis presented in Chapter 2 focuses on the factors governing variability in weed diversity and abundance. It was very clear that weed densities were consistently low on certain farms and consistently high on other farms. Farms with many hours of hand-weeding were also the farms with higher weed densities. It appears that the farmers with low weed densities and few hours of hand weeding deliberately take a long-term approach to weed control, for example by removing flowering individuals of certain weed species from grain fields. Farms with high weed densities also had a higher species richness than farms with low weed densities. The apparent trade-off between weed density and diversity raises important questions for policymakers, if they believe that one of the aims of organic farming is to increase biodiversity.

Crop planting patterns to minimise weed seed production

On farm monitoring of weed populations often leads to new questions concerning weed ecology and the interaction with management. During the 1997 survey, two questions arose. The first question was whether it was better to use a wider or narrow row spacing in cereal crops if the criterion for evaluation was the number of seeds produced per seedling at the start of the season. The second question was whether the order of crops in a crop rotation could affect weed population dynamics.

The context for the first question is the method of weed control in spring cereals (wheat, barley, oats), used by many organic farmers, including all but one farmer in the weed monitoring study. Typically a wide row spacing (22-30 cm) is used in order to be able to use a mechanical hoe, which is considered to control weed plants in cereal crops better than other implements. However, because of the wider row spacing it is likely that weed plants will grow larger and produce more seeds than in a narrower row spacing. In a narrow row space, though, more weed plants might survive weed control. Chapter 3 contains the results of an experiment designed to address these questions. By combining data on weed seed production and survival it was possible to calculate seed production per seedling, which is a common currency for comparing the effects of the different treatments. Three weed species were studied: ladysthumb (*Polygonum persicaria*), wild buckwheat (*Polygonum convolvulus*), and common chickweed (*Stellaria media*). The results showed that, taking into account differences in mortality, seed production was lowest in the more narrowly spaced crop. Weed mortality in the wide row spacing would have to increase in order to reach the levels of seed production found in the narrowest row spacing. It seems, therefore, that organic farmers would be better off using a narrow row spacing and less intensive weed control measures. On-farm trials on a wider variety of soils, with other weed species, and higher crop sowing densities would be useful for investigating the wider validity and applicability of the results and for convincing farmers.

The row spacing experiment was unique in comparison to most other studies on weed-crop competition. First the emphasis was on weed seed production rather than on plant densities as the criteria for evaluating different treatments. Secondly, the experiment focused on survival and reproduction of individual weed plants. Most weed-crop competition studies have focused on plant density and when weed mass has been measured, it has usually been on a unit area basis, rather than on an individual basis. An important disadvantage of making measurements on a unit area basis is that knowledge of the variability between individuals is lost. As it is individuals that interact with the local environment (biotic and abiotic), an understanding of the variability between individuals is crucial for evaluation and developing weed management strategies cf. (Harper 1964).

Predicting individual weed mass and survival

In the row spacing experiment presented in Chapter 3, the individual as the unit of reference arose naturally from the criterion that weed seeds should not replace themselves. While such a perspective necessarily resulted in a laborious experiment, one of the advantages was that it was possible to investigate whether there was a relationship between the local environment of a weed plant, its mass (a measure of potential reproductive output) and chance of survival. By understanding which weed plants contribute most to future generations and how their performance is related to their local environment, it may be possible, for example, to find optimal combinations of crop row spacing and mechanical control or to answer such questions as whether different crop planting patterns lead to different weed spatial patterns.

Descriptors of the local environment include the local density of crop plants around a target weed plant, its distance to the nearest crop plant, or direct measures of resource availability. In the row spacing experiment described in Chapter 3, measurements were made of the distance between each weed plant and the nearest crop plant. In Chapter 4, these descriptors of the local environment were used to form statistical predictors of individual weed plant mass and survival, such as those found by Weiner (1982) and Silander and Pacala (1985). Using logistic regression, it was found that individual weed mortality increased with increasing distance from the crop row only in the widest row spacing treatments, where hoeing could be carried out.

With regard to plant mass, the same form of the predictor (of 32 tested predictors) gave the best fit for all three species studied, even though the growth habits of each species were different. The predictor had a linear form (in the parameters), with the distance measures squared, $w = b_0 + b_1 u^2 + b_2 v^2$, where w is the predicted mass of a plant, u is its distance to the nearest crop plant, v is the crop row spacing where the plant is located, and the b_i are parameters estimated from the data. While this linear form is applicable only for a limited range of distances, because plants will not grow to an infinite size as distance increases, it is not likely that the distances in a cereal crop will be much larger than those measured in the experiment. Furthermore, this model is intuitively satisfying because one might expect that the amount of resources available (particularly light) would be related to the area available, i.e., distance squared.

Crop rotations and weed population dynamics

In Chapter 5, the second question raised by studying on-farm weed populations is addressed, namely does the order of crops in a rotation affect weed population dynamics. It is known that crop rotations with a higher diversity of crops tend to have less weed problems (Leighty 1938, Fream and Robinson 1949). Furthermore the farms in the survey were required to follow a crop rotation that alternated mown crops (cereals, legumes) with lifted crops (potatoes, onion, carrots). A natural question is whether such a rotation is necessarily the best one, considering that seeds produced during the years of a mowed crop may lead to an increase in the hours of hand weeding needed during the following year of lifted crops. Experimental studies of the effects of crop rotations on weed populations have tended to focus on comparing monocultures with a crop rotation and possibly the interaction with different tillage methods (Kegode et al. 1999, Blackshaw et al. 2001). Frequently the analysis in such studies has focused on determining which treatment had the largest effect at the end of the last crop in the rotation cycle, rather than on whether the weed population has increased or decreased over a complete rotation cycle. In comparing different rotations it is possible that the weed population size will be much larger in one crop than in another crop.

One approach towards answering the question of whether the order of crops matters for weed population dynamics is to use a mathematical model of how a weed population changes over time in a crop rotation. A mathematical model necessarily involves many simplifications. However, because the assumptions and structure of the model are known, with enough effort it is possible to explain the results fully. This does not imply that the results will reflect reality, but the insights gained can lead to new ideas for management and to more focused experiments.

Using a model of weed seedbank population dynamics, we showed that the order of crops in a rotation affects the weed population growth rate and its sensitivity to changes in underlying parameter values. In this periodic matrix model, the seed population was structured by depth in the soil, i.e., seeds at different depths could differ in their ability to germinate, reproduce or survive. A variety of rotations were examined, all based on two crops, one in which the population declined and the other in which it increased. By examining the reproductive value and stable depth distribution of seeds in the different rotations, it was possible to explain how the differences in growth rates and elasticities (proportional sensitivities) arose.

Some of the implications for weed management are that it is important to consider crop order when designing a crop rotation and when making changes to weed management strategies within a crop. The long-term impact on the population growth rate of a proportional change in weed survival, for example, may depend on both the crop in which this change is made and the position that a given crop holds in the cycle. It is also likely that weed population size and short-term dynamics will be affected by the interaction of initial conditions (the distribution of seeds over the soil) and the crop with which a new rotation is started. Such effects will be investigated both theoretically and experimentally in an upcoming project.

While periodic matrix models have been applied to organisms in natural ecosystems (Gotelli 1991, Hoffmann 1999), there has been little systematic examination of the effects of different orders of events (fire, flooding, grazing) on population growth rates or possibilities for management, rather the focus has been on randomly recurring events. As the results from this analysis show, it would be useful for researchers and managers of other ecosystems to consider effects of event order and how differences in population growth rates arise.

CHAPTER 2

Variability in Weed Species Diversity and Abundance: Results from Monitoring Annual Broadleaf Weeds on Five Organic Farms

ABSTRACT

Knowledge of the variability of weed diversity and abundance on farms and the relation with management practices is critical for identifying potential weed problems, evaluating the effectiveness of current management strategies, discovering new strategies developed by farmers, and for clarifying decisions that must be taken by policymakers. Addressing these issues is particularly important in organic farming systems, due to the high costs of hand weed control and loss of yield due to weeds. Regular monitoring of weeds on the same group farms, which are on the same soil type and using a similar rotation, allows investigation of the effects of year and also of weed population changes over time. For the years 1995, and 1997 through 2001, weed populations were monitored at the end of the season on every field on five organic farms in the Netherlands and weed management information was collected from the farmers. There were differences between farms in weed species diversity and abundance, and in the amount of mechanical and hand weed control applied. *Stellaria media* was by far the most dominant species, with a relative abundance close to one and median densities of about 10 plants m^{-2}. Farms with low weed species diversity had low densities and few hours of hand-weeding. The factors farm, crop, and hand and mechanical weed control explained variation in weed densities. Cereal and potato crops had the highest densities, while grass-clover, onion, and carrot crops had the lowest densities. Weed densities declined with increasing number of mechanical control operations. Weed densities and hours of hand weed control were positively correlated, reflecting densities at the start of the season. This study raises questions concerning trade-offs between low weed densities and increased species richness, and concerning the strategies farmers use for weed management.

Adapted from: Mertens, S. K. Variability in weed species diversity and abundance, and growth rates: results from six years of monitoring annual broadleaf weeds on five organic farms. In preparation.

INTRODUCTION

When a population is in need of management, whether because it is on the edge of extinction due to human causes or because it interferes with the functioning of another ecosystem, then it is critical to understand the underlying causes of natural fluctuations in the population size, the interactions with exogenous interference and the consequences for management. Examples of the former are fisheries on the verge of collapse (Myers et al. 1997), while examples of the latter are invasive exotic plants (Zavaleta et al. 2001) or, according to most farmers, weeds in an agro-ecosystem. Variability at the community or individual level can also be of importance. For example, do management strategies increase species diversity or change the species composition? Or, are individuals of a certain genotype selected by repeated application of a certain management tactic? Management itself can be a cause of variability of populations and depending on its effect, different adjustments to future management may be necessary.

Non-crop plants, i.e. weeds, growing in competition with crop plants are an example of a group of organisms in need of management. While weeds can play a beneficial role (Datta and Banerjee 1979, Vieyra-Odilon and Vibrans 2001), too many of them at the wrong time or place will cause unacceptable loss of yield (Parker and Fryer 1975, Bridges and Anderson 1992), while controlling them creates other costs (Akobundo 1990, Chandler 1991). It is therefore crucial to determine how variable weed populations are, what the sources of variability are, and whether it is possible to manipulate the factors determining variability. In considering weeds in agro-ecosystems, one may be interested in variability in species composition and diversity, in population abundances of a species or a group of species, or one may be interested in genetic or phenotypic variability. Because farmers are a population in themselves, variability in weed management strategies and the interaction with weed diversity and abundance is also of interest.

Depending on the comparisons one chooses to make, one will always find differences. For example if one compares a desert and coral reef, one will surely find variation in species diversity and abundance. Likewise, if one compares the diversity and abundance of weeds on farms where herbicides are being used, with those on farms where herbicides are not being used, the species diversity, composition and abundances are also likely to differ and the reasons may be rather clear and easily testable in an experiment. A rather more interesting question is how variable weed communities and population abundances are over time on a set of farms, which are on similar soil types and using similar approaches to crop production.

Understanding variability in weed species diversity and abundance over time and between farms is particularly important with regard to farming systems where synthetic pesticides are not used, i.e., 'organic' farming systems. At a political level, a government may want to promote organic farming with the aim of increasing species diversity. At an economic level, organic farmers may be faced with high costs of hand weed control. Relevant questions are: Do organic farms have higher levels of plant species diversity? Do trade-offs exist between species diversity and abundance? Do all organic farms have the same levels of weed abundances? Are populations increasing or decreasing? Is there a relationship between management strategies and population densities and growth rates?

Surveys and regular monitoring of weed communities and populations can provide answers to these questions. While elucidating causes and effects is more difficult than in an experimental setting, on-farm studies can lead to new insights concerning factors of importance as well as lend or remove support for existing theories on factors governing weed populations (Derksen 1996). Importantly, more information on the range of variability in weed abundance and diversity is available.

Most investigations of on-farm weed populations have taken the form of surveys whose aims were either to identify problematic or potentially problematic species (Froud-Williams and Chancellor 1982, Lemerle et al. 2001) or to investigate effects of management or environmental variables on the weed community (Saavedra et al. 1990, Andreasen and Streibig 1991). Occasionally a survey may be repeated in order to discern broad trends in weed populations, such as shifts in species composition (Thomas 1991, McWhorter 1993, van Acker et al. 2000). Typically each edition of the survey uses a different set of fields, so that changes in weed populations at the field level are not discernible. There is an implicit assumption that a region has an "average" management strategy and that the farmers change their strategies in a similar way over time.

There are very few examples of monitoring of on-farm weed populations on the same fields over time. An exception is a study by Davies and colleagues (1997), where the populations of weed seedbanks and plant densities were monitored twice during the conversion period of two organic farms. The closest comparable studies have been experiments to compare various aspects of different types of farming systems. In these studies (Dessaint et al. 1992, Marshall and Arnold 1994, Mayor and Dessaint 1998, Squire et al. 2000), an effort has been made to keep methods similar to on-farm practices for each type of farming system and weed seedbank or plant densities were monitored regularly during the course of the experiment. However, as the aim of these studies was to compare different farming systems, very little information was available on the variability in weed populations and communities within a farming system.

In 1995, a survey was carried out on organic farms in the Netherlands in order to identify which weed species were the most problematic (i.e., contributing most to the time spent hand-weeding) and whether there was any relationship with the management strategies being used (Schotveld and Kloen 1996). In 1997, the survey was repeated for the annual broadleaf population in the same fields in order to determine whether the populations differed between years. In order to determine whether weed populations were increasing or decreasing and to have more data to investigate the effects of management, the survey was continued until 2001. The purpose of this chapter is to describe the broad differences between farms in weed diversity, abundance and management practices, and to investigate the factors contributing to variability in weed abundances. Future analysis of the data will consider the effects on growth rates of the weed populations.

METHODS AND MATERIALS

Background to the project

Monitoring of weed populations on the farms began in 1995 with monthly observations of populations of blooming and seed-setting weeds on each of the farms (Schotveld and Kloen 1996). In 1997 the monthly observations were repeated, however the density of vegetative as well as blooming and seed-setting plants were monitored (Mertens 1998). In 1998 a decision was made to continue monitoring the weed populations, but to limit observations to August only.

The five farms in the weed monitoring project formed part of a larger project on developing 'prototype' or model methods for organic farming (Vereijken et al. 1994) and in which a multitude of aspects of the farming system were monitored. The farms were selected for inclusion in the prototyping project on the basis of the farmers' interest in following a prescribed rotation. The project was limited to farms in the Flevoland region. When weed monitoring was re-initiated in 1997, only the five farms that had been in the prototyping project the longest were selected.

Study sites

Geographical region

All farms in the survey were located in the central clay region of the Netherlands, at about 52° North and 5° East, in the province of Flevoland. The soils in the region are marine clays with varying fractions of sand. The entire area consists

Table 1. Background information on farms in the survey.

Farm	Area (ha)	Year of conversion to organic management	Farm type
3	42.9	1991	Commercial
5	25.5	1990	Commercial
6	34.9	1990	Commercial
8	32.3	1990	Commercial
9	22.8	1979	Research

of polders, land that was claimed from the sea through dike construction and drainage. Three of the farms are located on the Noord-Oost Polder, which was opened in 1942 and two farms are located in the Oostelijk Flevoland Polder, which was opened in 1957. The topography is flat and the elevation ranges from about sea level to several meters below sea level.

General description of farms

Organic farming methods were used on all farms and therefore pesticides and synthetic fertilisers were not applied. Four of the farms were arable and Farm 8 had a beef herd, although the cattle were not grazed on-site (Table 1). The area of these farms ranged from about 23 to 43 ha. When weed monitoring was initiated in 1995, the farms were following a prescribed rotation (Vereijken et al. 1994, Vereijken et al. 1995) which consisted of alternating mown type crops with root or row vegetables. There was some flexibility in choice of crops. The main crops were potatoes, carrots, onions, cereals, and legumes (Table 2), and two farms incorporated a grass-clover crop in their rotation. Some crops, particularly legumes had often been harvested before weeds were monitored. During 2000-2001, two of the farms experienced large changes (loss or acquisition of land) which resulted in changes to their rotations, and another farmer started to include lettuce in his rotation. While there were patterns in the sequence of crops found on each farm, there were relatively few fields where the rotations in 2001 began with the same crops as in 1995. Table A1 (Appendix) lists the crops grown on each field for the period 1995-2001.

Monitoring Procedure

Weed populations

Weeds were monitored in 10 quadrats arranged along a diagonal transect in each field. The quadrats had an area of 1 m^2, however different shapes were used in order to maintain the same proportion of crop row to inter-row space found in the field as a whole. The quadrats were spaced approximately 25 meters apart. Each year the transects were in approximately the same place.

Factors influencing weed densities

Screening for important factors. Factors influencing weed densities were investigated by fitting a linear mixed-effects model of all *a priori* selected factors that could be influencing weed densities. These factors were farm, year, crop, hours of hand-weeding and number of mechanical control operations, and interactions between crop and weed control (both mechanical and hand-weeding). The random component of the model was fields within farms. Factors with $p \leq 0.1$ were excluded from the model in a stepwise fashion. Once a model including only important factors was achieved, contrasts between factor levels were investigated. The model was fit in the statistical package R, using the linear mixed-effects function (lme).

Effects of the factors were investigated for blooming and total average densities per field of *S. media* and of the other species excluding *S. media*. The data were log-transformed in order to satisfy the assumptions of normality. However, because there were quadrats with densities of zero, a constant had to be added. In order to determine which constant would yield residuals that fulfilled the assumption of normality, preliminary fitting of the models with different constants was carried out in order to examine which constant would be most appropriate for the analysis of each data set.

The full model was first fit using the coarsest level of grouping the crops (level 2), which required only four degrees of freedom. At several stages in the analysis, the effect of using the lower level of grouping (level 1) was analysed by comparing the Aikake Information Criterion (AIC) values of models with the two different levels of grouping. At any point in the analysis, if a more detailed level yielded a lower AIC, then the model selection procedure was repeated, using the level 1 crop grouping. The AIC is a measure of the amount of information in the data that is explained by the model and takes into account the number of parameters fitted (Burnham and Anderson 1998). It is calculated as $-2\ell + 2p$, where ℓ is the log-likelihood resulting from fitting the data and p is the number of parameters in the model. The lower the AIC, the better the fit of the model.

Investigating the effects of factor levels. After the most parsimonious model was found, the effects of the various factors were investigated by examining the coefficients of the models. For the factors other than farm, the coefficients were tabulated to show the contrasts between the different levels of each factor (e.g., differences between years or crops). In tabulating the contrasts, the aim was to identify general patterns, for example that one crop generally has a higher weed density than other crops. The structure of the data is too unbalanced to draw inferences concerning the value of particular factor levels. An absolute *t*-value greater than 2 was used as a guide to which factor levels are 'important' (the critical *t*-value for a 5% significance level is 1.96).

RESULTS

Patterns in weed abundance diversity and management

Over the six years of the survey a total of 25 species were observed. *S. media*, with an average density close to 18 plants m^{-2}, was by far the dominant species (Table 3). No other species had average densities above 1. *S. media* was also the most abundant species on each farm with average densities ranging from 10 to 32 plants m^{-2} (Table A2 in Appendix). Considering the dominance of *S. media*, for the remainder of the descriptive statistics, results are presented on the total weed densities on each farm with and without *S. media*.

Table 3. Mean density and standard deviation per plot, averaged over fields, farms and year.

Species	Density (m^{-2})
Capsella bursa-pastoris (L.) Medicus	0.662 (3.410)
Cardamine hirsuta L.	0.002 (0.063)
Chenopodium spp.	0.151 (0.749)
Galeopsis tetrahit L.	0.001 (0.032)
Galium aparine L.	0.001 (0.032)
Galingsoga parviflora Cav.	0.001 (0.032)
Lamium spp.	0.050 (0.759)
Matricaria discoidea DC.	0.195 (1.485)
Myosotis arvensis (L.) Hill	0.001 (0.032)
Oenothera biennis (L.)	0.014 (0.164)
Plantago spp.	0.021 (0.207)
Polygonum aviculare L.	0.098 (0.561)
Polygonum convolvulus L.	0.052 (0.354)
Polygonum persicaria L.	0.115 (0.837)
Ranuculus sceleraturs L.	0.201 (1.722)
Rorippa palustris (L.) Besser	0.151 (0.848)
Senecio vulgaris L.	0.851 (10.66)
Sinapis arvensis L.	0.001 (0.032)
Solanum nigrum L.	0.313 (1.849)
Sonchus asper (L.) Hill	0.663 (3.382)
Stellaria media (L.) Vill.	17.852 (36.129)
Taraxacum officinalis Web.	0.375 (2.170)
Thlaspi arvense L.	0.033 (0.397)
Urtica urens L.	0.306 (3.454)
Veronica persica Poiret	0.466 (4.928)

Table 4. Summary statistics on weed species diversity, density, and weed control.

	Species diversity		Total weed density		Blooming weed density		Weed control	
Farm	Mean	Total	+ *S. media*	− *S. media*	+ *S. media*	− *S. media*	Hand	Mechanical
	—number—		———number m^{-2}———				hours ha^{-1}	—number—
3	12.6	18	19.9	2.6	4.2	0.3	32.8	4.1
	(2.1)		(26.0)	(3.4)	(4.7)	(0.6)	(37.6)	(1.5)
5	16.4	20	42.4	9.7	8.7	1.0	81.6	3.5
	(3.0)		(40.2)	(14.0)	(8.2)	(1.7)	(99.7)	(1.6)
6	11.2	15	14.8	4.7	3.6	0.4	30.5	3.5
	(1.3)		(12.3)	(6.3)	(4.6)	(0.7)	(41.4)	(1.4)
8	8.0	15	19.4	0.7	9.8	0.1	14.0	1.6
	(2.0)		(37.8)	(1.1)	(24.4)	(0.3)	(16.8)	(1.4)
9	14.2	21	16.9	6.3	6.2	1.8	47.1	4.7
	(3.4)		(30.0)	(15.6)	(14.1)	(4.1)	(72.7)	(2.9)

Viewed from a variety of angles, several patterns emerge with regard to differences between farms. Farm 8 had the lowest number of species observed per year, by far the lowest total and blooming weed densities when *S. media* was excluded, and the fewest mean hours of hand-weeding and number of mechanical control operations (Table 4). When *S. media* was taken into account, the average weed density on Farm 8 was much higher, and no longer the lowest of all farms. Farms 5 and 9 were at the other end of the spectrum, with higher number of species observed, high densities of blooming plants, and more hours of hand-weeding and mechanical control operations. Farm 5, though, had high total weed densities, while those on Farm 9 were relatively low.

The high average for total weed densities on Farm 8 can be explained by examining the boxplots of the total and blooming densities for all species (Fig. 1). Because of the skewed nature of the data, the densities have been plotted on the log scale. The median total density on Farm 8 (Fig 1a) is the lowest of all farms. The high average densities on Farm 8 are therefore due to a few fields with very high densities, and which were composed mainly of *S. media* (compare Fig. 1a-b with Fig. 1c-d). Farm 5 remained as the farm with the highest densities in all categories.

Rank-abundance diagrams indicate how evenly total abundance (over all species) is shared by the various species present on a farm (Fig. 2). If there are equal numbers of each species, then points will fall on a horizontal line when a random ranking is assigned to the species. The more negative the slope of the line drawn through the points, the more unequal the distribution of species. Farm 8 again stands out as being the farm with the most uneven distribution of species, while Farm 9 has the most even distribution. Within farms, there appear to be differences between years

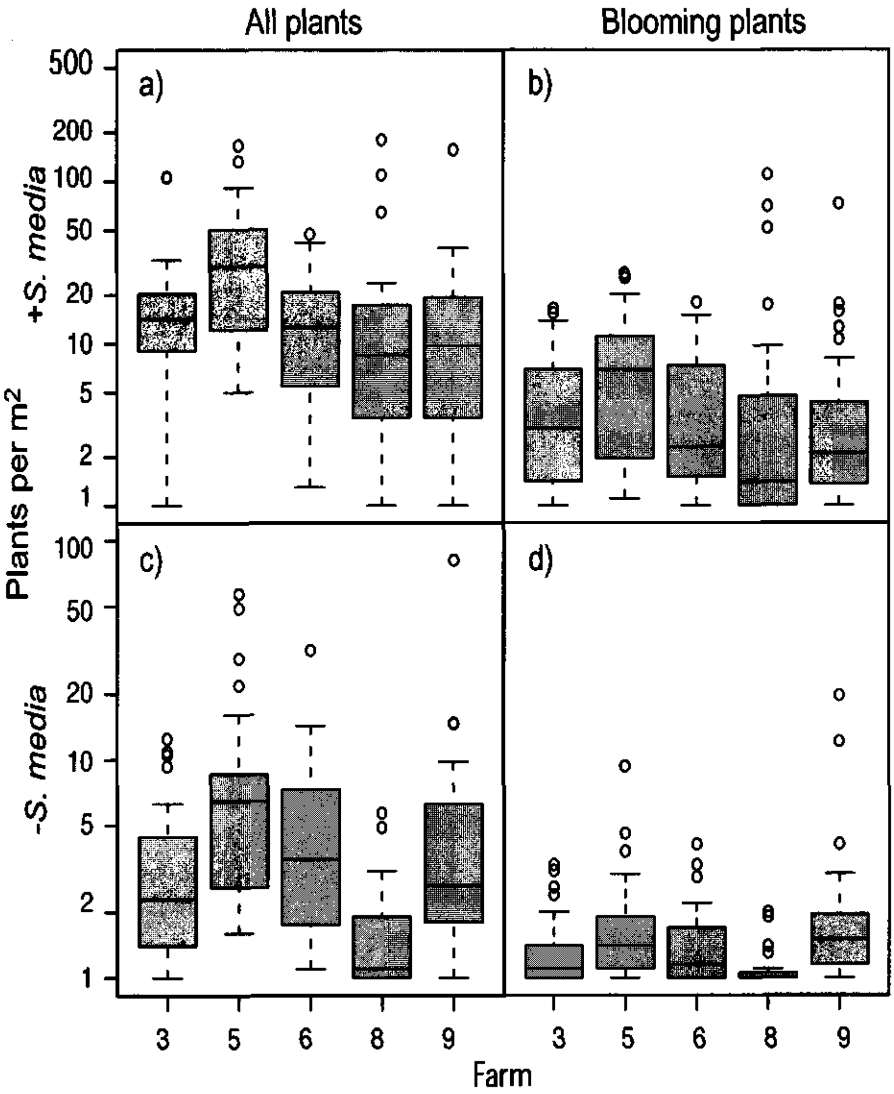

Fig. 1. Box plots of weed densities (log scale) per field, with and without *S. media* populations.

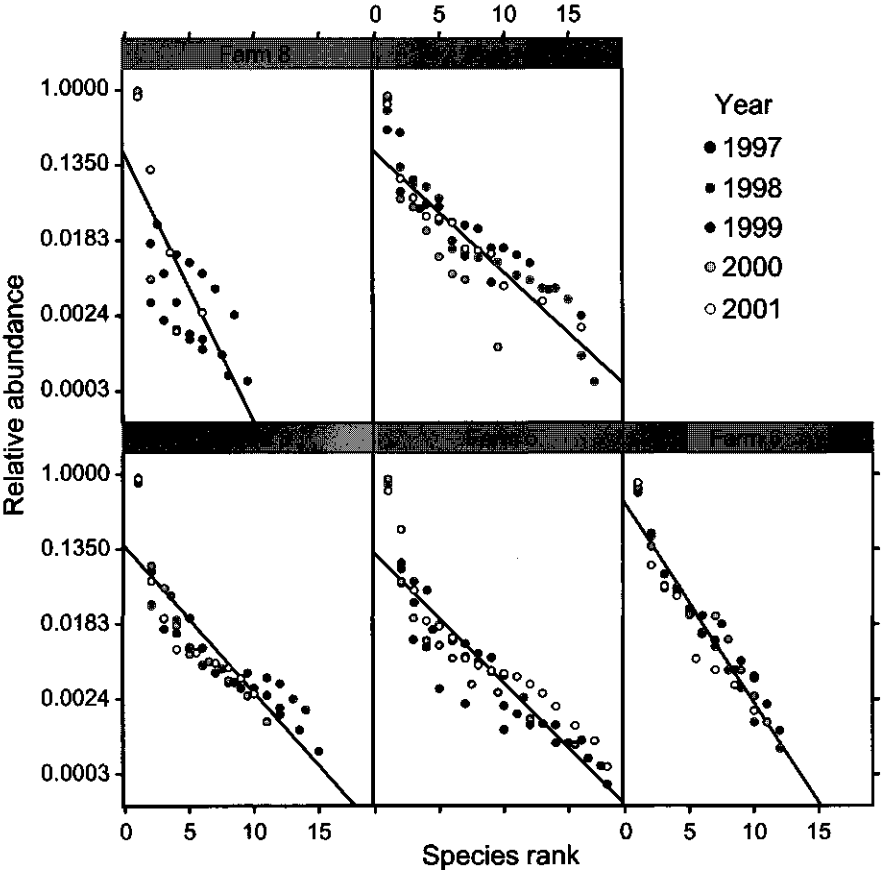

Fig. 2. Rank-abundance diagrams. Relative abundance and ranks averaged over year each farm, where abundance was the mean over all fields.

in species richness and evenness. This may in part be due to differences in the number of fields and the type of crops monitored in a given year.

Compared to other species, *S. media* was much more evenly distributed over quadrats, as it occurred in a large fraction of quadrats (Fig. 3), and its mean density, given that it occurred, was much higher than for the other species. On Farms 3 and 8 most of the other species occurred on a small fraction of the quadrats, whereas on the other farms more species were found on a higher fraction of quadrats. The occurrence density also tended to be higher as the fraction of plots with a species increased. Some species on each farm were rather clumped – they occurred on a small fraction of quadrats but their occurrence density was relatively high. These clumped species differed from farm to farm.

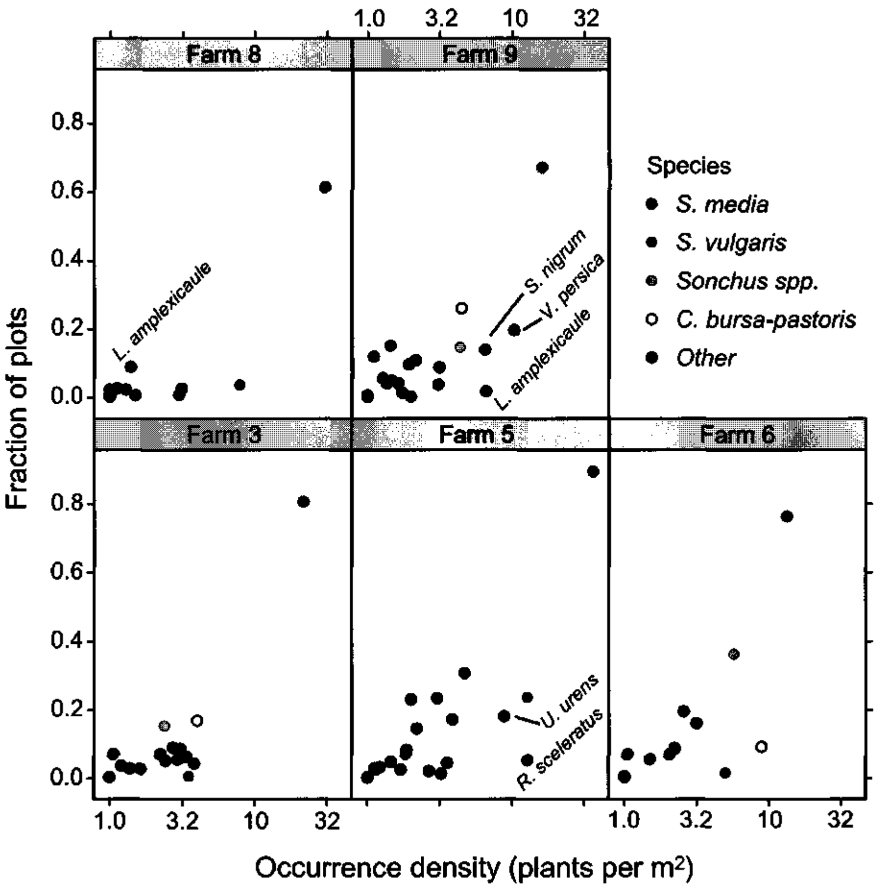

Fig. 3. Mean weed density of each species per plot, given that the species occurs on the plot, against the fraction of plots with the species.

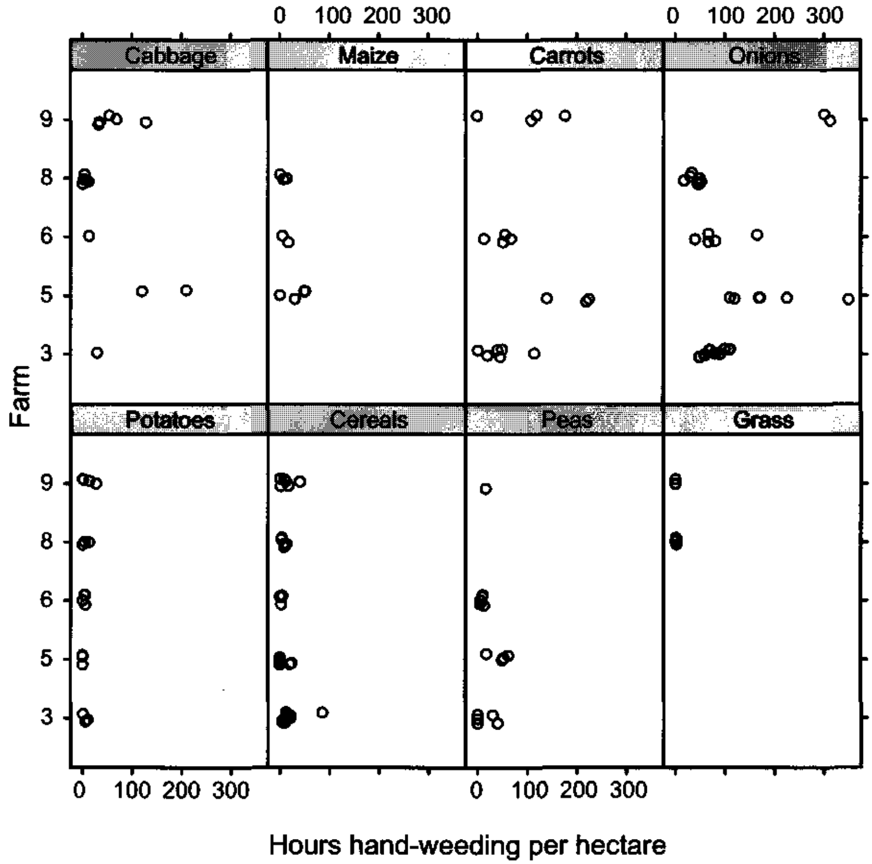

Fig. 4. Dot plots of hand-weeding on each farm for each crop type (level 1 grouping). Vertical random jitter has been added to increase visibility of overlying points. Not all crop types were grown on each farm.

Hand-weeding was concentrated in carrot- and onion-like crops (Fig. 4), and no hand-weeding was carried out in grass-clover crops. Levels of hand-weeding were also low in potato and cereal crops. The number of mechanical control operations was lowest in grass-clover crops and also tended to be lower in potato crops (Fig. 5). In cereal crops, Farm 8 carried out no mechanical control and Farm 9 consistently had the highest number of control operations.

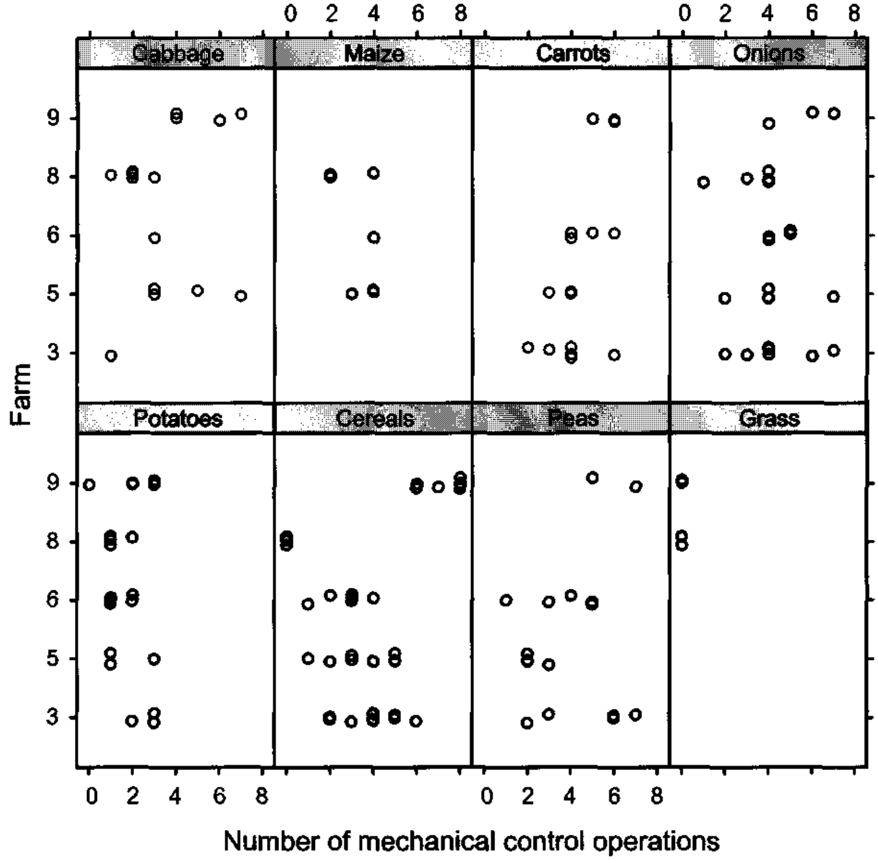

Fig. 5. Dot plots of mechanical control operations on each farm for each crop type (level 1 grouping). Vertical random jitter has been added to increase visibility of overlying points. Not all crop types were grown on each farm.

Factors influencing weed densities

The factors with important effects on weed densities varied slightly between the four groups of data (populations of all and blooming/seed-setting plants, with and without *S. media* – Table 5). For example, there were effects of mechanical control and hand-weeding on both total and blooming populations of *S. media*. For the populations of other weed species, there was an effect of hand-weeding only for the blooming population and no effect of mechanical control on either the total or blooming population. A better fit was achieved by the more fine level of crop

Table 5. Results of screening data for important effects. Results are given only for factors with $p \leq 0.1$. No interactions were found between crop group and hand-weeding or mechanical control.

	Total population				Blooming population			
	S. media		Other species		*S. media*		Other species	
Factor	F	*p*-value (df)	F	*p*-value (df)	F	*p*-value (df)	F	*p*-value (df)
Intercept	307.5	<0.000 (1, 97)	1.6	0.2080 (1, 95)	154.4	<0.0001 (1, 122)	192.2	<0.0001 (1, 127)
Farm	2.6	0.0589 (4, 25)	14.9	<0.0001 (4, 25)	1.7	0.1798 (4, 25)	9.7	<0.0001 (4, 127)
Year	6.0	0.0002 (4, 97)	4.6	0.0021 (4, 95)	8.2	<0.0001 (5, 122)	–	–
Crop group 1	–	–	7.4	<0.0001 (7, 95)	10.4	<0.0001 (7, 122)	6.2	<0.0001 (7, 127)
Crop group 2	3.8	0.0121 (1, 97)	–	–	–	–	–	–
Mechanical control	7.8	0.0064 (1, 97)	–	–	6.4	0.0129 (1, 122)	–	–
Hand-weeding	3.4	0.0678 (1, 97)	–	–	–	–	5.2	0.0146 (1, 127)
Time of observation[a]	–	–	–	–	2.8	0.0971 (1, 122)	5.7	0.0183 (1, 127)

[a] Relative to time of crop harvest

grouping (see Table 2) for all populations, except the total population of *S. media.* The effect of farm was most important for the total and blooming population of *S. media.* There was some effect of time of observation relative to harvest time only for the blooming populations, and particularly for the population of species other than *S. media.*

The coefficients for hours of hand-weeding were positive but small, such that weed densities and hours of hand-weeding were found to be slightly correlated (Table 6). On the other hand, the coefficients for mechanical control were negative, indicating that fewer weeds were found as the number of mechanical weed control operations increased. Densities of blooming plants were slightly smaller as the time

Table 6. Coefficients for hours of hand weeding and number of mechanical control operations.

		Hours hand-weeding		Mechanical control operations		Time of observation relative to harvest	
	df	Coefficient (St. error)	t-statistic (*p*-value)	Coefficient (St. error)	*t*-statistic (*p*-value)	Coefficient (St. error)	*t*-statistic (*p*-value)
S. media total	97	0.0038 (0.0020)	1.8473 (0.0678)	−0.1725 (0.0574)	−3.0073 (0.0034)	–	–
S. media blooming	121	–	–	−0.1044 (0.0433)	−2.4041 (0.0178)	−0.0056 (0.0033)	−1.6720 (0.0971)
Other species blooming	127	0.0055 (0.0023)	2.3460 (0.0205)	–	–	−0.0131 (0.0055)	−2.3904 (0.0183)

Table 7. Contrasts and *t*-values (in parentheses) for the factor *crop*. The contrasts give the effect of year in a row relative to the year heading each column. Results are given for models where *crop* had $p \leq 0.1$.

	S. media					Other species				
value	1995	1997	1998	1999	2000	1995	1997	1998	1999	2000
					Total population					
1997	–	–	–	–	–	–	–	–	–	–
1998	–	0.749 (3.02)	–	–	–	–	0.335 (0.968)	–	–	–
1999	–	–0.298 (–1.169)	–1.047 (–4.145)	–	–	–	–0.864 (–2.429)	–1.199 (–3.312)	–	–
2000	–	0.605 (2.288)	–0.144 (–0.544)	0.904 (3.391)	-	–	–0.264 (–0.704)	–0.599 (–1.570)	0.600 (1.576)	–
2001	–	–0.059 (–0.234)	–0.808 (–3.261)	0.24 (0.946)	–0.664 (–2.517)	–	–0.359 (–1.014)	–0.694 (–1.926)	0.505 (1.357)	–0.096 (–0.253)
					Blooming population					
1997	0.570 (2.878)	–	–	–	–	–	–	–	–	–
1998	1.295 (6.546)	0.7255 (3.694)	–	–	–	–	–	–	–	–
1999	0.762 (3.814)	0.1919 (0.951)	–0.534 (–2.618)	–	–	–	–	–	–	–
2000	0.485 (2.308)	–0.0843 (–0.402)	–0.810 (–3.778)	–0.276 (–1.287)	–	–	–	–	–	–
2001	0.534 (2.659)	–0.035 (–0.170)	–0.761 (–3.662)	–0.2271 (–1.077)	0.049 (0.226)	–	–	–	–	–

interval between observation and harvest increased. Using the *t*-values as a rough guide for the importance of contrasts between the levels of the categorical variables (year and crop), most differences between years were found for the total population of *S. media* (Table 7). In general, 1998 appears to have had higher weed densities, but the effect was important only for the *S. media* population. The important effect of year in 1995 is due to the counting method used in 1995, such that when densities were higher than four plants per m^2, they density class was five plants per m^2. With regard to contrasts between crops (Table 8), in all four populations potatoes and cereals had more weeds than other crops and grass-clover crops had fewer weeds than other crops. Carrot and onion crops also tended to have fewer weeds than most other crops. The contrasts for the blooming population of the species other than *S. media* were less strong, in part due to the high proportion of observations with zero density.

Table 8. Contrasts and *t*-values (in parentheses) for the factor year. The contrasts give the effect of a crop in a row relative to the crop heading each column. The number of contrasts for the total population of *S. media* is lower because the coarse crop grouping level gave a (level 2) better fit (see Table 2 for the crop grouping levels).

	S. media							Other species						
Crop	Potatoes	Cereals	Legumes	Grass	Cabbage	Maize	Carrots	Potatoes	Cereals	Legumes	Grass	Cabbage	Maize	Carrots
	Total population													
Cereals	0.087 (0.373)	–	–	–	–	–	–	−1.0401 (−2.5586)	–	–	–	–	–	–
Legumes	−1.17 (−2.875)	−1.257 (−2.838)	–	–	–	–	–	−1.0324 (−2.1636)	0.0077 (0.0174)	–	–	–	–	–
Grass	−0.587 (−2.154)	−0.674 (−2.725)	–	0.584 (1.234)	–	–	–	−3.5752 (−6.0935)	−2.5351 (−4.4981)	−2.5427 (−4.0357)	-	–	–	–
Cabbage	–	–	–	–	–	–	–	−2.4444 (−4.9528)	−1.4043 (−3.1139)	−1.412 (−2.6342)	1.1308 (1.9099)	–	–	–
Maize	–	–	–	–	–	–	–	−0.8816 (−1.6365)	0.1585 (0.3119)	0.1509 (0.2585)	2.6936 (4.0097)	1.5628 (2.6858)	–	–
Carrots	–	–	–	–	–	–	–	−1.8998 (−4.0577)	−0.8597 (−2.065)	−0.8674 (−1.7596)	1.6754 (2.6976)	0.5446 (1.0368)	−1.0182 (−1.8063)	–
Onions	–	–	–	–	–	–	–	−0.9781 (−2.3304)	0.062 (0.1656)	0.0543 (0.1204)	2.597 (4.5185)	1.4663 (3.1216)	−0.0966 (−0.1864)	0.9217 (2.0672)

Table 8. continued.

	S. media							Other species						
Crop	Potatoes	Cereals	Legumes	Grass	Cabbage	Maize	Carrots	Potatoes	Cereals	Legumes	Grass	Cabbage	Maize	Carrots
	Blooming population													
Cereals	0.4659	–	–	–	–	–	–	–0.058	–	–	–	–	–	–
	(2.1149)							(–0.166)						
Legumes	–0.3588	–0.8247	–	–	–	–	–	–0.539	–0.481	–	–	–	–	–
	(–1.3719)	(–3.6228)						(–1.274)	(–1.258)					
Grass	–1.3429	–1.8088	–0.9841	–	–	–	–	–2.068	–2.01	–1.529	–	–	–	–
	(–4.1656)	(–5.3275	(–2.6468)					(–3.884	(–3.915)	(–2.673)				
Cabbage	–0.054	–0.5199	0.3048	1.2889	–	–	–	–1.194	–1.136	–0.655	0.8739	–	–	–
	(–0.1865)	(–1.8962)	(1.0064)	(3.6319)				(–2.493)	(–2.445)	(–1.293)	(1.5621)			
Maize	–0.3222	–0.7881	0.0366	1.0207	–0.2682	–	–	–0.879	–0.821	–0.34	1.1891	0.3152	–	–
	(–1.0494)	(–2.7512)	(0.115)	(2.5928)	(–0.8615)			(–1.759)	(–1.711)	(–0.644)	(1.9665)	(0.6098)		
Carrots	–0.5754	–1.0413	–0.2166	0.7675	–0.5214	–0.2532	–	–1.267	–1.209	–0.728	0.8008	–0.073	–0.388	–
	(–2.0731)	(–4.1809)	(–0.7816)	(2.0692)	(–1.985)	(–0.84)		(–2.715)	(–2.74)	(–1.536)	(1.3822)	(–0.164)	(–0.743)	
Onions	–0.4305	–0.8964	–0.0717	0.9124	–0.3765	–0.1083	0.1449	–1.26	–1.202	–0.721	0.8078	–0.066	–0.381	0.0069
	(–1.7685)	(–4.4096)	(–0.298)	(2.582)	(–1.483)	(–0.3869)	(0.6163)	(–2.884)	(–2.975)	(–1.591)	(1.4451)	(–0.149)	(–0.756)	(0.0173)

DISCUSSION

The aim of this paper has been to describe variability in weed diversity, abundance, and management practices and to explore the relation between weed densities and factors such as farm, year, choice of crop, hours of hand-weeding, and number of mechanical control operations. The results show that there is variation due to farm, year, and management practices. However, because factors affecting weed densities are intertwined, for example crop choice will influence the management options, it is difficult to unravel cause and effect. Examining the relationships from various angles and using anecdotal information from the farmers, it is possible to identify likely relations and to provide avenues for management, particularly through raising questions about the aims of management.

Community aspects

A frequently used argument for supporting policies to reduce use of herbicides and to encourage organic farming, is that such practices will contribute to increasing biodiversity (Kleijn et al. 2001, LNV 2002). There is evidence that higher use of herbicides does lead to reduced number of weed species (Ebregt et al. 1988, Crawley 1997, Squire et al. 2000, Mäder et al. 2002). An important question is whether it is possible to have a high level of weed species diversity and still maintain weed densities at low enough levels so that a farmer is able to reach financial targets. From the observations on these farms, it appears that weed diversity is positively correlated with weed density. The level of diversity may still be higher than that found on conventionally managed farms, but it appears that managing for a low weed density, regardless of the method, is likely to lead to a lower species diversity – that there will be fewer species and the community is more likely to be dominated by a single species. If weed control pressure is not reduced because of low weed densities, then rare species are likely to become locally extinct.

The possible trade-off between species diversity and weed abundance raises the question of what the goal of increasing weed diversity in organic systems is. Is it because some plants are aesthetically important? Is it that increasing diversity contributes to increasing crop yield by harbouring predators of crop pests? Or that certain weeds are an important food source for other organisms that have ecological or aesthetic value beyond crop production? A better understanding of the ecological function that different weed species play in an agro-ecosystem may help to clarify the objectives of increasing biodiversity in agricultural settings. Squire and colleagues (2000) suggest that, in evaluating weed diversity, species could be weighted by their functional role.

If the importance of a weed species is for aesthetic values or ecological roles beyond crop production, then it is important to know how increasing such populations will affect crop yield and financial aspects, in order to develop management strategies and policies that will achieve multiple goals. Furthermore it may be necessary to consider the spatial structure of such weed populations at the landscape level, and whether concentrations of certain weeds (patches) play a role in the metapopulation dynamics of dependent organisms. The metapopulation dynamics of weeds may be less important from the perspective of serving as a host to another organism, because of the possibility of selective hand-weeding. Of course, if such a species is unwanted in other fields or farms, then it is crucial to consider the metapopulation dynamics and dispersal characteristics of the species.

Factors influencing weed densities

For effective management of weed populations, it is critical to know which factors are influencing a weed population, the magnitude of their effect, and whether it is possible to exert any control over important factors. In screening for factors influencing weed density, it was clear given the summary analysis of the data that some factors, such as farm, would have an effect. The effect of farm can come about through choice of crop, location of the farm, or the management strategy adopted by the farmer. While there were some differences in the crops grown, the effect of farm was probably in most part due to the weed management strategy. On Farms 3 and 6, and particularly on Farm 8, attention is given to removing seed-bearing plants, even if there is not a threat to current yield. On Farm 8, for example, flowering and seed-bearing plants of species other than *S. media* are removed from the wheat fields, while on Farm 3, time allowing, seed-bearing plants are removed from the onion field prior to harvest. In contrast, on Farm 5, germinating seedlings surrounded seed-bearing plants that have been observed to be left in the field after weeding.

The finding that weed densities were positively correlated with hours of hand-weeding is an indication that the weed densities prior to control were very high, rather than hand-weeding being a cause of high plant densities. Understanding how hours of hand-weeding are related to weed densities at the start of the season will be important in developing models of weed population dynamics in organic farming systems and for finding optimal methods of hand control. For example does the removal rate (plants removed per minute) depend on the weed population density? One might expect that the removal rate would be a type 2 functional response (Holling 1959), where the removal rate first increases with density and then levels off. As the density increases, one does not need to travel as much to reach the next weed. On the other hand, at higher densities search time may increase because more weeds may be hidden by the crop, and therefore at a certain density the removal rate might decrease.

The effects of year were in the range of those for the factor crop, suggesting that factors beyond a farmer's control may have just as high an impact on weed densities as controllable factors. However, as the effect of year may have been influenced by the combination of crops sown in a given year, it is difficult to conclude from this study the actual degree of the impact of year. In improving weed control strategies it would be useful to have more concrete data on the variation due to uncontrollable factors and their possible interaction with weed management strategies.

The pattern that cereal crops tend to have higher weed densities is not surprising given the difficulty of hand-weeding in a cereal crop. While the greater competitiveness of cereal crops relative to many weed species allows production of a reasonable yield, even in the presence of weeds, including too high a proportion of cereal crops in a rotation can lead to high inputs to the weed seedbank. These inputs of weed seeds will lead to extra efforts in controlling weeds in subsequent, less competitive crops. While the results indicated that weed densities were lower with more mechanical weed control operations, this does not necessarily mean that a higher kill rate will lead to lower weed densities in the long term. Future weed densities depend on the amount of weed seeds produced. Mertens and Jansen (Mertens and Jansen 2002) have shown that the kill rate must be very high in cereal crops which are sown at a wide enough row spacing to accommodate mechanical control, in order to have a seed production level as low as that found in a narrowly spaced crop. Farm 8 uses such a strategy of sowing the wheat crop at a narrow spacing and undersowing with clover much earlier than the other farms. Consequently no mechanical weed control is carried out in the wheat crop.

A second clear pattern that emerged was that grass-clover crops had very low weed densities compared with all other crops. There is much evidence suggesting that a properly managed grass-clover crop has very few weeds (Lueschen et al. 1993, Davies et al. 1997, Ominski et al. 1999, Sjursen 2001) and also that farmers perceive that they have fewer weed problems when the proportion of grass-clover years increases in the rotation (Entz et al. 1995). For the two farms that did include grass-clover crops in their rotation, this crop consistently had fewer weeds than the other crops. However, considering that Farm 9 had rather high overall weed densities, and that the sample consisted of just two farms, it is difficult to conclude whether the grass-clover crop is contributing to long-term reductions in weed densities.

The effect and role of a grass-clover ley in weed management may be viewed from several perspectives. On the one hand it can serve to deplete the weed seedbank. The strength of such an effect may however depend on the species composition of the weed seedbank, as some weed species have persistent seedbanks (Roberts and

Feast 1972, 1973). On the other hand, if the weed seedbank increases only slightly, a grass-clover ley can allow farmers to focus their resources on weed control in other crops, such as onions. Doing so gives the possibility of reducing the weed population much more than if wheat, for example, had been planted instead of grass-clover. The position that the grass-clover ley has in the crop rotation may also be important (Mertens et al. 2002). For example reductions in the weed population may be greater if the grass-clover ley precedes an onion crop. On Farm 8 such a strategy is adopted. The farmer reasons that the weed seedbank population, particularly that of *S. media*, declines during the grass-clover ley and that remaining seedlings are grazed by insect larva in preference to onion seedlings. Then, with the combination of flame weeding and mechanical control, the weed population is reduced to such levels that very few hours of hand-weeding are necessary. It is important to recall that on Farm 8, the weed population is dominated by *S. media.* In contrast, on Farm 9, the densities of species with persistent seedbanks are relatively higher. Furthermore the grass-clover ley usually occurs before a wheat crop, which, from the perspective of weed management, may not be the most beneficial position in the crop rotation. The impact of the grass-clover ley on reducing the weed population may therefore be less than could be expected.

Considerations for future studies

The aims of this study have been broad, and the methods used in monitoring have necessarily included some compromises. In this study the same quadrat size and number has been used regardless of the question at hand, e.g., species diversity or species abundance. It is well known that the number of species observed increases with the area surveyed. A more true impression of species richness may be achieved by monitoring a larger fraction of the field. Because some species are rare, while they may be present in a quadrat one year, the following year they may be just outside the quadrat. Therefore the quadrat size may need to vary between species, given the estimated abundance of each species at the start of the study.

Management information, such as hours of hand-weeding or number of mechanical control operations give an indication of the approach a particular farmer uses for weed management. The goals a farmer has regarding weeds, the strategy used and the reasons for the operations carried out are much more difficult to quantify. These more qualitative aspects, however, provide valuable clues to variation in weed diversity and abundance as well as useful directions for research to improve weed management strategies. Some farmers may have a high density because they do not weed intensively in order to encourage a more diverse flora. Or it could be due to an injury that prevented mechanical control at a crucial period, and allowing many weeds to reproduce at the end of the season. Such qualitative aspects cannot be captured via quantitative measures alone.

As weeds are an essentially human-constructed problem, a better integration of the human dimensions, e.g., political, economic, and social aspects, into the study of weed ecology can help to focus research on relevant questions and help to design more effective management strategies. Long-term monitoring studies that incorporate quantitative data on weed populations, management, and environment, with qualitative information about farmer goals, strategies, tactics, and mishaps, are one method of incorporation human aspects with the biological aspects.

APPENDIX

Table A1. Crops growing on each farm in the period 1995 to 2001.

	Field					
Year	1	2	3	4	5	6
Farm 3						
1995	Barley	Spelt	Poppy	Onions	Cabbage	Carrots
1996	Carrots	Onions	Potatoes	Peas	Barley	Wheat
1997	Wheat	Peas	Barley	Potatoes	Carrots	Onions
1998	Onions	Potatoes	Carrots	Wheat	Wheat	Beans
1999	Beans	Wheat	Wheat	Carrots	Onions	Potatoes
2000	Potatoes	Carrots	Onions	Oats	Beans	Lettuce
2001	Lettuce	Oats	Lettuce	Cabbage/Onions	Potatoes	Celery
Farm 5						
1995	Peas	Oats	Onions	Potatoes	Carrots	Flax
1996	Leek	Potatoes	Spelt	Peas	Beans	Belgian endive
1997	Oats	Wheat	Belgian endive	Onions	Potatoes	Maize
1998	Carrots	Onions	Peas	Wheat	Maize	Potatoes
1999	Wheat	Oats	Potatoes	Carrots	Onions	Cabbage
2000	Belgian endive	Potatoes	Cauliflower	Wheat	Carrots	Shallots
2001	Maize	Pumpkin	Onions	Beans	Beans	Wheat
Farm 6						
1995	Potatoes	Onions	Celery	Wheat	Wheat	Peas
1996	Maize	Spelt	Peas	Onions	Carrots	Potatoes
1997	Onions	Carrots	Potatoes	Wheat	Beans	Maize
1998	Carrots	Beans	Corn	Onions	Potatoes	Wheat
1999	Beans	Potatoes	Wheat	Carrots	Maize	Onions
2000	Potatoes	Peas	Onions	Beans	Wheat	Carrots
2001	Pumpkin	Wheat	Carrots	Potatoes	Onions	Beans
Farm 8						
1995	Maize	Grass	Cabbage	Potatoes	Wheat	Onions
1996	Peas	Onions	Wheat	Grass	Potatoes	Maize
1997	Wheat	Maize	Potatoes	Onions	Grass	Peas/Broccoli
1998	Potatoes	Peas/Broccoli	Grass	Maize	Onions	Wheat
1999	Wheat	Wheat	Onions	Peas/Broccoli	Maize	Potatoes
2000	Shallots	Potatoes	Cabbage	Wheat	Peas/Broccoli	Grass
2001	Cabbage	Grass	Onions	Onions	Potatoes	Shallots
Farm 9						
1995	Carrots	Wheat	Carrots	Onions	Potatoes	Oat
1996	Potatoes	Onions	Peas	Oats	Wheat	Carrots
1997	Wheat	Oats	Potatoes	Carrots	Onions	Peas
1998	Onions	Carrots	Grass	Peas	Wheat	Potatoes
1999	Wheat	Peas	Celery	Potatoes	Carrots	Grass
2000	Belgian endive	Potatoes	Wheat	Grass	Peas	Sugar beet
2001	Peas	Grass	Belgian endive	Sugar beet	Potatoes	Wheat

INTRODUCTION

In Northern Europe agricultural policies are being implemented to encourage farming systems that do not use herbicides or other artificial inputs (Lucas and Pau Vall 1999). In the Netherlands, for example, currently about 1% of agricultural land is managed without artificial inputs and the goal is to increase this to 10% by 2010 (LNV 2000). A major concern for these farmers is weed control.

In cereal crops, farmers relying on non-herbicide-based systems of weed control often use a wider row spacing of 23 to 30 cm compared to their conventional (herbicide-applying) colleagues, who typically sow in the range of 9 to 12 cm. The wider row spacing allows mechanical weed control with a hoe using goosefoot or V-shaped blades, as well as with a harrow. In narrower spaced crops only the harrow can be used. The efficacy of harrowing is highest with weed seedlings, while a hoe is able to control plants with more developed root systems (Rasmussen and Ascard 1995). Consequently hoeing, particularly in combination with harrowing, tends to be more effective, in terms of fraction of weeds killed, than harrowing alone.

Much previous work has shown, however, that weed biomass and density in cereal crops is reduced with a narrower crop row spacing, a higher planting population, or a combination of both (Teasdale and Frank 1983, Medd et al. 1985, Champion et al. 1998). Furthermore it is known that that seed production per plant tends to increase with biomass (Samson and Werk 1986, Thompson et al. 1991). Thus one expects that crop spatial arrangement will also affect weed seed production. The few studies addressing seed production per weed plant and crop spatial arrangement support this contention (Wilson et al. 1995, Teasdale 1998, Young et al. 1999).

The decision to use a row spacing suitable for hoeing may therefore carry the trade-off of higher seed production per weed plant. A crucial question is whether the increased efficacy of hoeing is great enough to balance potential increases in seed production of surviving plants caused by a wider row spacing. From a long-term perspective a reasonable criterion for effective weed management is a declining weed population, which implies that weed seeds are not able to replace themselves. Minimising seed production per seedling can be an important part of lowering the weed population growth rate. It does not matter, though, whether seed production per seedling is decreased by lowering the density of plants by killing them or by using interference from the crop to decrease seed output per adult plant.

Our aim was to investigate whether seed production per surviving plant is higher in a widely spaced wheat crop and, if so, whether more aggressive weed control can compensate for it. We considered three weed species common to the Netherlands and having different growth habits: wild buckwheat, ladysthumb, and chickweed, growing in spring wheat sown at three row spacings and two sowing densities. Spring wheat is commonly grown by farmers in the Netherlands who do not use herbicides. The three row-spacing treatments (10, 20, and 30 cm) encompassed the range of spacings used in practice and in which the 30 cm spacing allows hoeing. The lower sowing density (140 kg ha^{-1}) was typical, while the high density (180 kg ha^{-1}) was considered to be the upper limit of sowing densities that farmers would use.

MATERIALS AND METHODS

Experimental Methods

Study Site

The experiment was conducted in 1999 and 2000 at the Lovinkhoeve Experimental Farm (52°41' N and 5°53' E), near Marknesse in the Netherlands. The experiment was in a different field each year. The soils on both fields were calcareous polder vague soils with a loamy surface, a particle distribution of 12% sand, 68% silt, 30% clay (de Vos et al. 2000), and had 2.3% organic matter and a pH of 7.4 (AB-DLO 1997). Each year the crop preceding the spring wheat crop was sugar beet. The experimental fields had been managed without pesticides or inorganic fertilisers since 1995.

Cultural Practices

The fields were moldboard ploughed in the winter, and in April of each year cattle manure was injected. This was immediately followed by seedbed preparation and sowing. See Table 1 for details on dates of operations and amounts of manure. Weed control consisted of harrowing or hoeing and harrowing. Harrowing was carried out with an Hatzenbichler spring tine harrow with a working width of 12 m, and hoeing with a Rabe hoe with a working width of 3 m (10 rows) and using 20 cm wide V-shaped blades.

Experimental Design

To expedite field operations a randomised split-plot design with four replicates was used for testing the effects of row spacing/weed control intensity (associated with main plots) and sowing density (associated with sub-plots). Main plots were 3 m by 80 m and split plots were 3 m by 40 m. Three levels of row spacing were used, 10, 20, and 30 cm. The two sowing densities were 140 and 180 kg ha^{-1}. This corresponded to 330 and 430 seeds m^{-2} for the cultivar Lavette and 350 and 450 seeds m^{-2} for the cultivar Baldus. In 1999 the row spacing/weed control combinations used were (a) 10 cm and harrowing twice, (b) 20 cm and harrowing twice, and (c) 30 method of harvesting these plants was to step 60 cm from the used area and harvest the first *n* individuals encountered in each row, with the number *n* determined so that about 10 plants were harvested per treatment, with approximately an equal number from each row. A total of 404 individuals were harvested.

Weed harvest and processing. For all experiments, surviving weed plants were harvested 12 weeks after seedling germination (4 weeks before the crop was harvested). This harvest time represented a balance between minimising seed loss due to shedding and allowing as many mature seeds as possible to be produced.

Immediately after harvesting the plants were dried at 80°C for 24 hours. Prior to weighing they were re-dried for two hours at 80°C and sealed. Seed production was determined by randomly drawing 10 plants from six (1999) or five (2000) dry-mass classes in each of the three row spacing treatments, combining plants across replicates and sowing densities. Plants were threshed and the viable seeds were separated using a Dakota Seed Blower and then counted by hand. The airflow in the blower was adjusted so that immature, cracked and aborted seeds were blown out, leaving only seeds that would have passed the test of being squeezed with forceps.

Data Analysis

Weed Seed Production

Seed production per plant. Weed seed production per surviving plant was modelled by regressing seed production per plant against individual plant dry mass. Effects of year, population (planted or natural), and row spacing/sowing density treatment were investigated by including these terms sequentially in the model. In determining which regression model to use for seed production, we examined which factors had significant F-probabilities ($p \leq 0.05$), the possible causes of differences between the models, and whether models with more parameters resulted in large differences in the predictions of seed number.

Average seed production per seedling. First the average seed production *per surviving plant* of each species was calculated by inserting the average biomass per plant in the regression equation for seed production per plant. Average seed production *per seedling* was then calculated by multiplying average seed production per surviving plant by the estimated mean fraction of plants surviving in a given row spacing/sowing density treatment:

$$\hat{S}_{kl} = \hat{h}_{kl}\hat{Y}_{kl} \qquad (1)$$

where $\hat{S}_{kl}$ is the average seed production per seedling in the *k*th row spacing level and *l*th sowing density level, $\hat{h}_{kl}$ is the mean fraction of plants surviving, and $\hat{Y}_{kl}$ is average seed production per plant, as calculated with the regression equation for seed production. Mean plant survival was given by the predicted means resulting from logistic regression of plant survival. The logistic regression model was fitted in a stepwise fashion to account for the split-plot design.

Presentation of results. Results of calculations of seed production per plant and per seedling were plotted on graphs where the *x*-axis represents a range of seed production per surviving plant ($\hat{Y}_{kl}$), the *y*-axis represents plant mortality (M_{kl}), and where isolines indicate constant amounts of seeds per seedling for a range of seeds produced per surviving plant and all possible mortality levels. The equation for the isolines is

$$M_{kl} = 1 - S_{kl}/Y_{kl} \tag{2}$$

where M_{kl} is plant mortality, and S, Y, k, and l are as given for equation 1. For a given treatment, the average fraction of plants dying and seeds per surviving plant have been measured. These pairs are plotted on the graph and the number of seeds produced per seedling can be inferred from the position of each point in relation to the isolines. Note that by rearranging equation 2 so that $S_{kl} = (1-M_{kl})Y_{kl}$, one arrives at equation 2 because $h_{kl} = 1-M_{kl}$.

Effects of Row Spacing and Sowing Density

Dry mass per plant. Calculating seed production per seedling involves combining variables with different distributions; consequently it is difficult to directly compute effects of the treatments on seed production per seedling. However, it is straightforward to calculate the effects of the treatments on plant dry mass. Furthermore the effects of survival can be incorporated by considering dead plants as having zero mass. Analysis of plant dry mass gives an indication of the effects of the treatments on seed production per individual (plant or seedling) because of the linear relation between seed production and plant dry mass.

Effects of the treatments on the biomass of surviving plants and all plants were investigated by fitting a generalised linear model, based on the normal distribution, to the log-transformed plant dry weights (Neter et al. 1996a). For the analysis including dead plants, the transformation was log (dry mass + 1) in order to avoid taking the logarithm of zero. The model was fitted sequentially in order to generate the appropriate block and error terms for a split-plot design. Data from different years and populations were analyzed separately.

Crop yield. Analysis of variance using error terms appropriate for a split-plot design was used to analyze crop yield. Data for each year were analyzed separately.

RESULTS AND DISCUSSION

Weed Seed Production

Seed Production per Plant

For all species, seed number per plant clearly increased with dry mass per plant (Fig. 1). Using the arithmetic average of plant dry mass (Table 2), we calculated average seed production per surviving plant (consider *x*-coordinates of points in Fig. 2). Up to 3 times more seeds were produced per surviving plant in the 30 cm treatments than in the 10 cm treatments. Differences in seeds produced per surviving plant reflect differences in plant dry mass, and are discussed in connection with effects of row spacing and sowing density.

Table 2. Arithmetic means of plant dry mass and estimated mean fraction of surviving plants. In 2000, wild buckwheat seedlings were planted only in the 10 cm treatments (both sowing densities) and in the 30 cm, 140 kg ha^{-1} treatment.

Species	Year (population)	Row spacing	Plant mass		Survival	
			sowing density (kg ha^{-1})			
			140	180	140	180
		cm	g plant^{-1}		fraction	
Wild buckwheat	1999 (natural)	10	0.546	0.404	0.9	0.9
		20	1.071	0.757	0.9	0.9
		30	1.162	1.331	0.6	0.6
	2000 (planted)	10	0.188	0.180	0.9	0.9
		20	-	-	-	-
		30	0.254	-	1.0	-
Ladysthumb	1999 (natural)	10	0.426	0.378	0.9	0.8
		20	0.814	0.547	1.0	0.9
		30	1.153	0.591	0.6	0.5
	2000 (planted)	10	0.402	0.303	0.8	1.0
		20	0.363	0.396	1.0	0.8
		30	0.397	0.438	1.0	1.0
	2000 (natural)	10	0.421	0.421	-	-
		20	0.860	0.662	-	-
		30	1.102	0.789	-	-
Common chickweed	1999 (natural)	10	0.328	0.280	0.8	0.8
		20	0.470	0.363	0.9	0.9
		30	0.727	0.639	0.6	0.5
	2000 (planted)	10	0.107	0.092	1.0	1.0
		20	0.121	0.108	1.0	1.0
		30	0.145	0.142	1.0	1.0

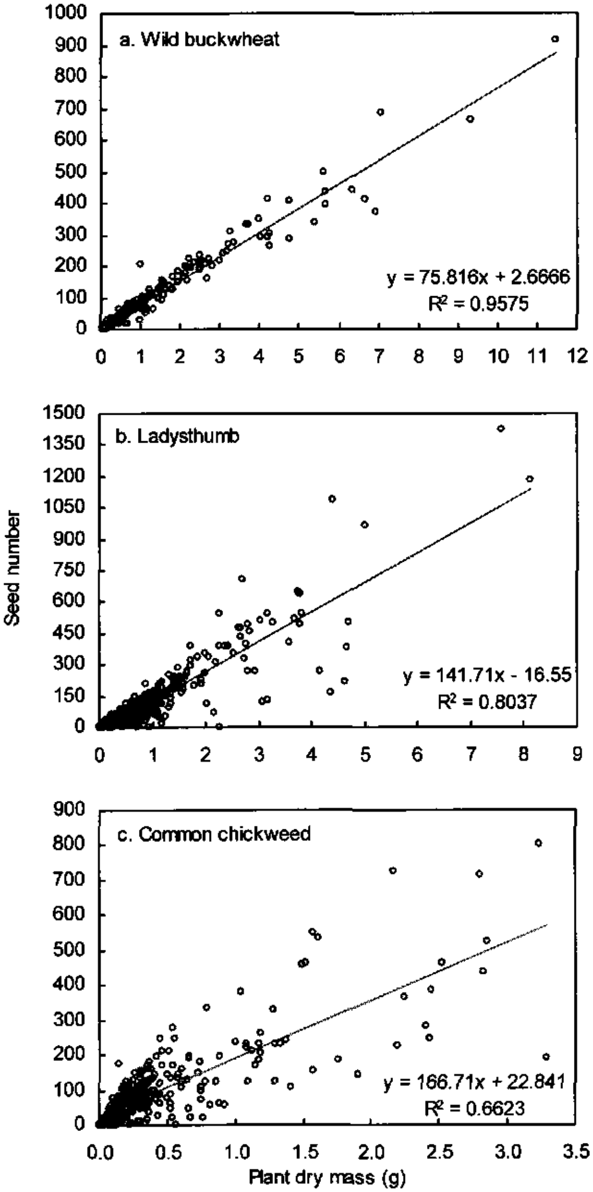

Fig. 1. Relationship between plant dry mass and seed number.

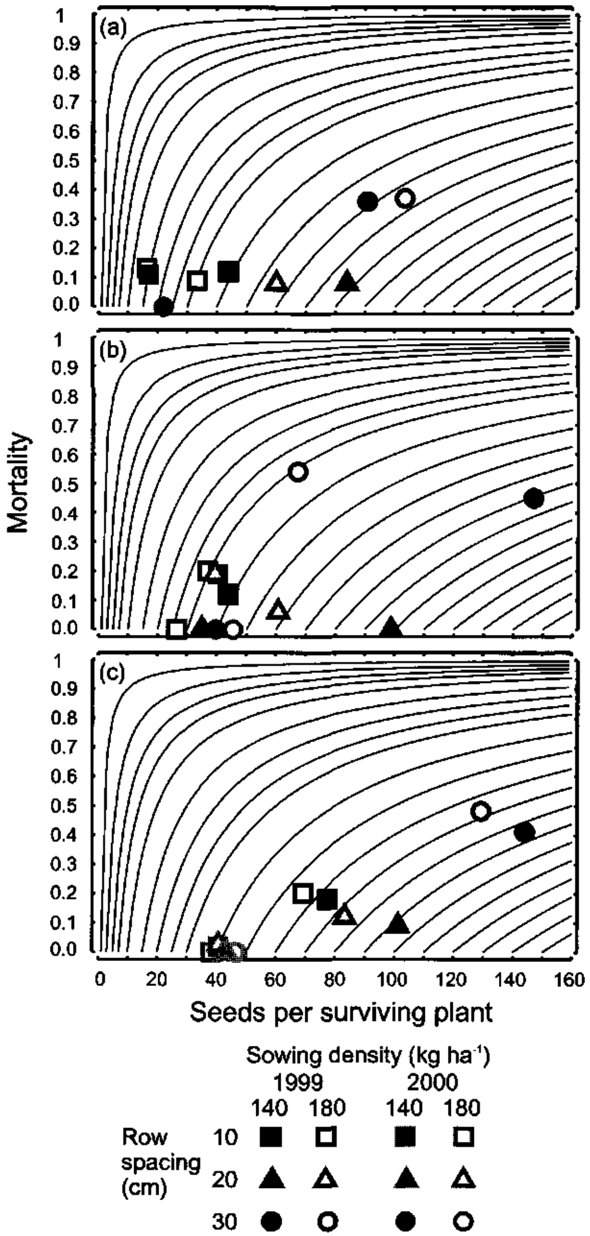

Fig. 2. Isoline graphs of seed number per seedling for given levels of seeds produced per surviving plant and levels of mortality. Isolines are of equal numbers of seeds per seedling and value can be read from intercept with *x*-axis. (a) wild buckwheat, (b) ladysthumb, and (c) common chickweed.

The simplest model for seed production, including only dry mass per plant, was used for each species. There were significant effects of different factors for each species: for wild buckwheat there was a significant effect of year (p = 0.013); and for ladysthumb and common chickweed, there was a significant effect of row spacing (p = 0.005 and p = 0.034, respectively), and of an interaction between row spacing and sowing density (p = 0.043 and p = 0.007, respectively). These significant effects are due to overfitting, as the few observations of plants with a high dry mass had a high leverage, particularly when factors besides dry mass were included in the model. There was no systematic pattern in the predictions of the models including the different factors, as one might expect if there was a biological reason for the effects. We therefore opted to model seed production using only dry mass per surviving plant. For each species, this one-variable model slightly overestimated plant mass in the 10 cm treatments, and slightly underestimated plant mass in the 30 cm treatments, compared to the models including the factors with significant effects.

It is likely that seed production per surviving plant, particularly in the 30 cm treatments may have been underestimated, if plants had been allowed to remain in the field until crop harvest and if all seeds could have been collected. During harvesting and cleaning the seeds it appeared that large plants may have had a higher fraction of immature seeds, which could perhaps have matured by the time of crop harvest. At the time of harvest very few seeds appeared to have been shed from the wild buckwheat and ladysthumb plants and care was taken not to lose any during the harvest. For common chickweed, as it started flowering earlier, the fraction of seeds shed was higher than for the other two species, but losses were probably less than 10%. For all species, a higher fraction of seeds was probably lost from larger plants than from smaller plants. If seed production of the larger plants was indeed higher than we measured, then the slopes of the regression line for seed production would have been higher, and therefore the average amount of seeds per surviving plant would have been higher, particularly for larger plants, than the results we obtained here.

Average Seed Production per Seedling

After taking into account plant survival (Table 2), average seed production was still lower in the 10 cm spacing than in the 20 and 30 cm treatments and was generally lower in the 180 kg ha^{-1} treatments than in the 140 kg ha^{-1} treatments (Fig. 2). Seed production per seedling in the 10 cm treatments was about one half to three quarters of that found in the 30 cm spacing, for all sowing densities. The exception was ladysthumb (experiment 2, 140 kg ha^{-1}), where the same level of seed production per seedling was achieved in both the 10 and 30 cm treatments. In the 20 cm treatments, particularly at the higher sowing density, the average seed production per

Usefulness of the Method

In this work we have used the individual as our unit of reference, e.g., seed production is reported per plant or per seedling rather than per plot or per unit area. The individual as a unit of reference arises naturally from the criterion that weed seeds should not replace themselves. While such a perspective necessarily results in laborious experiments, it provides a number of advantages. Firstly, one can immediately interpret results from the perspective of weed population dynamics, e.g., for the time interval and conditions observed, one has an impression of whether the weed population is growing (seeds are more than replacing themselves), or declining (seeds are not replacing themselves). Secondly, weed plants usually have a heterogeneous spatial distribution. Therefore when plant mass or seed production is reported per unit area or per plot, or when the efficacy of weed control is reported with reference to a control plot, the results may be difficult to interpret as the density is unknown. For the same reason it is difficult to compare results between studies. Thirdly, non-linear relations may be present, for example between seed production and plant mass, or between mortality and plant density. If one wished to predict average seed production per plant from a non-linear relation between seed production and plant mass, then the mass of individual plants is needed rather than average mass per plant as calculated from total mass per plot divided by plant density.

Other advantages of an individual perspective are that one obtains many more data points per unit area and that one can measure resource availability in terms of effects on individual plants. For the former advantage, with more data points one can obtain better estimates of the shape and parameters of distributions for plant mass or seed production per plant. With respect to the latter advantage, one can measure the local density or other aspects of the local environment around a target weed plant. For example, the mass of a target plant may bear little relation to densities reported on a per unit area basis because weed density is heterogeneous; what matters is how many plants were close to the target weed plant.

In this study, we have been concerned with the combined effects on mortality and seed production of crop planting pattern and weed control. By taking this combined perspective it is possible to save space and time because the factor 'no weed control' does not need to be included in the experiment. If one wished to attribute separately the effects to crop planting pattern and weed control, the additional 'no control' factor is of course necessary to avoid confounding of the results.

Implications of Results for Non-Herbicide Weed Management

Our aim has been to examine whether a widely spaced wheat crop, in combination with more intensive weed control, produces more or less weed seeds than a wheat crop grown under a narrow row spacing with less intensive weed control. The results indicate that it would indeed be beneficial, at least for the weed species concerned and in spring wheat, to use a narrow row spacing and less intensive methods of control. Although more plants survived in the narrowly spaced treatments, their seed production was so low that the lower plant survival in the wide row spacing could not counterbalance the higher seed production per plant. While the higher sowing density (180 kg ha^{-1}) tended to decrease seed production, the differences were not large. We expect, however that a sowing density higher than 180 kg ha^{-1} may have a greater effect, particularly in the 10 cm treatment. The recent work of Weiner et al. (2001) indicates that using uniform crop planting pattern and a high sowing density could lead to even greater reductions in weed size and hence greater reduction in weed seed production.

As we examined effects of row spacing/weed control and sowing density on only three weed species, it is useful to consider whether the conclusions may apply to other species, and to winter cereal crops. In spring crops the benefits of using a narrow row spacing are likely to carry over to most annual species. The three species considered here have rather different growth forms, with common chickweed and particularly wild buckwheat being able to forage for light by winding their stems through and up the crop. All three species still showed significant effects of the row spacing treatment. This suggests that a substantial effect of a different row spacing and sowing density may be on early growth, and that the effects cannot be overcome by an ability to forage for resources. Using a narrow spacing may not have large benefits over a wide row spacing and hoeing when weeds are able to emerge earlier than the crop and when early crop growth is slow, a situation common in fall and winter sown crops. Considering the large area devoted to winter cereal crops in Northern Europe and North America, further research on trade-offs between crop spatial pattern and control would, however, be useful.

CHAPTER 4

Local Predictors of Biomass and Survival for Weeds Growing in a Crop

ABSTRACT

Key questions in weed ecology concern the probability of a weed surviving and the number of seeds it will produce. We ask whether weeds growing in a crop experience different local environments, and whether these local environments can be used to predict individual survival and reproductive potential. In an experiment with spring wheat, we created a variety of environments by imposing three row spacing/weed control treatments and two sowing density treatments on the crop. The widest row spacing level was associated with mechanical hoeing and harrowing, while the other two row spacing levels were associated with harrowing or no control. The local environment around each weed plant was described by the distances to the nearest crop and other weed plant, and the local crop row width. The survival and dry mass of three naturally occurring weed species (*Polygonum convolvulus*, *Polygonum persicaria* L. and *Stellaria media* (L.) Vill.) was measured. Plant survival declined with distance to the nearest crop plant only in the wide row spacing, where weed control was with a mechanical hoe. Plant dry mass for all species increased linearly with the square of the distance to the nearest crop plant and the square of the local row spacing. Reciprocal predictors of plant mass did not fit the data well. Local predictors, based on local environments, can be used to predict individual weed survival and reproductive potential and thus provide a means to examine the effect of crop planting patterns and weed control on weed population dynamics.

Adapted from: Mertens, S. K. Local predictors of biomass and survival for weeds growing in a crop. Submitted.

INTRODUCTION

Plants, as sedentary organisms, grow and reproduce in response to their local environment and variability in local environments is thought to be responsible in part for the variability in plant size (Harper 1977). The local environment around a plant can be described by the local density of other plants, the amount of unoccupied space, or specific measures of resource availability.

Research on weed-crop competition has rarely been conducted at the level of individual weed performance in relation to the local environment. Early research was more concerned with the effect of weeds on crop yield (e.g., Bleasdale 1960, Appleby et al. 1976, Buchanan and Hauser 1980, Martin et al. 1987), and therefore attention was given to the environment of crop plants. With the increasing focus on developing weed management strategies where weeds are not allowed to replace themselves in future generations, more attention is being given to the effects on weed plant performance due to competition with the crop. Most of the studies (e.g., Teasdale and Frank 1983, Medd et al. 1985, Champion et al. 1998) have examined either effects on weed density or on weed mass per unit area, implicitly assuming that the mean environment of an individual plant is an adequate description of what it experiences. But, the environment is likely to be different for individuals in different locations (Fig. 1). The range of possible environments will depend on the crop planting pattern (dictated by the row spacing and sowing density) and the evenness with which the crop emerges. Therefore an individual-based approach to studying the effects of crop spatial arrangement on weed performance may be more appropriate. The few studies (Teasdale 1998, Young et al. 1999) that have examined the effects of the local environment on individual weed plants have manipulated the placement of plants so that information on differences in environments in a more typical weed-crop setting is unknown.

A central question in weed ecology and management is which weeds contribute most to future generations and how their performance is related to their local environment. In order to address this question it is necessary to know whether there are differences in the local environment that weed plants experience and whether these differences are reflected in measures of plant performance. We addressed these aspects using naturally occurring populations of *Polygonum convolvulus, Polygonum persicaria* L. and *Stellaria media* (L.) Vill., growing in spring wheat at three row spacings and two sowing densities. Different row spacing levels were associated with different types of mechanical weed control. In the widest row spacing, mechanical hoeing and harrowing were applied, while in the two narrower row spacing levels only

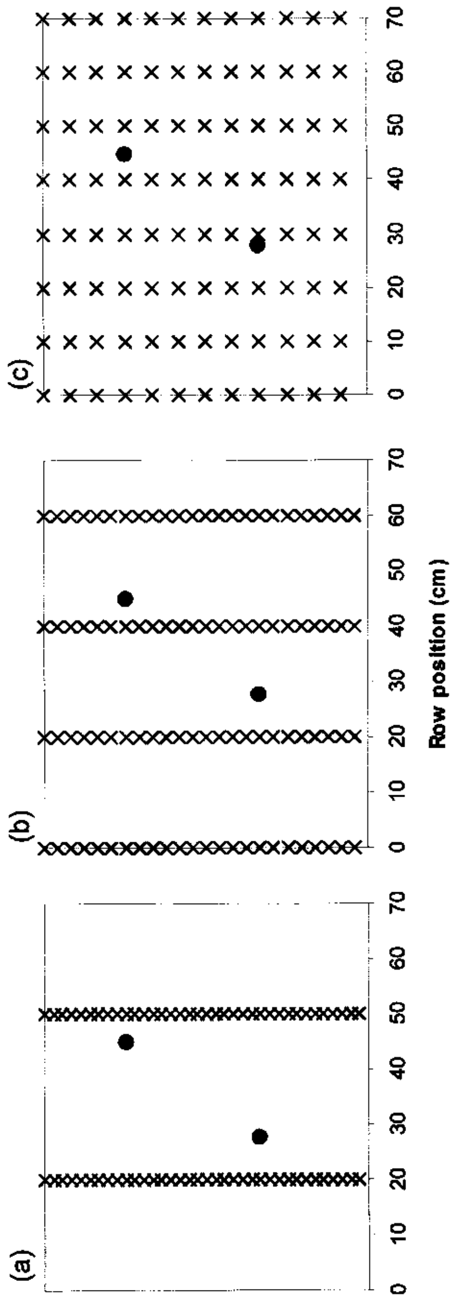

Fig. 1. Neighbourhood perspective of weeds growing a crop at different row spacings, where ✖ indicates a crop plant and ● indicates a weed plant. The density of crop plants in each figure is the same, as are the co-ordinates of the weed plants.

harrowing or no control was applied. The measures of plant performance were survival and plant mass. Because there is a close relationship between plant mass and seed production, mass can be used as a measure of reproductive potential (Samson and Werk 1986, Weiner 1988, Thompson et al. 1991). Below we briefly review past work on descriptors of the local environment and predictors of plant performance.

Descriptors of the local environment

The local environment around a plant can be described using either summary measures (local density or space available) or specific measures such as local levels of light, water or nutrients. Studying plant performance in relation to specific measurements of resource availability is important for establishing the biological processes influencing plant performance. Changes in a plant's local environment, however, are most likely to come about through changes in summary measures, such as distance to, or size of neighbouring plants. Summary measures also have the advantages that they are simple to measure, are not specific to a particular system, and that future environments can be calculated from the past environment using spatially explicit models of plant population dynamics.

The most common summary descriptors of the local environment around a target plant have been the density of neighbouring plants around a target plant (Weiner 1982, Firbank and Watkinson 1987) or the amount of unoccupied space (Mead 1966, Firbank and Watkinson 1987). In the neighbourhood approach, the number of neighbouring plants is counted in an area surrounding the target plant, giving the neighbourhood density. An optimal neighbourhood can be found by using a radius that gives the best fit to the relationship between target plant mass and neighbourhood density (Silander and Pacala 1985). The relationship between plant performance and other descriptors such as the biomass or size of neighbouring plants, their distance to the target plant or their angular dispersion relative to the target plant has also been investigated (Ross and Harper 1972, Mack and Harper 1977, Weiner 1982, Silander and Pacala 1985). Local density approaches have tended to be more informative compared to area-available approaches.

In this study we used distance measures, such as the distances to the nearest crop plant and nearest other weed plant, and the local row spacing, to describe the local environment around target weed plants rather than neighbourhood density. Because crop plants are arranged in a regular pattern, the number of crop plants for a given neighbourhood size is likely to be the same for different target weed plants, unless the neighbourhood size is very different from a multiple of row width. Weed plants are also likely to be affected most by crop plants in the adjacent rows and therefore the neighbourhood size is likely to be closely related to row width and distance to the nearest crop plant.

Predictors for plant mass and survival

Local predictors of plant performance are the models relating plant mass, reproductive effort, or chance of survival to descriptors of the local environment. Local predictors of plant mass have often been based on models developed to study the relationship between yield (mass or reproductive output per unit area) and density (Kira et al. 1951, Bleasdale and Nelder 1960, de Wit 1960, Holliday 1960). In a review by Willey and Heath (1969), two main forms of relationships between yield and density are given – linear ones with or without quadratic terms, and nonlinear ones, principally of a hyperbolic form. A hyperbolic form of predictor is intuitively satisfying because it can be derived from assumptions concerning plant growth over time, because the parameters have biological interpretations, and because as density goes to zero, yield per unit area will reach a constant level.

Local predictors of plant mass typically use the local density in place of mean density and predict individual plant mass rather than mass per unit area. Area available or distance measures can be incorporated by using the reciprocal of these descriptors. Some studies have used multiple linear regression to relate measures of the local environment to plant performance (Hickman 1979, Waller 1981), while others have used non-linear equations analogous to those developed to describe yield-density relations (Soetono and Puckridge 1982, Weiner 1982, Silander and Pacala 1985). Different basic forms of local predictors for plant mass have rarely been compared. In this study we fitted both linear and reciprocal forms of the local predictors and examined the effect of using linear, quadratic, or cubed transformations of the local descriptors.

Local predictors of plant survival have rarely been developed and when they have, results have not been consistent (Pacala and Silander 1990). Because local densities must often be so high to induce mortality (Harper 1961, Watkinson and Lonsdale 1983), plants in such situations may all experience nearly identical neighbourhoods and therefore the chances of survival will be similar for all individuals. In other situations, where an outside control agent can be applied, survival may be related to the local environment of a plant. For example in an agro-ecosystem, the effectiveness of mechanical control or herbicide spraying may be influenced by the distance a weed plant is from a crop plant. Local predictors of plant survival can then be developed using, e.g., logistic regression since survival is a binary variable.

METHODS AND MATERIALS

Experimental methods

General. The experiment was conducted during 1999 and 2000 with spring wheat (*Triticum aestivum* L.) at the Lovinkhoeve Experimental Farm in the Netherlands and in 1999 at the Wageningen University Unifarm. In 1999 the variety was Lavette, while in 2000 it was Baldus. Table 1 summarises the experimental set-up at each of the locations and the sample sizes for each of the species. Further details of the experimental method at the Lovinkhoeve site are given in Chapter 3.

At the Lovinkhoeve site, the row spacing levels were 10, 20, and 30 cm and the sowing densities were 140 and 180 kg ha^{-1}, corresponding to 330 and 430 seeds m^{-2} for the cultivar Lavette and 350 and 450 seeds per m^{-2} for the cultivar Baldus. A split-plot design with four replicates was used, where row spacing/weed control intensity was associated with main plots and sowing density was associated with sub-plots. Weed control consisted of only harrowing with a spring-tine harrow (in the 10 and 20 cm treatments), or hoeing and harrowing (only in the 30 cm treatments). The harrow consisted of thick wires, 50 cm long, mounted 10-20 cm apart on a 12 by 2 m frame that was dragged behind the tractor. It was used in all treatments. The hoe consisted of 10, 20-cm wide, V-shaped blades that were dragged behind the tractor and could only be used in the 30 cm treatments. In 1999 harrowing was carried out twice and hoeing was carried out once. In 2000, because of weather conditions, no control was possible.

At the Unifarm site, there were two replicates of three row spacing levels: 9.3, 18.6, and 27.9 cm and the sowing density was 140 kg ha^{-1}. The only weed control was manual hoeing in the 27.9 cm treatments using two passes with a 15 cm hoe blade pushed just under the soil surface.

Study species and method. The three weed species considered in this study were naturally occurring populations of *Polygonum convolvulus, Polygonum persicaria*, and *Stellaria media*. Following the fate of individual plants was made possible by marking individuals with aluminium rings and recording the co-ordinates of their positions in each plot. At the Lovinkhoeve site in 1999, for most of the plots, all individuals of *P. convolvulus* and *P. persicaria* present in a plot were marked. Due to high densities at the Unifarm site and one plot at the Lovinkhoeve site (for *P. convolvulus* only) the individuals were randomly selected. Because of the range in sizes of *S. media* plants, only those with four true leaves were considered. For 2000, data were only collected for *P. persicaria*, as there were insufficient numbers of naturally occurring *P. convolvulus,* and *S. media* individuals. Furthermore the naturally occurring *P. persicaria* population was sparse and could only be identified at the time of harvesting. Therefore no mortality data were available.

Table 1. Overview of experimental set-up, data collected, and sample sizes in each of the three experiments.

	1999		2000
	Lovinkhoeve	Unifarm	Lovinkhoeve
Experimental set-up			
Row spacing (cm)	10, 20, 30	9.3, 18.6, 27.9	10, 20, 30
Sowing density (kg ha^{-1})	140, 180	140	140, 180
Number of replicates	4	2	4
Variety of spring wheat	Lavette	Lavette	Baldus
Individual plant performance			
Plant mass	Yes	Yes	Yes
Plant survival	Yes	Yes	Yes
Neighbourhood descriptors			
Distance to nearest crop plant (cm)	Yes	Yes	Yes
Local row spacing (cm)[a]	Yes	Yes	Yes
Distance to nearest other weed plant	Yes	Yes	No
Sample sizes (varied row spacing)			
Polygonum convolvulus (# surviving)	906 (733)	258 (200)	0
Polygonum persicaria (# surviving)	578 (444)	249 (186)	402 (402)
Stellaria media (# surviving)	1041 (790)	0	0

[a] In 2000 the local row spacing was measured as the gap width. See section Methods and Materials (Neighbourhood descriptors), and Fig 2 for explanation.

For all experiments, the above-ground part of surviving weed plants was harvested 12 weeks after seedling germination, 4 weeks before the crop was harvested. Immediately after harvesting the plants were dried at 80°C for 24 hours. Plants were then weighed and survival was noted.

Neighbourhood descriptors. The descriptors of a weed's neighbourhood were the distance of a target weed plant to the nearest crop plant, the distance to the nearest other weed plant, and the local row width (Fig. 2). Measurements of the local row width were made because the row spacing within each treatment varied due to effects of the tractor wheels during sowing (the wheels caused furrows which then pushed the pipes of the sowing machine away from their neutral position). Per row there was little variability and therefore the row width was measured at the start of each row. In 2000, when there was a gap in the row wider than the width of the row where the weed plant was located, then the local row spacing was measured at the position of the plant. The distance to the nearest other weed species was not collected in 2000, as exploratory analysis showed no relationship between target plant mass and distance to the neighbouring weed plant.

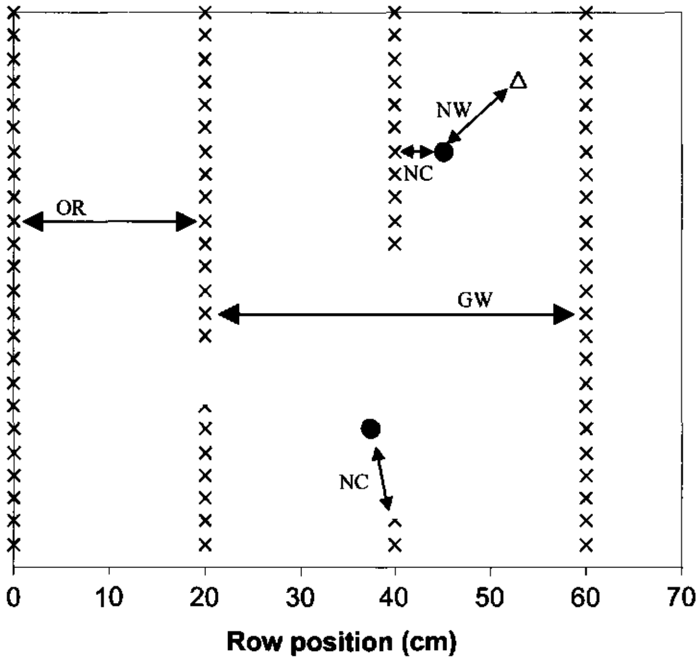

Fig. 2. Neighbourhood measures used. GW - gap width. OR - observed row spacing. NC - distance to nearest crop plant. NW - distance to nearest weed plant. **X** indicates a crop plant, ● indicates target weed plant, and Δ indicates a non-target weed plant.

Data analysis

Variability in descriptors of local environment, and weed mass. We used schematic box plots to summarise the variability in the data of distances to the nearest crop plant and of the dry mass of weed plants. For the observed row widths we present the minimum, maximum, and median widths.

Local predictors of weed survival and mass. Logistic regression models were used to investigate the effect of distance to the nearest crop plant and observed row spacing on plant survival. The probability for the *i*th weed to survive was related to the descriptors of the local environment (u_i and v_i) through:

$$\pi_i = \frac{\exp(a_0 + a_1 u_i + a_2 v_i)}{1 + \exp(a_0 + a_1 u_i + a_2 v_i)} \tag{1}$$

As survival is a binary variable, it follows the binomial distribution with the parameter π_i, resulting in the following log-likelihood function for the parameters (a_0, a_1, and a_2), given the data of whether a plant survived or not (Y_i is 1 or 0), where n is the number of observations (Neter et al. 1996b):

$$\ell(a_0, a_1, a_2; Y) = \sum_{i=1}^{n} \left[Y_i (a_0 + a_1 u_i + a_2 v_i) + \ln(1 + \exp(a_0 + a_1 u_i + a_2 v_i)) \right] \quad (2)$$

The parameters were estimated in Genstat (release 4.21), using step-down regression. As previous analysis (Chapter 3) showed that row spacing/weed control treatment had an effect on weed survival, parameters were estimated separately for each row spacing/site combination (the weed control treatments were site-dependent).

The descriptors of the local environment that were most related to above-ground dry mass of the weed plants were found using Spearman rank correlations. Only distance to the nearest crop plant (u_i) and observed row width (v_i) showed a relation with plant mass (Appendix, Table A1). Therefore predictors of plant mass were based on only these two variables. Two general predictors of plant mass were investigated, where the predicted mass of the *i*th plant ($w_{pi}(\mathbf{v}_i; \mathbf{b})$) was a function of the neighbourhood descriptors (vector $\mathbf{v}_i$), given the parameters (vector $\mathbf{b}$). The first model form describes a linear relation with regard to the parameters,

$$w_{pi}(\mathbf{v}_i; \mathbf{b}) = b_0 + b_1 u_i^{\,q} + b_2 v_i^{\,q} + b_3 u_i^q v_i^q \quad (3)$$

while the second form describes a reciprocal relation:

$$w_{pi}(\mathbf{v}_i; \mathbf{b}) = \frac{b_0}{1 + b_1 / u_i^q + b_2 / v_i^{\,q} + b_3 / (u_i v_i)^q} \quad (4)$$

The parameters, b_0, b_1, b_2, and b_3, were estimated from the data and q was a parameter for transformations of the variables with q = 1, 2, and 3 being considered. In order to avoid division by zero, 1 was added to all u_i. For both of these predictors, reduced models were created by setting parameters associated with particular variables to zero. Table A2 of the Appendix lists all the models fitted.

The parameters were estimated using maximum likelihood methods based on the gamma distribution, with the following log-likelihood function for the parameters (α and $\mathbf{b}$), given the data of observed plant masses (w_o):

$$\ell(\alpha, \mathbf{b}; w_o) = \sum_{i=1}^{n} \left[\alpha \left\{ \ln\left(\frac{\alpha w_{oi}}{w_{pi}(\mathbf{v}_i; \mathbf{b})} \right) - \frac{w_{oi}}{w_{pi}(\mathbf{v}_i; \mathbf{b})} \right\} - \ln w_{oi} - \ln \Gamma(\alpha) \right] \quad (5)$$

where w_{oi} is the observed mass of the ith plant, n is the number of plants in the sample, α is the shape parameter of the gamma distribution, and $w_{pi}(\mathbf{v}_i; \mathbf{b})$ is given by equation 3 or equation 4. The decision to use the gamma distribution was because the data appeared to follow the gamma distribution, a finding supported by other studies (Pacala and Silander 1990), because the link function of gamma distribution has a reciprocal form which is appropriate for the predictor given in equation 4 (McCullagh and Nelder 1989), and because predictions can be kept on the original scale of measurement. Furthermore inspection of plots of residuals against fitted values showed no trend.

The fitting procedure involved first using a random search for parameter estimates that yielded the lowest negative log-likelihood value. These estimates were then used as starting values for the minimisation routine of Mathematica Version 3.0 (Wolfram 1996). The Aikaike Information Criterion (AIC) was used as the basis for model selection. More traditional goodness-of-fit measures (likelihood-ratio test or F-test) were not appropriate for model selection because the two model forms (equations 3 and 4) were not nested and because the log-likelihood function was not based on the normal distribution.

A low AIC value resulting from a particular model indicates that a larger amount information contained in the data is explained by the model relative to the other models examined (Burnham and Anderson 1998). The AIC is calculated as $-2\ell + 2p$, where ℓ is the log-likelihood value resulting from a particular model and p is the number of parameters estimated. For each model, the difference in AIC (ΔAIC) was calculated relative to the model with the lowest AIC. The model with the lowest ΔAIC was used for further analysis. All predictors given in the Appendix (Table A2) were fit to the data for each combination of species, site, and year. Based on the model finally selected, we tested for differences between sites and years for each species and for effects of the three row spacing/weed control levels and the two sowing density levels, using the likelihood-ratio test statistic (Hilborn and Mangel 1997)

$$LR = 2\left\{ \ell(w;m_a) - \sum_s \ell(w;m_s) \right\}, \tag{6}$$

where w are the data, m_a is a single model fit to the data aggregated over year, site, or experimental treatment and where m_s are models that are fit to the data separated by year, site, or experimental treatment and the log-likelihoods resulting from each model are summed. The likelihood ratio test statistic (*LR*) has an approximate χ^2-distribution with the degrees of freedom given by the difference in the number of parameters between m_a and the total number of parameters over all the m_s. Standard errors of the parameters for the models with the best fit on the basis of the likelihood-ratio test were then calculated in Genstat (release 4.21). The goodness-of-fit was measured by comparing the deviance with the residual degrees of freedom. If the value of the deviance is near that the number of residual degrees of freedom, then the fit is considered good (McCullagh and Nelder 1989).

RESULTS

Variability in descriptors of local environment and plant mass

The distribution of distances to the nearest crop plant was rather symmetrical around the median value (Fig. 3). The minimum distance was zero for all treatments except one. The median and range of distances increased with increasing row spacing. Distances that were larger than half the treatment row spacing were due to occasions when crop plants were missing from the crop row, or the observed row width was wider than the treatment row width. The median distances in the Lovinkhoeve 2000 experiment (Fig. 3iii) were lower in the 180 kg ha^{-1} sowing density treatment than in the 140 ha^{-1}. This was most likely due to the smaller sample size than to an effect of the sowing density treatment.

For the observed row widths, the range in widths was smallest for the 27.9 and 30 cm treatments (Table 2). The median row widths were close to the treatment row spacing. In 2000, 40 plants were in gaps, with 34 of the plants in the 10 cm row spacing treatment. In that treatment the gap size ranged from 11 to 24 cm, with a median gap size of 16 cm. In the 20 cm treatment the five plants were in gaps of 36 and 38 cm, while only one plant was in a gap (58 cm) in the 30 cm treatment.

The distribution of plant masses was highly skewed towards high masses for all treatments (Fig. 4). Maximum plant masses were often well over 10 times the median plant mass. The minimum plant mass in each treatment was usually close to zero grams. In the 180 kg ha^{-1} sowing density treatments, median plant masses tended to be lower than in the 140 kg ha^{-1} sowing density treatments.

Table 2. Observed row widths (cm) for each row spacing treatment in each experiment.

	Lovinkhoeve						Unifarm		
	10 cm		20 cm		30 cm		9.3 cm	18.6 cm	27.9 cm
	1999	2000	1999	2000	1999	2000	1999		
Minimum	5	4	13	14	–	26	4	11	20
Maximum	20	18	26	25	–	33	18	22	29
Median	10	10	20	20	–	30	9	18	28

– no observations available.

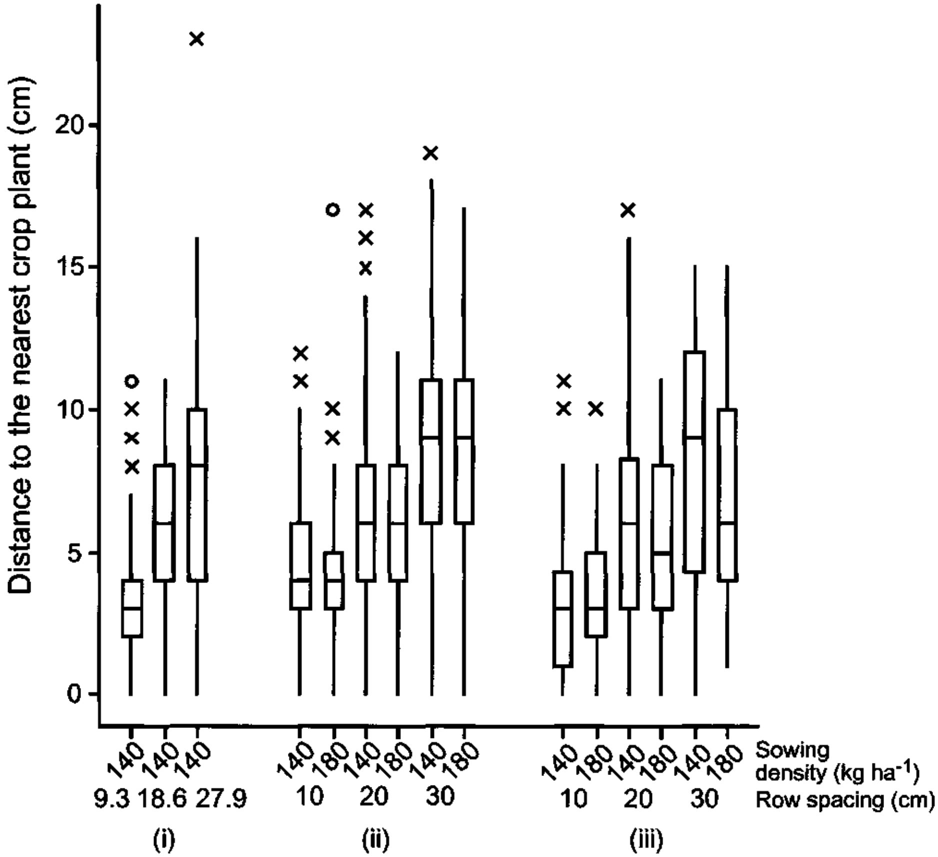

Fig. 3. Box plots of distances to the nearest crop plant. (i) Unifarm 1999. (ii) Lovinkhoeve 1999. (iii) Lovinkhoeve 2000. The ends of the boxes bound the plant masses containing the middle 50% of the data (interquartile range). The line dividing the box indicates the median distance. The whiskers extend to the most extreme values within 1.5 interquartile ranges from the ends of the box. Observations marked with × are minor outliers and are in the region of 1.5 to 3.0 interquartile ranges from the ends of the box. Observations marked with o are major outliers and are in the region of more than 3.0 interquartile ranges from the ends of the box.

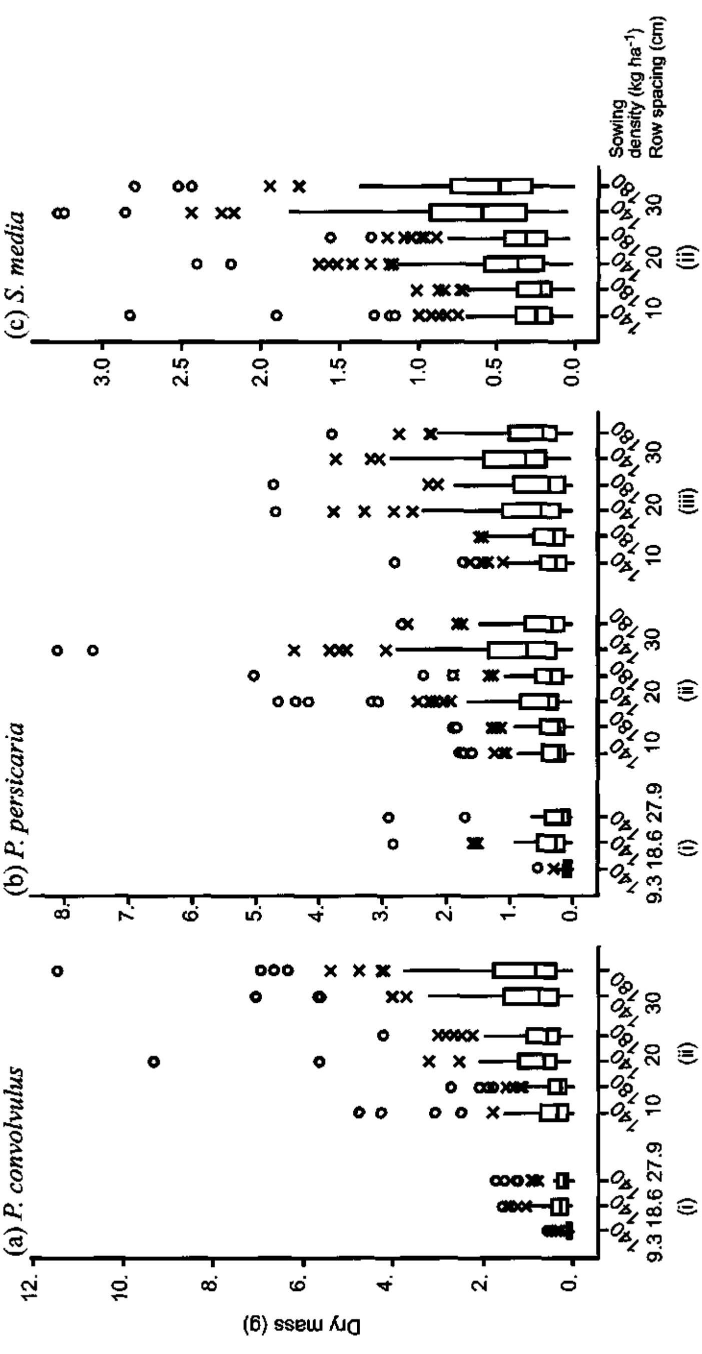

Fig. 4. Box plots of weed dry mass. (i) Unifarm 1999. (ii) Lovinkhoeve 1999. (iii) Lovinkhoeve 2000. See the caption of Fig. 3 for explanation of the symbols.

Local predictors of plant survival and mass

Plant survival. There was a significant effect on individual weed survival of only distance to the nearest crop plant in the widest row spacing treatments at both sites (Table 3). Survival decreased with increasing distance from the crop plants (Fig. 5). Visual inspection of the fitted predictor and the observed values shows good agreement, except for cases where there were few observations. At the Unifarm site, survival dropped more suddenly with distance from the nearest crop plant compared to the Lovinkhoeve site (Fig. 5(ii)a-b). The decrease in plant survival with increasing distance in the wide row spacing was due to mechanical hoeing.

Plant mass. When the predictors of plant mass were ranked by the difference in AIC (ΔAIC) calculated over all species and experiments, the model $w_{pi} = b_0 + b_1 u_i^2 + b_2 v_i^2$ was clearly the most parsimonious overall predictor (Table 4). It was the best model for *P. convolvulus* and *P. persicaria*, and the second best for *S. media*. In the Appendix (Table A3) we show the ΔAIC for all the models for each species. As the linear predictor with squared variables was clearly the best model, we investigated whether the fit was affected by aggregating data over sites and years, or separating it according to experimental treatment. Fitting the model to data aggregated over sites and years did not lead to a lower AIC (Table 5). When the model was fit to data separated by sowing density, the fit was much improved for all species in the 1999 experiment (Table 6). In 2000 the fit was not improved by separating the data by

Table 3. Effect of distance to the nearest crop plant and observed row width on plant survival, measured as approximate *p*-values from the analysis of deviance for the logistic regression. The regression model was fit to data separated by row spacing treatment. Two degrees of freedom were lost by fitting the model.

	Lovinkhoeve			Unifarm		
	Dist. to nearest crop plant	Observed row width	Residual df	Dist. to nearest crop plant	Observed row width	Residual df
	10 cm			9.3 cm		
P. convolvulus	0.662	0.937	351	0.847	0.678	6
P. persicaria	0.144	0.281	191	0.290	0.557	82
S. media	0.875	0.880	346	–	–	–
	20 cm			18.6 cm		
P. convolvulus	0.183	0.309	196	0.578	0.987	79
P. persicaria	0.555	0.313	152	0.053	0.951	76
S. media	0.770	0.467	324	–	–	–
	30 cm			27.9 cm		
P. convolvulus	<0.001	–	349	<0.001	0.117	84
P. persicaria	<0.001	–	236	<0.001	0.248	82
S. media	<0.001	–	362	–	–	–

– no observations available.

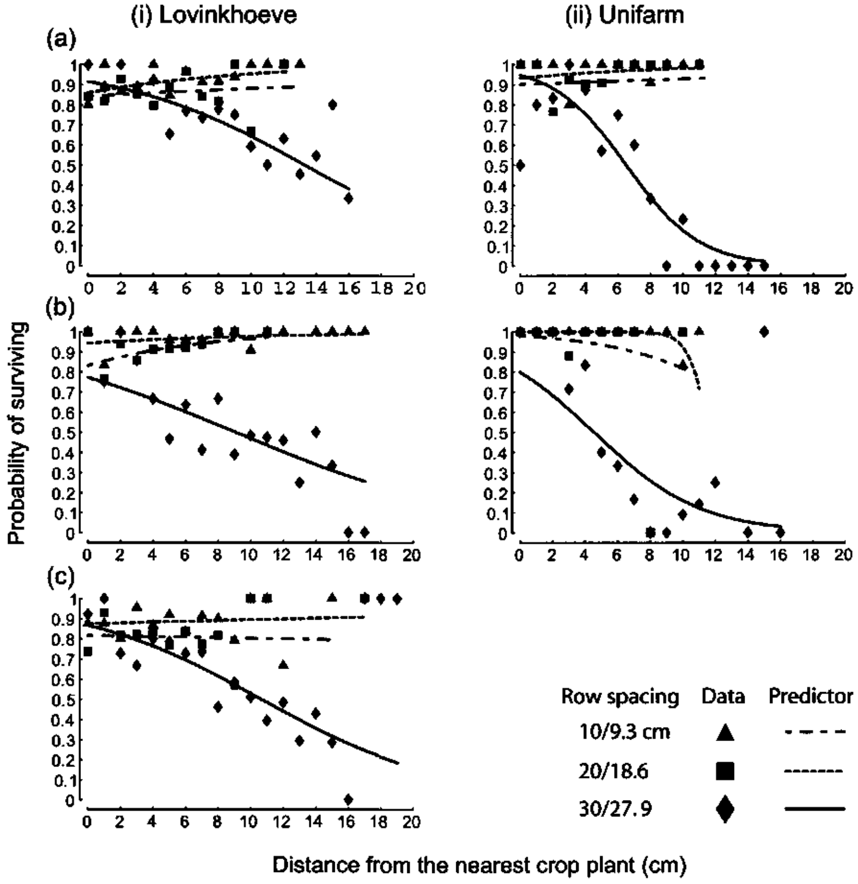

Fig. 5 Relationship between chance of survival and distance from the nearest crop plant (1999 data only). (a) *P. convolvulus.* (b) *P. persicaria.* (c) *S. media.*

Table 4. The four predictors of plant mass with the lowest ΔAIC for each species and over all species.

Model	*P. convolvulus*	*P. persicaria*	*S. media*	Total
$b_0 + b_1 u_i^{\ 2} + b_2 v_i^{\ 2}$	0.0	0.0	1.9	0.0
$b_0 + b_1 u_i^{\ 3} + b_2 v_i^{\ 3}$	0.2	–	5.2	24.4
$b_0 + b_1 (u_i + v_i)^2$	13.9	–	0.0	29.8
$b_0 + b_1 u_i^{\ 1} + b_2 v_i^{\ 1}$	–	–	–	33.6
$b_0 + b_1 (u_i + v_i)^1$	17.0	–	–	–
$b_0 + b_1 (u_i v_i)^1$	–	4.7	–	–
$b_0 + b_1 v_i^{\ 1}$	–	9.0	–	–
$\dfrac{b_0}{1 + b_1 / u_i^{\ 1} + b_2 / v_i^{\ 1}}$	–	17.7	–	–
$b_0 + b_1 (u_i + v_i)^3$	–	–	5.2	–

– predictors with a ranking higher than 4 for a given species.

Table 5. Difference in model fit between years and sites for *P. convolvulus* and *P. persicaria* for the predictor $w_{pi} = b_0 + b_0 u_i^2 + b_0 v_i^2$.

	AIC			
Contrast	Aggregated data (# of parameters)	Separate data (# of parameters)	ΔAIC	Likelihood ratio test statistic (*p*-value)
P. convolvulus				
Sites	no convergence	792.9 (8)	–	–
P. persicaria				
Sites	277.0 (4)	232.3 (8)	47.7	55.7 (<<0.0001)
Years	4664.1 (4)	797.3 (8)	3866.8	3874.8 (<<0.0001)
Years and sites	705.2 (4)	641.4 (12)	63.8	71.8 (<<0.0001)

Table 6. Difference in model fit between sowing densities for all three species at the Lovinkhoeve site for the predictor $w_{pi} = b_0 + b_0 u_i^2 + b_0 v_i^2$.

	AIC			
Year	Aggregated data (# of parameters)	Separate data (# of parameters)	ΔAIC	Likelihood ratio test statistic (*p*-value)
P. convolvulus				
1999	999.7 (4)	990.8 (8)	8.9	16.9 (0.002)
P. persicaria				
1999	388.2 (4)	385.2 (8)	3.0	11.0 (0.027)
2000	409.1 (4)	409.1 (8)	0.0	0.0 (1.00)
S. media				
1999	66.6 (4)	60.7 (8)	5.9	13.9 (0.007)

Table 7. Deviance, residual degrees of freedom, and parameter values with the standard errors in parentheses resulting from fitting the model $w_{pi} = b_0 + b_0 u_i^2 + b_0 v_i^2$ to the data sets in the table.

	P. convolvulus			*P. persicaria*				*S. media*	
	1999			1999			2000	1999	
	Lovinkhoeve		Unifarm	Lovinkhoeve		Unifarm	Lovinkhoeve	Lovinkhoeve	
	Sowing density (kg ha^{-1})								
	140	180	140	140	180	140		140	180
Deviance	283.0	370.1	141.7	224.6	191.2	169.7	370.6	247.2	189.8
Residual df	297	428	196	237	199	182	398	422	360
b_0 (× 10^{-1})	2.84	2.25	0.43	1.44	2.71	0.40	2.41	2.18	1.91
	(0.55)	(0.33)	(0.14)	(0.44)	(0.56)	(0.18)	(0.45)	(0.25)	(0.22)
b_1 (× 10^{-4})	5.02	8.01	4.00	4.70	2.52	5.77	4.70	4.26	3.52
	(1.46)	(1.26)	(0.76)	(1.46)	(1.19)	(1.25)	(1.45)	(0.69)	(0.52)
b_2 (× 10^{-3})	6.69	3.96	2.83	5.96	2.29	2.23	4.02	1.55	1.10
	(1.34)	(1.00)	(0.55)	(1.21)	(1.22)	(0.68)	(0.94)	(0.48)	(0.46)

sowing density treatment. Fitting the model to data separated by rowing spacing treatment failed to converge for most data sets.

The fit of the final models was good as the deviance values were close to the number of residual degrees of freedom. The parameter values resulting from fitting the selected model were positive, so plant mass increased with increasing distance from a crop plant and increasing row width. Confidence intervals based on the standard errors in Table 7 would exclude zero. For all species, the intercept was of magnitude 10^{-1}. The parameter b_2, associated with distance to the nearest crop plant was one order of magnitude larger than b_1. Therefore plant mass increased faster with distance from the nearest crop plant than with increasing row width. Plants at the Unifarm site were predicted to be smaller than their counterparts in 1999 at the Lovinkhoeve site, regardless of the sowing density treatment.

DISCUSSION

In this study we have sought to identify which weed plants will contribute most to future generations and whether there is a pattern in the contributions. We have considered naturally occurring weed plants growing in a spring wheat crop at three row spacing/weed control levels and two sowing densities. We first examined whether weed plants experienced different environments, both within and between crop planting patterns. Secondly, we identified predictors of plant mass and survival based on descriptors of the local environment.

Weed plants experienced a range of local environments both between and within the experimental treatments. For all species, plant mass increased with the square of the distance to the nearest crop plant and the square of the observed row crop emergence? – Do different crop planting patterns lead to different weed spatial patterns?

Almost 40 years ago, Harper stated that there was a widening gulf between experiments on individuals and experiments in populations and he wished to focus attention on 'the reaction of a plant to its neighbours as a critical, often the most critical, part of the autecology of a species and to suggest that this type of study has a cementing and unifying function in the science of plant ecology' (Harper 1964). His remarks are very relevant to weed ecology today because most ecological studies of weeds have been at the level of the population. We have shown that individual weed plants in a crop have different probabilities of survival and have different reproductive potentials and that these differences are related to differences in the local environments perceived by the individuals. It is therefore not sufficient to remain at the population level for the development of management strategies. Further insights on the ecology of weeds will come about through an increased focus on the role of the individual.

APPENDIX

Table A1. Spearman rank correlations between mass per plant and local predictors. See section *Methods and Materials: Experimental methods* and Fig. 2 for descriptions of the various distance measures.

Site	Species	Nearest crop plant	Observed row width	Nearest weed plant
Unifarm 1999	*P. convolvulus*	0.34***	0.37***	–0.10
	P. persicaria	0.33***	0.39***	0.16*
Lovinkhoeve 1999	*P. convolvulus*	0.35***	0.37***	0.09*
	P. persicaria	0.38***	0.30***	0.05
	S. media	0.29***	0.37***	0.05
Lovinkhoeve 2000	*P. persicaria*	0.38***	0.40***	–

Levels of significance: *** ($p \leq 0.0005$), **($0.0005 < p \leq 0.001$), *($0.001 < p \leq 0.05$)

Table A2. Codes for the models fitted to the data. The entries of the table are the abbreviations for each model/variable combination that was fitted to the data. The letter 'l' of the coding stands for the linear model form, while the 'r' stands for the reciprocal model form. Models with only one variable are given in (a) and models with two or variables are given in (b).

(a)

Variable	—Model form—	
x	$b_0 + b_1 x$	$\frac{b_0}{1 + b_1 / x}$
u^1	lu^1	ru^1
u^2	lu^2	ru^2
u^3	lu^3	ru^3
v^1	lv^1	rv^1
v^2	lv^2	rv^2
v^3	lv^3	rv^3
$(u+v)^1$	$l(u+v)^1$	$r(u+v)^1$
$(u+v)^2$	$l(u+v)^2$	$r(u+v)^2$
$(u+v)^3$	$l(u+v)^3$	$r(u+v)^3$
$(uv)^1$	$l(uv)^1$	$r(uv)^1$

(b)

Variables		————Model form————			
x_1	x_2	$b_0 + b_1 x_1 + b_2 x_2$	$b_0 + b_1 x_1 + b_2 x_2 + b_1 x_1 x_2$	$\frac{b_0}{1 + b_1 / x_1 + b_2 / x_2}$	$\frac{b_0}{1 + b_1 / x_1 + b_2 / x_2 + b_3 / x_1 x_2}$
u^1	v^1	lu^1v^1	lu^1v^1x	ru^1v^1	ru^1v^1x
u^2	v^2	lu^2v^2	lu^2v^2x	ru^2v^2	ru^2v^2x
u^3	v^3	lu^3v^3	lu^3v^3x	ru^3v^3	ru^3v^3x

Table A3. Ranking of models for each species by the sum of the AIC values over all and their differences relative to the model with the lowest AIC sum over each data set per species and over all data sets.

P. convolvulus		*P. persicaria*		*S. media*		——Total——	
Model	ΔAIC	Model	ΔAIC	Model	ΔAIC	Model	ΔAIC
lu^2v^2	0.0	lu^2v^2	0.0	$l(u+v)^2$	0.0	lu^2v^2	0.0
lu^3v^3	0.2	$l(uv)^1$	4.7	lu^2v^2	1.9	lu^3v^3	24.4
$l(u+v)^2$	13.9	lv^1	9.0	$l(u+v)^3$	2.3	$l(u+v)^2$	29.8
lu^1	17.0	ru^1v^1	17.7	lu^3v^3	5.2	lu^1v^1	33.6
$l(uv)^1$	17.8	$l(u+v)^2$	17.9	$l(u+v)^1$	8.4	$l(uv)^1$	50.5
$l(u+v)$	26.7	lu^3v^3	21.0	lu^3v^3x	8.9	$l(u+v)^3$	60.3
$r(u+v)^1$	26.7	$r(u+v)^1$	28.2	lu^1v^1	9.6	$l(u+v)^1$	61.4
$l(u+v)^3$	29.0	$l(u+v)^1$	28.2	$r(u+v)^1$	14.6	$r(u+v)^1$	67.6
ru^1v^1	32.8	$r(u+v)^2$	28.7	lv^2	21.4	ru^1v^1	75.1
$r(u+v)^2$	42.9	$l(u+v)^3$	30.9	lv^3	22.3	$r(u+v)^2$	114.0
$r(uv)^1$	63.7	$r(uv)^1$	40.0	ru^1v^1	26.5	$r(uv)^1$	172.5
lv^1	83.1	ru^2v^2	47.0	ru^1v^1x	28.5	lv^1	196.1
$r(u+v)^3$	85.8	$r(u+v)^3$	62.7	lv^1	29.3	lv^2	197.0
lv^2	87.5	lu^2	64.2	$l(uv)^1$	29.9	rv^1	216.2
rv^1	88.3	lu^1	68.6	rv^1	43.4	$r(u+v)^3$	226.2
lv^3	104.5	lu^3	79.7	$r(u+v)^2$	44.4	lv^3	235.8
rv^2	107.5	lv^1	85.6	ru^2v^2	64.1	lu^2	275.0
lu^2	107.8	rv^1	86.4	$r(uv)^1$	70.8	rv^2	275.7
lu^3	110.1	lv^2	90.0	rv^2	75.5	lu^3	296.1
lu^1	123.3	rv^2	94.7	$r(u+v)^3$	79.7	lu^1	301.7
rv^3	139.6	ru^3v^3	99.1	ru^3v^3	98.4	rv^3	371.2
ru^1	163.4	ru^1	105.9	lu^2	105.0	ru^1	411.1
ru^2	215.7	lv^3	111.0	rv^3	106.6	ru^2	554.2
ru^3	234.4	rv^3	126.9	lu^3	108.2	ru^3	624.7
lu^1v^1x	–	ru^2	179.2	lu^1	111.6	lu^1v^1x	–
lu^2v^2x	–	ru^3	225.9	ru^1	143.8	lu^2v^2x	–
lu^3v^3x	–	lu^1v^1x	–	ru^2	161.2	lu^3v^3x	–
ru^2v^2	–	lu^2v^2x	–	ru^3	166.4	ru^2v^2	–
ru^3v^3	–	lu^3v^3x	–	lu^2v^2x	–	ru^3v^3	–
ru^1v^1x	–	ru^1v^1x	–	lu^3v^3x	–	ru^1v^1x	–
ru^2v^2x	–	ru^2v^2x	–	ru^2v^2x	–	ru^2v^2x	–
ru^3v^3x	–	ru^3v^3x	–	ru^3v^3x	–	ru^3v^3x	–

– no convergence in parameter estimation.

CHAPTER 5

Weed Populations and Crop Rotations: Exploring Dynamics of a Structured Periodic System

ABSTRACT

The periodic growing of a certain set of crops in a prescribed order, called a crop rotation, is considered to be an important tool for managing weed populations. Nevertheless, the effects of crop rotations on weed population dynamics are not well understood. Explanations for rotation effects on weed populations usually invoke the diversity of environments caused by different crops that a weed population encounters. Using a periodic matrix model, we show that the number of different crops is not the sole factor, and that the sequence of a given set of crops can play an important role. In the model the weed population is structured by seed depth in the soil, and ploughing moves seeds between layers. For illustration of concepts, we use parameter values thought to be characteristic for *Polygonum persicaria* growing in carrots (crop A) and spring wheat (crop B) in the Netherlands. We systematically examine the population growth rates for *P. persicaria* and their sensitivity to changes for all rotations of two to six years based on crops A and B. We include eight scenarios that differ in the effects of ploughing and seed survival over winter. Differences between rotations can be striking. For example the weed population growth rate in the baseline rotation AABB (assuming 100% winter survival) is nearly 25% lower than in rotation ABAB. The elasticity (a measure to quantify the effect of proportional changes in model parameters on population growth) to seedling survival is nearly 75% higher in the B years of rotation ABAB than in the B years of rotation AABB. Changing parameter values changes the relation between population dynamics and rotation organization, but not the conclusion that there are consequences for population dynamics and management due to choice of a rotation. While our example is an agronomic one, the question – Does sequence matter? – and the methods applied should be of interest to researchers and managers concerned with the periodic management of other ecosystems.

Adapted from: Mertens, S. K., F. van den Bosch, and J. A. P. Heesterbeek. 2002. Weed populations and crop rotations: exploring dynamics of a structured periodic system. Ecological Applications. 12: 1125-1141.

INTRODUCTION

Crop rotation –the growing of different crops in recurring succession on the same land– has long been advocated as a method to increase crop yields and reduce inputs (Leighty 1938, Fream and Robinson 1949). Explanations for increased yields of crops grown in a rotation system rather than as a continuous monoculture crop include the periodic changes in the environment that prevent particular pests, diseases, and weeds from dominating, and the decreased stress on the soils by including crops that require less cultivation or that increase nutrient and organic matter inputs (Crookston 1984, Crookston et al. 1991). The development of problematic weed populations is thought to be prevented by the diverse environments that weed populations encounter over the course of a crop rotation cycle (Liebman and Dyck 1993, Liebman and Gallandt 1997). For example, sowing dates, weed-control methods, and competition from the crop will differ from season to season as the crop species change.

Each of the diverse environments is characteristic of a given crop. A crop rotation, by definition, extends over several cropping seasons. A rotation's organisation includes the crop species, their proportion and order, and the length of the rotation (number of cropping periods). A natural question is whether the organisation of a crop rotation, given a set of crops, will affect weed-population growth rates. For example, would a rotation of alternating carrot and wheat crops result in a different weed-population growth rate than a rotation consisting of two consecutive years of carrots followed by two consecutive years of wheat?

Up to now there have been few experimental or theoretical studies that directly and systematically address the effect of crop sequence on weed-population growth rates. Most studies have concentrated on comparing a continuous monoculture crop with one or more different rotations, usually in combination with different tillage or weed control treatments (Martin and McMillan 1984, Schweizer et al. 1988, Blackshaw et al. 1994, Doucet et al. 1999, Kegode et al. 1999). Some modelling studies of weed population dynamics have included crop rotations, but did not systematically examine the effect of different crop rotations based on their set of crops (Gonzalez-Andujar and Fernandez-Quintanilla 1991, Jordan et al. 1995, Lindquist et al. 1995, Squire et al. 1997).

In a more general ecological setting, the realisation of the importance of the timing of events in a periodic system is not new; Darwin and Williams (1964) found that the season of hunting affected the population growth rate of an age-structured population of rabbits. More recent studies have concentrated on the frequency of nominally periodic events, such as fire and drought (Gotelli 1991, Gross et al. 1998, Hoffman 1999), but have not examined the effect of systematically different orders of events on growth rates or on possibilities for management. Golubov et al. (1999) in their study of *Prosopis glandulosa* (honey mesquite) calculated the periodic growth rates for all combinations of their four, yearly transition matrices. However their aim was to obtain a confidence interval for the periodic growth rate. The population dynamics of annual weeds in a crop rotation represent a very simple periodic system, but one allowing multiple avenues for intervention, for example through changing the rotation itself or through changing the weed population's vital rates, through management, in a particular crop. A better understanding of weed population dynamics in crop rotations may contribute insights applicable to the understanding and management of species in other ecosystems.

Our purpose is the systematic examination of the effects of different crop rotations on weed population dynamics and on possibilities for management. Our questions pertain to how the proportion of crops, their order, and number affect the population growth rate of a depth-structured seedbank and the growth rate's sensitivity to changes in life-cycle processes. Answering these questions with field experiments, because of their long-term nature, is practically difficult. We therefore find answers through use of a mathematical model that captures essential features of our system but that is simple enough to allow in-depth investigation of the processes affecting weed population dynamics in crop rotations. Our investigation is restricted to a weed with a semelparous life history, growing in two crops, where its seedbank is structured by depth and seeds can be moved vertically in the soil by ploughing. A particularly suitable description is a periodic matrix model. This choice also allows application of a considerable body of theory (de Kroon et al. 1986, Caswell 1989, Caswell and Trevisan 1994, Benton and Grant 1999, de Kroon et al. 2000). We illustrate concepts with parameter values characteristic for *Polygonum persicaria* L. (redshank) growing in a variety of rotations, composed of carrots and spring wheat in the Netherlands.

METHODS

Model construction

The transition matrices. As the ability of a seed to germinate and emerge varies with depth (Vleeshouwers 1997a), and as tillage operations redistribute seeds in the soil (Cousens and Moss 1990), a weed seed population can be considered as being structured by the depth at which seeds are located. We distinguish two soil layers,

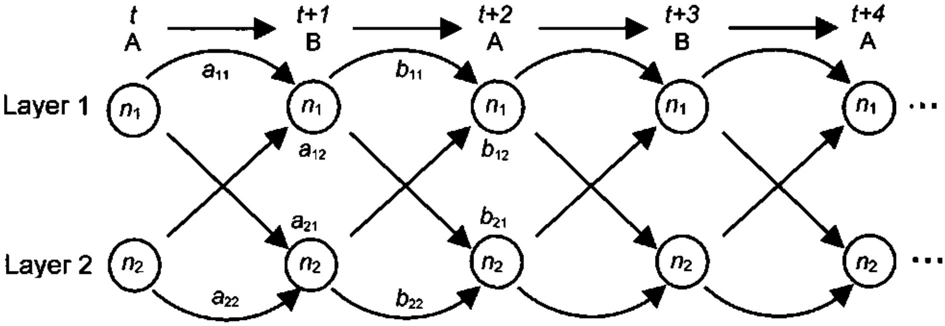

Fig. 1. Transitions in a two-year rotation of crops A and B. Weed seeds in soil are in either layer 1 or 2, and n = the number of weed seeds in layer 1 or 2 at time t; a_{ij} = the contribution of one seed in layer j at time t to the population of seeds in layer i at time $t+1$.

where the top layer is indexed 1 and the bottom layer indexed 2. The number of seeds in soil layers 1 and 2 at time t can be represented as a vector, $\mathbf{n}(t)$:

$$\mathbf{n}(t) = \begin{pmatrix} n_1(t) \\ n_2(t) \end{pmatrix} \tag{1}$$

We regard time in discrete steps of 1 yr, where one crop is grown per year. Each time step the weed seed population in each soil layer can be calculated by applying a matrix of transition rules to the population vector resulting from the previous time step. The transition rules, also called transitions, describe seed survival, reproduction, and movement between soil layers. These rules, and therefore the matrices, will be different depending on the particular crop grown each year. We consider two crops only, A and B, and assume that the transition rules only depend on the crop in question and not the crop that was grown, say, in the previous year. For a two-year rotation of crops A and B, the seeds will follow the transitions given in Fig. 1. These yearly transitions yield matrices **A** and **B**, for the respective crops, e.g., for crop A

$$\mathbf{A} = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix} \tag{2}$$

where the element a_{ij} of matrix **A** is the contribution of one seed in layer j, at time t, to the population of seeds in layer i, at time t+1. The population over a complete cycle of the rotation AB, is given as:

$$\mathbf{n}(t+2)=\mathbf{BAn}(t), \tag{3}$$

i.e., first apply the transition matrix **A** and then the matrix **B** (since crop A is grown first, followed by crop B).

In order to distinguish different years within a rotation cycle and in keeping with the terminology of Caswell and Trevisan (1994), we call each year of a rotation a 'phase' and number the phases with respect to some 'reference rotation.' Defining rotation AB as the reference rotation, then crop A occurs in phase 1, denoted $A^{(1)}$, and crop B occurs in phase 2, denoted $B^{(2)}$. The rotation $B^{(2)}A^{(1)}$ is the cyclic permutation of AB, and starts with phase 2 of the reference rotation AB. Different cyclic permutations of some reference rotation will have the same population growth rate, but other properties, such as the distribution of seeds over soil layers at the end of the rotation, will differ for each cyclic permutation of the reference rotation. Cyclic permutations of a given rotation will have identical population growth rates because in the long term the rotations are identical. Properties such as the depth distribution of seeds are expected to change because processes occurring during the previous crop act on the depth distribution present at the start of that crop. More details on these effects are given in following sections.

We also wish to distinguish rotations that cannot be cyclically permuted to give identical rotations. Rotations ABAB and AABB are such rotations, and we call them 'essentially different.' Essentially different rotations are expected to produce different population growth rates.

In general, for some given rotation, the dynamics are:

$$\mathbf{n}(t+p)=\mathbf{M}^{(h)}\mathbf{n}(t) \tag{4}$$

where **M** is the matrix product of the yearly transitions, starting in phase *h*, where *h* will be in $\{1, 2, 3,..., p\}$, and *p* is the length (period) of the rotation. We define reference rotations lexicographically, so that the largest block of consecutive A crops in the rotation occurs first. Thus, for example, rotations consisting of consecutive blocks of two A crops and two B crops will have the reference rotation AABB, whose matrix product is $\mathbf{M}^{(1)}=\mathbf{B}^{(4)}\mathbf{B}^{(3)}\mathbf{A}^{(2)}\mathbf{A}^{(1)}$. If the rotation starts with the last B crop, giving rotation BAAB, the matrix product is $\mathbf{M}^{(4)}=\mathbf{B}^{(3)}\mathbf{A}^{(2)}\mathbf{A}^{(1)}\mathbf{B}^{(4)}$.

For our example crops, A and B, we systematically examine all essentially different cropping sequences of two to six years, as well as monocultures of both crops. In practice crop rotations do not usually exceed six years. For each rotation length, all possible ratios of the two crops and all essentially different orders are

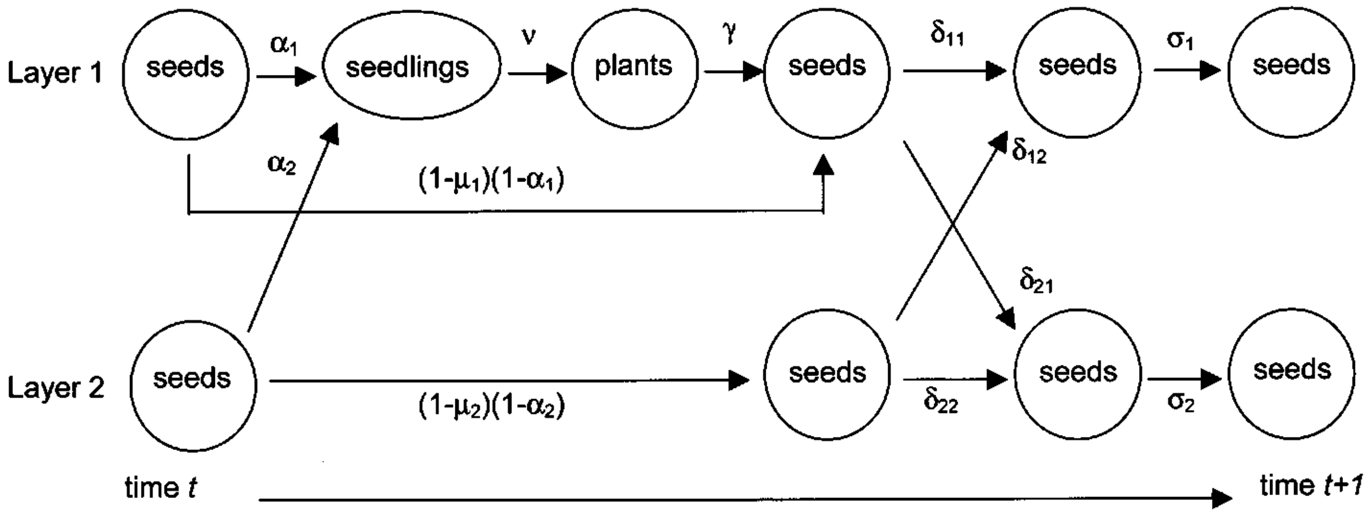

Fig. 2. Weed life history used in defining the transition rules. See section *Methods: Life history underlying transitions* and Table 1 for explanation of symbols. The life cycle begins in the spring of one year and ends in the spring of the following year.

investigated. We also examine the effect of increasing rotation length while keeping the proportion of each crop the same for the series AB, AABB, AAABBB, and so on.

Life history underlying the transitions. As it is difficult to directly measure the transitions a_{ij} and b_{ij}, and as it is not possible to directly manipulate them because they are composed of a variety of biological and management processes, we must consider a weed's life cycle and the parameters that underlie transitions from one stage to the next. Fig. 2 illustrates the life cycle for a summer annual weed growing in a crop, where tillage occurs in the fall. By following the paths seeds take over their life, one arrives at the transition values. For example, the contribution of this year's seeds in layer 1 to next year's population in layer 1, i.e., a_{11} or b_{11}, can be broken down as follows: at time t a certain fraction α_1 emerge from the top layer, of which a fraction ν plants survive, with each surviving plant producing γ seeds. The newly produced seeds are added to the fraction of seeds that did not emerge and that survived, $(1-\mu_1)(1-\alpha_1)$, where μ_1 is the fraction of seeds in the top layer that died or were lost. The seeds are then moved between layers by ploughing in the fall, with a fraction δ_{11} remaining in layer 1, i.e., moving from layer 1 back to layer 1, and then a fraction σ_1 survive over the winter to time t+1. In short the transition rule for remaining in layer 1 of crop A is $a_{11} = \alpha_1\nu\gamma\delta_{11}\sigma_1 + (1-\mu_1)(1-\alpha_1)\delta_{11}\sigma_1$. The other transitions can be calculated in a similar fashion, giving for crop A

$$\begin{aligned} a_{12} &= \alpha_2\nu\gamma\delta_{11}\sigma_1 + (1-\mu_2)(1-\alpha_2)\delta_{12}\sigma_1 \\ a_{21} &= \alpha_1\nu\gamma\delta_{21}\sigma_2 + (1-\mu_1)(1-\alpha_1)\delta_{21}\sigma_2 \\ a_{22} &= \alpha_2\nu\gamma\delta_{21}\sigma_2 + (1-\mu_2)(1-\alpha_2)\delta_{22}\sigma_2 \end{aligned} \tag{5}$$

Each transition consists of two terms, the first one representing reproduction, and the second representing survival. The subscripts on the parameters for seed movement (δ_{ij}) indicate transfer of seeds from layer j to layer i. All parameter values can depend on the crop and can therefore be different for crops A and B.

Parameter values used. For the purposes of illustration we have used parameter values that resemble those for *Polygonum persicaria*, growing in crops similar to carrots (crop A) and spring wheat (crop B), under non-herbicide weed-management regimes in the Netherlands (Table 1). The life cycle begins 1 April and continues until 31 March the following year. The depths of the soil layers are 0-5 cm for layer 1 and 5-20 cm for layer 2. Vleeshouwers (1997a) has shown that *P. persicaria* does not usually emerge from depths > 5 cm. The parameters for seed movement are based on a ploughing matrix experimentally measured by Cousens and Moss (1990).

The values of the parameters for emergence and mortality are derived from experiments by Vleeshouwers (1997b) on the emergence and fate of *P. persicaria* seeds in relation to the timing of disturbance (e.g., seedbed preparation, shallow cultivation).

Table 1. Baseline ($\sigma_1=1$) parameter values (based on *Polygonum persicaria* growing in carrots (A) and spring wheat (B) under non-herbicide weed-management regimes in the Netherlands.

Parameter	Description	Crop A	Crop B
α_1	seedling emergence from layer 1	0.45	0.15
α_2	seedling emergence from layer 2	0.00	0.00
μ_1	seed mortality layer 1	1.00	0.3
μ_2	seed mortality layer 2	0.20	0.20
v	fraction of seedlings surviving weed control	0.001	0.60
γ	seed production per surviving plant	400	90
σ_i	survival over winter	1.00	1.00
δ_{11}	fraction of seeds remaining in layer 1	0.02	0.02
δ_{12}	fraction of seeds moving from layer 2 to layer 1	0.29	0.29
δ_{21}	fraction of seeds moving from layer 1 to layer 2	0.98	0.98
δ_{22}	fraction of seeds remaining in layer 2	0.71	0.71

The timings of disturbances used by Vleeshouwers (1997b) are similar to those that would occur for seedbed preparation of carrots (crop A) and spring wheat (crop B). Experiments by Roberts and Neilson (1980) indicate that seed age does not have an important effect on the probability of emergence of *P. persicaria* seedlings. Under a non-herbicide weed-management regime, the fraction of seedlings surviving control (v) is much lower for carrots than for spring wheat, because of the increased efficacy of mechanical and hand control in carrot crops. The number of seeds produced per surviving weed (γ) is much higher in carrots than in wheat because a carrot crop is less competitive than a wheat crop. As there is no information concerning winter survival of *P. persicaria* seeds these parameters (σ_i) have been set to 1.

Using the parameter values for crops A and B in the above setting (the 'baseline ($\sigma_1=1$)' parameter set) and the equations for the transition elements (equation 5), we obtain the following matrices

$$\mathbf{A}=\begin{pmatrix}0.0036 & 0.2320\\ 0.1764 & 0.5680\end{pmatrix}$$
$$\mathbf{B}=\begin{pmatrix}0.1739 & 0.2320\\ 8.5211 & 0.5680\end{pmatrix} \qquad (6)$$

In the analysis of different rotations it is useful to appreciate that in the top layer of crop A, before ploughing, about 0.2 seeds are produced per seed ($a_{11}+a_{21}$), while in the top layer of crop B, also before ploughing, about 9 seeds are produced per seed ($b_{11}+b_{21}$). In the bottom layer of both crops, 0.8 seeds per seed are produced before ploughing ($a_{12}+a_{22}$, $b_{12}+b_{22}$,).

Table 2. Parameter values used for each crop in each scenario.

	Scenario															
	Baseline				No-till A				No-till B				No-till A and B			
	$\sigma_l = 1$		$\sigma_l = 0.8$		$\sigma_l = 1$		$\sigma_l = 0.5$		$\sigma_l = 1$		$\sigma_l = 0.5$		$\sigma_l = 1$		$\sigma_l = 0.5$	
Parameter	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B
δ_{11}	0.02	0.02	-	-	0.98	-	0.98	-	-	0.98	-	0.98	0.98	0.98	0.98	0.98
δ_{21}	0.98	0.98	-	-	0.02	-	0.02	-	-	0.02	-	0.02	0.02	0.02	0.02	0.02
δ_{12}	0.29	0.29	-	-	0.02	-	0.02	-	-	0.02	-	0.02	0.02	0.02	0.02	0.02
δ_{22}	0.71	0.71	-	-	0.98	-	0.98	-	-	0.98	-	0.98	0.98	0.98	0.98	0.98
σ_l	1.00	1.00	0.80	0.80	-	-	0.50	-	-	-	-	0.50	-	-	0.50	0.50

Notes: For convenience we repeat the relevant baseline (σ_l=1) parameter values and for the other scenarios we show only differences with respect to the baseline (σ_l=1) scenario. The name of each scenario indicates in which crop tillage (ploughing) is not carried out, and the level of winter survival in the top soil layer.

We also investigated the effect of changing the values for winter survival in the top layer (σ_l) and for seed movement (δ_{ij}). These two parameters were chosen because there is great uncertainty in the values for survival over winter, and because in many agricultural regions minimum-tillage cropping systems are used. In such systems ploughing is carried out less frequently or plough types are used that do not invert the soil. Not ploughing is expected to decrease seed survival over winter because crop residues left on the soil surface may, for example, increase microbial activity or populations of seed predators. The values for these seven additional scenarios are given in Table 2. Throughout this chapter we use the terms 'ploughing' and 'tillage' interchangeably. We label the scenarios, for example, as no-till A (σ_l=0.5), to indicate the scenario where ploughing is not carried out at the end of the A phases so that most seeds remain in each layer, and where only half of the seeds in the top layer of the A phases survive over the winter. We examine the population growth rates and elasticities for all essentially different rotations up to six years long.

Model analysis

Growth rate. When examining different crop rotations, a question of primary importance is how fast a weed population grows in each crop rotation. The growth rate over a complete rotation cycle is given by the dominant eigenvalue (λ) of the matrix product $\mathbf{M}^{(h)}$ (Luenberger 1979, Caswell 1989, Caswell and Trevisan 1994). For $\lambda > 1$ the population will eventually increase geometrically, for $\lambda < 1$ the population will eventually decrease geometrically. In order to compare rotations of different lengths, we need a mean growth rate per year. This is given by the geometric mean of the cycle growth rate

$$\hat{\lambda} = \lambda^{(1/p)} \tag{7}$$

where p is again the length of the rotation cycle.

Stable depth distribution and reproductive value. Insight into differences in the growth rates and their sensitivities to changes is gained through examining the stable depth distribution and reproductive value. The stable depth distribution is the distribution of seeds over the various soil layers, approached over the long term. The reproductive value is a measure of the contribution of seeds in a given layer to future population growth, and is also approached over the long term. For an annual weed, when emergence and reproduction does not depend on seed age, the reproductive value will depend on a seed's probability of surviving until able to reproduce, and the amount of future reproduction (cf. Caswell 1989). In a periodic system the stable depth distribution and reproductive values are cyclically stable. When examined from one projection period to the next these quantities do not change. They will, however, differ from one phase to the next.

Mathematically, the stable depth distribution and reproductive value correspond, respectively, to the right ($\mathbf{w}^{(h)}$) and left ($\mathbf{v}^{(h)}$) eigenvectors associated with the dominant eigenvalue (λ) of $\mathbf{M}^{(h)}$. Usually the right eigenvector is normalized so that the elements sum to 1, while elements in the left eigenvector are divided by the value of the first element so that the reproductive values of lower layers are relative to that in the top layer. The eigenvectors are defined as

$$\begin{aligned} \mathbf{M}^{(h)}\mathbf{w}^{(h)} &= \lambda\mathbf{w}^{(h)} \\ \mathbf{v}^{(h)^{\mathrm{T}}}\mathbf{M}^{(h)} &= \lambda\mathbf{v}^{(h)} \end{aligned} \tag{8}$$

where T indicates the transpose and h indicates a phase in the rotation and is in $\{1,2,\ldots p\}$ and p is the length of the rotation. The phase index on the eigenvectors indicates the rotation matrix with which they are associated. The eigenvectors, though, are achieved at the end of a rotation starting with phase h. We therefore display the eigenvectors with the final phase with which they were achieved rather than with the starting phase of the rotation from which they were calculated. Thus in rotation AABB, the stable depth distribution after phase $\mathbf{B}^{(3)}$ is the right eigenvector $\mathbf{w}^{(4)}$, associated with the matrix $\mathbf{M}^{(4)} = \mathbf{B}^{(3)}\mathbf{A}^{(2)}\mathbf{A}^{(1)}\mathbf{B}^{(4)}$. The left eigenvector $\mathbf{v}^{(4)}$ indicates the reproductive value of seeds in each layer at the end $\mathbf{B}^{(3)}$ and gives the contribution of seeds to future generations starting with phase $\mathbf{B}^{(4)}$.

Elasticity analysis. The response of λ to perturbations in the transition elements and the underlying parameters is likely to depend on the composition of the crop rotation. These responses are usually represented as either sensitivities or elasticities. Sensitivities give the absolute change in λ in response to an absolute change in a transition element or underlying parameter. Elasticities give the proportional change in λ in response to a proportional change in a transition elements or underlying parameter (de Kroon et al. 1986). We focus on elasticities, as in a weed-management context it is more typical to consider proportional rather than absolute changes in parameters. See Caswell (2001) for further discussion of differences between sensitivities and elasticities.

The calculation of elasticities is based on that for sensitivities. An elasticity is the product of the ratio of a transition element or parameter to the growth rate and of its sensitivity. Caswell and Trevisan (1994) provide an equation for calculating the sensitivity matrices for the phases in a periodic matrix model

$$\mathbf{S}_C^{(h)} = \left[\mathbf{C}^{(h-1)}\mathbf{C}^{(h-2)}\ldots\mathbf{C}^{(1)}\mathbf{C}^{(p)}\mathbf{C}^{(p-1)}\ldots\mathbf{C}^{(h+1)}\right]^{\mathrm{T}}\mathbf{S}_M^{(h)}. \tag{9}$$

$\mathbf{S}_C^{(h)}$ is the matrix of sensitivities, with elements $\partial\lambda/\partial c_{ij}^{(h)}$, of either crop A or B in phase *h*. $\mathbf{C}^{(h)}$ is either matrix $\mathbf{A}^{(h)}$ or $\mathbf{B}^{(h)}$, and $c_{ij}^{(h)}$ is an element corresponding to one of these two matrices in phase *h*. The first term on the right-hand side is obtained as follows: cyclically permute the crop matrices of the rotation so that the *h*th crop matrix ($\mathbf{C}^{(h)}$) occurs first, then exclude this matrix, and transpose the resulting product. The second term, $\mathbf{S}_M^{(h)}$, is the sensitivity matrix of the product matrix **M**, rotated to phase *h*. The elements, $\partial\lambda/\partial m_{ij}^{(h)}$, of $\mathbf{S}_M^{(h)}$ are calculated using the right ($\mathbf{w}^{(h)}$) and left ($\mathbf{v}^{(h)}$) eigenvectors

$$\frac{\partial\lambda}{\partial m_{ij}^{(h)}} = \frac{v_{\mathrm{i}}^{(h)} w_{\mathrm{j}}^{(h)}}{\mathbf{w}^{(h)}.\mathbf{v}^{(h)}} \tag{10}$$

where $m_{ij}^{(h)}$ are the elements of $\mathbf{M}^{(h)}$, and $\mathbf{w}^{(h)}.\mathbf{v}^{(h)}$ is the inner product of the right and left eigenvectors of $\mathbf{M}^{(h)}$ (Caswell 1989). The elasticities associated with the transitions in each phase of a crop rotation can then be calculated as

$$e_{ij}^{(h)} = \frac{c_{ij}^{(h)}}{\lambda}\frac{\partial\lambda}{\partial c_{ij}^{(h)}} \tag{11}$$

where $\partial\lambda/\partial c_{ij}^{(h)}$ are the elements of $\mathbf{S}_C^{(h)}$, given in Equation 9. The elasticities in each phase sum to 1, thus the element containing the largest elasticity must always have an elasticity > 0.25.

The elasticities to the transition elements are a useful guide in pointing out, in a general way, how the growth rate will respond to changes. However, changes in the transition elements can only be made by adjusting the parameter values. Therefore it is of practical interest to examine the elasticities to the parameters, for each phase of the rotation. The general expression for calculating the elasticity to the underlying parameters is obtained by applying the chain rule for differentiation, giving

$$\frac{x}{\lambda}\frac{\partial\lambda}{\partial x}=\frac{x}{\lambda}\sum_{ij}\frac{\partial\lambda}{\partial g_{ij}}\frac{\partial g_{ij}}{\partial x} \qquad (12)$$

for some parameter x in a matrix **G** with elements g_{ij} (Caswell, 1989). In a periodic system, as with the transition elements, one must consider the phase in which the parameters occur, so that the elasticity to a parameter in the h^{th} phase is:

$$\frac{x^{(h)}}{\lambda}\frac{\partial\lambda}{\partial x^{(h)}}=\frac{x^{(h)}}{\lambda}\sum_{ij}\frac{\partial\lambda}{\partial c_{ij}^{(h)}}\frac{\partial c_{ij}^{(h)}}{\partial x^{(h)}}. \qquad (13)$$

Again, $\partial\lambda/\partial c_{ij}^{(h)}$ are given by elements of $\mathbf{S}_C^{(h)}$ (Equation 9).

Simulation and yearly growth rates. With the models considered here, most of the characteristics of a weed's population dynamics can be obtained through direct analysis of the matrices. The iterated solution to the model, however, aids understanding through the possibilities of graphical representation and calculation of yearly growth rates given an initial population. Each simulation started with 10 seeds per layer. The yearly growth rates were calculated by dividing the population size at time t+1 by the population size at time t, once the rotation growth rate and stable depth distribution were 99.99% of the analytically calculated quantities.

RESULTS

Having the basic crop matrices and a means of analyzing periodic matrix models, we can now systematically examine a variety of crop rotations. First we present results of the effects of different crop rotations on mean weed population growth rates per year ($\hat{\lambda}$) and of effects on the elasticity of the growth rate to transition elements and parameters. Then, using the stable depth distributions and reproductive values, we give a biological explanation for the differences in growth rates and elasticities, between rotations and between the scenarios indicated in Table 2.

Effects of crop rotation on growth rate

We first examine, for all scenarios, general patterns in the relationship between $\hat{\lambda}$ and the proportion of each crop. Subsequently we consider the effect of crop order and increasing rotation length.

General patterns in $\hat{\lambda}$. For each scenario, $\hat{\lambda}$ decreases as the fraction of crop A increases (Fig. 3a-d). The mean annual population growth rate of the baseline

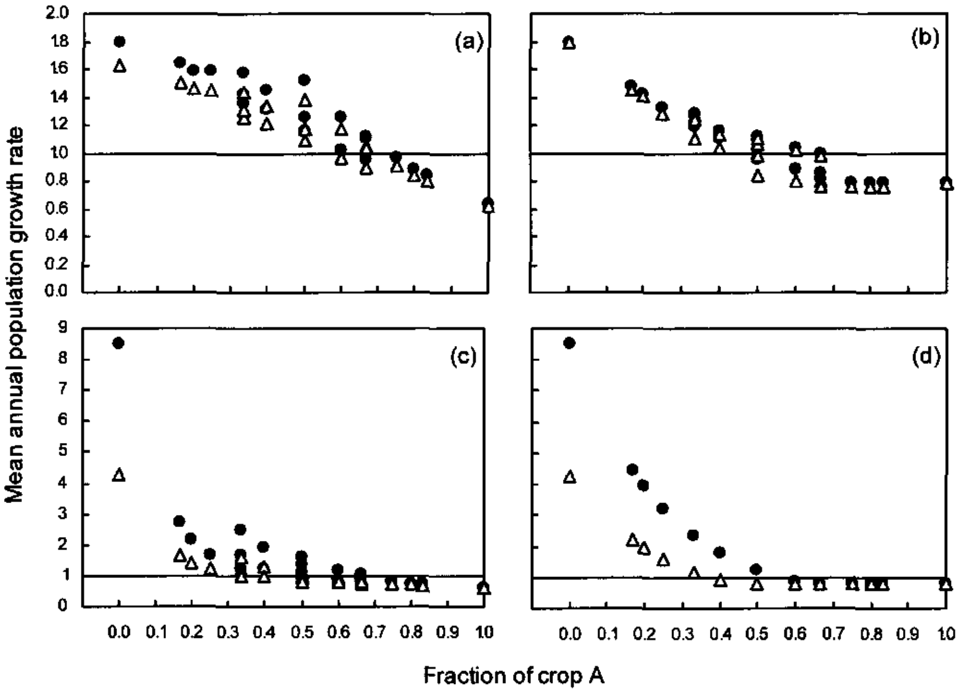

Fig. 3. Mean annual population growth rates ($\hat{\lambda}$) for all four scenarios and all essentially different rotations up to six years long of crops A and B. (a) Baseline scenarios. (b) No-till A scenarios. (c) No-till B scenarios. (d) No-till A, B scenarios. Solid circles indicate scenarios with seed survival over winter $\sigma_1=1$, open triangles indicate scenarios with (a) $\sigma_1=0.8$, and (b)-(d) $\sigma_1=0.5$. In the no-till scenarios for a particular crop, the values for the parameters governing seed movement are such that very little movement of seeds between layers occurs. See Tables 1 and 2, and section *Methods: Model construction: Parameter values used* for a complete explanation of the parameter values used in the scenarios.

($\sigma_1=1$) monoculture B is about 1.79 and that of the baseline A monoculture is about 0.63. The form of the decrease varies between scenarios. For example, scenarios that do not include ploughing at the end of the B years result in a more concave pattern in the relationship between $\hat{\lambda}$ and the fraction of crop A compared to the baseline and no-till A scenarios. In the no-till A ($\sigma_1=0.5$) scenario, rotations with a low fraction of B have a $\hat{\lambda}$ lower than that of a monoculture of A (Fig. 3b). In the scenarios where ploughing is not carried out in the B years, the $\hat{\lambda}$ of the monoculture B is much higher than the baseline situation. Adding a low proportion of crop A, though, causes a large decrease in $\hat{\lambda}$ (Fig. 3c-d). Decreasing survival over winter in the top layer tends to decrease $\hat{\lambda}$, but the effect is less in rotations with a high proportion of crop A.

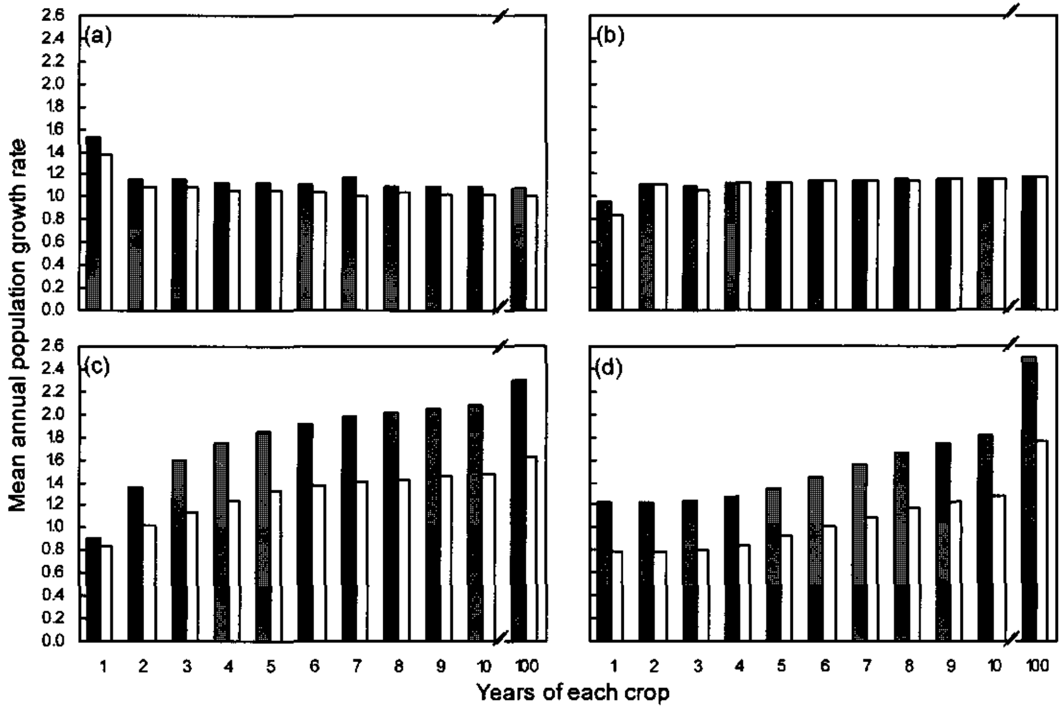

Fig. 4. Effect of increasing crop rotation length on mean annual population growth rate, λ , where equal amounts of each crop are used and the rotations use the simplest pattern, giving the sequence AB (one year of each crop), AABB (two years of each crop), AAABBB, and so on. (a) Baseline scenarios. (b) No-till A scenarios. (c) No-till B scenarios. (d) No-till A, B scenarios. Dark gray bars indicate scenarios with σ_1=1, open bars indicate scenarios with (a) σ_1=0.8, and (b)-(d) σ_1=0.5. In the no-till scenarios for a particular crop, the values for the parameters governing seed movement are such that very little movement of seeds between layers occurs. See Tables 1 and 2, and section *Methods: Model construction: Parameter values* used for a complete explanation of the parameter values used in the scenarios.

Table 3. Effect of the order of crops (A and B) on $\hat{\lambda}$, the mean weed population growth rate per year.

	Fraction	Baseline		No-till A		No-till B		No-till A, B	
Rotation	crop A	$\sigma_1 = 1$	$\sigma_1 = 0.8$	$\sigma_1 = 1$	$\sigma_1 = 0.5$	$\sigma_1 = 1$	$\sigma_1 = 0.5$	$\sigma_1 = 1$	$\sigma_1 = 0.5$
B	0.00	1.791	1.629	1.791	1.791	8.521	4.261	8.521	4.2610
ABABBB	0.33	1.568	1.429	1.185	1.108	1.674	1.209	2.345	1.1820
ABBABB	0.33	1.419	1.312	1.263	1.239	1.242	1.014	2.342	1.1730
AABBBB	0.33	1.356	1.258	1.282	1.267	2.480	1.586	2.342	1.1821
AABBB	0.40	1.312	1.217	1.164	1.135	1.940	1.310	1.812	0.9217
ABABB	0.40	1.455	1.338	1.106	1.037	1.227	0.981	1.809	0.9106
ABAB	0.50	1.520	1.383	0.949	0.844	0.912	0.831	1.228	0.7868
AABB	0.50	1.154	1.084	1.112	1.100	1.358	1.017	1.231	0.7903
AABAAB	0.67	1.110	1.041	0.820	0.756	0.863	0.779	0.788	0.7848
AAABAB	0.67	1.124	1.051	0.858	0.794	0.823	0.765	0.790	0.7850
AAAABB	0.67	0.945	0.900	0.988	0.982	1.041	0.862	0.799	0.7867
A	1.00	0.633	0.621	0.784	0.784	0.633	0.633	0.784	0.7840

Effects of crop order. For all scenarios except where ploughing is not carried out in both crops, the $\hat{\lambda}$ for a given fraction of crop A can differ substantially depending on crop order (Table 3). For example, in the baseline (σ_1=1) scenario, rotation ABAB has a $\hat{\lambda}$ of 1.52, while rotation AABB has a $\hat{\lambda}$ of 1.15. For certain scenarios and fractions of crop A, crop order can mean the difference between an increasing or a decreasing population. For example in the no-till B (σ_1=0.5) scenario, rotation ABABB has a $\hat{\lambda}$ of 0.98 while rotation AABBB has a $\hat{\lambda}$ of 1.31. In the baseline scenarios, patterns in which each crop is in a consecutive block have a lower $\hat{\lambda}$ than patterns that have alternating years of crops A and B. In the other scenarios, patterns with each crop in a consecutive block have the highest growth rate for a given rotation length and fraction of each crop.

Effects of rotation length. When rotations increase in length following the pattern AB, AABB, AAABBB, and so on, the trend in $\hat{\lambda}$ tends to decrease in the baseline scenarios (Fig. 4a). In the no-till A scenarios, $\hat{\lambda}$ appears to level off at 1.82, which is close to the $\hat{\lambda}$ for a monoculture of B in the baseline scenario (Fig. 4b). In scenarios where tillage does not occur in the B years, the $\hat{\lambda}$ increase and there is a large effect of decreased survival over winter (Fig. 4c-d).

Effects of crop rotation on elasticity of growth rate

We first examine elasticities of $\hat{\lambda}$ to transitions and underlying parameters for the baseline (σ_1=1) monocultures and rotations ABAB and AABB. We then examine patterns in the highest elasticities found for each rotation of all eight scenarios.

Elasticities to baseline transitions per phase. In the A monoculture, the highest elasticity value is to transition a_{22}, which is the transition related to remaining in the bottom layer (Fig. 5a). With a value of ~0.8, it is much higher than the elasticities to the other transitions. The elasticity values found for the B monoculture (Fig. 5b) are more evenly spread, with transitions b_{12} and b_{21} having the highest value. Rotation ABAB (Fig. 5c) has a regular pattern of elasticities, with the highest elasticity alternating between the transitions $a_{12}^{(1),(3)}$ and $b_{21}^{(2),(4)}$, governing movement between layers. (See section *Methods: Model analysis: Elasticity analysis* for explanation of symbols.) The pattern of elasticities for rotation AABB is more complicated (Fig. 5d). Overall the highest elasticity is for transition $a_{22}^{(1)}$, that of remaining in the bottom layer during the first A crop. In the other phases, the transitions governing movement of seeds between layers and of remaining in the bottom layer tend to have the highest elasticity values.

Elasticities of underlying parameters. As with the elasticities for the transitions, the crop rotation influences the impact of changes in a particular parameter on the growth rate (Table 4). We again focus on the baseline (σ_1=1) rotations ABAB and AABB, and also compare them with the monocultures of A and B. In the next section we will investigate the reasons for differences in elasticities.

Table 4. Elasticity of weed-population growth rate to baseline (σ_1=1) parameter values. For rotation ABAB values for only years 1 and 2 are given, as years 3 and 4 are the same as years 1 and 2, respectively. See Table 1 for explanation of parameters.

	Monoculture		ABAB		AABB			
Parameter	A	B	$A^{(1)}$, $A^{(3)}$	$B^{(2)}$, $B^{(4)}$	$A^{(1)}$	$A^{(2)}$	$B^{(3)}$	$B^{(4)}$
α_1	0.0936	0.3959	0.0044	0.7855	0.0546	0.0546	0.4772	0.4772
α_2	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
μ_1	–0.2861	–0.0126	–0.0133	–0.0251	–0.1668	–0.1668	–0.0152	–0.0152
μ_2	–0.2266	–0.1423	–0.2489	–0.0364	–0.2364	–0.2364	–0.1203	–0.1203
ν	0.0936	0.4011	0.0044	0.7958	0.0546	0.0546	0.4835	0.4835
γ	0.0936	0.4011	0.0044	0.7958	0.0546	0.0546	0.4835	0.4835
δ_{11}	0.0005	0.0418	0.0010	0.0010	0.0002	0.0031	0.1119	0.0031
δ_{12}	0.0931	0.3888	0.8533	0.0034	0.0544	0.5159	0.4071	0.0515
δ_{21}	0.0931	0.3888	0.0034	0.8533	0.0544	0.0515	0.4071	0.5159
δ_{22}	0.8133	0.1806	0.1424	0.1424	0.8910	0.4295	0.0740	0.4295
$\sigma 1$	0.0936	0.4306	0.8543	0.0044	0.0546	0.5190	0.5190	0.0546
$\sigma 2$	0.9064	0.5694	0.1457	0.9956	0.9454	0.4810	0.4810	0.9454

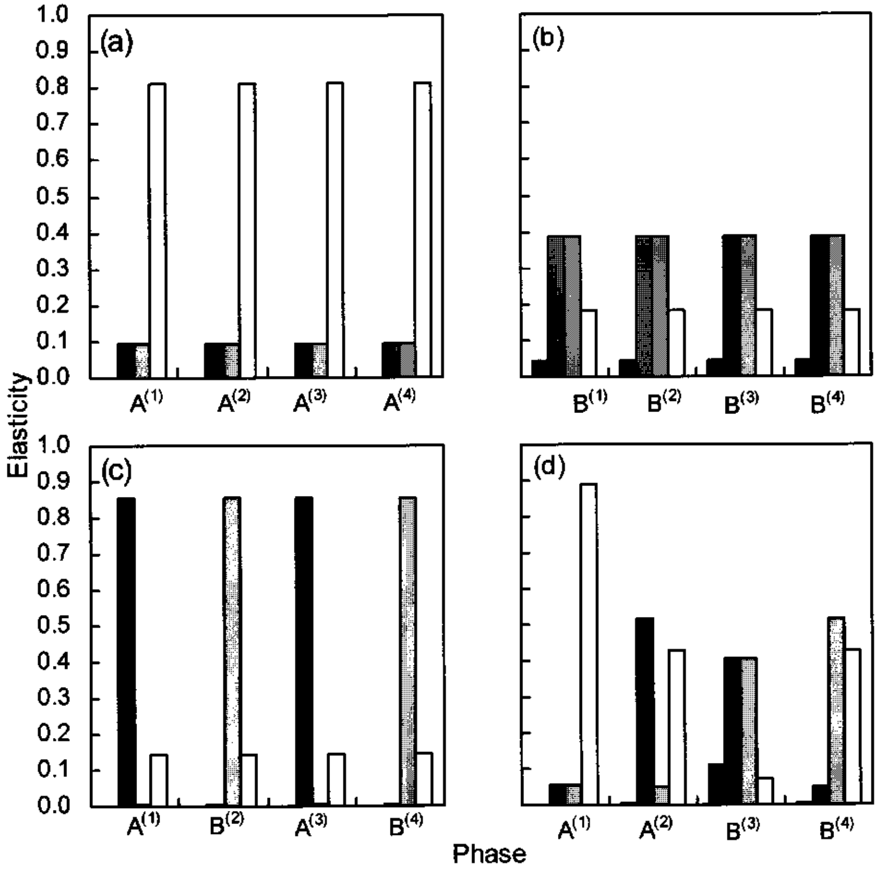

Fig. 5. Elasticities of transition elements in the baseline ($\sigma_1=1$) scenario. (a) Monoculture A. (b) Monoculture B (a) Rotation ABAB. (b) Rotation AABB. The transitions $c_{ij}^{(h)}$ for crop A or B of phase h are indicated as follows: $c_{11}^{(h)}$, black; $c_{12}^{(h)}$, dark gray; $c_{21}^{(h)}$, light gray; $c_{22}^{(h)}$, open bars.

The highest elasticity values tend to be to the parameters for survival over winter (σ_i), in either or both of the soil layers. In monocultures of A and B, winter survival in the bottom layer is most important, but in crop A it has a much larger elasticity than in crop B. In phase A of rotation ABAB, survival over winter in the top layer is most important, while in phase B winter survival in the bottom layer is most important, and has a much larger elasticity than a B monoculture. For rotation AABB, winter survival in the bottom layer has a higher elasticity in the first and the last phases than in the middle two phases.

The value of the parameter for seedling survival (ν) is likely to depend heavily on weed-control methods and is therefore the process over which a farmer usually has the most influence. It also has the same elasticity as the parameter for seed production (γ) because in this model γ is density-independent and multiplication with ν yields a single parameter –seeds produced per emerged seedling. The elasticity of ν differs between rotations and between phases in a rotation. In a monoculture of A the elasticity of ν is low compared to the elasticities of the other parameters, while in a monoculture of B, ν has an elasticity similar to many of the other parameters. In rotation ABAB the elasticity of ν is lower in the A phases compared to an A monoculture. In the B phases the elasticity of ν is larger relative to a B monoculture. In rotation AABB the elasticities of ν during the A phases are also very low, while during the B phase they are somewhat larger than in a B monoculture but not nearly as large as during the B phase of rotation ABAB. The elasticities for ν do not necessarily remain the same for the same crop in different phases within a rotation. For example in the baseline (σ_I=1) rotation AABABB, the elasticity of ν is much greater during phase $B^{(3)}$ than during any other phase (Fig. 6).

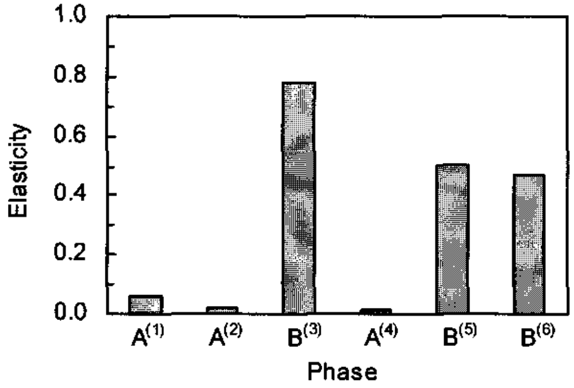

Fig. 6. Elasticities of the parameter for seedling survival (ν) in rotation AABABB (baseline (σ_I=1) scenario).

Elasticity patterns in all scenarios. An overview of the effect of changing parameter values can be seen in graphs of the highest elasticity to a transition per rotation against the fraction of crop A (Fig. 7a-d). As it is not possible to include the rotation or phase in the graphs, we give these results in the Appendix. In the baseline scenarios the values of the highest elasticities appear to increase with the fraction of crop A (Fig. 7a). Crop order, however, can cause differences in the values as well as the transition and phase in which they occur. For the baseline rotations where consecutive A crops occur, then the highest elasticities are to a_{22}. When A and B crops alternate, then the highest elasticities are to transitions a_{12} and b_{21}. In the no-till A scenarios, the highest elasticity values are to transition a_{22} for all rotations (Fig. 7b). As the fraction of crop A increases, then the elasticity values approach 1. In the no-till B scenarios the relation is more complicated (Fig. 7c). There is some pattern: Rotations with a majority of crop B tend to have the highest elasticity to transition b_{11}, while those with a majority of crop A have the highest elasticity to transition a_{22}. In between, the dominant elasticity is to transition b_{22}, but other transitions may also carry the highest elasticity. In both the no-till A and B scenarios, the pattern of transitions carrying the highest elasticity is similar to that for the no-till B scenarios but the values tend to be close to 1 (Fig. 7d).

Causes of differences in growth rates and elasticities

Using the baseline ($\sigma_1=1$) monocultures and rotations ABAB and AABB, we elucidate the causes of some of the differences described in the preceding subsections. Because we have examined a small set of the infinite number of theoretically possible rotations, some points may appear as outliers in the figures of the population growth rates and elasticities (Figs. 3 and 7). Such points are not outliers in a statistical sense because values are due to the same deterministic processes at work for any other point. Therefore the reasoning applied below to differences between rotations ABAB and AABB can be used to explain differences between other rotations, as well as to differences between scenarios.

Depth distributions and baseline ($\sigma_1=1$) growth rates. In both monocultures, the bottom layer has a higher proportion of seeds than the top layer (Table 5), reflecting how ploughing moves almost all seeds from the top layer to the bottom layer and moves only about a third of the seeds in the bottom layer to the top layer. The fraction of seeds in the top layer of A is, however, about twice that found in the top layer of crop B. In crop B, due to high seedling survival and reproduction by seeds in the top layer, a greater proportion of the total population ends up in the bottom layer compared to crop A.

In the modelled crop rotations, the depth distribution of seeds achieved after

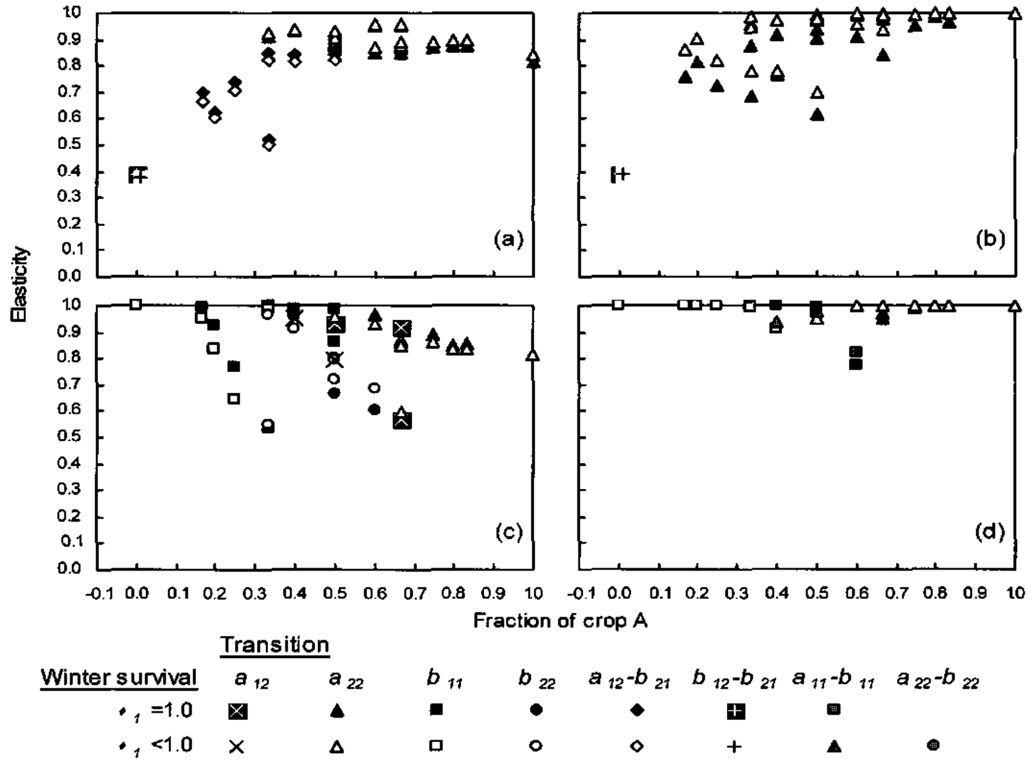

Fig. 7. Highest values of elasticities to transition elements for all scenarios and all essentially different rotations up to six years long. (a) Baseline scenarios. (b) No-till A scenarios. (c) No-till B scenarios. (d) No-till A, B scenarios. For panel (a) the weed seed survival over winter σ_1=0.8, and (b)-(d) σ_1=0.5. In the no-till scenarios for a particular crop, the values for the parameters governing seed movement are such that very little movement of seeds between layers occurs. See Tables 1 and 2, and section *Methods: Model construction: Parameter values used* for a complete explanation of the parameter values used in the scenarios. This figure is based on the data in the Appendix.

Table 5. Baseline ($\sigma_1=1$) depth distribution of seeds (fraction in each layer), seed reproductive values (relative to value in layer 1) at the end of the indicated phase, and growth rates per phase in both layers and for the total population.

		Seed depth distribution		Reproductive	Annual population growth rate		
Crop rotation	Phase	Layer 1	Layer 2	value, layer 2	Layer 1	Layer 2	Total
Monoculture							
	A	0.269	0.731	3.568	0.633	0.633	0.633
	B	0.125	0.875	0.190	1.791	1.791	1.791
ABAB							
	$A^{(1)}, A^{(3)}$	0.285	0.715	0.068	3.060	0.581	0.756
	$B^{(2)}, B^{(4)}$	0.071	0.929	17.330	0.755	3.972	3.054
AABB							
	$A^{(1)}$	0.279	0.721	6.686	1.183	0.603	0.698
	$A^{(2)}$	0.268	0.732	0.340	0.604	0.636	0.627
	$B^{(3)}$	0.074	0.926	0.074	0.806	3.694	2.919
	$B^{(4)}$	0.164	0.836	3.406	3.071	1.250	1.385

each phase only approaches that of the corresponding monoculture crop. This occurs because the distribution resulting after each phase depends on the preceding distribution as well as on the transition values of the current phase (Table 5).

For example, when a baseline A crop precedes a baseline B crop, there will be a greater proportion of seeds in the top layer before the B phase compared to a B monoculture (Table 5). Therefore more seeds will be produced during the B phase compared with a B monoculture and they will be on the top layer before ploughing. After ploughing the proportion of seeds on the bottom layer is greater than in a B monoculture. This is because before ploughing there was a greater proportion and number of seeds in the top layer than in a B monoculture. Ploughing moved more seeds to the bottom layer and fewer seeds to the top layer, leading to a decline in the number of seeds in the top layer and a very large increase in the bottom layer. The overall growth rate for a B phase following an A phase is thus larger than the yearly growth rate in a B monoculture (Table 5). Similar reasoning can be used to show that, after an A phase, if the initial distribution of seeds is higher in the bottom layer compared with an A monoculture, then the proportion and absolute number of seeds in the top layer will increase, as will the total number of seeds over both layers. Such a situation occurs when the preceding phase is crop B. The stable depth distribution for a given phase in a rotation can be thought of as a transient distribution when compared to a monoculture situation.

For the baseline rotations ABAB and AABB, the different values of $\hat{\lambda}$ can be explained as follows. Compared with the A phases of rotation AABB, the A phases

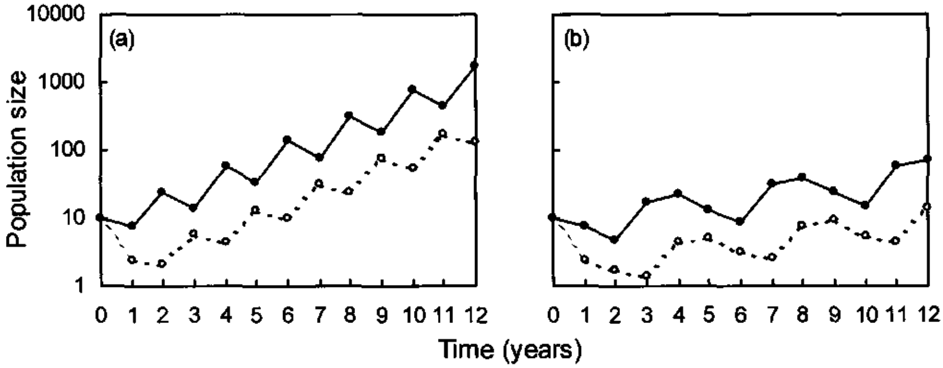

Fig. 8. Simulated population dynamics of baseline (σ_1=1) scenario. (a) Rotation ABAB. (b) Rotation AABB. Broken lines and open circles indicate the population in the top layer and thick lines and solid circles indicate the population in the bottom layer.

of ABAB result in a higher proportion of seeds in the top layer and thus also a greater population in the top layer (Table 5). These seeds can then produce many more seeds during the following B phase. Similarly, the B phases of ABAB result in a higher proportion and number of seeds in the bottom layer than the B phases of AABB. Therefore, before ploughing in the following A year, fewer seeds are lost from the bottom layer than from the top layer. Consequently during each phase of ABAB, the population will grow faster than in the same crop in rotation AABB, leading to a higher growth rate over the entire rotation cycle. The alternating pattern of crops thus increases the population of the top layer by the end of an A year, and sets the population up for another round of high reproduction in the next B year (Fig. 8a). In contrast, at the end of phase $A^{(1)}$ in rotation AABB, while the proportion of seeds in the top layer is similar to that of the A phases of ABAB, during the second phase very few seeds will be produced because it is an A phase. In fact, the population declines more than in an A monoculture (Table 5). Phase $A^{(2)}$ acts as a brake, slowing the yearly growth rate in each of the following phases compared to the corresponding crop growth rates in rotation ABAB (Fig. 8b).

Reproductive values, depth distributions, and baseline elasticities. Unlike the growth rates, the elasticity of the growth rate to changes in transitions depends on what will happen to a seed in the future as well as the probability of which layer it will end up in at the end of the previous crop. Elasticity values therefore depend both on the reproductive value and the depth distribution of seeds. While reasons for differences in the stable depth distributions depend on previous distributions and transitions, differences in the reproductive values are due to differences in future environments.

In an A monoculture the reproductive value of the lower layer is more than 3.5 times that of an individual in the top layer, i.e., most contributions to future generations come from seeds in the bottom layer (Table 5). This is because prior to ploughing in crop A, the seed population decreases less in the bottom layer. On the other hand, in a B monoculture, because of high seed survival and reproduction in the top layer before ploughing, the reproductive value of a seed in the top layer is ~5 times that of seed in the bottom layer. In a rotation, the different sequences of following crops will alter the reproductive values of each phase.

For example, after phase A of rotation ABAB, the reproductive value of the top layer is almost 15 times that of the bottom layer, which contrasts sharply with that found in a monoculture of A (Table 5). In the ABAB rotation, the seeds in the top layer at the end of an A phase can produce many new offspring during the following B year. Furthermore the newly produced seeds will be moved to the bottom layer prior to the next A phase where their chances of survival are higher than in the top layer. Such reasoning can be used to explain the different reproductive values in the B phase and in other rotations.

Understanding the causes of differences in reproductive values, we can now explain the differences in the elasticities. The high elasticity found in transition a_{12} of rotation ABAB, for example, can be accounted for by the high reproductive value of seeds in the top layer and because most of the seeds that are in the top layer came from the bottom layer. Likewise, the transition b_{21} has a high elasticity because most of the seeds in the bottom layer were in the top layer before ploughing, and once in the bottom layer they have a high reproductive value. Therefore management practices that decrease the proportion of seeds in the top layer at the end of an A phase or the amount of reproduction during the B phase are likely to have the largest impact on the growth rate. This result concurs with that of the elasticities of the parameters, where, for example, winter survival in the top layer of A and in the bottom layer of B both have high elasticities. Through considering the stable depth distribution, and reproductive and parameter values, the transition and parameter elasticities for other rotations can similarly be explained.

Explaining differences between scenarios. The different patterns found between scenarios in the growth rates and elasticities can broadly be understood by considering the analysis of the baseline monocultures and simple rotations presented in the last section. As examples we consider why rotations with alternating years of A and B have lower growth rates in the no-till scenarios than in the baseline scenarios, why not ploughing in both crops leads to little effect of crop order and why growth rates of certain rotations in the no-till A (σ_1= 0.5) scenarios can be lower than that of the crop A monoculture. Finally we examine reasons for the effects of increasing rotation length on $\hat{\lambda}$. Differences in elasticity patterns between and within scenarios can be explained by considering how seeds are distributed over the soil layers and their capacity for future reproduction. Such an exercise follows the reasoning used earlier for the baseline ($\sigma_1=1$) ABAB and AABB rotations and therefore we do not devote space to it here.

In rotations in which tillage is not carried out for either crops A or B, the $\hat{\lambda}$ are lower for those rotations in which crops A and B alternate. In the no-till B scenarios, this is because, for an alternating pattern of crops A and B, seeds produced in a B crop remain in the top layer and then are mostly removed during the following A phase. In the no-till A scenarios, seeds that were buried at the end of the B year are not brought back to the surface before the next B year and so cannot reproduce. The effect of consecutive blocks of crops in the no-till scenarios is to either store seeds until they can be brought back to the surface after the first B phase (no-till A scenarios) or to cause a large build up in the population during the B years that is not offset by decreases during the A phases (no-till B scenarios). Considering the elasticity patterns found in the analysis of the baseline ($\sigma_1=1$) ABAB rotation (Fig. 5a), this is not a surprising result.

When ploughing is not carried out in both crops, the lack of difference between $\hat{\lambda}$ for rotations that differ only in crop sequence is because not ploughing effectively decouples the dynamics of the two layers. Thus two, nearly separate populations are created and therefore order of multiplication of matrices and crop order does not have a large effect. Structure, however, still does play a role as $\hat{\lambda}$ for each rotation is not a simple (geometric) average of the monoculture growth rates. The decoupling of the layers also causes the highest elasticity of each phase to be close to 1 because the annual growth rates are dominated by a single transition.

Rotations with $\hat{\lambda}$ lower than that of the lowest monoculture may occur when introduction of another crop with a higher monoculture $\hat{\lambda}$ moves seeds to a layer where they will be removed faster than they will be replaced by the increase caused by the crop with a higher monoculture $\hat{\lambda}$. For the no-till A, ($\sigma_1=0.5$) scenarios, the majority of seeds in a monoculture of crop A will be in the bottom layer. The inclusion of a single B crop in rotations of 3 to 5 A crops, permits ploughing so that many seeds are moved to the top layer where they are removed from the population. The low survival over winter compensates for the slight increase in population during the B year.

The patterns observed in Fig. 4, for the effects of increasing rotation length, can also be explained by the same reasons for the differences in crop order. When rotations are extended to a common rotation length, the shorter rotations just have more repeating units. Conversely, longer rotations have longer spans of each crop in a consecutive block. In the baseline scenarios, rotations with each crop in a block had the lowest $\hat{\lambda}$ for a given number and fraction of each crop. For the other scenarios the opposite was the case. It is not clear, however, whether the $\hat{\lambda}$ will reach a limit if rotation length were further extended. In the no-till A scenarios, $\hat{\lambda}$ appears to level off, but it may also be increasing very slowly.

DISCUSSION

Our goal has been to show how different types of crop rotations affect weed population dynamics. We have used a periodic matrix model and examined a variety of crop rotations, and the effects of crop order, rotation length, and proportion of each crop. Of prime importance is the conclusion that the order of crops will affect the population growth rate. Our conclusion rests on the form of the model, i.e. that the population is structured, and that life cycle parameters change with the crop being grown. Only when life-history parameter values lead to a non-structured population, does the order have little effect on the population growth rate.

The sequence of crops in rotation also affects the sensitivity of the growth rate to changes, at both the levels of the transition elements and the underlying parameters. The differences in growth rates and elasticities between rotations, and between phases within rotations are in general due to how mixtures of crops, in comparison to monocultures of each crop, alter both the distribution of seeds over soil layers and the contribution of a seed in a particular layer to future generations. Below we consider extensions of our approach, and the implications for weed management and understanding of crop rotations.

Extension of the method

The approach taken in this chapter can be extended to include aspects such as density dependence, effects of environmental variation on vital rates, and increasing the number of soil layers. Doing so is not likely to change our qualitative conclusion and comes at the expense of analytical tractability, therefore complicating the interpretation of results. For example, aperiodically fluctuating populations due to density-dependent vital rates may obscure the effects of the crop rotation cycle. Our interest is not in forecasting what the population will be, rather it is in projecting what the population would be should the given conditions (parameter values) remain constant (Caswell 1989). Understanding population projections provides a sound basis for developing more complex models, while in the empirical arena it results in more precise hypotheses and thus in better experimental designs.

Division of the soil column into more layers is likely to lower weed population growth rates over a rotation cycle because seeds will reside much longer in layers from where they cannot emerge and thus have a greater chance of losing viability. In situations where accurate quantitative prediction of the future population is of interest, division of the soil into more layers or use of an integral projection model would most likely be necessary (Easterling et al. 2000).

Because weed populations can be structured in many other ways, such as by seed age, size of rhizomes, or seed position relative to a ridge, our approach can be applied to other situations besides those where the seed population is structured by depth in the soil and the seeds are moved by ploughing.

Implications for management

The outcomes of decisions concerning crop rotation sequences have implications for weed management, in both the long and short term. As different rotations can have different growth rates, the amount of time to reach a target weed population will be different for each rotation. If other, non-weed management aspects are equal, then the rotation with the lowest weed population growth rate would be the most sensible. One way of thinking about the difference in growth rates between rotations is, e.g., to imagine how much seedling survival (ν), needs to be changed in order to achieve the same growth rate of another rotation. In crop B of the baseline (σ_1 [weed survival over winter]=1) rotation ABAB, seedling survival would have to be decreased from 0.6 to 0.28 in order to achieve the same growth rate found for the population in rotation AABB. This would require an 80% increase in effectiveness of weed control. Thus rotation AABB provides the equivalent of an extra, efficient weed control operation without the effort.

Short-term management decisions will also be affected by the choice of a particular rotation because of different elasticity patterns resulting from different rotations. As a rule of thumb the largest impact on the population growth rate is achieved by changing the values of the parameters with the largest elasticities. Decreasing seedling survival in a given crop may be more effective in one rotation than in another rotation. Furthermore, within a rotation, the strategy may be more effective in one phase than in another phase (each year of a rotation is called a 'phase'). This not to say that the process with the highest elasticity is necessarily the best or most convenient one to manipulate. As de Kroon et al. (2000) point out, there may be limits to the degree of change that can be induced in a particular process.

Our model, as with any periodic linear model, shows that the population growth rate, given by the dominant eigenvalue, will not be affected by the starting phase of the rotation. The size of a future population will, however, be affected by the starting crop and the initial distribution of seeds over the soil column. Taking the baseline (σ_1=1) rotation AB as an example, if most of the seeds are in the top layer, then it may be beneficial to start with the A phase of the rotation. Few seeds will be produced and then most of them will be moved to the bottom layer, where their reproductive value will be low. Therefore the amount of new seeds produced in the following B phase will be less than if the B phase occurred first. As the size of the weed population can affect the costs of control and can reduce crop yield, it may be important to consider the initial seed distribution and starting crop when a change to another rotation is contemplated. The starting distribution of seeds also has practical consequences for empirical studies of long-term weed growth rates in crop rotations. Experiments should be carried out long enough to overcome any transient effects and the starting distribution of seeds over the soil column should be measured, an observation also made by Mohler (1993).

From a management perspective, it is tempting to ask whether there are critical values of the monoculture growth rates for which order would not affect the population growth rate over a rotation cycle. Such reasoning, though, ignores the crucial role of population structure. For a structured periodic system the population growth rate is not the product of the monoculture growth rates because the order of crops changes the population structure, which in turn affects the growth rate the following year. Consequently rotation population growth rates may show little relation to the product of the monoculture population growth rates. In a structured periodic system, order will not matter only when there is no difference in right eigenvectors between the yearly transition matrices (Caswell 2001) or when processes in one crop yield a matrix that is the inverse of the other crop or the inverse of the product of the other matrices. Such situations are unlikely to occur. The only other possibility is if the life history for the weed species in each of the crops leads to transition matrices that are similar. The elasticity of the population growth rates to the underlying parameters may differ though, because the sums and products of parameter values determining the value of a particular transition may be the same for each crop, but the values of corresponding parameters in each crop may be different.

Toward an improved understanding of crop rotations

As stated at the outset, impacts of crop rotations on weed populations are typically attributed to the diversity of environments, which are thought to prevent a weed population from becoming unmanageably large. While there is undoubtedly much truth in this explanation, it is now possible to specify underlying processes more precisely as well as to provide some qualifications. Critically, not just the diversity of environments matters, but also the sequence of environments interacting with the population structure. Two rotations can be equally diverse, i.e., having the same number and proportion of crops, but still can have different weed population growth rates depending on their order. Furthermore, one can now begin to imagine rotations that could increase a weed problem compared to a monoculture of any of the component crops. This could perhaps happen when germination and emergence depend on seed age and the population is structured by position in the soil. Particular sequences could enhance the fraction of seeds emerging beyond that found in a monoculture. The observation of how growth rates change as rotation length increases is perhaps interesting from a mathematical perspective but has less practical relevance for weed populations.

Use of simple, analytically tractable models to examine crop rotations goes far in giving the ability to explain how biological processes and effects of management interact differently under different rotations. Jordan et al. (1995) observed, in simulations of a structured weed population with a four-year rotation (oats/clover, corn, soybean, corn), that different sensitivities resulted between the first and second corn years. While these could have been due to differences in the ploughing regimes between the two corn crops, some of the differences could be due to the rotation itself. They were not able, however to explain the processes underlying the differences in sensitivities and concluded that 'crop rotations are complicated historical sequences, and effects of an event or process on weed population dynamics may be very different depending on timing within the rotation' (Jordan et al. 1995, p. 395). In this chapter we have been able to explain such effects.

The present analysis raises the question of why a particular crop rotation is being used and whether the arguments given for this choice actually hold. In the Netherlands, for example, crop rotations tend to follow an ABAB pattern, alternating competitive crops (grains, potatoes) with non-competitive crops (sugar beets, onions), and where is done after each crop. Typical reasons for the alternating pattern relate to soil, weed, and disease management. Given our findings we wonder whether the ABAB pattern, with tillage occurring after each crop, is the ideal one, at least as far as weed management is concerned. With regard to soil and disease management there has been no systematic investigation of the effects of crop order, number, and proportion on these aspects of crop production. It is possible that they may show dynamics qualitatively similar to the results presented here for weed populations.

Taking a theoretical approach frees one to ask apparently absurd questions, such as what would happen if ploughing did not occur prior to a carrot crop. From a standard agronomic perspective there may be little sense in not tilling before a carrot crop. From a weed-management perspective, such a practice may be beneficial and should, for example, stimulate investigation of new crop husbandry methods or development of varieties that grow well without tillage. An improved theoretical approach to crop rotations we hope will contribute to more creativity in finding solutions for managing weed populations.

APPENDIX

Supplementary results on highest elasticities

For each crop rotation scenario, the highest elasticity value occurring in each rotation is given, along with the transition and phase in which it occurs. Fig. 7 is based on the elasticity values and transitions shown below.

		Baseline				No-till A				No-till B				No-till A and B			
		$\sigma_1 = 1$		$\sigma_1 = 0.8$		$\sigma_1 = 1$		$\sigma_1 = 0.5$		$\sigma_1 = 1$		$\sigma_1 = 0.5$		$\sigma_1 = 1$		$\sigma_1 = 0.5$	
Rotation	Fraction crop A	Elast.	Trans.	Elast.	Trans.	Elast.	Trans.	Elast.	Trans.	Elast.	Trans.	Elast.	Trans.	Elast.	Trans.	Elast.	Trans.
B	0.00	0.389	$b_{12}^{(1)}, b_{21}^{(1)}$	0.380	$b_{12}^{(1)}, b_{21}^{(1)}$	0.389	$b_{12}^{(1)}, b_{21}^{(1)}$	0.389	$b_{12}^{(1)}, b_{21}^{(1)}$	1.000	$b_{11}^{(1)}$	1.000	$b_{11}^{(1)}$	1.0000	$b_{11}^{(1)}$	0.9998	$b_{11}^{(1)}$
ABBBBB	0.17	0.698	$a_{12}^{(1)}, b_{21}^{(6)}$	0.664	$a_{12}^{(1)}, b_{21}^{(6)}$	0.762	$a_{22}^{(1)}$	0.860	$a_{22}^{(1)}$	0.992	$b_{11}^{(3)}$	0.954	$b_{11}^{(3)}$	0.9999	$b_{11}^{(3)}, b_{11}^{(4)}$	0.9996	$b_{11}^{(3)}, b_{11}^{(4)}$
ABBBB	0.20	0.625	$a_{12}^{(1)}, b_{21}^{(5)}$	0.601	$a_{12}^{(1)}, b_{21}^{(5)}$	0.817	$a_{22}^{(1)}$	0.904	$a_{22}^{(1)}$	0.926	$b_{11}^{(2)}$	0.834	$b_{11}^{(3)}$	0.9997	$b_{11}^{(2)}, b_{11}^{(4)}$	0.9994	$b_{11}^{(3)}$
ABBB	0.25	0.743	$a_{12}^{(1)}, b_{21}^{(4)}$	0.708	$a_{12}^{(1)}, b_{21}^{(4)}$	0.723	$a_{22}^{(1)}$	0.824	$a_{22}^{(1)}$	0.770	$b_{11}^{(2)}$	0.644	$b_{11}^{(2)}$	0.9997	$b_{11}^{(2)}, b_{11}^{(3)}$	0.9982	$b_{11}^{(2)}, b_{11}^{(3)}$
AABBBB	0.33	0.910	$a_{22}^{(1)}$	0.922	$a_{22}^{(1)}$	0.957	$a_{22}^{(1)}$	0.988	$a_{22}^{(1)}$	0.998	$b_{11}^{(4)}$	0.986	$b_{11}^{(4)}$	0.9997	$b_{11}^{(4)}$	0.9905	$b_{11}^{(4)}$
ABABBB	0.33	0.850	$a_{12}^{(1)}, b_{21}^{(2)}$	0.820	$a_{12}^{(1)}, b_{21}^{(2)}$	0.688	$a_{22}^{(3)}$	0.779	$a_{22}^{(3)}$	0.986	$b_{11}^{(4)}$	0.966	$b_{22}^{(2)}$	0.9996	$b_{11}^{(4)}, b_{11}^{(5)}$	0.9941	$b_{11}^{(4)}, b_{11}^{(5)}$
ABB	0.33	0.522	$a_{12}^{(1)}, b_{21}^{(3)}$	0.503	$a_{12}^{(1)}, b_{21}^{(3)}$	0.879	$a_{22}^{(1)}$	0.944	$a_{22}^{(1)}$	0.535	$b_{11}^{(2)}$	0.547	$b_{22}^{(3)}$	0.9994	$b_{11}^{(2)}$	0.9938	$b_{11}^{(2)}$
AABBB	0.40	0.931	$a_{22}^{(1)}$	0.938	$a_{22}^{(1)}$	0.920	$a_{22}^{(1)}$	0.975	$a_{22}^{(1)}$	0.988	$b_{11}^{(3)}$	0.952	$a_{12}^{(2)}$	0.9985	$b_{11}^{(3)}, b_{11}^{(4)}$	0.9112	$b_{11}^{(3)}, b_{11}^{(4)}$
ABABB	0.40	0.843	$a_{12}^{(1)}, b_{21}^{(2)}$	0.814	$a_{12}^{(1)}, b_{21}^{(2)}$	0.768	$a_{22}^{(3)}$	0.779	$a_{22}^{(1)}$	0.956	$b_{22}^{(2)}$	0.911	$b_{22}^{(2)}$	0.9992	$b_{11}^{(4)}$	0.9378	$a_{11}^{(3)}, b_{11}^{(5)}$
AAABBB	0.50	0.862	$a_{22}^{(1)}, a_{22}^{(2)}$	0.884	$a_{22}^{(1)}, a_{22}^{(2)}$	0.980	$a_{22}^{(1)}$	0.996	$a_{22}^{(1)}$	0.987	$b_{11}^{(4)}$	0.962	$a_{22}^{(2)}$	0.9897	$b_{11}^{(4)}, b_{11}^{(5)}$	0.9552	$a_{22}^{(1)}, a_{22}^{(2)}$
AABABB	0.50	0.920	$a_{22}^{(1)}$	0.931	$a_{22}^{(1)}$	0.906	$a_{22}^{(1)}$	0.971	$a_{22}^{(1)}$	0.861	$b_{11}^{(5)}$	0.802	$b_{22}^{(3)}$	0.9956	$b_{11}^{(5)}$	0.9807	$a_{22}^{(1)}$
AABB	0.50	0.891	$a_{22}^{(1)}$	0.907	$a_{22}^{(1)}$	0.975	$a_{22}^{(1)}$	0.994	$a_{22}^{(1)}$	0.934	$a_{12}^{(2)}$	0.797	$a_{12}^{(2)}$	0.9940	$b_{11}^{(2)}$	0.9761	$a_{22}^{(1)}$
AABBAB	0.50	0.920	$a_{22}^{(1)}$	0.931	$a_{22}^{(1)}$	0.936	$a_{22}^{(1)}$	0.980	$a_{22}^{(1)}$	0.860	$b_{11}^{(3)}$	0.792	$b_{22}^{(6)}$	0.9956	$b_{11}^{(3)}$	0.9807	$a_{22}^{(1)}$
AB	0.50	0.853	$a_{12}^{(1)}, b_{21}^{(2)}$	0.824	$a_{12}^{(1)}, b_{21}^{(2)}$	0.617	$a_{22}^{(1)}$	0.702	$a_{22}^{(1)}$	0.662	$b_{22}^{(2)}$	0.721	$b_{22}^{(2)}$	0.9934	$a_{11}^{(1)}, b_{11}^{(2)}$	0.9815	$a_{22}^{(1)}, b_{22}^{(2)}$
AAABB	0.60	0.846	$a_{22}^{(1)}, a_{22}^{(2)}$	0.871	$a_{22}^{(1)}, a_{22}^{(2)}$	0.994	$a_{22}^{(1)}$	0.999	$a_{22}^{(1)}$	0.965	$a_{22}^{(2)}$	0.930	$a_{22}^{(2)}$	0.7739	$b_{11}^{(4)}$	0.9966	$a_{22}^{(1)}, a_{22}^{(2)}$

Appendix continued.

		Baseline				No-till A				No-till B				No-till A and B			
		$\sigma_1 = 1$		$\sigma_1 = 0.8$		$\sigma_1 = 1$		$\sigma_1 = 0.5$		$\sigma_1 = 1$		$\sigma_1 = 0.5$		$\sigma_1 = 1$		$\sigma_1 = 0.5$	
Rotation	Fraction crop A	Elast.	Trans.	Elast.	Trans.	Elast.	Trans.	Elast.	Trans.	Elast.	Trans.	Elast.	Trans.	Elast.	Trans.	Elast.	Trans.
AABAB	0.60	0.955	$a_{22}^{(1)}$	0.958	$a_{22}^{(1)}$	0.909	$a_{22}^{(1)}$	0.962	$a_{22}^{(1)}$	0.600	$b_{22}^{(3)}$	0.682	$b_{22}^{(3)}$	0.8236	$b_{11}^{(3)}, a_{11}^{(4)}$	0.9983	$a_{22}^{(1)}$
AAAABB	0.67	0.851	$a_{22}^{(1)}, a_{22}^{(3)}$	0.874	$a_{22}^{(1)}$	0.998	$a_{22}^{(1)}$	0.999	$a_{22}^{(1)}$	0.920	$a_{12}^{(4)}$	0.867	$a_{22}^{(3)}$	0.9497	$a_{22}^{(2)}$	0.9978	$a_{22}^{(1)}, a_{22}^{(3)}$
AAABAB	0.67	0.871	$a_{22}^{(1)}, a_{22}^{(2)}$	0.892	$a_{22}^{(1)}, a_{22}^{(2)}$	0.978	$a_{22}^{(1)}$	0.994	$a_{22}^{(1)}$	0.865	$a_{22}^{(2)}$	0.849	$a_{22}^{(2)}$	0.9717	$a_{22}^{(1)}, a_{22}^{(2)}$	0.9993	$a_{22}^{(1)}$
AAB	0.67	0.952	$a_{22}^{(1)}$	0.957	$a_{22}^{(1)}$	0.845	$a_{22}^{(1)}$	0.936	$a_{22}^{(1)}$	0.566	$a_{12}^{(2)}$	0.598	$a_{22}^{(1)}$	0.9748	$a_{22}^{(1)}$	0.9990	$a_{22}^{(1)}$
AAAB	0.75	0.870	$a_{22}^{(1)}, a_{22}^{(2)}$	0.891	$a_{22}^{(1)}, a_{22}^{(2)}$	0.955	$a_{22}^{(1)}$	0.990	$a_{22}^{(1)}$	0.892	$a_{22}^{(2)}$	0.862	$a_{22}^{(2)}$	0.9962	$a_{22}^{(1)}, a_{22}^{(2)}$	0.9995	$a_{22}^{(1)}, a_{22}^{(2)}$
AAAAB	0.80	0.878	$a_{22}^{(1)}, a_{22}^{(3)}$	0.896	$a_{22}^{(1)}, a_{22}^{(3)}$	0.988	$a_{22}^{(1)}$	0.997	$a_{22}^{(1)}$	0.849	$a_{22}^{(3)}$	0.837	$a_{22}^{(3)}$	0.9987	$a_{22}^{(2)}$	0.9998	$a_{22}^{(2)}$
AAAAA B	0.83	0.878	$a_{22}^{(1)}, a_{22}^{(4)}$	0.896	$a_{22}^{(1)}, a_{22}^{(4)}$	0.996	$a_{22}^{(1)}$	0.999	$a_{22}^{(2)}$	0.853	$a_{22}^{(4)}$	0.835	$a_{22}^{(2)}$	0.9992	$a_{22}^{(2)}, a_{22}^{(3)}$	0.9998	$a_{22}^{(2)}, a_{22}^{(3)}$
A	1.00	0.813	$a_{22}^{(1)}$	0.842	$a_{22}^{(1)}$	1.000	$a_{22}^{(1)}$	1.000	$a_{22}^{(1)}$	0.813	$a_{22}^{(1)}$	0.813	$a_{22}^{(1)}$	0.9997	$a_{22}^{(1)}$	0.9999	$a_{22}^{(1)}$

Notes: In order to distinguish different years within a rotation cycle, each year of a rotation is called a "phase," and the phase for each crop in a rotation are numbered chronologically and denoted by a superscript in parentheses. For crop A the element a_{ij} of transition matrix A is the contribution of one weed seed in soil layer j at time t to the population of seeds in layer i at time t+1. Weed seed survival over winter is σ_1.

CHAPTER 6

Perspectives

This thesis has sought to understand aspects of weed-crop competition and population dynamics with the immediate aim of decreasing the amount of mechanical and hand weed control needed by organic (non-herbicide using) farmers in Western Europe. The questions studied ranged from the practical –is it better to use a wider or narrower row spacing in cereal crops to minimise weed seed production?, to the more theoretical –how does the order of crops in a rotation affect weed population dynamics?

The results stemming from the studies presented in Chapters 2 to 5 and the experience of carrying out this research have lead to many more questions and also to views on directions for research on weed ecology and management. The objective of presenting these perspectives is to provoke thought and discussion, and along the way, point out some potentially interesting research questions. The objectives are neither to give a comprehensive research strategy nor to directly discuss extensions of the results of Chapters 2 to 5. With regard to the latter point, the reader is referred to the discussion contained in the chapters themselves. With regard to the former point, it is felt that it is generally unproductive to claim that there can be a best method for carrying research on weed ecology –a diversity of research angles is critical for progress in any field. Therefore some important aspects, for example spatial dynamics of weed populations or specific biological processes such as effects of cover crops, are not considered, or at least not in detail.

HUMAN DIMENSIONS OF WEED ECOLOGY AND MANAGEMENT

If one were to ask a weed what it was, it would probably answer that it considered itself a plant, and that it was people that had classified it as a weed. Most weed ecologists and farmers would agree that agricultural weeds are a subjective issue. A plant growing in a mountain meadow or along a roadside might elicit comments on its pretty flowers or on how butterflies gather nectar from it. The same plant in a crop field may raise groans of annoyance that the population still has not disappeared. As long as agricultural fields have been present, there have been unwanted plants able to live in the same environment, and often at the expense of the crop plants.

The human dimension of weed ecology and management plays a role at many different levels, ranging from the daily decisions that a farmer may take concerning weed control, to policies that are set in place in response to societal or other concerns. In most work on weed ecology it is assumed that a farmer's goal is to reduce weed densities. Consequently most studies are oriented towards reducing weed numbers, usually in the short term. Recently, however, awareness has been growing of the need to consider longer-term aspects. With the interest in reducing herbicide use, more emphasis has been put on economic aspects, and specifically examining what strategies and factors are important if the goal is to maximise (future) profits rather than to minimise weed densities (Pandey and Medd 1991, Wallinga 1998). At the policy level, the human dimension of weed management comes into play when laws are passed which restrict or remove access to certain herbicides, or incentives are created to increase biodiversity in agro-ecosystems.

At all levels, and particularly with regard to organic farming, there may be a greater diversity of objectives than is realised and some of them may be in conflict with each other. Furthermore very little is known about the long-term consequences of human decisions, whether they are at the farm or policy level. For example, a potential conflict between objectives may be the desire to increase weed diversity on the one hand and to minimise hours of hand-weeding on the other hand. The results from Chapter 2 and other studies suggest that there may be a trade-off between weed diversity and density. At the farm level, some farmers have a very clear strategy to reduce weed population densities over the long term, while others appear to be reacting in order to prevent excessive crop yield losses. Is the latter a deliberate strategy? A lack of understanding of long-term dynamics? A lack of resources to make the investment in reducing weed population densities in the long term? Other aspects of the farm which take priority? Is it something about the soils on the farm? Such questions need to be addressed in order to focus research on relevant aspects of weed management, but also so that farmers understand the wider consequences of their decisions.

Farmers and scientists may also differ in their perception of what the problem is. For example, results from the 1995 survey of ecological farms (Schotveld and Kloen 1996) indicated that while *Stellaria media* (chickweed) was deemed to account for most of the time of hand-weeding, it was not the species that the farmers were most worried about. Instead, with regard to annual weeds, they were more concerned about *Chenopodium* spp. and *Solanum nigrum* (black nightshade). Nevertheless much recent work in Wageningen (Franke 1998, van Orsel 1998, Pannebakker 1999, van

Delden 2001) has concentrated on *S. media* as result of the finding that *S. media* was the dominant species on ecological farms. It would be useful to know why the farmers were more worried about the other species. Could it be that these species present a larger threat to crop yields than *S. media* or are more difficult to control? Some farmers may even consider *S. media* as a useful cover crop in cereal crops, provided they have an effective short-term management tactic for less competitive crops like onions.

LONG-TERM MONITORING AND EXPERIMENTS

Over the last 20 years, recognition of the importance of long-term ecological data has been growing. The reasons for the importance of long-term experiments and monitoring studies include the ability to observe the effects of slow ecological processes, the effects of rare events, cyclic behaviour that may recur at intervals longer than most studies, and to have better estimates of variability in the data (Woiwood 1991). For example some processes such as complex interactions between plant or animal populations, resources, and environmental perturbations may not be discernible through short-term experiments and monitoring studies (Brown et al. 2001). Studies of long-term fisheries data have helped to clarify causes and rates of ecological change, but have also provided ideas for management that would not have occurred based on recent observations alone (Jackson et al. 2001). Long-term data sets also allow testing of ecological theory (in the form of results from mathematical models) and discrimination of environmental noise from various ecological processes (Woiwood 1991, Bjørnstad and Grenfell 2001). Testing of theory and separating noise from signal are crucial aspects of being able to forecast system dynamics, which is an important goal of research on weed ecology.

While agricultural experiments have provided ecologists with some the longest data sets, such as the Broadbalk and Park Grass experiments at Rothamsted (Woiwood 1991, Johnston 1994), there have been very few long-term experiments or monitoring studies of weed population dynamics. Numerous studies have been carried out to quantify various weed life-history processes, and many models have been constructed to simulate weed population dynamics. However, very little is known about the actual dynamics of weed populations and the relative importance of factors influencing weed population dynamics and their interactions. The few existing long-term studies (>10 years) of weed populations have tended to either focus on before and after snapshots of weed communities (e.g., Hume 1982), or have looked just at indices of total weed population magnitudes rather than the densities of specific species (e.g., Aebischer 1991). While these studies have provided useful information, the most relevant information may come from the analysis of permanent plots in 'commercial' fields or long-term experiments. This is because of the sedentary nature of most plants, the presence of a seedbank, and the desire of farmers to know the consequences of different factors. Aggregating data across fields would obscure such relations.

For non-herbicide weed management, a long-term perspective towards management is essential and therefore knowledge and understanding of weed population dynamics in the long term needs to be built up. For example crop rotations are considered to have an important effect on weed population dynamics but few studies continue beyond one or two rotation cycles, which is not likely to be enough to get beyond transient dynamics. Particular questions of interest to weed management include whether weed populations appear to reach a stable equilibrium? How long does it take for populations to return to equilibrium after a perturbation? What is the effect of environmental stochasticity? Does it overshadow effects of control? Are there cycles in herbivores or seed predators that influence weed population dynamics. For farmers that rely on hand-weeding, a stable equilibrium in weed control may be more important than a stable weed population. Firbank (1991) has pointed out that long-term studies of weed population dynamics would help to resolve questions of whether the dynamics of some species are more predictable than other species or whether a seedbank dampens population changes.

Establishing long-term experiments and monitoring studies requires much thought, and studies of weed population dynamics have particular requirements. More general considerations for long-term experiments have been outlined by Leigh et al. (1994), and include keeping a simple design, using large plots, having a uniform site, and preventing soil movement across soil boundaries. Particular considerations for weed studies include how large an area is needed to have meaningful estimates of the weed plant population or the number of cores needed for seedbank estimates, and when to make counts of weed plant densities – at the start or end of the cropping season. The amount of control may be related to the population size at the start of the season, whereas the population size at the end of the season will determine the population size in the following season. Some of these aspects may have to be adjusted according to the species being considered. For example a species which has a low density may require a larger monitoring area in order to avoid spurious variability such that one year there is a plant in the plot and the next year there is one just outside the plot. For species with several generations per year, it may be of interest to monitor the population during each generation.

To make sense of observations of weed population dynamics, it is useful to have information on management practices and certain environmental parameters. How much information, though, is enough but not too much? On the one hand detailed information, for example on precise amounts and composition of fertilisers, may appear desirable, but may result in data overload and too much work, particularly if it is farmers that must provide the information. On the other hand, without enough management or environmental information, it may be difficult to explain patterns that are observed in the data. As one might expect, the data collected will depend on the question and the resources available.

Finally, there are the questions of how long a study should be continued and how to analyse the data. Again, the answers will depend in part on the hypothesis that is being tested. With regard to the length of the study, if parameters are being estimated from the data, then it is critical that the number of observations exceeds the number of parameter values that need to be estimated. Furthermore, while it is useful if there is a clear question at the outset of the study, the value of the data may only become evident as time passes and new theories and methods of analysis are developed.

THEORIES AND MODELS FOR WEED POPULATION DYNAMICS

In developing meaningful long-term experiments or monitoring studies, theories or hypotheses that can be expressed in a mathematical model are useful for focussing attention on the question at hand and the required data. Frequently, however, models of weed population dynamics have been developed with the aim of predicting weed population size in order to ultimately assist farmers with decisions on what strategies and control methods to apply. However, the record of predictions from models of weed population dynamics has been poor (Firbank 1989, Cousens and Mortimer 1995), and has to do with inherent variability in estimates of parameter values, measurement error, effects of magnification of errors through time, and unknown biological processes. However, for certain management strategies (e.g., threshold weed control), even a large error in predicted weed densities may not affect the decision (e.g., to control or not to control, Wallinga et al. 1999)

Some types of weed population models, however, rather than trying to make quantitative predictions of weed population dynamics, have instead aimed to examine the qualitative behaviour and to identify the key processes shaping such behaviour. For example Wallinga and van Oijen (1997) demonstrated how the discontinuity due to control decisions based on threshold weed densities leads to unpredictable weed population dynamics. While the exact quantitative dynamics observed in this model are not expected to be mirrored in reality, it provides another perspective for viewing changes in weed population size and the consequences of control. Furthermore, the clarity and simplicity of the conclusions allow well-defined experiments to be set-up in order to determine whether actual weed populations show some of the same qualitative behaviour as shown by the models. The model of weed population dynamics and crop rotations presented in Chapter 5 follows this spirit of developing theory rather than predicting population size.

If data sets of weed population dynamics were available and if these were long and large enough, it would be possible to apply other methods of analysis. In doing so both goals of quantitative prediction of weed population dynamics and improved understanding of the processes governing weed population dynamics might become within the grasp of weed ecologists. These methods can range from linear and non-linear time series analysis where predictions are based on purely statistical analysis of past patterns, to more involved fitting of models based on biological processes. For example, Kendall et al. (1999) demonstrated how competing hypotheses which might explain the cyclic dynamics observed in a laboratory population of blowflies can be evaluated. After constructing models based on biological processes (birth, death, and transition between life history stages) and different assumptions concerning competition, they estimated parameters from the data using several methods and then simulated the population dynamics (including measurement noise) resulting from the different models and parameter fits. A general difficulty with comparing biologically-based models with data is the absence of a well-defined measure of goodness-of-fit. Kendall et al. (1999) tackled this problem by calculating a variety of 'probes.'(mean, median, period and amplitude, to mention a few), which described the observed and simulated time series. As the probes may not be independent, they used principle component analysis to account for correlation and then compared the data and simulations graphically in principle component space. Using this method, they were able to conclude that one hypothesis concerning competition was more plausible than the other and that the level of discrimination between hypotheses was greater than if they had used the goodness-of-fit criterion (r^2) that was maximised when estimating the parameter values from the data. Methods of discriminating between competing hypotheses based on single goodness-of-fit criteria (comparison of likelihood values, or information theoretic criteria) are, however, much more common (e.g., Dennis et al. 1995, Hilborn and Mangel 1997, Burnham and Anderson 1998).

Another avenue for combining theory and data is to use what are called 'partially specified' (Wood 2001) or 'semi-mechanistic' (Ellner et al. 1998) models of population dynamics. In such models known biological aspects are included, while unknown aspects are derived from the data. For example Ellner et al. (1998) do not specify the rate of transmission of measles from infected to susceptible individuals, but rather examine the fit of the model when different general functions are used. Compared with a mechanistic and a statistical time series model, the partially specified model gave the best fit and also provided additional insights, through suggesting underlying mechanisms and the relative importance of unpredictable noise. Allowing functions to be derived from the data can also help to avoid super-sensitivity of population dynamics to model structure (Wood and Thomas 1999). In such cases several functional forms may give equally good fits to the data for the process of interest, but may result in very different population dynamics. Currently most weed population dynamic models to not include functional responses. However, in the effort to create more 'realistic' models or models that fit observed time series, incorporation of functional responses may become more common, whether it is dependence of control decisions on density, response of germination to temperature, or effectiveness of weed control in relation to soil moisture.

EXPERIMENTS AND THE INDIVIDUAL IN THE POPULATION

The above emphasis on long-term studies and analysis of weed population dynamics is not to suggest that there is no role for short-term experiments in weed ecology. Such experiments will always have a place, for example, to investigate the effects of weed-crop competition, the effectiveness of different control methods, or the forms of density dependence that may be present. Resources might be better allocated and experimental designs improved, however, if more thought is given to the role of individual weed plants in the population and by not loosing sight of long-term aspects. With regard to the latter point, taking a long-term approach requires a focus on how all aspects of a weed's life cycle influence future populations. Such a perspective can lead to considerations of whether there are trade-offs between different management strategies. As shown in Chapter 3, one strategy leads to a lower weed density, but not to a lower level of seed production, while the other strategy leads to a higher weed density but lower seed production.

With regard to the former point, because plants are sessile and therefore influenced by their local environment (biotic and abiotic), taking an individual approach allows investigation of how local factors affect various life-cycle processes such as survival or seed production. An understanding of such relations can provide insights leading to refinement in or new forms of weed control and management. Measurements on an individual basis also provide a better description of the distribution of responses. Such data is useful in developing stochastic models of weed population dynamics. Furthermore, adoption of an individual approach helps to avoid measurement errors due to the spatial heterogeneity of weed plants and seeds. For example, as shown in Chapter 4, weed survival due to mechanical hoeing may depend on the distance a weed plant is from the crop row. If survival is measured just by calculating the ratio of densities before and after weed control, then misleading survival rates may result, as the weeds are not likely to have a random spatial distribution. It may not always be necessary or possible to take an individual approach, but just by trying to think more from the perspective of a weed plant or seed may help to focus hypotheses and to avoid shortcomings in experimental design resulting from taking a density or population based approach.

ADAPTIVE MANAGEMENT

The need to manage exploited populations, particularly fisheries, without driving the population to collapse and in the face of incomplete and uncertain knowledge has lead to the concept of 'adaptive management' (Shea 1998). The idea, as espoused by Walters (1986) was that management should be an adaptive process, whereby 'we learn about the potentials of natural populations to sustain harvesting mainly though experience with management itself, rather than through basic research or the development of general ecological theory'. With weeds there are parallels – there is much uncertainty and there is usually a clear goal, though usually related to keep the population below rather than above a certain level. In a sense agriculture has its roots in adaptive management, however until recently the link with rigorous observations and analysis of cause and consequence has been lacking. Adaptive management, in its more formal definition and application can be a useful starting point for linking long-term studies, experiments, and ecological and economic theory in order to achieve specific goals regarding weed management.

Walters (1986) gave three ingredients for adaptive management: mathematical modelling, statistical analysis, and formal optimisation. Together these three aspects were expected to focus attention on uncertainties and how the propagate over time, generate, alternative hypotheses, and provide a range of management options. Implicit in these ingredients is the importance of monitoring and defining a clear objective. Some of the limitations of taking an adaptive management approach relate to potential irreversibility of decisions, and costs of monitoring (Shea et al. 2002).

In a weed management context, the simplest form of adaptive management would be to consider the weed populations observed over the last few years and then to choose the management strategy in response to past trends and future goals. An aspect that is particularly important in a weed management context is that a farmer is dealing with a community of weed species and strategies that may reduce the population of one species may result in population increases of another species.

An example of how adaptive management could be applied in a weed context, might start with the observation that the population of early germinating weeds had been increasing over the last few years and was getting to levels that prevented economic goals from being achieved. Possible responses for an organic farmer might include planting fall crop, delaying planting of the current crop species, or using a different form of direct weed control such as flame weeding instead of hoeing. Each of these choices carries its own costs and risks. Delaying sowing could result in lower yields, planting a fall-sown crop might result in undesirable increases in a different weed species, while a different control method might be more effective, but only in a narrow window of opportunity. An additional question is for how long a particular strategy be should implemented. For example should a fall-sown crop be planted for more than one year? Past knowledge in combination with dynamic models (preferably including an economic component and environmental stochasticity) could provide some guidance through evaluating future consequences. Once a decision has been implemented, then regular monitoring must continue in order to evaluate the consequences of the decisions and thereby to provide feedback for improving future decision-making. For example, how similar were the predicted results (long and short term) to the observed outcome. If they were very different, was it due to an unexpected event (rain at a crucial time), lack biological knowledge, or inclusion of too many details in the model, leading to magnification of error? Even if outcomes were close to predictions, could there have been another explanation for the observations?

A limitation of adaptive management in a weed context may be the variety of decisions that can be made and the interactions between different decisions. Therefore it may be difficult or even impossible to discern a final answer for a particular decision – the outcome may be due to past decisions or to the particular combination of decisions made. Furthermore, the impact of a decision may be very different whether it is viewed in the long or the short term and therefore a variety of time-horizons should be considered.

Current decision support systems and farm consultants do already attempt to bring together available knowledge, and possible outcomes. They are, however, more oriented towards herbicide-using farmers and often do not consider effects beyond one season or effects of environmental stochasticity (e.g., Wiles et al. 1996). Furthermore there is usually no framework for monitoring the impacts of a practice once it has been carried out. Decision support systems that have included long-term weed population dynamics do seem to raise farmer awareness of the long-term implications of using certain control methods (Pannell 2001). Incorporating game playing into evaluation of different management strategies would be useful from both an educational perspective but also for learning how decision making takes place and to develop a wider range of strategies (e.g., Milner-Gulland et al. 2001).

CONCLUSION

The perspectives discussed in this chapter should not be considered as prescriptions, but rather as a limited number of aspects that could warrant more thought in research on weed ecology and in the development of weed management strategies. In particular, the human dimensions of weed management should not be ignored, both in terms of a better understanding of the aims of weed management and in terms of how management decisions affect weed population dynamics. However, few theories concerning weed population dynamics can be tested or management strategies evaluated without access to long-term data sets. To see the benefits, one has only to consider the use to which long-term data sets of communicable diseases have been put, from evaluating vaccination strategies to inferring contact patterns, which have analogies with weed control and dispersal, respectively. Considering the costs of controlling weeds – both financial and environmental, and the risks posed by herbicide resistant crops, it would be worthwhile for weed ecologists, farmers, and funding bodies to initiate some simple long-term studies on weed population dynamics.

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Samenvatting

ACHTERGRONDINFORMATIE

In Europa wordt de kans steeds groter dat men mensen zal zien die handmatig onkruid wieden. De bezorgdheid over het milieu, het belang van gezond voedsel en het schrappen van certificering van een reeks herbiciden zijn enkele redenen voor de toename van handwieden. Hoewel de omstandigheden sinds de tijd van het schilderij op de omslag van dit proefschrift verbeterd zijn, is dit nog steeds erg zwaar werk en is het moeilijk om mensen te vinden die zulk werk willen doen. In andere delen van de wereld, waar de belangrijkste vorm van onkruidbestrijding nog steeds handmatig is, bestaat een tekort aan arbeid vanwege de migratie naar stedelijke gebieden en de HIV/AIDS-epidemie. Hier lijdt de voedselproductie onder.

Bij mechanische en handmatige onkruidbestrijding worden onkruidplanten uitgeroeid, zodat de onkruidpopulatie niet te omvangrijk wordt. Net als ieder ander levend organisme worden onkruidplanten beïnvloed door hun omgeving. Als we weten hoe de omgeving rond een onkruidplant haar overlevingskans, reproductie en verspreiding beïnvloedt, ofwel als we de ecologie van onkruid kennen, zouden we andere methoden kunnen vinden om de onkruidpopulatie te reguleren in plaats van deze planten alleen proberen uit te roeien. Ecologische kennis van onkruid heeft zich door de eeuwen heen ontwikkeld met behulp van observaties van telers en meer recent door wetenschappelijk onderzoek.

Een voorbeeld van een manier waarop de kennis over onkruidecologie wordt gebruikt, is uitgesteld zaaien. Veel onkruidsoorten hebben een bepaalde periode waarin ze ontkiemen en opkomen. Als het zaaien van het gewas een paar dagen kan worden uitgesteld en het opkomen van onkruid kan worden aangemoedigd door valse zaaibedden te creëren, dan kan de onkruidpopulatie met een substantieel deel worden teruggebracht in het werkelijke zaaibed dat later wordt gecreëerd.

Hoewel er veel bekend is over onkruidecologie, valt er nog veel te leren. De kennis van onkruidecologie kan worden ontwikkeld op het gedetailleerde niveau van specifieke soorten of op het algemene niveau van de manier waarop onkruidplanten en populaties met de omgeving en met de beslissingen van de telers interacteren. Gedetailleerde kennis zal waarschijnlijk eerder leiden tot directe toepassingen, maar is erg tijdrovend. Algemene principes kunnen echter inzicht verschaffen dat tot nieuwe en ongebruikelijke ideeën kan leiden om onkruidpopulaties te beheren.

Dit proefschrift heeft tot doel de gedetailleerde en algemene kennis over verschillende aspecten van onkruidecologie te ontwikkelen. Op gedetailleerd niveau ligt de nadruk op hoe gewasrij-afstand in combinatie met verschillende soorten mechanische bestrijding de onkruidzaadproductie beïnvloedt. Op een algemener niveau ligt de nadruk op hoe gewasrotatie, vooral de gewas-volgorde, de wisselende grootte van onkruidpopulaties beïnvloedt. Tussen het algemene en gedetailleerde niveau in ligt de nadruk op de factoren die de onkruidpopulaties beïnvloeden op biologische boerderijen.

Hoewel de vragen die in dit proefschrift aan de orde komen een breed gebied beslaan, is het centrale thema de noodzaak van een lange-termijn visie voor onkruidbeheer. Dit komt omdat de onkruidzaden die het ene jaar worden geproduceerd, bijdragen aan de toekomstige onkruidpopulaties. Een betrouwbare evaluatie over onkruidbeheersystemens kan alleen gemaakt worden als er wordt gekeken naar de effecten op langere termijn. Op z'n minst moet er worden gedacht aan de gevolgen voor het volgende groeiseizoen. Een lange-termijn visie betekent echter niet dat de populatiedynamica van onkruiden in ieder hoofdstuk wordt geobserveerd of gesimuleerd met computermodellen. In Hoofdstuk 3 was bijvoorbeeld het doel van het experiment de onkruidzaadproductie te minimaliseren, maar de motivatie voor het experiment was de vermindering van de onkruidpopulaties op de lange termijn.

KORTE SAMENVATTING VAN DE HOOFDSTUKKEN

Formulering van het probleem

In Hoofdstuk 2 worden de resultaten besproken van de regelmatige observatie van onkruid op biologische boerderijen. Door onkruid op bepaalde boerderijen te observeren, is het mogelijk om beter te begrijpen wat het probleem is, als er al een probleem is, en is het ook mogelijk om de waarschijnlijke oorzaken van het probleem te vinden. Alleen wanneer het probleem bekend is, kunnen oplossingen worden gevonden. Een statistische analyse kan worden gebruikt om te onderzoeken of er een verband bestaat tussen de waargenomen onkruidpopulatie en verschillende controleerbare en oncontroleerbare factoren. Informatie van en discussie met telers over hun aanpak kan helpen bij de verklaring van de verspreidingspatronen van de onkruidpopulaties.

De analyse uit Hoofdstuk 2 richt zich op de factoren die de variabiliteit van onkruiddiversiteit en -overvloed bepalen. Het onkruid werd in totaal zes jaar (1995 en

1997 tot 2001) geobserveerd op vijf biologische boerderijen en van ieder veld legden de telers informatie vast over het beheer van onkruid en gewassen. Het was overduidelijk dat de onkruiddichtheid op bepaalde boerderijen consequent laag was en op andere juist hoog. De boerderijen met veel uren handmatig onkruid wieden waren ook de boerderijen met een hogere onkruiddichtheid. Het lijkt erop dat de telers met lage onkruiddichtheid en weinig uren handwieden opzettelijk een lange-termijn aanpak hanteren voor onkruidbestrijding door bijvoorbeeld de bloeiende planten van een bepaalde onkruidsoort te verwijderen van de graanvelden. Boerderijen met een hoge onkruiddichtheid kenden ook meer onkruidsoorten dan boerderijen met een lage onkruiddichtheid. Het klaarblijkelijke verband tussen onkruiddichtheid en het aantal onkruidsoorten roept belangrijke vragen op voor beleidsmakers, als zij van mening zijn dat één van de doelen van biologische landbouw het verhogen van de biodiversiteit is.

Gewasplantpatronen om de onkruidzaadproductie te minimaliseren

In Hoofdstuk 3 worden de resultaten besproken van een experiment over het effect van gewasrij-afstand en mechanische bestrijding op onkruidproductie. Biologische telers maken normaal gesproken gebruik van een ruime rij-afstand (22-30 cm) voor graangewassen (gerst, haver, tarwe) om een mechanische schoffel te kunnen gebruiken, die als een van de betere onkruidbestrijdingsmiddelen wordt beschouwd. Maar door de ruime rij-afstand zullen de onkruidplanten waarschijnlijk groter worden en meer zaden produceren dan bij een nauwere rij-afstand. Bij een nauwere rij-afstand kunnen echter meer onkruidplanten de onkruidbestrijding overleven. Als we het aantal geproduceerde zaden gebruiken om de verschillende opties te evalueren, willen we graag weten welke combinatie van gewasrij-afstand en mechanische bestrijding de minste zaadproductie oplevert.

De opzet van het experiment bestond uit drie rij-afstanden (10, 20 en 30 cm) en twee zaaidichtheden (140 en 180 kg ha^{-1}). Bij de opzet van 30 cm werd er gebruik gemaakt van mechanisch schoffelen en eggen om het onkruid te bestrijden. Bij de opzet van 10 en 20 cm gebruikte men alleen een eg om het onkruid te bestrijden. Er werden drie onkruidsoorten onderzocht: perzikkruid (*Polygonum persicaria*), zwaluwtong (*Polygonum convolvulus*) en vogelmuur (*Stellaria media*). Om de zaadproductie te berekenen was het noodzakelijk om te weten hoeveel planten de onkruidbestrijding overleefden en hoeveel zaden er door de overlevende planten werden geproduceerd. Hiervoor werden de planten allemaal gemarkeerd voordat de onkruidbestrijding plaatsvond.

Uit de resultaten bleek dat, rekening houdend met de verschillen in effectiviteit van de verschillende onkruidbestrijdingsmethoden, de zaadproductie het laagst was bij de nauwere gewasrij-afstand. De onkruidmortaliteit bij de ruime rij-afstand zou moeten toenemen om het niveau van de zaadproductie bij de nauwere rij-afstand te evenaren. Het lijkt er daarom op dat biologische telers beter een nauwere rij-afstand kunnen gebruiken en minder intensieve onkruidbestrijdingsmaatregelen moeten nemen. Proeven op boerderijen met meer variëteit in bodem, met andere onkruidsoorten en hogere zaaidichtheden van gewassen, zouden nuttig zijn om de bredere geldigheid en toepasbaarheid van de resultaten te onderzoeken en zo de telers te overtuigen.

Het voorspellen van de individuele massa en overlevingskans van onkruid

In Hoofdstuk 4 werden extra gegevens van het experiment uit Hoofdstuk 3 gebruikt om te onderzoeken of de massa en de overlevingskans van individuele onkruidplanten voorspeld kan worden met de informatie van hun lokale omgeving. Als we begrijpen welke onkruidplanten het meeste bijdragen aan toekomstige generaties en hoe overleving en reproductie verbonden zijn met hun lokale omgeving, kunnen we bijvoorbeeld optimale combinaties van gewasrij-afstand en mechanische bestrijding vinden. Of we kunnen de vraag beantwoorden óf verschillende gewas plantpatronen leiden tot verschillende ruimtelijke patronen van onkruid.

Het lokale milieu rond een onkruidplant kan op vele manieren worden omschreven. Voorbeelden hiervan zijn de lokale dichtheid van gewasplanten rond een doel-onkruidplant, de afstand tussen de doel-onkruidplant en de dichtstbijzijnde gewasplant of directe metingen van groeivoorwaarden, zoals de hoeveelheid beschikbaar licht of water voor een doel-onkruidplant. Bij het experiment over rij-afstand, dat beschreven wordt in Hoofdstuk 3, werden er metingen verricht van de afstand tussen iedere onkruidplant en de dichtstbijzijnde gewasplant. In Hoofdstuk 4 werden deze metingen van de lokale omgeving gebruikt om statistische vergelijkingen op te stellen die gebruikt kunnen worden om de massa en de overlevingskans van individuele onkruidplanten te voorspellen.

Met betrekking tot de plantmassa werden er met de gegevens 32 verschillende vergelijkingen getest, waarbij verschillende combinaties werden gebruikt van de twee metingen van de lokale omgeving. Het is verrassend dat eenzelfde vergelijking de best passende relatie gaf voor alle drie de onderzochte soorten. De vorm van de vergelijking was $w = b_0 + b_1u^2 + b_2v^2$, waar de w de voorspelde massa van een plant is, u de afstand tot de dichtstbijzijnde gewasplant is en v de rij-afstand is waartussen de onkruidplant zich bevindt. De b_i zijn geschatte parameters uit de gegevens die per soort verschilden. Deze lineaire vorm is alleen toepasbaar voor een beperkte reeks afstanden, omdat de planten niet tot een oneindige hoogte groeien als de afstand groter wordt. Het is echter niet waarschijnlijk dat de afstanden bij een graangewas veel groter zullen zijn dan de afstanden die in het experiment gemeten zijn. Het model is voldoet intuïtief, omdat men zou verwachten dat de hoeveelheid beschikbare groeivoorwaarden (vooral licht) in relatie zouden staan met het beschikbare gebied, i.e. het kwadraat van de afstand. Met betrekking tot de onkruidmortaliteit werd gevonden dat alleen de afstand van de gewasrij nodig was om de overlevingskans van het onkruid te voorspellen en dan alleen bij de ruime rij-afstand waar mechanisch schoffelen werd gebruikt. Bij de andere opzetten hadden de onkruidplanten dezelfde overlevingskans ondanks hun lokale omgeving (zoals is beschreven aan de hand van de afstanden tot de dichtstbijzijnde gewasplant en gewasrij).

Gewasrotatie en populatiedynamica van onkruiden

In Hoofdstuk 5 komt de vraag aan de orde of de gewasvolgorde in een rotatie de populatiedynamica van onkruiden beïnvloedt. Als men bijvoorbeeld twee gewassen heeft – peen en tarwe – en een eis van twee jaar voor ieder gewas, dan zijn er twee mogelijkheden voor een vierjarige rotatie: peen-tarwe-peen-tarwe of peen-peen-tarwe-tarwe. De vraag is nu in welke van deze rotaties de onkruidpopulatie het langzaamst groeit en waarom? De meeste experimentele en gesimuleerde onderzoeken van onkruidpopulatie waren geneigd de nadruk te leggen op de vergelijking tussen monoculturen en een gewasrotatie en mogelijk ook op de interactie met verschillende ploegmethoden. Uit deze onderzoeken bleek dat gewasrotaties met een hogere diversiteit aan gewassen minder onkruidproblemen leken te hebben dan monoculturen. De manier waarop de gewasvolgorde de populatiedynamica van onkruiden beïnvloedt, is echter nooit onderzocht.

Aangezien experimenten met gewasrotatie een noodzakelijk lange tijdspanne vereisen, is het gebruik van een wiskundig model een manier om de bovengenoemde vraag te beantwoorden. Een wiskundig model houdt noodzakelijkerwijs vele vereenvoudigingen in. Maar omdat de veronderstellingen en de structuur van het model bekend zijn, is het met voldoende inspanning mogelijk om de resultaten volledig te verklaren. Dit betekent niet dat de resultaten de werkelijkheid weerspiegelen, maar de verkregen inzichten kunnen leiden tot nieuwe ideeën voor beheerstrategiën en tot meer gerichte experimenten.

Met het model zou het aantal onkruidzaden in twee bodemlagen kunnen worden berekend voor verschillende gewasrotaties, bestaande uit twee gewassen. Er werden twee bodemlagen gebruikt, omdat de ontkiem- en overlevingskansen van een zaadje afhankelijk zijn van de diepte waarin het zich in de bodem bevindt en omdat zaden in verschillende bodemlagen ook verschillende kansen hebben om naar andere lagen te worden bewogen door middel van ploegen.

Uit berekeningen bleek dat het populatiegroeicijfer tussen rotaties met verschillende gewasvolgordes verschilde. Bij de peen-tarwe-peen-tarwe rotatie groeide de onkruidpopulatie bijvoorbeeld veel sneller dan bij de peen-peen-tarwe-tarwe rotatie. Als er niet geploegd werd na het tarwegewas groeide de populatie bij de peen-peen-tarwe-tarwe rotatie sneller. Er werd ook ontdekt dat als het onkruidbeheer veranderd werd, door bijvoorbeeld meer of minder onkruid te bestrijden, het resultaat anders zou zijn afhankelijk van het gewas waar de verandering was aangebracht en van de positie die het gewas had in de rotatie. De onkruidbestrijding bij tarwe met 20% verhogen zou bijvoorbeeld een beter resultaat opleveren dan ditzelfde te doen bij peen, en bij de peen-peen-tarwe-tarwe rotatie zou het uitmaken of de verandering in het eerste of tweede tarwejaar was aangebracht.

Het gevolg hiervan voor onkruidbeheer is, dat het belangrijk is om aandacht te schenken aan de gewasvolgorde wanneer men een gewasrotatie ontwerpt en wanneer men veranderingen aanbrengt aan de onkruidbeheersstrategie binnen een gewas. Het is ook waarschijnlijk dat de grootte van de onkruidpopulatie en de korte-termijn dynamica zullen worden beïnvloed door de interactie van begincondities (de verdeling van zaden over de bodem) en door het gewassoort waarmee een nieuwe rotatie wordt begonnen. Daarom kan het voor de telers belangrijk zijn, wanneer zij overgaan op een nieuwe gewasrotatie, om te onderzoeken hoe groot de onkruidzaadpopulatie is en hoe de zaden over de bodem verspreid zijn. Het zou nuttig zijn om enkele lange-termijn veldexperimenten op te zetten om een aantal ideeën te testen die zijn voortgekomen uit het werk met modellen.

PERSPECTIEVEN

In de loop van het onderzoek, dat in dit proefschrift beschreven wordt, werden er enkele ideeën ontwikkeld die tot algemenere benaderingen van het onderzoek in onkruidecologie hebben geleid. Ten eerste is het van belang dat de menselijke factor niet wordt vergeten – waarom bijvoorbeeld sommige telers een lange-termijn visie voor het beheer van onkruidpopulaties hebben en anderen niet. Ten tweede zou het, aangezien onkruidbeheer bij biologische landbouw een lange-termijn probleem is, nuttig zijn om meer informatie te krijgen over de lange-termijn dynamica van onkruidpopulaties op boerderijen en in goed ontworpen experimenten. Zulke gegevens kunnen helpen bij het bepalen of menselijke factoren meer invloed hebben dan factoren zoals het weer. Ten derde, met toegang tot lange-termijn gegevens, is het mogelijk om hypothesen te toetsen zoals die betreffende de resultaten van gewasvolgorde (Hoofdstuk 5), of om recentelijk ontwikkelde methoden te gebruiken van tijdreeksanalyse en van het aanpassen van populatiedynamische modellen aan meetgegevens. Zulke modellen zouden een beter voorspellend vermogen hebben dan de meer gebruikelijke deterministische modellen die geen 'random' variatie opnemen. Verder dient er bij het ontwikkelen van modellen voor populatiedynamica van onkruiden meer aandacht te worden geschonken aan de wijze waarop de onkruidbestrijding is gesimuleerd. Letten biologische telers bijvoorbeeld op de omvang van de onkruidpopulatie of roeien ze altijd een vast gedeelte van de populatie uit? Ten vierde is het belangrijk, bij het ontwerpen en uitvoeren van experimenten, om niet de plaats van de individuele plant in de populatie uit het oog te verliezen. Individuele planten dragen namelijk bij aan de toekomstige generaties. Hoe beter we de variabiliteit begrijpen tussen individuele planten en de factoren die verantwoordelijk zijn voor deze variabiliteit, des te waarschijnlijker het zal zijn dat de beheersstrategie aangepast kan worden, opdat de strategie de grootste impact heeft. Ten vijfde en tenslotte zouden onkruidecologen, bij het ontwikkelen van een onkruidbeheersstrategie, een flexibel beheer moeten overwegen, die met name voor de visserij is ontwikkeld. Bij de visserij bestaat er namelijk veel onzekerheid over informatie vanwege onvolledige kennis en vanwege de random variatie. Een flexibel beheer houdt in dat er veranderingen aan een systeem, bijvoorbeeld een gewassysteem, worden aangebracht en dat vervolgens de manier waarop de populatie verandert wordt geobserveerd, nadat de verandering in het beheer is aangebracht. Dit beheer houdt in dat de observatie, de modellen en kleine experimenten gecombineerd worden in een continue poging om één of meer doelen te bereiken. Bij een visserijsysteem zou er bijvoorbeeld ieder jaar een evaluatie kunnen worden gemaakt van de populatiegrootte en vervolgens wordt dan de kennis van het resultaat van veranderingen gebruikt voor de methoden voor het volgende visjaar. Een teler die onkruid beheert, zou rekening kunnen houden met speciale problemen die in het laatste jaar zijn voorgekomen en het beheer in het huidige jaar aanpassen om de langetermijn impact op gewasopbrengst en andere kosten te kunnen minimaliseren.

Curriculum vitae and Publications

The author, Shoshana Karina Mertens (Shana), was born in 1967 in Santiago, Chile. Her higher degrees are from the University of Chicago (1989, B.A. in biology), the Free University of Brussels (1992, M.A. in human ecology) and Wageningen Agricultural University (1998, M.Sc. in ecological agriculture), all received with some sort of honours. In 1998 she began her Ph.D. research on weed ecology at the former Institute for Agrobiology and Soil Fertility (AB-DLO) and the former Department of Theoretical Production Ecology (Wageningen Agricultural University). In November 2002 she will start a three-year project at Rothamsted Experimental Station, in which she will be developing methods of analysing transient dynamics in periodic matrix models, and also carry out field and controlled environment experiments to test some of the hypotheses suggested by the modelling work.

During and in between her studies, Shana has supported herself with jobs ranging from teaching/laboratory assistant to content editing of science textbooks. In particular she spent four years (1992-1996) working on environmental policy in Brussels. She first worked at the Environmental and Development Research Centre on European-Amazon issues, where her primary task was the organisation of a European-Amazon Roundtable Meeting at the European Parliament. Subsequently she was based at Climate Network Europe, where she co-ordinated a series of evaluations of public participation in Global Environment Facility (GEF) climate change projects and wrote a guide to the GEF in order to facilitate participation of non-governmental organisations. Her primary interest, however, is in scientific research rather than in political campaigning. She has had a life-long curiosity for natural history, particularly the ecology of plants, as well as interest in the interface between humans and their environment. In the future she hopes to continue to pursue her interests in plant ecology, ecosystem structure, ecological management, and human impacts, particularly through linking mathematically modelling with experimental and monitoring studies.

PUBLICATIONS

Ecology papers (published and in press)

Mertens, S. K., and Jansen, J.. (2002) Weed seed production, crop planting pattern, and mechanical weeding in wheat. *Weed Science.* In press.

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